

**Neural Circuitry and Behavior;
Synaptodendritic Microprocesses and Conscious Experience:
Data and Theory**

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Abstract

Neurons are ordinarily conceived to be the computational units of the brain. The majority of processing theories since the seminal contribution of McCulloch and Pitts (1943) have taken the axonal discharge of the neuron, the nerve impulse, as the currency of computation. However, this framework for computational theory has led to considerable misunderstanding between neuroscientist and those interested in computational processing. Successful computational networks depend on highly--often randomly--interconnected elements. The more complex the computation, the more connections are needed: the law of requisite variety (Ashby, 1960). Neuro-scientists know that neurons are connected nonrandomly, often sparsely, and always in a specifically configured fashion (see Crick & Asanuma, 1986, for a neuroscience view of connectionist computational theory). In short, current computational processing emphasizes a minimum of constraints in the processing wetware or hardware; in the current neuroscience framework wetware is highly constrained. Misunderstanding is alleviated when the computational framework is broadened to include the microprocessing that takes place within dendritic networks. Not only are axonal-dendritic synapses that connect neurons subject to local influences in these networks, but innumerable local circuit operations provide the unconstrained high connectivity needed in computational procedure (Bishop, 1956; Pribram, 1960, 1971; Schmitt, Dev, & Smith, 1976). Local circuit neurons are found in many locations in the sensory and central nervous system (see Table, p. 9, in Shepard, 1981). The processing capability of such neurons (primarily inhibitory) is often dendro-dendritic. (See e.g., Rakic, 1976; Sloper, 1971.) Data manifolds are presented that map these dendritic fields.

Junctions (axodendritic and dendo-dendritic) between neurons in the form of chemical synapses and electrical gap junctions occur within overlapping dendritic arborizations (Fig 1.2). These junctions provide the possibility for processing as opposed to the mere transmission of signals. The term neurotransmitters applied to chemicals acting at junctions is, therefore, somewhat misleading. Terms such as neuroregulator and neuromodulator convey more of the meaning of what actually transpires at synapses.

Nerve impulse conduction leads everywhere in the central nervous system to such junctional dendritic microprocessing. When nerve impulses arrive at synapses, presynaptic polarizations result. These are never solitary but constitute arrival patterns. The patterns are constituted of sinusoidally fluctuating hyper- and depolarizations which are insufficiently large to immediately incite nerve impulse discharge. The delay affords opportunity for computational complexity. The dendritic microprocess thus provides the relatively unconstrained computational power of the brain, especially when arranged in layers as in the cortex.

The neurophysiologist can readily study the output--spike trains-- of neurons when they act as channels but he has only limited access to the functions of the interactive dendritic junctional architecture because of the small scale at which the processes proceed. A major breakthrough toward understanding was achieved, however, when Kuffler (1953) noted that he could map the functional dendritic field of a retinal ganglion cell by recording impulses from the ganglion cell's axon located in the optic nerve. This was accomplished by moving a spot of light in front of a paralyzed eye and recording the locations of the spot that produced a response in the axon. The locations mapped the extent of the responding dendritic field of that axon's parent neuron. The direction of response, inhibitory or excitatory, at each location indicated whether the dendrites at that location were hyperpolarizing or depolarizing.

The current study explores 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.

In our experiments, sensory input is generated by the spacings of the grooves on the cylinders and the speed with which the cylinders are rotated. The results 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. (Figure 1). 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.

According to signal processing theory, the general shape of a field potential manifold is the same for each combination of spatial and temporal frequencies. 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 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.

In our simulations 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. 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. Figure 2 depicts manifolds and contours derived from these simulations. Note the close fit to the experimentally derived manifolds and contours shown in Figure 1. 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.

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

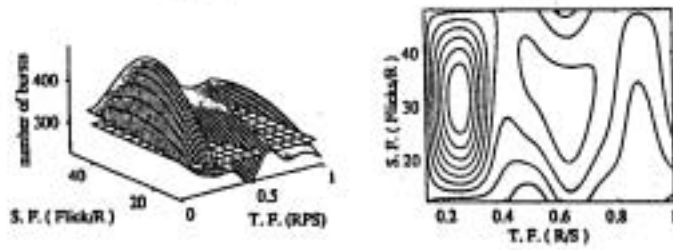
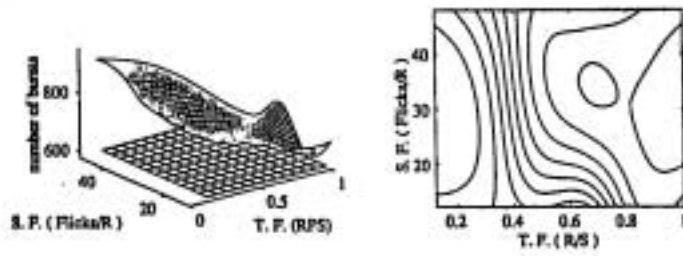
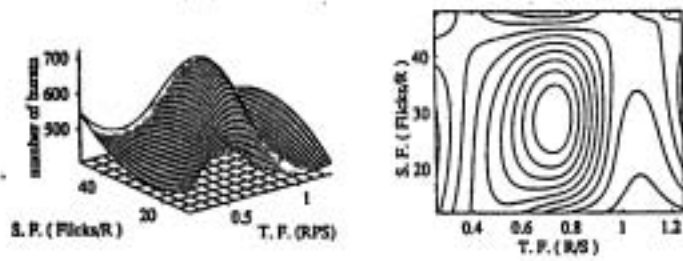
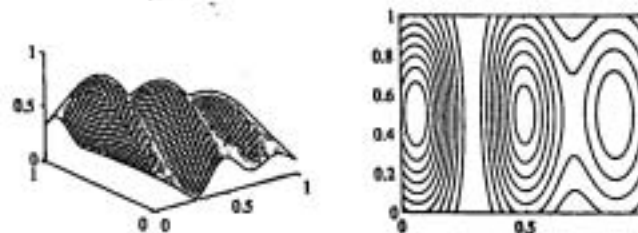
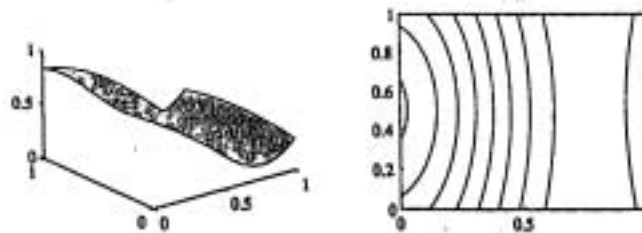
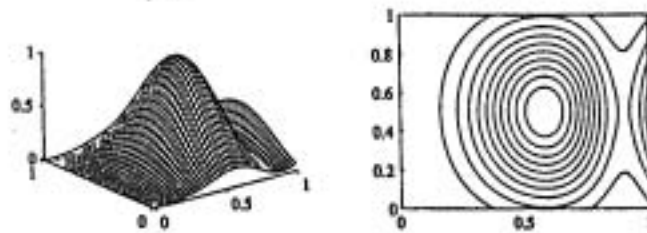


Figure 1

Figure 2



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.

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