



**Figure 11.** Comparison of spike train statistics for nonburst cell *e047* to those for a simple numerical model. The statistics for the neuron (*left column*) were computed by averaging over 15 trials at  $c = 0.128$ . The spikes (*top trace*) are less clustered than random, as demonstrated by the absence of short intervals in the ISI and the dip at low frequencies in  $S'(f)$ . The corresponding numerical model (*right column*) consists of a computer-generated Poisson process (mean rate, 86 Hz) superimposed with a Gaussian-distributed refractory period (mean, 5 msec; SD, 2.0 msec; truncated at 0 and renormalized). The model does not account for initial transients in the data and averages over the equivalent of 1000 2-sec-long trials, so the PSTH is flat and all plots are less noisy for the model. The levels of PSTH and power spectrum (above 200 Hz) demonstrate that the resulting process has an overall mean rate matching that of the neuron. The absence of short intervals in the ISIs and the dips at low frequencies in the power spectra are in close agreement between the neuron and the model. This model is *not* intended to be a best fit for the data, but rather a demonstration that the location and size of the dip are qualitatively accounted for by a random process with a stochastic refractory period of appropriate duration. The *solid curve* superimposed on the neuron's spectrum (*bottom left*) corresponds to the analytical power spectrum for a Poisson process with a refractory period (Eq. 15) with  $\lambda = 58$  Hz and  $\sigma = 3.5$  msec. Again, this qualitatively accounts for the dip.

for the observed cell to fire an action potential in the short time interval  $t_1 + t$  and  $t_1 + t + dt$ , assuming that it had fired at time  $t_1$ . For the binary data we have here (per sampling interval of  $\Delta t = 1$  msec, either zero or one spike can occur),  $p(t)$  is directly proportional to the autocorrelation function  $R(t)$ . For our nonbursting cells (e.g., Fig. 2, cell *d*),  $R(t)$  (not shown) is well fitted by a constant minus a small Gaussian around the origin, indicating a reduced probability of firing around  $t = 0$ . We therefore assume for the renewal density

$$p(t) = \lambda - \lambda e^{-(t^2/2\sigma^2)}. \quad (14)$$

Replacing  $p(t)$  into Equation 13 yields the power spectrum of

an infinite train of Poisson-distributed  $\delta$ -impulses with refractory period

$$S_{\text{Poisson}}(f) = \lambda(1 - \sqrt{2\pi}\lambda\sigma e^{-2(\pi f\sigma)^2}), \quad (15)$$

for  $f \neq 0$ . In order to ensure that  $S_{\text{Poisson}}$  is always positive, the maximum firing rate must be limited:  $\lambda \leq 1/(\sqrt{2\pi}\sigma)$ . This spectrum, parameterized by two parameters, the mean rate  $\lambda$  and the width of the refractory period  $\sigma$ , is constant for large values of  $f$  but dips toward its minimum at  $f = 0$ . Figure 10 shows  $S_{\text{Poisson}}(f)$  for  $\lambda = 40$  Hz and for  $\sigma = 1, 2, 4,$  and  $8$  msec. A longer refractory period causes a deeper trough at low frequencies. Note that this result appears at odds with intuition,