Periodic forcing of a model sensory neuron

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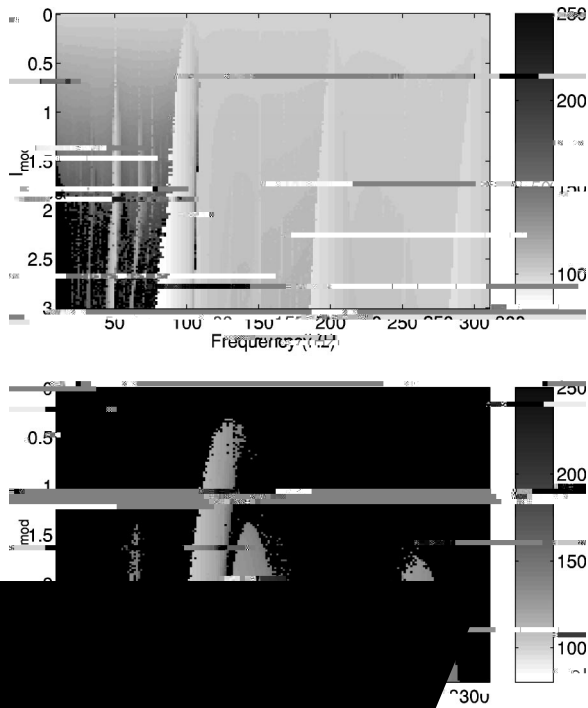
FIG. 5. A transient sinusoidal modulation of the input current switches system (A1)–(A6) from bursting to periodic firing. Parameters are $I_b=9$, I_{mod} is 1.5 for $1200<t<1400$, and the forcing frequency is 125 Hz. Top, V_s and $I-90$; bottom, p_d

...ency of forcing space
...$_b+I_{mod}\sin(2\pi ft)$. Top,
...rsting. Bottom, $I_b=8.7$;
...e color indicates the maxi-
...Hz (reciprocal of the mini-

...periodically modulated is
...bursting behavior and peri-
...cked to the forcing. Only one
...culated at each of the points in
...ity appears as the "speckles" of
...d dark within light regions. This
...when the reduced model presented
...lly 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 $I_{mod}\neq0$. It is de-
...values 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 burst-
...pressed almost immediately and the neuron is in-
...fire at the same frequency as the forcing. In Fig. 6,
...requency doublet occurs within 100 ms of the onset
...ng. We now examine the effects of including noise in
...namics of the ghostburster.

IV. STOCHASTIC RESONANCE

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

tion of a small amount of noise to a system receiving a sub-threshold 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 $I\approx5.6$ 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 ghost-burster can also show stochastic resonance near the periodic → 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