## Periodic forcing of a model sensory neuron

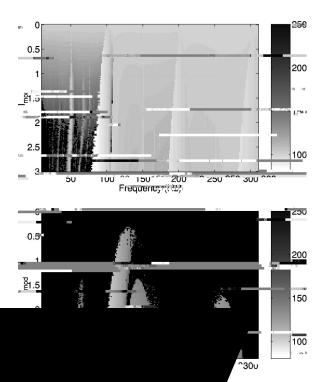
Carlo R. Laing

how these other systems respond to time-varying inputs. It is likely that this information would also help in understanding how coupled bursting systems behave, an area of recent interest [19]. Here we choose to study the ghostburster, as it is well characterized experimentally and has a clearly defined and relevant periodic input.

A two-variable model of the bursting pyramidal cell stud-

## III. SINUSOIDAL INPUT

We now investigate the effects of sinusoidally modulating the somatic input current to the ghostburster, replacing



hency of forcing space  $I_b + I_{mod} \sin(2\pi f t)$ . Top, arsting. Bottom,  $I_b = 8.7$ ; color indicates the maxi-Hz (reciprocal of the mini-

periodically modulated is bursting behavior and pericked to the forcing. Only one culated at each of the points in ity appears as the "speckles" of id dark within light regions. This when the reduced model presented ally forced, in the vicinity of the 1:1 as found to arise from a subcritical t orbit.

ee that the boundary between periodic or is deformed when  $I_{mod} \neq 0$ . It is devalues for some frequencies and to higher frequencies. This suggests that if  $I_{mod}$  is d from zero to a nonzero value, the neuron d to switch from periodic firing to bursting, depending on the value of  $I_b$  and the forcing amples of both of these types of behaviors are s. 5 and 6, where a sinusoidal modulation of I is a few hundred milliseconds. In Fig. 5, the burstpressed almost immediately and the neuron is infire at the same frequency as the forcing. In Fig. 6, requency doublet occurs within 100 ms of the onset ing. We now examine the effects of including noise in namics of the ghostburster.

## **IV. STOCHASTIC RESONANCE**

Stochastic resonance is a well-known phenomenon in onlinear dynamical systems [27,28]. Put simply, the addi-

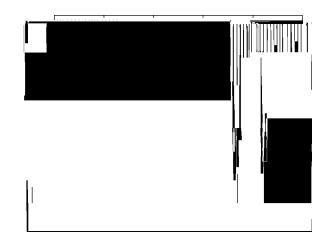


FIG. 5. A transient sinusoidal modulation of the input current switches system (A1)–(A6) from bursting to periodic firing. Parameters are  $I_b=9$ ,  $I_{mod}$  is 1.5 for 1200 < t < 1400, and the forcing frequency is 125 Hz. Top,  $V_s$  and I-90; bottom,  $p_d$ 

tion of a small amount of noise to a system receiving a subthreshold signal may make the signal observable. When no noise is added, the signal is, by definition, unobservable, and if large amounts of noise are added, the signal is swamped by the noise. Thus, if the signal to noise ratio for a periodic signal is plotted as a function of noise level, it will have a maximum at some intermediate intensity of noise. This maximum may have some functional significance for an "observer" of the system.

As seen in Fig. 2, the ghostburster (A1)–(A6) has two current thresholds, i.e., there are two values of *I* such that, if *I* is transiently increased above these values, there is a qualitative change in the behavior of the system. The first threshold, at  $I \approx 5.6$  involves a saddle node on a circle bifurcation, i.e., excitable dynamics between a fixed point and periodic firing, so the system is capable of exhibiting stochastic reso-

nance near this threshold [28]. We now show that the ghostburster can also show stochastic resonance near the periodic  $\rightarrow$  burst threshold that occurs for larger bias current *I*, provided that bursts are used to form the output signal, rather transient increase in synaptic input to such a model neuron could be robustly signaled by the production of a burst.

The results presented here are for an input signal and noise added to the soma only. Biophysically, however, inputs to a neuron are thought of as coming via the dendrites. Also, it is not clear what relative contribution do the soma and dendrite make to the overall level of noise in a neuron. Thus, it would be interesting to see whether stochastic resonance occurs in the ghostburster when the signal is injected to the dendrite and noise appears in either the soma or dendrite. We investigated these possibilities and found that stochastic resonance does occur, regardless of the location (soma or dendrite Time is measured in milliseconds and voltages are measured in millivolts. Subscripts s and d refer to somatic and dendritic variables, respectively. m and