*Figure 15.* Comparison of spike train statistics for burst cell *j001* to those from a simple numerical model. The statistics for the neuron (*left column*) were computed by averaging over 15 trials at $c = 0.256$. The spikes (*top trace*) are more clustered than random, as demonstrated by the excess (62%, truncated on plot) of intervals in the 1, 2, and 3 msec bins of the ISI. The PSTH is particularly noisy because spikes occur in bursts. The corresponding numerical model (*right column*) is an extension of that used for nonburst cells (see Fig. 11) in which each spike generated from an underlying Poisson process with refractory period is now replaced by a burst of spikes where the burst length and the temporal structure of spikes within the burst are chosen to match the data (see Results). Similar to the nonburst model, this is not intended to be a best fit to the data, but a demonstration that a process firing bursts randomly with a burst-related refractory period can account qualitatively for the location, size, and shape of the peak near 33 Hz and the dips near the origin and at higher frequencies. The *solid curve* superimposed on the neuron's spectrum (*bottom left*) corresponds to the analytical power spectrum given by Equation 17 with $\lambda = 20.4$ events/sec, $\sigma = 12.5$ msec, $A = 550$ spikes/sec, and $L = 2.55$ msec. This cell is one of the 10% of cells whose peak in the 40 Hz range is twice as tall as the dip at higher frequencies.

Neuron

Model
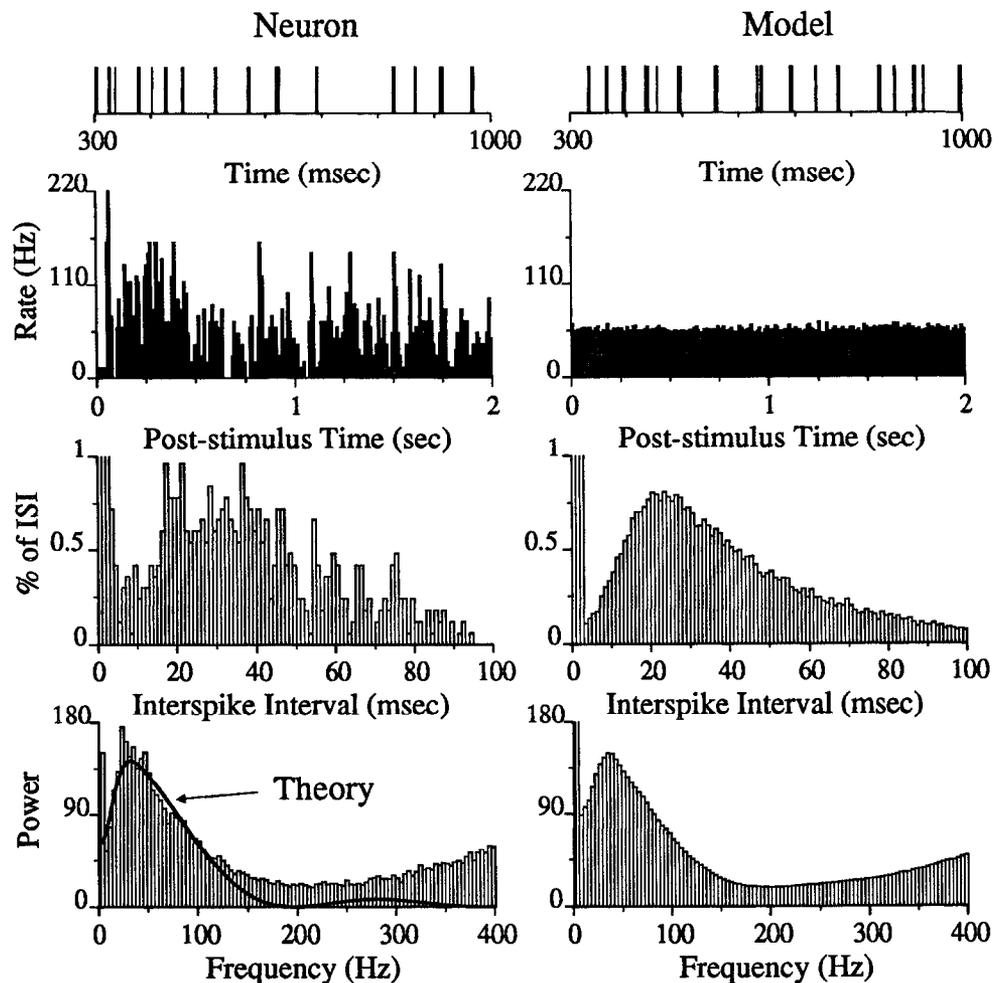
process, the variance should be equal to the mean, while for a fractal point process the variance can be larger than the mean (Teich, 1992; Usher et al., 1994). A number of studies have used this measure as indicative that the firing of cortical cells in striate and extrastriate monkey cortex are consistent with a description of spiking as a Poisson process (Tolhurst et al., 1983; Parker and Hawken, 1985; Vogels et al., 1989; Zohary et al., 1990; Snowden et al., 1992). Thus, at least for long spike trains in the trained monkey, the associated ISI and the power spectrum are compatible with the notion that the underlying point process can be described by an almost memoryless Poisson process with refractory period.

Bursting cells

More complex temporal dynamics are shown by the large fraction of cells (131 of 212) that frequently discharge in bursts, that is, two to four spikes within 2–8 msec or less (see the raster plots in the top row of Fig. 2). The fraction of the total number of spikes in a train that are less than 3.5 msec apart (our measure of "burstiness," B) ranges from an extreme value above 60% to 0. Unfortunately, we were not able to separate our 212 cells into two clearly segregated subpopulations using this or a related measure, since the distribution of cells varies continuously from strongly bursting to nonbursting (Fig. 3). Thus, any grouping of cells into "bursting" and "nonbursting" will be arbitrary to some extent. However, the amount of burstiness associated with in-

dividual cells remains relatively constant for all visual stimuli tested and, in particular, is independent of motion coherence (Figs. 5, 6, and our definition of P in Data analysis in Methods). Furthermore, we found no systematic relationship between burstiness and the onset or the duration of the experiment for the majority of cells. Finally, it should be remembered that due to the perceptually demanding nature of the experiment, the monkey had to be highly alert throughout each trial. These observations argue against the possibility that the bursting is related to the onset of drowsiness or sleep.

Intracellular current injection into cells in rodent slices of sensory-motor cortex has revealed three distinct types of neurons (McCormick et al., 1985; Connors and Gutnick, 1990; Agmon and Connors, 1992). The majority of these *in vitro* cells respond to the sustained current by a train of action potentials, which adapt within 50–100 msec to a more moderate discharge rate ("regular-spiking" cells). A second class of neurons, only infrequently recorded from, is capable of high discharge rates with little or no adaptation ("fast-spiking" cells). A third set of neurons respond to the depolarization by generating a short burst of two to four spikes, followed by a long hyperpolarization. This cycle of burst and hyperpolarization persists for as long as the current stimulus persists ("intrinsically bursting"). In slice tissue, the regular-spiking cells correspond to pyramidal neurons, fast-spiking cells to GABAergic nonspiny stellate cells, and the intrinsically bursting cells to layer V pyramidal cells (Agmon