Stochastic resonance in the amphibian auditory system? It's just a matter of time

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Abstract: Noise has traditionally been a factor to minimize or eliminate for optimum performance of a communication system. Recently, it has been proposed that in some cases, noise may benefit information transfer and that its existence in sensory systems may be an adaptation to enhance detection of weak signals. One possible mechanism that could take advantage of noise to enhance signal transmission is a physical phenomenon known as stochastic resonance (SR). In order to study such effects in auditory neurons, we made use of the ability of amphibians to function over a range of ambient temperatures, and thus over a range of internal noise levels. The goal of the present study was to determine the effect of temperature (and internal noise) on information transmission in the frog. To this end, core temperature shifts were induced experimentally and the resulting changes in signal-to-noise ratio (S/N) were quantified. Although our results do not demonstrate SR in the sense that the S/N passes through a maximum at a particular internal noise intensity, we do demonstrate the profound influence of the internal noise on the S/N derived from the neural spike trains. Moreover, recent field and behavioral data will be presented and interpreted in the framework of stochastic resonance.

The goal of the present study was to determine the effect of internal noise on information transmission in the frog auditory periphery. To achieve this, we experimentally shifted core temperature to manipulate the internal noise level, and examined the resulting changes in signal-to-noise ratio of the auditory nerve spikes. Thus, we measured how the signal-to-noise ratio of the encoded stimulus at the level of the auditory nerve was affected by temperature-induced changes in the internal noise level.

This study was motivated by the possibility that the internal noise in the anuran auditory system might play a significant role in the transmission of information along the nerve fibers. In fact, the background noise in the anuran auditory system is much greater than one might expect, if one assumes that it represents only the effect of a noisy transducer. The high noise level in this system and others suggests that its presence may provide some selective advantage. Possible hypotheses include: 1) that unavoidable noise drives a system to evolve a mechanism to take advantage of the noise, and 2) that high noise levels per se are useful and therefore natural selection favors them. These two hypotheses are not mutually exclusive; e.g., after evolving a mechanism to take advantage of noise (hypothesis 1), it may have become useful to provide additional fluctuations over and above those already present as a result of imperfect or noisy signal transduction to increase the effectiveness of this mechanism (hypothesis 2).

What could provide the basis for such a mechanism? One possible mechanism that could take advantage of noise to enhance signal transmission is a physical phenomenon known as stochastic resonance (SR; for a review see Wiesenfeld and Moss, 1995). Stochastic resonance is a strictly nonlinear effect, most often observed in systems with bistable energy potentials, driven by noise and a weak (subthreshold) coherent signal. It is also evident in threshold systems similar to the earliest models for the stochastic behavior of sensory neurons and in subthreshold operation of the Fitzhugh-Nagumo model neuron (see Narins et al., 1997 for references). The noise, which may be either internal to the system, as in certain noisy sensory neurons, or externally-applied, for example in the process of weak signal detection in a noisy environment, adds to the signal to produce superthreshold "spikes" which occur at more-or-less random times, but are to some degree coherent with the signal. The signal is described as "weak", indicating that in the absence of noise it alone is incapable of crossing the threshold and hence generating a spike. Measures of the information content of the spike train, such as the signal-to-noise ratio derived either from power spectra or from interspike interval histograms, quantitatively show the degree of coherence. SR is characterized by maximum information transfer at some optimal level of the noise intensity, which usually falls off above and below this optimum.

Northern leopard frogs, Rana pipiens pipiens were anesthetized 1 h prior to surgery with sodium pentobarbital and placed on a Peltier plate where a dorsal approach was used to expose the eighth cranial nerve. Recordings from individual auditory nerve axons were obtained using glass micropipette electrodes with impedances of 20-80 MΩ. Signal-to-noise ratios for individual auditory neurons were determined by first presenting a constant tone to the frog and collecting the times of action potentials. Each spike in the spike train was converted (by the window discriminator)
to a standard rectangular pulse of width $\Delta t = 0.59$ ms. A Fast Fourier Transform (FFT) was computed for these 2048 points, and a power spectrum was obtained; ten such spectra were averaged. The general shape of the resulting power spectra is that of a sinc function ($\text{sinc} x = \sin x / x$). A measure of the internal noise intensity in the neuron in the absence of a periodic stimulus is represented by the amplitude of the power spectrum at low frequency. The resulting mean power spectrum typically exhibited a narrow peak located at the tone frequency that stood out above the broadband background 'noise'. The noise level was measured directly from the power spectrum as the noise amplitude at the base of the signal peak, while the signal strength (area above the noise but beneath the signal peak) was determined by integrating the power spectrum in the vicinity of the stimulus frequency and measuring the change in this plot at the signal frequency. The resultant signal-to-noise ratio (SNR) was calculated from a standard definition.

Power spectra were collected at as many temperatures as possible during the time the electrode was in contact with a fiber. Linear regression slopes for the relationship of SNR to temperature, SNR to noise, and noise to temperature were calculated for each fiber. These slopes were compared for fibers originating in the saccus, the rostral end of the amphibian papilla (AP\textsubscript{ROSTRAL}, CF $\leq$ 500 Hz), and the caudal end of the amphibian papilla (AP\textsubscript{CAUDAL}, CF $> 500$ Hz). However, all of the slopes of the functions relating SNR to temperature for saccular and AP\textsubscript{CAUDAL} fibers are positive whereas more than half of the slopes of these functions for the rostral AP\textsubscript{CAUDAL} fibers are negative (Fig. 1). This observation suggests that rostral and caudal AP fibers differ in their responses to temperature. In addition, increasing the temperature resulted in nominal increases in internal noise intensities, and these, in turn, were accompanied by increasing SNR. These results cannot easily be explained on the basis of linear filter theory.

Preliminary evidence from acoustic playback experiments with calling male frogs in their natural habitat suggest a possible role of background noise for improving behavioral responses. Synthetic call notes were broadcast both alone and embedded in progressively higher levels of broadband masking noise to individual calling males of the Puerto Rican arboreal frog, \textit{Eleutherodactylus coqui}. Surprisingly, low-to-intermediate levels of masking noise resulted in the highest calling rate from the males tested. This result could be interpreted as a manifestation of the "capture" effect whereby attention is focused on the calls being broadcasted, since neighboring males' calls are being masked by the broadband masking noise. Additional experiments are needed to test this hypothesis.

![Figure 1](image1.png)

**FIGURE 1.** Signal-to-noise ratios plotted against temperature for 49 fibers innervating (a) the saccus (n=19), (b) the rostral (low frequency) region of the amphibian papilla (n=15), (c) the caudal (mid frequency) extension of the amphibian papilla (n=15). Each signal-to-noise ratio was calculated as $10 \log_{10}(S/N)$ in dB, where $S$ is the signal power and $N$ is the noise power. Temperature was incremented in steps of 1 or 2°C.

**REFERENCES**


**ACKNOWLEDGMENTS**

Supported by NIH Grant DC-00222 to PMN.