The Journal of Neuroscience, May 1994, 14(5): 2870–2892

# Power Spectrum Analysis of Bursting Cells in Area MT in the Behaving Monkey

**Wyeth Bair,[1] Christof Koch,[1] William Newsome,[2] and Kenneth Britten[2]**

[1]Computation and Neural Systems Program, California Institute of Technology, Pasadena, California 91125 and
[2]Department of Neurobiology, Stanford University School of Medicine, Stanford, California 94305

**It is widely held that visual cortical neurons encode information primarily in their mean firing rates. Some proposals, however, emphasize the information potentially available in the temporal structure of spike trains (Optican and Richmond, 1987; Bialek et al., 1991), in particular with respect to stimulus-related synchronized oscillations in the 30–70 Hz range (Eckhorn et al., 1988; Gray et al., 1989; Kreiter and Singer, 1992) as well as via bursting cells (Cattaneo et al., 1981a; Bonds, 1992). We investigate the temporal fine structure of spike trains recorded in extrastriate area MT of the trained macaque monkey, a region that plays a major role in processing motion information. The data were recorded while the monkey performed a near-threshold direction discrimination task so that both physiological and psychophysical data could be obtained on the same set of trials (Britten et al., 1992). We identify bursting cells and quantify their properties, in particular in relation to the behavior of the animal.**

**We compute the power spectrum and the distribution of interspike intervals (ISIs) associated with individual spike trains from 212 cells, averaging these quantities across similar trials. (1) About 33% of the cells have a relatively flat power spectrum with a dip at low temporal frequencies. We analytically derive the power spectrum of a Poisson process with refractory period and show that it matches the observed spectrum of these cells. (2) About 62% of the cells have a peak in the 20–60 Hz frequency band. In about 10% of all cells, this peak is at least twice the height of its base. The presence of such a peak *strongly* correlates with a tendency of the cell to respond in bursts, that is, two to four spikes within 2–8 msec. For 93% of cells, the shape of the power spectrum did not change dramatically with stimulus conditions. (3) Both the ISI distribution and the power spectrum of the vast majority of bursting cells are compatible with the notion that these cells fire Poisson-distributed bursts, with a burst-related refractory period. Thus, for our stimulus conditions, no explicitly oscillating neuronal process is required to yield a peak in the power spectrum. (4) We found no statistically significant relationship between the peak in the power spectrum and psychophysical measures of the monkeys' performance on the direction discrimination task. (5) For cells firing bursts, ROC (receiver operating characteristic) analysis shows that the "event" rate, where an event is either a single burst of spikes or an isolated spike, is on average a more sensitive measure of visual stimulus direction than the total number of spikes, used previously (Britten et al., 1992), implying that the number of spikes in a burst is less stimulus dependent than the overall firing rate or the rate of bursts.**

***[Key words: behaving monkey, extrastriate cortex (MT), oscillations, power spectrum, interspike interval analysis, bursting]***

What neural code is used by the brain to decipher sensory events and translate them into a percept of the visual scene? Because the mean firing frequency in response to a sensory stimulus is reproducible under identical stimulus conditions and varies predictably and smoothly with such stimulus parameters as velocity, contrast, orientation, and so on, it is widely held to be the primary variable relating neuronal response to sensory experience (Lettvin et al., 1959, or the 5. dogma in Barlow, 1972). This belief is supported by the existence of a quantitative relationship between the firing rates of single cortical neurons and psychophysical judgements made by behaving monkeys (Werner and Mountcastle, 1963; Barlow et al., 1987; Newsome et al., 1989a; Vogels and Orban, 1990; Zohary et al., 1990; Britten et al., 1992). Some electrophysiologists have focused on the idea that the detailed dynamics of the neuronal response may carry significant information (e.g., Poggio and Viernstein, 1964; Chung et al., 1970; Strehler and Lestienne, 1986; Optican and Richmond, 1987; Abeles, 1990; Eskandar et al., 1992; Zipser et al., 1993; see also Bialek et al., 1991). A great deal of attention has recently been given to the reports of stimulus-induced semisynchronous neuronal oscillations in the 30–70 Hz range in the visual cortex of the anesthetized cat (Eckhorn et al., 1988; Gray and Singer, 1989; Gray et al., 1989; Ghose and Freeman, 1992) and the awake monkey (Kreiter and Singer, 1992). Moreover, Gray et al. (1989) report that oscillating neurons up to 10 mm apart can be phase-locked with a phase-shift close to zero; that is, these neurons usually fire within ±3 msec of each other (for a review, see Singer, 1994).

Only a few reports have focused on the possible significance of bursting for neuronal coding. Cattaneo et al. (1981a,b) report that complex (but *not* simple) cells in area 17 of anesthetized

Received June 21, 1993; revised Oct. 20, 1993; accepted Oct. 26, 1993.

We thank a number of individuals with whom we discussed these findings over the last two years, in particular Francis Crick, Joel Franklin, Ehud Zohary, and William Softky. This work was supported by the Office of Naval Research, the Air Force Office of Scientific Research, the National Science Foundation, the National Eye Institute, and the McDonnell-Pew Program in Cognitive Neuroscience. W.B. received support from a National Science Foundation Graduate Fellowship and is now supported by the L. A. Hanson Foundation. K.B. received support from an NIMH training grant to the Department of Neurobiology at Stanford University.

Correspondence should be addressed to Wyeth Bair, Computation and Neural Systems Program, 139-74, Division of Biology, Pasadena, CA 91125.