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Representation of Cortical Unit Response to Texture and Orientation of Tactile Gratings in the Rat

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Abstract. Data obtained as a result of experimental procedures must become encoded and/or displayed in some form to assure communication. The decision as to what form is chosen is not a trivial one. Interpretation hangs on that decision. We have chosen two forms of display of data obtained in mapping receptive fields of units in somatosensory cortex responding to whisker stimulation. Vector representation is a popular form that allows ready interpretation, communication and manipulation. However, the vector representation is less complete than one that maps the entire field in terms of spectral density. Spectral density maps provide a deeper understanding of the response of the cortex because of their greater detail but suffer from being highly convoluted and therefore difficult to use per se in further analyses.

1. Introduction

The whisker system of the laboratory rat has emerged as a model system for the study of cortical processing. Although the system was first studied systematically by developmental neuroanatomists, it quickly became the staple of neural systems analysis (e.g. SIMONS and CARVELLE, 1989), and more recently has attracted those interested in understanding processing in restricted regions of neural tissue (NICOLELIS *et al*., 1997; NICOLELIS, 1997). For example, NICOLELIS has argued that local representations of whisker stimulation in both thalamus and primary somatosensory cortex are more distributed and plastic than previously thought. Similarly, SIMONS and his collaborators have begun to develop models of local processing within primary somatosensory (barrel) cortex (SIMONS and CARVELLE, 1989).

That distributed processing over groups of neurons accounts for some aspects of cortical processing is not under dispute, nor is the idea a new one (PRIBRAM, 1971, 1991; GEORGOPOULOS *et al.*, 1983; GALLISTEL, 1990). It is the nature of this distributed processing (and the particular methods used to collect and display unit recordings) that remains unsettled. For example, through his use of large arrays of low impedance microelectrodes to record from large populations of neurons, NICOLELIS (1997) has discerned spatio-temporal codes to represent different dimensions of vibrissal (whisker) stimulation. On the other hand, SIMONS (1995) recording discharge patterns from single units within cortical barrels in response to patterns of stimulation among several (up to four) whiskers described excitatory and inhibitory interactions among comparatively small groups of neurons. This latter approach is consistent with those used to develop models of neuronal interactions within primary visual cortex (SAUL and HUMPHREY, 1992; MURTHY and HUMPHREY, 1999; SAUL, 1999).

A further issue is raised when one tries to describe the population response within a patch of cortical tissue. Traditionally, investigators have represented a population code in terms of vectors. For example, GEORGOPOLOUS *et al.* (1982) found that a vectoral representation of unit activity in primary motor cortex accurately represented the direction of arm movements by monkeys. When the hand of a primate moves through space, the activity of any given motor neuron is highest for a particular direction of movement, and decreases as the direction of movement departs from this preferred orientation. The preferred orientation can be represented as the peak of a cosine wave with values approximating the preferred orientation forming a crescendo to the peak. In this manner preferred orientations can be represented by a vector, which in a field of 360 degrees, points in a cell's preferred direction. The magnitude of a cell's response is reflected in the length of the vector, thus weighting the contribution of each neuron in a population. Vectors of individual neurons are then combined to produce a population vector which points in the direction of movement, its length proportional to the instantaneous speed of movement (GEORGOPOLOUS *et al.*, 1983).

Others have represented the population code in terms of a spatially distributed surface distribution of unit activity. For example, WILSON and MCNAUGHTON (1993) found that groups of neurons in the hippocampus demonstrated spatially distinct patterns of activity when rats moved in a particular direction in a familiar environment as compared the animal's movement in a novel environment. NICOLELIS *et al.* (1997) similarly demonstrated reproducible spatiotemporal patterns of discharge across a population of barrel cortex neurons in response to whisker stimulation. More recently KING *et al.* (2000) have used unit recordings from barrel cortex to construct surface distributions to represent patterns of cortical activity in somatosensory cortex. Through the use of a model based on signal processing principles, they showed that these surface distributions represented cortical processing in the spectral domain. Therefore, both spatiotemporal and spectral codes may operate simultaneously within an area of cortical tissue.

The purpose of the current experiments is to investigate the relative advantages and limitations of vectors and surface distributions in the representation of texture and orientation in the population responses of units composing the rat's barrel (somatosensory) cortex.

2. Procedures

2.1. Subjects

A total of 21 Holtzman albino rats, five male and 16 female, 80–140 days old and weighing 275–540 grams were used in two sets of experiments. All animals were maintained on ad libitum food and water. Twelve hours before surgery rats were deprived of food and water to reduce the risk of surgical (anesthesia) complications. The rats were treated in accordance with the APA guidelines for Ethical Principles for the Use of Vertebrate Animals in Research.

In addition, all experimental protocols were reviewed and approved in advance by the university's Animal Care and Use Committee.

2.2. Apparatus, recording and survey

Prior to surgery each rat was anesthetized with , an ip. injection of sodium pentobarbital (50 mg/ml) at a dose of 50 mg/kg body weight, plus 0.05 cc of atropine sulfate (0.4 mg/ml). Incremental doses of pentobarbital were administered as needed to maintain sluggish corneal and tail pinch reflexes.

In many experiments, including our own, that explore the organization of the somatosensory systems in rats, passive stimulation of the whisker system is accomplished by passing the stimulus across the whiskers. This is similar to drifting gratings across the visual field in explorations of the visual system. In the current experiment we sought to take a step in the direction of what a rat actually does to explore his world with his whiskers. In order to approximate that condition of active whisking in anesthetized animals electrical stimulation of the buccal nerve was chosen.

To this end, an incision was made in the right cheek of the animal approximately one cm behind the mystacial (whisker) pad to expose the buccal nerve (ventral branch of the facial nerve). Once the nerve was dissected from the surrounding tissue, the nerve was connected by silver electrodes to a square-wave stimulator. The stimulator was powered by a 9 volt battery and was set to pulse the nerve at frequencies of 4, 8, or 12 stimulations per second.

For the brain recording, another incision was made along the midline of the scalp to expose the skull. The bone over the somatosensory cortex was drilled at a location approximately 4 mm posterior and 5–7 mm lateral to bregma. A microelectrode (A-M Systems Inc., Everett, WA) of 2–3 MOhm impedance was angled at 15 degrees and lowered to the surface of the intact dura with the aid of a Kopf Stereotaxic instrument. The exposed area of brain was bathed in 0.9% saline solution during the course of the experiment.

After the recording microelectrode was located just above the surface of the dura, the rat was placed in a Faraday cage (to reduce electrical interference). Then the microelectrode was lowered through the dura into the brain with the aid of a hydraulic micromanipulator (Trent Wells, South Gate, CA) until spikes were obtained (usually at depths between 300 and 900 microns. Raw data were passed through a 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, then amplified with a gain

of 20,000. For each location we attempted to identify the principle whisker for the unit responses that we observed.

One of five teflon textured disks was then placed against the rat's whiskers at a distance of 1–2 cm from the animal's face. Due to the fact that it is difficult to place the disks close to the rat's smaller more anterior whiskers, locations that generated responses from the larger, more posterior whiskers were used for recording. The disks (Cupp Tool Corporation, Blacksburg, VA) consisted of gratings with widths of 200, 400, 600, 800 and 1000 microns, respectively. The disks were rotated to orientations of 0, 30, 60, 90, 120 and 150 degrees relative to horizontal.

Baseline neural activity as a function of the rate of stimulation of the buccal nerve, was recorded prior to the insertion of each of the five disks. Then experimental recordings were made for each of the five disks at each of the six orientations. For nine of the animals (20 locations) only the 8 Hz nerve stimulation rate was used. For the other 12 animals (12 locations) three different buccal nerve stimulation rates were used for each combination of disk and orientation. Therefore a total of 36 recording sessions made up these experiments. The order in which the textured disks were used was randomized before recording from each location. For each textured disk, stimulation of the nerve began with either the 4 Hz stimulation rate and ascended to the 12 Hz rate, or began with the 12 Hz rate and descended to the 4 Hz rate. For each successive orientation the order of progression through the three stimulation rates was reversed from that of the previous orientation. The orientation of the disks always began with the angular orientation of 0 degrees and progressed up to the angular orientation of 150 degrees. Each disk was loosely mounted to a piece of plexiglass so that angular orientation could be systematically changed without disturbing the placement of the disk against the animal's whiskers.

Each recording lasted for 25 seconds. Approximately 60 seconds elapsed between recordings to allow changing the disk's orientation and the stimulation frequency. A longer period was required (up to 5 minutes) when the disk had to be changed. All recordings were digitized at a sample rate of 30,000 and stored to a 486 computer using Brain Wave Software (Data Wave Systems, Longmont, CO). At the end of a recording session a small lesion was made at the recording electrode site by passing a 2 milliamp current for approximately 0.5 second. Once awake, the animal was maintained on ad libitum food for approximately 2 weeks, then sacrificed with an overdose of pentobarbital, and perfused transcardially with formal saline. The brain was removed and placed in 10% buffered formalin until frozen sections could be made. Each brain was placed in a 40% sucrose solution for seven days before slicing. Brain tissue was sliced coronally in 25 micron sections with a Cryocut 1800 cryostat (Cambridge Instruments, Heidelburg, Germany) and stained with thionin.

All data were first digitally filtered at a highpass of 300 Hz to remove low frequency artifact generated by the stimulator. In-house software was used to separate spikes on the basis of spike amplitude and descending slope. Next, spikes generated over the 25 second recording interval were counted for each data file. Thus in experiments in which nerve stimulation rate was not varied, 30 files were recorded for each location. In those experiments in which nerve stimulation rate was varied, there were 90 files for each experimental location.

3. Results

3.1. Baseline measurements

Baseline measurements were taken under both buccal nerve stimulation (no texture disc present) and non-stimulation conditions. Our results showed that whisking produces an increase in unit activity at all stimulation rates. These data also indicate that the 12 Hz nerve stimulation rate generates significantly more spikes than the 4 and 8 Hz stimulation rates at each of the nine locations in which all three whisk rates were tested. (Results of the Analyses of Variance are available from the authors.)

3.2. Surface distributions

Analyses of the baseline data indicated that baseline spike counts change systematically with buccal nerve stimulation rate. Therefore, baseline rates have to be taken into account before the experimental data, consisting of stimuli differing in orientation and in texture (that is, groove width measured as spatial frequency) can be interpreted. Therefore, a "Spike Factor" was used to allow for direct comparisons of unit activity across different rates of buccal nerve stimulation. The Spike Factor (SF) is defined as: (Ts–Bs)/Bs where Ts is the total number of spikes during a particular stimulation condition, and Bs is the number of baseline spikes during buccal nerve stimulation with no textured disc present.

Surface distributions of the spike factor measure were constructed for each location. A separate set of surface distributions was constructed for each brain location. Each set contained surface distributions and their associated contour maps for each of the three buccal nerve stimulation rates. Figure 1 portrays these three dimensional surface distributions and their associated contour maps. The surface distributions were derived by a cubic interpolation (spline) procedure. The contour maps were abstracted from the surface distributions by plotting contours in terms of equal numbers of spikes per recording interval (100 msec).

3.3. Sinusoidal regression and population vectors

The same data were used to generate sinusoidal regression curves and population vectors for preferred orientation and texture. The population vector was computed as that orientation at which the greatest change from baseline firing was achieved by the data fit to a cosine wave using a least squares regression. Both maxima (/*) indicating excitatory and minima (/) indicating inhibitory changes from the idealized regression were plotted. As there were six orientations, six regressions were plotted for each buccal nerve stimulation rate (4 Hz, 8 Hz, 12 Hz).

An example at 4 Hz is shown for each of two brain locations (recording sites): A set of regression curves and the associated population vectors is presented in Figs. 2 and 3. Essentially two to five response peaks were obtained for each combination of buccal nerve stimulation rate, texture and orientation. With this procedure, sinusoidal regression indicated a preferred orientation that is within one standard deviation of baseline activity for the each buccal stimulation rate.

However, one can also see that within a given location the "preferred" orientation changed not only as a function changes in buccal nerve stimulation rate, but also as a

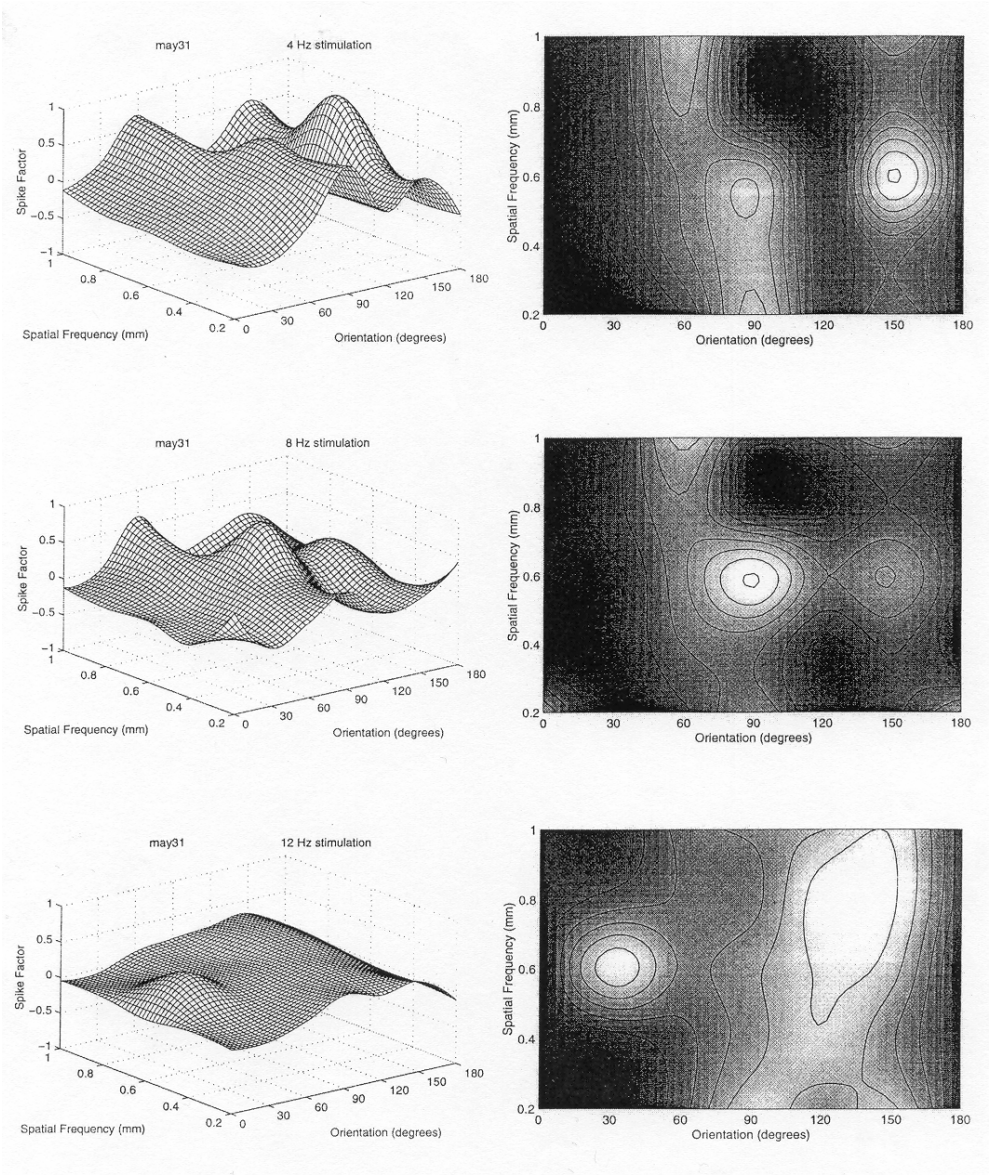

Fig. 1. An example for the three dimensional representation of the surface distribution and associated contour map of the electrical response to buccal nerve stimulation. The surface distributions were derived by a cubic interpolation (spline) procedure. The contour maps were abstracted from the surface distributions by plotting contours in terms of equal numbers of spikes per recording interval (100 msec). The buccal nerve stimulation whisked the rat's whiskers against teflon discs whose textures (groove widths that determined the spatial frequency of the disc) varied from 200 to 1000 microns and whose grooves were oriented from 0 to 180 degrees. Separate plots are shown for each frequency of buccal nerve stimulation 4 Hz, 8 Hz, and 12 Hz (top to bottom).

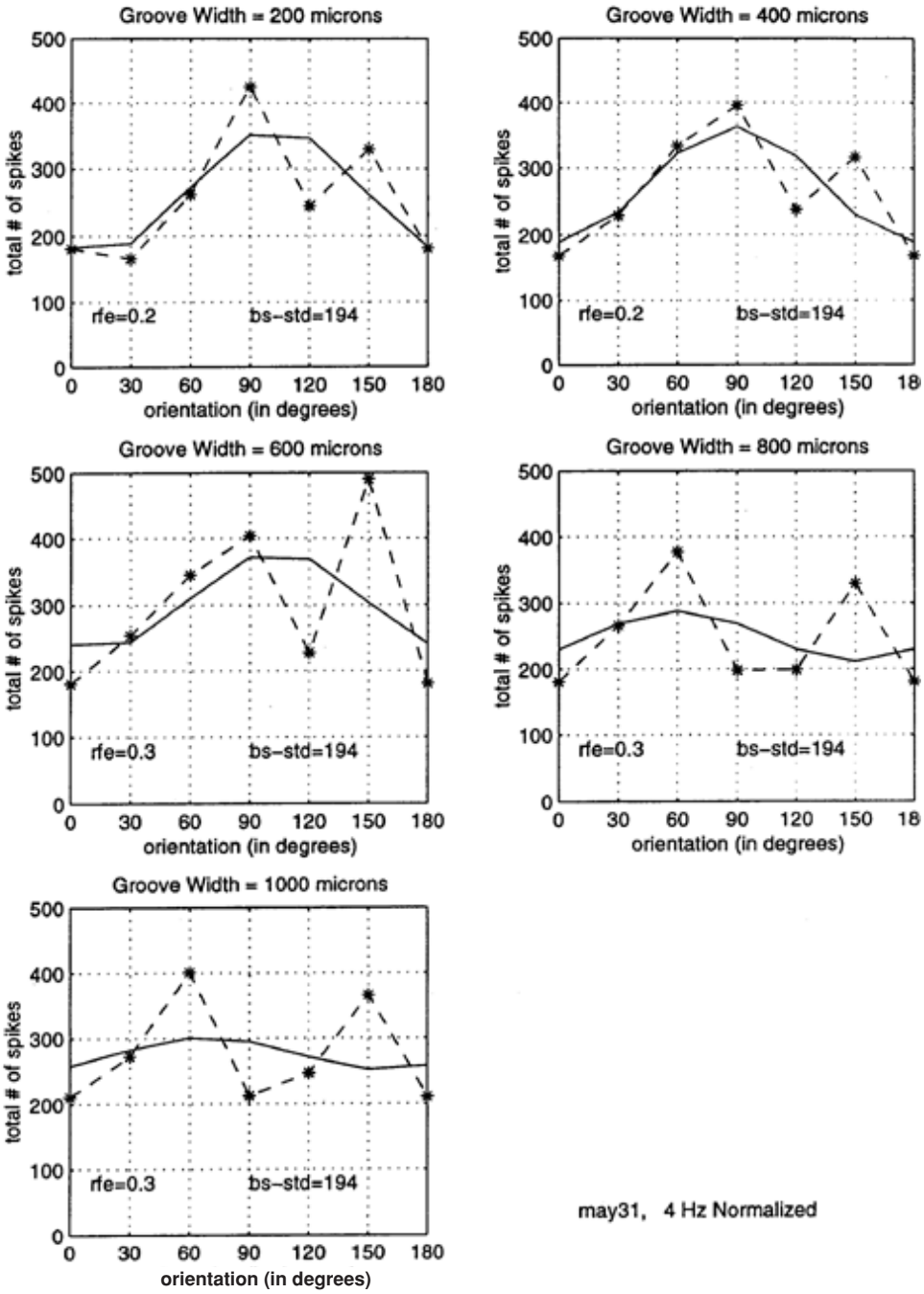

Fig. 2. The cosine regressions of the total number of spikes for the orientation of the stimulus for the 4 Hz condition are shown.

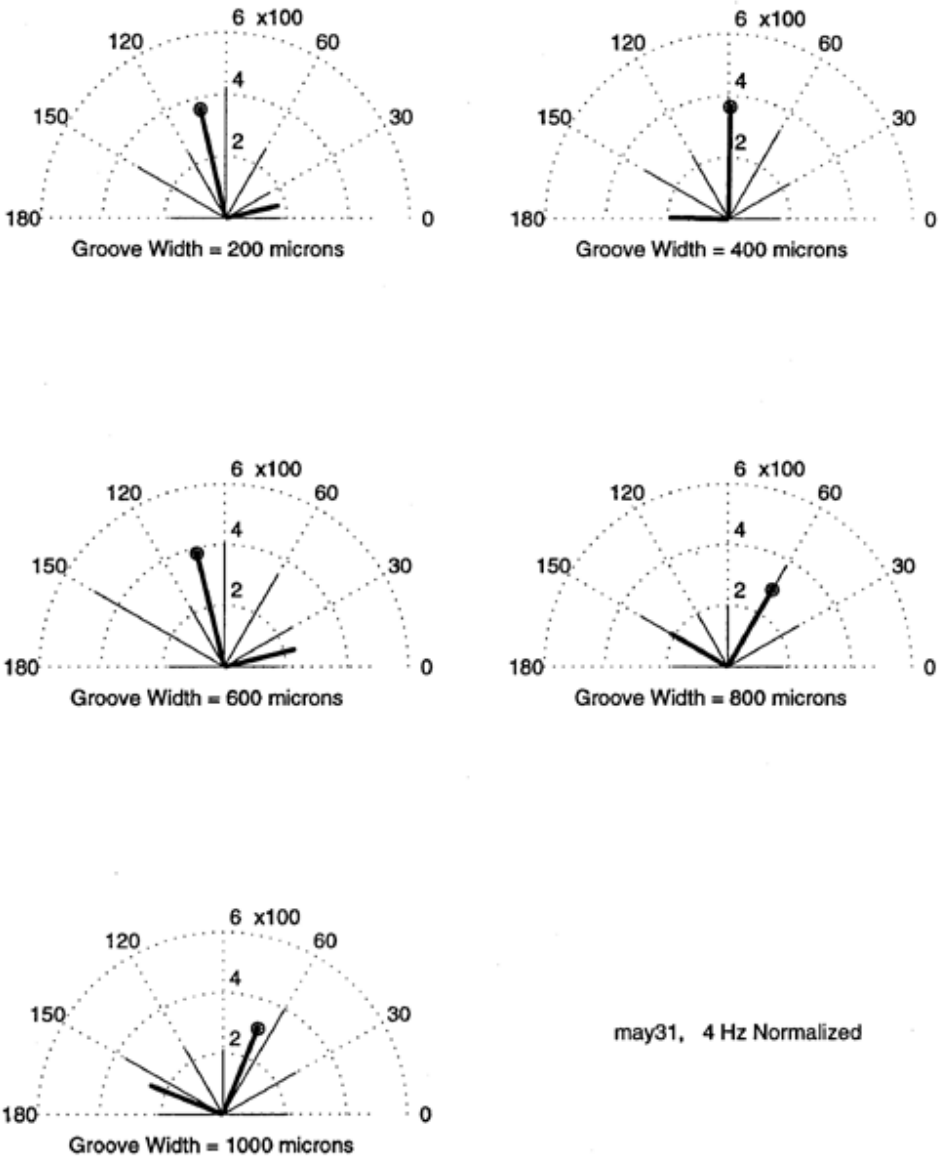

Fig. 3. The angle at which the maximum (/*) and minimum (/) of greatest change from baseline firing rate occurs (again for 4 Hz) is given.

function of changes in texture. Thus, "preferred" orientation changed as a function of changes in the stimulation parameters. When inspecting data for a particular buccal nerve stimulation rate, none of the locations possessed exactly the same preferred orientation across texture gratings.

4. Discussion

In our previous paper we mapped the surface distribution of electrical field potentials in dendritic arbors in terms of spectral density. Most studies of this sort have analyzed data in terms of vectors. We undertook the current study to determine the relationship between vector representations and spectral density maps. We had no difficulty in constructing vector representations from regression equations fitted to the maxima and minima of the wave forms constituting the spectral maps.

We found that a "preferred" orientation can reasonably be constructed for each texture grating, and that a population vector can be extracted displaying that "preferred" orientation. However, the preferred orientation changes as a function of texture grating. Further, the pattern of change across texture gratings is different for each rate of buccal stimulation.

If analyzed only for a particular texture grating at a particular buccal nerve stimulation rate, one would be left with the impression that each location represents a feature detector for a particular orientation. This would be misleading since the unit responses represented by the surface distributions show that neural activity at a location within barrel cortex changes as a function of texture grating, texture orientation and buccal nerve stimulation rate.

Thus population vectors are a reasonable choice when one is trying to extract the neural representation of a single dimension as in studies of movement. However, in the study of representations of multidimensional stimuli (as in the present experiments) surface distributions are a more informative choice.

We conclude that each representation has virtues and drawbacks: The spectral density maps are more complete but often convoluted and difficulty to use for further analyses (we had one map that looked somewhat like a Klein bottle); the vector representation is simpler to interpret and use for further processing, but does not provide a complete picture of what is happening in the dendritic arbor.

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