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How does stochastic resonance work within the human brain? – Psychophysics of internal and external noise

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ABSTRACT

We review how research on stochastic resonance (SR) in neuroscience has evolved and point out that the previous studies have overlooked the interaction between internal and external noise. We propose a new psychometric function incorporating SR effects, and show that a Bayesian adaptive method applied to the function efficiently estimates the parameters of the function. Using this procedure in visual detection experiments, we provide significant insight into the relationship between internal and external noise in SR within the human brain.

1. Introduction

Noise is inevitably present in both man-made and natural systems, and has traditionally been considered as a detriment to signal detection and information transmission. But surprisingly, during the past few decades, noise has been discovered to be of benefit; for example, the noise-enhanced detection and transmission of weak signals are possible in certain nonlinear systems via a mechanism known as stochastic resonance (SR; for review, see [1–3]).

The concept of SR was originally put forward as a possible explanation for the apparent periodicity of Earth's ice ages in the seminal papers by Benzi and collaborators [4,5]. The term "stochastic resonance" was initially invented in order to describe the process whereby the response of a bistable dynamical system subject to feeble periodic forcing (i.e., signal) undergoes resonance-like behavior as a function of the level of random perturbation (i.e., noise). In 1994, however, Wiesenfeld and coworkers found that non-dynamical systems with threshold-like properties also show the hallmark of SR, an inverted U-shaped relationship between the detection performance of a nonlinear system and noise [6–9] (Fig. 1). Now, the term SR is expanded to include any phenomenon whereby a nonlinear system — whether dynamical or non-dynamical — can detect an otherwise undetectable signal by the addition of a particular, non-zero level of noise to the signal. SR has stimulated research in a variety of fields and, as a result, SR-type phenomena have been observed in a wide variety of systems, including physical [10,11], chemical [12], and biological systems [13–15].

In this article, we first review how the concept of SR has impacted on research in neuroscience, and point out that the previous studies have overlooked the interaction between internal and external noise. Then, we introduce the results of psychophysical experiments that point to the hypothesis that the internal noise within the brain substantially influences SR in visual perception.

2. Stochastic resonance in neuroscience

Noise is ubiquitous in the nervous system: at the level of a single neuron, there is membrane noise related to the dynamics of ion channels, and furthermore, the convergence of multiple independent random synaptic inputs will contribute to a source of noise at the level of neuronal networks. Additionally, environmental noise will also contribute to a source of noise. Therefore, effects of noise have attracted widespread attention in neuroscience. It seems that the roles of noise on motor control and planning have been investigated from a different point of view of SR. For example, Cabrera and Milton [16] found that, during stick balancing, parametric noise results in corrective movements that occur on all time scales including those shorter than the time delay of feedback, contributing to the stability of the stick. Given the many roles of noise other than SR, especially in motor control (for example, see

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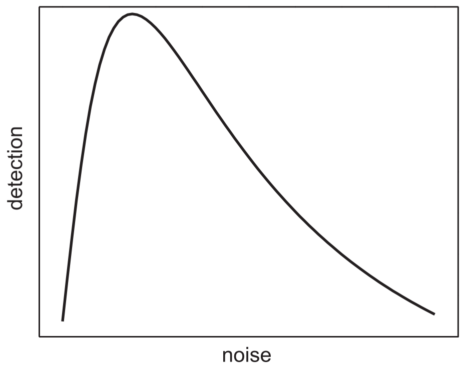

Fig. 1. The signature of stochastic resonance (SR). The measure of detection performance such as a signal-to-noise ratio (SNR) has its maximum at an intermediate level of noise.

[17,18]), we cannot provide a comprehensive review in this paper. Therefore, we restrict our focus to SR.

Time delays, which arise, for example, due to finite axonal conduction velocities, processing times, and so on, are also present in the nervous system. SR effects can arise from the interaction between noise and delay [19]. In addition, in bistable time-delayed dynamical systems, there is the possibility that long-lived transient states can arise, referred to as metastability [20]. These observations might be relevant to the noise-induced neural synchronization, which we refer to later in this section. We thus consider that time delays may be an important factor in information processing in the nervous system, but we will not deal directly with time delays in this paper.

Because sensory neurons in their coarse behavior operate as a threshold system [21], researchers have thought that the threshold SR may play a significant role in sensory perception. Roughly speaking, studies on SR in sensory biology have evolved from the level of sensory receptors to that of neuronal networks within the central nervous system (CNS).

Probably the first study suggesting the existence of SR in the sensory system was reported by Longtin and colleagues [22]. They investigated the interspike interval histogram (ISIH) recorded from real, periodically forced sensory neurons. They found two features: first, the modes are located at integer multiples of the stimulus period, and second, the mode amplitudes decay rapidly, approximately exponentially. The authors neither measured nor controled the noise level directly, but concluded, from theoretical analysis, that these features cannot exist without noise. The more direct experimental evidence of SR in the sensory system was first reported by Douglass and colleagues [13]. They applied electric stimuli of periodic signal and noise to crayfish mechanoreceptor cells, and recorded the spike trains from the cells. The measured signal-to-noise ratio (SNR), a measure of the sensitivity, showed a maximum at an optimal noise intensity, a hallmark of SR. These works have been limited to the treatment of systems with periodic signals; on the contrary, Collins and colleagues presented a theory for characterizing SR-type behavior in excitable systems with aperiodic signals (aperiodic stochastic resonance, ASR; [23]), and demonstrated ASR experimentally in rat cutaneous mechanoreceptors [24]. SR in sensory receptors was also found in the *auditory* system of leopard frogs [25]. Furthermore, Cordo and coworkers [26] found SR-like phenomena in sensory receptors of *human* subjects.

SR-like phenomena are observed in neuronal activities recorded not only from sensory receptors but also from large-scale neuronal networks. Srebro and Malladi [27] recorded electroencephalography (EEG), which reflects a mass response of a very large number of cortical cells, from human subjects and investigated the visual evoked potential (VEP) produced by visual stimuli consisting of a temporally modulated checkerboard pattern (served as periodic signals), plus spatio-temporal noise. There was a peaked relationship between VEP (amplitude and power) and added noise level, the hallmark of SR. SR in neuronal networks (i.e., EEG activity) was also found in human *somatosensory* system [28]. A problem of these studies is that they adopted the so-called single receptor design, where both signal and noise are injected into the same receptor (Fig. 2A). The fact that SR-like phenomena were observed in EEG does not always guarantee that SR occurred not in the sensory periphery but in the brain, because, in single receptor design, signals and noise can interact in the sensory periphery before reaching the CNS. To dissociate SR occurring in the CNS from SR occurring in the peripheral nervous system, one has to adopt a double receptor design, where signals and noise are injected into two distinct receptors from which neuronal inputs first converge in the CNS (Fig. 2B).

Using a double receptor design, Manjarrez and colleagues [29] demonstrated the occurrence of SR in the CNS, in anesthetized cats. They applied periodic tactile stimuli with an indenter placed on the glabrous skin of the central pad of the hind paw and noisy tactile stimuli with an additional indenter placed on the glabrous skin of the third digit of the hind paw. This protocol ensured that the signal and noise were mixed not in the skin but in the somatosensory regions of the CNS. All the cats showed distinct SR behavior in the spinal and cortical evoked field potentials (EFPs). However, SR observed in cortical EFPs still does not guarantee that SR is occurring in the *brain*, because it may reflect SR occurring in the spinal cord. The occurrence of SR in higher levels of the CNS, the brain, was first demonstrated in human subjects by Hidaka and colleagues [30] for the brain stem reflexes and later by Mori and Kai [31] in the cortex. In the latter study, the researchers separately stimulated the right eye with a subthreshold periodic optical signal and the left eye with noise, and recorded EEG activity. This protocol (a double receptor design) ensured that the signal and noise were first mixed in the visual cortex. For all the subjects, brainwave entrainment to the signal had the bell-shaped dependence on added noise intensity, which is the signature of SR.

As described above, SR has been observed in neurophysiological data recorded from every level of the nervous system, from the level of sensory receptors to that of neuronal networks within the brain. Because these neurophysiological studies do not deal directly with functional aspects of SR, more recent studies have focused on the noise-induced enhancement in behavioral or functional performance in animals [15] and humans. Probably the first experimental evidence of behavioral SR in humans was

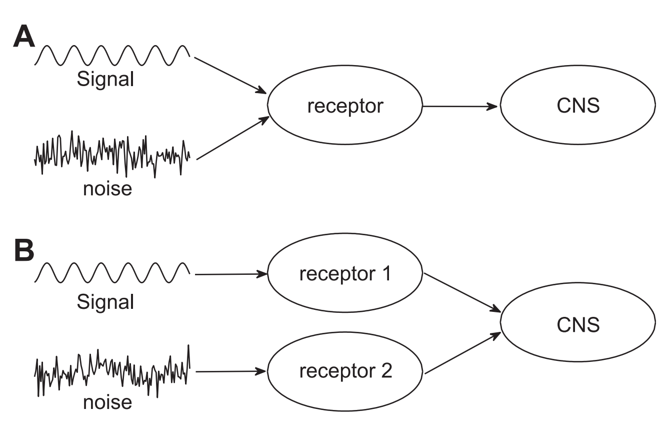

Fig. 2. (A) Single receptor design. In this design, signals and noise interact in the receptor. Therefore, one cannot dissociate SR occurring in the central nervous system (CNS) from SR occurring in the sensory periphery. (B) Double receptor design. In this design, signals and noise converge in the CNS. Therefore, this design can be used to test whether SR occurs in the CNS.