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CALIFORNIA INST OF TECH PASADENA DIV OF BIOLOGY
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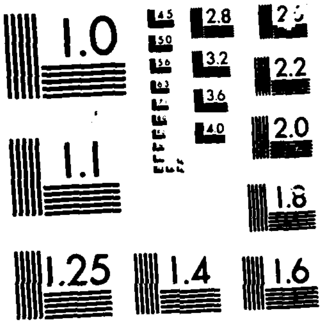

MICROCOPY RESOLUTION TEST CHART

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Technical Memorandum

Contract #N 00014-85-K-0068

Work Unit: NR 196-083

Office of Naval Research

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20. ABSTRACT (Continue on reverse side if necessary and identify by block number)

We have used a combination of physiological and anatomical approaches to elucidate the functional organization of visual cortex in the macaque monkey. One project was a single cell analysis of texture vision, using texture patterns of the type developed by Julesz for human psychophysical studies. Many cells tested in area V2 responded to static or moving texture gradients in ways which were not predictable on the basis of responses to individual texture elements and which correlated with the preattentive discriminability of these texture patterns to human observers.
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A second project involved the development of a computerized technique for generating two-dimensional maps of cerebral cortex. An algorithm based on simulated annealing procedures was used to construct a complete map of primary visual cortex, thereby demonstrating its suitability for dealing with anatomical data from highly convoluted regions of cortex.

A third project involved the use of voltage-sensitive dyes to monitor activity patterns in visual cortex. This technique offers great promise for analyzing the organization of large neural ensembles with high spatial and temporal resolution. Keywords:

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Principal Investigator: David C. Van Essen

Division of Biology

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The research supported by this contract has been aimed at elucidating the functional organization of mammalian visual cortex. We use a combination of physiological and anatomical techniques to identify different visual areas and to characterize how information processed within each area and distributed among areas. There have been three major components to our overall effort during the past year. The first project is an analysis of texture vision as assayed by monitoring the activity of single neurons in areas V1 and V2 of the macaque in response to texture patterns of the type developed by Julesz and collaborators. The second project is the development of a computerized technique to generate two-dimensional maps of cerebral cortex, for use in determining the functional organization of different visual areas. The third project is the application of an optical technique for monitoring the physiological activity of visual cortex with high spatial and temporal resolution. Substantial progress has been made on each of these projects, as described in the sections below.

Physiology of Texture Vision

Our sense of vision involves simultaneous operation of two distinct components: an attentive system that provides detailed scrutiny of one object at a time in the visual field, and a pre-attentive system that continuously scans the entire visual field in parallel and selects items of particular salience for further scrutiny by the attentive system (Julesz, 1984). The pre-attentive system appears to specialize in providing information about visual texture, i.e., the arrangement of features that provide surfaces with their characteristic appearance. One of the keys to Julesz' recent approach has been to simpify the analysis of texture vision by concentrating on patterns that consist of an array of discrete, overlapping elements, called textons. In essence, this approach has allowed a detailed dissection of which characteristics of a pattern are important in texture discrimination and which characteristics are irrelevant.

Our general aim has been to identify and characterize cells in monkey visual cortex that may be involved in mediating the perception of texture. We have used the texture patterns devised by Julesz and have used stimulation paradigms that are based on the concepts that have emerged from his psychophysical studies. In the preliminary experiments carried out to date, we concentrated on two paradigms. The first was directed at attention-related mechanisms for detecting the presence of local texture differences (texture gradients). The second was directed at the analysis of "texture contours" whose presence is signaled by borders across which there is a texture gradient. This project has been carried out by Ted DeYoe, Jim Knierim, Dov Sagi, Bela Julesz, and myself.

Our experimental preparation is the anesthetized, paralyzed macaque monkey. We made extracellular recordings from single nerve cells in areas V1 and V2, using recording procedures standard for this laboratory (Manusell and Van Essen, 1983). Visual stimuli were generated on a Hewlett-Packard CRT monitor using a software and hardware system provided on loan by Bela Julesz. Data acquisition and analysis was carried out on our existing PDP 11/34 computer.

Texture Gradients using Static Center-Surround Patterns

The salience of any given texton to the pre-attentive system depends critically on the context in which it is presented, i.e., its relationship to nearby textons. A texton of any sort is immediately obvious if it is presented in complete isolation or if it is presented within a field of textons having different attributes, such as color or orientation. If, however, it is embedded within a field of identical textons, it does not stand out.

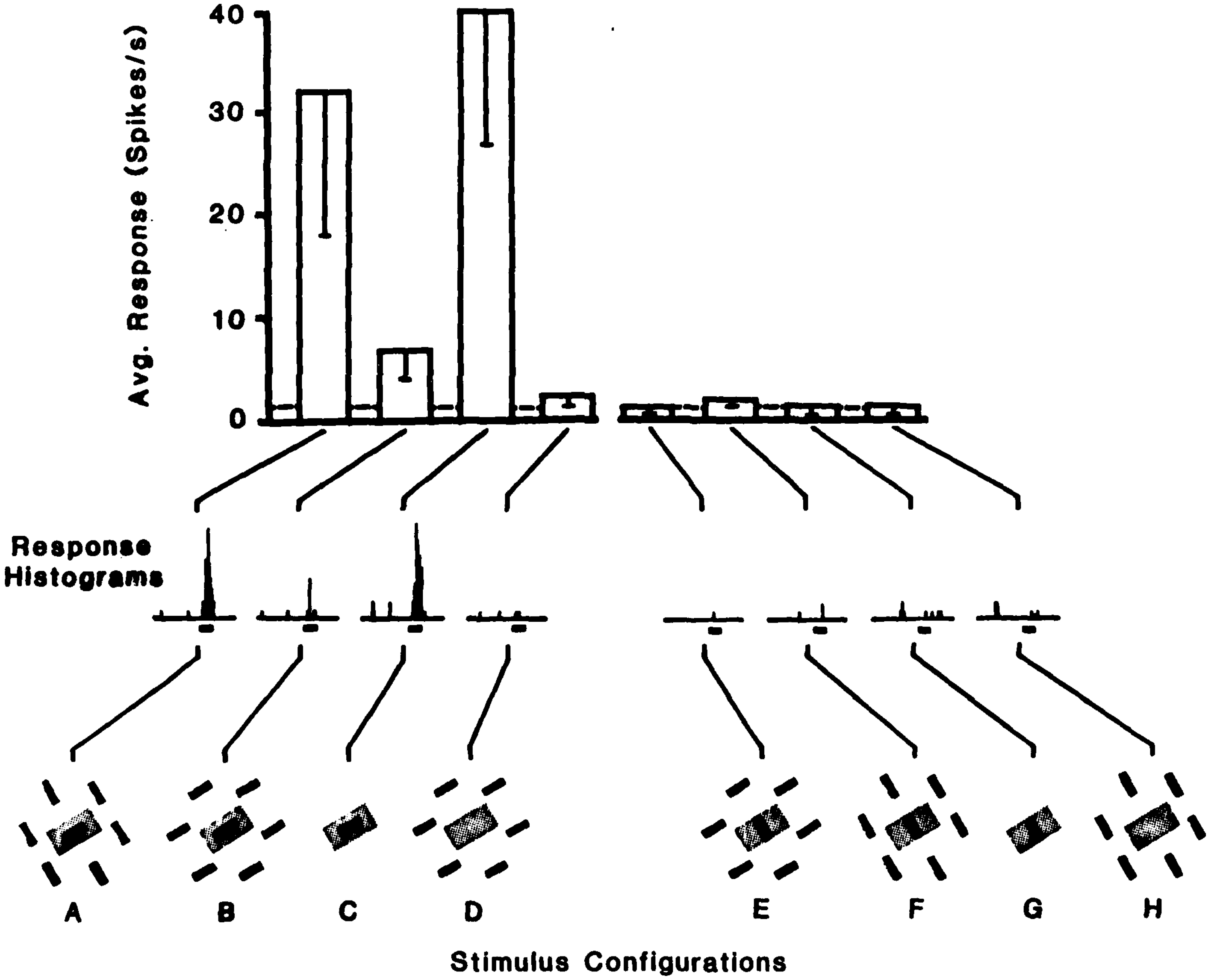
We tested for neural correlates of these psychophysical observations using patterns consisting of a central region lying, within the receptive field of the neuron under study, and a larger surround region lying completely outside the neuron's "classical" receptive field. Textons consisted of small elongated bars of light, and each texton was placed either at the cell's preferred orientation or perpendicular to it. All possible combinations of center and surround patterns were tested on each cell, and results from one particularly interesting cell are illustrated in Figure 1. The bottom row shows the eight different stimulus patterns; the middle row shows peristimulus response histograms determined from 10 pseudorandomly interleaved repetitions of each stimulus; and the top row shows bar histograms of the average response rate. The cell responded well to stimulus C, a single bar of the optimal orientation and placed within the receptive field. It also responded well to stimulus A, consisting of the same central bar surrounded by bars of the orthogonal orientation. In contrast, there was only a weak response to stimulus B, in which the central stimulus was surrounded by bars of identical orientation. The remaining portion of the figure illustrates several control patterns, demonstrating that the cell did not fire, for example, to the surround when presented without the central bar. In short, the response of this cell mimic several key features of human texture vision: the response is large if the stimulus within the receptive field is salient to the pre-attentive system, either because of a texture gradient (stimulus A) or a combined texture and luminance gradient (stimulus C), whereas the response is small if the central bar is not pre-attentively salient, because there is no texture gradient (stimulus B).

Thus far we have obtained good recording data from 37 cells in V1 and V2 when using this paradigm. A pronounced suppressive effect of the stimulus surrounded was found for at least one stimulus configuration in 16 of 22 V2 cells and 8 of 15 V1 cells. For some cells the surround effect was non-specific. More interestingly, for 7 cells in V2 and 2 cells in V1 the interaction was dependent on both center and surround: there was substantial suppression for matching orientations but little or none for contrasting orientations. Thus, the responses of such cells correlate with the perceptual salience of the center texture element.

Responses to Moving Texture Contours

A texture pattern that moves relative to its background suddenly stands out, a fact that works to the disadvantage of prey and to the advantage of predators. We have

FIGURE 1


Avg. Response (Spikes/s)
40
30
20
10
0
Response
Histograms
A
B
C
D
E
F
G
H
Stimulus Configurations

analyzed the responses of cell in V1 and V2 to moving texture patterns of the type illustrated in the upper part of Figure 2. A "texture bar," consisting of a vertical column of short horizontally oriented textons, is embedded in a field of vertically oriented textons (Frame 1). On each successive frame, the texture bar moves one column to the right. To a human observer, this sequence appears as a bar moving steadily to the right ("apparent motion"), with a smoothness that depends on the spatial separation of columns and the temporal separation of frames.

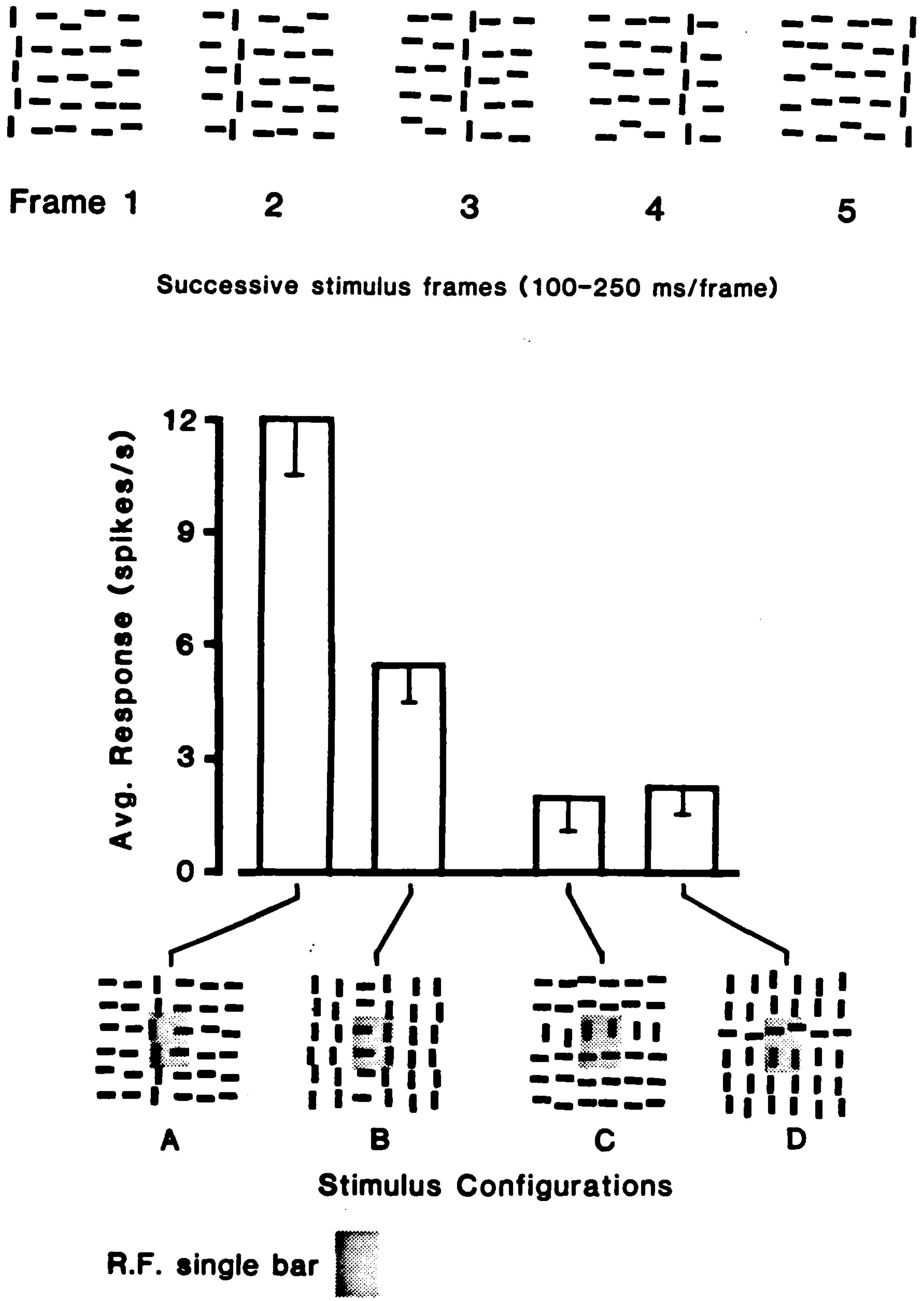
The lower portion of Figure 2 illustrates the responses of a cell in area V2 to the apparent motion of a texture bar. The cell responded best to rightward motion of a texture bar consisting of vertical textons, but there was also a good response when the orientation of the textons in the texture bar and surround were reversed. However, there was amuch weaker response to downward motion of a horizontal texture bar, irrespective of texton orientation. Thus, the responses of this cell were determined mainly be the configuration of the texture bar, rather than the composition of the individual texture elements.

In more recent experiments, we have obtained similar results using patterns consisting of textons at oblique orientations to the texture bar, thereby eliminating any subtle luminance cues that might otherwise be used for discriminating apparent motion. These and other controls have convinced us that the responses of many cells in V2 (26 of 40 tested) encode useful information about moving texture patterns. In contrast, only 2 of 16 cells in V1 that were tested in a comparable fashion responded to the motion of the texture bar rather than the texture elements. Much more experimentation will be necessary, however, to fully clarify the nature of this information encoding in V2 and V2 to establish its relevance to texture perception.

Computerized Mapping

The convolutions of cerebral cortex in many species imposes major difficulties in carrying out precise analyses of the functional organization of different visual areas.

Oriented Contour Stimulus

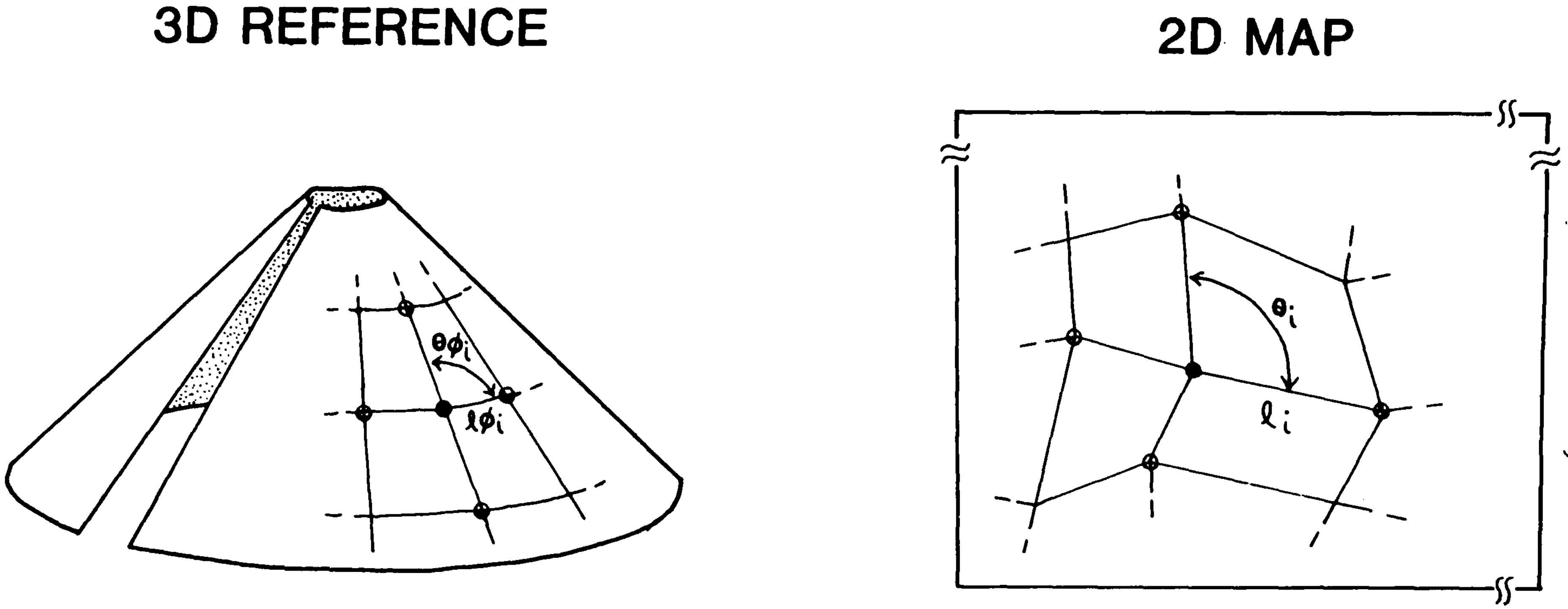


For about a decade we have been able to circumvent many of these difficulties by displaying our experimental findings on two-dimensional maps of the cortical surface (Van Essen and Zeki, 1978; Van Essen and Maunsell, 1980). Our original procedure for generating these maps was an entirely manual method, and it had the disadvantages of being difficult to learn, tedious to implement, and limited in overall accuracy. It has long been one of our goals to develop a completely computerized procedure for constructing two-dimensional maps, and George Carman in my lab has now succeeded in this endeavor.

The initial database for the computerized mapping procedure comes from the contours of cortical layer 4 (the middle layer) from histological sections taken at closely spaced intervals (0.5 mm) through the hemisphere. These contours are digitized on a graphics tablet and stored in disk memory on our Masscomp 535 computer. Each of these contours is smoothed and sampled at intervals of 0.5 mm. The resultant set of points form a three-dimensional reference surface used in the mapping procedure. (Each point has an x,y coordinate from its location within the section and a z coordinate from the level of the particular section to which it belongs.) For each point on this reference surface, a corresponding point is created on a two-dimensional mapping surface. The initial configuration of the two-dimensional surface is not crucial: the algorithm succeeds when all points on the lattice are started at a singularity, so that topologically correct ordering of points can be restored even when initially absent from the map.

The heart of the mapping algorithm is an iterative procedure that gradually transforms the 2-D map into its proper configuration. This is achieved using a metric of local distortion, called the energy, which reflects the deviation of the local geometry on the 2-D map from the desired geometry present in the 3-D surface. The basic strategy is to randomly move the points on the map so as to minimize the deviations of lengths and angles on the 2-D map from the corresponding distances and angles on the 3-D reference surface. This comparison between actual and desired local relationship for one lattice point and its four neighbors is illustrated in Figure 3. The sum of energies for all points

FIGURE 3



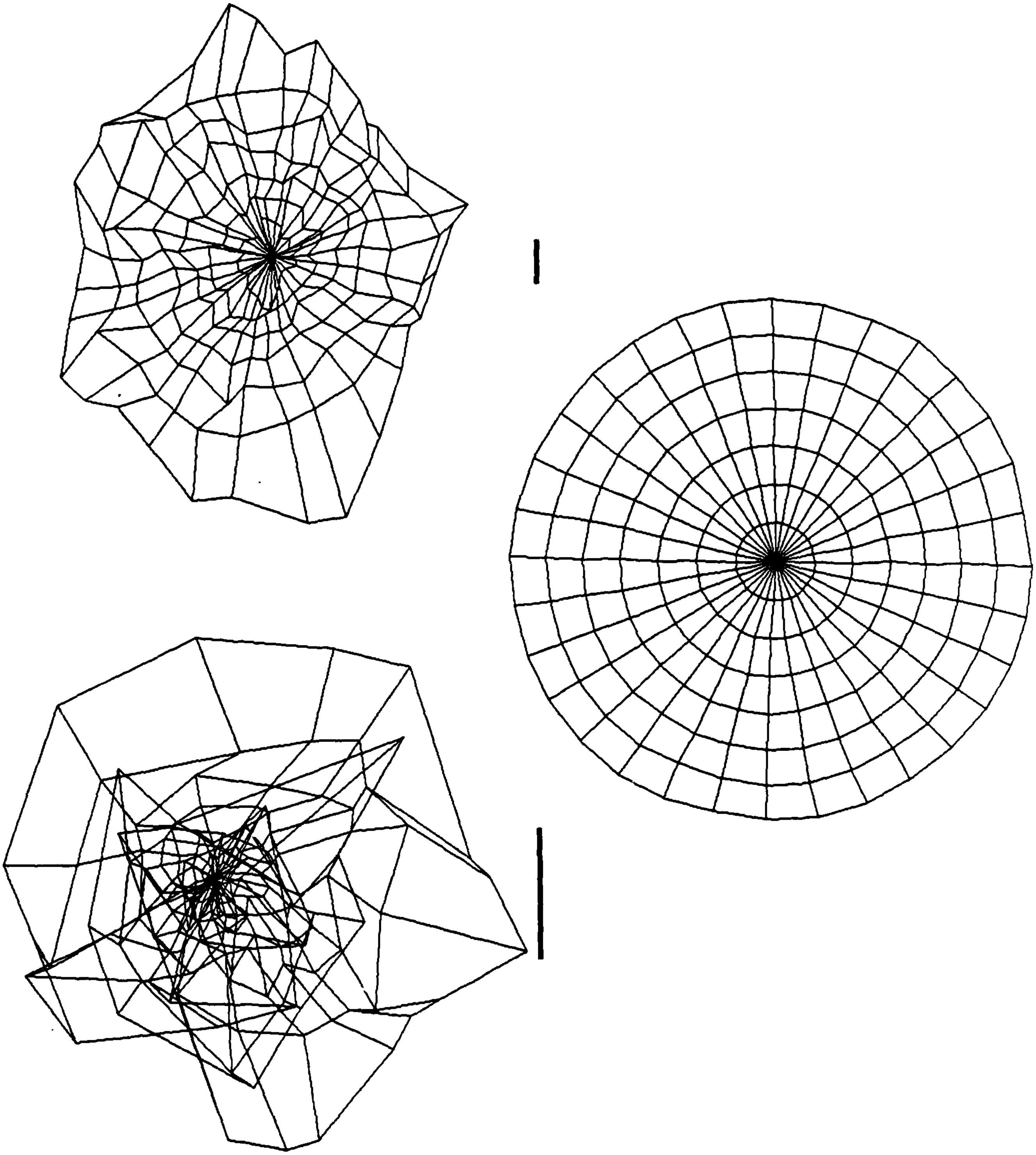
yields a global energy, which must be minimized in order to generate an optimal 2-D map of the reference surface.

To find this global energy minimum, we subject the 2-D map to stimulated annealing (Kirkpatrick et al., 1983). In our implementation of this iterative algorithm, a point is chosen randomly from the lattice, and a small random displacement of that point is attempted within the plane of the map. Displacements resulting in a more accurate local geometry (decrease in energy) are always accepted, while those resulting in a less accurate local geometry (increase in energy) are accepted with a probability dependent upon a control parameter termed the "temperature." Initially, the temperature is set high in order to allow positions of points of the map to become randomized. The temperature is then gradually reduced over successive iterations, allowing the points to approach their optimal local geometries and resulting in the emergence of an optimal global conformation of the map.

We initially developed and tested this algorithm by generated 2-D maps of mathematically precise 3-D geometrical surfaces such as cones and hemispheres. For example, Fig. 4 shows three stages in the generation of an unfolded map of a hemisphere. The lattice on the top left is at an early stage of annealing, and parts of the map are not even in a topologically correct order. The lattice on the top right is topologically correct, but still has considerable local disorder. Finally, the lattice on the bottom represents a map essentially at its global energy minimum, achieved after ca. 258 iterations and 1.5 hours of computational time.

The current mapping algorithm appears to be fairly robust, in that it can generate accurate 2-D maps from a variety of 3-D surfaces, and it is flexible with regard to the starting configuration of the lattice and the precise sequence of temperature changes during annealing. Reaching this level of performance was not an easy feat, however. There are many subtleties to the algorithm that must be recognized and respected, and experience has revealed that even minor flaws can lead to highly aberrant maps as the final product. Thus, the testing of the algorithm on mathematically well-defined surfaces was crucial to its eventual success.

FIGURE 4



We next applied this approach to real neuroanatomical data, starting with a map of striate cortex (V1). We used contours from the same hemisphere that had previously been mapped by LeVay et al. (1985) using our standard manual procedure. Figure 5 shows an intermediate stage (left) in the annealing of this map, and the final, minimum-energy stage (right), reached after 250 iterations and 24 hours of computation. In this display the continuous lines represent the contours associated with individual sections through the cortex; the connections between lattice points on adjacent sections are omitted for clarity, even though they were equally important in generating the map.

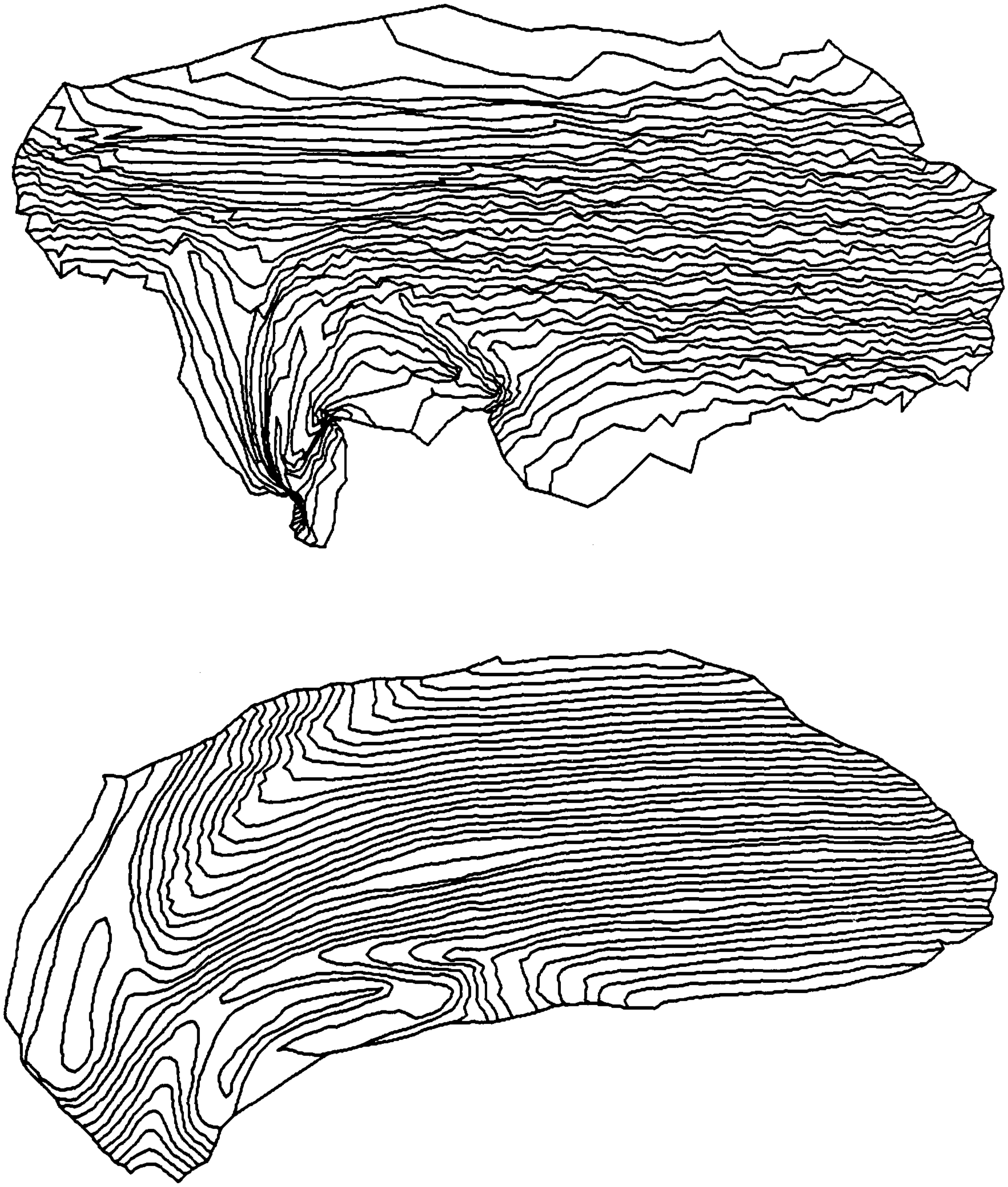
The computerized 2-D map is similar to our earlier manual version in its general configuration, but it has several important advantages. Both have some residual distortions that cannot be removed because of the intrinsic curvature of the cortex (Van Essen and Maunsell, 1980). However, the distortions on the computerized map are smaller; moreover, their magnitude can be calculated and displayed precisely. The computerized procedure is more reliable, does not depend on subjective judgements, and frees the neuroanatomist from having to learn a tricky and tedious procedure.

There remains a considerable amount of work left before all stages of computerized map-making are refined and completely automated. Of particular importance is the procedure for linking corresponding points on adjacent sections, in order to create a completely connected lattic for the 3-D reference surface. We are currently exploring several possible options for most efficiently and reliably executing this task. Ultimately, we plan to have a complete package of algorithms that will be made available to interested users in the neuroscience community.

Optical Monitoring of Brain Activity

Recently, a promising new technique has been developed for monitoring brain activity using an optical technique rather than standard electrical recording methods. This approach relies on the use of special organic dyes which, when applied to the brain, change their absorbance or fluorescence in proportion to the degree of local neural

FIGURE 5



activity (Orbach and Cohen, 1983; Grinvald, 1985). By mounting an array of photodetectors onto a microscope viewing the brain surface, it is possible to monitor the level of neural activity simultaneously at each of 100 different locations. This technique offers a combination of high temporal and spatial resolution that is unavailable with any other recording technique.

During the past year, Dr. Harry Orbach has been involved in setting up the experimental apparatus for this project and carrying out pilot studies. This has entailed extensive design and assembly of the various hardware and software components that are needed for the specific projects we will be undertaking, with the hardware being constructed by engineer Herb Adams and the software developed by Dave Bilitch. The major system components include: 1) a rat head-holding device which keeps the animal securely and stably positioned, and which is compact enough to fit on a microscope stage; 2) a transparent chamber for viewing the exposed cortical surface while minimzing cortical pulsations; 3) a microdrive for advancing electrodes into cortex to allow simultaneous optical and electrical measurements; 4) modifications of a Zeiss University microscope to allow insertion of the animal under the objective and positioning of the photodector array on a vertical phototube; 5) linkage of 100 photodetectors through individual low-noise amplifiers to the multiplex A/D port of the Masscomp; 6) development of software for 100-channel data acquisition, analysis and graphical display; 7) construction of a projection system for presenting simple patterns (bars and edges of light) for use as visual stimuli; and 8) programming of an IRIS video graphics system for presentation of more comlex stimulus patterns (e.g., oriented gratings).

These various developmental stages are now largely completed, and we have been able to carry out preliminary experiments. Most experiments to date have been done on rat visual cortex. One major objective has been to obtain simultaneous optical and electrical recordings in response to restricted visual stimuli. We feel that such an analysis will provide crucial but currently unavailable information concerning the relationship between electrically and optically mediated events in the cortex. To date, we have gotten good electircal responses in some experiments and clear optical signals in other experiments; for a variety of technical reasons the combined experiment has not yet worked, but we expect it to succeed soon.

Another project already underway is to search for new dyes that give large optical signals, as the low signal-to-noise is a crucial limiting factor in most CNS experiments. We are planning to try a variety of dyes, some fast-acting for good temporal resolution, but also some that integrate over longer time periods, thereby trading temporal resolution for the prospect of a stronger signal.

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