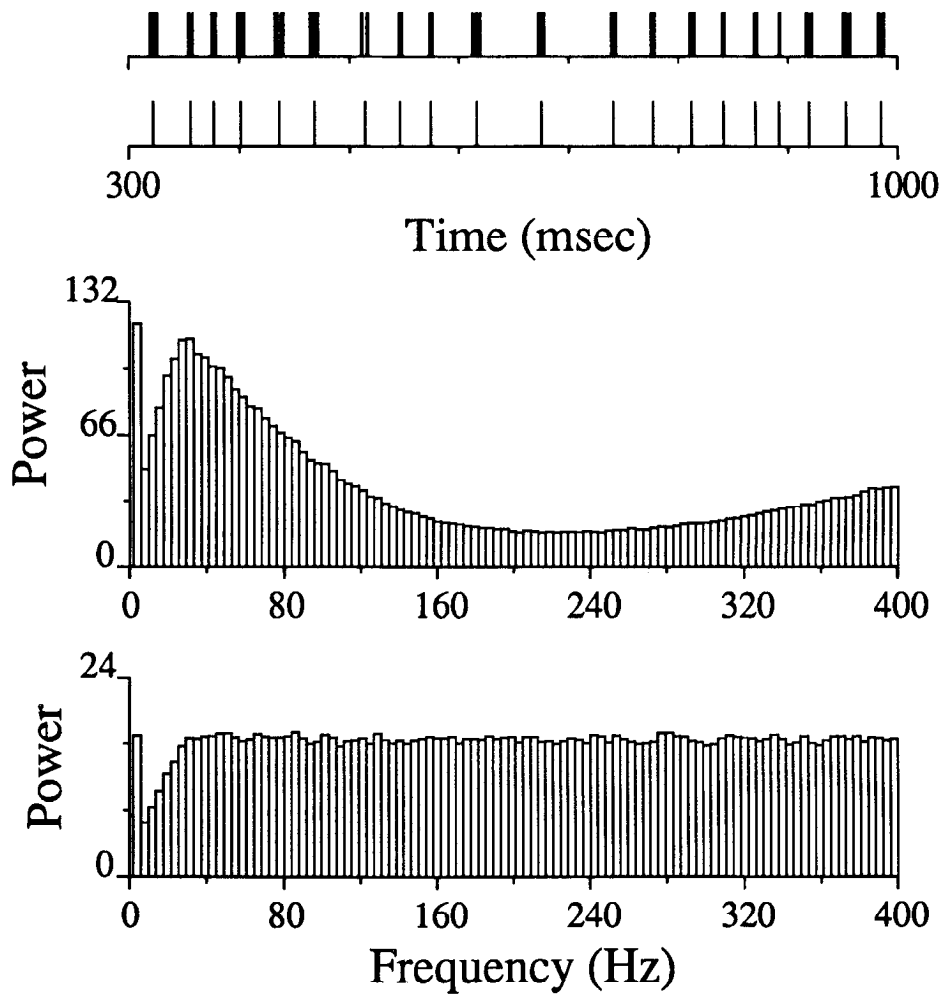

Figure 17. A demonstration that a peak in the power spectrum may be due to the presence of bursts, rather than regularity in their temporal alignment. When bursts from a neuron (*upper impulse plot*) are replaced by single spikes (*lower impulse plot*), the peak in the original power spectrum (*upper spectrum*) disappears (*lower spectrum*). A burst is defined as the longest subtrain of consecutive action potentials with no ISI greater than 8 msec (using 3 msec gives a very similar result). Each burst is considered to be an event at the mean occurrence time of all action potentials within that burst. This supports our notion that the bursts themselves are randomly placed (with a burst-related refractory period) and are *not* locked to a regular oscillatory pattern.

a process that randomly fires bursts followed by a refractory period is then given by the product of these two equations (Eq. 17). Given that one function is increasing with f and the second one decreasing, the product of the two will have a local maximum. In our case, if bursts are treated as boxcar functions that are about 4 msec wide, occur at a frequency of between 10 and 20 Hz, and are followed by a refractory period of between 10 and 25 msec (see table, Fig. 16), the peak in $S'(f)$ lies in the 20–50 Hz range (Fig. 15). These values were obtained from the distribution of the bursts themselves and can also be justified on biophysical grounds (Connors and Gutnick, 1990). We find it surprising to what extent simple analytical models can account for the observed ISI distributions and power spectra of bursting cells at frequencies less than 100 Hz. Our computer simulation of such a firing process, which differs from the analytical model by resolving the boxcar bursts into individual impulses and the renewal density into a stochastic refractory period, gives a better match of $S'(f)$ at higher frequencies.

If the occurrence of every burst in a spike train is replaced by a single action potential throughout the entire spike train (and isolated action potentials remain single spikes), the power spectrum $S'(f)$ totally changes its character (Fig. 17), from a spectrum with a peak to a flat spectrum with a dip at low frequencies, compatible with our notion that bursts themselves are distributed according to a Poisson distribution with a burst-related refractory period. If, for instance, the peak in the spectrum is due to periodically occurring bursts, our procedure should have revealed a spectrum with a clear peak, rather than the flat spectrum with a dip. We believe that our method of replacing bursts with "events" is a useful diagnostic tool for removing the confounding influence of bursts on the power spectrum, revealing the underlying dynamics.

Another way in which a neuronal "oscillator" model differs from our "random burst" model is in the distribution of IBIs; the former gives rise to an IBI distribution tightly clustered around the inverse of the oscillation period, while the latter model is associated with a decaying exponential IBI modified by a refractory period.

As discussed in the previous section (Bursting cells), our data are consistent with the random burst model (Fig. 14); however, the two models are difficult to distinguish when the oscillator model becomes less regular. We can show using computer-generated data what is expected in the case of the oscillator model. Figure 18 demonstrates the appearance of the ISI and spectrum $S'(f)$ in the case of a neuron which fires isolated spikes (top) or bursts (bottom) with an approximately Gaussian ISI or IBI. In the case of isolated spikes, the power spectrum remains flat with a dip related to the apparent refractory period induced by the Gaussian ISI for distributions with a broad range of SDs ($\sigma \geq 12$ msec). Once the SD becomes smaller (Fig. 18, top; $\sigma = 7$ msec), a prominent peak arises in the spectrum (see Fig. 18, upper right arrow) related to the inverse of the mean of the