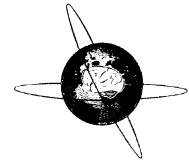




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Stochastic resonance and sensory information processing: a tutorial and review of application

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Abstract

Objective: To review the stochastic resonance phenomena observed in sensory systems and to describe how a random process ('noise') added to a subthreshold stimulus can enhance sensory information processing and perception.

Results: Nonlinear systems need a threshold, subthreshold information bearing stimulus and 'noise' for stochastic resonance phenomena to occur. These three ingredients are ubiquitous in nature and man-made systems, which accounts for the observation of stochastic resonance in fields and conditions ranging from physics and engineering to biology and medicine. The stochastic resonance paradigm is compatible with single-neuron models or synaptic and channels properties and applies to neuronal assemblies activated by sensory inputs and perceptual processes as well. Here we review a few of the landmark experiments (including psychophysics, electrophysiology, fMRI, human vision, hearing and tactile functions, animal behavior, single/multiunit activity recordings). Models and experiments show a peculiar consistency with known neuronal and brain physiology. A number of naturally occurring 'noise' sources in the brain (e.g. synaptic transmission, channel gating, ion concentrations, membrane conductance) possibly accounting for stochastic resonance phenomena are also reviewed. Evidence is given suggesting a possible role of stochastic resonance in brain function, including detection of weak signals, synchronization and coherence among neuronal assemblies, phase resetting, 'carrier' signals, animal avoidance and feeding behaviors.

Conclusions: Stochastic resonance is a ubiquitous and conspicuous phenomenon compatible with neural models and theories of brain function. The available evidence suggests cautious interpretation, but justifies research and should encourage neuroscientists and clinical neurophysiologists to explore stochastic resonance in biology and medical science.

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1. Introduction

Stochastic resonance (SR) is essentially a statistical phenomenon resulting from an effect of noise on information transfer and processing that is observed in both man-made and naturally occurring *nonlinear* systems (Moss, 1994, 2000; Moss et al., 1994; Wiesenfeld and Moss, 1995, for reference). Since the early 1980s, it has provided theoretical and experimental researchers with a rich source of research topics (mostly in the physical sciences), with frequent reports

published in both physics and interdisciplinary journals. In the early 1990s, a crucial paper delineated the role of noise in neural encoding and phase-locked responses of sensory neurons to weak periodic stimuli (Longtin et al., 1991). SR was then documented in experiments on neural encoding in invertebrates (see Appendix A), with interest and application in sensory biology, neuroscience and medical science soon appearing and growing (Chiou-Tan et al., 1996, 1997). A recent review focuses on biological applications and the noise-dependent synchronization of oscillators – a process of potential importance in neuroscience and medicine (Anishchenko et al., 1999).

The purpose of this review is to draw attention to this extremely simple phenomenon, its possible functional role in

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brain processes and the potential application in neuroscience and clinical neurophysiology. Although still a subject of research, SR has already found a direct application for efficient encoding of auditory information used in cochlear implants (Morse and Evans, 1996). Recent research points toward clinical applications involving electromyography of the human median nerve (Chiou-Tan et al., 1996), augmentation of muscle function (Chiou-Tan et al., 1997) and the human tactile sense (Collins et al., 1997; Priplata et al., 2003).

The nonlinearities peculiar to cortical dynamics, sensory information processing and neuronal function motivate research on SR. In this respect, the study of electrophysiological signals appears a privileged approach, and SR may help understand the neuronal mechanisms underlying the responses to sensory inputs. Under the assumption of substantial correlation between neuronal function and recorded signals, in fact, the stimulus-dependent transient recruiting of neurons from discrete brain locations that results in the episodic coherence and synchrony of signals at some given frequency and is modulated both globally and regionally can be approximated to resonance (Basar, 1992; Basar and Bullock, 1992; Varela, 1995; Nuñez, 1995; Varela et al., 2001).¹ Noise is ubiquitous in the CNS, although somehow difficult to characterize (see Section 9).

2. What is SR?

SR is a nonlinear phenomenon whereby the addition of a random interference ('noise', as it is almost universally called) can enhance the detection of weak stimuli or enhance the information content of a signal (e.g. trains of action potentials or signals generated by a neuronal assembly). An optimal amount of added noise results in the maximum enhancement, whereas further increases in the noise intensity only degrade detectability or information content. The phenomenon does not occur in strictly linear systems, where the addition of noise to either the system or the stimulus only degrades the measures of signal quality (see for reference: Benzi et al., 1981; Moss, 1994, 2000; Moss et al., 1994; Wiesenfeld and Moss, 1995; Ward et al., 2002). Additional information is given in Fig. 1.

In its simplest manifestation, referred to as 'threshold SR' or 'non-dynamical SR', stochastic resonance results

¹ Resonance defines in physics the enhanced response of a system for some values of the input parameters. The core feature of this enhancement is its occurrence when the driving frequency of the input matches the system natural or inherent frequency (i.e. the intrinsic characteristics of the circuit). If applied – with due approximation – to stimulus-related neuronal activation and signals, this concept would indicate frequency-dependent neural assemblies or circuitry properties and suggest some functional specificity with respect to frequency of brain signals. Experimental evidence indicates that cell and circuit properties determine to some extent the frequency of neuronal membrane oscillations (König et al., 1992; Jefferys et al., 1996; Herculano-Houzel et al., 1999; Sannita, 2000, 2003; Solessio et al., 2002).

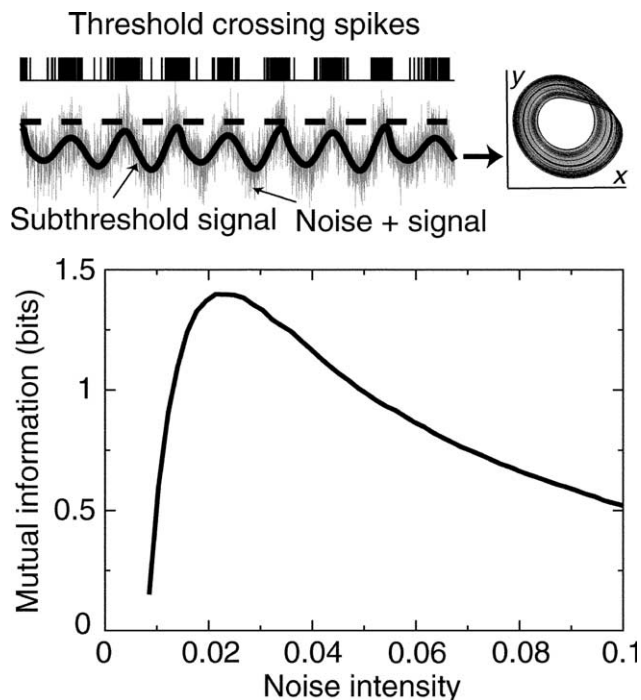


Fig. 1. Noise-enhanced information in a threshold system. The threshold, Δ_0 , is the distance between the mean of the subthreshold stimulus (thick solid line) and the threshold (dashed line). The stimulus, $x(t)$ was generated from the Rössler system: $\dot{x} = -(y+z)$; $\dot{y} = x+0.15y$; $\dot{z} = 0.2+z(x-7.1)$. The attractor $x(t)$ versus $y(t)$ is shown on the right. The band limited, Gaussian noise $\xi(t)$ (irregular light line) was generated from: $\dot{\xi} + (2/\tau)\xi + (1/\tau)\xi = (1/\tau^2)\sqrt{2D}w(t)$, where D is the noise intensity, $w(t)$ is Gaussian noise with zero correlation time and the correlation time, $\tau = 0.05$. The lower panel is the mutual information between spike trains generated by noise alone and noise plus stimulus. The optimal noise intensity is $D_{\text{opt}} \cong 0.022$ for which the information is a maximum. The information in the spike train can be quantified by computing the mutual information (I) between a spike train (top panel) occurring in the absence of a stimulus (i.e. with noise alone) and the spike train resulting from the stimulus plus the noise, $I = H_0 - H_S$, where the latter two quantities are the Shannon entropies without, H_0 , and with, H_S , the stimulus present. They are each defined by $H = -\sum_{i=1}^n P_i \log P_i$, where P_i is the probability of finding a spike in a certain time interval of the spike train, and n is the total number of intervals the time axis is divided into (Shannon, 1948). How to calculate the entropies specifically for spike trains can be found in Strong et al. (1998).

from the concurrence of a threshold, a subthreshold stimulus, and noise (Gingl et al., 1995). These ingredients are ubiquitous in nature as well as in a variety of man-made systems – which accounts for the observation of SR in many fields and conditions. The phenomenon also exists in another form ('dynamical SR') which appears only in stochastic, nonlinear, dynamical systems. Indeed, SR was thought to exist only in its dynamical form throughout most of its history, commencing with its discovery as a possible approach to explain periodic recurrences in the Earth's Ice Ages (Benzi et al., 1981, 1982; Nicolis, 1982, 1993). An adequate description of this form of SR requires the theory and mathematics of dynamical systems, a treatment that can be found in Gammaitoni et al. (1998). This review will focus

on the threshold version of SR. The restriction is appropriate, as natural systems such as the animal and human brain, visual and auditory systems, and behavior lack the rigorous and quantitative theories needed to apply dynamical SR.

2.1. How threshold crossings enhance detectability and information content of sensory neural discharges

Fig. 1 outlines the 3 ingredients contributing to threshold SR mechanisms in an example where the subthreshold stimulus was generated by a chaotic system (a Rössler attractor) that conveniently mimics the oscillatory processes occurring in the brain and shares the physiological relevance of chaotic systems (Strogatz, 1994). The Rössler system is not strictly periodic. Instead, its ‘frequency’ varies in time around some preferred value; in this respect, it approximates the variability of the signals related to brain function most often encountered in neuroscience and medicine, such as the EEG or MEG signals (e.g. Srebo and Malladi, 1999; Tass et al., 2003). Alternatively, the dynamics of the attractor can be shown by means of its so-called ‘phase portrait’, i.e. by plotting the instantaneous amplitude of one variable versus another. The phase portrait of the Rössler attractor, $x(t)$ versus $y(t)$ (as defined by the equations in the caption), is shown in the inset of Fig. 1 (right).

The paradigm is that information about the subthreshold stimulus is encoded by the sequence of threshold crossings. The stimulus is by itself below threshold, never crosses it, and is therefore undetectable. When noise is added to the stimulus, threshold crossings occur with greater probability near the peaks of the stimulus where it comes closest to the threshold. The noise (with Gaussian distribution and band limited to an upper cut-off frequency significantly larger than the characteristic frequencies contained in the stimulus) is shown in Fig. 1 by the thin irregular line. Positive-going threshold crossings of the stimulus plus the noise are indicated by the sequence of identical marker pulses, here called the ‘spike train’, shown in the topmost tracing. Though noisy (i.e. with spikes occurring irregularly in time), such sequences contain a large amount of information about the subthreshold signal. When compared with a situation in which the noise alone is present, in which threshold crossings occur completely at random, this additional information allows the stimulus to be detected and characterized.

This paradigm actually represents an early, simple, stochastic neuron model (McCullough and Pitts, 1943) also applicable to ion channels. Additional features can be added to the neuron model, for example to provide for a refractory time or a dynamic threshold with a post-firing relative recovery time. A FitzHugh–Nagumo model (Moss et al., 1993) or a full Hodgkin–Huxley model (Braun et al., 1998) can also be employed. Though the quantitative results across these different models vary, the qualitative or overall features of the processes described here are

preserved. A comprehensive discussion of modern information theory applied to neural discharges is given by Rieke et al. (1997). The mutual information for various noise intensities results in the graph shown in the lower panel of Fig. 1. We note that the optimal noise intensity for this example is approximately 0.022 for which value I is a maximum. This occurrence of the maximum mutual information at a non-zero noise level is the signature of SR.

2.2. The signal-to-noise ratio

A convenient measure of the quality of the signal output by the threshold system and representing the subthreshold stimulus (e.g. a spike train representing the times when stimulus + noise exceeded the threshold) is the signal-to-noise ratio (SNR) computed from a time average of the power spectrum of the signal.

The role of noise is to sample the stimulus. This means that the larger amplitude excursions of the noise cross the threshold and provide a ‘sample’ of the subthreshold signal’s amplitude at a given instant in time. For good information transmission, the sampling rate should be greater than the stimulus frequency (see also Section 8).²

3. SR in sensory biology and animal behavior

The original experiment that demonstrated SR in sensory biology made use of the predator avoidance system of the crayfish (Douglass et al., 1993; Pei et al., 1996; Wilkens and Douglass, 1994; for a review on nonlinear processes in the crayfish mechanoreceptor system see Bahar and Moss, 2003a,b). A paradigmatic demonstration of SR enhancing the perception of sensory information and also affecting animal behavior comes from experiments on the feeding behavior of the juvenile paddlefish (Russell et al., 1999). Evidence from animal studies indicates that they can perceive the enhancement of information available in the peripheral sensory system with the addition of external noise, and that they can make use of this noise-enhanced information, for example for feeding or predator avoidance. These experiments (see Appendix A for detailed information) nevertheless raised questions about the SR

² This measure is more suitable when the stimulus is a purely periodic function, $A \sin(\omega_0 t)$, of amplitude A and frequency ω_0 . For threshold SR the SNR (in units of decibels) has been calculated as follows (Moss et al., 1994): $\text{SNR} = 10 \log_{10} \left[\frac{2\omega_n \Delta_0 A^2}{\sqrt{3}\sigma^4} \right] \exp\left(-\frac{\Delta_0^2}{2\sigma^2}\right)$ where ω_n is the upper cut-off frequency of the noise, Δ_0 is the distance between the mean of the stimulus and the threshold, and σ is the standard deviation of the (Gaussian) noise. This formula is subject to only two approximations that seem to be well justified in most applications: $\omega_n \gg \omega_0$, and $\Delta_0 \gg A$. The combination of the inverse noise intensity (σ^4) in the prefactor and inverse σ^2 in the exponent of the formula results in a graph with a maximum of the SNR located at an optimal (non-zero) value of the noise intensity, similar to the graph of mutual information versus noise intensity in the lower panel of Fig. 1.

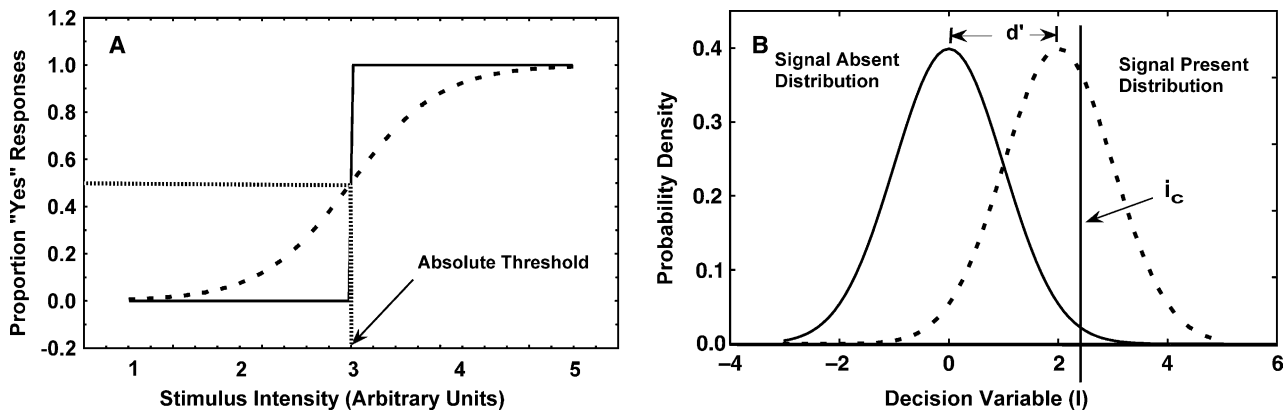


Fig. 2. Theories of psychophysics. (A) Classical threshold theory fixed absolute threshold assumption (solid line) for the experiment in which near-threshold stimulus intensities are presented many times each for a detection response ('yes'), with curve typically fitted to actual data (curved dashed line) and statistical threshold determination at 0.5 proportion 'yes' responses (dotted line). (B) Signal detection theory. A particular, not-always-detected, stimulus intensity is presented on signal present trials and no stimulus at all on signal absent trials. Over many trials the noisy sensory responses are Gaussian distributed as indicated. On each trial, the observer responds 'yes' if the sensation magnitude (decision variable, I) is above a criterion, i_c , and 'no' otherwise. Proportions of 'hits' ('yes' when stimulus present) and 'false alarms' ('yes' when stimulus absent) corresponding to areas under signal present and signal absent curves to the right of i_c are used to calculate d' , the standardized distance between the means of the distributions.

phenomena and sensory perception that could be addressed only through experiments with humans, e.g., by psychophysical approaches.

4. SR in human psychophysics experiments

In order to demonstrate SR in human perception it is necessary to use psychophysical techniques that precisely characterize the responses of the sensory systems to physical signals (e.g. Fechner, 1966; Norwich, 1993), and this has been done (e.g. Ward, 2002; Ward et al., 2002; Sections 4–6 of this paper). Classical psychophysical theory postulated a fixed absolute threshold for perception, but typical experimental results rarely support this assumption (Fig. 2A). Either the absolute threshold varies randomly according to a roughly Gaussian distribution, or the threshold is 'soft' (i.e. the logistic or a similar function describes the transfer function of the human sensory system). Opinion is divided as to which is the case, although under extremely low-noise conditions a fixed threshold can be discerned. For example, Hecht et al. (1942) found an absolute threshold of 6 photons for light detection, therefore suggesting that environmental noise may be responsible for the lack of a fixed threshold under more usual experimental conditions.

Extremely low-noise experimental conditions are rare. Green and Swets (1966), among others, argued that stimulus detection typically was a signal-to-noise problem and suggested a variant of statistical decision theory (called signal detection theory; SDT) to replace the classical theory (Fig. 2B). The index of sensitivity in SDT experiments, d' , is independent of the position of the criterion relative to the two distributions, and thus avoids problems caused by varying motivation of observers. It is the preferred measure

of performance in modern psychophysics. The d' measure should be maximal at some non-zero level of added noise if SR is operating in a signal detection experiment. Notice that in this theory, there is no threshold as such, only a decision-related nonlinearity whose position is not fixed. This raises some problems for the interpretation of SR experiments (e.g. Tougaard, 2000; Ward et al., 2002).

An early result of psychophysics (the 'negative masking') deserves mention here. In psychophysics, as in physics, noise usually interferes with detection and identification of a signal – a process called masking. Some studies on masking in audition, vision and touch have reported that at very low levels of signal and mask intensity, it is easier to detect the signal in the presence of the mask than alone when the two are added in phase with each other (see Laming, 1986, for a review). Higher intensities of the mask have the usual interfering effect, making detection of the weak signal more difficult. This phenomenon is explained by the energy addition of the signal and the mask, making signal + mask discriminable from the mask alone when signal + mask is near threshold, but not when the mask is very intense or very weak. Although these studies never found out-of-phase or incoherent noise maskers to have this effect (which would have been early evidence of SR), some more recent studies to be described shortly do find this effect with incoherent noise 'maskers'. This type of SR, which could be called Type E (for energy), can be contrasted with SR in which energy addition of signal and noise is not sufficient to explain the SR. In this situation, which can be called Type I (for information), stimuli are equated for energy and the critical feature is the transmission of a signal modulation across the nonlinearity, usually a threshold.

Many psychophysics experiments have demonstrated in humans a threshold for visual perception (Norwich, 1993)

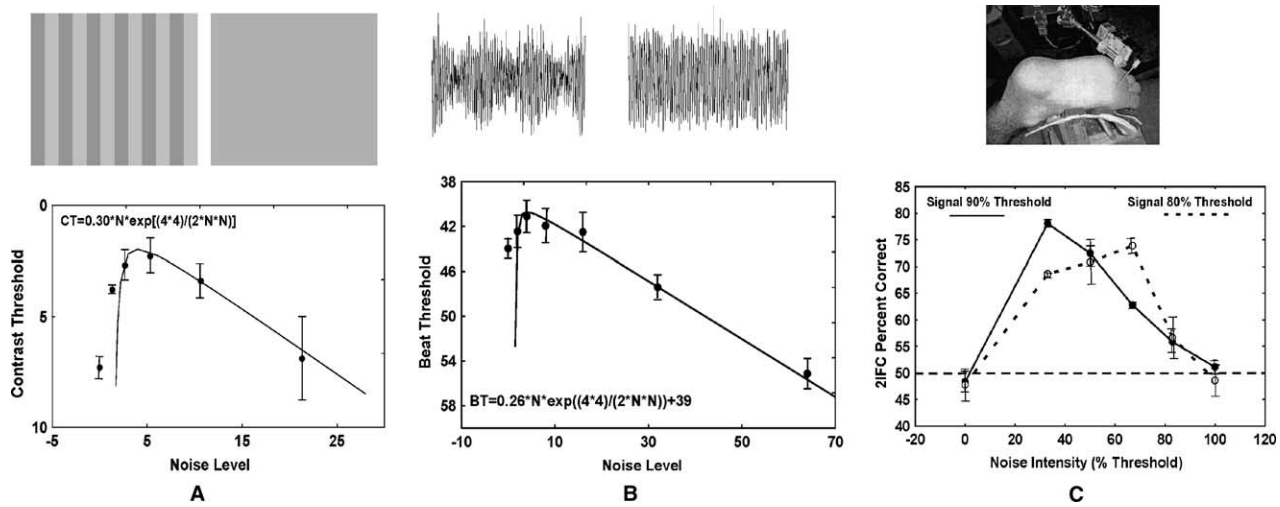


Fig. 3. Results of psychophysical SR experiments in (A) vision (Ward et al., 2001), (B) audition (Ward et al., 2001), and (C) touch (Wells et al., 2001). Top panels represent the stimulus situation, and bottom panels represent the data. For vision, the discrimination was between a grating and a uniform stimulus, for audition between a 3 Hz beat and a non-beating stimulus, and for touch, the photograph shows the experimental setup with a tactile stimulator vibrating at 25 Hz just touching the foot sole. The y-axes in (A) and (B) (average thresholds over all observers) are reversed, so that the minimum thresholds appear in the figures as maximum sensitivities at small, but non-zero, levels of added noise.

as well as effects of noise and SR phenomena in the perception of gratings, ambiguous figures, letters, and in the 3-dimensional perception of autostereograms (Riani and Simonotto, 1994; Speranza et al., 1997; Simonotto et al., 1997, 1999; Piana et al., 2000; Ditzinger et al., 2000; Ward, 2002; Ward et al., 2002). SDT experiments have demonstrated that SR can improve the observers' sensitivity to weak visual signals (Section 4.1). Other studies have investigated the effects on human perception of SR relative to an artificial physical threshold (Section 4.2).

4.1. SR and the detection of weak visual signals

Several studies focused on the human threshold for detection of luminance changes across space (Ward et al., 2001). In an experiment, observers were requested to recognize striped and non-striped visual stimuli (Fig. 3A). Contrast was increased/decreased in small steps according to an SDT-based adaptive technique and depending on the observer's correct/incorrect answer. To add noise, the gray level of each pixel in the stimulus was increased/decreased by different random amounts from a Gaussian distribution with a particular standard deviation. The average luminance of striped and non-striped stimuli was equated at all noise levels. The added noise apparently renders weak spatial modulations in luminance more detectable, by lowering the contrast threshold at which they can be detected in agreement with the Type I SR paradigm.

Following a different approach, Kitajo et al. (2003) had observers adjust the strength of handgrip to the brightness of a slowly varying visual signal presented to one eye (in this case, the visual stimulus was above threshold, but its variations were subthreshold). Noise was presented to

the same eye, or to the other eye, by adding random luminance steps (successive samples from a Gaussian distribution) at a rapid rate compared to the slow variation of the stimulus. The coherence of variation between handgrip strength and visual signal was greater for intermediate levels of noise in both conditions, indicating that the slow subthreshold variations were amplified by intermediate levels of noise to the point where they helped drive fluctuations in observers' handgrip force. Conceivably, when signal and noise were added to separate eyes their combination occurred somewhere in the visual system after inputs from the two eyes combined in visual cortex.

4.2. Visual perception of SR: psychophysical and fMRI studies with an artificial threshold

Perceptual response to SR has been studied in several experiments in which the threshold was neither



Fig. 4. Visual images of Big Ben on a 256 gray scale with spatial resolution of 256 by 256 pixels. The original photograph is suppressed beneath a threshold of $\Delta_0 = 30$. Noise from Gaussian distributions is added to the gray scale values in each pixel. Left-to-right the standard deviations of the noise are $\sigma = 10, 90$ and 300 , respectively. The information content in each pixel is 1 bit: if the gray scale value in that pixel is greater than threshold (30) the pixel is painted black. Otherwise it remains white. Reproduced from Simonotto et al. (1997), with permission.

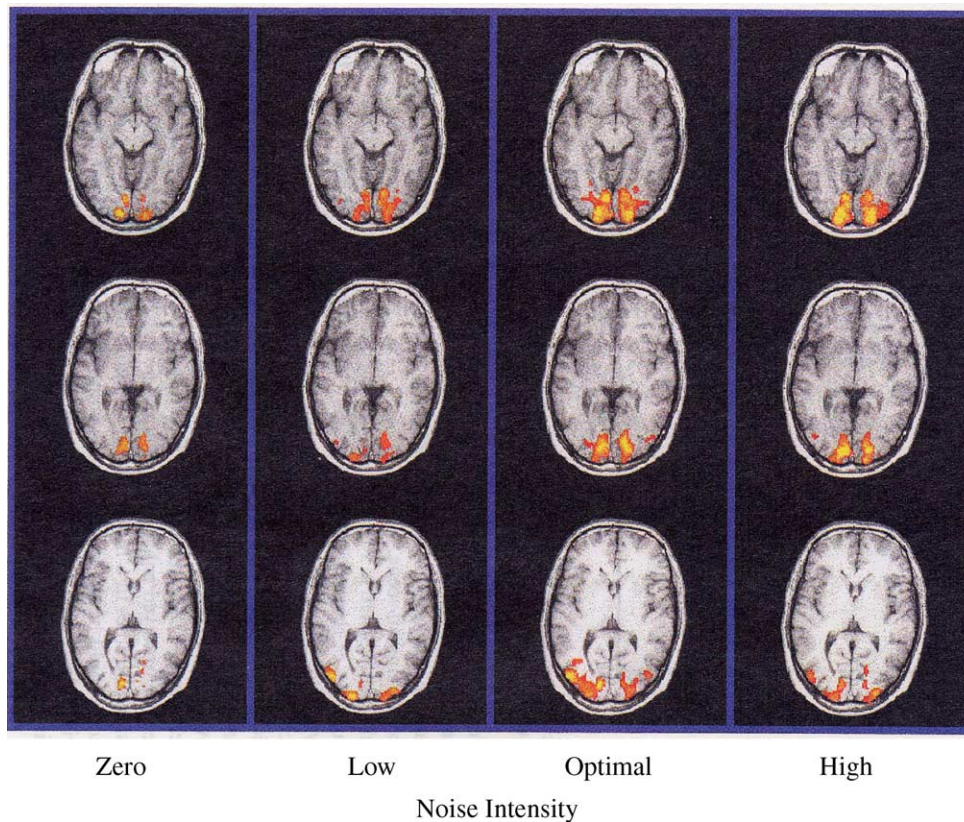


Fig. 5. fMRI statistical maps (color) for 4 stimulations representing a range of noise intensities. The volume of activated regions can be determined from sets of cross-sections at differing vertical heights. Active volumes, represented by colored areas, are clearly largest for an intermediate level of noise (third column). Reproduced from [Simonotto et al. \(1999\)](#), with permission.

physiological nor perceptive, but rather built into the visual scenes displayed to the subjects. The purpose of the artificial threshold was to suppress images below threshold and to allow subthreshold visual stimulation of a sensory system that operates across wide ranges of luminance and contrast. In one study ([Simonotto et al., 1997](#)), the scene was black and white on a 256 gray scale. The paradigm applied to the gray scale value in each pixel was identical with the SR paradigm put forth above. Each pixel was black whenever the gray scale value of the image plus noise (a random selection from a Gaussian distribution on 1–256) exceeded the artificial threshold, or remained otherwise white. The noise intensity was determined by the standard deviation of the Gaussian distribution. An example is provided in [Fig. 4](#), where the picture was suppressed beneath a threshold and the aforementioned paradigm applied. In the actual experiment the noise was dynamical, i.e. in each pixel the noise added to the suppressed image was a function of time (the process is included in an interactive video made available at <http://neurodyn.umsl.edu/~simon/sr.html>). As shown in the figure and the video, there is an optimal noise level enhancing the observer's perception of the image. In the actual experiment a visual stimulus consisting of stripes of various widths was used and subjects were requested to determine the best contrast level at which they could

distinguish between two fine stripes. A minimum in this contrast level signaled the optimal noise ([Simonotto et al., 1997](#)). A follow-on experiment focusing on letter recognition has recently been reported ([Piana et al., 2000](#)).

Documenting that dynamical noise in a threshold system can enhance the accuracy of perception of the scene, however, provides no indication of whether the enhancement is due to temporal averaging of the noise by the retinal cells or reflects instead visual processing in the visual cortex. An fMRI study applying a similar visual protocol indicates that neural activation in visual cortex appears improved by optimal noise ([Fig. 5](#)). The results do not allow a comprehensive understanding of the neural mechanisms involved, yet a conspicuous observation was that the optimal noise was the same for all subjects at a fixed threshold and within the experimental statistical precision ([Simonotto et al., 1999](#)).

4.3. SR, brain multistability and the perception of ambiguous figures

Looking at ambiguous figures results in spontaneous alternation between different stable percepts or interpretations in the absence of a physical change of stimulus ([Attneave, 1971](#)) (Necker's cube, where randomly

switching attention from one corner to another causes alternation between foreground and background percepts, is a classic example; Necker, 1832). This stochastic phenomenon, referred to as visual bistability or multistability, engages separated specialized cortical areas, but is also associated with intermittent inhibition of structures putatively maintaining perceptual stability. Both antagonistic connectivity within the visual system and events initiated by brain areas that integrate sensory and non-sensory information seem to be involved (Kleinschmidt et al., 1998; Long and Olszewski, 1999; Leopold and Logothetis, 1999; Vetter et al., 2000). The dual perception of perspective of Necker's cube has been modeled based on bistable energy potential with additional noise and appears consistent with SR theory (Riani and Simonotto, 1994).

5. SR in human hearing

The auditory system is fundamentally nonlinear (Eguiluz et al., 2000) and there is physiological evidence for SR to occur in human hearing. For instance: (1) the hair bundles of the inner hair cells exhibit SR with respect to mechanical stimulation, with the critical amplitude of noise to give maximum sensitivity of the hair cells being just about that provided by Brownian motion of the surrounding fluid (Jaramillo and Wiesenfeld, 1998); (2) noise added to the auditory stimulus enhances vowel coding in experimental animal models predicting the response of the human auditory nerve to vowels coded by a cochlear implant (Morse and Evans, 1996); (3) thresholds for detection and discrimination of pure tones by people with cochlear or brain-stem implants are decreased by the addition of an optimum amount of broad band noise (Zeng et al., 2000); and (4) the absolute threshold for pure tone detection by normal hearing individuals is decreased in the presence of non-zero levels of added noise (Zeng et al., 2000).

In these studies, SR is characterized by mechanisms of Type E, in which subthreshold noise and stimulus combine in energy to exceed the threshold and become detectable. However, SR of Type I is also involved in human audition. An experiment in which normal hearing listeners were requested to recognize which of two ~ 70 Hz sounds was beating at 3 Hz is summarized in Fig. 3B (Ward et al., 2001). The two sounds were equated for carrier frequency and total energy and differed only in the envelope modulations of the 3 Hz beats. Gaussian noise was added digitally to the two sounds before presentation through a D-to-A converter and special sound-attenuating headphones. An adaptive technique based on SDT was used, in which beat amplitude was increased/decreased in small steps depending on whether the previous response was correct or in error. The curve of the average beat thresholds against the amount of added noise was congruent with Type I SR, in that the sensitivity to the beats was highest for

a non-zero level of added noise (Fig. 3B). It should be noted that the optimal amount of noise is near the absolute threshold for the noise alone under these conditions. The identification of Type I and Type E SR phenomena suggests that audition can be improved in case of hearing loss by adding noise to hearing aids or cochlear implant outputs (e.g. Moss et al., 1996).

6. SR in human tactile experiments

Probably the first observation of Type E SR for tactile sensation was by Collins et al., who found that a non-zero level of random vibration added to the stimulator enhances the detection of weak touches (indentations by a mechanical stimulator) on the observers' fingers (Collins et al., 1995, 1996a). In a later report, such enhancement was found to occur only for near-threshold stimuli, with masking by noise being observed for stimuli above threshold (Collins et al., 1997). Ivey et al. (1998) reported similar psychophysical results and showed how the tuning curves of the relevant mechanoreceptors were affected by the addition of noise, with most information being transmitted at intermediate levels of noise. Richardson et al. (1998) documented that direct electrical stimulation of the touch receptors with a randomly varying electrical current added to a touch stimulus resulted in SR for tactile sensation.

More recently, Type I SR has been demonstrated for touch in experiments in which stimuli vibrating at various frequencies were applied to the foot soles of young and elderly adults (Wells, 2002; Wells et al., 2001) (Fig. 3C). Noise was added digitally to the sinusoidal signal sent to the stimulator through a D-to-A converter. The touch stimuli were equated for total energy by setting the power of the noise stimulus to equal that in the signal + noise stimulus. The only difference therefore was a weak sinusoidal modulation (80% or 90% of threshold) in the stimulus that subjects were requested to identify. For both younger and elderly observers, the proportion of correct responses (proportional to d' in this paradigm) was maximal at a non-zero level of added noise (scaled as percentage of noise threshold) (Fig. 3C). Moreover, SR occurred at all 4 vibration frequencies studied (25, 50, 250, and 400 Hz), therefore implicating all 4 cutaneous receptor systems for touch. The optimum noise level was below noise threshold; it varied over frequencies and groups, but was never higher than 66% of threshold and was detectable by itself only exceptionally. In another experiment, observers' ability to discriminate small differences in the frequency of vibration around 25 and 250 Hz was also improved by the addition of small amounts of touch noise, but only when the vibrations themselves were very weak (110% of non-noise threshold or less). However, only one level of noise was used in this experiment (the optimum noise level for the 90%-of-threshold signal in the previous experiment) and enhanced

discrimination at higher signal levels might be observed if more noise were added.

Application of these findings seems possible. Thresholds for vibration are significantly elevated in the elderly for frequencies above ~ 40 Hz (Wells et al., 2003), but were significantly reduced by SR phenomena in these experiments (nearer to the young subjects' thresholds). There is promise that SR paradigms (induced for example by randomly vibrating shoe inserts) may improve posture and balance in debilitated patients or in the elderly. Indication in this regard comes from the observation that noise reduces postural swaying in the elderly to levels near those of younger subjects without added noise and improves balance (Priplata et al., 2002, 2003).

7. SR, nonlinear visual phenomena and visual mechanisms

Visual information is processed in parallel, with retinotopic projection to cortex through several major pathways from any given retinal location and parallel analysis of the relevant physical properties of visual input. Evidence indicates (quasi) independent and often antagonistic parallel submodalities of processing (an arrangement usually referred to as 'channeling'), that in several instances depend on factors such as selective (linear or nonlinear) threshold and subthreshold summation. Nonlinearity appears to be a widespread characteristic of neuronal mechanisms involved in vision (for instance, simple cells in V1 feed forward to complex cells with a threshold nonlinearity according to the canonical model by Hubel and Wiesel) (Maunsell and Van Essen, 1983; Heeger et al., 1996; Koch and Segev, 2000). Synchronization and phase locking to stimulus of segregated cortical neurons responding to specific properties of visual input (local luminance, contrast, orientation, color, etc.) are also needed for a proper cortical activation to occur and an electrophysiological response to be eventually evoked. Several aspects of this functional arrangement are consistent with SR theory and with the results of modeling and experiments (see also Section 9).

At the retinal level, the sensitivity of bipolar 'on' cells is improved in vertebrates by subthreshold, otherwise undetectable light stimulation. This effect is mediated by cGMP-activated membrane channels and improves light discrimination via a facilitating feedback mechanism that increases the signal above background noise with characteristics consistent with retinal physiology and compatible with SR (Shiells and Falk, 2002). Improved detection of weak signals mediated by processes compatible with SR has been described in the context-dependent response of activated cortical cells, whereby enhancement or depression follow upon weak and strong stimuli respectively, due to the differential effects of excitatory and inhibitory current and noise conveyed by the lateral connections (Stemmler et al.,

1995). In primary visual cortex, membrane potential noise promotes spiking and contributes to the contrast invariance of orientation tuning (Anderson et al., 2000). Micro-movements of the eyes reportedly improve visual acuity with features consistent with SR and have been suggested as a possible source of internal 'noise' contributing to vision (Hennig et al., 2002).

8. SR and electrophysiological signals

With due approximation, the amplitude and SNR of electrophysiological mass responses to sensory stimulation depend on the size and degree of activation of the activated neural assembly(ies) as well as on synchrony among responding neurons. Although of common use, 'signal-to-noise ratio' or comparable definitions are in several instances ambiguous when applied to brain signals (Ryan, 1989; Regan, 1989). Signals such as the spontaneous background EEG are usually (dis)regarded as 'noise' with respect to stimulus- or event-related electrophysiological events, in a pragmatic approach that helps deal with methodological problems like the EEG nonstationarity and incomplete definition as a signal. However, spontaneous brain signals reflect neuronal interaction and changes in brain functional states that can be relevant to sensory information processing. To assimilate the background EEG to ('physiological') noise with respect to the stimulus- or event-related responses in a SR paradigm therefore appears pertinent, but caution and strict control of the experimental conditions are advisable.

Electrophysiological techniques could therefore provide privileged approaches to the investigation of SR in the CNS, also in consideration of the nonlinear characteristics common to (spontaneous and evoked) brain signals and distributed nonstationary cortical sources (Nuñez, 1995). The available evidence seems consistent with this expectation. In agreement with the noise-enhanced spindle function (Cordo et al., 1996) and tactile sensation (Collins et al., 1996a,b), added noise improves the cortical somatosensory response to mechanical tactile stimulation in healthy subjects, with an inverted-U function of the response amplitude at increasing noise amplitudes and improved SNR at optimal noise levels (Manjarrez et al., 2002a). Phenomena consistent with SR were observed at the spinal and cortical stages of the sensory encoding in anesthetized cats, with the coherence between spinal and cortical responses to tactile stimulation also following a SR function that was abolished in cortex but not in spinal structures after sectioning of the dorsal columns and the ipsilateral dorsolateral funiculus. This observation has been interpreted as an indication that SR favors coherence among interacting neuronal structures/mechanisms and has a functional role in the CNS (Manjarrez et al., 2002b, 2003).

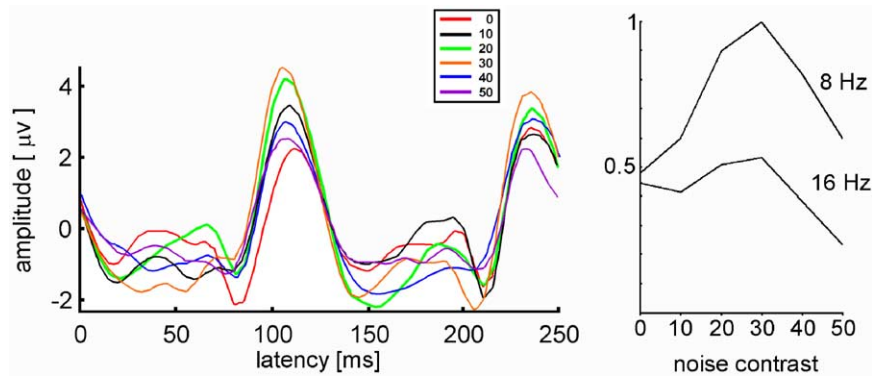


Fig. 6. (Left) Superimposed averaged VEPs from one subject (one cycle of stimulation) at the indicated levels of contrast of added noise; the average VEP amplitude was enhanced by noise by a factor of about 1.6 up to a 30% noise contrast, to be diminished with the noise contrast being increased further. (Right) Power of the 8 and 16 Hz harmonics as a function of noise contrast, with maximum power around 30% noise contrast; average across 13 subjects. The stimulus (black and white grating; spatial frequency: 4 cycles/degree; contrast: 20%) was counterphase reversed at 4 Hz (8 reversal/s). Recording from occipital vs. vertex. Adapted from [Srebo and Malladi \(1999\)](#).

Noise effects on the electrophysiological responses to visual stimulation above threshold match the SR model like those on perceptual responses to subthreshold visual signals (see Section 4.1). Optimal noise increased the response amplitude and power of the first even harmonics of the cortical response to steady-state contrast stimulation (steady-state VEPs). This effect was suggested to arise mainly from activation of complex cells in striate visual cortex based on the nonlinear properties that these cells and the steady-state VEPs share ([Srebo and Malladi, 1999](#)) ([Fig. 6](#)). Following an alternative approach, white noise and a rhythmic, transient luminance stimulus were presented simultaneously and independently to the two eyes arguing that any SR phenomena observed in the electrophysiological response recorded at occipital locations should originate in visual cortex. The normalized power density in the alpha frequency range featured an inverted-U correlation with noise that appears consistent with SR and was interpreted as reflecting the stimulus/noise-related synchronization of responding neurons ([Mori and Kai, 2002](#)).

9. SR and neuronal function

The role of neurons in information processing often depends on thresholds and nonlinearity of function ([Koch and Segev, 2000](#)). Accordingly, the SR paradigm is compatible with single-cell models. It actually represents an early, simple, stochastic neuron model ([McCullough and Pitts, 1943](#)) applying to individual neurons (such as neocortical pyramidal cells and simple or complex cells of visual cortex) as well as at the subcellular level ([Bulsara et al., 1991](#); [Bezrukov and Vodyanoy, 1995](#); [Astumian et al., 1997](#); [Anderson et al., 2000](#); [Rudolph and Destexhe, 2001](#)). The SR paradigm can be extended to ion channels when described by simple two-state models, as experimentally demonstrated by [Bezrukov and Vodyanoy](#)

(1995). Some contiguity among cellular or subcellular mechanisms and processes occurring in neuronal population is conceivable.

9.1. SR and synaptic transmission

‘Internal noise’ can be tentatively defined in models and single-cell experiments with greater approximation than in psychophysics studies, and ‘noise’ sources potentially improving sensory information processing by SR mechanisms are numerous in nature. For instance, synaptic transmission (a nonstationary and nonlinear process because of varying contributions from depolarizing and hyperpolarizing currents) is noisy. Noise is a fundamental aspect of channel gating and also originates from sources such as fluctuations in the transmitter quanta released by nerve terminals, number of activated postsynaptic receptors, ion concentrations, membrane conductance, effects of previous action potentials, etc. ([Traynelis and Jaramillo, 1998](#); [White et al., 1998, 2000](#); [Koch and Segev, 2000](#)). Synaptic noise affects relatively simple neuronal systems (such as the discharge of motoneurons depending on the weighted contributions of multiple inputs; [Poliakov et al., 1996](#)) and even small amounts of synaptic noise from dendritic synapses improve the response to independent, subthreshold synaptic stimuli in agreement with the SR paradigm ([Stacey and Durand, 2001](#)). The detection of distal synaptic inputs by CA1 hippocampus neurons is improved by noise, and the noise level needed to obtain this effect in models is comparable to physiological noise in slices and in vivo ([Stacey and Durand, 2000](#)). Changes in applied electric fields and light levels proved efficient in mimicking ‘intrinsic noise’ in SR studies on in vitro hippocampal cells and on the caudal photoreceptors of the crayfish, respectively; instead, the lack of effects of increased temperature under these experimental conditions points at

some requirement for specificity (Pei et al., 1996; Gluckman et al., 1996).

9.2. SR, neuronal synchronization, phase locking, and frequency-dependent phenomena

SR enhances phase locking and coherence and promotes synchronization in neuronal systems, according to simulation studies and experiments (Neiman et al., 1998, 1999; Bahar et al., 2002; Bahar and Moss, 2003a; Balazsi et al., 2001; Neiman and Russell, 2002; Tass et al., 2003; Pikovsky et al., 2001).³ An alternative description based on accurate systematic theory (Zhou et al., 1990) characterizes SR as a statistical process in which the time distribution of events is not structured in the absence of periodic activation, but can be synchronized by external signals (Neiman et al., 1998). The cells of the electrosensory organs of the paddlefish rostrum behave like noise-mediated oscillators that can be synchronized by an external input (Neiman et al., 1999) (see Appendix A). A correlation between SR effects and an increase in stochastic phase synchronization between the neuronal response and a periodic stimulus has been demonstrated (Bahar and Moss, 2003a).

These observations are pertinent when investigating sensory information processing in animals and man. The recording itself of (electric or magnetic) mass responses to sensory inputs (and the amplitude and SNR variations following upon changes in the stimulus properties or brain state) reflects stimulus-induced or -enhanced phase locking and synchronization of activated neurons. It is not inconceivable that the frequency components of the signal may act like signals or noise depending on function and conditions (see Section 8). Experiments on the shark multimodal sensory afferents indicate that the membrane oscillations near the spike-triggering threshold determine the basic rhythms of impulse generation, but superimposed noise actually triggers impulses (Braun et al., 1994). This observation suggests a functional arrangement whereby background oscillations and external events cooperate to determine a response. If applicable to other experimental conditions, this arrangement appears in agreement with the functional role suggested for the oscillations in

the ~20–80 Hz frequency interval ('gamma' band) that occur spontaneously due to intrinsic cell properties (Llinás, 1998; Silva et al., 1991; Nuñez et al., 1992) and are enhanced into coherent spatiotemporal patterns by sensory (olfactory, auditory, visual) stimulation. These oscillatory responses are observed in membrane/local field potentials and spiking rate as well as in (macro)electrodes or neuromagnetic recordings and are thought to mediate in stimulus-induced neuronal synchronization through interneurons/pyramidal cell coupling (see for reference: Gray and Singer, 1989; Gray and McCormick, 1996; Engel et al., 1992; Singer, 1993; Traub et al., 1999; Sannita, 2000, 2003). In visual cortex, both oscillatory mass responses phase-locked to stimulus (that reflect its physical properties with dynamics anticipating the VEPs) (Sannita et al., 1995, 1999; Sannita, 2000; Tzelepi et al., 2000; Narici et al., 2003) and gamma activities with longer latencies (~280 ms or above) and no phase locking to stimulus have been described and can coexist. The latter activity is observed in concomitance of 'cognitive' processes involving selective attention, focused arousal, visuomotor integration, etc., with different topographic distribution than the phase-locked response (see for reference: Singer and Gray, 1995; Tallon-Baudry and Bertrand, 1999; Sannita, 2000). The suggested core function is to provide spatiotemporal mechanisms by which the activity in separate cortical columns or regions is temporarily coordinated (Gray and Singer, 1989; Engel et al., 1992; Singer, 1993; Sannita, 2000). A role as 'cortical information carrier' has been proposed (Bressler, 1990) that would be consistent with SR theory (Sannita, 2000). The SNR curve in neuronal networks depends in fact on the signal frequency, whereby SR is a possible frequency-dependent amplification mechanism (Gluckman et al., 1996). Models including interneurons and electric synapses describe stimulus-related modulation from low to higher frequencies and synchronization in the ~20–80 Hz interval (Di Garbo et al., 2002). The hypothesis that SR may specifically regulate the oscillatory responses and synchronization in this frequency range (as suggested by Gluckman et al., 1996) remains undocumented. The concept can nevertheless expand to include the nonlinear phenomena and chaotic behavior of neocortical dynamics and signals structure and their physiological implications. A detailed treatment of the issue is given by Nuñez (1981, 1995).

10. SR and models of brain function

The results of most experiments on SR and the effects of noise on sensory functions match those of modeling and simulation, circumstantially supporting a close relationship between neuronal mechanisms and SR theory. The embodiment of SR processes in the real brain is a different matter, however, as the variety of SR observations that relate to brain may not specifically indicate a function. Despite indication that noise occurs

³ Synchronization occurs when a nonlinear oscillator with a stable limit cycle is subjected to an external time-dependent force or is coupled with another oscillator. It is usually understood as the locking between instantaneous phases of a state variable of the oscillator and depends on the circuit natural frequency (Neiman et al., 1998; Brown and Kocarev, 2000). In neuroscience it is often referred to as a 'neural activity at any level of congruence above that of coincidence in a fraction of the neighboring generators or a volume of tissue, in broad-band range or in a defined frequency band', without required agreement in phase across frequency bands. Coherence implies that: (1) two neurons (or neuronal aggregates) have a component of the energy at a given frequency following a common driver; (2) one drives the other; (3) they reciprocally cooperate; or (4) there are common characteristics with a phase delay that is constant over time (Bullock and McClune, 1989).

naturally, to identify ‘internal’ noise in the CNS and to incorporate in the SR theory any of the possible sources of neuronal noise (ion channel or synaptic noise, noise built into the stimulus, light, eye micro-movements, etc.; Stemmler et al., 1995; Pei et al., 1996; White et al., 1998, 2000; Traynelis and Jaramillo, 1998; Stacey and Durand, 2000, 2001; Shiells and Falk, 2002; Hennig et al., 2002) remains a major and still unresolved problem. Once ‘internal’ noise originating from any source is defined, also crucial is how to change it in the brain under experimental control or to monitor and relate to function its spontaneous or state-related fluctuations. The issue regarding a possible role of SR in evolution is also critical. SR has been connected with the evolution of the frog auditory system (Jaramillo and Wiesenfeld, 1998). However, the hypothesis that any (neuronal) system has evolved an internal, or natural, noise optimal for some general process (including sensory information processing) has never been tested experimentally under controlled conditions and may hardly be.

A cautious interpretation of the available evidence is that there is no unambiguous demonstration that naturally occurring noise actually enhances information transmission and processing, nor is it documented that neuronal systems do optimize the noise intensity for maximum information or efficacy of processing. Yet some indication that SR models may reflect mechanisms that are operative in the CNS seems to exist and justifies research. The caveats mentioned above and the requirements for experimental demonstration notwithstanding, SR appears to be a ubiquitous and remarkable phenomenon congruent to the available theories on brain function (e.g. Nuñez, 1995; Tass, 1999), with widespread potentialities in both biological and medical protocols and a privileged field of application in neuroscience.

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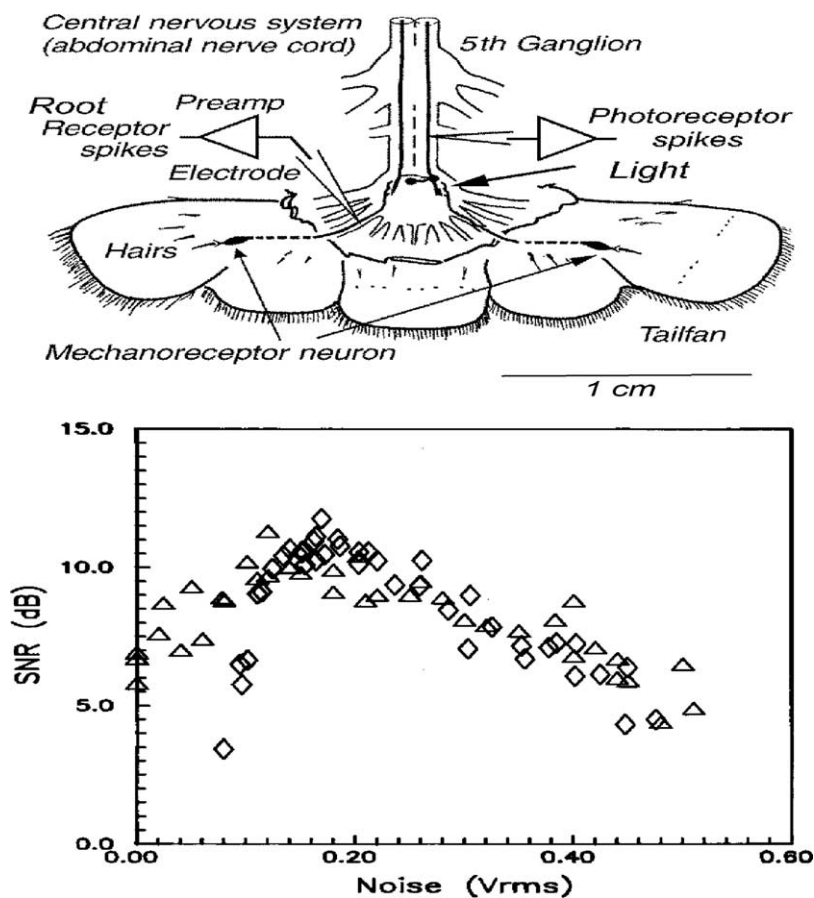


Fig. A1. Diagram of the crayfish (*Procambarus clarkii*) tail-fan with hydrodynamically sensitive mechanoreceptors (upper panel). Extracellular recordings were made from the sensory neurons in the root (left preamplifier). The SNR in decibels computed from power spectra of the measured root receptor spike trains with periodic subthreshold hydrodynamical forcing (triangles). The horizontal scale is the noise intensity measured in Volts-rms input to an electromechanical transducer that moved the tail-fan preparation relative to the saline solution in which it was immersed with a combination of sinusoidal (10 Hz) plus Gaussian, band limited (25 Hz) noise (0.5 Vrms was equivalent to sinusoidal peak amplitude of motion of 122 nm). A simulation by an electronic analog neuron model is shown for comparison (diamonds). Adapted from Moss et al. (1993).

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Appendix A. SR in predator avoidance and at the perceptive level in feeding behavior

The tail-fan of crayfish is covered with hydrodynamically sensitive hairs, each one innervated by sensory neurons that converge on interneurons in the sixth ganglion (upper panel of Fig. A1). Recorded spike trains from the sensory neurons of the crayfish during periodic stimulation are similar to those shown in the paradigm described in Section 2.1 and Fig. 1, with the measured SNRs (obtained from the power spectra of the measured spike trains) showing a maximum at an optimal noise intensity (lower panel of Fig. A1, triangles). This behavior was also

mimicked by an electronic analog simulator of a model neuron (Moss et al., 1993; lower panel of Fig. A1, diamonds). The experiment was repeated with many improvements using the cercal system of the cricket, a non-aquatic animal of the same phylum as the crayfish with a very similar neural architecture for predator avoidance based on the perception of air motion (Levin and Miller, 1996). Results were similar in the two experiments, the major difference being the sensitive frequency ranges (6–15 and 90–150 Hz for the crayfish and cricket, respectively).

The passively electrosensitive paddlefish features a long anterior rostrum, which is covered with tens of thousands of electrosensitive organs that detect and track the weak electric fields generated by the swimming and feeding motions of its favorite prey zooplankton *Daphnia* (Wilkens et al., 1997). The electric field around the *Daphnia* is dipole-shaped. Thus, the further individual plankton is from the rostrum, the weaker the electrical signature at the rostral surface, dropping beneath the animal's perceptive threshold at some limiting distance. The animal's perceptive abilities in the presence of a weak signal from prey are improved when external noise is added in the form of a random electric field applied parallel to the fish long axis (Russell et al., 1999; top panel of Fig. A2). The results of this study support the hypothesis that these subthreshold signatures

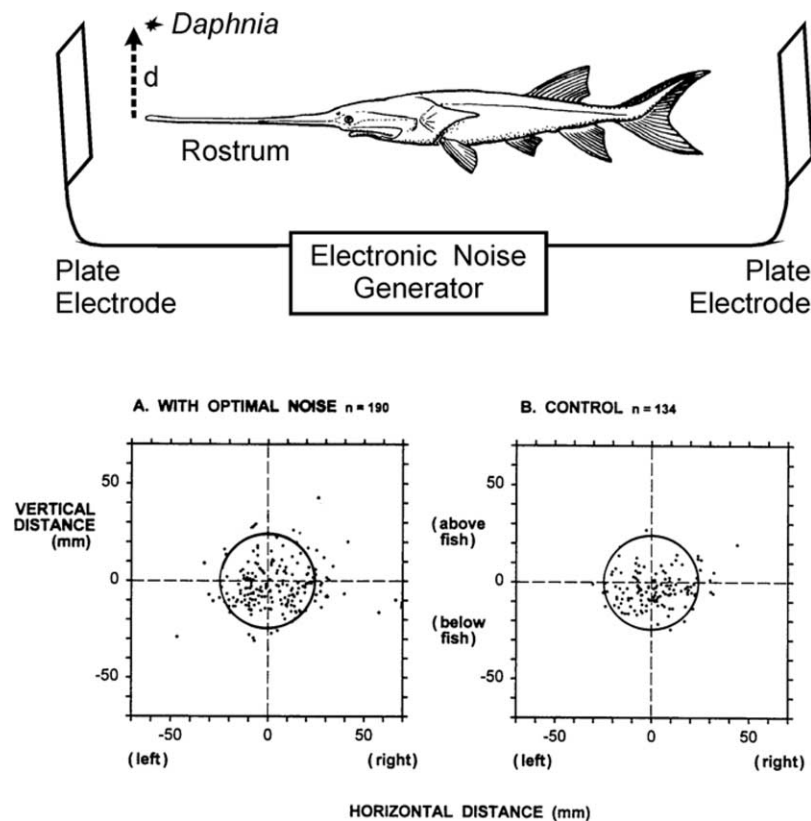


Fig. A2. Diagram of the paddlefish *Polyodon spathula* swimming in the swim mill between a pair of parallel plate electrodes. A weak ($0.1\text{--}100\ \mu\text{V}/\text{cm}$) noisy electric field was generated across the fish. The locations of *Daphnia* crossing a plan perpendicular to the tip of the rostrum (radius d measured from the origin at the tip) are marked as shown in the lower panels (left panel: captures in the presence of optimal noise; right panel: captures with no noise). Adapted from Russell et al. (1999).

can be enhanced by externally added electrical noise, and that the fish would be able to extend the distance range of its capture distribution in the presence of optimal noise (Russell et al., 1999, 2001; Freund et al., 2002) (see bottom panel of Fig. A2).

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