Figure 18. The difference between peaks in the power spectrum due to regular oscillation and peaks due to bursts. The *top six plots* show computer-generated data for the Gaussian ISI model with a mean of 25 msec. The *left column* shows a series of ISI histograms in which the SD, σ, of the Gaussian distribution is varied. For $\sigma > 12$ msec, there is no observable peak in the power spectra (*right column*), only a dip due to the apparent refractory effect imposed by the Gaussian. At $\sigma = 12$ msec, a peak is just beginning to form at 40 Hz (the inverse of the mean of the ISI), and as σ decreases further, the peak (shown by *arrow* for $\sigma = 7$ msec) rapidly increases in size. A similar progression occurs for the Gaussian IBI model (*bottom set of six plots*) in which spikes from the Gaussian ISI model are replaced by bursts. However, in the Gaussian IBI model, the spectrum has a broad bulge that sweeps up to a peak near 40 Hz due to the structure of the bursts (see Fig. 17), and this peak is present for all values of σ. A narrower peak appears above the broad peak due to bursts only when the variance of the Gaussian IBI becomes small. We therefore make a distinction between a peak in the power spectrum that is due to the local temporal structure of bursts and a peak that is due to a very narrow ISI or IBI distribution, which is a sign of regularity, that is, oscillation, in the timing of spikes or bursts. It is common to see sharp peaks of the type pointed to by the *arrows* when neurons respond to artifacts in a stimulus, such as the 60 Hz refresh rate of a cathode-ray tube.

Gaussian ISI. The bottom portion of Figure 18 shows a similar result, except that the isolated spikes are replaced by bursts (see the bimodal ISI distributions) and the peak due to small values of σ is superimposed on the peak due to bursts, explained in Poisson-distributed bursts in Results. The narrow, that is, more localized, peak should be associated with oscillations since it arises due to the regularity of the ISI and *not* due to the interaction of bursting with the refractory period. Localized peaks in the power spectrum, although not observed in our data, are associated with ringing in the cross-correlogram that has been reported in data from other laboratories.

Treating bursts as signaling events

Because of the possible special relevance of bursts to signaling in the brain (e.g., Koch and Crick, 1994), we evaluated to what extent bursts convey a different message from that conveyed by a collection of individual spikes. Following Cattaneo et al. (1981a,b) and Bonds (1992), we plotted the tuning curve as a function of motion coherence for three different measures of cell response (Fig. 8*a*): spikes/second, events/second—where an event is either a burst of spikes or an isolated spike—and spikes/event. Different from Bonds (1992), the average spikes/event (which includes individual spikes) does *not* vary with motion coherence *c*. Furthermore, if the event/second response is scaled up by the mean number of spikes per event, it closely follows

the spike rate tuning curve (Fig. 8*b*). Thus, events or bursts per se have the same overall dependency on *c* as does the spike rate. However, due to elimination of the variability in the number of spikes per event when using event count, the variance of the scaled-up curve, $\mu_M(c)$, is less than the variance associated with the mean spike rate, $\mu_S(c)$, in particular around low values of motion coherence.

Because of the reduced variability of this measure, we expect it to be a more reliable indicator of the direction of motion of the stimulus. This intuition is confirmed by our analysis. We repeated the original ROC analysis (based on signal detection theory) of Newsome et al. (1989a) but allowed more flexibility in defining the signal on which the ideal observer would operate. They assumed that an ideal observer (referred to as the "Stanford" observer) counts each action potential in the 2-sec-long spike train from an MT cell and uses this number as the basis for his analysis. We added a twist to this by weighting bursts differently from single spikes. While each isolated action potential contributed 1 toward the final sum, all spikes in a burst make a total contribution of α. Setting $\alpha = 1$ implies that the entire burst only contributes as much as a single, isolated action potential toward the final decision.

The result, as shown in Figure 9, is unambiguous. Setting $\alpha = 1$, corresponding to using the event rate as the neuronal signal, improves the neuronal threshold for most of the 41 strong burst