



Maps of Surface Distributions of Electrical Activity in Spectrally Derived Receptive Fields of the Rat's Somatosensory Cortex

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Abstract. This study describes the results of experiments motivated by an attempt to understand spectral processing in the cerebral cortex (DeValois and DeValois, 1988; Pribram, 1971, 1991). This level of inquiry concerns processing within a restricted cortical area rather than that by which spatially separate circuits become synchronized during certain behavioral and experiential processes. We recorded neural responses for 55 locations in the somatosensory (barrel) cortex of the rat to various combinations of spatial frequency (texture) and temporal frequency stimulation of their vibrissae. The recordings obtained from single and multi-unit bursts of spikes were mapped as surface distributions of local dendritic potentials. The distributions showed a variety of patterns that are asymmetric with respect to the spatial and temporal parameters of stimulation, and were, therefore, not simply reflecting whisker flick rate. Next, a simulation of our results showed that these surface distributions of local dendritic potentials can be described by Gabor-like functions much as in the visual system. The results provide support for a model of distributed cortical processing that imposes a physiologically derived frame (the limited extent of a dendritic patch) and an anatomically derived (axonal) sampling of the distributed process. This combination provides a complex Gabor wavelet that encodes phase, which is necessary to processing such details as edges and texture in a scene. The synchronization across cortical areas that make the Gabor wavelet processes within restricted cortical areas available to one another (the binding problem) proceed at a "higher order" level of integration. Both levels of distributed processing accomplish computation in the conjoint spacetime and spectral domain.

Key words: Gabor wavelets, holography, phase space, receptive fields

1. Introduction

In the mid-1960s, Leith and Upatnicks (1965) found ways to produce optical holograms using the mathematical formulation proposed by Dennis Gabor (1948). Engineers (e.g. van Heerden, 1963), psychophysicists (e.g. Julez and Pennington, 1965) and neuroscientists (e.g., Barrett, 1969; Pollen, 1971; Pribram, 1966) immediately saw the relevance of holography to the hitherto intractable issues of brain function in perception (e.g., constancies) and memory (e.g., distributed store).

This early promise was temporarily derailed by the advent of computer-friendly associative nets based on massively parallel programming architectures. For example, Longuet-Higgins and his group, inspired by Crick (Willshaw *et al.*, 1969), proposed that a non-holographic amplitude modulated associative memory model based on correlations (that did not rely on phase encoding) could handle a large storage capacity and efficient representational memory. On the other hand, van Heerden (1970a & b) noted that holographic (distributed spectral) principles account for aspects of perception that cannot be addressed by non-holographic associative nets. Van Heerden used a holographic process that encodes coherence (in which the phase spectrum is preserved) rather than just correlation. Indeed, the argument is best presented in his own words:

Willshaw, Buneman and Longuet-Higgins have proposed a nonholographic associative memory model for the brain (Willshaw *et al.*, 1969, p. 9601). They also criticize the proposal made by myself (van Heerden, 1963, p. 393) and by Pribram (1966, 1969) that the brain would be organized on the holographic principle. They say: "How could the brain Fourier-analyse the incoming signals with sufficient accuracy . . ."

I agree with the contention of Willshaw, Buneman, and Longuet-Higgins, in their response to my communication (van Heerden, 1970), that the associative net they proposed (Willshaw *et al.*, 1969) performs the specified functions as well as the hologram. Two of the most striking capabilities of human memory, however, are not present in their network. The first is our ability to recognize a person we know, when he appears in our field of view, which may contain a hundred more people. The sudden flash of recognition . . . this absolute certainty of "this is he and it can be nobody else" is . . . evoked only by an extremely reliable and fast form of information processing in our brain. This function of recognizing is also performed by the two-dimensional hologram, as the appearance of a bright light point in the image plane of the optical arrangement, and the brightness and sharpness of the light point are a scientific measure of the degree of recognition.

The second capability is our ability, after recognizing a person, to recall quickly a considerable amount of the information we have about this person. In an optical arrangement, the recognition signal given by the two-dimensional hologram provides the instruction for generating total recall of the relevant information from a three-dimensional hologram . . .

In a book on the subject (van Heerden, 1968) I discussed . . . how the brain could work physically very well as a three-dimensional hologram. If we have a three-dimensional network of neurones, in which each neurone is connection to a few adjacent ones, and if a neurone in a certain layer, in receiving a signal, will send this on to a few neurones in the next layer, then signals will propagate in this network as a wave propagates in an elastic medium. If, moreover, the ability of the neurones to propagate received signals can be permanently enhanced by frequent use, then the network must act as a three-

dimensional hologram, with a storage capacity of the order of the number of neurones present in the network . . .

(For a more complete exchange between Willshaw *et al.* and van Heerden see Pribram, 1971, pp. 153–157).

Despite Van Heerden's argument, for a time visual scientists became engaged in showing that the idea of a global Fourier holographic transformation was untenable. But neurophysiologists (Pollen, 1971; Pribram *et al.*, 1973; Robson, 1975) had, from the beginning, insisted that the spread function – the spectral, holographic-like process – was limited to patches of single, albeit overlapping, spatially restricted, receptive fields. Engineers (see Bracewell, 1989, for review) soon showed that patch holography could and did produce coherent three-dimensional images when inverse transformed, a technique that became basic to optical image processing in tomography.

These advances in understanding did not immediately register when it came to discussions of possible neural implementations of a primarily optical information process. Thus, Crick (1994) reasserted his earlier opinion that “nothing resembling a Fourier transformation exists in the brain,” and 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.”

We disagree with Churchland. A large body of evidence has accumulated over the past decades that maps visual cortical function in terms of the constrained Fourier process. DeValois and DeValois (1988) presented an extensive review of the evidence, much of it their own, in favor of a spectral Fourier-like description of the receptive field properties of cells in the primary visual cortex. In a similar manner, Vadim Glezer reviewed his and other Russians' work on the spectral holographic-like receptive field properties of visual cortical cells in his book, *Vision and Mind* (1995) (see also Pribram, 1991).

We believe that these disparate views are due to a failure to take into consideration the level or scale at which processing is being investigated: The focus of Churchland's inquiry is the neural circuit, whereas it is at the level of synaptodendritic processing that holographic-like transactions among fluctuating hyper- and depolarizations can take place (see Shepherd *et al.* 1985).¹

Level of processing is largely ignored even in massively parallel neural net simulations, the focus of Churchland's evaluation: What needs to be emphasized is that it is the weighting of connections *between* “neurons” as, for instance, in encoding the phase relations among neural hyper- and depolarizations – not the amplitudes (discharges rates) of neurons themselves – that provide the distributed processing necessary to learning. This is not to deny the importance of assemblies

¹ The retina works almost exclusively on the basis of such continuous hyper- and depolarizations. Only when processing reaches the ganglion cell layer are sustained spikes generated. Nerve impulses, spikes, then transmit the information generated by the retinal process to the brain.

of neurons operating as modules (e.g. Pribram, 1991; Favorov and Kelly, 1994a, b) or that of systems in neural "information processing". The clinical syndromes of agnosias due to localized cerebral lesions indicate that information retrieval from stored memory is accomplished by virtue of systems localized in one or another region of the brain. This difference between processing at the level of systems and that which occurs at the level of dendritic receptive fields (within modules) can be conceptualized in terms of a surface structure operating on a deeper, distributed processing web (Pribram, 1997).

Direct recording of the electrical activity within the dendritic receptive fields is difficult. But a technique for mapping the dendritic configuration of responses to sensory stimulation of a single neuron has been available and in constant use since 1953. In that year Kuffler (1953) showed that he could map the dendritic field of a retinal ganglion cell's axon located in the optic nerve. By stimulating a receptor or a set of receptors in a variety of dimensions and using the density of unit responses recorded from axons, the configuration of the functional responsivity of the synaptodendritic receptive field of each axon are obtained.

Using Kuffler's technique, maps of the receptive fields of dendrites of neurons located in the primary visual cortex were shown to conform to Gabor wavelets (constrained sinusoids) rather than to simple Fourier transformations of the stimulus (Barrett, 1969, 1973; Daugman 1990; Marcelja, 1980; Pribram, 1991; von der Heydt *et al.*, 1992). Gabor (1946), working to determine the efficiency with which a telephone message could be sent across the Atlantic cable, had noted that there was a limit to the compressibility of an intelligible phonic signal. Mathematically this limit was a half of a wavelength.

To reach this conclusion, Gabor utilized a phase space in which one axis represented frequency, the other time. Whereas most analyses represent data in terms of *either* frequency (holographic-like spectrum) *or* time (Minkowsky spacetime), the phase space utilizes *both* frequency (spectrum) *and* time (spacetime). Specifically, Gabor used a Gaussian envelope to constrain the spectral (frequency) domain because the Fourier transform of a Gaussian is also a Gaussian.

In Gabor's own words:

Fourier's theorem makes of description in time and description by the spectrum two mutually exclusive methods. If the term 'frequency' is used in the strict mathematical sense which applies only to infinite wave-trains, a 'changing frequency' becomes a contradiction in terms, as it is a statement involving both time and frequency. The terminology of physics has never completely adapted itself to this rigorous mathematical definition of 'frequency'. For instance speech and music have a definite 'time pattern' as well as a frequency pattern. It is possible to leave the time pattern unchanged, and double what we generally call 'frequencies' by playing a musical piece on the piano an octave higher, or conversely, it can be played in the same key, but in different time." (p. 431)

The finding that Gabor wavelets better represented the configuration of the receptive fields of cells in the visual cortex solved the problem posed by the fact that ideally, the Fourier transform extends the frequency domain to infinity which is neurologically infeasible.² On the other hand, the phase space representation includes spacetime and therefore "seduces" one toward thinking *solely* in spacetime terms.

The finding that Gabor wavelets accurately represent the maps of receptive fields of cells in the primary visual cortex, make it possible that processing occurs largely in ordinary spacetime configuration space or largely in holographic-like spectral form – or simultaneously in both. In earlier experiments using brain electrical stimulation we showed that, at both the lateral geniculate and the cortical level, the inhibitory surrounds and flanks of receptive fields could be augmented or diminished: Inferior temporal lobe and putamen stimulation increased the inhibitory surrounds; anterior frontal lobe and caudate nucleus stimulation practically wiped out these surrounds (Spinelli and Pribram, 1967; Lassonde *et al.*, 1981). The surrounds were interpreted to be represented by the Gaussian envelop of the Gabor wavelet which suggested that when the surround was maximized, processing proceeded in the spacetime domain; when the surround was minimized, processing emphasized the spectral domain and was more holographic-like (Pribram, 1991, Lecture 10 and Epilogue). On the basis of these results, our view is that both types of processing occur and that we need to firmly establish the level at which, and the conditions under which, one or the other type tends to dominate.

To accurately define the level, or scale, at which we are working, our first steps were to study the timing of the relationship between the magnitude of the dendritic depolarizing process and the axonal spikes of the same neuron that ordinarily make up recordings of unit activity. These experiments inquired whether, indeed, the axonal spikes can reasonably be viewed as representations of dendritic receptive field maps.

Next we investigated the possibility of mapping *purely spectral* parameters of a sensory input by plotting the number of spikes generated by varying both that input's spatial and temporal frequency. The response maps show the surface distributions of the magnitudes of depolarization within the dendritic receptive field of the neuron(s) as gauged by the spikes per second that are correlated with these magnitudes.

Finally, we simulated these distributions by computer programs to determine their fit to a Gabor function.

² Gabor pointed out that his use of the phase space (a Hilbert space) was identical to this use by Heisenberg in microphysics. Therefore he labelled his wavelets, "logons" or "quanta of information." He warned that this use indicated only that the relationship was formally the same and did not mean that the communication of information was taking place at the quantum level. The same caveat applies, of course, to the finding that the receptive fields of visual cortical neurons can be mapped as Gabor wavelets.

The rat somatosensory system was chosen for convenience and because the relation between whisker stimulation and central neural pathways has been extensively studied (Armstrong-James, 1995; Simons, 1995). The whisker system has the putative advantage over the visual system that greater control over the spatial location of receptors can be exercised. However, as noted by Simons (1995), "... In its function the whisker field may be more similar to a continuous receptive sheet, like skin or retina, than its punctate anatomical structure might suggest." (268) Also, in this modality as in our studies in vision noted above, there is a good deal of evidence that the classical receptive field properties are altered by extra-field stimulation (Paradisio *et al.*, 1996; Vidyasagar and Henry, 1996).

2. Methods

Whiskers were stimulated by means of a set of rotating textured cylinders, each grooved with equally spaced teeth, the tooth width and grooves subtending equal angles. (The rotating cylinder were meant to mimic the drifting of gratings across the retinal receptors in vision.) The cylinders were rotated counter-clockwise against the right whisker array so that the whisker(s) were deflected posteriorly and rebounded anteriorly. Three cylinders (2cm. In diameter and 5 cm. In length) were used with grooves and teeth each measuring 30°, 15°, and 7.5°, respectively (corresponding to 12, 24 and 48 teeth/cylinder). These textures were approximately the same as the coarser of those used by Carvell and Simons (1990). The cylinders were rotated at 8 different speeds, varying from 22.5 deg/sec to 360 deg/sec.

Whiskers were identified according to accepted nomenclature. In 32 experiments [in 25 rats] single whiskers were isolated and stimulated; additionally, in 23 of these experiments a group of four to six primary whiskers comprising portions of one or two columns of the mystacial pad was in 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 drifting gratings.)

Electrodes were Teflon coated stainless steel (Haer) ranging in impedance between 1 and 3 megohms. The electrodes were implanted with the rat under intraperitoneal barbiturate anesthesia (50 mg/kg) with 0.05 ml subcutaneous atropine sulfate to suppress excess bronchial secretions. The rat was placed in a stereotaxic headholder, and a small (.5 cm.) round opening was made in the skull. A microelectrode was lowered slowly through the opening at approximately 4 mm posterior and 4-5 mm lateral to bregma by means of a hydraulic micromanipulator until good unit responses were recorded, usually at a depth of approximately 600-700 micra. Histological examination showed the electrode tracts to end in layer IV of the somatosensory cortex.

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. The recorded signal was band limited between 300 and 3000 Hz.,

and amplified with a gain 20,000. One hundred seconds of continuous voltages sampled at the rate of 32,000 samples per second were digitized and stored via a BRAINWAVE (DataWave, Inc.) system onto a PC-486 computer. The raw data were then transferred for processing in a Silicon Graphics workstation. Approximately 1/3 to 1/2 gigabytes of data representing both single spikes and bursts of spikes were recorded at each cortical location. Our data include both single and multi-unit activity – that is, single spikes and bursts of spikes. When single spikes were used, their origin from a single neuron was ascertained by a sorting procedure using template matching based upon spike amplitude and recovery slope. (We used recovery slope rather than ascending slope because we found ascending slope to be highly positively correlated with amplitude.) More often we used multi-unit bursts of spikes, especially during whisker stimulation since our records show a great deal of superposition of spikes (defined in terms of a spike arising during the ascending or descending slopes of another spike) during such bursts. Furthermore, the number of multi-unit bursts increase dramatically during stimulation. On the average (during a 100 second record) the baseline has 350 isolated single spikes, 152 bursts, and 26 superpositions; the stimulation record has 265 spikes, 218 bursts, and 307 superpositions.

2.1. RELATION BETWEEN SINGLE AND MULTI-UNIT ACTIVITY

As our analyses were derived from both multi-unit bursts and from single units, we sought to determine the relationships between the surface distribution maps derived from multi-unit bursts and those derived from single units composing the bursts. In nine experiments, single whiskers were isolated and stimulated. Whiskers were identified according to accepted nomenclature as described by Simons (1978). In our analyses of four such records, we found that the surface distribution constructed from multi-unit bursts encompassed those of the individual units composing the bursts: For instance, a burst-produced distribution surface appears to be composed of surface distributions from the four single unit which compose that burst. The four single-unit distributions show a gradual change in shape corresponding to slight changes in location within the burst map. The figures describing these results are available from the authors.

3. Results

3.1. THE FIELD/SPIKE DUAL

We obtained evidence that we are indeed mapping the varying magnitudes of the fields of electrical activity which we assume to be occurring in the dendrites of the neurons from whose axons we are recording spikes: Multi-unit bursts of spikes (as well as individual action potentials) were recorded with a high pass filter and simultaneously with a low pass filter (see also Verzeano *et al.*, 1970). This procedure allowed us to compare the time course of the recordings provided we adjusted for

the relative delay produced by the low pass filter. In our recording apparatus this delay amounts to 8–10 msec. Figures 1a and 1b show that the onset of the field effect precedes or co-occurs with that of the initiation of spikes. Spike occurrence becomes most likely just prior to the occurrence of the maximum amplitude of the depolarizing field and ceases as the field decays (Figure 1b). Out of 2,369 field/spike recordings, 1,573 or 61% showed this relationship; when recordings made during sensory stimulation were separately considered, the ratio went to 75%. The remaining cases were made up of 796 instances where the field effect was recorded without any evidence of correlated spike activity.

3.2. THE CONFIGURATION OF THE AMPLITUDES OF SURFACE DISTRIBUTIONS

Fifty-five maps were constructed of the number of bursts or spikes per 100 seconds of stimulation generated at each spectral location as determined by the spatial and temporal parameters of an input. According to our assumption of the field/spike dual, the spike activity above or below baseline³ which resulted from whisker stimulation represents a surface distribution of the amplitudes of local dendritic potentials. Spatial frequencies of the structure are scaled in terms of grooves per revolution, while temporal frequencies are scaled in terms of revolutions per second. Both are plotted on normalized axes. 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 (Figures 2a and b, 3a and b and 4a and b). These parameters co-determine the rate at which a whisker (or set of whiskers) is flicked. If flick rate were critical, an equal flick rate ought to generate an equal number of spikes or multi-unit bursts irrespective of whether the flicks are produced by the spatial (texture) or the temporal (rotation speed) stimulus. For instance, if flick rate were critical, a cylinder with 24 grooves rotating at one revolution per second should generate an equal number of spikes and the same surface distribution of local field potentials as a cylinder with 12 grooves rotating at two revolutions per second. This expectation was not fulfilled, most likely due to the fact that a change in rotation speed results in a change in acceleration of whisker deflection, which a change in the spacing of grooves does not. Thus, the three-dimensional mapping of the surface distribution of the amplitudes of local field potentials is asymmetrical with respect to the spatial and temporal axes of the stimulus. Representatives of the 55 maps are shown in Figures, 2, 3, 4.

4. Simulation

In order to discern whether, indeed, our data fit ordinary signal processing procedures, a simulation of the experimental method was executed.

³ Our baselines were composites of 100 sec of pre- and 100 sec of post-stimulation recordings. In a separate study (Xie, M. *et al.*, 1994) using the same baseline data, we showed the spike trains to be stochastic (and, in longer runs, stationary), not deterministically chaotic.

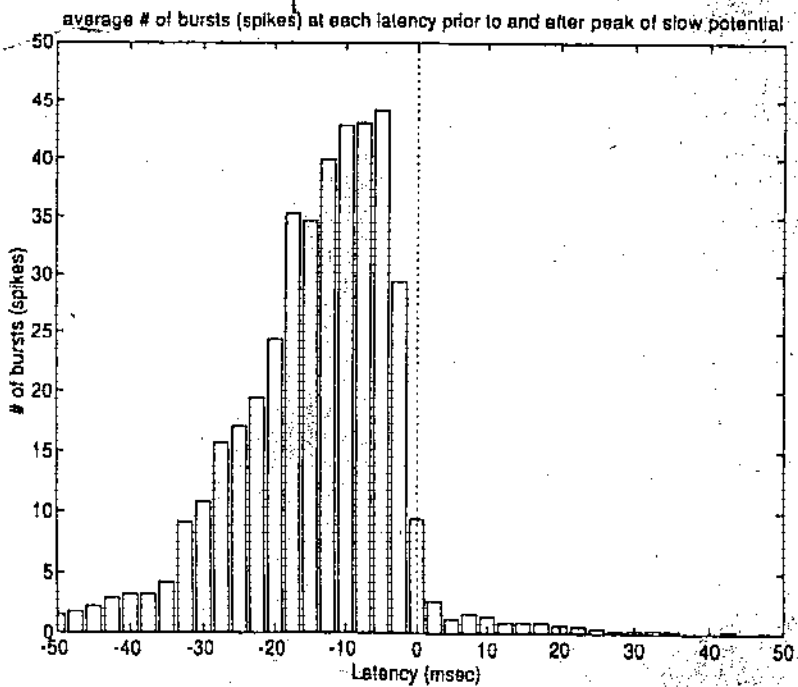
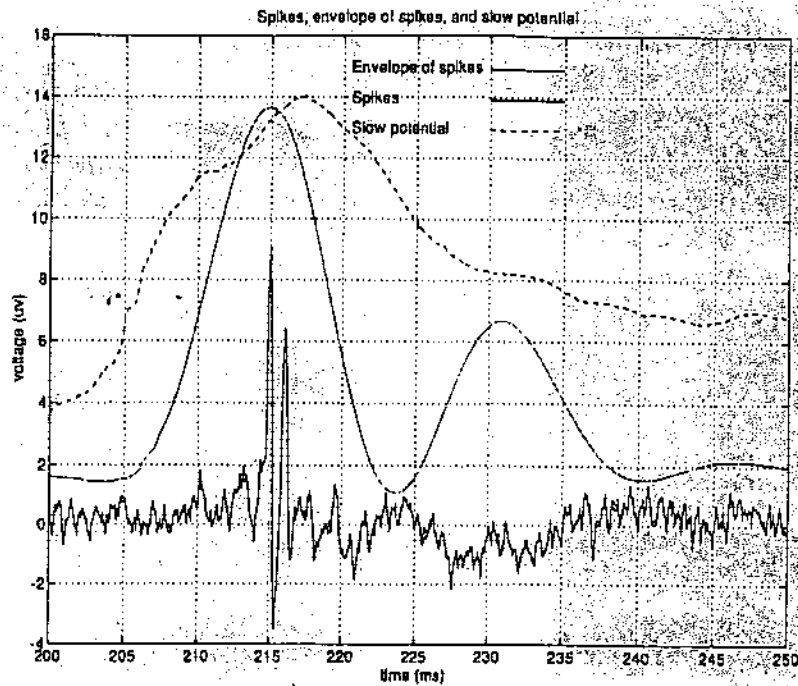


Figure 1a-b. Figure 1a is an example of the relationship between spikes and multi-unit bursts to coincident local field potentials. Figure 1b shows this relationship over 1,573 bursts. The peak of the slow potential is marked zero. Note that the ascending slope of the field potentials precedes that of the spikes and bursts. If the field potentials were a consequence of the burst, the peak should coincide with or come later than the maximum number of bursts.

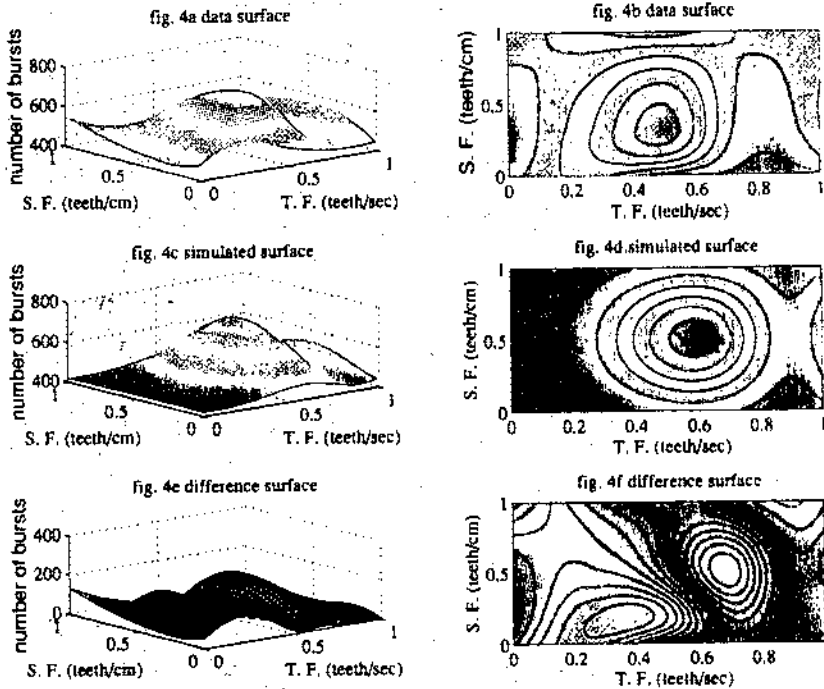


Figure 2, 3, 4. Examples of local field surface distributions (2a, 3a, 4a) and their associated contour maps (2b, 3b, 4b) derived by cubic interpolation (spline) procedure from recorded whisker stimulation. The contour map was abstracted from the surface distribution by plotting contours in terms of equal numbers of bursts per recording interval (100 secs.). Each figure shows baseline activity (no whisker stimulation) at a given electrode location as a plane located in terms of number of bursts per 100 secs. The x axis represents temporal frequency (T.F.) in revolutions per seconds (RPS). The y axis represents spatial frequency (S.F.) in terms of the number of flicks per revolution (Flicks/R). Figures 2c, 3c and 4c are examples of simulated surface distributions of local field potentials and their associated contour maps (2d, 3d, 4d) to be compared with the empirically derived maps presented in Figures 2a & b, 3a & b, and 4a & b. Figures 2e and f, 3e and f, and 4e and f show the difference between the surface distributions mapped from the data and those mapped from the simulations. *Note that the coordinates of the difference maps range from 0 upward while those of the surface distributions mapped from data and simulations range from a much higher level upward.*

4.1. FRAMING

The first stage of the simulation was to construct a putative map of the surface distribution of fluctuating amplitudes of local field potentials in patches of cortex. In order to provide a pattern of peaks and valleys similar to that shown by our data, we chose a rectangular window in the spatiotemporal domain to constrain a two dimensional sinusoidal signal, because when the extent of the signal is pruned of noise, a rectangular region is obtained in the results of experiments recorded from visual cortical neurons (Gaska *et al.*, 1994). In addition, the rectangular window

allows for maximum resolution of frequencies (Zeevi and Daugman, 1981). The use of such a window generates a sinc function in the spectral domain.⁴

In our simulations, each plot shows the surface distribution of a spectral density function of a rectangular windowed two-dimensional sinusoidal signal. When, in other experiments, only a single frequency of stimulation is used, a spatial "connection" matrix can be constructed from recordings made with multiple electrode arrays to represent the data (Barcala *et al.*, 1993; Chapin *et al.*, 1996; Nicolelis *et al.*, 1996; Ahissar *et al.*, 1996; McLaughlin *et al.*, 1996). In our version of such a matrix, the surface distribution of the amplitudes of local field potentials in a patch of cortical tissue can be conceived to act as an "ideal" filter which processes incoming signals. This ideal filter when activated generates a sinc function which is defined as:

$$\text{sinc}(\omega) = \frac{\sin(\omega)}{\omega} \quad (1)$$

for all values of the spectrum that activate the filter (Kamen, 1990).

As we used two parameters of stimulation, spatial and temporal frequency, the sinc function becomes two dimensional as follows:

$$F(\omega_1, \omega_2) = A \sin c(\omega_1) \sin c(\omega_2) \quad (2)$$

for all values within the range of values specified for (1) above, and where ω_1 and ω_2 correspond to the representation of spatial and temporal frequency in the computational space.

In simulating our data, the sinc function must, therefore, be defined for a range of stimulus parameters within a computational space in which an incoming signal is processed. Each signal generates a sinc function within that space, the peak of which will be located at some given temporal and spatial value. Therefore, the actual sinc function generated by each two-dimensional signal will be displaced from the origin of the computational space by the difference between the spectral frequencies which define the computational space and the actual frequencies generated by the incoming signal. The sinc function produced by the incoming signal will thus be defined by:

$$F(\omega_1, \omega_2) = A \sin c(\omega_1 - \omega_{01}) \sin c(\omega_2 - \omega_{02}) \quad (3)$$

where A is a scaling constant, ω_1 and ω_2 are spatial and temporal frequencies of the computational space, and ω_{01} and ω_{02} are the spatial and temporal frequencies of the signal.

⁴ We experimented with other types of window such as a Gaussian function and found little difference in the results of simulation: the sinc function provided somewhat sharper boundaries between the various isopotential representations.

Systematically changing the parameters of stimulation, therefore, serves to systematically "move" the sinc function generated by the incoming signal within the computational space in which the signal is processed.

4.2. SAMPLING

The second stage of the simulation adds another axis to the computational space by taking a limited sample of the sinc function using a Gaussian function. In vision, convergence of visual-nerve fibers onto the lateral geniculate nucleus has made it possible to conceive of each geniculate cell as acting as a "peephole" sampling a part of the retinal mosaic (Pribram, 1991, p. 74; Hashemiyoony and Chapin, 1996). In the somatosensory modality, a similar convergence onto the principle nucleus of the trigeminal nerve in the brain stem makes it possible to consider the cells in the ascending trigeminal pathway as sampling the mystacial mosaic. The Gaussian represents such a sample, a peephole, and has the advantage that its Fourier transform is also a Gaussian and thus can be readily applied to the spectral domain. When this sample represents the output of a single neuron it is limited by the spatial extent of the local field potentials fluctuating among that neuron's dendrites. When a surface distribution is modeled from multi-unit bursts, the spatial constraint is assumed to portray a greater reach. Sampling, which manifests as a point process, 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. This filter is multiplied with the sinc function to yield a display of the surface distribution.

Figures 2c and d, 3c and d and 4c and d depict distribution and contour maps derived from these simulations. Note the close fit to the experimentally derived surface distributions and contours shown in the difference manifolds of Figures 2e and f, 3e and f, and 4e and f. Statistical analyses are presented in Table I. As noted, a total of 55 surface distributions were experimentally generated. Of those three were essentially flat. Of the remaining 52, we simulated six; all but two of the remaining 46 have a shape that can be seen to be successfully simulatable with the technique described.

5. Discussion

To summarize: We simultaneously recorded neuronal spike activity and field potentials from 25 rats, and the results showed the density of spike activity represented the distribution of field potentials. Then, using simple spikes and bursts of spikes, we mapped the distribution of receptive dendritic field potentials in the somatosensory cortex generated by rotating grooved cylinders.

The surface distributions 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

visual cortex (Daugman, 1990; Pollen and Taylor, 1974; Pribram and Carlton, 1986; Pollen and Gaska, 1997). This suggests that such a processing medium is ubiquitous in cortical networks.

6. The Complex Form of Gabor Functions and the Importance of the Phase Spectrum

A recent review by Tai Sing Lee (1996) continues and expands the simulation procedures begun in our experiments and specifies the phase space sampling schemes needed for image reconstruction. Lee succinctly recapitulates and brings up to date the evidence as presented originally by Gabor (1946) and reviewed with respect to brain processes by Pribram (1991) (bold ours):

On the theoretical side, [the] important insight ... advanced by Marcelja (1980) and Daugman (1980, 1985), [is] that ... cells in the visual cortex can be modeled by Gabor functions [which can be used as a starting point for developing a theory of efficient reconstruction of an image]. The 2D Gabor functions proposed by Daugman are local spatial bandpass filters that achieve the theoretical limit for conjoint resolution of information in the 2D spatial and 2D Fourier domains.

Gabor (1946) showed that there exists a "quantum principle" for information: the conjoint time-frequency domain for 1D signals must necessarily be quantized so that no signal or filter can occupy less than a certain minimal area in it. This minimal area, which reflects the inevitable trade-off between time resolution and frequency resolution, has a lower bound in their product, analogous to Heisenberg's uncertainty principle in physics. He discovered that Gaussian-modulated complex exponentials provide the best trade-off. The original Gabor elementary functions, in the form proposed by Gabor (1946), are generated with a fixed Gaussian while the frequency of the modulating wave varies. These are equivalent to a family of "canonical" coherent states generated by the Weyl-Heisenberg group ... A signal can be encoded by its projection onto these elementary functions. This decomposition is equivalent to the Gaussian-windowed Fourier transform ...

Daugman (1980, 1985) generalized the Gabor function to the following 2D form to model the receptive fields of the orientation-selective simple cell ... The 2D Gabor function is a product of an elliptical Gaussian and a complex plane wave. The careful mapping of the receptive fields of the visual cortical cells by Jones and Palmer (1987) confirmed the validity of this model. **Mathematically, the 2D Gabor function achieves the resolution limit in the conjoint space only in its complex form.** Since a complex-valued 2D Gabor function contains in quadrature projection an even-symmetric cosine component and an odd-symmetric sine component, Pollen and Ronner's (1981) finding that visual cells exist in quadrature-phase pairs therefore showed that the design of the cells might indeed be optimal. The

fact that the visual cortical cell has evolved to an optimal design for information encoding has caused a considerable amount of excitement not only in the neuroscience community but in the computer science community as well. Gabor filters, rediscovered and generalized to 2D, are now being used extensively in various computer vision applications (Bovik *et al.*, 1990; Lee *et al.*, 1992).

Neurophysiological evidence (DeValois and DeValois, 1988) suggests that the spatial structure of the receptive fields of visual cells having different sizes is virtually invariant. Daugman (1993) and others (Bovik *et al.*, 1990) have proposed that an ensemble of such cells is best modeled as a family of 2D Gabor wavelets sampling the frequency domain in a log-polar manner. This class is equivalent to a family of affine coherent states generated by the affine group. The decomposition of an image f into these states is called the *wavelet transform* of the image A particular Gabor elementary function can be used as the mother wavelet to generate a whole family of Gabor wavelets. (1-2)

By numerically computing the frame bounds for this family of wavelets in different phase space sampling schemes, he finds that the phase space sampling density provided by the visual cells in the primary visual cortex is sufficient to form an almost tight frame that allows stable reconstruction of the image by linear superposition of the Gabor wavelets. Running his simulations, Lee (1996) came up with a surprising conclusion: "... two to three orientations are sufficient for complete representation of the image" (p. 11). Further:

... there are at least two advantages to such a redundant representation: first, an image can be represented and easily reconstructed as a linear superposition of the receptive field structures of the visual cells weighed by their firing rates; second, high precision information can be computed and stored by a population of low-precision neurons. (p. 12)

Lee then asks whether the surplus redundancy in representation could be due to a limitation in a neuron's ability to transmit only three or four bits of information. In fact, temporal coding carried in the spike train of a single neuron is more often 1/2 a bit or less (Richmond and Opticon, 1987). Thus, the dendritic fields of visual cells, modeled by Gabor wavelets, with surplus redundancy provide an ideal medium for representing surface texture and surface boundary with high resolution. The amount of redundancy provided by extreme oversampling in a tight frame may be exaggerated in the Lee simulation. When more than a few stimulus components are being sampled, this density of sampling is necessary to providing fidelity.

Important for us is that, as noted by Lee, Gabor functions, *unless they encode complex representations of frequency, do not fully describe the potential of these surface distributions*, the "ideal filter." Phase encoding is necessary for faithful reproduction of the stimulus. Amplitude encoding, as provided by correlations performed by non-holographic associative networks, provides only a gross approx-

imation to the stimulating surface (Caelli and Hubner, 1983 as quoted in Pribram, 1991, Figure 2.5, p. 37; Oppenheim and Schafer, 1989).

An excellent *simulation* using Gabor functions has been developed by Christoph von der Malsburg and his group in a dynamic link architecture (Lades *et al.*, 1993). Their network achieves image processing via computations similar to those described here: they use Gabor wavelets to compose a linear filter operation in which an image is convolved with a family of wavelets. This family is self similar under the application of the group of translations, rotations, and scaling. This procedure was also proposed by Pribram (Carlton, 1988; Pribram and Carlton, 1986; Pribram, 1991) to deal with the perception of objects. However, Pribram based his proposal on a four-dimensional rather than a two-dimensional dynamic. Critical to his proposal is movement, which the van der Malsburg group point out is the next step to be considered in their simulation.

Bell and Sejnowski (1996) confirm the importance of phase encoding in terms of the advantages of an independent component analysis (over a principal component analysis) (underline ours):

The failure of correlation-based [processing] is most clearly shown by the filters they produce when trained on stationary ensembles of signals. The filters are typically *global* ..., sensitive to different spatio- or temporal frequencies, but with non-zero weights extending throughout the filter. They reflect only the amplitude spectrum of the signal and ignore the phase spectrum where most of the suspicious *local* coincidences in natural signals take place. An edge in an image, for example, is a coincidence in the phase spectrum, since if we were to Fourier analyse it, we would see many sine waves of different frequencies, all aligned in phase where the edge occurred

To illustrate formally that second-order statistics only carry information about the amplitude spectrum, consider the autocorrelation function of a signal, which contains all its second-order structure. The Fourier transform of this is the power spectrum, which is the square of the amplitude spectrum. Thus the two carry identical information.

To demonstrate intuitively that what we consider as the informative part of a natural signal is captured in the phase spectrum, Fourier transform the signal, remove the phase information, and transform it back to the space or time domain. It will then look or sound like noise, typically with a $1/f$ amplitude spectrum. All the visual or auditory features that our perceptual system thinks of as 'signal' will be lost. On the other hand, if we remove the amplitude information, and preserve the phase, the signal will be distorted but remain recognisable. (sic.)

This points to a curious paradox: correlation-based learning algorithms are sensitive to exactly the part of natural signals which we regard as least meaningful (amplitude), and ignore the part of the signal which we find most meaningful (phase). To encode the phase of signals, we need an algorithm that is sensitive to higher-order statistics. (261-262)

Independent component analysis thus provides a readily accessible technique to implement the findings of Caelli and Hubner and augments the argument made by van Heerden (albeit in a learning rather than a recognition context) quoted in the introduction. Independent Component Analysis, by being sensitive to higher order statistics provides the procedure necessary for recording phase encoding in electrical recordings of brain activity – an essential requirement if cortical processing is mathematically at all like that of an optical hologram.

7. Conclusion

Research using extracellular microelectrode recording allows the mapping of dendritic surface distributions of field potentials. Such mapping has shown that Gabor wavelets provide a reasonable fit to surface distributions recorded from primary visual cortex. In the current experiment, we have obtained evidence for a similar fit between surface distributions of dendritic field potentials and Gabor functions in the primary somatosensory barrel cortex. This finding suggests that Gabor functions or some similar Hermite polynomials are good descriptors of the surface distributions of dendritic field potentials in sensory cortex. These functions encode complex representations of the sensory stimulus. Complex representations imply that phase is an essential attribute to edge and texture representation. If this is so, the next step in research needs to demonstrate that transient phase locking to periodic stimulation occurs in such surface distributions in order that such details as edges can be extracted from scenes.

8. Implications for Future Research

The neurophysiological community has come to terms with the distributed nature of what can be conceptualized as the "surface structure" of cortical processing (Pribram, 1997). The accepted view is that distribution entails the necessity of binding together the disparate sites of processing. Binding is accomplished by temporal synchronization of spatially distinct oscillating neural processes. However, as Steven Schiff (Fitzgerald, 1999) has pointed out: "All really interesting things that go on in the brain happen in states of partial synchrony" (17). Such partial synchronization is best represented by transient phase locking. To date, the emphasis has been that under the conditions which produce binding, no phase lead or lag is present (see the interchange between Jay McClelland and Pribram, 1998, pp. 551–556). More recently, using EEG recordings, Varela (Lachaux, Rodriguez, Martinerie and Varela, In Press) and his group have shown transient phase locking to occur only at the moment a person perceives a recognizable figure. Taking such experiments a step further, Bressler (1994) has traced the paths of phase synchronization during performance of a visual discrimination task.

At the microelectrode level of recording (conceptualized as the deep structure of cortical processing, Pribram, 1997), Saul and Humphrey (1990, 1992a, b) have

found cells in the lateral geniculate nucleus that produce phase lead and phase lag in the cortical processing initiated by them. In the somatosensory system, Simons and his group (Simons, 1995), have analyzed the timing of the thalamocortical process to show how it enhances "preferred" features and dampens "non-preferred" ones – that is, to show how it sharpens sensory discrimination. They have used single pulse stimuli in their experiments. As one of the postdoctoral students in their group pointed out, were periodic stimulation used, their timing coincidence would amount to phase locking. In fact, most natural sensory stimulation is periodic ... otherwise rapid adaptation cancels out sensation. Currently, recordings made with multiple microelectrodes and data analysis with sufficiently powerful computers makes it possible to more readily obtain additional data of this sort and to determine the conditions under which phase – and not only amplitude – encoding occurs. These are definitive steps in bringing the neural network (PDP) simulations to include spectral processing, steps that help realize the promise articulated by Van Heerden (quoted in the introduction) in understanding the functions of the brain in perception and memory provided by the holographic process.

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