Spatial Mapping in the Primate Sensory Projection: Analytic Structure and Relevance to Perception*

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Abstract. The retinotopic mapping of the visual field to the surface of the striate cortex is characterized as a logarithmic conformal mapping. This summarizes in a concise way the observed curve of cortical magnification, the linear scaling of receptive field size with eccentricity, and the mapping of global visual field landmarks. It is shown that if this global structure is reiterated at the local level, then the sequence regularity of the simple cells of area 17 may be accounted for as well. Recently published data on the secondary visual area, the medial visual area, and the inferior pulvinar of the owl monkey suggests that the same global logarithmic structure holds for these areas as well. The available data on the structure of the somatotopic mapping (area $S-1$) supports a similar analysis. The possible relevance of the analytical form of the cortical receptotopic maps to perception is examined and a brief discussion of the developmental implications of these findings is presented.

Introduction

The primary sensory projection of the brain is a topographic mapping of the receptor periphery onto the central neural processor. Early workers such as Talbot and Marshall [29] (retinostriate projection), Apter [7] (retinotectal projection), Woolsey [36] (somatotopic projection), and Lorenté de No [20] (auditory projection) established the basic existence and structure of these mappings using relatively crude slow-wave recording techniques. Subsequent work, making use of more refined and sophisticated single-unit mapping methods, has served in recent years to greatly increase the detailed knowledge of the structure of the various sensory mappings, and has extended

their domain of definition to include a variety of thalamic and mid-brain structures as well.

The existence of orderly spatial mapping in diverse neural structures would seem to have considerable importance to the functional aspects of sensory neurophysiology: in each modality, a receptor surface (the retina, the cutaneous surface, the basilar membrane) is mapped, through sub-cortical relay nuclei, to an essentially two-dimensional (laminar) representation at the cortical surface. This representation of the sensorium in terms of a receptor sheet mapped onto a cortical surface has led Arbib [8] to characterize the brain as "a layered, somatotopically organized computer".

The view of the primary sensory projection as a planar (although "distorted") map of the sensorium underlies a basic controversy that has existed for the past thirty years. Somjen [26] has provided a concise statement of this question:

"The issue of the cortical movie screen, popular at first, discredited later... and defended once again, is still not resolved. The presence of these topographically organized projection areas can hardly be mere accident, of course. Besides the retina and the body surface, the receptor sheet of the cochlea also finds a representation of sorts in several regions of the brain. What kind of significance can we attach to them?"

The present work is a critical examination of this question, which begins by analyzing the anatomical and physiological data that has accumulated during the past twentyfive years on the detailed structure of the retinotopic mapping of the striate cortex (area 17). It is possible to present a simple analytic description of the retinotopic mapping, using complex variables to represent points in the visual and cortical planes. The retinotopic mapping is thus found to be a complex logarithmic (conformal) mapping of the visual field onto the cortical surface. Furthermore, the available evidence suggests that the receptotopic

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mappings of the secondary visual cortex, the inferior pulvinar, and the somatosensory cortex, may be described by the same mathematical formalism. In addition, it is pointed out that the local receptive field structure of the striate cortex, as represented by Hubel and Wiesels [17] model of the hypercolumn, may very well be the consequence of a complex logarithmic mapping on a local scale. The possible relevance to visual perception of the complex logarithmic mapping will then be investigated by studying the mapping of a visual stimulus. This demonstration will support, in a graphic way, the conclusion that the preprocessing of the two-dimensional brightness distribution available at the retina, by the complex logarithmic retinotopic mapping, may possibly play a role in the analysis of form invariant information. Finally, a brief discussion of the seemingly ubiquitous presence of complex logarithmic structure in the sensory projection will be presented with respect to the developmental mechanisms that could lead to this structure in a biological system.

Global Retinotopy

The notion of retinotopy may be traced back to the pioneering anatomical investigations of Polyak [23], who suggested, on the basis of the anatomy of the visual cortex, that a mathematical projection of the retina on the cortex must exist. Talbot and Marshall [29] confirmed this hypothesis with physiological methods, and the extensive investigation of Daniel and Whitteridge [11] provided a source of precise, quantitative data; however, a mathematical analysis of the retinotopic mapping has never been presented.

In subsequent work, making use of single cell recording techniques, the locus of accurate topographical representation in the striate cortex has been limited to layer IVc, where the receptive fields are predominantly small and circularly symmetric, and the cortical afferents arriving from the lateral geniculate nucleus (LGN) arrive and terminate [17]. In the subsequent discussion of global topography, it will be understood that it is mainly layer IVc of the striate cortex that is accurately retinotopic. Following this discussion of global topography, the local remapping of cortical afferents to simple cells, which are located mainly in the cortical laminae surrounding layer IVc, will be separately analyzed.

Daniel and Whitteridge measured the cortical magnification factor by recording slow wave and multiple unit responses to spots of light in the visual periphery, and then reconstructing the electrode tracks from histological sections. They defined the cortical magnification factor as the distance moved (in millimeters) across the cortical surface corresponding to one degree of movement of a point stimulus in the visual field [11].

Daniel and Whitteridge found that the cortical magnification factor is the same along all radii, regardless of the angular coordinate, and is the same whether measured radially or along the circumference; thus the magnification factor is radially symmetric.

The cortical magnification data was used to construct a three dimensional model, which accounted closely for the surface area of the cortex, and could be simply folded to duplicate the actual folding pattern of the striate cortex. However, their investigation was largely phenomenological: "no simple equation was found to fit the data".

Daniel and Whitteridge presented their cortical magnification data graphically. For the present analysis, data published in their original work were measured, and fit by computer to a power law. The fit is excellent over the entire range of measured date (from 1° to 50°):

Figure 1A

$$M(r) = 6^\star(r)^{-0.9} \quad (C.L. = 95\%) . \tag{1}$$

$M(r)$ is the magnification factor in millimeters/degree, and the variable r measures the eccentricity in degrees. The choice of r as the variable representing eccentricity is made in order to simplify the geometry by approximating the visual sphere by its tangent plane. The spherical polar coordinates of eccentricity and azimuth may be approximated by the polar coordinates of the tangent plane (r and ϕ). The polar coordinate ϕ is identical to the azimuthal spherical coordinate. The polar coordinate r is approximately proportional to the eccentricity:

$$r = R \sin \Theta \cong R\Theta . \tag{2}$$

Where r is the tangent plane radial polar coordinate, R is the radial distance of the tangent plane from the retina, and Θ is the eccentricity. The approximation of Equation (2) is accurate to 98% for the central 20 degrees of visual field. Furthermore, for a tangent plane that is placed 57.3 cm from the eye, the polar coordinate r in the tangent plane is numerically equal (in cm) to the eccentricity in degrees.

The fit of Equation (1) is the best power fit to the data of Daniel and Whitteridge. For the central foveal representation (less than 1° of eccentricity), no magnification data is available; it is assumed that the inverse dependence on eccentricity tapers off in a gradual way for this central-most part of the visual field. For the central 20 degrees of visual field, a simple straight line fit to the inverse magnification is in excellent agreement with the data. In order to include peripheral parts of the visual field (beyond 20°), Equation (1) may be used, which is very close to an

inverse linear dependence on eccentricity for the entire visual field. Thus, the exponent of r in Equation (1) is sufficiently close to unity to be replaced by it; that is supported by the later work of Hubel and Wiesel [18], who find that the inverse magnification curve is closely approximated by a straight line. In light of the previous discussion, it is possible to simplify the analysis of Daniel and Whitteridge's data, expressed in Equation (1) by the approximation:

$$m = k/r . \cdot \tag{3}$$

Where k is a constant, r represents eccentricity from the fixation point (foveal representation) and m is the magnification. Cortical magnification is a differential quantity: small changes in cortical position are related to small changes in visual field position. Since we are interested in the analytic form of the retinotopic mapping, and not its derivative, we must find an analytic function whose derivative is radially symmetric and is proportional to $1/r$. The analytic function that has this property is the complex logarithm:

$$w = \ln(z) \tag{4}$$

where w represents a point in the cortical plane and z represents a point in the visual plane, which may be represented as:

$$z = r \exp(i\phi) . \tag{5}$$

Equation (4) may be written in real variables as:

$$z = \ln r$$
$$y = \phi \tag{6}$$

with the point (x, y) located in the cortical plane and the point (r, ϕ) located in the visual plane.

Magnification is defined for a complex (conformal) mapping as the amount by which an infinitesimal line segment is "stretched" by the mapping $f(z)$ [1]. This is exactly analogous to the physiological definition of magnification. In general, the magnification of a conformal mapping may be written as: (1)

$$m(z_0) = \lim_{z \to z_0} \left| \frac{f(z) - f(z_0)}{z - z_0} \right| = |f'(z_0)| . \tag{7}$$

Substituting the logarithm function for $f(z)$, we have:

$$|f'(z_0)| = \left| \frac{k}{z_0} \right| = \left| k \frac{e^{-i\phi}}{r_0} \right| = \frac{k}{r_0} . \tag{8}$$

Thus, the magnification of the complex logarithm has the required logarithmic dependence on eccentricity, and is radially symmetric, satisfying the experimental findings of Daniel and Whitteridge. In order to verify this analysis, it is possible to examine the mapping of global visual field landmarks and compare these to the predicted mappings of the same stimuli under the logarithmic mapping. It should be emphasized that this is a totally independent verification. The (differential) cortical magnification, as a measurement, is independent of the (global) measured representations of the vertical and horizontal meridians, and other visual landmarks.

The mapping of global visual field landmarks, as measured by Talbot and Marshall and Daniel and Whitteridge is shown in Figure 1B.

The vertical meridian is wrapped around the visual projection, and forms the border of area 17; *circles of constant eccentricity are mapped to vertical straight lines*. Alongside the experimental data is presented the predicted mappings of the same visual field landmarks. There is excellent agreement between the measured and predicted geometries.

Thus, the phenomenological aspects of the retinotopic mapping discussed above, and illustrated in Figures 1A and 1B support the hypothesis summarized by Equation (4).

The characteristic features of planar mapping which indicate the underlying presence of logarithmic spatial structure are summarized in Table 1, and are derived in Appendix 1.

These features may be thought of as the "signature" of the complex logarithmic mapping. Wherever these "signatures" are evident in a receptotopic mapping, the presence of a logarithmic spatial structure may be inferred. This situation is analogous to plotting data on semi-logarithmic paper. Exponentually distributed data is difficult to characterize by eye; if one takes the (exponential) data points representing the growth of a bacteria colony and plots them on linear graph paper, they may seem to be derived from an exponential distribution. However, if the same data is plotted on semi-logarithmic paper, the resultant straight line fit is satisfying confirmation that the underlying distribution actually is exponential. In a similar manner, once the underlying signatures of the complex logarithmic mapping are familiar, it becomes very much

Table 1. Geometry of the logarithmic conformal mapping

$\log z$	$=$	w
1. Concentric circles (exponentially spaced)		Vertical lines (equally spaced)
2. Radial lines (equal angular spacing)		Horizontal lines (equally spaced)
3. Logarithmic spirals ($\varrho = Ae^{k\phi}$)		Inclined straight lines slope $= l/k$; intercept $= -(\log A)/k$

The three geometric patterns on the left are the level lines (1), or streamlines, of the logarithmic conformal mapping. Numbers 1 and 2 may be thought of as limiting cases of the logarithmic spiral; No. 1 for $k = 0$ and No. 2 for $k = \infty$

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A

B

| TɛM | DɛW | W= LNZ |

C

VISUAL HEMIFIELD
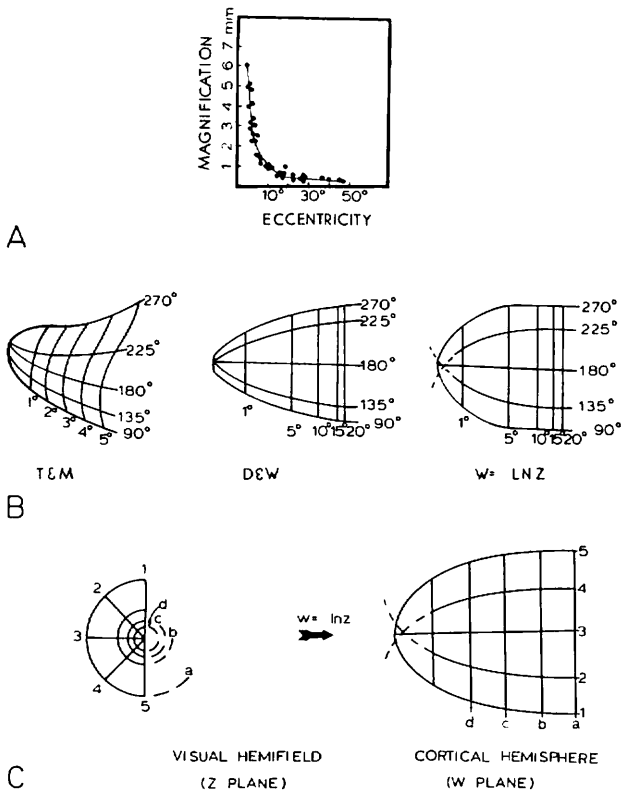(Z PLANE)

CORTICAL HEMISPHERE
(W PLANE)

Fig. 1. A The cortical magnification data of Daniel and Whitteridge. Through the points is drawn the best fit to the data for a power law, as described in the text. **B** The measured and predicted mapping of visual landmarks in striate cortex. The upper (90°) and the lower (270°) vertical meridians, the horizontal half meridian (180°), the octants (135° and 225°) and the circles of constant eccentricity are drawn as measured by Talbot and Marshall, and Daniel and Whitteridge. The data of Talbot and Marshall, on the left, does not show the correct (logarithmic) spacing between the lines of constant eccentricity; their experiment is the pioneering measurement of this data. The data of Daniel and Whitteridge is much more accurate, and is shown in the center. This is a projection, onto a horizontal plane, of a three dimensional model; the meridians and octants are equally spaced, as they are in the theoretical prediction of these mappings under the logarithmic conformal mapping. The theoretical prediction, on the right, actually represents a vertical meridian that is infinitesimally displaced from the origin; otherwise the curved part of the contour would actually be a right angle. The horizontal meridian is an average of a line infinitesimally above and below the precise horizontal meridian. With these qualitative reservations, there is great similarity between the data and the theoretical prediction of the data under the logarithmic mapping. **C** The global retinotopic mapping under the logarithm function. Concentric circles (exponentially spaced) and radial straight lines are mapped onto the equidistant cartesian grid on the cortex. Note the density (derivative) of the exponentially spaced lines gives a linear dependence on the eccentricity; this is observed as a linear scaling of the receptive field size in the visual plane, with a constant (hypercolumn) size in the cortex

easier to identify the presence of complex logarithmic structure. This analogy is particularly applicable to neuroanatomical data because of the complex folding and bending characteristic of neural structures. Virtually all the "surfaces" alluded to in this paper are

actually highly complex, convoluted, doubly curved surfaces, for which the "planar" structure must be inferred by histological reconstruction, and then by projection onto a planar map. Naturally, the maps that result from this procedure are often difficult to interpret merely by their visual appearance. However, the signature of spatial logarithmic structure, as outlined above, is easy to see and provides satisfying confirmation of the underlying mathematical structure of the neural maps.

The previous analysis has demonstrated that the retinotopic mapping of the striate cortex may be mathematically described as a complex logarithmic mapping. The characteristics of logarithmic spatial structure that support this statement are summarized in Table 1. In the case of the striate cortex, excellent measurements are available, and these satisfy all the requirements specified in Table 1 for the existence of logarithmic spatial structure. For other cortical and sub-cortical areas and modalities, the experimental data is much less comprehensive. Nevertheless, the signature of the complex logarithm is so characteristic that it is possible to identify a receptotopic mapping as a logarithmic mapping, even in the absence of the detailed data available for the striate cortex.

In the following discussion, the lateral geniculate nucleus, the secondary visual cortex, the inferior pulvinar, and the somatosensory cortex, will be discussed with respect to specifying the analytic structure of their receptotopic maps.

The Optic Tract and the Lateral Geniculate

The magnification factor for the lateral-geniculate nucleus (LGN) is the same from as that for the striate cortex, up to a scale factor [9] and therefore is of the same form as Equation (3) above. Since cell density in both the LGN and the striate cortex is roughly constant with respect to eccentricity [18] most workers in the physiology of the geniculo-striate system have assumed that the origin of the magnification curve lies in the form of the density of the retinal ganglion cells themselves [9] which follow a distribution of the form of Equation (3). As in the previous discussion, it is evident that a (differential) magnification curve of the form of Equation (3) implies a logarithmic radial structure for the LGN retinotopic mapping, and thus raises the possibility that the source of the complex logarithmic structure of the striate cortex may lie in the LGN (and possibly the retinal ganglion cells). However, the available maps of the LGN show that this is not the case. Lines of equal azimuth and elevation from a grid which is approximately cartesian in the visual plane. They also form an approximately cartesian grid in the LGN [9]. The form of the

magnification curve is clearly in evidence in these plots, causing the central representation of the visual field to occupy a disproportionately large area. Nevertheless, the angular part of the complex logarithmic mapping is not present at the level of the LGN, and must occur in the projection of the LGN onto layer IVc of the striate cortex. Thus, the complex logarithmic structure of the striate cortex seems to be effected in two separate steps: 1) the form of the density of retinal ganglion cells, leading to a logarithmic *radial* structure in the optic tract, and LGN, 2) the projection of the LGN onto the cortex, where the angular reorganization of optic tract fibers is effected that leads to the final form of the striate cortex retinotopic map, as in Equation (4) above.

Secondary Visual Cortex

The quantitative data available on the secondary visual cortex is much less documented that that for the striate cortex. However, in recent years, the secondary visual cortex of the primate and the lower mammals has begun to be extensively studied. In a recent investigation of the organization of the second visual area (area 18) of the owl monkey, Allmann and Kaas [5] have published receptive field plots corresponding to straight line trajectories across the surface of visual area V–II. Their data is reproduced in Figure 2. It is evident from this figure that the image, under a straight line across the surface of V–II, is a spiral pattern of receptive fields in the tangent plane. Referring to Table 1, it can be seen that the mapping which images a spiral onto a straight line is the logarithmic conformal mapping.

In order to emphasize this point, Allman and Kaas' figure is reproduced in Figure 2. Also shown in this figure is a logarithmic spiral, for reference, and a semi-logarithmic polar plot of the receptive field centers corresponding to straight line trajectories in the periphery. Recalling that the equation of the logarithmic spiral is $r = Ae^{k\phi}$, it can be seen that the log of the radius should be linear with respect to the polar angle. The straight line plots (and the coefficients of linear regression) presented in Figure 2 support this statement. This procedure is not intended to be quantitative, but merely to support the observation that the spiral receptive field structure reported by Allman and Kaas does in fact represent a logarithmic structure.

Allman and Kaas emphasize in their paper that area V–I (area 17) is a "simple topological transformation of the visual hemifield" and call this a "first order transformation". They refer to V–II as a "second order transformation" because they feel that the simple retinotopy of the striate cortex is not maintained there. This is because area V–II forms a belt around the striate cortex (V–I) such that points above and below the horizontal meridian are mapped to points quite far apart in the cortical representation. However, aside from this peculiarity of the representation of the horizontal meridian, it would seem that the global structure of secondary visual cortex is described by a logarithmic spatial conformal mapping, as is the primary visual area.

In subsequent work, Allman and Kaas [6] have mapped the global receptive field structure of the medial visual area of the owl monkey. This data is shown in Figure 3.

Again each trajectory across the surface of the cortex corresponds to a logarithmic spiral trajectory in visual space. Also shown in Figure 3 is a plot on semilogarithmic paper of the radial versus the angular coordinates of the receptive field centers. These plots support the characterization of the receptive field trajectories as logarithmic spirals, analogous to those presented above for the secondary visual cortex (V–II). This characterization of the secondary visual cortex (area 18) and the medial visual area of the primate cortex as logarithmic conformal mapping is expected. Clasically, area 18 is described as a "mirror image" of area 17 [5], and the medial visual cortex is explicitly an image of the striate cortex [6]. The "mirror image" description of area 18 is called into question by the analysis of Allman and Kaas, cited above. Nevertheless, logarithmic spatial structure is clearly evident in these areas.

Somatosensory Cortex

The primate dorsal column-medial lemniscal component of the somatosensory projection subserves the modalities of touch and kinesthesis. One more synapse (at the level of the gracial or cuneate nuclei) than the visual system separates the cutaneous periphery from the primary cortical processor. The cutaneous periphery is represented by a map-like representation of the body, located in the post-central gyrus of the cerebral cortex (area S–1). This is termed the somatotopic map. The elegant experimental observations of Werner and Whitsel are of particular interest to the present discussion. Instead of determining the projection of the body to the cortex, Werner and Whitsel [34] measured the projection of straight lines of cells in the cortex (S–1) to the surface of the limbs. They found that "the receptive fields of the neurons progress, essentially, in bands around the limb, much as did the laces of a Roman soldier's footwear ...the sum total of all RF's represented in any mediolateral traverse of the cortical map describes a continuous spiral path around the limb". Coupling this observation with that of Mountcastle [21], that the size of the cutaneous
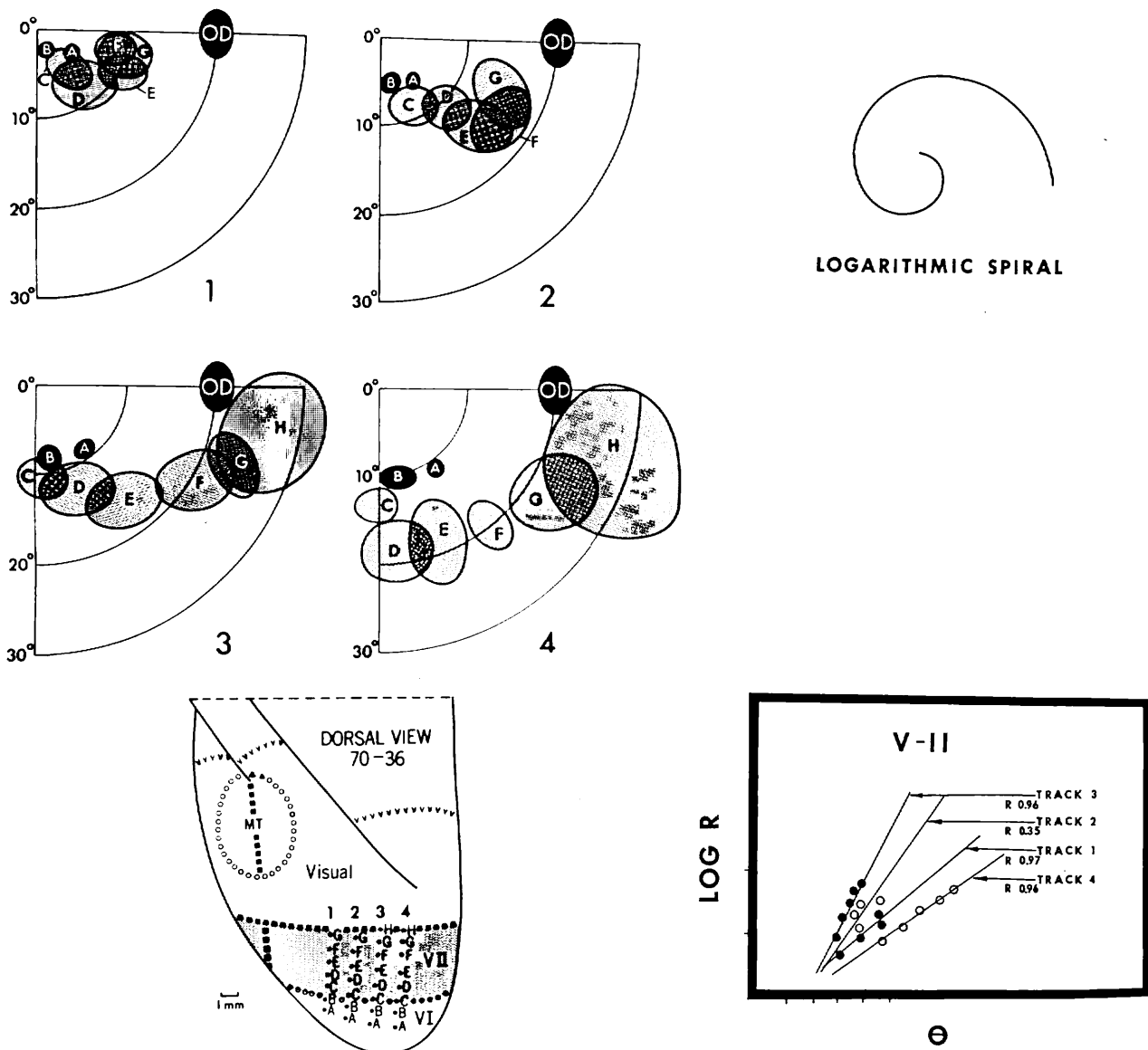
Fig. 2. On the left is reprinted the data of Allman and Kaas showing their results for the measurement of receptive field size and position, corresponding to straight lines across the secondary visual area of the monkey. The perimeter charts labeled 1, 2, 3, and 4 correspond to the anatomical locations indicated in the lower part of the figure. On the right is an example of a logarithmic spiral. Below the spiral is a semi-logarithmic plot of the radial position of the receptive field centers with respect to the corresponding angular positions. The hypothesis that these receptive field trajectories lie along logarithmic spirals is equivalent to the hypothesis that this semi-logarithmic plot should be linear. The coefficients of linear correlation to the best (least-squares) fit to a straight line are shown in the figure. The measurements were made directly from the figure of Allman and Kaas, starting from the first RF in V–II

receptive fields linearly increases with distance from the distal point of the limb, it is clear that the somatotopic mapping takes straight lines (in the cortex) to logarithmic spirals in the cutaneous periphery. This conclusion is supported by the further observations of Werner and Whitsel [35] that for rostro-caudal trajectories across the surface of S–1, "the sequence of receptive fields describe circular paths around the limb". With reference to Table 1 and Appendix 1, *the mathematical structure that this*

implies for the somatotopic mapping is the logarithmic conformal mapping, centered about the distal point of the limb. To summarize the parallels between the visual and (somatic) maps: receptive field size for the visual (somatic) map scales linearly with distance from the foveal (distal) point of the receptor surface. Straight lines in the cortical representation correspond to receptive fields trajectories that are concentric circles, logarithmic spirals, or radial straight lines, depending on the orientation of the cortical
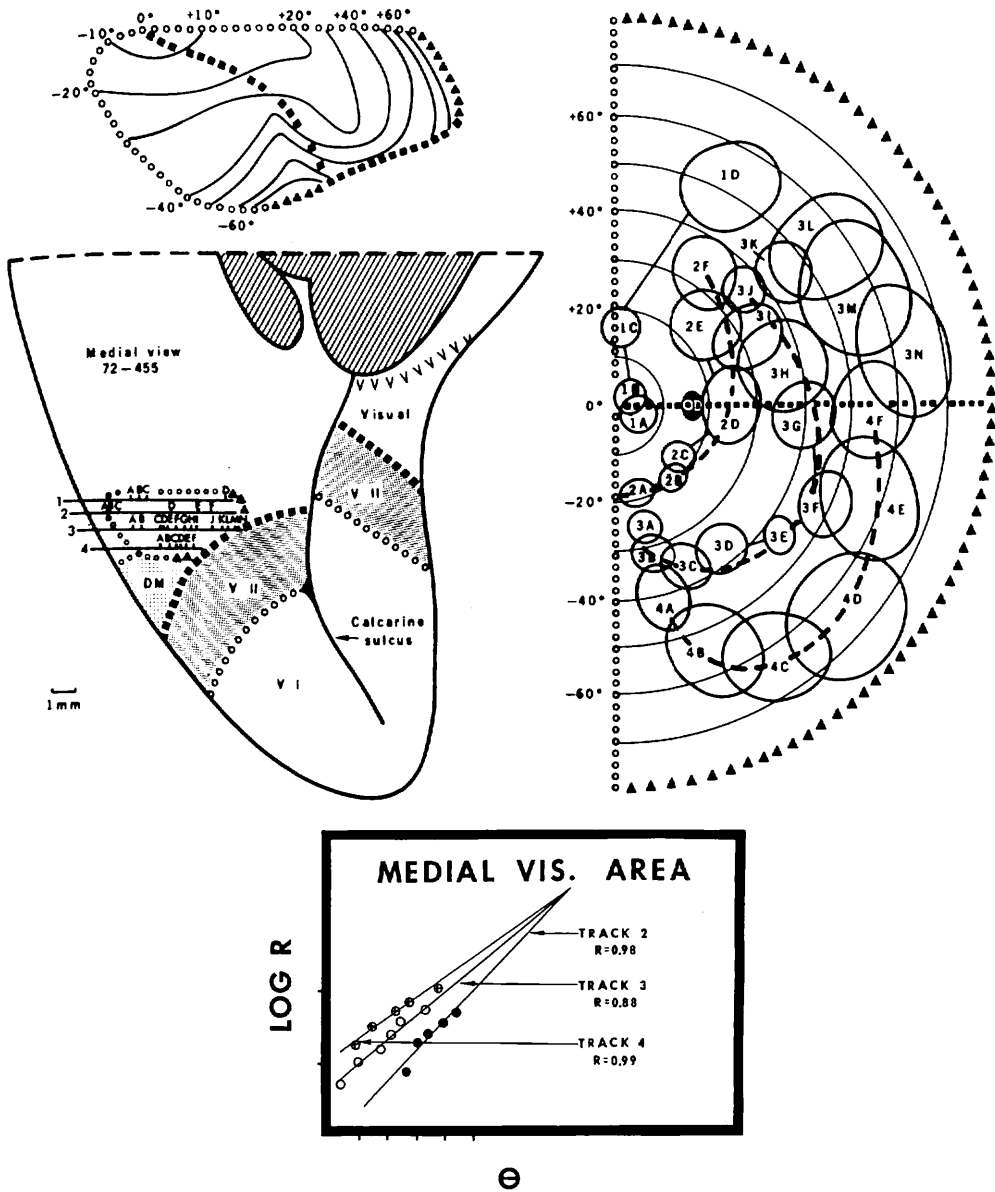
Fig. 3. Above is reprinted the figure of Allman and Kaas showing their measurements of receptive field size and position, corresponding to straight lines across the medial visual area of the monkey. On the right, sections of logarithmic spirals have been drawn through the receptive field trajectories (dashed lines), corresponding to the contiguous straight line tracks across the cortex shown on the right. Below is shown a semi-logarithmic plot of the radial position of the receptive field centers with respect to the corresponding angular positions. The hypothesis that these receptive field trajectories lie along logarithmic spirals is equivalent to the hypothesis that this semi-logarithmic plot should be linear. The coefficients of linear correlation to the best (least-squares) fit to a straight line are shown in the figure. The measurements were made directly from the figure of Allman and Kaas, starting from the first *RF* in the medial visual area

trajectories. Again, as in these case of the secondary visual areas, this discussion of the somatotopic mapping is qualitative; nevertheless, the observations of Werner and Whitsel, and Mountcastle imply that the analytic structure of the somatotopic mapping is the same as· that found previously to account so parisomeously for the structure of visuotopic mappings.

The importance that this analysis has with regard to visual-haptic coordination of eye-limb activity is obvious, and will be discussed in more detail later in this paper. Additionally, the motor representation of the cortex is itself a mirror-image of the somatotopic representation. Thus, the visual, somatotopic, and motor maps of the primary cortical representation may be described, at least approximately. by the same mathematical function: the complex logarithm. A similar situation is known to exist in the superior colliculus, where superimposed visual, motor, somatic,
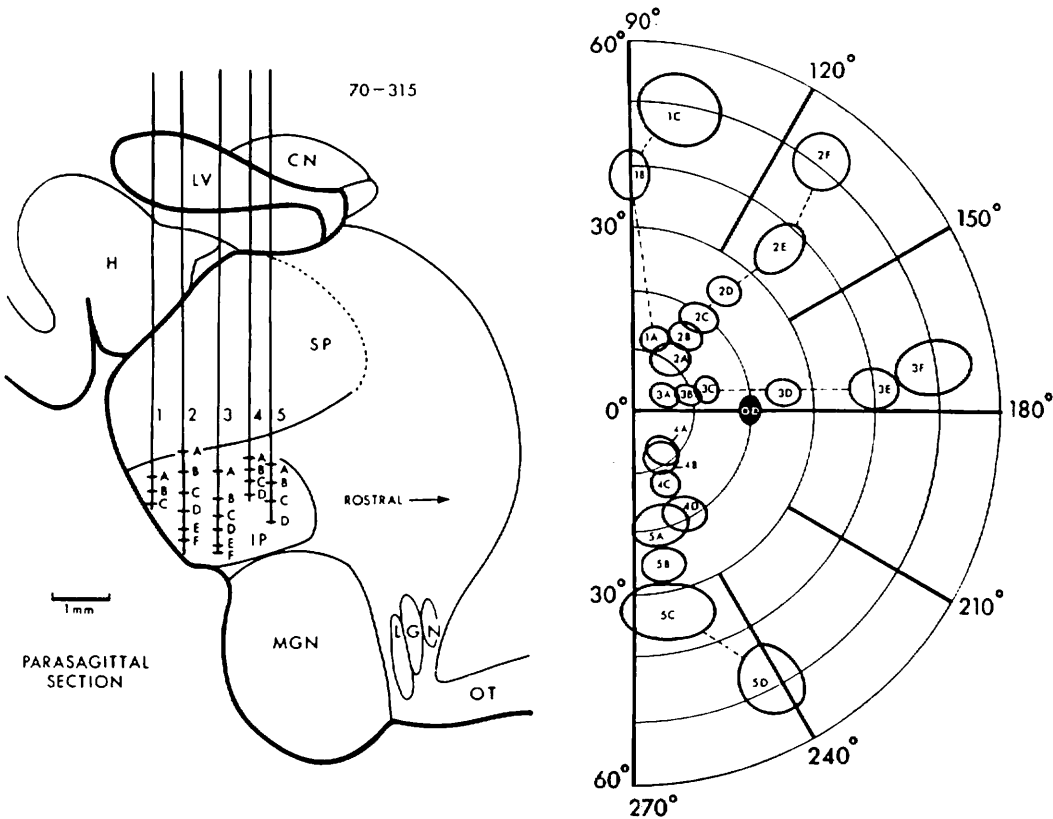
Fig. 4. A recent map of the retinotopic structure of the primate inferior pulvinar has been provided by Allman and Kaas. The visual field trajectories and the corresponding thalamic trajectories are shown in the figure. Clearly, parallel straight line trajectories in the inferior pulvinar correspond to radial straight line trajectories in the visual field. With reference to Table 1, this observation gives tentative support to the classification of the retinotopic structure of the pulvinar as a complex logarithmic map, like that of the primary and secondary visual cortex. It can be predicted from this data that, had the thalamic trajectories been rotated by 90 degrees, circular visual field trajectories would have been obtained; an intermediate angle of rotation would yield logarithmic spiral trajectories, as shown in Figures 2 and 3, for the secondary visual cortex

and auditory maps exist. These (linear) collicular maps are in registration with one another, both anatomically and functionally [13] and are thought to subserve the functional capabilities of the superior colliculis that have to do with visual orientation. The results of the present paper are very intriguing in this light, because they suggest the existence of a basic principle of sensory-motor function. A primary algorithm of the sensory system of the brain seems to be the creation of maps of the relevant sensory-motor spaces, in registration with one another. This is apparently the plan utilized by the (linear) tectal system and the (logarithmic) cortical system, as a general principle of sensory information processing.

Inferior Pulvinar

The inferior pulvinar is a large thalamic nucleus located in close proximity to both lateral geniculate and the superior colliculus. The pulvinar is a somewhat mysterious structure, both anatomically and

functionally, and has been described as "terra incognita of the thalamus" [33]. Recently, it has been established that the inferior pulvinar receives a retinotopic projection of the visual field, in the primate [4]. A parasagital section of the brain, showing a number of straight line electrode trajectories, along with the corresponding receptive field plots, is shown in Figure 4.

It is clear from this figure that straight line trajectories in the brain correspond to radial straight line receptive field plots. Consequently, (with reference to Table 1 and Appendix 1), the retinotopic mapping of the pulvinar may be described, insofar as available data allows, by the complex logarithm function. This figure represents the only available data to date on the mapping of the inferior pulvinar, no magnification data is available. Consequently, the assignment of a complex logarithmic structure to the retinotopic map of the pulvinar is only tentative.

Allman and Kaas speculate that the source of the retinotopy of the pulvinar may lie either in the LGN, the superior colliculus, or the cortex. The puta-

tive logarithmic structure suggested in this paper would tend to group the pulvinar with the geniculo-striate system, (which is generally logarithmic in structure) rather than with the tecto-fugal system (superior colliculus) which is generally linear in the structure of its retinotopy. Consequently the above analysis may provide some hints as to the function and anatomical relationship of this poorly understood thalamic visual area.

Sequence Regularity in the Striate Cortex

The previous analysis of the various receptotopic mappings of the sensory projection was concerned with the global nature of these mappings, with the mapping of entire receptor surfaces (the retina, the cutaneous surface) onto the corresponding central receiving areas. In the case of the striate cortex, the global logarithmic spatial structure holds at the level of layer IVc where the afferent input to the cortex arrives from the LGN [17]. In the surrounding laminae of the cortex, this precise topographic mapping is no longer valid; as is well known, the simple and complex cells in these laminae are responsive to straight line stimuli tuned about a range of angular orientation, and with definite stimulus velocity characteristics [16]. The local structure of the striate cortex has recently been examined in exquisite detail by Hubel and Wiesel in a series of paper culminating in their recent elegant demonstration of sequence regularity and the "hypercolumn" model [17]. A brief summary of this model, and the demonstration of sequence regularity among the simple cells of the striate cortex, will be presented, in order to demonstrate that the local mapping of cortical (LGN) afferents to the simple cells may be characterized as a logarithmic mapping, on the scale of a single hypercolumn.

In the original paper of Hubel and Wiesel [16] reporting the existence of simple cells, they speculated that the orientation tuning property of these simple cells arises from the convergence of a row of geniculate cells onto a single simple cell, as shown in Figure 5. Although the question of modeling the origin of simple cell orientation tuning is an active field of research in itself, the original model of Hubel and Wiesel is correct in its substantial details.

Recently, Hubel and Wiesel [17] have specified in detail the spatial arrangement of these columns, or slabs, of simple cells. The striate cortex of the macaque (and likely of the cat) is subdivided into two independent and overlapping series of columns termed "orientation slabs" and "ocular dominance columns". Each orientation slab represents tuning of

simple cells over an angular range of 10–15 degrees. The width of these slabs is 25–50 μ. Thus, over a cortical traverse of from 0.5–1 mm, a complete traverse of the angular tuning variable (180°) is accomplished. This is the same distance which two ocular dominance columns span; the complete angular set of orientation tuning slabs, coupled with the binocular representation of two ocular dominance columns, is a functional unit of the striate cortex, called a hypercolumn.

This demonstration of "sequence regularity" shows, in the words of Hubel and Wiesel, that the striate cortex "after all is a remarkably uniform and homogeneous structure". In order to account for this regularity of orientation tuning, we have to deal with a situation as depicted in Figure 5. Each row of geniculate cells converges onto a slab of cortical cells, and the rows of geniculate cells rotate through regular angular increments, as the cortical representation moves through parallel slabs. It is obvious that in order to simultaneously satisfy the requirement of sequence regularity, as well as orientation tuning, the mapping that describes the wiring of LGN afferents to cortical simple cells must be very precisely constrained. In fact, with reference to Table 1, it is evident that the *formal mapping which takes equal angular strips to parallel strips is the complex logarithm.* If one describes the local mapping of LGN afferents (located in layer IVc) to simple cells (located in the surrounding laminae) by a local complex logarithmic mapping, about the hypercolumn center, then it is possible to satisfy the requirement that *rows of LGN cells converge onto simple cells in a spatially regular way such that equal angular increments in visual space correspond to equal linear steps in cortical space.* The analysis would seem to be particularly harmonious with the thinking of Hubel and Wiesel on this subject. They view each hypercolumn as a quasi-independent unit of the cortex ... "capable of analyzing a region of visual field equal to the local field size" [17]. The image evoked by their model is of a cortex that is spanned by a mosaic of quasi-independent patches, each of which is responsible for the analysis of a small area of the visual field. The receptive fields are globally located across the surface of the cortex by a similar complex logarithmic mapping that describes the global relationship of the entire retinal surface to the cortical surface. The cortex is thus a concatenated logarithmic structure, whose structure in the large mirrors that of its local elements. This structure has a simple developmental rational, which will be discussed later in this paper. Furthermore, this concatenated logarithmic structure has some very potent information processing characteristics which may be of direct relevance to visual perception. These will now be illustrated.
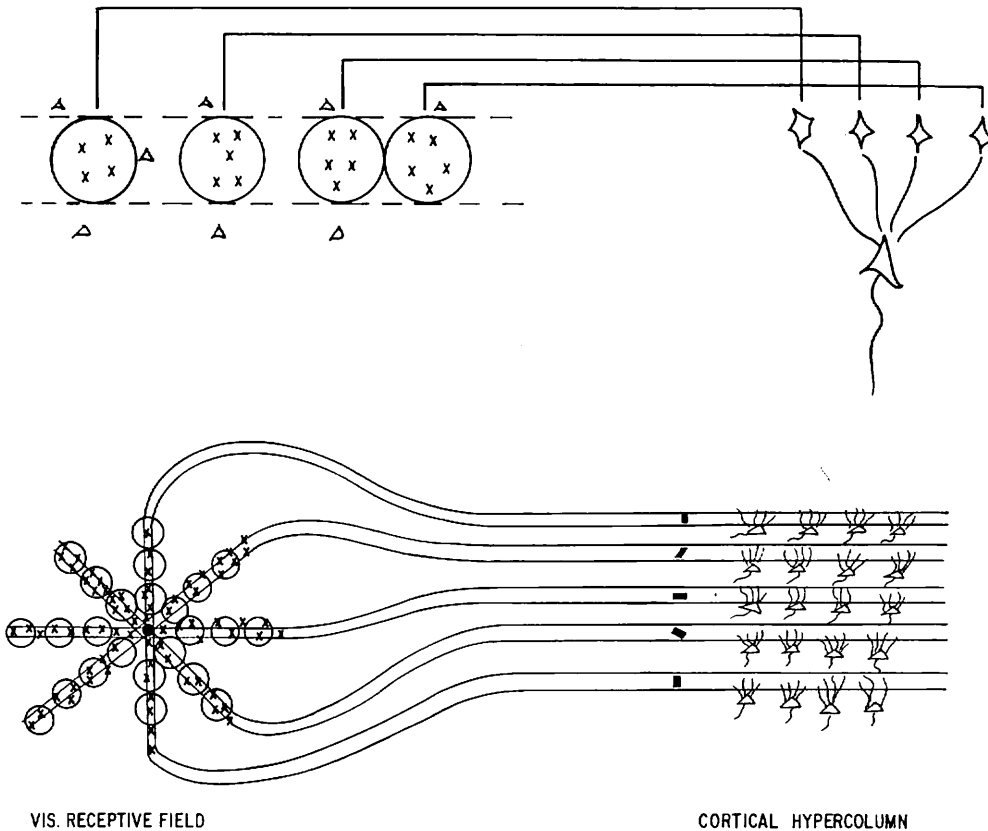
VIS. RECEPTIVE FIELD   CORTICAL HYPERCOLUMN

Fig. 5. Figure 5 shows a schematic representation of Hubel and Wiesel's suggestion for the origin of the orientation tuning of the simple cells of the striate cortex. A row of LGN cells (corresponding to a row of excitation at the retinal surface) converges onto a simple cell, whose response properties will then show orientation tuning. The recent demonstration of sequence regularity by Hubel and Wiesel is schematically represented in the bottom part of the figure. Here, a number of rows of LGN cells, arranged in equi-angular steps, are shown as they must project to the simple cells in order to maintain both orientation tuning and sequence regularity. The geometric statement of the sequence regularity property is that *equi-angular* steps in the visual (LGN) plane correspond to equal *linear* steps in the cortical plane. With reference to Table 1, it can be seen that the complex logarithm function provides this property. Consequently, it may be hypothesized that the projection, within the approximate area of representation of a receptive field at the cortex, of cortical afferents to simple cells, may be formally described as a local complex logarithmic mapping

Perceptual Consequences of Logarithmic Structure

Many years ago, Polyak [23] advanced the suggestion that there may exist a mathematical representation of the retina in the cortex. The present work supplies the mathematical form for this mapping: the complex logarithm of Equation (4). The anatomical and physiological thrust of this paper ends here. However, the fundamental reason for studying the anatomy and physiology of the visual system is to gain insight into its functional aspects. At present, our fundamental knowledge of perception is slight. Julesz [19] has said: "We still lack a physiological psychology of... visual perception. One of the greatest obstacles to its attainment is our inability even to guess the neural levels where certain perceptual phenomena might occur". One of these illusive perceptual phenomena is size invariance. We have no problem recognizing a familiar stimulus, whether it is near or

far from us in space. The locus of retinal excitation due to the face of a friend is very different if that friend is sitting next to us. or is across the room. According to Sutherland [28], this size invariance property is one of the fundamental aspects of the visual system that any neural theory of perception must explain. The following discussion will demonstrate that the complex logarithm has a natural size invariance property. This mathematical fact, coupled with the previous anatomical and physiological analysis, suggests that the psychological property of size invariance may be subserved by the anatomical structure of the striate cortex. This is a hypothesis at present: it may be merely accidental that the mathematical properties of the retinotopic map automatically provides a size scaling effect. However, the lack of any viable neural theory for the existence of size invariance in visual perception makes this suggestion an attractive working hypothesis.
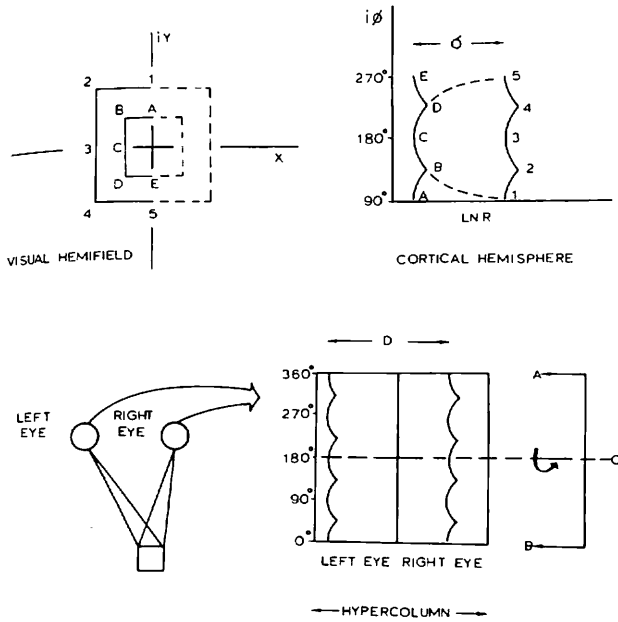
Fig. 6. The size-scaling property of the complex logarithm is graphically illustrated. The top of the figure shows the mappings of a large and small square, as they would appear across the surface of the unfolded and flattened cortex. The image of the square is an invariant; size dilitation merely causes this invariant image to shift across the cortical surface. The bottom of the figure shows the analagous mapping, under the local (hypercolumn) logarithmic mapping. In this figure, a small square element of the image space corresponding to a visual receptive field is depicted; the slightly different size of the retinal images are normalized by the complex logarithmic mapping. The relative shift, on the scale of a hypercolumn, is a possible cue for the disparity of the stimulus, since this relative shift is proportional to the relative difference in size of the left and right eye projections

A two dimensional contrast distribution (for example the grain of a photographic emulsion) may be represented as the locus of points (complex variable z_j) of each independent element of the pattern. The operator for size dilitation in complex variables is simple multiplication by a real constant k. The point z_j $(r_j e^{i\phi} j)$ is then taken to the point z_j $(kr_j e^{i\phi} j)$. The locus of points $\log(z_i)$ is mapped to the locus $\log(kz_i) = \log(z_i) + \log(k)$. Thus, in the logarithmic (cortical) plane, size changes in the image plane reduce to a simple translation. The size of the image is thus invariant. This mathematical property of the complex logarithm is illustrated in Figure 6.

Chaikin and Wieman [10] have exploited this property of the complex logarithm, in a computer oriented pattern recognition approach. An earlier work in computer oriented pattern recognition [22] pointed out an additional useful property of processing pictorial information via the complex logarithm: multiplicative effects in the picture plane become additive effects in the logarithmic plane. Thus, the intensity distribution of a scene may be written as:

$$I(x, y) = R(x, y) U(x, y) \qquad (9)$$

where R is the reflectance distribution of the stimulus and U is the illumination distribution of the ambient lighting. In the complex logarithmic plane the above relation becomes:

$$\log I(x, y) = \log R(x, y) + \log U(x, y). \qquad (10)$$

Thus, the reflectance and illumination may be treated separately and then additively combined. This simplification is not possible in the linear image plane.

These potent information processing capabilities of the complex logarithm have been exploited by workers in articial pattern recognition. As regards the problem of neural pattern recognition, it is not possible to state unequivocally whether or not the brain helps itself to the advantages of image processing outlined above. Nevertheless, it is a striking fact that both the primary and secondary visual cortex, the inferior pulvinar, and the somatotopic cortex as well, represent a complex logarithmic mapping of the sensory receptor surface onto a central neural surface. The preprocessing of spatial information by the complex logarithm may well be a crucial step in the functioning of the sensory system.

The size scaling property of the complex logarithm may have relevance to stereopsis. When the eyes fixate a stimulus, the two corresponding retinal projections will be, in general, of slightly different size. This size difference will be normalized by the complex logarithmic structure of the retinotopic map (both for the cortical projection as a whole, and for the local, hypercolumnar logarithmic structure described earlier). Psychological studies of steropsis have demonstrated the existence of this binocular "perceptual zooming" effect. Random dot stereograms may still be fused, even though the size scaling of the left and right images differs by up to 15% [19].

The need for a size-scaling mechanism in the visual system has been emphasized by a number of authors [19, 24, 25, 28]. Richards has pointed out that there is a correlation between size-scaling under changes in the vergence angles of the eyes (Emmerts Law) and binocular rivalry. He concludes that the neural site of size scaling precedes the site of binocular combination; it is after the chiasm, but before the cortex [24]. This is supported by the analysis of this paper, which locates the site of size-scaling to the projection of the LGN onto the striate cortex. It must be emphasized that the various psychological phenomena grouped under the general label of "size invariance" (Emmerts law, perceptual zooming; Sutherlands conception of size invariance) are diverse; no attempt is made to present a specific model. Rather, it is merely to be

pointed out that the cortical visuotopic mappings, which may be mathematically represented by the complex logarithm, operate on visual data that is automatically scaled for size, by the anatomical structure of the cortex. Whether this is an accident of anatomy, or has direct functional significance, is of course, a matter for further experimental study.

One of the principal cues for steropsis is binocular disparity; random dot stereograms which present a correlated (shifted) image to the left and right eyes create a very potent illusion of depth, as discovered by Wheatstone in the last century, and recently exploited by Julesz's [19] elegant investigations. Perhaps the neural basis of disparity as a cue for depth perception lies in the fact that the complex logarithm links a (cortical) shift to a (visual plane) size change, as derived above. Thus, the slightly different projections of the two eyes are normalized by the complex logarithm to the identical cortical pattern, with the shift proportional to the size difference, and ultimately, the disparity of the stimulus.

The fact that both the somatosensory and visual maps have the same logarithmic spatial structure has obvious relevance to the problem of cross-modal intergration of sensory information. Consider the following remark of Somjen [26]: "...What boggles the imagination is how the non-linearity of the somatic projection be matched with the different structure of the non-linearity of the visual projection. For while it is true that the somatic sensory figurines are more or less mirror images of the motor figurines, there is no correspondence whatsoever between the somatic projection and the visual projection. If eye-hand coordination is to be guided by the brain charts of visual space and of body-image, the two cannot be scaled by discordant nonlinear transformations."

Since a result of the present work is that both the primary sensory projection of each limb and the visuotopic projection of the retina, are *both* described by the complex logarithm, Somjens' particular objection to the perceptual relevance of the receptopic mappings is eliminated. As Gibson has emphasized from the psychological point of view the visual and haptic worlds are of "one piece" [14]. The fact that the visual and haptic maps available at the cortical level are of the same analytic structure provides a link between the psychology and the neurophysiology of the spatial senses.

The previous discussion of the complex logarithmic mapping and perception is speculative. Nevertheless, potentially rich insight into perceptual processes is apparent once the mathematical form of the retinotopic mapping is understood. This is particularly true since the topographical structure of the sensory system is at the present time felt to be of minor importance to

sensory perception. This attitude is typified by the widely quoted study of Doty [12] (performed in 1958, before any of the "modern" results of cortical physiology had been accumulated), which concluded: "The topographical arrangement of the retino-cortical projection is in itself of minor importance or no importance in the visual analysis of geometrical patterns." Recently, Towe has analyzed this question with regard to columnar structure of visual and sensory-motor cortex. The crucial question concerns the fine-grain nature of the sensory mappings: are they continuous? Towe [30] remarks: "whether such (continuous) shifts, if reduced to the limits of experimental resolution, would continue to exhibit this (topographic) property has never been formally determined". This question, like many others in sensory neurophysiology, is still an open one. In the light of the results of the present work, it is timely to reopen, both experimentally, and theoretically, the issue of the relevance of the receptotopic mapping properties of the sensory system to the functional aspects of perception.

Morphology, Development and Logarithmic Spatial Structure

The assertion that something as forbidingly mathematical sounding as a logarithmic conformal mapping is a ubiquitous structural principle in the brain has a firm foundation in morphological biology. In the seminal work of D'Arcy Thompson [32], "On Growth and Form", first published over fifty years ago, the many common examples in biology 'of logarithmic spatial structure are discussed. They range from the beautiful shell of the Nautilus (and many other molluscans) to the horns of the ram, and the florets of the sunflower. Thompson suggests that there is a mathematical law of growth which is common to these diverse species. The characteristic shared is the property that a structure "shall widen and lengthen in the same unvarying proportions: and this simplest of laws is that which nature tends to follow. The shell, like the creature within it, grows in size but does not change its shape; and the existence of this constant ...similarity of form...may be made the basis of a definition of the equiangular (logarithmic) spiral".

Another important fact concerning logarithmic structure is that the real and imaginary parts of the complex logarithm are harmonic functions that are solutions to the diffusion equation (the laplacian) in polar coordinates [1]. Thus, a diffusion related growth process, in which a central active site releases a diffusing morphogenic substance would have its dynamics described by the complex logarithm. The lines of equal concentration would be given by

the real part of the complex logarithm and the lines of flow, or streamlines, by the imaginary part.

The suggestion that the striate cortex is a concatenated logarithmic structure (both locally and globally logarithmic) also has a simple interpretation in terms of developmental systems. Compound structure is frequently seen in biology, wherever an organism consists of a number of similar parts, and in which the development of the parts repeats more or less exactly the development of the whole organism. Examples are branching systems such as compound leaves, inflorescences, the lung trachae, blood vessels and so forth. Recently, the powerful mathematical apparatus of formal automation theory, or developmental languages, has begun to be applied to the growth and structure of biological organisms. Compound structure is particularly simple to model in this framework, and Lindenmeyer languages with a single recurrence formula have been found to be well suited to model compound developmental systems [15]. In any case, the compound logarithmic spatial structure suggested for the striate cortex in this work might be the simple expression of a common biological growth law.

The formal language theory approach to growth and development is essentially a combinatorial, finite mathematical method. Contrasting to this is the work of René Thom [31], who has tried to apply the differential topology of many dimensional spaces to the same general problem. In addition to these two lines of research, the present work suggests that the properties of a simple and familiar concept such as conformal mapping may in fact be useful in describing as complicated a morphological structure as the mammalian nervous system. These three lines of thought represent an initial assault on the formidable mathematical problem of describing form and structure in biology. It is fitting to close this work with a statement of D'Arcy Thompson, who wrote, over fifty years ago:

"How far even mathematics will suffice to describe, and physics to explain, the fabric of the body, no man can foresee. It may be that all the laws of energy, and all the properties of matter... are as powerless to explain the body as they are impotent to comprehend the soul. For my part, I think it is not so..."

Appendix 1

Associated with each analytic function $f(z)$, is a conformal mapping which affords an excellent visualization of the properties of the function $f(z)$. Conformal mapping enters naturally into many branches of mathematical physics, and in this way accounts for the immediate usefulness of complex function theory. When a conformal mapping is defined by an explicit analytic function $w = f(z)$, we naturally wish to gain information about the specific geometric properties of the mapping. One of the most fruitful ways is to study the correspondence of curves induced by the point trans-

formation. The special properties of the function $f(z)$ may express themselves in the fact that certain simple curves are transformed into curves of a well known character. This information strengthens our visual conception of the mapping.

The complex logarithm may be written as:

$$f(z) = \ln z = \varrho + i\phi \tag{1}$$

using the polar form for the complex variable z. Thus, circles in the z plane (constant ϱ) are transformed into straight lines in the w plane, parallel to the imaginary axis. Likewise, radial straight lines (constant ϕ) are transformed into straight lines in the w plane, parallel to the real axis. Logarithmic spirals in the z plane ($\varrho = Ae^{k\phi}$) are transformed to straight lines in the w plane, making a slope of $1/k$ with the real axis. Circles and radial straight lines are limiting cases of logarithmic spirals, with the constant k approaching 0 and ∞ respectively. Thus, in general, the complex logarithm maps logarithmic spirals to straight lines.

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