# Stochastic resonance and the benefits of noise: from ice ages to crayfish and SQUIDs

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**Noise in dynamical systems is usually considered a nuisance. But in certain nonlinear systems, including electronic circuits and biological sensory apparatus, the presence of noise can in fact enhance the detection of weak signals. This phenomenon, called stochastic resonance, may find useful application in physical, technological and biomedical contexts.**

SINCE the early days of radio, when the random arrival of electrons at the anode of a vacuum tube translated into an audible and annoying hiss at the loudspeaker, engineers have sought to minimize the effects of noise in electronic circuits and communication systems. But recent research has established that noise can play a constructive role in the detection of weak periodic signals, via a mechanism known as stochastic resonance (SR). In essence, SR is a nonlinear cooperative effect in which a weak periodic stimulus entrains large-scale environmental fluctuations, with the result that the periodic component is greatly enhanced.

Stochastic resonance is now known to occur in a wide range of physical systems; however, it was originally proposed as an explanation of the periodic recurrences of the Earth's ice ages, which exhibit a 100,000-year periodicity. In 1981, a group of European scientists[1-3] described a general dynamical mechanism whereby small periodic perturbations could be greatly amplified by large environmental fluctuations. In the case of the ice ages, a weak periodicity in the insolation stemming from variations in the Earth's orbital parameters might cause regular transitions in a bistable energy potential used to model long-term changes in global climate[4]. Although the proposition that the glacial–interglacial cycles are indeed periodic and linked to the Earth's orbital motions has been a matter of recent debate[5,6], the possible role of SR in palaeoclimatology is a topic of continuing interest[7,8]. These discussions notwithstanding, SR as a physical process is now firmly established as a genuine and even common phenomenon.

Experimentally, SR was first demonstrated with a noise-driven electronic circuit known as a Schmitt trigger[9]; this work was also the first to characterize the phenomenon in terms of a signal-to-noise ratio. It took five more years before the interest of physicists ignited, sparked by the demonstration of SR in a bistable ring-laser experiment[10]. Stochastic resonance has been reported in a wide variety of physical systems[11,12], and the classical theory[12-20] is well in hand. Now SR has crossed disciplinary boundaries: its role in sensory biology is being explored in experiments on single crayfish neurons, and in perceptive brain function by experiments on people's ability to resolve ambiguous figures. These new efforts, together with attempts to exploit SR for technological advantage, are the main trends in current research on this topic. There are even indications that SR may affect research in medical and environmental science.

## The mechanism

The basic picture of SR can be illustrated using a mechanical analogy. Imagine a particle subject to friction, moving in a double-well potential. A weak signal serves to periodically modulate the potential by alternately raising and lowering the wells relative to the barrier (Fig. 1*a*). Here, "weak" means that the modulation is far too small to excite the particle over the barrier. On the other hand, the presence of random noise alone is sufficient to induce (irregular) switching between the wells. In the high-friction limit, the dynamics can be modelled by the differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t}=-\frac{\mathrm{d}U}{\mathrm{d}x}+F(t)+A\sin(\omega t)$$

where $U$ is the bare potential, $A\sin(\omega t)$ is the signal, and $F$ is the noise. Stochastic resonance is a nonlinear cooperative effect whereby the small signal entrains the noise-induced hopping, so the transitions are surprisingly regular. What is more, the regularity can improve with the addition of more noise. In this way a small regular influence can have a large effect if environmental fluctuations are available to be tapped.

There is another way to view SR which is enlightening when thinking about applications, both in technology and biology. It concerns the problem of detecting weak signals in a noisy environment. Imagine that the system and signal are hidden from view, and that we gain information only by observing the system's output as a time series of switching events. In SR the system becomes a more sensitive detector as more noise is added, at least up to a point: it is optimally sensitive at some non-zero level of input noise.

Today, we know that SR is even more general than the bistable picture implies. Even simpler systems[21], including those with a single potential well[22] and integrate-and-fire[23] dynamics can exhibit SR or SR-like properties. The latter is a common model for neurons wherein a steady input is integrated until the result exceeds a critical threshold whereupon the neuron 'fires', and resets the 'integrator' to zero. In fact, the simplest possible system[24] consists only of a threshold, a subthreshold signal and added noise, as depicted in Fig. 1*b*. Whenever the noise plus the signal crosses the threshold in one direction, it triggers a narrow pulse in the output (Fig. 1*c*). The nonlinearity in this system is simply the on/off nature of the output. This version of SR has obvious appeal for those working in sensory biology, as neurons are excitable systems with properties similar to those depicted in Fig. 1*b*, *c*: when some internal threshold is crossed the neuron 'fires' and then resets itself to await another threshold-crossing event.

Stochastic resonance should not be confused with 'dither', also known as stochastic linearization, a technique wherein periodic or random forcing is intentionally introduced to overcome regions of 'dead' dynamical behaviour in self-regulating systems. A familiar example is the use of dither to cancel the effect of gear backlash which, in servo mechanisms, often leads to undesirable effects such as gear chatter.

## Quantifying SR

The most common way to quantify SR is through the signal-to-noise ratio (SNR). This is readily obtained from the output by forming the power spectrum, which measures the frequency content of a time series. A typical result is shown in Fig. 1*d*, taken from numerical simulations of a threshold-crossing system. The signal shows up as a sharp peak located at the signal frequency riding on a broadband noise background; the SNR is the ratio

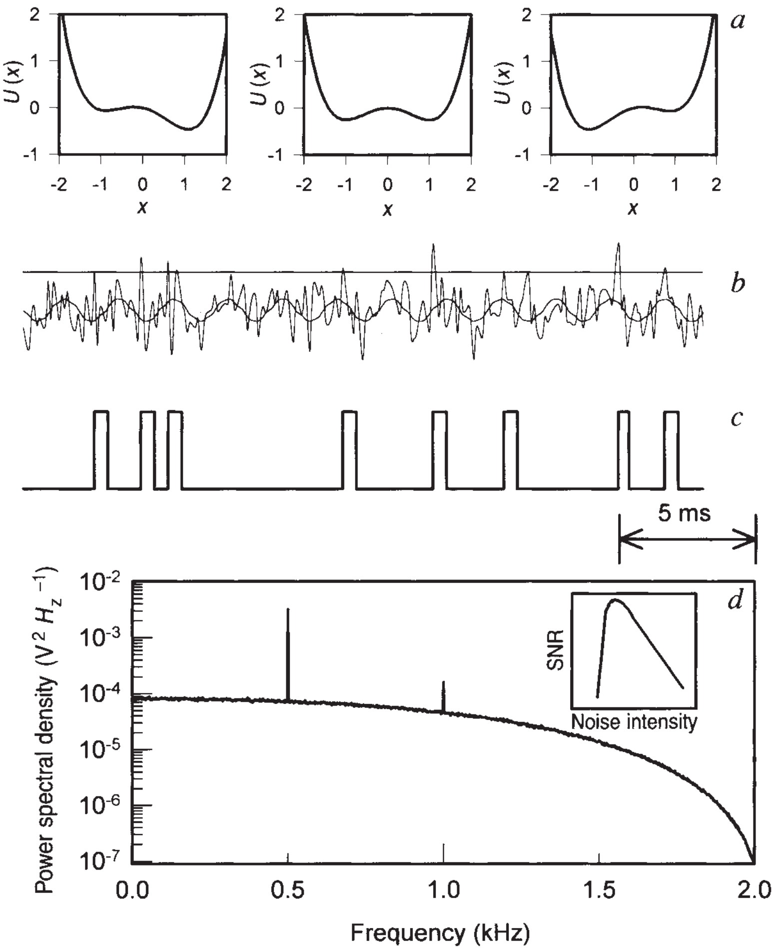


FIG. 1 *a*, A bistable potential, weakly modulated by a periodic signal. *b*, The simplest instance of stochastic resonance (SR) consists of a threshold (shown by the straight line) and a subthreshold sinusoidal signal with added gaussian noise. Each time the signal plus the noise increases across the threshold, a pulse of standard shape is written to the time series shown in *c*. *d*, Power spectrum of a long time series of the pulses shown in *c* has a broadband noise background whose amplitude at zero frequency is related to the mean pulse repetition rate and hence to the noise. The signal feature is the sharp peak located at the signal frequency (0.5 kHz in this case) riding on the noise background. The SNR is defined as 10 $\log_{10}(S/N_0)$ in decibels (dB) where $S$ is the area enclosed above the noise background, and $N_0$ is the amplitude of the noise background at the signal frequency. Inset, the characteristic signature of SR, that is, a maximum in the SNR at an optimal value of input noise intensity.

of the strength of this peak to the background level (see Fig. 1 legend). Remarkably, theories for all three main types of SR—the bistable potential model, the fire-and-reset excitable system model, and the simple threshold model—result in the same general formula (apart from some constant factors of order one in both the prefactor and the exponent) for the SNR:

$$\mathrm{SNR} \propto \left(\frac{\varepsilon \Delta U}{D}\right)^2 \mathrm{e}^{-\Delta U/D} \qquad (1)$$

where $\varepsilon$ is the input signal strength, $D$ is the input noise intensity and $\Delta U$ is a constant related to the barrier height or the threshold. The signature of stochastic resonance is that this SNR is zero for zero added noise (that is, $D \rightarrow 0$: no noise implies no switching or threshold crossings, hence no output), rises sharply to a maximum at some optimal noise intensity, and decreases gradually for larger noise intensity as randomization overrides the cooperative effect. The detailed shape of this curve depends on the signal frequency and other system parameters; Figs 3 and 4 show typical examples.

Although the power spectrum is the most widely used coherence measure, it is not the only possibility. An alternative is the residence-time probability distribution[25] depicted in Fig. 2*a*–*c*, more familiarly known to experimental biologists as the interspike interval histogram[26]. This measure is composed of a set of peaks which are widely spread for very small noise but become more coherent for larger noise intensity. This qualitative structure of the histogram is very common, and is not in itself a signature of SR. Rather, SR is identified with the more particular behaviour shown in Fig. 2*d*, where the amplitudes of the lower-order peaks pass through individual maxima with increasing noise intensity[25,27]. Similar histograms from both neuron models[27] and actual biological preparations[28] show SR or at least a strong connection between the ability of a sensory neuron to transmit coherent information and its internal or external noise[29,30].

## SR in biology

Is it possible that noise-mediated detection or transmission of weak signals plays a significant role in biology? Sensory neurons are notoriously noisy, and in their coarse behaviour operate as threshold systems. Could SR account for the exquisite sensitivity of some animals to weak coherent signals embedded in a noisy environment? This question prompted a series of experiments with a simple, perhaps even primitive, sensory system: the mechanoreceptor hair cells of the crayfish *Procambarus clarkii*[28]. These cells are specialized to detect weak, coherent water motions produced, for example, by the approach of a predator, perhaps a swimming fish. In these experiments, a piece of the telson together with the nerve cord and the sixth ganglion was excised and mounted in crayfish saline on an electromechanical transducer. Signal and noise generators drove the transducer so that the hair cell's motion through the saline was a combination of coherent and random motions. Electrophysiological recordings were made from a single cell stimulated with a weak (subthreshold) signal. Most cells tested showed clear evidence of SR (Fig. 3).

A familiar and frequently used theoretical model of a neuron, known as the Fitzhugh–Nagumo equations, gave similar results. These were implemented using an analogue electronic circuit operating in the subthreshold regime and stimulated with gaussian noise and a weak sinusoidal signal[31]. Figure 3 shows data from both the crayfish experiment (squares) and the Fitzhugh–Nagumo simulation (diamonds); both data sets show the characteristic signature of SR. The crayfish data do not decrease rapidly for small noise because of the residual internal noise of the neuron. The solid curve shown in Fig. 3 is a fit to the data using equation (1). Thus theory, simulation and experiment all provide support for the notion of SR as a viable mechanism in sensory biology.

It is possible, although not yet demonstrated, that SR is a common phenomenon in sensory biology. Virtually all sensory systems operate as threshold detectors, and the crayfish mechanoreceptor example demonstrates that the efficiency for detecting weak signals can be enhanced by the addition of external noise. This is obviously helpful in noisy environments, but might even be useful where external noise is not available. Neurons can also have substantial amounts of internally generated noise, and it is natural to ask whether this apparently undesirable noise source can serve a useful function. This remains an important open question: to date, experiments designed to study the role of the internal noise have been inconclusive[30].

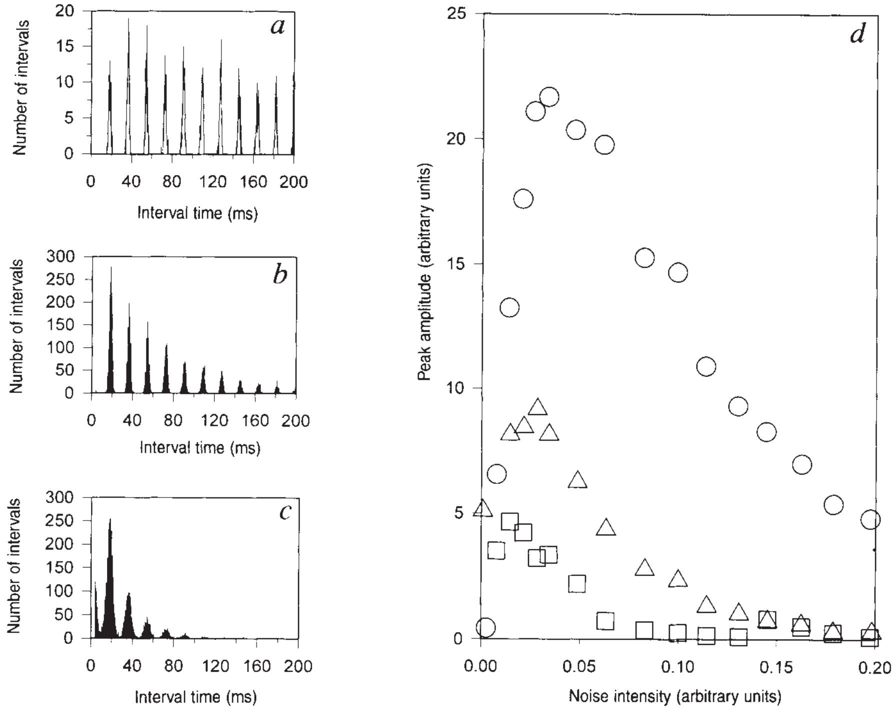


FIG. 2 *a–c*, Interspike interval histograms, as measured on an electronic Fitzhugh–Nagumo neuron model[31] for increasing noise intensity. The area under the first peak represents the total number of action-potential spikes that occur at every cycle of the periodic stimulus. The areas under the higher-order peaks represent events that skipped stimulus cycles. The tendency of the noise to concentrate area under the first peak represents increasing coherence. *d*, Behaviour of the amplitudes of the higher-order peaks with increasing noise intensity for a bistable system[25]. The circles, triangles and squares represent data for the second-, third- and fourth-order peaks, respectively.

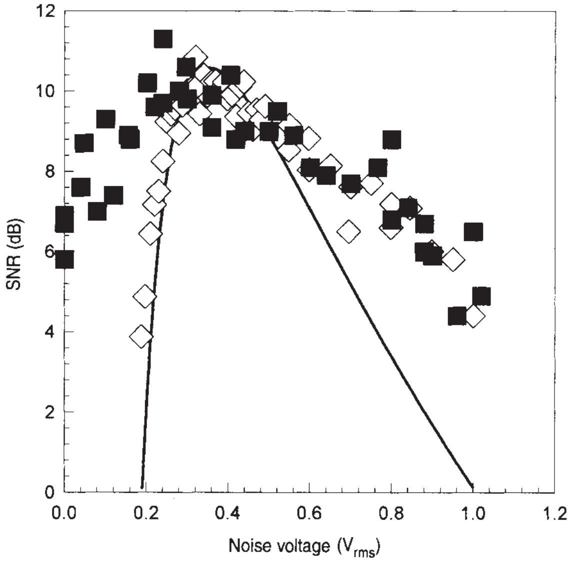
## Technological applications

Researchers are just beginning to pursue possibilities for technological exploitation of SR. With a view to possible applications in magnetic sensing, a group associated with Quantum Magnetics, Inc. (San Diego) demonstrated SR in a bistable superconducting quantum interference device (SQUID) loop[32,33]. Future directions for this work can be threefold. First, the passage of individual fluxons into and out of the loop are macroscopic quantum tunnelling events and thus are candidates to demonstrate quantum SR. Investigation of these events would be of fundamental interest; recent theoretical work[34] predicts subtle differences from the classical case with respect to underlying symmetries of the system. Second, SQUIDs fabricated from high-temperature superconducting materials are in principle much cheaper to operate, but are inherently noisy. It may be possible to optimize their performance in some applications by using SR to exploit the internal noise for weak magnetic signal detection. Third, researchers are actively considering arrays of coupled SQUIDs to boost the sensitivity of these bistable systems even further.

With an eye to electromagnetic communications, a recent study[35] reported using SR to improve detection of a weak carrier signal, operated in both amplitude- and frequency-modulated modes (AM and FM). An interesting twist here is that the detector was a bistable system (known as Chua's circuit), the two states of which were chaotic. Although there is no obvious advantage in using a chaotic detector, chaos does not impede the effect[36,37], illustrating yet again the generality of SR. Possibly indicative of the approaching technological exploitation, both Chua's circuit and the Quantum Magnetics SQUID have been implemented on silicon chips.

Physicists at the Georgia Institute of Technology (K.W. *et al.*, unpublished results) are studying the role that SR could play in enhancement of trigger-threshold detectors. In practice all detectors have a minimum threshold; inputs smaller than this are 'invisible'. The traditional approach to detector design is to make this threshold as small as possible, while isolating the system from noise as much as possible. However, at some point each of these objectives becomes either impractical or prohibitively expensive. An economical alternative may be, for a given thresh-

FIG. 3 Results of our experiment with crayfish mechanoreceptors (filled squares) compared to the electronic Fitzhugh–Nagumo simulation (diamonds) and the theory given by equation (1) (solid curve)[21]. The horizontal axis represents externally applied, gaussian noise: hydrodynamic noise in the case of the mechanoreceptor, and electronic noise in the case of the neuron model. The crayfish data do not decrease rapidly for small noise because of the residual internal noise of the neuron.



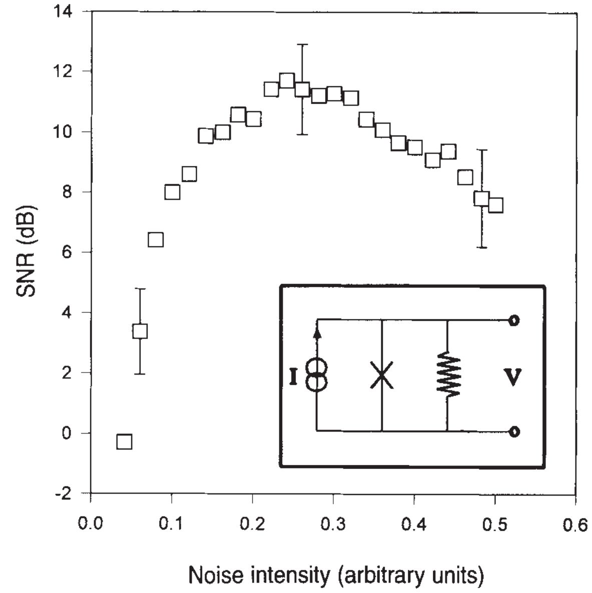


FIG. 4 Main figure, data from a numerical simulation of a trigger-reset system based on a Josephson junction as nonlinear element[48]. Inset, circuit diagram of the Josephson system, consisting of an ideal junction (cross), quasiparticle resistance, and current source *I* which is the sum of three components—constant bias, weak periodic signal and noise. The output is the voltage, *V*.

old value, to allow enough noise to produce operation at the optimal value on the SNR curve. An example of SR in such a threshold device is shown in Fig. 4, generated from numerical simulations of a device that uses a superconducting Josephson junction as the nonlinear element.

## Further examples

The possible role of SR is being pursued in other areas of science as well. One such study concerns human perception of simple ambiguous figures, for example the Necker cube[38], which may be viewed as a bistable process with an inherent noise. Bistability arises in the perception of which one of a pair of diagonally opposed corners of the transparent cube is in the foreground, and the perception spontaneously switches between the two alternatives. The switching is a random (or possibly a low-dimensional chaotic) process, and the fluctuation intensity can be controlled by the size and/or aspect ratio of the cube[39]. A weak 'signal' can be introduced by moving a marker sinusoidally along a diagonal joining the two corners. In this way the eye, and hence the observer's attention, is weakly biased alternately between the two possible perceptions. Recently researchers demonstrated SR in a neural-network simulation of this process[40]; an experiment by this same group using human subjects is in progress.

A controversial issue, currently the focus of an intense public health debate, is the effect (if any) of extremely low frequency electromagnetic fields on living tissue[41–43]. Theoretical estimates consistently predict the interaction energies of such fields after penetrating tissue to be up to three orders of magnitude smaller than the average energy of thermal fluctuations. How could such low-level coherence affect living cells[44]? A concise review of this problem, including a summary of recent experimental results, is given in ref. 45. Recently, it was suggested that SR may play a role[45–47]: voltage-sensitive ion channels in cell membranes behave like threshold devices in regard to external fields, randomly switching between open and closed states in response to thermal fluctuations. If SR is relevant, the effect of weak extremely low frequency electromagnetic fields might be greatly amplified. Whether any such enhancement is large enough to have significant biological ramifications is at this stage purely speculative. □

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