I was particularly struck some years ago by the title of a very interesting book called Seeing the Light (1). This book's subtitle was "Optics in Nature, Photography, Color, Vision and Holography" and it struck me then that we take for granted that we see the light but do not always recognize it when we are designing optical systems. At the time of writing this introduction I have just finished reading Arthur Zajonc's book, Catching the Light (2), subtitled "The Entwined History of Light and Mind." Perhaps I should not be commenting here on other books, but they were important in my thinking about the current volume in our series and, in particular, this introduction.

In this series, we have so far omitted any detailed consideration of how a human being interacts with optical systems. One very special and important way is that the output of many optical systems presents information directly to the human observer and the observer receives that information through his eyes. This is obviously true for output images whether they be directly formed through an optical system or indirectly formed through an optical and electronic system. Many of these images have been processed in particular ways before the human observer receives the final image. Thus, I would hope that the system designer takes into careful consideration that the human being becomes an integral part of the total system. To achieve that result requires some detailed understanding of the human visual system.
Introduction to Chapter 8

In this chapter we move from psychophysical studies of inhomogeneity into the neural architecture that underlies it, and the fascinating mathematics that govern the whole system. Since Dr. Schwartz is the leading exponent of this field (and of the kind of computer modeling that makes it tractable), we could not have a better guide. The reader may note that this architectural approach to the visual system neatly complements the finer-scale, receptive-field approach described by Martinez-Urelias in Chapter 4; both have important roles to play.

When I first met Eric Schwartz, he had only recently taken the plunge into neuroscience, from a promising career in high energy physics that included a Ph.D. from Columbia and several publications in the field. To make the break, he went through a postdoc at New York Medical College and then moved to New York University School of Medicine.

In the late 1970s, I came across one of Dr. Schwartz's papers in *Biological Cybernetics*. I wanted to learn more about his work because I was fascinated by the prospect of a sophisticated mathematical model of the so-called retinocortical projection: the geometrical transformation from the retinal image to the cortical one, based on conformal mapping in the complex domain. Clearly this machinery plays a fundamental role in how we perceive the objects and events in the real world around us.

At that time it was my duty, as chairman of the Vision Technical Group of the Optical Society of America, to put together a symposium on current
exciting topics in visual science for the 1978 OSA meeting in San Francisco. What better way, I thought, to pick Eric's brain (both real and modeled) than to invite him to come to San Francisco and tell us all about it. (This was before the days of any official OSA interest in computer vision or computational neuroscience. Eric's talk was published in *Vision Research*.) By hearing him speak, I also learned that his talent for exposition is as great as his scientific insight.

Now I have done the same thing to him again, more or less. Eager to have an up-to-date report on his studies of visual brain architecture in the primate, I invited him to write it for me. Professor Schwartz is currently at Boston University in the School of Medicine (Anatomy and Neurobiology), the School of Engineering (Electrical Engineering and Computer Systems), and the Faculty of Arts and Sciences (Cognitive and Neural Systems), with a full schedule of teaching and research duties. Nevertheless, he somehow managed to find time to oblige me. I'm sure you will be glad he did.

In addition to reporting his own work, Eric has provided us with a masterful account of the history of this subfield, complete enough so that anyone who is interested can dive right in. I know of no comparable survey in the literature. In any case, this chapter has a little something for everyone, including a recent engineering application.

8

**Topographic Mapping in Primate Visual Cortex:**

**History, Anatomy, and Computation**

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I. INTRODUCTION

This chapter presents the history and an estimate of current understanding of the spatial architecture of primary visual cortex (V-1, striate cortex, area 17) in primates. Special emphasis is placed on experimental techniques, mathematical and computational analyses, and the relevance of V-1 architecture to current work in machine vision. An attempt has been made to provide a representative coverage of the primary literature, but completeness in this regard is not claimed. Rather, the intention is to provide an overview of the difficulties, both conceptual and experimental, that have characterized this field for the past 50 years, and to provide some insight into the importance of spatial architecture in visual cortex to both biological and machine vision.

History is divided into four periods in which the status of understanding mapping in V-1 is surveyed:

*Preclassical*: prior to physiological demonstration of cortical topography
*Classical*: initial demonstrations of topography, but no analytic characterization
*Middle*: first attempts at magnification factor data fitting and introduction of complex log model.
Modem: use of 2-deoxyglucose, awake behaving preparations, computer flattening, and conformal mapping

Then follows a summary of the detailed mathematical methods in current use for modeling visual cortex topography, consisting of three parts:

One-dimensional: use of scalar magnification factor to characterize V-1

Two-dimensional: parametric fits to the two-dimensional cortical map function using two and three parameters are presented, along with current experimental evidence

High-dimensional: incorporation of additional, nontopographic dimensions, such as ocular dominance and orientation tuning (protocolumns and polymaps)

Next, the characterization of psychophysically measured spatial scaling functions is reviewed briefly in terms of cortical magnification factor. Emphasis is on methodological problems with many of the measurements that have been performed.

Finally, we review computational applications of cortical architecture. Particular emphasis is placed on recent activity in building space-variant active vision systems and multiresolution vision systems, in which the design principles of primary visual cortex have played an important motivating role.

II. HISTORY OF TOPOGRAPHIC MAPPING

A. Preclassical Period

The existence of distinct scotomas caused, for example, by penetrating missile wounds of occipital cortex, suggested to Minkowski [1], Holmes [2], and Poliak [3] that there must be a maplike representation of the visual field in cortex. However, there appears to have been little further thought on this subject prior to the classical period described in the next section, when V-1 topography, as well as lateral geniculate nucleus (LGN) topography [4] and somatosensory topography [5] were directly demonstrated for the first time. This is curious, since there have been extensive speculations about the mental bases of vision for many hundreds (or thousands) of years. (See Ref. 6 for a historical review.) The space-variant nature of our visual systems, which is evident to casual (if informed) self-experimentation, appears to have been little discussed prior to the 1940s and is, on the part of laymen, largely unknown today. The overwhelming majority of us believe implicitly, as can be demonstrated with a classroom full of students, that the visual world is constant, space-invariant, and Euclidean. The profound illusion that more peripheral locations have the same resolu-

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B. Classical Period

In the early 1940s Talbot and Marshall [7] used electrophysiological techniques to demonstrate the existence of a well-defined topographic map in monkey visual cortex and provided some of the first speculations concerning the functional utility of such a representation. Nearly 20 years later, Daniel and Whitteridge [8] performed the second experiment in this area, using several species of monkeys and apes, and introduced one of the key terms in the field: cortical magnification factor. However, neither Talbot and Marshall nor Daniel and Whitteridge took the next step of providing an analytic fit to their data, an activity that did not begin until the 1970s, as will be shown after a brief discussion of these two landmark experiments.

1. Talbot and Marshall

In 1941 Talbot and Marshall provided the first direct physiological evidence for the existence of an orderly map of visual space to the surface of primary visual cortex. They modified the standard Horsely-Clark stereotactic headholder to allow a wide angle of visual field to be projected onto the retina, immobilized the eye by sewing the conjunctiva to a fixed metal ring, and proceeded to plot the location of cortical stimulation sites referenced to retinal stimulation sites, using evoked potential recordings obtained from a "moist thread or an insulated needle." Using this apparently crude electrode technology, they produced a map of visual cortex that agrees reasonably well with later experiments.

Talbot and Marshall used the term "cortical discrimination," defined as a ratio of retinal distance (degrees) divided by cortical distance (millimeters). This is equivalent to the inverse of the "magnification factor" (later defined by Daniel and Whitteridge, to be discussed below. They stated: "... the spacing of contours is inversely proportional to discrimination in the cortex" [7, p. 1257] and reported that in cat, the cortical discrimination averaged 5 deg/mm at 30° and 1 deg/mm centrally. In the monkey, they found that the discrimination averaged 18 minutes of arc/mm at 5° and 2 minutes of arc/mm centrally. This measurement of foveal discrimination (inverse magnification factor in more modern terms) appears to be larger
than most later measurements of cortical magnification in the monkey, which generally have been in the range of 6-10 mm/deg, although Dow and his colleagues, working with behaving monkeys in a very accurate experiment, have reported peak values of cortical magnification in this range.

In addition to introducing the concept of (inverse) cortical magnification, under the term “cortical discrimination,” Talbot and Marshall also introduced several seminal ideas. They suggested that vernier acuity and stereo acuity might be related to the huge expansion in the central cortical representation, and they speculated in a similar vein about stereoscopic fusion, suggesting that “… disparate images … converge to common neurons at the cortex [7, p. 1261].

Using relatively crude physiological equipment, Talbot and Marshall obtained a relatively accurate map. They introduced the fundamental ideas of cortical scaling and magnification factor, as well as the notion that spatial representation of the visual field, at the cortex, might be of functional significance to vision.

2. Daniel and Whitteridge

Roughly 20 years later, Daniel and Whitteridge, using cortical evoked potentials (2 mm silver balls) as well as multiunit recording (electrodes with tip size between 10 and 2 μm), confirmed Talbot and Marshall’s study. Daniel and Whitteridge introduced the term “cortical magnification,” defined as the reciprocal of “cortical discrimination”—that is, the ratio of a cortical distance to a corresponding retinal distance (mm/deg)—and provided a plot of cortical magnification versus retinal eccentricity.

Curiously, Daniel and Whitteridge stated [8, p. 211] that

No simple equation has been found to fit the data. Neither plotting the data on a semi-log basis nor plotting reciprocals of the data gives a straight line.

But, in fact, the reciprocal of their data is fairly close to a straight line, and in the absence of any error analysis could be approximated as a linear function. Starting with the analysis of Schwartz [9], virtually all later workers in this area have made this approximation. The question of what constitutes a “fit” has only recently begun to be addressed and is obviously of central importance to this area (see below).

Daniel and Whitteridge also introduced the notion of “brain flattening.” Since cortex is essentially a two-dimensional sheet [1200 mm² (per hemisphere, Macaque-V-1) by roughly 2 mm thick], Daniel and Whitteridge constructed a three-dimensional clay model of cortex, then flattened it by orthogonal projection. Methods for representing cortical maps on flattened surfaces have become an active area of research. Van Essen and Maunsell [10] used a “hand tracing” method to provide flattened models of V-1, as well as the entire extra striate visual cortex. Tootel et al. [11] using physical flattening via pressing cortex between glass slides, to provide flattened specimens of 2-deoxyglucose (2DG) labeled V-1. Our lab [12-14] developed computational methods to provide quantitative brain flattening in order to begin to provide estimates of the errors involved in measuring cortical topography (and see Ref. 15).

A second experimental statement of Daniel and Whitteridge is also of great importance. They stated that cortical magnification was both locally isotropic and globally symmetric:

Magnification factor measured radially over a small distance was found not to differ significantly from the magnification factor measured along the corresponding circumference … there is no significant difference between magnification factors for different radii.

Thus, although Daniel and Whitteridge made a clear distinction between local and global symmetry in 1961, many later workers in this area have confused the two. This point is of great importance, since it can be shown (see below) that local isotropy and global symmetry are in general mathematically inconsistent.

A good way to see this is to consider the derivative of the function \( \log(z + a) \) on the horizontal meridian (i.e., the real axis) and on a vertical meridian (e.g., the upper vertical meridian, which corresponds to the positive imaginary axis in this model). These are

\[
|f'| = \frac{k}{x + a} \quad \text{for } x \text{ real} \tag{1}
\]

\[
|f'| = \left| \frac{k}{a + iy} \right| = \frac{k}{\sqrt{a^2 + y^2}} \quad \text{for } y \text{ imaginary} \tag{2}
\]

These differ by a maximum amount of \( \sqrt{2} \) at \((a, 0)\) and \((0, a)\). Thus, there is a 41.4% difference in magnification at 0.3° on the horizontal and vertical meridians if the constant \(a\) is 0.3°. Correspondingly, the integrals of the horizontal and vertical meridians differ by about 30% for \(a = 0.3\). These lengths can be evaluated by noting that the integral of magnification factor, as above, is an elliptic integral. Alternatively, the complex logarithm function can be plotted, and a piece of string laid along the image of the different meridians! Therefore, Daniel and Whitteridge’s report of local and global isotropy cannot be correct. This point will be established further in this chapter, under the detailed discussion of conformal mapping.

The issue of local isotropy, and cortical mapping in general, is further
confounded by the existence of ocular dominance columns, which essentially provide a double map instead of the single map conceptualized by Daniel and Whitteridge. It has been only in the last several years that computational tools for modeling such multiple maps, which we term poly-maps, have been developed [16]. These issues of local isotropy, and the existence of multiple columnar systems in V-I, are among the most difficult, both conceptually and experimentally, in this area. They are still a matter of debate, and we return to them later in this chapter.

Finally, Daniel and Whitteridge introduced a seminal idea in cortical physiology. They pointed out that the cortical distance corresponding to the minimal angle of resolution worked out to about 67 μm or “the distance occupied by about five cells in the densest part of layer IV of the cortex” [8, p. 218], independent of eccentricity. Plotting the minimal angle of resolution (in man) against inverse cortical magnification factor (in monkey), they showed that the two curves were almost identical. They concluded [8, p. 218]:

The minimal angle of resolution would correspond to about 67μm in both the fovea and extreme periphery. Two peaks of excitation would have to be separated by this distance and by a corresponding number of cortical cells for them to give rise to separate sensations.

Daniel and Whitteridge sharpened the scaling argument introduced by Talbot and Marshall and laid the stage for the cortical hypercolumn model of Hubel and Weisel [17]. Moreover, this analysis presaged a large amount of psychophysical activity beginning in the late 1970s, which sought to relate various notions of cortical magnification factor with spatial scaling functions measured in experiments on acuity, stereo acuity, motion, vernier acuity, and stereo fusion.

C. Middle Period

The classical period of work in the area of visual cortex topographic mapping was circumscribed by only two papers, published over the period of 1941 to 1961, outlined above. Beginning in the early to mid-1970s, work in this area began to pick up momentum, beginning with the analysis of feline retinal ganglion cell density and receptive field overlap. Burkhardt Fischer approximated the density of retinal ganglion cell receptive fields in terms of an inverse linear function of distance from the fovea and pointed out that “an isotropic coordinate” system for the retina was obtained by integrating the retinal ganglion cell density function [18]. He suggested several different forms of logarithmic structure for an “isotropic” coordinate system, one of which was the complex logarithmic mapping whose detailed structure is discussed below.

Fischer did not relate his ideas to cortical magnification, nor to cortex at all. His model was for structure in “the optic tract” of the cat, and it was intended to provide an isotropic system in which equal steps of distance corresponded to equal numbers of ganglion cells in the cat retina. Fischer’s work was the first to attempt to provide a two-dimensional model of any aspect of the visual system, and was, as we will shortly see, very close to providing a model for the cortical map, since it turned out that the cortical topographic map was (at least approximately) one of the “isotropic” representations of the retina that Fischer was conceptualizing.

Fischer’s notion of an isotropic representation of the retina, like that of Daniel and Whitteridge, reached full expression the next year when Hubel and Weisel published their “hypercolumn” model, which suggested that equal areas of cortex (hypercolumns) represented invariant structures not only for topography, but also for ocular dominance and orientation representations (17).

1. Complex Logarithmic Model

In 1976 I presented abstracts at the American Physiological Society and the Society for Neuroscience [9] reporting that a simple fit to Daniel and Whitteridge’s cortical magnification data was close to inverse linear. It was suggested that a complex logarithmic map of the visual field to the surface of visual cortex provided a simple (two parameter) fit to the cortical map. Moreover, it was pointed out in these papers and in subsequent journal articles [19-21] that the local hypercolumn structure of cortex suggested that the geometric properties of the complex log function were consistent with a miniature recapitulation of the overall complex log topographic map. In other words, each hypercolumn (of which there are roughly 1000 in each hemisphere) received an afferent projection in layer 1Vc of the form of a miniature complete topographic map of the small patch of visual space represented by that hypercolumn cortical patch. Also, in this work, it was pointed out the size, rotation, and projection invariance properties of the complex log map suggested a possible role for these geometric features of the visual system in visual computation, and that retinal cell density seemed to match cortical magnification [21]. This work did not reach the mainstream of the vision community, however, until 1978, when Donald Kelly

*It should be emphasized that most cortical maps that have been studied have evidence of one or more submodalities in the form of columnar interlacing. Therefore the poly-map is the prototypical cortical structure.
generously invited me to present it at a symposium at the Optical Society of America, and shortly afterward with publication of a summary of these ideas in the journal *Vision Research* [22].

At the present time, the complex logarithmic approximation to cortical topography has been accepted as a reasonable approximation [23–25]. In fact, no one has yet provided an alternative two-dimensional analytic model.●

In recent years, our lab has developed more general modes of V-1 topography in terms of conformal mapping and has demonstrated experimentally that a conformal model provides an excellent fit to global cortical topography. We have constructed accurate numerical “brain flattening” algorithms and have begun to place “error bars” on the data and the fits, an activity that is noticeably absent in the literature spanning the half-century from 1941 to 1992! Obviously, it is not possible to talk about a goodness of fit without an error estimate, and, in fact, the original observation of Daniel and Whitteridge (that “no simple mathematical function was found to fit the data”) is not meaningful in the absence of some error estimate. We will return to this issue later.

At present it is much less clear whether the local spatial structure of visual cortex, on the scale of a single hypercolumn, is also characterized by the complex logarithmic mapping. This idea was motivated by the observation of Hubel and Weisel [17] that “sequence regularity” characterized the hypercolumn geometry. They stated that thin (50 μm × 400 μm) slabs of cortex contained neurons responsive to a single orientation of stimulus and that these slabs (orientation columns) were stacked along the cortex in a highly regular, parallel fashion.

Consider the following question: What analytic function has the property that it maps regularly rotating “slabs” in one domain to parallel “slabs” in another domain? Since the complex log function has this property, it does seem possible that the complex log mapping, which clearly characterizes the global architecture of visual cortex, may well characterize the local architecture as well. This was the basis for my suggestion that the cortex may be a “concatenated complex log mapping” [9], and the structure of the vortex street (from hydrodynamics) was used as the paradigm of a net of local logarithmic mappings [20]. Variants of this model were subsequently proposed by Dodson [27] and by Cavanagh [28], but it is safe to say that

relatively few workers in the mainstream of vision were much interested in this idea.

Recently, however, the new techniques of optical recording from visual cortex have provided dramatic images of the orientation column structure in visual cortex [29,30]. These workers have begun to describe the hypercolumn pattern in terms of “vortex” or “pinwheel” structures. And, in our lab, we have recently provided what we believe to be a fundamental mathematical insight [31–33] into the nature of orientation maps, cortical vortices, and the hypercolumn map. Briefly, we have found that if one constructs an orientation map in a planar domain (as V-1 is believed to be in terms of orientation-tuned neurons), and if the map is to be continuous in both orientation and topography, the production of local logarithmic or vortex patterns is unavoidable. This follows directly from a basic topological theorem (nonretraction of $S^1 \to R^2$). There will be no further discussion of this subject here, except to point out that the geometrical properties of the complex log are almost certainly involved in the detailed local structure of V-1 hypercolumns, as is indicated by the current vogue of using the term “vortex” to represent the hypercolumn, as well as for somewhat deeper mathematical reasons that are discussed in detail in the papers cited above.

2. M-Scaling

In the late 1970s, Drasdo [34] and Rovamo and Virsu [35] provided fits to the spatial structure of human magnification factor, using a mixture of human and monkey data, and retinal and cortical measurements. Virsu and Rovamo [36] introduced the term “M-scaling” to refer to the idea that the spatial variation of visual acuity might parallel the curve of their “cortical-retinal” magnification curves, as also had been suggested earlier [19,21].

One problem with this work was that a mixture of cortical and retinal data was used to estimate the “M-curve.” This is problematic, since it is only an assumption, even at the present time, that a measure such as retinal ganglion cell density is related in any way to a measure of cortical magnification. These are, in principle, completed unrelated physiological data. One consequence of this approach is that the fits obtained for the monkey by Virsu and Rovamo had a flatter variation with eccentricity than is currently accepted (see Ref. 37 for review). This is because retinal ganglion cell density, and human acuity, are relatively flatter than modern estimates for (inverse) cortical magnification factor. By mixing retinal and cortical data, Virsu and Rovamo obtained good fits to functions such as human acuity, but at the cost of a kind of circular reasoning. The question of whether retinal ganglion cell density, cortical magnification factor, and human visual acuity are matching functions can be determined only by studying each phenomenon separately, and obtaining separate functional forms and error

*Van Essen has constructed a linear interpolation of data points to provide a two-dimensional map, but no function was presented to model the data. Johnston [26] has suggested that the projection of a tilted plane matches the cortical map, an idea that had been discussed [22] in a publication that also pointed out that this approach works only outside the foveal representation. This approximation is poor; it cannot simultaneously fit the central and parafoveal representations.
bars. This has not yet been done! The approach of Drasdo and Virsu and Rovamo, which has been to estimate human cortical magnification factor by mixing retinal, cortical, and psychophysical data, and then to compare them by "eyeball" estimation, has led to a great deal of confusion in this area. This issue will be returned to later in this chapter, in a discussion of Wassle's recent contributions to the question of homology between retinal, cortical, and psychophysical measurements of spatial scaling.

3. Ocular Dominance and Cortical Topography

An approximate back-mapping of the cortical ocular dominance column pattern, at the level of the retina, was presented in 1976 [9]. Slightly later, Hubel and Freeman [38] presented a two-dimensional estimate of cortical topography, by an ad hoc method of symmetrically stretching radii of a semicircle by the estimate of cortical magnification factor at each point. They then used this to estimate the structure of the ocular dominance column pattern, when projected by their map function back to the retina. They did not provide an analytic or numeric fit to these data, other than a one-dimensional magnification function.

Both these approaches suffered from one major flaw: the ocular dominance column pattern was viewed as an "image," and this image was mapped via a cortical map function to the (two) retinas. But this is not correct, since in fact both retinas map, completely, to one cortical hemisphere. Each of the retinal maps must be "squeezed," or otherwise made to fit, into a single cortical hemisphere. But the methods used by Schwartz [9] and Hubel and Freeman [38] simply mapped the ocular dominance column image, at the cortex, into its retinal representation, via an estimated map function. The issue of "shearing" or "warping" the ocular dominance column local topography was not addressed.

The details of exactly how the ocular dominance column submaps fit together to form the observable cortical map in layer 1Vc of primate cortex is of crucial significance to understanding the fine details of cortical topography. A recently developed algorithmic approach to modeling such "poly-maps" [16] is briefly discussed later in this chapter.

D. Modern Period

Beginning in the early 1980s, a variety of new experimental techniques were applied to studying V-I topography, which are briefly reviewed here.

1. Awake Behaving Monkey Studies

The laboratory of Bruce Dow provided several important measurements of V-I topography, using awake monkeys that were trained to visually fixate a target. All earlier experiments had been performed with animals whose eyes were fixed, either by sewing them to a metal ring or by the use of curare derivatives to paralyze the ocular muscles.

As a result of allowing the monkeys to use their own ocular motor system to provide a stable reference for the topographic measurements, Dow and his colleagues avoided one of the principal sources of error in these measurements, namely, the error in physiologically plotting the representation of the fovea on a tangent screen or computer monitor.

Usually, a reversible ophthalmoscope is used to first plot the fovea, and then, by mechanically reversing the instrument, to project the ophthalmoscope beam on the tangent screen. This procedure is difficult: parallax, mechanical error, and difficulty in judging the exact center of the fovea contribute to an error Van Essen et al. have estimated to be about 0.5° [23]. In our work, we have been able to statistically regress out this eye fixation error and have found that an error of 0.5° – 1.0° is in agreement with our experience. But, because of the huge cortical magnification factor, an error of this size is a reasonable fraction of the cortex! Since no other lab, prior to our recent experimental work, had attempted to statistically correct for this error, we can assume that eye fixation plotting error is a significant source of error in estimations of the intercept of a linear approximation of (inverse) cortical magnification factor with the horizontal axis (i.e., visual angle).

Dow's methodology is notable for eliminating several of the major sources of variance associated with the use of paralyzed animals. For one thing, Dow and his collaborators obtained data from the central fovea (down to 15 minutes of arc), which appears to be a unique achievement in this field: Hubel and Freeman reported data only peripheral to 4°, Van Essen reported data peripheral to 2°, and Daniel and Whitteridge's data stopped at 1°. This is important because the linear regression that is used to determine the parameters of the magnification function is very sensitive to data near the origin. Also, Dow's method, using an awake monkey to control eye fixation, presumably reduced to a negligible amount the usual error of plotting the position of an immobilized eye.

Dow's measurements suggested that magnification factor was locally isotropic. The observation of locally isotropic magnification is mathematically equivalent to the fact that the cortical map is conformal, as shown below. Dow fit the data to a two-dimensional conformal map function using the complex log approximation and reported excellent results.

2. 2-Deoxyglucose: Human Studies with Positron Emission Transaxial Tomography (PETT)

Prior to the late 1970s, all measurements of cortical topography were obtained via electrophysiological techniques, using either field potentials (Talbot and Marshall), or single- and multiunit recording (Daniel and Whitter-
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Tootell et al. [1] were able to produce outstanding 2DG images using a ring-and-ray pattern similar to that used in earlier PETG images [39, 40]. When these data were presented for the first time at the Association for Research in Vision and Ophthalmology (ARVO), there was a spontaneous standing ovation! Unfortunately, these excellent 2DG data were never analyzed by Tootel et al. to produce a two-dimensional estimate of the monkey topographic map.

Since the 2DG method produces a two-dimensional image of a stimulus pattern, at the surface of the cortex, it would seem that a two-dimensional fit would be the analysis of choice. In fact, a two-dimensional fit of the data of Tootel et al. [11], using the complex log function [42], was found to provide a “good approximation” [24] to the 2DG data. The use of 2DG to study cortical topography was further pursued in animal work, starting in 1984, by my lab at NYU Medical Center (in collaboration with Tom Albright, Amar Munsif, and David Rosenbluth), and this work has been analyzed via fitting a two-dimensional conformal mapping to the data, resulting in an excellent approximation to the two-dimensional cortical topographic map. This work is described below, after a brief discussion of the technical details underlying the notion of conformal mapping.

III. MATHEMATICAL MODELING OF V-1 SPATIAL ARCHITECTURE

Having briefly outlined the history of an area that has obviously received intense and continuous experimental activity over the past 50 years, we now turn to a detailed analysis of the mathematics of topographic mapping. First, the nature of one-dimensional fits to cortical magnification is outlined. Next, it is shown that the simplest two-dimensional correlate of a one-dimensional inverse linear magnification curve is provided by the complex logarithm function. The mathematical details of this function are explained, and some quantitative estimates of the nature of space-variant vision, both in biological and computer terms, are provided. In particular, the number of “degrees of freedom,” or equivalent pixels, of the human visual field, is estimated. Then, a generalization of the complex log function, using a numerical conformal mapping model is reviewed. Finally, the notion of cortical mapping, in the presence of multiple columnar systems (polymaps as in Ref. 16), is reviewed.

A. One-Dimensional Models

Virtually all psychophysical approaches to cortical magnification factor have been based on the use of a one-dimensional map function, of the form
\[ M_{\text{cortex}}(\theta) = \frac{k}{\theta + a} \]  

(3)

where \( M_{\text{cortex}}(\theta) \) represents the cortical magnification factor (i.e., the differential change in cortical position with respect to retinal eccentricity \( \theta \)) and \( k \) and \( a \) are two constants that specify the fit.

It is important to realize that magnification factor is essentially a "derivative." It represents the ratio of small changes in cortical location to corresponding small changes in retinal location. The question then, naturally arises: What is it the derivative of? We should first note that since there are two possible directions at each location in the cortex, and two independent directions in the retina, it is not immediately clear how to specify the ratio of cortical difference to retinal difference as a scalar function. This represents a mathematical difficulty that has largely been ignored in physiological and psychophysical studies involving the retinotopic map. The simple use of a scalar magnification factor, which is nearly universal, can hold only under limiting circumstances, which amount to an assumption of local isotropy. Since a map that is locally isotropic is also, by definition, a conformal map, there are very significant consequences to the usual assumption of scalar magnification factor. On the other hand, the isotropic nature of the map is an experimental question, which is not automatically true. To clarify this issue, we will embark on a brief but necessary digression concerning the nature of the derivative of a map from a planar region to a planar region, following an earlier exposition of this subject [43], in this context.

B. Two-Parameter Fit to the Cortical Map Function: The Complex Logarithm

In Schwartz [9,19,22] it was shown that if one represents the cortical map function in complex variables as

\[ w = k \cdot \log(z + a) \]  

(4)

then the magnitude of the derivative of this map function is

\[ |w'| = \left| \frac{k}{z + a} \right| \]  

(5)

Figure 1 shows the geometry of this mapping, and Figure 2 shows approximations using this function to V-1 topography in several different species.

A function of a complex variable is by definition analytic, or conformal, which is equivalent to the assumption of local isotropy. This is the only condition under which the usual scalar magnification function is sufficient to characterize the cortical map.

Figure 1 The conformal mapping of the unit half-disk by \( \log(z + a) \), shown here with \( a = 0.1 \). The vertical meridian in the domain (half-circle as a model for the retina) is mapped to the curved boundary at left in the range (model of the cortex). In the central, or foveal, region the map is asymptotically linear, turning to a logarithmic geometry in the region > a. (From Ref. 71.)

The constants \( k \) and \( a \) may be determined by plotting inverse magnification factor against eccentricity, which is linear: intercept = \( a/k \) and slope = \( 1/k \). In this two-parameter fit, only the constant \( a \) is of qualitative significance to the "shape," or the "foveal" extent of the map. The constant \( k \) merely provides a normalization. However, if one is interested in the numerical value of magnification factor in units such as millimeters per degree, then both parameters are significant.

The physical interpretation of the two constants may be understood as follows. The constant \( k \) is essentially a normalization factor, which for most purposes is uninteresting. The constant \( a \) determines the extent of the linear regime of the cortical map, which we suggest should provide the definition of the term "fovea." Consider the asymptotic forms of the map function \( \log(z + a) \):

\[ \log(z + a) = \log(a) + \frac{z}{a} \quad \text{for } z < a \]  

(6)

\[ \log(z + a) = \log(z) \quad \text{for } z > a \]  

(7)

For \( z > a \) the map is essentially logarithmic, while for \( z < a \), the map is essentially linear. Current estimates for the magnitude of \( a \) are in the range of 0.3–0.8°, which corresponds roughly to the usual definition of the
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"fovea." It has been proposed [22] that this change in the behavior of the cortical representation, from linear to logarithmic, be used as a quantitative estimate of the size of the "fovea." In any case, the constant \( a \) above is best understood in terms of the location of change in the geometric behavior of the cortical map.

In the psychophysical literature, another interpretation is in current use for these parameters. Cortical magnification factor is represented as [37]

\[
M_{\text{cortex}}(\theta) = \frac{M_{\text{cortex}}(0)}{1 + E/E_2}
\]

In this parameterization, \( E_2 \) is the eccentricity at which magnification has fallen by a factor of 2. The two descriptions are equivalent, since they are both linear functions.

Thus,

\[
a = E_2 \quad \quad \quad \quad \quad \quad \quad \quad k = M_{\text{cortex}}(0)E_2
\]

Here we use the \([k, a] \) parameter set, which explicitly makes the connection to cortical map geometry via the interpretation of \( a \). The "halving" of cortical magnification factor in the interpretation of the \([M(0), E_2] \) parameter set suggests no physiological interpretation. However, the two descriptions are equivalent, since they model inverse cortical magnification factor as a linear, scalar function.

1. Geometry of Complex Log Function

Now, if one asserts that a scalar function is sufficient to model cortical magnification factor, one has implicitly assumed that the two-dimensional structure of the cortical map is given by a function of the form

\[
w = k \cdot \log(z + a)
\]

whose derivative (in absolute magnitude) is

\[
|w'| = \left| \frac{k}{z + a} \right|
\]

In fact, functions of the complex log type do provide a fairly good fit to all existing data. For example, as shown in Reference 22, the data of both Talbot and Marshall and Daniel and Whitteridge are approximately fit to a map function of the form \( \log(z + a) \) with the constant \( a = 1^\circ \), as shown in Figure 2. Dow et al. found that a function of this form provided a good fit to their data, using a constant \( a = 0.3^\circ \). The data of Tootel et al. [11] are fit, to a "good approximation," by the same complex log function with \( a = 0.3^\circ \). Van Essen et al. [23] reported an inverse linear magnification,
with constant \( a = 0.8^\circ \), and Van Essen has stated that the complex log
model is a good approximation, although there may be localized departures
from isotropic mapping near the representation of the lower vertical meridian.

It appears that there is a rough consensus that primate visual cortex is,
to a first approximation, a complex logarithmic structure characterized by
a “foveal” constant \( a = 0.3 \) to \( a = 0.9^\circ \) [37].

The complex log mapping may be regarded as a warping of a conventional scene. This is illustrated in Figure 3.

2. Two-Parameter Mapping

One problem with the simple complex log fit is that it begins to fail around
15-20\(^\circ\), where the actual shape of the cortex requires that the boundaries
of the map begin to close in to make a closed, vaguely elliptical surface (see
below; Fig. 10 for the shape of the central 10\(^\circ\) of cortex, and Figs. 6 and 9
for the shape of the entire cortex). Also, cortical magnification is somewhat
sublinear beyond 20-40\(^\circ\) of visual field. Both these problems can be simply
addressed, however, by the use of a second logarithmic function, which
requires one additional parameter, as suggested elsewhere [44]:

\[
\begin{align*}
  w &= k \left( \log \left( \frac{z + a}{b} \right) \right); \quad a = 0.3^\circ, \ b = 50^\circ \\
  \end{align*}
\]

Thus, simple two- and three-parameter fits provide a good approximation
to the topographic map structure in primate V-1. However, these fits, as
well as the numerical conformal fit that is to be presented shortly, are based
on the existence of “isotropy”: the local cortical magnification must be a
scalar (i.e., independent of local direction).

To fully understand the nature of “cortical magnification,” we need to
take a brief diversion into tensor calculus. It is necessary to take a close
look at the nature of the “derivative” of a cortical map function [44].
Although this area is both obscure and elementary (in a mathematical
sense), it is impossible to understand the details of topographic mapping
without grasping the following argument, which has been largely ignored
in both the psychophysical and physiological literatures.

3. Regular Mappings of Two-Dimensional Surfaces into
   Two-Dimensional Surfaces

For a regular map \( F: \Omega \to \Omega’; \ F: (x,y) \to (f(x,y),g(x,y)) \), the Jacobian is:

\[
J = \begin{vmatrix}
\frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\
\frac{\partial g}{\partial x} & \frac{\partial g}{\partial y}
\end{vmatrix} = \begin{vmatrix} f_x & f_y \\
g_x & g_y
\end{vmatrix}
\]

As mentioned in earlier work [43], it is instructive to rewrite the Jacobian
in terms of its symmetric and antisymmetric parts:

Figure 3  Texture mapping of digitized image with complex logarithmic map.
(From Ref. 71.)
2J = S + A = (J + J') + (J - J')
= \begin{bmatrix} 2f_x & f_x + g_y \\ f_y + g_x & 2g_y \end{bmatrix} + \begin{bmatrix} 0 & f_y - g_x \\ g_y - f_x & 0 \end{bmatrix}

It is further useful to rewrite the symmetric part as the sum of a diagonal and a traceless matrix:

\[ S = \begin{bmatrix} 2f_x & f_x + g_y \\ f_y + g_x & 2g_y \end{bmatrix} = D + T = \begin{bmatrix} \text{tr} & 0 \\ 0 & \text{tr} \end{bmatrix} + \begin{bmatrix} 2f_x - \text{tr} f_x + g_y \\ f_y + g_x, 2g_y - \text{tr} \end{bmatrix} \]

where \( \text{tr} \) represents the trace of the Jacobian (i.e., \( \text{tr} = f_x + g_y \)).

The traceless component of the Jacobian can be diagonalized by an orthogonal transformation \( R \), since it is symmetric and positive definite, which we write explicitly:

\[ RTR^{-1} = \begin{bmatrix} \lambda & 0 \\ 0 & -\lambda \end{bmatrix} \]

The differential structure of a regular mapping has been dissected into the sum of three geometric invariant components:

A rotation (the antisymmetric part \( A \))
A dilation (the diagonal part \( D \))
A shear (the traceless part \( T \))

The shear component is a compression along one axis and an expansion of equal magnitude along another axis, of magnitude equal to \( \lambda \). The directions of the principal axes are given by the rotation matrix \( R \). In the case that the mapping has no shear, \( T \) (the traceless, symmetric part of the Jacobian) is zero and the differential structure of the mapping is characterized by only two numbers: the rotation and the dilation. The dilation is the "magnification factor," and this is the single number that usually emerges from physiological or anatomical experimental work.

In the literature, the apparent compression of the cortical magnification factor (CMF) perpendicular to the axes of ocular dominance columns is sometimes expressed as a ratio of gain along the two axes. In the analysis above, if we consider only the symmetric portion

\[ RSR^{-1} = RDR^{-1} + RTR^{-1} = D + RTR^{-1} = \begin{bmatrix} \text{tr} + \lambda & 0 \\ 0 & \text{tr} - \lambda \end{bmatrix} \]

and examine the ratio of the two nonzero terms, we obtain the "compression ratio" of the mapping.

Having provided the necessary analysis, we conclude by pointing out that the characterization of a neural map by microelectrode measurements of "magnification" (i.e., by comparison of small changes in one neural layer with small changes in another) requires four such measurements at each point, to retrieve the Jacobian matrix. This has never been reported in any physiological experiment and would be technically difficult to accomplish. However, obtaining only a single magnification measurement at each point, as in conventional magnification experiments, is sufficient only if the mapping is conformal (i.e., if the "shear" component is zero). In the absence of a direct measurement of the Jacobian of the cortical map, our strategy has been to use numerical and analytic conformal maps to model the cortex. If these work, then the shear component is negligible and we don't, in fact, need to perform the very difficult experiment that would be required to provide the Jacobian. This strategy, which seems to be effective for primate V-1, will now be reviewed.

4. Numerical Conformal Mapping

We have performed [45] a series of 2DG studies of primate retinotopic mapping, using computer reconstruction and computer brain flattening, together with numerical conformal mapping, to provide an isotropic map fit to primate topography in V-1. Before presenting some preliminary results of this work, we provide some background material on the properties of isotropic map functions and conformal mapping.

C. Application of Conformal Mapping to Cortical Topography

Conformal mappings may be defined in a number of equivalent ways, which emphasize different aspects of their geometric or analytic properties [46]:

Complex analytic functions \( f(z) = (u(x,y), v(x,y)) \), for

\[ \frac{df}{dz} \neq 0 \]

represent conformal mappings.

The real and imaginary parts of the map function satisfy the Cauchy-Riemann equations:

\[ \frac{\partial u}{\partial x} = \frac{\partial v}{\partial y} \quad \text{and} \quad \frac{\partial v}{\partial x} = -\frac{\partial u}{\partial y} \]

A conformal mapping is locally isotropic. This means that an element of infinitesimal area is magnified equally in all directions. In the language of the preceding section, conformal mappings have no shear component. Infinitesimal angles are preserved by conformal mapping.
The real and imaginary parts of the map function are harmonic conjugate functions; that is, they satisfy the Laplace equation

$$\nabla^2 u(x,y) = \nabla^2 v(x,y) = 0$$

and their level curves intersect orthogonally.

This property provides important practical application to areas of potential theory (electrostatics, fluid mechanics, etc.) where the Laplace equation occurs.

The Riemann mapping theorem (see Appendix) guarantees the existence and uniqueness of conformal mappings between regions. It is of fundamental importance, since it states that given any two planar brain regions (e.g., retina and cortex), there is a unique conformal mapping between them which is specified by the "shape" of the regions, a single point correspondence, and angle specifying the relative orientation of the domain and range regions.

[Riemann]: Given a region, there exists a conformal mapping of this region onto the unit disk [46]. The mapping is made unique by fixing the mapping of a single point in the region onto the center of the unit disk, and fixing the orientation of the unit disk. (See Appendix for a further discussion of the Riemann mapping theorem.)

The use of this theorem in the present context consists in mapping two regions into the unit disk, which then implicitly provides the desired map function.

The Riemann theorem is perhaps surprising in that it does not seem intuitively possible that all the details of a two-dimensional map could be specified by a single point and orientation. However, this may be understood better by considering the one-dimensional analogy. If one species the boundary points of a curve (i.e., two points) and states that the curve must satisfy the equation

$$\frac{dy}{dx^3} = 0$$

the curve must be a straight line (i.e., zero curvature), and we then know all the internal points only from the boundary conditions, which are simply the end points of the line. In two dimensions, the Laplace equation condition that is one of the possible defining characteristics of a conformal mapping, as summarized above, is a direct generalization of the specifica-
tion of a straight line in one dimension. Conformal mappings thus are the generalizations to mappings of $$R^2 \to R^2$$ of the straight line as a mapping of $$R^1 \to R^1$$! This is why they are so widely used as a modeling tool in engineering, physics, and mathematics. Conformal mappings are the simplest possible regular mapping in two dimensions.

1. Numerical Conformal Mapping of the Retina to the Cortex

Now we describe a method for constructing numerical conformal mappings from one finite region to another which is applicable when only the shapes of the two regions to be mapped (and a point and orientation correspondence) are known. This is the condition of most interest in the current physiological context.

In this approach, one of the regions of interest is triangulated (e.g., using a Voronoi method [47]). The second region may then be triangulated by mapping the nodes of the initial triangulation to the second region, then using the initial connectivity matrix* to triangulate the second region. It is important to point out, however, that this joint triangulation is potentially problematic. There is no guarantee that the connectivity matrix of a triangulation will describe a triangulation when its nodes have been mapped to a new region: some of its edges might then intersect, violating the definitions of triangulation. For a given mesh, a joint triangulation can always be generated by adding pairs of points to the original point mapping, as proven by Saalfeld [48]. Saalfeld gives a constructive existence proof that the joint triangulation can be generated, but this method requires exponential refinements (subdivisions) of its triangles. In our experience, no special means of generating valid triangle maps has been necessary, since any reasonably well-chosen mesh size leads to a valid triangle map.

We begin with the case of mapping an arbitrary region to the unit disk and then discuss mapping between two arbitrarily shaped regions.

2. Mapping an Arbitrary Region to the Unit Disk

Henrici has surveyed existing numerical conformal mapping algorithms [49]. For arbitrary shaped regions (which are approximated by polygonal boundaries with large numbers of vertices), Symm's algorithm (Appendix) is preferable.†

The Symm algorithm is initialized with a description of the boundary of the region to be mapped and the point in this region that is the preimage of the center of the unit disk; it returns the mapping of the boundary and interior region to the unit disk.

To create a mapping from one region to another, we start by generating

*The connectivity matrix can be defined as a binary-valued Cartesian product on the set of points in the region. If two points are connected by an edge, the matrix entry is 1, otherwise 0. In this way the topology of the triangulation map is specified.

†We thank Nick Trefethen for helpful discussion on this point.
the mapping from each region onto the unit disk, either analytically or using the Symm algorithm. We then triangulate the range set from the second region mapping. Optimized point location [50] is used for each point in the range set of the first region mapping to determine which triangle from the range set of the second mapping contains that point. The affine mapping determined by this triangle and its counterpart in the domain of the second region mapping is used to map the included point from the first region range set to the second region. A cleaner solution would make use of a general method capable of mapping the unit disk to an arbitrary region, thus avoiding the numerical inversion of the Symm mapping. Some ideas on how this might be done are outlined by Saalfeld [49].

IV. APPLICATION TO VISUAL CORTEX: COMPUTER SIMULATION VIA TEXTURE MAPPING

In the case of visual cortex, there is considerable experimental evidence that the mapping of the retina to the surface of primary visual cortex is approximately isotropic. Thus, to model the representation of a visual image on the surface of the cortex, we need to construct a conformal approximation to this map and to perform a conformal texture map of given visual field images. To illustrate this process, we show a numerical flattening we performed recently of the surface of primary visual cortex of the monkey.

In this work, we were able to identify a single point (the representation of the blind spot, or optic disk) in the eye and an orientation (the orientation of the horizontal meridian). These observations, together with the flattened representation (and its boundary), were sufficient to generate the cortical map function [51].

The agreement of this method of determining the cortical map, and direct microelectrode measurements of the cortical map function, is excellent. Figure 4 shows a natural scene, mapped via this conformal approximation. The details of its construction are outlined in the Appendix.

A. Numerical Conformal Mapping of 2DG Computer-Flattened Cortex

During the long history of attempts at measurement and modeling of the primate V-1 topographic map, there has never been, to my knowledge, an attempt to assess the "error" in a particular functional fit.

In fact, there has been a very wide range in the reported values of the constant \( a \) in the linear magnification fit: Dow has reported the smallest value (about 0.3°), while Virsu and Rovamo and Tootal have reported values in the range of 1.5°-2°, and Hubel and Freeman [38] report 4°. Is this range of variance due to normal differences between animals or to error in experimental procedure? And, more to the point, how is it possible to compare different measures, such as retinal ganglion cell density, visual acuity, or stereo fusion area, with cortical magnification factor, when one or both of the derived curves has no error analysis supplied?

To provide a high precision estimate of the two-dimensional cortical
map function, we set out several years ago to provide the following data and computational procedures.

1. Computer Flattening
To mathematically model the cortex, it is convenient to work in a planar model. Numerical methods for conformal mapping have been published for planar domains only. Differential geometry is best avoided in numerical problems, and the cortex is relatively flat. (We have measured the mean and Gaussian curvature of primate V-1 and find that curvature of cortex does not preclude an accurate flattening [12,13].) We have found that it is possible to flatten cortex with a mean local error of roughly 5% [14,52-54] and have applied this method to the reconstruction of primate ocular dominance columns and to primate topography in V-1. Figure 5 shows the wire frame model of a flattened cortex, reconstructed from serial sections. This experiment was from a macaque that had one eye enucleated and whose brain was subsequently stained for cytochrome oxidase, revealing the structure of the ocular dominance column pattern, which was computer mapped from digitized images of the serial sections into the flattened cortical representation [14]. Note the representation of the blind spot in Figure 6. The blind spot (optic disk) in macaques is located at about 17° of eccentricity on the horizontal meridian, as shown in Figure 6. We will return to the significance of this particular type of data shortly.

2. Numerical Map Fitting
As outlined above, we have developed several fitting methods using complex logarithmic functions, and also a more general numerical conformal mapping method. We have also outlined the conditions under which local shear in the map function might be modeled, although we have not performed any numerical analysis of sheared mappings. Using the numerical conformal mapping procedure outlined above, and described in detail recently [55], we have modeled the details of a 2DG experiment which is now described.
3. 2DG Measurements of V-1 Topography

2-Deoxyglucose is a metabolic marker. When radioactively labeled, it can be injected, and then, following some paradigm for stimulation, the brain can be imaged to detect the relative pulse density of neurons, in terms of their metabolic activity, following the stimulation.

2DG has been used in humans, using PETT scanning to reconstruct the pattern of firing [39,40]. The stimulus pattern in this case was a logarithmically structured stimulus, similar to that shown in Figure 7.

A similar use of this technique was provided by Tootell et al. [11], who used monkeys and physical brain flattening (i.e., pressing the opercular part of monkey visual cortex between glass slides). In this and subsequent accounts of this research, these workers modeled their data with a simple, one-dimensional magnification curve. Initially they claimed contradictions with the complex logarithmic model and their data. However, a simple complex log fit to their data was subsequently published [42], followed by agreement that the complex log provided a "good" fit to their data [24]. Figure 8 shows the data, with a complex log model superimposed. This log map had an $\alpha$ of 0.3°, in agreement with the data of Dow et al. It appears to provide a good fit to the data of Tootel et al., except for a region near the intersection of the inferior occipital sulcus and the calcarine cortex, where the 2DG images seem to be significantly sheared. This coincides with a region in which Van Essen [23] reported observing anisotropies (shear) in V-1 topography and also coincides with some of our recent 2DG computer-flattened models, as shown in Figure 9.

We are in the final stages of analyzing a series of 2DG experiments, using computer flattening and conformal mapping. The result from one experiment is shown in Figure 9. In this experiment, monkeys were shown stimuli like that of Figure 7, following paralysis, eye position plotting, and injection with $^{14}$C-labeled 2DG. Following about 40 minutes of stimulation, the monkeys were sacrificed, their brains were removed, and one hemisphere was physically flattened while the other hemisphere was blocked for subsequent coronal section on a cryostat. The autoradiography of the physically flattened hemisphere is shown in Figure 10. The computer-
Figure 6 Using a flattened cortical model of the type shown in Figure 5, the density of cytochrome oxidase was texture mapped from the original serial sections (obtained from a one-eye-enucleated monkey). This shows the ocular dominance column pattern. Note the representation of the optic disk, which is the dark region along the horizontal meridian. The data were hand-traced after computer plotting to provide a "black-white" representation.

flattened, reconstructed other hemisphere is shown in Figure 9. Both these figures correspond to the stimulus shown in Figure 7.

Using a single intersection of the ring-and-ray pattern as one of the constraining data needed to apply the Riemann mapping theorem to construct a conformal model of the data, as outlined above and elsewhere [55], the conformal map of the stimulus of Figure 7 was produced (Fig. 11). The superposition of this conformal model and the computer-reconstructed autoradiographic data are shown in Figure 12. It is clear that the agreement between the conformal model and the data is excellent. However there appears to be evidence of some shear in the lower corner of the map data, which is at the intersection of the inferior occipital sulcus and the lip of the calcarine sulcus. This is the same phenomenon seen in the data of Tootel et al. shown above (Fig. 8) and has also been described by Van Essen [23]. It is remarkable, however, that this feature, which appears to be common in macaques, is quite localized to the lip of the lower calcarine sulcus. This feature, which we call the calcarine anomaly, represents a localized departure from the otherwise excellent fit of an isotropic (conformal) map to V-1 topography.

Figure 7 Example of the 2DG visual stimulus used in the 2DG experiment discussed in the text.

Figure 8 The 2DG data of Reference 11, overlaid with a complex log mapping of constant $a = 0.3$, from Reference 42.
In this study, we performed a regression to find the best fit conformal map to our data. In the regression, we allowed both eye position and cyclostom to be the free variables, and the error function for the fit was the summed square difference of data landmarks (e.g., intersections of rings and rays) with corresponding conformal map landmarks. We used a nonparametric regression procedure (Nelder Simplex Method [56]) and were able to determine the best fit to the eye position and cyclostom of the paralyzed monkeys. It appears that this procedure has provided an excellent fit (Fig. 12). There is a significant error associated with plotting the retinal landmarks of paralyzed monkeys. Van Essen [23] estimate this error to be about 0.5° typically. In the data shown in Figure 9, we found a one-degree error, and we also obtained an estimate of 11° for cyclostom from the regression. This is in good agreement with the cyclostom of paralyzed monkeys and with our measured value for cyclostom in this particular case. We therefore feel that our regression procedure has allowed us to null out the significant error due to imprecise retinal plotting in these procedures.

In the near future, we plan to publish analyses for several monkeys and to provide an estimate of “error” for the whole procedure. At the present time, we have hand-sketched “error bars” in Figure 12, to represent the distance between the computer-predicted feature and the actual measured feature in the map (features are corners of “boxes,” intersections of rings and rays). It is evident that the average error is considerably less than 1
mm, over perhaps 10-15 mm of cortex. Since the error of brain flattening is roughly 5%, we feel that this error is about as small as is possible to achieve under these conditions.

In summary, the average error in this fit is considerably less than 10%, although there is an error of 4-5 mm (perhaps 30%) localized in the lower left corner of the operculum in Figure 12, in the region of the calcarine anomaly. Put another way, if we have a technique that reliably indicates the visual field coordinates of a single point in the cortex, then (if we have access to the anatomical “shape” of the cortical boundary), we can reproduce the entire cortical map to within an accuracy of roughly 1 mm. This somewhat counterintuitive result illustrates the power of these techniques.

What is the cause of the calcarine anomaly? We have not found any correlation to excessive Gaussian curvature of cortex in that region, although the intersection of the lip of the calcarine and the inferior occipital cortex is one of the most severely folded parts of the macaque visual cortex. Perhaps a shear may be introduced in the developmental events leading to the creation of the sulcal pattern of the cortex. Perhaps the cause lies in an idea suggested by Tootel et al. [11]: that in this region the compression of the ocular dominance column pattern is less than 2:1. It is difficult to say, although the location of this anomaly in the region of major sulcus folding, and its topographic location in the vicinity of about 8° on the upper vertical meridian, make it unlikely that the anomaly is driven by any functional considerations.

In summary, we offer these preliminary data as an estimate of the reliability of conformal approximations of cortical topography in V-1. We believe that this is the first time a regression or error analysis has been performed on the two-dimensional structure of V-1 topography.

4. Application to Reconstruction of Human V-1 Topography

One major application of the use of numerical conformal mapping has been validated by the monkey data shown in Figure 12: namely, it provides an entirely new method for estimating topographic map structure in primates, as pointed out by Weinshall and Schwartz [51]. To reconstruct a conformal approximation to a topographic mapping, access to the following data will suffice:

1. A single point correspondence
2. The relative orientation of the two domains
3. A flattened representation of the boundary of the cortex

This follows directly from the Riemann mapping theorem and is shown by construction in Figure 12, since the computer model in that figure was...
constructed from a single point (ring-and-ray intersection) and the flattened cortical representation. Note that the alternative to this procedure is to perform an exhaustive (physically and figuratively!) point-by-point physiological mapping of differential magnification factor measurements. Difficult and error prone as this approach is in monkey research, it is impossible (for legal and ethical reasons) in human research. However, anatomical data on the V-1 boundary are readily available in both monkey and human data. (Magnetic resonance images are now capable of noninvasively providing submillimeter resolution of tissue density, which is sufficient to model the boundaries of human cortex, and to flatten human cortex using our flattening software, to excellent precision.)

Now, in the human, physiological mapping methods have been applied in only a few, very limited experiments. PETT scanning, even with current resolutions in the range of 5–7 mm, is much too coarse to provide a reliable estimate of the human map. But, human ocular dominance columns from postmortem examination of one-eyed patients have been reconstructed [57] using the same cytochrome oxidase stain used in the monkey experiment summarized in Figure 6.

To demonstrate the feasibility of this method, we used the columnar pattern, as shown in Figure 6, to measure the position of the optic disk, which is clearly evident in the figure. This provides us with a landmark at 17° on the horizontal meridian. We then constructed the unique conformal mapping that corresponds to this constraining data point. The result is shown in Figure 13.

By numerical differentiation, we have found that the magnification function obtained from this map is essentially indistinguishable from microelectrode estimates of V-1 cortical magnification [51]. Therefore, this approach provides a novel route to estimating cortical magnification factor, and one that is applicable to humans. Thus, by either reconstructing the ocular dominance column postmortem in one-eyed humans, or, perhaps, by using echo-planar magnetic resonance imaging (MRI) techniques to find a single visual landmark, followed by computer flattening of the MRI-measured sections of human cortex, we would be able to reconstruct a highly reliable estimate of human V-1 topography. Moreover, if this were done in an MRI paradigm, we would have the added benefit of a living subject, thus allowing psychophysical study of the individual whose anatomy has been characterized. An experiment of this kind is currently being planned. The basic calibration of the method, together with the necessary algorithms, has been provided in the context of the monkey work outlined above. If successful, it may be possible to provide the first reliable estimate of human V-1 topography. At the present time, we see no other viable route to this extremely important data.

Figure 13 Numerical conformal map, made from a computer-flattened ocular dominance column preparation (Fig. 6), using the known location of the optic disk to constrain the complete conformal map.

B. Corrections to the Archival Literature on Cortical Topography

At this point, we have reviewed the history of topographic mapping in primate V-1 and have shown a complete analysis of the mathematical structure of a simple regular mapping of a two-dimensional surface, such as the retina, into another two-dimensional surface, such as the cortex. Three different isotropic models have been outlined. All work well, with the numerical conformal mapping just shown providing the best performance. Within the possible exception of a localized region near the calcarine-infero-occipital intersection, the primate V-1 map appears to be well characterized as an isotropic mapping. Before proceeding to analyze the consequences of the existence of higher dimensional mapping in V-1, particularly ocular dominance column structure, we briefly summarize some of the insights gained so far, in the form of a series of brief statements (lemmas). Then, each lemma will be used to clear up misstatements and misconceptions that have accumulated over the years in this field.
1. Some Lemmas on Isotropic (conformal) Maps

Lemma 1 (Inverse linear magnification factor) The use of an inverse linear magnification factor scalar function to summarize a mapping is valid if and only if the mapping is locally isotropic. Otherwise, the magnification is summarized by the Jacobian of the map, a two-dimensional tensor function that geometrically represents an infinitesimal rotation, dilation, shear, and direction of shear. No direct measurement of the cortical magnification tensor has yet been performed, although the evidence in this chapter suggests that except for the region of the calcarine anomaly, cortical magnification is in fact a scalar quantity.

Lemma 2 (Complex log) There is only one two-dimensional conformal map function that corresponds to a magnification factor that is of the inverse linear form: the complex logarithm.

Lemma 3 (Global symmetry) The complex log mapping does not have the same magnification function on the vertical, horizontal, or other meridians. In fact, the assumption of global symmetry is generally inconsistent with local isotropy.

Lemma 4 (Conformal mapping) If the magnification factor is locally isotropic but not of the inverse linear form, a conformal mapping more general than the complex logarithm must be constructed. Such a map function may have a relatively complicated one-dimensional functional form and certainly does not have to be globally symmetric (i.e., the same on the vertical, horizontal, or other meridians). Moreover, such a map function is uniquely determined by the specification of a one-point correspondence between retina and cortex, the slope at this point, and the boundary of the retinal and cortical surfaces.

Now, using these four lemmas, we can correct some misstatements.

2. Daniel and Whitteridge

As noted above, Daniel and Whitteridge claim that the cortical map is both locally isotropic and globally symmetric. That this cannot be true (unless the cortical map is the identity) follows directly from the Riemann mapping theorem. If the map is locally isotropic, then it is conformal (by definition). Therefore, the map is uniquely determined by a single point. Stating global symmetry provides in effect an infinite set of point correspondences, which can be true only if the map is a trivial identity.

3. Sakitt

Barbara Sakitt [58] published a paper titled "Why cortical magnification factor cannot be isotropic." But, this title is a contradiction of the Riemann mapping theorem: there are an infinite number of isotropic maps which can be constructed between two arbitrary, simply connected regions. In fact, Sakitt followed a construction similar to that of Hubel and Freeman, of symmetrically stretching the cortical map along lines. This approach does not generate a conformal map.

4. Tootell

Tootell et al. [11], stated that since the vertical meridian is about 30% longer than the horizontal meridian in 2DG maps of V-1, the complex log mapping is not a good fit to cortical topography. Moreover, these authors suggested that this effect was rooted in the ocular dominance column pattern of V-1, since they do not believe that the left and right eye ocular dominance columns were "squeezed" by exactly a 2:1 shear to fit together, as measured by Le Vay et al. [59]; rather, they cite an apparent 30% shear to account for the lengthening of the vertical meridian.

This idea seems to be rooted in the same confusion of local and global isotropy outlined above. Global isotropy is not implied by the usual usage of the term "isotropic" map, and in fact, local and global isotropy are, in general, mutually inconsistent! Moreover, the 30% effect seen by Tootell et al. is in fact precisely that predicted by the complex log model, a point made in a subsequent paper addressed to these authors [42]. Tootell et al. [24] appear to have acknowledged this argument, in the form of an agreement that the complex log is a "good approximation" to V-1 topography. One consequence of this observation is that there is in effect little "residual" anisotropy caused by the ocular dominance column system. In other words, if the "net" cortical mapping is in fact isotropic, and we have shown data here to make that statement highly likely, then it appears that for everything to fit, the ocular dominance column system must be "squeezed" by close to a 2:1 factor.

In a more recent paper, the same authors [60] have escalated their position considerably, since they now claim that the cortical map is anisotropic (locally) by 100%. Their argument is that the ocular dominance columns are not "squeezed" at all and that the fitting together of two complete maps in V-1 causes a 100% shear! No two-dimensional map is presented to model this suggestion, nor is a great amount of data presented to support it. Moreover, the conceptual and computational issues of fitting together in a single cortical mapping multiple submodalities (such as ocular dominance and orientation columns) have only recently been addressed [16]. We now briefly review this aspect of cortical topography.

C. Higher Dimensional Models

1. Columnar Structure and Topography

The entire preceding discussion was predicated on the notion that visual cortex represents a "regular" mapping of the visual field—that is, a well-behaved, continuous map whose Jacobian is nonzero and finite. In fact, the situation is considerably more complex. In the input layers of V-1 (layer
IV), there are two complete maps, one for each eye, interlaced in the form of thin strips, or columns. We have shown a computer-flattened texture mapping of this ocular dominance column pattern from our lab (Fig. 6).

In addition, there are at least two more independent columnar systems in V-1: one for orientation and the so-called cytochrome oxidase puffs, which tend to occupy the singular regions where all orientations in cortex come together.

Recently, we developed computational methods to represent the cortex, including arbitrary columnar substructure [16]. This algorithm is reviewed here, along with some computer simulations of recent binocular 2DG data, which are well modeled by this approach.

2. Protocolumns and Protomaps

The details of the protocolumn algorithm are quite complex and depend on the manipulation of several data structures from computational geometry. But the general idea of it is simple: we imagine that the submodalities of the cortex (e.g., left eye input, or orientation input at some specific angle), constitute a complete map of retinal space. We call these maps "protomaps"; that is, they are the "regular" map before it has been "cut" into columns, which are then "squeezed" and packed together to make up the real, observable cortex. For ocularity, there are two protomaps: a left and a right eye protomap. For orientation, there are as many protomaps as distinct orientation values to be modeled. Thus, if we discretize orientation in terms of angular bins of 15° each, we would need to construct 12 protomaps for the orientation system.

The advantage of this conceptualization is that the protomaps are "regular" maps, which can be described by conventional continuum approaches, as we have outlined above.

To proceed with the algorithm, we then define "protocolumns." The protocolumns are constructed from the observed individual columns in the brain, by a warping transformation that expands the observed columns until they smoothly fill the cortex. This is sometimes called a "grow" operation in computer graphics; we have used a Voronoi diagram method to actually compute the protocolumn pattern. Thus, the protocolumn pattern represents a form of "proximity" diagram. For a given "real" column, its unique protocolumn is the locus of points nearest to that real column. Thus, for a typical single ocular dominance column in cortex, its protocolumn is a somewhat "fatter" version of itself, whose detailed shape is a function of that column and its near neighbors (see Fig. 14). This construction is designed so that the complete set of protocolumns perfectly tessellates the cortex. We then are able to image-warp from a protocolumn to its actual column and thereby construct a two-dimensional simulation of the topography and columnar structure of V-1.

Figure 14 Example of the protocolumn construction described in the text. Top: some of the steps of the algorithm that finds Voronoi polygons from the experimental column data. Bottom: the thresholded image of the ocular dominance column (left) and the corresponding protocolumn pattern (right). Each protocolumn is shaded with a different shade of gray, to help in visualization. Note that the protocolumns surround their corresponding columns, are about twice the thickness, and form a smooth, jigsaw-like tessellation of the cortex, which property follows from the definition of the Voronoi polygon construction used to create this protomap. (From Ref. 16.)
One consequence of this construction is that for "zebra skin"-like patterns, such as the V-1 ocular dominance column system, there is a roughly 2:1 compression between a column and its protocolumn. This agrees with an early estimate of the experimental "shear" within a cortical ocular dominance column [59] but is in significant disagreement with the recent estimate [60] that there is a 1:1 compression within a column, resulting in a 2:1 compression in the overall cortical map.

Figure 14 shows an example of the computation of a single protocolumn from its observed ocular dominance columns as well as the entire protomap of the left eye. Figure 15 compares a simulation of the protocolumn algorithm and a recent binocular 2DG experiment [61]. The agreement is good, but it should be stressed that there are few quantitative data available to constrain this fit.

Tootell et al. [61] in fact favor a model in which the protomap, to use our term, is actually isotropic and the "real" cortex is 100% anisotropic, and the local shear within an ocular dominance column is therefore something like 1:1. We favor a different model, in which the protomap is isotropic, the "real cortex" is isotropic, and there is a shear of 2:1 within an individual ocular dominance column.

We favor this type of model because, for one reason, it is very difficult to believe that there could be, in general, as good as fit as we have shown in Figure 12 to a highly anisotropic cortex. Tootel et al. in fact have not provided any two-dimensional modeling to support, or to clarify, their conjecture.

And, to avoid confusing the reader at this point with notions of columnar shear, we point out that virtually all methods of measuring cortical magnification factor operate on a scale larger than the size of individual cortical columns, so that the small-scale columnar structure is essentially averaged out. However, if there were anything much different from a 2:1 shear within individual columns, this effect would summate coherently over many columns* across the cortex and would be accompanied by a large macroscopic effect. We see no evidence of this, with the exception of the calcarine anomaly, and therefore assert that the most likely state of the local cortical shear is roughly 2:1, with the direction parallel to the column boundaries having a magnification factor twice that in the direction perpendicular to the local column boundary.

To conclude this section, Figure 16 shows a computer simulation, using a numerical conformal mapping and our protocolumn algorithm [16] to simulate a binocular spatial mapping, at the level of layer IVc of V-1: the natural scene has been digitized to span the range from 0 to 100°, with a maximum resolution corresponding to about 3 minutes of arc.

V. PSYCHOPHYSICAL-ANATOMICAL HOMOLOGY

A major theme of the literature on human retinocortical topography has always been the possible existence of scaling laws between psychophysical measurements and retinal and cortical anatomical measurements. Daniel and Whitteridge were likely the first to make this point, summarized earlier in this chapter, that the human minimum angle of resolution is similar in functional form to inverse cortical magnification. In later work, Schwartz [21] suggested that retinal ganglion cell density and cortical topography might be related by a particularly simple developmental rule: the retina (actually LGN) fiber input spreads across the cortex in the manner of an isotropic fluid. Fixing a single point then would be sufficient to provide a unique map.

During the 1980s many papers sought to link acuity, stereo acuity, vernier acuity, motion thresholds, and retinal receptor and retinal ganglion cell densities to cortical magnification factor. There are two major problems with this literature, however.

---

*Ocular dominance columns appear to be coherent, in the sense of running roughly parallel, over regions of the cortex that vary between several millimeters and perhaps 1 cm.
1. There has usually been no error analysis performed on any of the data. This is particularly problematic given the wide spread in the measurement of all the quantities involved. For example, different workers have found values of the constant $a$, which characterizes the cortical map, between 0.3 and 4°. This is a variation of more than 1000%. A recent PETT experiment [41] claims that human $a$ is 6°! And none of these experiments provides an estimate of error.

2. Human cortical magnification has never been reliably measured. Existing estimates of $a$, which tend to be in the range of 1.7–6° are based on extremely poor quality data and are many hundreds of percent higher than that found in monkey. The only reliable monkey measurements have been made with exhaustive microelectrode plotting and with 2DG analysis of serial sections. These techniques are not possible in human subjects. In fact, there are no techniques possible in human subjects, since careful microelectrode exploration is both illegal and unethical. Therefore human magnification factor is currently known by guesswork, not by measurement. This weakness greatly compromises the comparisons of human psychophysics to a largely unknown human magnification factor, or of monkey magnification factor to largely unknown monkey psychophysical data!

A recent review [37] attempts to rationalize this situation by suggesting that there are really two $a$ parameters, a retinal one in the range of 1.5–4.0° and a cortical one in the range of 0.3–0.8°. Table 1 summarizes psychophysical measurements and shows their relative $a$ values (called $E_2$ here) in slightly modified form.

The attempt to cluster the data is important, but it seems that the measurements in this field are simply spread over an extremely large range. For example, Wilson et al. [37] cite the data of Tootell et al. [11] as providing support for a value of 0.8° for $a$. But recently, it appears that the same data were presented with an analysis of 1.5° for $a$ by the same research group [60], which would move this measurement from one group of Wilson et al. to the other. And, recently, Wassle et al. [62] have provided evidence that the classical fits of retinal ganglion cell density have been contaminated by a background of displaced amacrine cells that have tilted the linear regression curves toward values of $a$ that are considerably too high. The new reanalyzed values of retinal ganglion cell density of Wassle et al. are in agreement with the recent $a$ of 1.5° [60], although evidently not in agreement with the value of $a$ of 0.8° from the same investigators using the same data set [11], and are in significant disagreement with the data of Dow et al.

There is clearly a problem here. One is reminded of the statement of Mark Twain: “The research of many learned men has already shed much
Table 1. Values of \( a \) from Psychophysical and Anatomical Sources

<table>
<thead>
<tr>
<th>Value of ( a )</th>
<th>Species</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>( a \in [1.5,\text{o},4,\text{o}] )</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Retinal cones</td>
<td>Human</td>
<td>92</td>
</tr>
<tr>
<td>( \beta ) ganglion cell density</td>
<td>Macaque</td>
<td>93</td>
</tr>
<tr>
<td>Gallion cell density</td>
<td>Macaque</td>
<td>94</td>
</tr>
<tr>
<td>Inverse cortical magnification</td>
<td>Macaque</td>
<td>62</td>
</tr>
<tr>
<td>Cortical receptive field size</td>
<td>Macaque</td>
<td>60</td>
</tr>
<tr>
<td>Minimum angle of resolution</td>
<td>Human</td>
<td>95</td>
</tr>
<tr>
<td></td>
<td></td>
<td>96,97</td>
</tr>
<tr>
<td></td>
<td></td>
<td>98</td>
</tr>
<tr>
<td></td>
<td></td>
<td>99</td>
</tr>
<tr>
<td></td>
<td></td>
<td>100</td>
</tr>
<tr>
<td>Contrast sensitivity</td>
<td>Human</td>
<td>101</td>
</tr>
<tr>
<td>Slow velocity discrimination</td>
<td></td>
<td>102,103</td>
</tr>
<tr>
<td></td>
<td></td>
<td>104,105</td>
</tr>
<tr>
<td>( a \in [0.3,\text{o},0.9,\text{o}] )</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inverse cortical magnification</td>
<td>Macaque</td>
<td>95</td>
</tr>
<tr>
<td></td>
<td></td>
<td>11,23</td>
</tr>
<tr>
<td>Optimal two-dot vernier acuity</td>
<td>Human</td>
<td>106</td>
</tr>
<tr>
<td>Abutting vernier acuity</td>
<td>Human</td>
<td>107,108</td>
</tr>
<tr>
<td>Vernier crowding zone</td>
<td>Human</td>
<td>99</td>
</tr>
<tr>
<td>Optimal three-dot bisection</td>
<td>Human</td>
<td>109,110</td>
</tr>
<tr>
<td>Stereo acuity</td>
<td>Human</td>
<td>111</td>
</tr>
</tbody>
</table>

Source: After Ref. 37.

more reliable retinal data is an important step toward clarifying the retinal component of this problem.

VI. MACHINE VISION

A. Vertical–Horizontal Pyramids

Variable resolution in spatial vision has been one of the principal themes in vision research for more than 30 years. Early in this era, this field bifurcated between “spatial frequency” enthusiasts and “space domain” partisans. There was a time when the Fourier transform was reified in vision, and it should be pointed out that a global convolution of this form, is, in a certain sense, the antithesis of a spatial map. There was also much contention among physiologists who preferred a spatial frequency interpretation to the space-domain receptive field interpretation originated by Hubel and Weisel. This contention reached its peak, if not its reductio ad absurdum, in a paper [63] showing that cortical simple cells were linear in their response to gratings but sinusoidal gratings were “better” stimuli, since a sinusoidal grating of a given amplitude had a larger cortical response than a slit of the same amplitude. It was later pointed out in a letter to Science that the normalization of a square slit and a sinusoid would be expected, on “energy” grounds, to differ by a factor of \( \sqrt{2} \! \)

More recently, this contention has faded away. There are relatively few who still argue that a Fourier transform is somehow performed in the brain. In any event, the waning of this form of argument makes an interesting historical counterpoint to the area of cortical topography.

Thus, it has been pointed out [64] that the variation of receptive field size across the surface of the cortex might be considered to be a form of “horizontal” multiple resolution representation, while the variation in receptive field size at a single location in the visual field might be considered to be a form of “vertical” multiple resolution. If so, the two major features of spatial vision could be viewed from a unified perspective.

Donald Kelly has extensively explored this idea [65] and has studied multiple-resolution representation using Gabor functions, together with complex log mapping to represent the spatial structure of the visual field. This work represents the only computational attempt to date to unify the spatial frequency description of cortical receptive fields with the space-variant facts of cortical topography (see Fig. 17).

The theme of “vertical–horizontal” space variance in vision provides a major thread in the context of machine vision. In fact, it can be argued that the only efficient approaches to real-time practical machine vision have been, and more to the point, will be, based on space-variant architectures.
For example, Burt and his collaborators [66,67] have provided “pyramid” algorithms for machine vision for more than a decade. By and large, multiscale, or pyramid, approaches to vision appear to be the only practical means of realizing real-time performance. This is because most early vision processing can be performed on a coarse-to-fine grid, greatly decreasing the processing required, so that refinement at high acuity needs to process only a relatively small area of the sensor.

In the early work of Burt, the operative metaphor was that of “spatial frequency.” A full image sensor was subsampled to provide perhaps four levels of a pyramid, with increasingly larger “receptive fields.” Burt and Adelson [66] showed that this results in a total amount of pixels that was $\Sigma 1/4 + 1/16 + \cdots = 4/3$ larger than the original single resolution frame. Therefore, a multiresolution pyramid “costs” little more than a conventional image but provides a potentially large speed-up on processing.

However, the original image itself is of order $N^2$, where $N$ is a large number in the range of 256–1000 pixels. Obviously $4/3 \cdot N \cdot N$ is a large number if $N \cdot N$ is a large number! This is the principal bottleneck in machine vision. Thirty frames per second of 0.256 million pixels is more than 7 million pixels per second, and each pixel must be processed in real time with many hundreds of machine instructions to complete a machine vision task.

More recently, Burt [68,69], and others have begun to use a “truncated” pyramid, in which the higher resolution levels are computed on smaller regions of the sensor. The highest resolution level of this truncated pyramid thus exists on the smallest segment of the sensor area. In other words, this is a discrete approximation to a foveal architecture!

Yeshuron and Schwartz [70] used the term “space-variant vision” to refer to machine vision performed with a sensor whose resolution varies smoothly across its surface, like that of the human visual system. The use of such sensors is rapidly becoming an important factor in machine vision: Burt’s truncated pyramid is one example, but more recently many other applications of space-variant vision have begun to emerge. In the next section, we review some work of our laboratory in this area, because it illustrates the potential of space-variant architectures in machine vision, and also because it may offer important insight into the nature of the constraints and architectural principles that are operative in human vision.

### B. Computational Function and Cortical Architecture

The nature of computational function in visual cortex is, at present, almost completely unknown. Despite an impressive amount of knowledge at all levels of the nervous system, from the level of ion channels and membrane
biophysics, neural trigger features, columnar and topographic architectures, and multivariato visual function throughout extrastriate cortex, there is no confident answer, at the present time, to the question: What are the computational functions of the visual cortex?

However, we can speculate on several aspects of visual computation, which are supported by the particular form of space-variant mapping that occurs in the cortex. We review several of these proposals, which have been advanced over the years. To begin, however, we choose a system that beyond any reasonable doubt follows directly from the analysis presented in this chapter and has had practical consequences to the recent design of machine vision systems.

1. Ten Thousand Pounds of Brain
The human visual system is able to cover a wide visual field, and to achieve high maximum resolution, without the need for an unreasonably large number of spatial channels. The foveating, or space-variant, construction of V-1 provides a dramatic form of data compression. Just how dramatic this compression is can be seen from the following simple estimate. Suppose we wish to "cover" a solid angle that is comparable to human vision (let us say about 100° × 100°), with a maximum resolution of 1 minute of arc. If we were to attempt this with conventional video sensor technology, we would require our sensor to have 6000 × 2 × 6000 × 2 pixels (the factor of 2 × 2 is for sampling). Figure 4 simulated a 16,000 × 16,000 pixel scene with the map function estimate from monkey V-1, which is represented by a simulated cortical representation of 16,000 pixels in total. In other words, we achieved, in Figure 4, a compression of about 16,000:1, by the use of a space-variant sensing strategy similar to that used in primate vision [14].

In a more careful analysis of this compression factor [71], we have defined a measure of sensor quality, which we term F/R quality, defined as the ratio of sensor field of view to maximum resolution, as outlined above. This is a measure of the spatial dynamic range of a sensor. Estimating a primate visual field of 140° (vertical) and 200° (horizontal), we estimated that the number of "pixels" in a complex log sensor such as the human retina is about 150,000. This number is consistent with the number of fibers in the optic tract (about 1,000,000), since we have not accounted for color, on-off and off-on pathways, noncortical afferents in the optic tract, and redundancy of sampling (see Chapter 4, which shows that orientation selectivity is a necessary consequence of chromatic decoding). We believe that a count of about 10^6 "pixels" or "sampling units" or "spatial degrees of freedom" is consistent both with cortical topography and with the number of fibers in the optic tract.

Nakayama has also provided a estimate of the number of "pixels" re-

quired to encode contrast [72]. He obtained an estimate of 25,000 "pixels" [72] somewhat lower than ours, but he did not provide any details of his calculation.

The number of pixels in a conventional, space-invariant sensor (e.g., a TV sensor) of the same F/R ratio, is 600,000,000.* These estimates for the space-variant and space-invariant pixel burden of vision sensors suggest that compression ratios of between 3500:1 and 10,000:1 are achieved.

Since the primate cortex is roughly 50% (exclusively) visual, and the human brain weighs about 3 pounds, we estimate that our brains would weigh many thousands of pounds if we were to maintain the same spatial dynamic range, but used a space-invariant, or nonfoveal architecture.

Since wide-angle vision with high acuity would appear to be of great selective advantage, and since a brain weighing 5000-30,000 pounds is not, it appears that we have identified at least one indisputable functional correlate of visual cortex spatial architecture.

2. Space-variant Active Vision
As we began to outline above, the use of space-variant architectures in machine vision has come to be an area of increasing importance. Starting with the pyramid algorithms of Burt, in the early 1980s there has been an increasing realization in the machine vision community that multiresolution sensing may be critical to achieve high performance, real-time machine vision.

During the past several years, with support from the Artificial Neural Network Technology Program of the Advanced Projects Research Agency (ARPA), we have built a machine vision system that utilizes the complex log geometry as its sensing strategy. The system we constructed has established extremely high performance on certain measures, which we now review.

3. CORTEX-I
We have constructed a miniature space-variant active vision system, using a complex logarithmic sensing strategy [74,75], which we call CORTEX-I. The benchmark application for this system was to acquire moving targets

*Shostak has estimated the following "pixel" estimates for the full visual field, using a space-invariant (nonfoveal) architecture [73]:

- Solid angle of human vision: 15,000 deg² (180° (horizontal) × 135° (vertical))
- Maximum resolution: 0.5 minute of arc
- Sampling factor: 2
- Space-invariant sensor size: 36,000 × 28,000 = 1,008,000,000 pixels

Shostak's estimate is larger than ours because he used an assumed 0.5 minute of arc, rather than a 1 minute of arc maximum resolution.
(automobiles), track them with the camera, and use pattern recognition techniques to read the license plates of the cars as they drove past the camera system. To accomplish this goal, a series of hardware and algorithmic problems had to be solved. At the hardware level, a novel actuator design was produced and implemented, called the spherical pointing motor. This design produced a 2-degree-of-freedom camera pointing device that was fast, very compact, and extremely inexpensive to produce. Additional hardware innovations were the production of subminiature camera and lens systems, a custom-built very-large-scale integrated (VLSI) sensor, and image processors based on digital signal processing. At the algorithmic level, it was necessary to develop attentional algorithms capable of locating in real time an object of interest (e.g., a license plate) in a complex scene containing moving objects, to track the object of interest, and to perform image processing and pattern recognition on the tracked object. This work is fully described in a recent series of papers [74–78].

The license plate reading benchmark was achieved [74] with a hardware system that occupied less than 0.5 cubic foot, weighed less than 10 pounds, and cost roughly $2000 in parts to build, including video camera, lenses, motors, and computer system. Figures 18, 19, and 20 show CORTEX-I, the custom “eye” spherical motor and camera system, and a sample of the license-plate-reading task, respectively.

The most notable aspect of this system was its ability to perform a difficult machine vision task, in real time, with the support of only 12 million instructions per second (MIPS) of processing power. This system is roughly 10–100 times smaller, cheaper, and computationally less powerful (in MIPS) than other contemporary machine vision systems. The reason for this economy can be traced directly to the use of a space-variant sensing strategy. Our system processed only 1400 pixels per frame, instead of the usual 64,000–256,000 pixels common in machine vision. In effect, we exploited the type of leverage outlined above for the human visual system (although not quite the same magnitude). And, the scaling down of our systems cost and size must be understood to apply not only to the sensor, but to the memory, the CPU power, and to almost all other aspects of the system.*

We are currently building a second-generation system, which will provide 200 MIPS or more, and which will be mounted on a miniature robot vehi-

*Like the human eye, and unlike conventional cameras, the log map sensor does not require high quality optics off-axis. This made possible very small and light lenses, which in turn allowed actuators to be very small and light. A number of synergistic benefits followed from the complex log sensor geometry.

Figure 18 The computer engine and camera of the machine vision system CORTEX-I. On the top of the rack is mounted a miniature active camera system, shown in more detail in Figure 19. The rack shown contains three digital signal processors (DSPs), one microprocessor, and several boards of custom electronics, including motor control, communications, and camera control. At the time of writing, this system was the smallest functional active vision yet constructed, by at least an order of magnitude. The output images of this system (bottom) represent a face and a license plate. The system was successfully demonstrated to acquire moving targets (vehicles), to locate the license plates on the moving vehicles using a model-based “attentional algorithm,” and to perform optical character recognition of the license plates in real time while tracking a moving target.
We expect the performance of this system to affirm the practical significance of space-variant image architectures.

4. Commodity Robotics

Machine vision and robotics have been disappointing in the marketplace. This is not because they have failed to perform at all. It is because the relatively modest performance that contemporary machine vision provides is not cost-effective. Almost all vision and robotic tasks are more cheaply performed, at the present, by human workers. We have recently argued that the availability of extremely low cost robotic and machine vision hardware, in the consumer price range, and with the functionality provided by the prototype CORTEX-1, will have a major impact on industrial and military applications, which we have likened to the impact of the low cost personal computer on computation in general. We have called this (so far hypothetical) phenomenon the PC-metaphor for machine vision, or the coming of "commodity robotics." For a number of years, we have predicted that high performance vision robots will ultimately use space-variant, active vision architectures: the factors of hundreds or thousands in data reduction that this provides are simply so great that any competition from a conven-

Figure 19 "Spherical pointing motor" built to control the active vision system camera of CORTEX-1. The camera (center) is about 5 mm x 10 mm. The whole system is about 1.5 inches on a side.

Figure 20 Frame from the final pattern recognition stage of CORTEX-1. This frame shows the optical character recognition algorithm classifying the characters on a stationary license plate, tracking the moving vehicle.

tional space-invariant system is unimaginable. Whether this will come to pass remains to be seen. However, judging by the rapidly increasing interest in machine vision groups to build active vision systems in general, and on space-variant or foveating systems in particular (see, e.g., Refs. 79-84), we feel confident that this trend will be realized within the next decade. And if it does, one more area of biological vision will have made an indisputable contribution to high performance machine vision.

5. Special Geometric Properties of the Complex Logarithm

One area of great activity has been the application of the special geometric properties of the complex log function to visual computation. These properties were known prior to the realization that primate cortex possessed
complex log geometry, but they were linked to the Fourier transform, via the “Mellin transform” [85, 86]. In the space domain, it was pointed out by several authors [9, 19, 87] that the complex log map possessed some intriguing properties of size, rotation, and projection invariance. These are summarized in pictorial form in Figure 21.

In a sense, the favorable size, rotation, and projection-invariant properties of the complex log map are bought at the expense of the severe breaking of translation symmetry that is implied by a space-variant mapping. At the present time, it is not known whether the symmetry properties of the complex log are significant. For one thing, they follow only on a complex log approximation to cortical topography that is valid outside of the foveal region (i.e., for visual angles greater than θ, where our best guess for θ is about 0.5°). Most likely, the geometric properties of the complex log mapping will find application in the simplification of optical flow, as sketched out in Figure 21 [22]. These aspects of the complex log have been most intensely investigated by George Chaiken [88], Carl Weiman [89], Guillio Sandini [80], and Ramesh Jain [90, 91].

**VII. CONCLUSION**

The means by which the brain provides a representation for spatial vision, or even whether the notion of representation is a viable concept, is at present unknown. A contingent of psychologists, cognitive scientists, psychophysicists, computer scientists, artificial intelligentsia, and worst of all, philosophers, has debated and argued over this issue for at least 20 years, with no end in sight. But the question of representation, in the brain, is the fundamental key to progress in understanding the nature of perceptual and cognitive brain activity. Until we know what, if anything, is being computed upon, the nature of the computation itself is one step further removed from our grasp.

In vision, the zeitgeist in this area tends to change once per generation. In the 1930s, 1940s, and 1950s, it appeared that spatiotemporal models were dominant. Lorenté de No introduced the notion of circulating temporal patterns of activity, the dramatic experiments of Talbot and Marshall drew attention to the notion of analog spatial representation, and the ideas of the gestalt psychologists, particularly Kohler, were intimately related to notions of analog spatiotemporal representation. Roy John and Walter Freeman developed notions of temporal coding to represent mnemonic and perceptual representations.

In the 1960s such young turks of the microelectrode as Barlow, Hubel, and Weisel overturned the dominant paradigm of analog representation in terms of a purely symbolic one: the single neuron feature extractor, representing perception and cognition in a purely nonspatial, hence purely symbolic, mode of the labeled “grandmother cell.”

In the 1970s, psychophysicists took a turn at paradigm leadership, introducing the notion that “spatial frequency” was the underlying basis for spatial representation in vision, which in turn stimulated a parallel school of physiologists to investigate the same hypothesis.

In the 1980s there was a resurgence in interest in topographic mapping, stimulated in part by the availability of new techniques of experimental
measurement and partly by a spurt of papers that sought to compare the spatial variation of acuity, stereo, and motion measures with retinal and cortical anatomy.

In the 1990s it appears that space-variant architectures, typified by the pyramid, and the log map, are on the point of becoming important sensor architectures for machine vision, with the likelihood that future high performance robotic vision systems will be based on the same sensor architecture used by the primate visual system. Moreover, these systems are likely to be “active” (i.e., based on robotic actuation), emphasizing the importance of a wide range of biologically motivated algorithmic areas such as attention and ocular motion control.

At the present time, it seems that only the feature filter and the spatio-temporal modes of representation have survived as viable proposals for the nature of visual representation. The notion that the brain is somehow performing Fourier, or “harmonic,” analysis seems to have faded away, with the (painfully slow) realization that the Fourier transform has an important, but very limited role to play in computational vision. The transfer of this idea to biological vision was a form of deus ex machina that has not stood up well to the observation that the moderate bandpass spatial filtering properties of the visual system are much better accounted for by a “pyramid” model, built over a space-variant mapping, than by a strict “Fourier transform” or “harmonic analysis” interpretation.* If so, the spatial structure of areas such as primary visual cortex are of fundamental importance to our attempt to understand the brain.

This chapter has reviewed attempts to model, and to measure, the topographic and columnar structure of visual cortex. Since columnar structure appears to occur jointly with topographic structure in cortical sensory systems, we have briefly reviewed constructions, such as the protomap, protocolumn, and cortical polymap [16], which have been introduced recently to make algorithmic sense of structures, such as V-1, which are both topographic and multimodal in a columnar fashion. Having introduced these ideas, we have a framework in which to understand visual cortex in terms of the simpler mathematical idea of “regular map” (i.e., a map with a well-behaved Jacobian), and we have reviewed the history, the mathematics (both analytic and numerical), and the current experimental status of modeling such neural maps. Preliminary data (Figs. 11–13) suggest that the topographic map of visual cortex is in fact quite well approximated by a

*The reader is alerted that this interpretation of the current status of the role of “Fourier theory” in vision may stimulate strong disagreement from some; it is presented here as an opinion of the current state of knowledge, if not a universal consensus.

conformal map whose structure is very close to the simple analytic model of the complex logarithm.

To fully present this idea, a fairly large amount of mathematical detail has been presented. The justification for doing this has been the primacy of this form of structure for understanding vision, and also the fact that the original papers presenting this work are scattered across several different literatures (computer graphics, physiology, neural modeling) in a way that makes it very difficult for the interested reader to obtain a full understanding of these methods. This chapter represents the first attempt to summarize all this material in one place, and the result is, clearly, quite a lot to expect of the reader. However, it would appear that coming to terms with the material presented here is, in the long run, an essential step in understanding the basic nature of spatial representation in primary visual cortex.

APPENDIX

Riemann Mapping Theorem

A typical statement of the Riemann mapping theorem is [46]:

Given any simply connected region Ω which is not the whole plane, and a point z0 ∈ Ω, there exists a unique analytic function f(z) in Ω, normalized by the condition f(z0) = 0, f'(z0) > 0, such that f(z) defines a one-to-one mapping of Ω onto the disk |w| < 1.

Our statement of this theorem is that uniqueness is specified by a point correspondence and an orientation. This is equivalent to the preceding statement: the point correspondence specifies the mapping of the point that maps into the origin of the unit circle f(z0) = 0. The statement that f'(z0) > 0 is equivalent to fixing the orientation of the unit disk, since it specifies that a (positive) scaling only, and no rotation, occur at this point. Other orientations of the mapping can be generated by multiplication of f(z) by e^a.

Symm Algorithm for Conformal Mapping

Symm has described an integral equation method for computing the conformal mapping of a given simply connected domain onto the interior of the unit circle. This method performs well for a domain described by a large number of (polygonal) vertices. It is based on the observation that a solution for conformally mapping a given simply connected domain D with boundary L, in the z plane, onto the unit disk |w| < 1, in the w plane, in such a way that a particular point z0 ∈ D goes into the center w = 0, is provided (up to arbitrary rotation) by:
\[ w(z) = \exp[\log(z - z_0) + \gamma(z, z_0)] \quad (14) \]

where \( \gamma = g + ih \) and \( g \) satisfies the boundary value problem

\[
\begin{align*}
\nabla^2 g &= 0 & \text{for} & \ z \in D \\
g &= -\log|z - z_0| & \text{for} & \ z \in \mathbb{L} 
\end{align*}
\] 

(15) (16)

This identity can be understood by observing that \( w(z_0) = 0 \).

On the boundary \( (z \in \mathbb{L}) \), \( w(z) = e^{i\omega(z - z_0)} \), i.e., \( |w(z)| = 1 \), so the boundary \( \mathbb{L} \) is mapped to the boundary of the unit circle.

For interior points \( z \in D \), we have \( w(z) < 1 \), since \( |w(z)| = 1 \) on the boundary, and \( w(z) \) must take its maximum in this region on the boundary, by the maximum principle [46].

Thus, Symm replaces the problem of finding \( w(z) \) to the problem of finding an analytic function \( \gamma(z) = \log(w) - \log(z - z_0) \); essentially, the problem is transformed from the original domain to a complex logarithmic representation of it.

Symm then goes on to outline methods of finding \( \gamma \), by means of setting up a set of Fredholm integral equations, which are numerically solved by standard methods.

One difficulty in implementing this work [46], not emphasized in it, is that line integrals of the argument of an analytic function are evaluated in this algorithm. Direct (i.e., naive) numerical implementation of the equations found in this reference is not correct; careful attention must be paid to ensuring that a continuous branch of the argument is used when a line integral of the argument of a complex function is performed.

**Conformal Mapping of the Retinal Image to a Flattened Section of the Cortex**

The problem of conformally mapping the retina to V-1, for example, can be regarded as a problem of mapping the half-unit sphere (an approximation to the retina) conformally to a flattened model of the surface of visual cortex. For flattening of cortex, we use an algorithm developed in our lab which achieves an average error of roughly 5\% in mapping a three-dimensional representation of visual cortex into two-dimensional form. The mapping problem is solved in our case by decomposing it into three steps:

1. Mapping the quarter-unit sphere (half of a retina) conformally to the half-unit disk.
2. Mapping the half-unit disk conformally to the unit disk, where the point in the half-disk that is mapped to the origin of the target disk is a parameter of this mapping, to be chosen dependent on the specific data.
3. Mapping the unit disk conformally to an arbitrary two-dimensional domain, the flattened brain data.

**TOPOGRAPHICAL MAPPING IN PRIMATE VISUAL CORTEX**

**Step 1:** We use the following stereographic projection (which provides a conformal mapping of the quarter-unit sphere to the half-unit disk):

\[
(\theta, \phi) \rightarrow \left( \frac{\cos \phi \sin \theta}{1 - \cos \phi \cos \theta}, \frac{\sin \phi}{1 - \cos \phi \cos \theta} \right) 
\]

(17)

where \( \theta \) and \( \phi \) are the corresponding eccentricity and azimuth of the unit sphere, and the output represents Cartesian coordinates in two dimensions.

**Step 2:** The following transformation \( T \) is a conformal complex transformation that maps the half-unit disk to the unit disk, where a point \( z_0 \) internal to the half-unit disk is mapped to the origin of the target unit disk, with a rotation of \( \alpha \) radians: \( T = H \cdot G \cdot F \), where

\[
F = \frac{z - i}{z + i}, \quad G = z^2H = \exp \left[ i\alpha \frac{(z - z_0)}{z - z_0} \right] \quad (18)
\]

**Step 3:** We use Symm's algorithm to conformally map a given simply connected domain onto the interior of the unit circle. The results of this approximation have been checked against direct microelectrode measurements of the map function of visual cortex [51] with excellent agreement.

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TOPOGRAPHICAL MAPPING IN PRIMATE VISUAL CORTEX

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