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Responses of Somatosensory Cortical Neurons to Spatial Frequency and Orientation : A Progress Report

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Pioneering work from Mountcastle's laboratory (1987, 1991) on the parietal cortex of monkeys demonstrated that unit responses to moving visual stimuli could be profitably viewed as population responses depicted in terms of neural population vectors derived from regression of neuronal response data to a sinusoid. This analysis indicated that the population vectors are directionality arranged in an opponent fashion along a single meridian. Their analysis further showed that opponent neuronal responses to directional movement of a stimulus could be modelled as a difference of gaussians (Motter, Steinmetz, Duffy and Mountcastle, 1987). Analysis of neuronal responses by population vectors was also used by Georgopolous (1983) in which vector representations of neuronal responses accurately predicted direction of arm movements by monkeys.

Similar investigations of the vibrissal system have not been pursued. The barrel cortex of the rat seems particularly well suited for such an analysis as unit recordings have indicated directional selectivities among neurons within the barrel cortex (eg. Simons, 1978). First described by Woolsey and Van der Loos (1970), the barrel cortex is the terminus of a system that extends from the two dimensional array of whiskers on the animal's vibrissal pad, via the fifth cranial nerve to the trigeminal brainstem nuclear complex, and from there to the ventral posterior medial thalamus (VPM), which relays the input to the somatosensory cortex (SI).

Although analysis by population vectors has not been performed for this system, response characteristics of neuronal populations have not been ignored. Research by Nicolelis, Lin, Woodward and Chapin (1993) and Nicolelis and Chapin (1994) indicate that, at least at the thalamic level, neurons in the vibrissal system of awake and lightly

anesthetized rats respond as ensembles, and in a systematically dynamic and distributed fashion.

Initial work in our laboratory (King, Xie, Zheng and Pribram, 1993) indicated that receptive fields could be systematically described in terms of three dimensional manifolds in the spectral domain. In that study, the spectral properties of the analysis were a function of stimulating the rat's whiskers by rotating a grooved cylinder across selected vibrissae. Thus, by plotting spatial against temporal frequency, the neural response to the frequency of stimulation could be shown. It was then demonstrated that these manifolds could be derived from Gabor-like functions, indicating that somatosensory processing is consistent with the physics of conventional signal processing theory. These data, and their modelling were interpreted as supporting a more general, distributed, and dynamic model of sensory processing (Pribram, 1991).

These data were acquired by recording neural activity during passive manipulation of the whiskers. The purpose of the present experiments is to actively move the whiskers across stationary textured gratings. Movement was produced by a repeated 8 Hz excitation of the dorsal branch of the facial nerve which moved the vibrissae in a horizontal motion similar to that described by Carvell and Simons (1990) in the awake rat during discrimination performance. The constant movement of whiskers across gratings differing in spatial frequency and orientation creates a spatial (rather than spectral) manifold which is ordinarily called a geodesic.

Methods

Twenty locations in 9 Holtzman albino rats (four female, five male) weighing approximately 300-500 grams were used in the experiments. The animals were lightly anesthetized with sodium pentobarbital (50 mg/kg of body weight, i.p.) supplemented with 0.05 cc of atropine sulfate to inhibit excess respiratory tract secretions. Electrodes were Teflon-coated stainless steel (Hare, Brunswick, ME) ranging from 0.63 to 4.20 Megohms impedance at 1 KHz. Electrodes were stereotaxically lowered, with the aid of a hydraulic micromanipulator, through a .5 cm diameter opening in the skull located approximately 2.5mm posterior and 5-6 mm lateral to bregma. Best responses to vibrissal stimulation were usually obtained at depths between 600 and 950 microns.

An incision approximately 2 cm in length was made on the right cheek of each animal in order to expose the marginal mandibular nerve, a branch of the seventh cranial nerve. A 0.5 cm section of the nerve was exposed, mounted on silver stimulating electrodes, and then stimulated with square-wave pulses (6.0 msec wide, 4 volt amplitude) with an electrically isolated stimulator. Each stimulation series was composed of a train of 300 stimuli (6 msec duration) separated by 0.125 sec for a total 50 seconds.

Five Teflon stimulus disks, each milled to one of five spatial frequencies, were presented at each of six orientations. The disks had alternating teeth and grooves of equal widths of 200, 400, 600, 800, and 1000 micrometers, respectively. Spatial orientations were 0 (horizontal), 30, 60, 90, 120 and 150 degrees. Whiskers were stimulated with each spatial frequency, at each orientation for a total of 30 stimulation conditions at each location. Twenty locations were tested.

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. Data were stored by a Brainwave system onto a 486 PC computer. Data were then transferred to a Silicon Graphics workstation where in house software was used to identify and count bursts of unit activity.

Data were analyzed in two ways. Following King et al. (1994), the total number of spikes at each of the 30 stimulation conditions was used to generate a 3-dimensional frequency distribution manifold for each location. Axes for each frequency distribution were spatial frequency and orientation.

Following Steinmetz, Motter, Duffy and Mountcastle (1987), we calculated a population vector based upon the responses across all orientations for a given spatial frequency grating. The population vector represents the orientation at which the maximal deviation from baseline of the neural response across spatial frequencies occurs.

Calculation of population vectors

The population vector is that orientation at which the greatest change from baseline firing rate would be achieved with the obtained data fit to a cosine wave. Since there were six orientations, the six points are fit to a cosine wave using least squares regression.

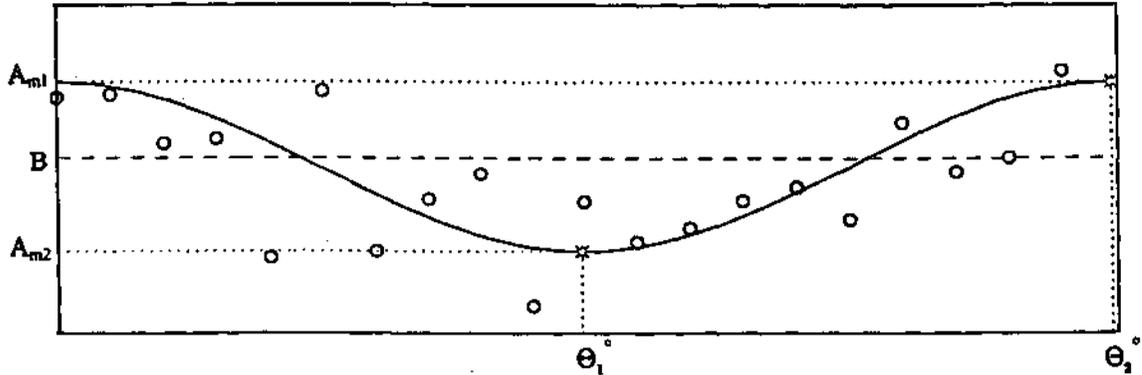


Figure 1. Cosine wave illustrating extraction of the orientation, θ° , and amplitude, A_m , components of the population vector. "B" represents baseline firing rate. Subscripts m1 and m2 represent maximal and minimal firing rates, respectively.

Therefore the population vector is defined as:

$$y = A_m \cos(\theta_i - \theta^\circ) \quad (1)$$

where y is the population vector, A_m is the maximal amplitude of the cosine function and θ° is the angle at which the maximum occurs.

When

$$\theta_i = \theta^\circ \quad (2)$$

y_i is at a maximum and

$$y = A_m \quad (3)$$

Equation (1) can be rewritten as:

$$y = A_m [\cos\theta \cos\theta^\circ + \sin\theta \sin\theta^\circ] + b_0 \quad (4)$$

Letting

$$\begin{aligned} b_1 &= \cos\theta^\circ \\ b_2 &= \sin\theta^\circ \end{aligned} \quad (5)$$

Equation (4) can be represented as:

$$y = A_m(b_1 \cos\theta + b_2 \sin\theta) + b_0 \quad (6)$$

Given the coefficients b_1 and b_2 . The angle and the magnitude of the population vector can be computed from:

$$\cot\theta = \frac{\cos\theta}{\sin\theta} = \frac{b_1}{b_2} \quad (7)$$

or

$$\theta = \cot^{-1}\left(\frac{b_1}{b_2}\right) \quad (8)$$

and

$$A_m = \sqrt{b_1^2 + b_2^2} \quad (9)$$

Since we have six orientations and three unknowns, we can solve for these using least squares regression in which:

$$y_i = b_0 + b_1 \sin\theta_i + b_2 \cos\theta_i \quad (10)$$

where $i=1,2,\dots,6$ orientations.

Since y_i and θ_i are known, let

$$\begin{aligned} \alpha_{i1} &= \sin\theta_i \\ \alpha_{i2} &= \cos\theta_i \end{aligned} \quad (11)$$

Therefore,

$$\begin{aligned} y_1 &= b_0 + \alpha_{11}b_1 + \alpha_{12}b_2 \\ y_2 &= b_0 + \alpha_{21}b_1 + \alpha_{22}b_2 \\ y_3 &= b_0 + \alpha_{31}b_1 + \alpha_{32}b_2 \\ y_4 &= b_0 + \alpha_{41}b_1 + \alpha_{42}b_2 \\ y_5 &= b_0 + \alpha_{51}b_1 + \alpha_{52}b_2 \\ y_6 &= b_0 + \alpha_{61}b_1 + \alpha_{62}b_2 \end{aligned} \quad (12)$$

Let

$$\alpha_{i,0} \equiv 1$$

and $i=1,2,\dots,6$. So, using the pseudoinverse of the 3×6 matrix, the preceding system of equations can be solved for b_0 , b_1 , and b_2 in the matrix form:

$$\begin{pmatrix} y_1 \\ y_2 \\ y_3 \\ y_4 \\ y_5 \\ y_6 \end{pmatrix} = \begin{pmatrix} \alpha_{10} & \alpha_{11} & \alpha_{12} \\ \alpha_{20} & \alpha_{21} & \alpha_{22} \\ \alpha_{30} & \alpha_{31} & \alpha_{32} \\ \alpha_{40} & \alpha_{41} & \alpha_{42} \\ \alpha_{50} & \alpha_{51} & \alpha_{52} \\ \alpha_{60} & \alpha_{61} & \alpha_{62} \end{pmatrix} \begin{pmatrix} b_0 \\ b_1 \\ b_2 \end{pmatrix} \quad (13)$$

The resulting values for b_1 and b_2 can be substituted into (8) to obtain θ^* , and A_m can be obtained from (9).

Results of Population Vector Analysis

A potentially confusing outcome occurs when A_m occurs at the lowest point of the cosine curve. In this case, sinusoidal regression results in a curve that is concave up. The maximum point on the curve is located 180° away from the orientations used in our experiment. Such is a logical outcome of studies involving orientation of gratings. The only possible orientations are from 0° to 180° . On the one hand this is not really a problem if one interprets the response of the cell in terms of inhibition. Sinusoidal regression provides the angle (θ^*) at which maximal displacement (A_m) from baseline occurs. In the case of excitation, the point of maximal displacement from baseline is a local maximum. In the case of inhibition, the regression simply provides the local minimum on the cosine curve. Figure 2 presents regression curves from which population vectors were obtained for one location. It should be noted that in this location both local maxima and local minima are represented for different spatial frequencies. Population vectors have been calculated and plotted for each spatial frequency across 20 locations in 9 animals

Note that the regression curves (Figures 2a,c,and d) from three spatial frequencies (200, 600 and 800 μm gratings) locate local minima, while regression curves (Figures 2b and d) from two other spatial frequencies (400 and 1000 μm gratings) locate local maxima. The

former are indicative of inhibitory responses while the latter indicate peaks of excitation. An initial problem, therefore, is the representation of inhibition with the population vector. One must be careful when reading population vectors derived from movement across gratings; realizing that such vectors represent excitatory as well as inhibitory responses to stimulation.

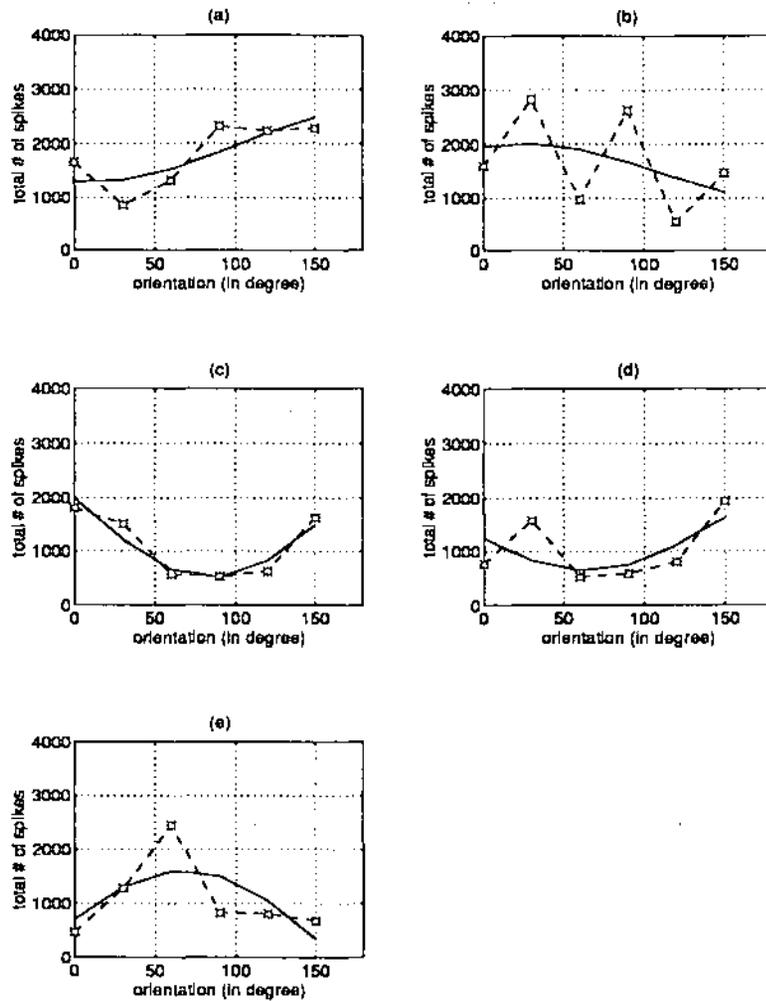


Figure 2. Sinusoidal regression curves resulting in identification of a local maximum (excitatory) vectors (2b and e), and local minimum (inhibitory) vectors (2a, c and d).

Figure 3 presents population vectors derived from the sinusoidal regression at each spatial frequency presented in Figure 2. Note that cells responding with excitation are "tuned" to two spatial frequencies (b and e, 400 and 1000um gratings, respectively) and have population vectors at 30° and 60° orientation. Also, inhibitory responses are "tuned" to three spatial frequencies (a,c, and d, 200, 600 and 800 mm gratings, respectively), with maximal inhibition occurring at approximately 10° 80° and 60° orientations, respectively.

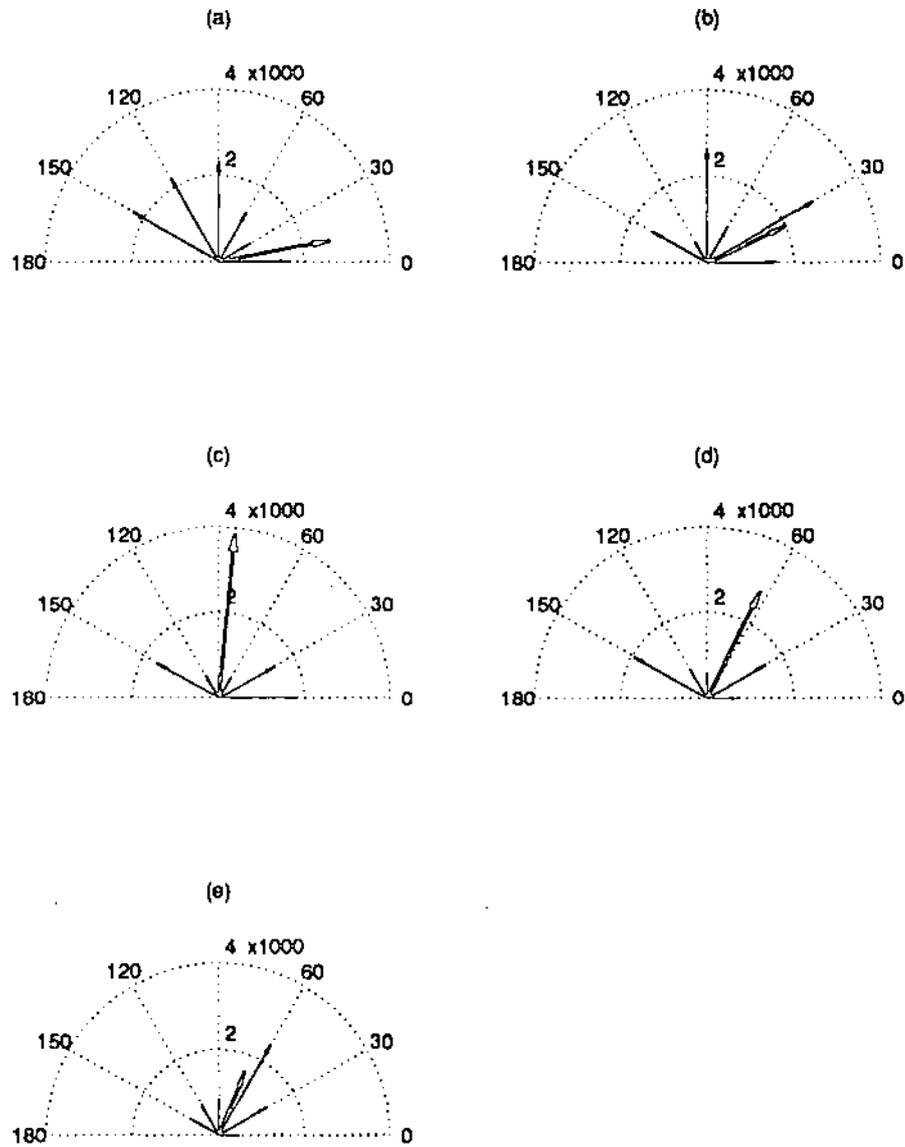


Figure 3. Population vectors derived from the sinusoidal regression curves depicted in Figure 2.

Response Manifolds

While vector representations have proven to be a very useful way to conceptualize processing in neural systems (Gallistel, 1990, Steinmetz et al, 1987), we have used two

dimensional manifolds to represent responses of populations of neurons to sensory stimulation (King et al., 1994). While the procedures used in the previous paper resulted in a spectral representation of the data, the procedures in the present paper results in a spatial representation of the data. An analogous representation of these response properties can be displayed as a three dimensional manifold (a geodesic).

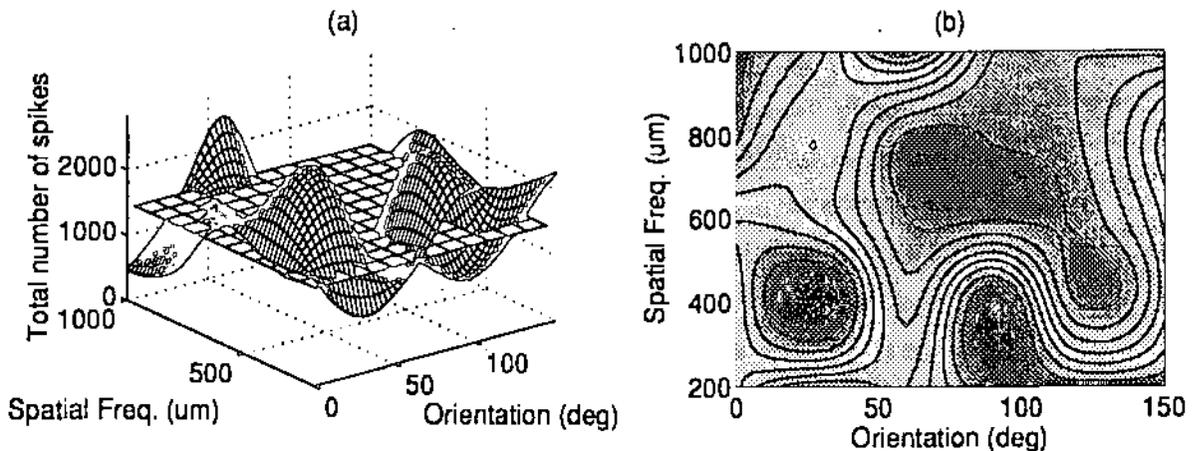


Figure 4. Response manifold (4a), and its associated contour map (4b) of population responses at one location in barrel cortex. Horizontal axes represent the five spatial frequencies and six orientations, respectively. The vertical axis represents number of bursts at each of the 30 combinations of stimulation parameters. The data are the same as those used to calculate population vectors in Figures 2 and 3.

To this end we constructed three dimensional manifolds in terms of distribution of number of bursts as a function of spatial frequency and orientation. Data were plotted as a function of the five spatial frequencies and six orientations used in our experiments. Neighboring points were connected using a cubic spline interpolation algorithm. Manifolds corresponding to the data set presented in Figures 2 and 3 are represented in Figure 4. Such manifolds have been constructed for each of the 20 locations from which we have recorded.

The initial advantage of this representation of the data is that a single manifold represents the data contained in five population vector representations. Second, the response manifold more clearly distinguishes between excitatory and inhibitory regions of the geodesic space.

One should notice that the manifold is constructed from the raw data points, and smoothed using a third degree polynomial. The population vectors, on the other hand, are fit to a cosine function. Therefore, the response manifold better represents changes in neuronal response from one orientation to another. The question is whether such changes in firing rates should be so represented or "smoothed" as with the population vector analysis. The most obvious case of such "smoothing" is depicted in Figure 2b. While the regression curve represents a single maximum at approximately 40° , the data indicate two maxima at approximately 30° and 90° , respectively.

To determine whether these points should be retained or smoothed, an experiment was conducted in which 10 baselines were recorded during stimulation of the facial nerve, but no grating was in place. Ten recordings were made in the following sequence of conditions: AAAAABBBBBBABABABAB, where "A" represents a baseline measured without stimulation and "B" represents a baseline recorded with seventh nerve stimulation, but no grating present. As there was no systematic difference between the sequential and alternating conditions, all As and Bs, respectively, were combined to calculate means and standard deviations for each of no stimulation and stimulation baselines. As in the 20 experimental locations, stimulation without a barrier resulted in an approximately fourfold increase in neural activity over the no stimulation baseline (from 500 units to 1700 units per recording interval). At firing rates comparable to those in the present experiment (20-60 spikes per second), the standard deviation of firing rates was 357 spikes per 50 second interval. This variation in baseline would not include the points at 30° and 90° orientations from Figure 2b. (That is, these points fall outside a ± 2 standard deviation range.) Therefore, a response manifold based on sinusoidal regression would "oversmooth" the data unless higher harmonics were used in the regression to accommodate multiple maxima and minima. Further, if one looks across different spatial frequencies at each orientation, then multiple maxima and minima also occur. It therefore seems that population vectors, representing a single maximum (or "best response") results in an oversimplification of the data.

Discussion

This representation complements that presented in King et al. (1994) for the spectral domain. Cortex may well be simultaneously processing in both domains. The procedures of our first study generated movement in the environment, and thereby resulted in a spectral representation. In the present study, movement of the animal's whiskers resulted in a manifold with a spatial representation.

This study further indicates that representations of the data based on population vectors oversimplify the data. The fact that orientation "tuning", is infrequently observed in the barrel cortex (Simons and Carvell, 1989) is not surprising according to a view of cortical processing based on a distributed model as suggested in Pribram (1991), and represented in the response manifolds presented in this paper.

The next step is to awaken the animal. Unit recordings from chronic preparations in which the animal is trained to systematically sweep its vibrissae across a grating will allow us to correlate the representation of population vectors with the animal's actual behavior. Nicolelis et al. (1993) have pioneered the development of such chronic preparations.

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