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**Spectral Density Maps of Receptive Fields
in the
Rat's Somatosensory Cortex**

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Abstract

To extend findings from visual neurophysiology we plotted responses for 48 locations in the somatosensory "barrel cortex" of the rat to spatial and temporal frequency stimulation of their vibrissae. The recordings obtained from bursts of spikes were plotted as response manifolds resembling field potentials such as those recorded with small macroelectrodes. The burst manifolds were shown to be composed of those obtained from single spikes, demonstrating continuity between two levels of analysis (single spikes and bursts).

A computer simulation of our results showed that, according to the principles of signal processing, the somatosensory receptive fields can be readily described by Gabor-like functions much as in the visual system. Further, changes with respect to direction of whisker stimulation could be described in terms of spatiotemporal (vectorial?) shifts among these functions.

As late as the 1950's, the structure of memory storage and the brain processes leading to perception remained enigmatic. Thus Karl Lashley (1950) could exclaim that his lifelong search for an encoded memory trace had been in vain, and Gary Boring (1929) could indicate in his *History of Experimental Psychology* that little was to be gained, at this stage of knowledge, by psychologists studying brain function.

All this was dramatically changed when engineers, in the early 1960's, found ways to produce optical holograms using the mathematical formulation proposed by Dennis Gabor (1948). The mathematics of holography and physical properties of holograms provided a palpable instantiation of distributed memory and how percepts (images) could be retrieved from such a distributed store. Engineers, (e.g. Van Heerden, 1963) psychophysicists, (e.g. Julesz and Pennington, 1965); and neuroscientists, (e.g. Pribram, 1966; and Pollen, Lee and Taylor, 1971) saw the relevance of holography to the hitherto intractable issues of brain function in memory and perception (Barrett, 1969; Campbell & Robson, 1968; and Pribram, Nuwer and Barron, 1974).

However, this early promise failed, for a variety of reasons, to take hold in the scientific community. The fact that neurophysiologically the holographic spread function is limited to single, albeit overlapping, receptive fields (patches) was not recognized by psychophysicists who, therefore, spent considerable energy in disproving globally conceived distributed functions. However, engineers, e.g. Bracewell (see review, 1969), soon showed that such patch holography could and did produce correlated three-dimensional images when inverse transformed, a technique that became the basis of optical image processing in tomography. The application of this principle to the receptive field structure (Robson 1975) overcame the psychophysical problem.

Further, it was unclear just how the principles involved in holography related to ordinary measures of brain physiology. For instance, the brain waves recorded with scalp electrodes are too slow to carry the required amount of information. Also, there seemed to be little evidence that the quadrature relation basic to performing a Fourier holographic transform could be found in the receptive field properties of the cerebral cortex. Finally, there was considerable confusion regarding just what needed to be encoded to provide a neural holographic process. These objections have, to a large measure, been met. The nanocircuitry of neural microtubules provides an adequately high frequency wave form for microprocessing in synaptodendritic receptive fields (e.g. Hammeroff, 1987). Quadrature has been shown in receptive fields within columns of the visual cortex (Pollen and Ronner, 1980). And, encoding of coefficients of intersections among waves, not of waves per se, was shown critical to the process (Pribram, 1991).

Despite this evidence, Churchland (1986), reflecting the received opinion of the neuroscience community, noted that: "the brain is like a hologram inasmuch as information appears to be distributed over a collection of neurons. However, beyond that, the holographic idea did not really manage to explain storage and retrieval phenomena. Although significant effort went into developing the analogy (see, for example, Longuet-Higgins, 1966) it did not flower into a creditable account of the processes in virtue of which data are stored, retrieved, forgotten, and so forth. Nor does the mathematics of the hologram appear to unlock the door to the mathematics of neural ensembles. The metaphor did, nonetheless, inspire research in parallel modelling of brain function" (pp. 407-408). In the same vein, Arbib (1969) states: "... we note that the Cambridge school of psychophysics (see Campbell, 1974 for an early review of their work) has psychophysical data showing that the visual cortex has cells that respond not so much to edges as to bars of a particular width or gratings of a certain spatial frequency. The cells of the visual cortex tuned for spatial frequency can be seen as falling into different channels depending on their spatial tuning. This might seem to support the contention that the brain extracts a spatial Fourier transform of the visual image, and then uses this for holographic storage or for position-independent recognition (Pribram, 1971). However, there is no evidence that the neural system has either the fine discrimination of spatial frequencies or the preservation of spatial phase information for such Fourier transformations to be computed with sufficient accuracy to be useful" (p. 134-135).

This view has also made its way into the popular literature on the subject. For example, Crick (1994) states "This analogy between the brain and a hologram has often been enthusiastically embraced by those who know rather little about either subject. It is almost certainly unrewarding, for two reasons. A detailed mathematical analysis has shown that neural networks and holograms are mathematically distinct. More to the point, although neural networks are built from units that have some resemblance to real neurons,

there is no trace in the brain of the apparatus or processes required for holograms." (p185).

That such statements can be made in view of so much evidence to the contrary -- see, for example, the volumes by Devalois and Devalois (1988) and by Pribram (1991) -- shows that something basic is at odds between the received view and those who have provided the evidence for the alternate view. We believe that the failure of holographic principles to take hold in neurophysiology is due to what is held to be the cerebral processing medium: ensembles of neurons or overlapping (receptive) fields of synaptodendritic arborizations. The distinction is a subtle one and concerns the level or scale at which processing is conceived to take place. Ensembles of neurons operating as systems (the current nomenclature is "modules"), communicating via axons, indeed have an important role to play: for instance, in information retrieval as indicated by localized clinical disabilities. Nonetheless, within modules, processing relies on distributed architectures such as those used in neural network simulations. It is our contention that, at this level of processing, the ensembles consist, not of neurons, but of patches of synaptodendritic networks.

What is needed is a method for mapping the activity of the overlapping synaptodendritic receptive fields in such a way as to convince the scientific community that something like a holographic process is indeed operating at the synaptodendritic level. Kuffler (1953), provided us with a major breakthrough when he showed that he could map patches of the dendritic field of a retinal ganglion cell by recording from its axon in the optic nerve. Kuffler's is a simple technique for making receptive field maps, which is now standard in neurophysiology. By stimulating a receptor or a set of receptors in a variety of dimensions and using the density of unit responses recorded from axons, a map of the functional organization of the synaptodendritic receptive field of that axon can be obtained. (See e.g. reviews by Bekesy, 1967 and Connor and Johnson, 1992 for somesthesia; and by Enroth-Kugel and Robson, 1966; and Rodiek and Stone, 1965 for vision).

Experiments by Barlow (1986) and by Gilbert and Wiesel, (1990) have shown that sensory stimulation beyond the reach of a particular neuron's receptive field can, under certain conditions, change that neuron's axonal response. Synaptodendritic patches are thus subject to changes produced in a more extended field of potentials occurring in neighboring synaptodendritic fields.

What is seldom recognized is that the Kuffler technique maps relations among local field potentials occurring in such extended overlapping dendritic arbors. The axon(s) from which the records are being made, sample a limited patch of this extended domain of overlapping receptive fields. Recently, Varela (1993) called attention to this relationship by demonstrating the correlation between burst activity recorded from an axon and the local field potentials generated in the synaptodendritic receptive field of that axon.

The current study also aims to explore the relations among local field potentials by mapping receptive field organization using the Kuffler technique. The specific questions posed and answered in the affirmative are 1) whether this technique can map the spectral properties of synaptodendritic receptive field potentials, and 2) whether such maps of receptive fields in the somatosensory cortex show properties of patch (quantum) holography (that is, of Gabor elementary functions) similar to those recorded from the visual cortex.

Methods and Results

The rat somatosensory system was chosen for convenience and because the relation between whisker stimulation and central neural pathways has been extensively studied (see review by Gustafson and Felbain-Keramidas, 1977). Whiskers were stimulated by a set of rotating cylinders, each grooved with equally spaced steps, the step width and adjacent grooves subtending equal angles. Three cylinders were used with their steps measuring 30deg., 15 deg., and 7.5 deg., respectively. The cylinders were rotated at 8 different speeds, varying from 22.5 deg./sec. to 360 deg./sec. (The rotating cylinders were meant to mimic the drifting of gratings across the retinal receptors in vision.)

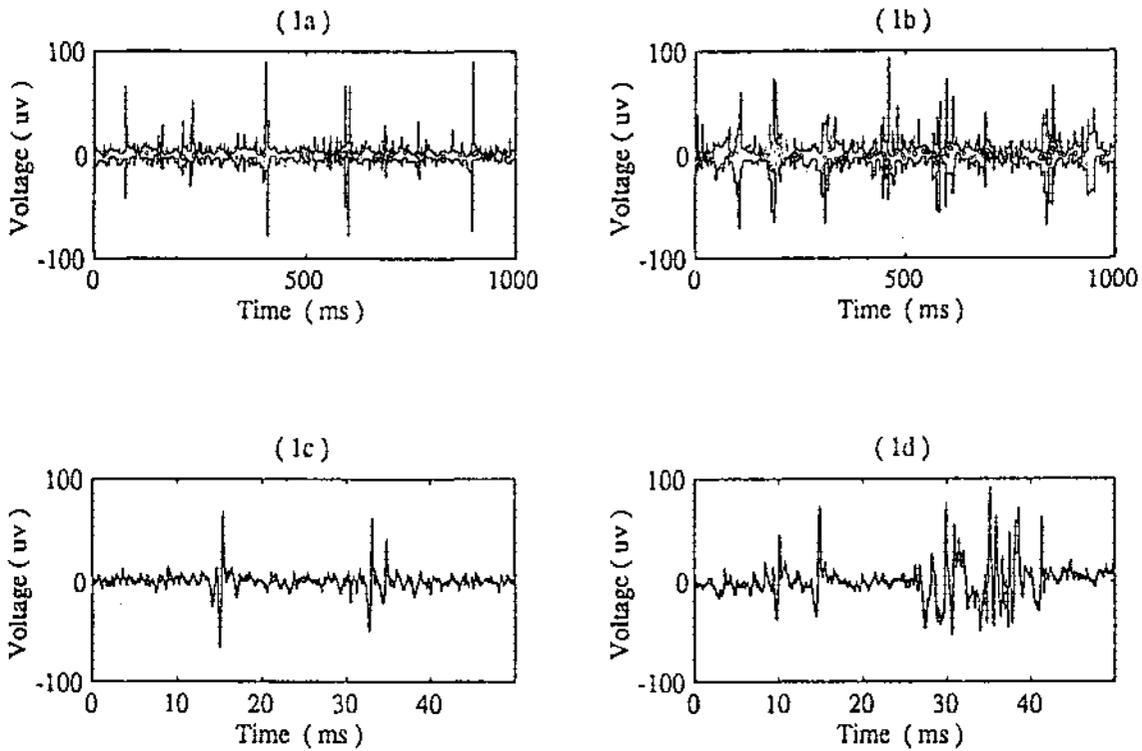
In most of our experiments an entire array of whiskers was subjected to contact with the rotating cylinders. This was done in order to bring the results of these somatosensory experiments into register with those performed in the visual system where an entire array of receptors is stimulated by the drifting grating.

Electrodes were teflon-coated stainless steel (Hare) ranging from 1-3 megohms impedance. Recordings were made from 48 locations using 23 different rats weighing 250-300 grams. Surgery was performed under pentobarbital anesthesia (50 mg/kg body weight, intra-peritoneally) supplemented with 0.05 cc atropine sulfate to inhibit excess respiratory tract accumulation of fluid. The rat was placed in a stereotaxic headholder (Kopf), and using a Zeiss surgical microscope, a small .25cm² round opening was made in the skull approximately 4 mm posterior and 4-5 mm lateral to bregma. An electrode was lowered slowly through the opening by means of a hydraulic micromanipulator until good responses were recorded, usually at a depth of 600-700 micra.

Records of raw data were obtained by means of an FET cathode follower which matched the impedance of the microelectrode to the input impedance of a Grass Model P5 preamplifier. The recorded signal was band limited between 300 and 3000 Hz and amplified with a gain of 20,000. One hundred seconds of continuous voltages were sampled at a rate of 32 KHZ and stored by a BRAINWAVE system onto a pc-486 computer. The raw data were then transferred for processing on a Silicon Graphics workstation. Approximately 1/3 to 1/2 gigabytes of data representing both single spikes and bursts of spikes were recorded during approximately one hour at each cortical location (Figures 1a-d).

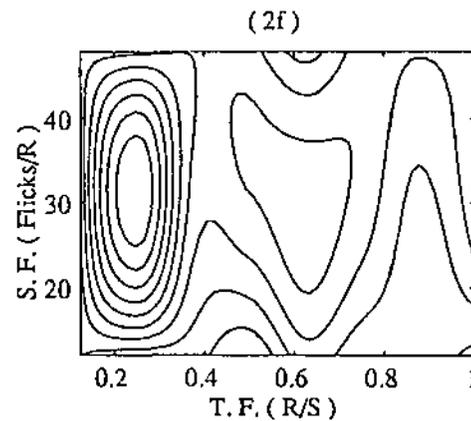
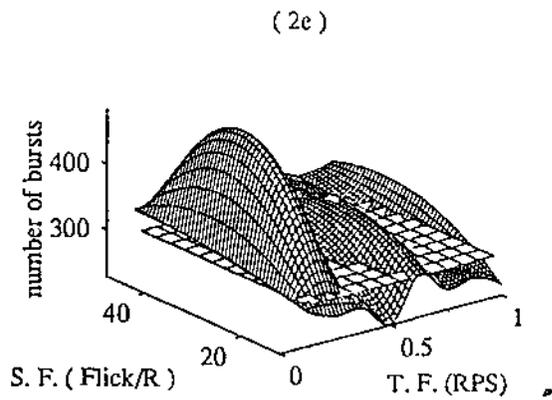
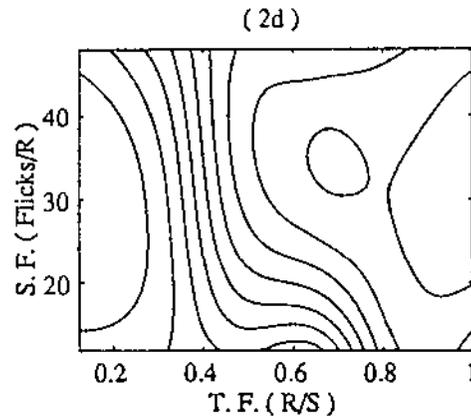
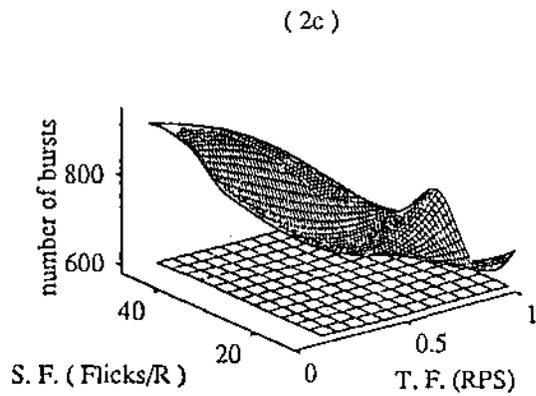
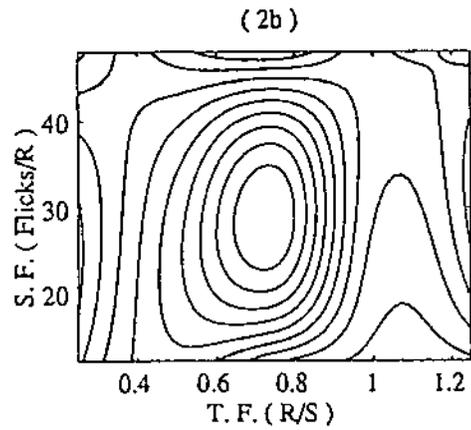
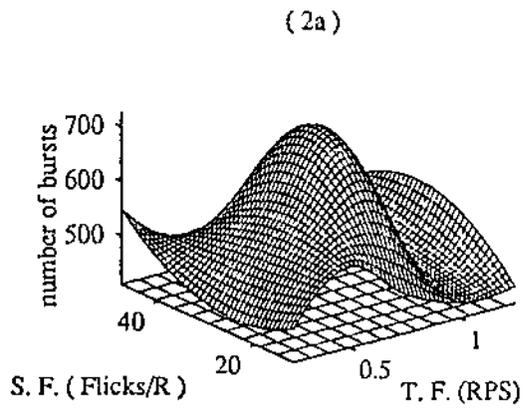
Our data include both single spikes and bursts of spikes. When single spikes were used, their origin from a single neuron was assumed by a sorting procedure using template matching (based upon spike amplitude and recovery slope). More often we used bursts of spikes, especially during whisker stimulation (Figures 1a and c). The reason for this is that our records show a great deal of superposition of spikes during such bursts (Figures 1b and d). Also, the number of bursts increases dramatically during stimulation. On the average, during a 100 second record, the baseline has about 350 single spikes, 152 bursts, and 26 superpositions, while the stimulation record has about 265 spikes, 218 bursts, and 307 superpositions. Note that the spikes are relatively independent during baseline (Figure 1a), but fire in bursts during stimulation (Figure 1b). Also, note that the burst rate during stimulation is not synchronized to whisker stimulation (figure 1b); actual whisker stimulation is occurring at about 3 stimulations (flicks) per second, while the burst rate is about 8 bursts per second. We believe that bursts of such overlapping multi-spike records reflect the activity of closely

related neurons and, therefore, are useful tools for mapping overlapping receptive field characteristics. One way to sample the synaptodendritic receptive field potential manifold is from spike train



Figures 1a-d. Figure 1a presents one second of a typical recording with no whisker stimulation (baseline). Figure 1b presents data from the same location during one second of whisker stimulation (spatial frequency = 24 grooves/rev.; temporal freq. = 0.125 rps). Figures 1c and 1d show individual units during 50msecs of baseline (1c) and the superposition of units during whisker stimulation.

recordings made with multi-electrode arrays. This approach was taken by Nicolelis et. al, (1993) to map the spatial distribution of responses in the ventral posterior medialis nucleus (VPM) of the thalamus to a vibromechanical stimulus of 1 Hz for 100 msec. to various sites on the mystacial pad of the rat. As they used only one frequency of stimulation, they described their receptive field configurations in classical spatial terms. Nonetheless, interesting from our standpoint is their finding that : "These quantitative representations revealed that receptive fields in the VPM are much larger and spatiotemporally complex than [heretofore] reported." In their study they used temporary local (lidocaine) anesthesia of a small area of the mystacial pad, and showed a dramatic reorganization of the receptive field manifold (the extent and relations among receptive fields) while the anesthesia was in effect. After the anesthetic wore off, the manifold returned to its original configuration.



Figures 2a-f. Examples of receptive field manifolds and their associated contour maps derived by an interpolation (spline) procedure from recorded whisker stimulation. The contour map was abstracted from the manifold by plotting contours in terms of equal numbers of bursts per recording interval (100secs.). Each figure shows baseline activity (no whisker stimulation) at a given electrode location as a gr-plane located in terms of number of bursts per 100 secs.

The stability of the receptive field manifold for a particular set of stimulus values makes it possible to map using a single electrode location as was done in our experiments. There are two ways to access a manifold. One can either move the electrode (or use an array of electrodes) and sample various portions of the manifold using a constant set of stimulus parameters, or one can keep the electrode in the same location and shift the manifold by systematically changing the stimulation parameters. Both methods require that the configuration of the manifold remain stable for any particular values tested. Evidence from the VPM study indicates that this requirement can reasonably be assumed to be met.

Axonal spike trains recorded from single electrodes can be attributed to three separable processes: 1) those due to the sensory input *per se*, 2) those that are intrinsic to the operations of the synaptodendritic field potentials and 3) those that reflect the output of the axon hillock. (Pribram et al 1981; Berger and Pribram, 1992). In our experiments, sensory influences are generated by the frequency (spectrum) of the stimulus as modulated by the spacings of the grooves on the cylinders and the speed with which the cylinders are rotated. The results thus provide maps of the number of bursts or spikes generated at each spectral location as determined by the spatial and temporal parameters of the sensory input. (Figures 2a-f). The activity above or below baseline which resulted from whisker stimulation is plotted as a manifold describing total number of bursts (or spikes) per 100 secs. of stimulation. Spatial frequencies are scaled in terms of grooves per revolution, while temporal frequencies are scaled in terms of revolutions per second. Thus, the density of stimulation of a whisker (or set of whiskers) is a function of both the spacings of the cylinder grooves and the speed with which the cylinder rotates. It is this density *per se* which composes the spectral domain.

In 27 experiments single whiskers were isolated and stimulated. Whiskers were identified according to accepted nomenclature as described by Simons (1978). The receptive field potential manifolds derived from such stimulations were irregular and poorly tuned to either spatial or temporal frequency. The intrinsic operations governing the configuration of the synaptodendritic field potentials are constrained by parameters such as the anatomical extent of each receptive field and the functional inhibitory and excitatory relationships among such fields. Our analyses were derived from both bursts of unit activity and from single units. We therefore sought to determine the relationships between the manifolds (field potential maps) derived from bursts and those derived from single units composing the bursts.

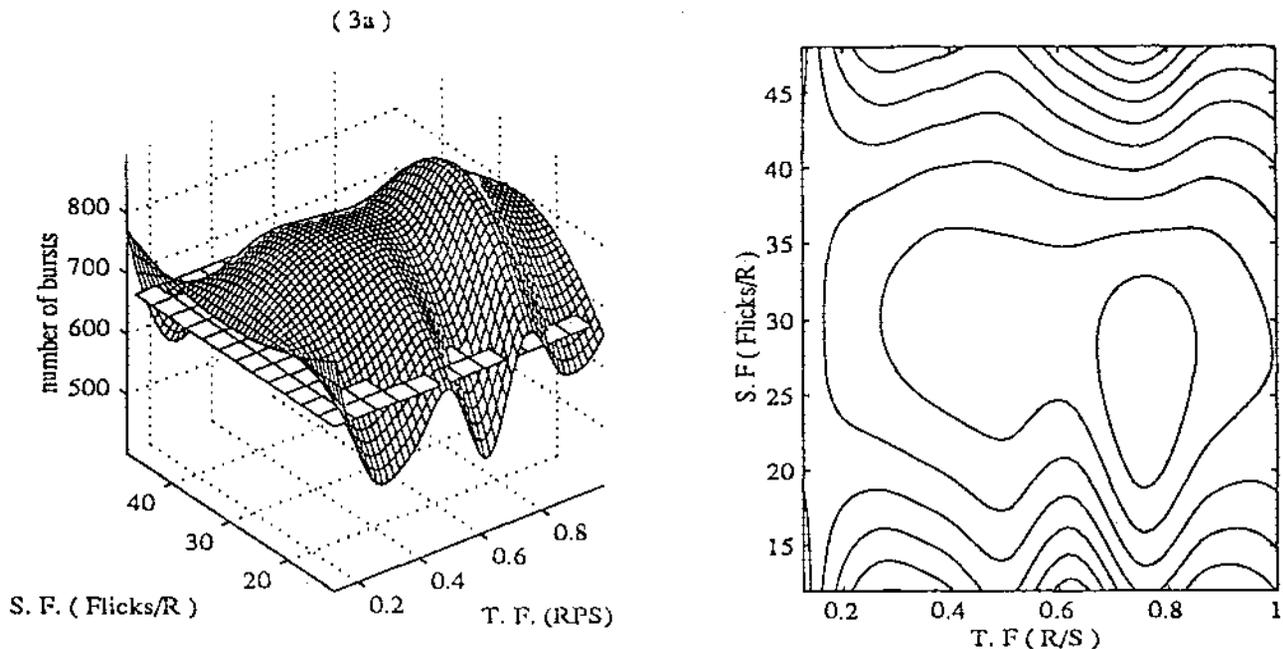
A manifold (Figure 3) constructed from bursts is shown to encompass those of the individual units composing the bursts: Figures 4a-d illustrate manifolds from the four single units which compose the bursts. These units were identified using a template constructed from a spike sorting procedure that discriminated the shape of the action potential (spike) on the basis of spike amplitude and recovery slope. The four single unit manifolds show a gradual change in shape corresponding to slight changes in location within the burst manifold: Figures 4a and b illustrate two peaks which progressively become combined into a single broad peak in the manifolds of Figures 4c and d. This demonstration of continuity between two levels of analysis (bursts and single units) strongly supports the view proposed by Pribram (1991) that extended networks of synaptodendritic fields serve as the processing medium, and therefore, single neurons are sampling from overlapping areas of the synaptodendritic

network.

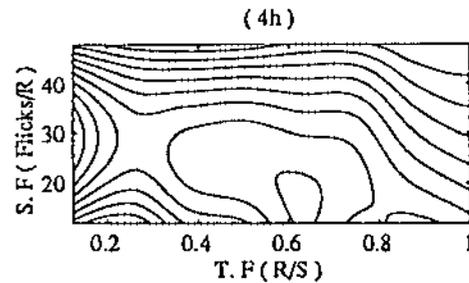
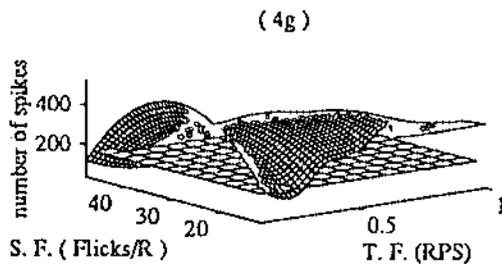
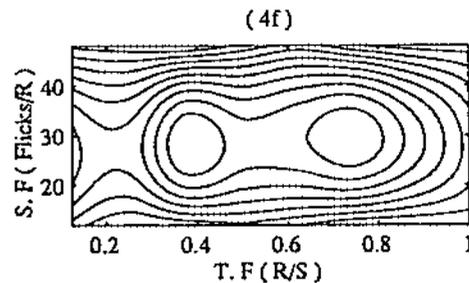
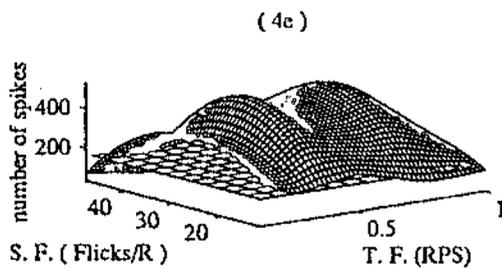
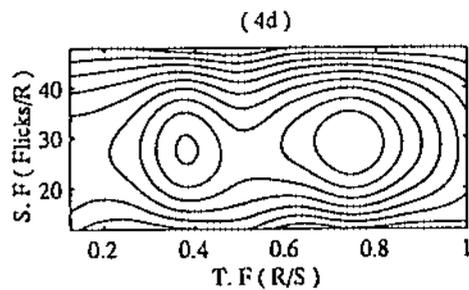
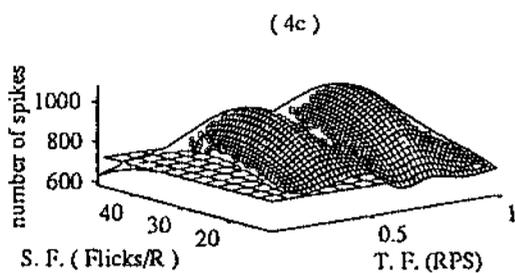
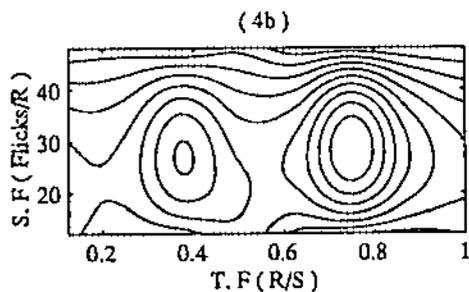
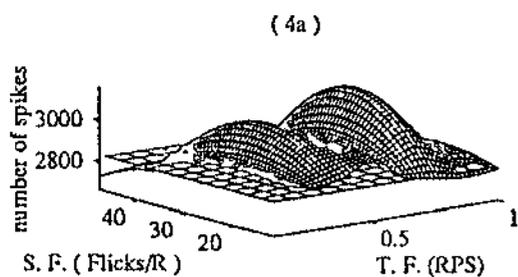
Simulation

According to signal processing theory, the general shape of a field potential manifold is the same for each combination of spatial and temporal frequencies (e.g. Fig. 5a). However, a central peak, reflecting the density of response for that spectral location in the manifold, will be shifted within the field according to the particular spatial and temporal stimulation values.

In order to discern whether, indeed, our data fit the requirements of signal processing theory, a simulation of the procedure was executed. The first stage of the simulation was to construct a putative truncated field potential manifold. Any extent of manifold is best described formally by a

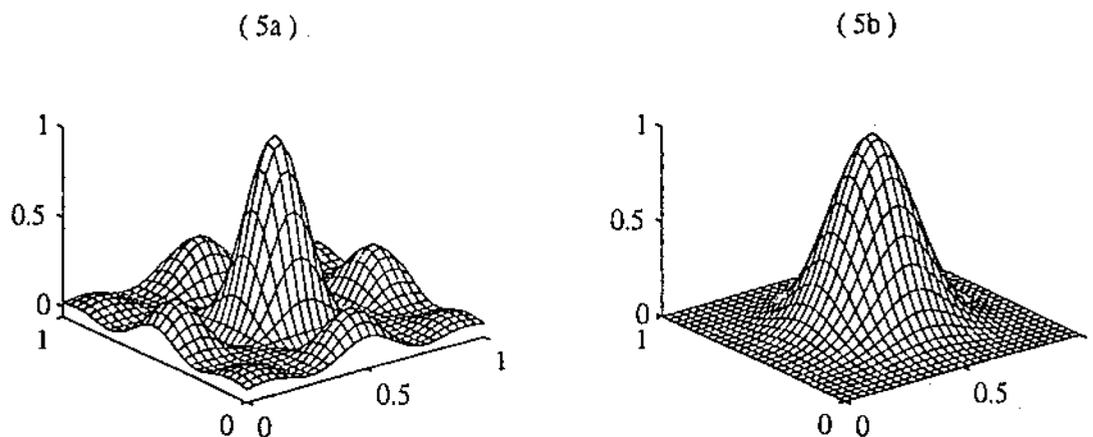


Figures 3a and b. Lateral (3a) view of an empirically derived burst manifold and its associated contour map (3b).



Figures 4a-h. These figures illustrate manifolds and their associated contour maps from four single units which compose the bursts used to construct the manifold in Figure 3.

truncated spectral function such as a constrained Fourier representation. Gabor (1946 p.431) defined such a function as follows: "Let us now tentatively adopt the view that both time and frequency are legitimate references for describing a signal and illustrate this . . . by taking them as orthogonal coordinates. Its frequency is exactly defined [only] while its epoch is entirely undefined. A sudden surge or 'delta function' (also called a 'unit impulse function') has a sharply defined epoch, but its energy is distributed over the whole frequency spectrum" Daugman (1990), McLennon (1993) and Pribram and Carlton (1986), have extended this illustration to include, in addition to the time parameter, two spatial dimensions.



Figures 5a and b. 5a presents a simulated manifold (mexican hat function) representing a spectral distribution induced by a single external stimulus (spatial and temporal frequency combination) across the cortical synaptodendritic field. 5b presents the second stage of the simulation as a probe consisting of a band-pass filter formed by a Gaussian (exponential) function.

We chose a rectangular window in the spatiotemporal domain to constrain the two dimensional sinusoidal signal. The reasons for this choice are: First, that the resulting spectrum generates a number of side lobes surrounding a central peak. In the visual system a number of side lobes has been observed at the lateral geniculate nucleus, (Hammond, 1972; Pribram, personal observation, 1974) and at the cortex (Pollen and Feldon 1979; Pollen and Pribram, personal observation 1972). The second reason for the choice of a rectangular window is that it reflects the spatial and temporal constraints on the extent of the distribution of the signal: the spatial constraint reflects the limits on spacings of the grooves on our cylinders; its temporal constraint, the limits on their rotation speed.

In addition, the rectangular window allows for maximum resolution of frequencies (see Zeevi and Daugman 1981; and Oppenheim and Shafer 1989 esp. Chapter 11, for review). The use of such a window generates a sinc function in the spectral domain.

In our simulations (Figure 6) each plot is a manifold of a spectral density function of a rectangular windowed continuous two-dimensional sinusoidal signal. When, in other experiments, only a single frequency of stimulation is used, a spatiotemporal "connection" matrix can be constructed from

recordings made with multiple electrode arrays to represent the data (Barcala, Nicoletis and Chapin 1993). Our version of such a matrix represents the variety of spatially and temporally constrained spectral data gathered in our experiments as a sinc function, centered at the frequency of each stimulation pair, i.e.

$$F(\omega_1, \omega_2) = A \text{sinc}(\omega_1 - \omega_{01}) \text{sinc}(\omega_2 - \omega_{02})$$

where A is a scaling constant, ω_1 and ω_2 are spatial and temporal frequencies of the spectrum, and ω_{01} and ω_{02} are the spatial and temporal frequencies of the stimulation. The function $\text{sinc}(\omega)$ is defined as :

$$\text{sinc}(\omega) = \frac{\sin(\omega)}{\omega}$$

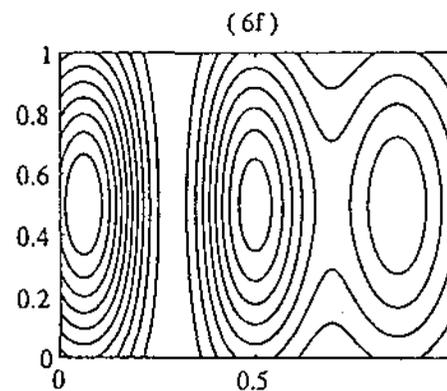
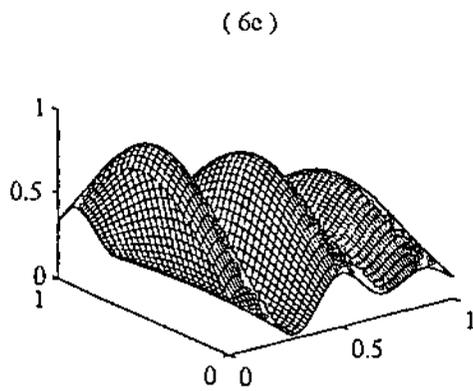
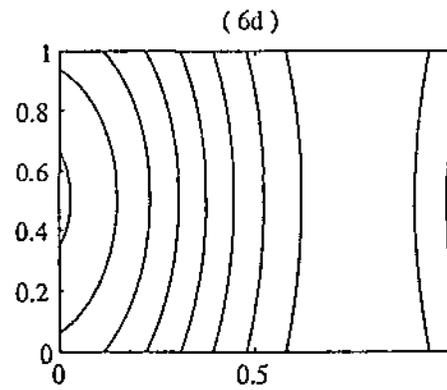
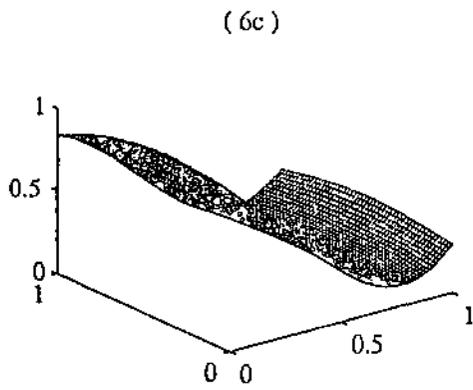
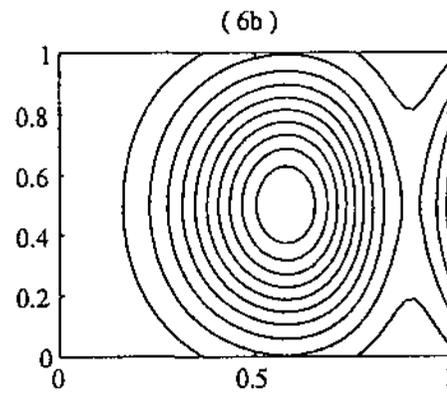
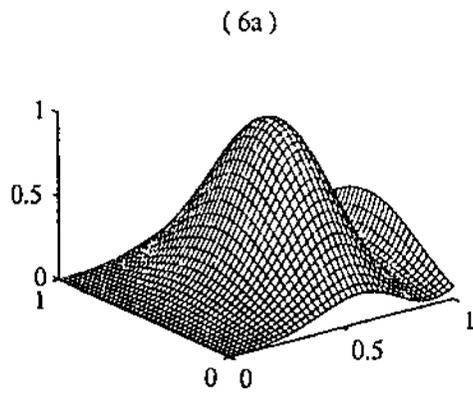
The second stage of the simulation uses as a probe, a Gaussian (exponential) function (Figure 5b). When this probe represents a single neuron it is limited by the spatial extent of the local field potentials fluctuating among that neuron's dendrites. When a burst manifold is modelled, the spatial constraint is assumed to portray a greater reach and is limited by the barrel (columnar) arrangement of the somatosensory cortex. Sampling is performed by the generative activity of the axon hillock, which, due to the upper and lower temporal limits of spike generation, functions as a bandpass filter which is the response of the sensory system. This filter is multiplied with the sinc function to yield a display of the manifold. Figures 6a-f depict manifolds and contours derived from these simulations. Note the close fit to the experimentally derived manifolds and contours shown in Figures 2a-f. A total of 48 manifolds were experimentally generated. Of those, three were essentially flat. Of the remaining 45, we simulated six; all but two of the remaining 39 have a shape that can be seen to be successfully simulatable with the technique described.

Discussion

The similarity of these manifolds obtained from recordings made from the somatosensory cortex to the receptive field characteristics demonstrated in the primary visual cortex (DeValois and DeValois, 1988; Pollen, and Taylor, 1974; Pribram and Carlton, 1986; Daugman, 1990) suggests that this processing medium is ubiquitous in the cortical synaptodendritic network.

The manifolds derived from our data are constructed of two orthogonal dimensions: one dimension reflects the spatial frequency of the stimulus and the other its temporal frequency. Because spatial and temporal variables constrain the spectral density response, a Gabor-like rather than a simple Fourier representation describes our results. Thus the results of our experiments can be interpreted in terms of an information field composed of Gabor-like elementary functions, that is, of truncated two dimensional sinusoids.

An unconstrained spectral representation is globally holographic; the constrained spectral domain, as in patch or multiplex holography, is termed holonomic. (For the derivation of this nomenclature,



Figures 6a-f. Examples of simulated receptive field manifolds and their associated contour maps to be compared with the empirically derived maps presented in Figures 2a-f. Axes are normalized from 0 to 1.

originated by Hertz, see Pribram, 1991 p. 27.). Holonomic constraints quantize an essentially spectral process. Gabor called the elementary function described by the intersection of his spectral and time parameters a "quantum of information." His reason was that he could address the problem of the efficiency of communication across the Atlantic cable in terms of "the formulation of Heisenberg's principle of indeterminacy in 1927. This discovery led to a great simplification in the mathematical apparatus of quantum theory which was recast in a form of which use will be made in the present paper" (1946, p. 432).

A possible resolution to the "binding problem" presents itself on the basis of these results. Processing of field potentials appears to be correctly described by patch holography: a manifold composed of Gabor-like elementary functions. Such descriptions are thus consistent with a quantum-type formulation. Non-local synchronization is a feature of quantum-type processes, and evidence has been presented that action-at-a-distance (saltation) is characteristic of processing in synaptodendritic arborizations (Shepherd et. al., 1985; Perkel and Perkel, 1985). Thus, spike trains recorded from axonal probes sampling isopotential loci within synaptodendritic manifolds would be expected to show synchronization.

The results of the experiments reported by Engel, Koenig, Kreiter and Singer (1991) support the conclusions presented here. Synchronization of frequencies was shown by them in records made from corresponding areas of the right and left visual cortices. Synchronization was disrupted by sectioning of the corpus callosum. As they note, the axonal transmission delay across the corpus callosum is approximately 6-8 msec. Reciprocal synchronization of frequencies within any single cycle of oscillation would, therefore, be difficult to achieve. Processing in the spectral domain, however, utilizes convolution-correlation algorithms, with the result that, over iterated cycles, phase coherence would come to be established. And, in fact, phase locking is what is reported by Engel et al to occur.

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