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5. Maurer and Salapatek [see (*4*)] made judgments of infant fixations on real adult faces. Since they did not measure fixations or the regions of the adult faces, their determination of regional fixations must be regarded as estimates. They reported as we do here an increase in face and eye looking to a still face between 4 and 8 weeks of age. Donnee [see (*13*)] measured fixations of infants as they scanned a face photograph.
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9 August 1977

Magnification in Striate Cortex and Retinal Ganglion Cell Layer of Owl Monkey: A Quantitative Comparison

Abstract. *Magnification, the relative size of the neural representation of a portion of the visual field, decreases more rapidly with increasing visual field eccentricity in striate cortex than in the retinal ganglion cell layer of the owl monkey (*Aotus trivirgatus*); the proportion of the cells in striate cortex devoted to central vision is much larger than the comparable proportion of retinal ganglion cells. Magnification in striate cortex is a power function of magnification in the retinal ganglion cell layer. A formula for convergence (ganglion cells to cortical neurons) follows from this relationship.*

Sensory surfaces project to mammalian neocortex in orderly topographic fashion. Sensory surfaces associated with behavioral specializations receive expanded representation, for example, the human and monkey hand, and the snout of the pig and coatimundi (*1*). Differential cortical representation may merely reflect differential innervation of the sensory surface or may be the consequence of an additional cortical adaptation.

In the mouse somatosensory system, cortical representation of the different whiskers may be described in terms of "peripheral scaling," that is, the number of cortical neurons per whisker is directly proportional to the peripheral innervation density (*2*). In the visual system, peripheral scaling describes the representation of the visual field (or retinal surface) in striate cortex of the cat (*3*) but not the rabbit (*4*). In primates, the central portion of the visual field receives a greatly expanded representation in striate cortex (*5–7*). Investigators disagree, however, as to whether this is solely because of increased ganglion cell density near the center of the retina (*8*) or whether the cortex provides additional "magnification" (*9*). The present study demonstrates that in the owl monkey, *Aotus trivirgatus*, the representation of the center of the visual field is expanded much more than might be expected from the distribution of retinal ganglion cells. This strongly suggests that, in primates, striate cortex is even more specialized than the retina for central vision.

We defined magnification in a given portion of a neural structure as the proportion of the structure devoted to the representation of a particular visual field zone divided by the proportion of the visual field represented (*7, 10*):

$$M(\phi_1,\phi_2) = \frac{N(\phi_1,\phi_2) \div N_{\text{tot}}}{A(\phi_1,\phi_2) \div A_{\text{tot}}} \quad (1)$$

where $M(\phi_1,\phi_2)$ is the magnification for the representation of the zone between two isoeccentricity contours of radii ϕ_1 and ϕ_2 with the center of gaze at the origin; $N(\phi_1,\phi_2)$ is the number of cells within the representation of that zone in a given structure; N_{tot} is the number of cells in the structure; and $A(\phi_1,\phi_2)$ and A_{tot} are the area of the zone and the total area of the visual field, respectively. For structures where cell density is invariant with respect to eccentricity, volume measurements yield equivalent values for magnification, and where the thickness of the structure also does not change as a function of eccentricity, magnification may be calculated on the basis of surface area.

We calculated magnification in striate cortex of the owl monkey using a three-dimensional model of the brain constructed on the basis of serial sections and receptive field data from a previous electrophysiological mapping study (*11*). These results were compared to calculations of magnification for the ganglion cell layer of the owl monkey retina (*12*) based upon ganglion cell counts along both horizontal and vertical meridians made from whole mounts by Webb and Kaas (*8*). The owl monkey is an excellent subject for studying quantitative relations between representations of the visual field in different structures because: (i) the ganglion cell layer is thin enough to permit cell counts from whole mounted retinas; (ii) ganglion cells are not displaced about a fovea as they are in most other higher primates; (iii) the ratio of rods to cones does not change as a function of eccentricity (*13*), implying equivalent (normalized) magnification functions for scotopic and photopic vision; (iv) the topographic representations of the visual field have been determined for more structures of the owl monkey visual system than for any other primate (*14, 15*); and (v) its relatively smooth brain makes it possible to map the cortical visual areas more accurately in the owl monkey than in other species with more convoluted neocortices.

The expanded representation of the center of the visual field in owl monkey striate cortex cannot be attributed solely to peripheral scaling (*16*). While magnification decreases monotonically as a function of eccentricity in both retina and striate cortex, the decrease is considerably more gradual in the retina, and cortical magnification for the central 10 degrees greatly exceeds retinal magnification (Fig. 1); that is, the proportion of the cells in striate cortex devoted to central vision is much larger than the comparable proportion of retinal ganglion cells. Functionally, this suggests that, in primates, striate cortex is even more specialized than the retina for processing information concerning the center of the visual field. Anatomically, this means that the ratio of retinal ganglion cells to neurons in striate cortex increases with eccentricity. More specifically, the relation between magnification for corresponding portions of striate cortex and the retinal ganglion cell layer is describable by a power function (Fig. 2):

$$M_C(\phi_1,\phi_2) = aM_R(\phi_1,\phi_2)^{2.35} \qquad (2)$$

where M_C is the magnification for striate cortex, M_R is the magnification for the retinal ganglion cell layer, and a is the proportionality constant. Malpeli and Baker (*9*) have recently suggested that a similar relation exists between retinal ganglion cell density and magnification (cubic millimeters per steradian) in striate cortex of the rhesus monkey. They were forced, however, to compare retinal cell counts from rhesus monkey to results for striate cortex (*7*) which represented a composite of four species (baboon, rhesus, cynomolgus, and vervet) (*17*).

It follows from our definition of magnification and the observed relation between retinal and cortical magnification that the ratio of ganglion cells to striate neurons is a power function of the area per ganglion cell (*18*):

$$\frac{N_R(\phi_1,\phi_2)}{N_C(\phi_1,\phi_2)} = k\left|\frac{A(\phi_1,\phi_2)}{N_R(\phi_1,\phi_2)}\right|^{1.35} \qquad (3)$$

where N_R and N_C are the numbers of retinal ganglion cells and striate cortical neurons, respectively, and k is the proportionality constant. A recent finding in the rhesus monkey (*19*) implies that although some primate retinal ganglion cells send collaterals to the superior colliculus, all ganglion cells send axons to the lateral geniculate nucleus (LGN). Nearly all the cells in the primate LGN project to striate cortex (*20*). Therefore, Eq. 3 describes anatomical convergence in the retino-geniculo-striate system, that is, the mapping of the retinal ganglion cell layer onto striate cortex. Convergence depends on eccentricity and thus on retinal area per cell. This may have implications for the study of the development of these connections. Experiments on the development of somatosensory and visual cortex suggest that portions of sensory surfaces compete for cortical representation (*21*). Our findings further suggest that in the developing primate retino-geniculo-striate system, competitive advantage decreases with eccentricity resulting in increased convergence. It would be of interest to know how such differential convergence is accomplished morphologically in terms of the organization of the neuropil at geniculate and striate levels and how this is reflected physiologically in changes in receptive field size.

The present results and those of recent physiological mapping studies (*15, 22*) suggest that in primates, each topographically organized visual structure may be unique in its differential magnification of the visual field. This is indicative of specialization of function in these structures. There exist particularly large differences with respect to magnification in the third tier of cortical visual areas. In the dorsolateral crescent of the owl monkey, approximately 75 percent of the area is devoted to the visual field zone from the center of gaze to 10 degrees, while only 4 percent of the medial area is devoted to the representation of this zone compared with 31 percent of striate cortex. Behavioral techniques are now available for the control of fixation during presentation of eccentric stimuli in monkeys (*23*). This makes possible psychophysical experiments in which stimulus eccentricity is an independent variable. More accurate specification of the relation between magnification and eccentricity at different levels of neural processing may permit determination of the structure involved in a perceptual task on the basis of psychophysical data.

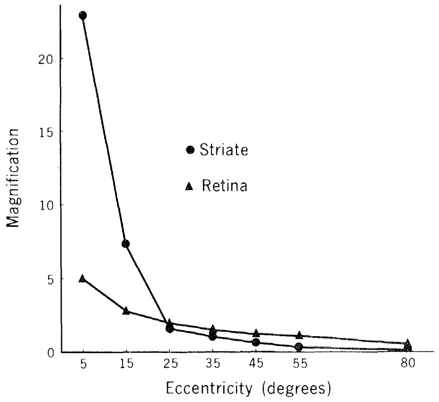

Fig. 1. Magnification in striate cortex and the retinal ganglion cell layer as a function of eccentricity. Values shown are for portions of retina and striate cortex corresponding to representations of concentric zones, each 10 degrees wide, in the visual field from 0 to 60 degrees and of the remainder of the visual field, the zone from 60 to 100 degrees.

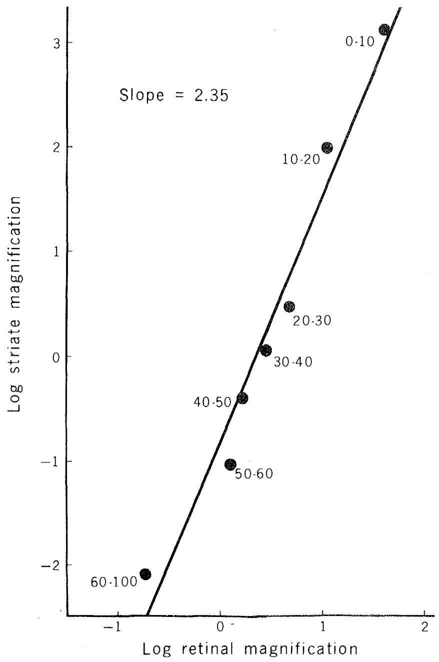

Fig. 2. Magnification in striate cortex as a function of magnification in the retinal ganglion cell layer. Values shown are for portions of retina and striate cortex corresponding to representations of concentric zones, each 10 degrees wide, in the visual field from 0 to 60 degrees and of the remainder of the visual field, the zone from 60 to 100 degrees.

Note added in proof. Our findings explain the results of recent autoradiographic studies (*24, 25*). After intraocular injection of tritiated proline, transneuronal labeling in foveal (dorsal) striate cortex is much less dense than in peripheral (calcarine) striate cortex in both squirrel monkeys and owl monkeys. This is because the ratio of ganglion cells to cortical neurons increases with eccentricity. In addition, degeneration caused by lesions of the LGN is less dense in dorsal striate cortex than in the calcarine fissure (*25*). These results and those of Malpeli and Baker (*9*) indicate that differential convergence in the primate retino-geniculo-striate system is accomplished in two steps: between retina and LGN and again between LGN and striate cortex.

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10. The present usage might be termed normalized cellular magnification to distinguish it from linear magnification (millimeters of cortex per degree of visual field) as defined by Daniel and Whitteridge (*6*). Our definition is similar to that employed by Malpeli and Baker (*9*) except that it is defined in terms of number of cells and normalized for greater ease of application to diverse structures. In choosing a cellular definition, we make no assumptions about the size or nature of functional elements above the cellular level.
11. See Allman and Kaas (*5*). Cell density and thick-

ness of striate cortex did not appear to vary systematically with eccentricity. Therefore, magnification was calculated from measurements of cortical surface area. The total area of the pial surface of striate cortex was 286 mm^2.

12. The point of maximum ganglion cell density which corresponds to the center of gaze is located 10 degrees nasal of the geometric center of the retina (*6*). Thus the visual field for the owl monkey extends out 90 degrees superior and inferior from the center of gaze along the vertical meridian, and 100 degrees out along the horizontal meridian. The formula for the proportion of the area of a sphere contained within the zone defined by two isoeccentricity contours is $A(\phi_1,\phi_2) = \cos \phi_1 - \cos \phi_2$. The application of this formula is complicated slightly by the position of the center of gaze. On the retina, $A(\phi_1,\phi_2) = (\cos \phi_1 - \cos \phi_2) A_{\text{tot}}$ for $\phi_2 \leq 80°$; $A(80°, 90°) = (\cos 80° - \cos 90° - 1/18) A_{\text{tot}}$, and $A(90°, 100°) - A_{\text{tot}}/18$. In the visual field, the proportion of the total area contained within a zone for $\phi_2 \leq 90°$ equals $0.9(\cos \phi_1 - \cos \phi_2)$, and the proportion for the zone from 90° to 100° equals 0.1.
    One degree of visual angle corresponds to 0.15 mm of retina (*6*). Although in some species the optics of the eye produce a nonlinear projection of the visual field onto the retinal surface, this does not appear to be the case in the owl monkey. The distance from center of gaze to blind spot is 20° and the contralateral visual field extends out 100° along the horizontal meridian (*12*). The length of the arc on the retina from center of gaze to optic disk is one fifth of the arc from center of gaze to retinal margin [A. E. Jones, *J. Comp. Neurol.* **125**, 19 (1965); (*8*)]. Therefore the number of millimeters per degree of visual angle must be approximately constant across the retina.
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16. Owl monkey striate cortex has been described as an example of peripheral scaling based on a proportional relation between linear magnification (millimeters of cortex per degree of visual field) and ganglion cell density (*6*). Peripheral scaling, however, requires either that linear magnification be proportional to distance between ganglion cells, or that ganglion cell density be proportional to number of cortical neurons per degree^2.
17. Malpeli and Baker (*9*) demonstrated that the proportion of the rhesus lateral geniculate nucleus devoted to central vision is greater than the comparable proportion of retinal ganglion cells. A mathematical description of the system is impeded, however, because only ganglion cell counts along the horizontal meridian are available in the rhesus monkey [E. T. Rolls and A. Cowey, *Exp. Brain Res.* **10**, 298 (1970)]. These yield biased estimates of magnification owing to the asymmetry of the macaque retina [J. M. Van Buren, *The Retinal Ganglion Cell Layer* (Thomas, Springfield, Ill., 1963)]. The displacement of ganglion cells about the fovea causes additional difficulties.
18. Equation 2 may be rewritten: $M_{\text{C}}(\phi_1,\phi_2) = aM_{\text{R}}(\phi_1,\phi_2) \times M_{\text{R}}(\phi_1,\phi_2)^{1.35}$; rearranging gives $M_{\text{R}}(\phi_1,\phi_2) \div M_{\text{C}}(\phi_1,\phi_2) = M_{\text{R}}(\phi_1,\phi_2)^{-1.35} \div a$. Substituting the definition of magnification and canceling terms results in Eq. 3 with $k = [\text{N}_{\text{R}}(\text{tot})^{0.35} \cdot A(\text{tot})^{1.35}] \div aN_{\text{C}}(\text{tot})$.
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Panhandling as an Example of the Sharing of Resources

The study of panhandling by Lockard *et al.* (*1*) provides a good example of how the ethological approach can be used in field studies of human behavior. However, there are some difficulties in interpreting their data.

Of the two studies reported, the first was conducted in the spring, the second in the fall. Lockard *et al.* concluded that there was a possible sex-by-season interaction since males were overall more successful in the spring than they were in the fall and since females were more successful than males in the fall. However, this finding is confounded. (i) The male confederates for the fall study were the same as those employed in the spring, but the females had not been previously employed. The amount of experience the confederates had could certainly affect the outcome of a request. (ii) The types of targets were different in the two studies in that family groups were also included in the fall study. From their second study only, it may be concluded that a possible sex-by-season interaction can be observed in panhandling. To generalize further, as the authors appear to do, would imply a four-way interaction: sex-by-season-by-target-by-experience.

Lockard *et al.* interpret nonfamilial sharing in terms of reciprocal altruism. In using altruism as an explanation, they indicate that giving a panhandler money is adaptive for the human species under certain conditions and important for survival. There are severe difficulties with this interpretation. Trivers (*2*) has noted that altruistic behavior is characterized by a relatively small cost to the donor and a great benefit to the recipient. If one considers the experimental manipulations of Lockard *et al.*, this condition does not appear to be met. It is not evident why only a dime was used as the amount requested. Aronson and Carlsmith (*3*) have argued that experiments designed to assess social processes must contain a balance of mundane and experimental realism. This means that the subjects must take the experimental context seriously, which these subjects apparently did. It also means that the experimental context must correspond to actual social processes as the subject is likely to view them. It is not reasonable to assume that a significant number of subjects in this experiment would view giving a dime to a panhandler as of great cost to them while greatly benefiting the panhandler. Even if the dime were given out of sympathy and that sympathy viewed as reciprocal altruism, one must still be cognizant of the cost-benefit ratio involved, as a variety of studies have shown [cited in (*2*)]. Further, reciprocal altruism is behavior that increases the fitness of both individual organisms and the social group, rather than increasing the fitness of one organism at the expense of another. Further, they do not provide a clear connection between an increase in fitness and the responses of their subjects.

Families were less willing targets than other groups, a phenomenon accounted for by Lockard *et al.* by the concept of kin selection. However, Wilson (*4*, p. 587) has argued that such a process involves the selection of genes from one or more individuals favoring or disfavoring the survival and reproduction of relatives (who are not offspring) possessing the same genes by common descent. Lockard *et al.*'s experiment does not present a situation in which there is great expense to the donor that would decrease his fitness while increasing that of the recipient (*4*). The experimental procedure is not at all analogous to the relevant processes. An explicitly social psychological interpretation of altruism that emphasized the motivational aspects of the targets' responses would be more appropriate. Lockard *et al.* do note that there are social psychological explanations for the refusal of groups to give a panhandler the requested dime (*5*). There are more cognitive explanations, which are difficult to relate to comparative research on the sharing of resources and to discussions of the evolution of sharing among humans. However, few other interpretations seem reasonable in light of the experimental design and the data reported.

Given the range of contexts within which panhandling can occur and the genetic diversity of the human species, it would not be unreasonable to presume that the responses of targets to panhandlers would vary as physical loca-