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Letter to the Editors

Stochastic resonance in the speed of memory retrieval

Marius Usher[1], **Mario Feingold**[2]

[1] Department of Psychology, Birkbeck College, University of London, London, WC1E 7HX
[2] Department of Physics, Ben-Gurion University, Beer Sheva, 84105, Israel

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Abstract. The stochastic resonance (SR) phenomenon in human cognition (memory retrieval speed for arithmetical multiplication rules) is addressed in a behavioral and neurocomputational study. The results of an experiment in which performance was monitored for various magnitudes of acoustic noise are presented. The average response time was found to be minimal for some optimal noise level. Moreover, it was shown that the optimal noise level and the magnitude of the SR effect depend on the difficulty of the task. A computational framework based on leaky accumulators that integrate noisy information and provide the output upon reaching a threshold criterion is used to illustrate the observed phenomena.

1. Introduction

An important question in the debate regarding the nature of the neural code is whether the irregularity of neural responses (Softky and Koch 1993) reflects a complex hidden signal or a noisy mode of information processing (Shadlen and Newsome 1994; Ferster and Spruston 1995). Although noise is usually thought to be detrimental to information processing, the phenomenon of stochastic resonance (SR) (Wiesenfeld and Moss 1995), whereby an optimal level of noise enhances the performance of a non-linear system, may provide an alternative rationale for a noisy neural code. Recently, SR has been reported in physiological systems affecting animal behavior (Douglass et al. 1993; Levin and Miller 1996; Collins et al. 1996a; Russell et al. 1999) and in human tactile (Collins et al. 1996b) and visual perception (Simonotto et al. 1997). Moreover, computational studies have shown that SR is expected to occur in neural responses (Collins et al. 1995; Stemmler et al. 1995; Stemmler 1996). An important question is whether the benefits of noisy processing are confined to sensory processes or whether they extend to central cognition. Here we present experimental data demonstrating SR in central cognitive processes and develop a computational framework that illustrates the mechanism that underlies this behavior.

Correspondence to: M. Feingold
(e-mail: mario@bgumail.bgu.ac.il)

2. Experimental evidence for SR in cognition

In our search for SR effects in central cognition, we focused on the task of memory retrieval for single-digit arithmetical multiplications (e.g. "$7 \times 8 =$?"). We used this task because it relies on a central cognitive process that, due to a high degree of pre-experimental training, is expected to show relatively low variability. We assumed that irrelevant acoustic input would induce noise (proportional to its loudness level in decibels) in the neural representations that mediate the computation of memory retrieval. The acoustic noise was delivered as sequences of random frequency tones. To obtain a single measure of performance that could be compared across noise levels, we focused on the speed of response (or its inverse, the response time – RT) while ensuring that incorrect responses were prevented. Otherwise, two independent measures, RT and accuracy, would be obtained involving complex dependencies, such as speed–accuracy tradeoffs (Luce 1986). To prevent errors from affecting the performance measure, participants were prompted by the computer software to make a new response if they produced an error, until the correct response was made. The RT recorded was the total time from stimulus presentation to the correct response.

Using this method, 19 participants were tested on their speed of memory retrieval for sets of arithmetical multiplications at six levels of auditory noise delivered by headphones, ranging from 51 dB to 90 dB.[1]

[1] The questions were grouped in blocks of four that were delivered at the same noise level (loudness of the tones). Six levels of noise were used and all the participants performed a set of practice trials with easier questions followed by two sets of six blocks. The first of these two sets was presented in ascending order of loudness and the second set in descending order.

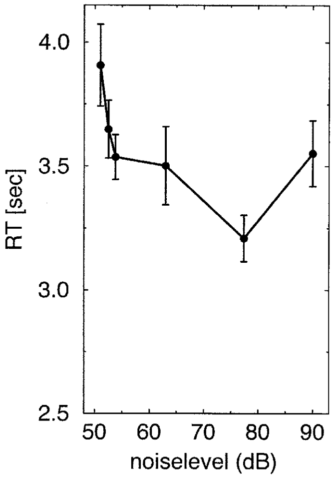

Fig. 1. Average RT as a function of noise for the 19 participants in the experiment (see text). *Error bars* correspond to one standard error

Response time performance as a function of noise (Fig. 1) indicates that up to an optimal level, the noise facilitates memory retrieval but at noise levels beyond the optimum, it slows down retrieval speed. Since experimental data is subject to statistical fluctuations due to a limited sample of measurements, it is necessary to estimate the statistical significance of the results.

This is done by calculating the probability of rejecting (or accepting) the null hypothesis, according to which the minimum in the RT at 77 dB is due to random fluctuations alone. Specifically, we estimate the probability, P, that the RT measured at 77 dB and the RTs measured at 50 dB and at 90 dB are statistical samples (based on 19 measurements, each one corresponding to one of the 19 participants in the experiment) from the same theoretical distribution.

Using the participant's t-test for 18 degrees of freedom we find that the probability, P, of accepting the null hypothesis is $P < .01$ ($t(18) = 3.07$) for 50 dB, and $P < .05$ ($t(18) = 2.37$) for 90 dB, where t is the difference between the two RTs normalized by the average of their standard errors.

It is standard in statistical analysis to reject the null hypothesis when its probability is lower than .05.

This result indicates that effects of SR, previously reported in perceptual processes (Collins et al. 1996b; Simonotto et al. 1997), also take place in more central cognitive processes. To understand the mechanism that may mediate this effect, we present in the following a simple neurocomputational model for noisy processing that provides a framework within which this behavior can be quantitatively examined.

3. A computational framework

The computational framework that we discuss in this section represents a highly simplified model of the actual process, a mere description that illustrates the main ingredients leading to SR-type behavior. It certainly does not describe the complex neural mechanism involved in retrieval of multiplication rules. This task is beyond the scope of this letter. Subject to these important limitations and for the sake of brevity, in what follows, we shall refer to the set of equations describing the competition between the correct and the incorrect answers as the "model".

In the process of performing single-digit multiplications, the participants in our experiment needed to make a connection between two input digits and a range of possible answers to decide which was the correct one. The answers can be thought off as response units that receive activation from the inputs on the basis of associations stored in memory. For simplicity, we assume that the unit that corresponds to the correct response, x_1, receives a standard input I_1 (chosen without restricting generality to be unity), whereas other units corresponding to incorrect answers receive a weaker input. Such input to the incorrect response units may be due to overlaps in the digit representations as proposed in previous neurocomputational models of numerical processing (Dehaene and Changeux 1996) and generates a distractor-type competition. We denote the unit that receives the second highest input as x_2 and its corresponding input as I_2.

The level of this input to an incorrect answer unit should reflect the difficulty of the question, namely, well-learned answers are thought to have lower competing distractors than less well learned ones.

Memory retrieval is modeled by activating the two inputs and generating a race process of the two response units, the correct one, x_1, and the incorrect one, x_2, (all other units receiving weaker inputs are neglected). To model the response time , we adopt the framework of race models, which are regularly used in computational models for choice RT in psychology (Luce 1986). Accordingly, when several response units are activated by the input, the one selected is the one that first reaches the activation level corresponding to the threshold. Moreover, the time it takes to select the response, RT, corresponds to the time it takes the activation to reach the firing rate threshold (see, for example, Grice 1972; Luce 1986). In these models, the variability that is ubiquitous in experimental RT data is accounted for by noise in the accumulation stage, resulting in a diffusion process (Ratcliff 1978). Recently, neural traces that provide support for this approach were reported (Hanes and Schall 1996). It was shown that the RT for eye movement is determined by the time it takes neural activation in the corresponding neurons to reach a specific level.

Here we assume that each response unit has the dynamics of noisy leaky accumulators (Grice 1971; Usher and McClelland 2000). This corresponds to the firing rate dynamics in cell populations (e.g. Wilson and Cowan 1972; Amit and Tsodyks 1991; but see Eggert and van Hemmen 2000, for a more complex scheme of neural population dynamics that takes into consideration patterns of synchrony within the population). In previous work (Usher and Niebur 1996), we found that the firing rate dynamics (Wilson and Cowan 1972; Amit and Tsodyks 1991) are well approximated by large computer

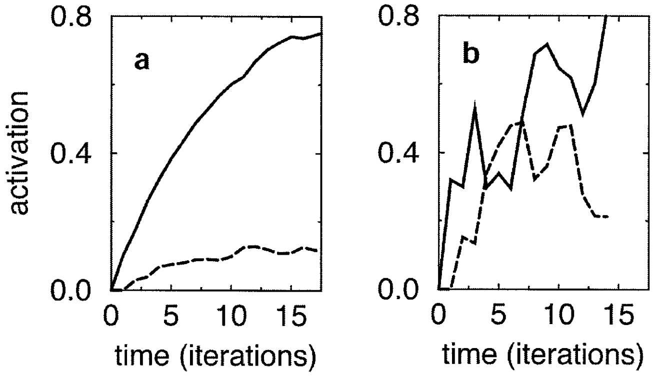

Fig. 2. The effect of noise on memory activations in the model for two accumulators. Eq. (1) is solved numerically with time step $dt = 0.1$, and independent Gaussian noise, ξ, with variance σ^2, is added to each unit at each iteration step. The activation of the correct unit, x_1, is shown by the *solid curve*; that of the distractor, x_2, corresponds to the *dashed curve*. **a** $\sigma = 0.036$; **b** $\sigma = 0.39$ ($I_1 = 1, I_2 = 0.23, \lambda = 1.2$, and $\theta = 0.77$)

simulations of integrate-and-fire neurons under conditions of noisy input and low firing rate. Since the units are assumed to receive Gaussian noise, the race process can be described as a diffusion process with drift I_i and with leak of activation, λ,

$$dx_i = (-\lambda x_i + I_i)dt + \xi\sqrt{dt} \ , \tag{1}$$

where dt is the time step and ξ is a Gaussian random variable with zero mean and standard deviation (SD) σ. The $\sqrt{dt}$ factor in Eq. (1) is a result of the fact that the variances rather than the SDs add up linearly in time (see Ricciardi 1977). This results in an Ornstein–Uhlenbeck diffusion process, which was recently used to explain a large amount of data from visual detection and choice latency paradigms (Smith 1995; Usher and McClelland 2000). The neural input–output response function assumed in this model is threshold linear. This is different from the logistic functions assumed in many connectionist and neural network models. However, in the range of low firing rates that prevails in cortical activity it provides a good approximation to experimental results (Ahmed et al. 1998). The race process between the two leaky accumulators and the effect of the neural noise (assumed to increase with the loudness of the auditory input) on this process is illustrated in Fig. 2. The noise speeds up the arrival of both accumulators to the response threshold. This speedup, however, is accompanied by a decrease in accuracy. Higher noise increases the probability of incorrect responses, that is, situations in which the unit with low match, I_2, reaches the threshold before the unit with high match, I_1.

To model the experimental data, we numerically simulated the process described above for different levels of noise, σ. In each simulation trial, the RT is the time when the correct unit reaches the threshold, θ. When the incorrect unit, x_2, reaches the threshold before the correct unit, x_1, the two accumulators are reset to zero and the process is restarted after a time delay of K iterations, which is a model parameter and accounts for the dead

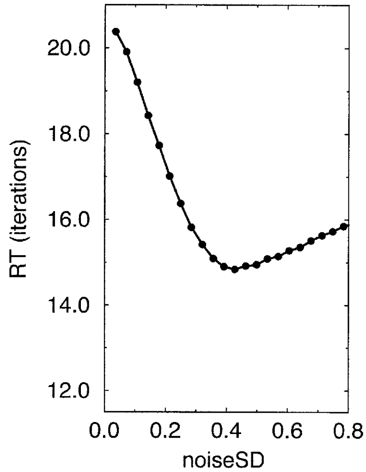

Fig. 3. The effect of noise on retrieval speed according to the model. Each point in the simulation is obtained by averaging the RT over 300,000 trials. $I_1 = 1, I_2 = 0.23, K = 14, \lambda = 1.2$, and $\theta = 0.77$. The *solid line* is obtained by simulating the process in which multiple attempts are made until the correct response is reached. The *symbols* are obtained by computing the values of T_1, T_2 in single-attempt simulations and n (see text)

time spent during the production of the incorrect response and the participants' preparation for a new attempt. The effect of noise on the speed of retrieval for the computer simulations is shown in Fig. 3 (solid line), demonstrating a stochastic resonance effect. This behavior is due to the fact that whereas a small degree of neural noise speeds up memory retrieval, larger amounts of noise induce incorrect retrievals that, in turn, cause delay. The tradeoff between the arrival times of the two racing accumulators to the response threshold, T_1 and T_2, and the number of retrieval attempts, n, required for a correct response of total latency RT can be explicitly formulated as

$$RT = T_1 + (T_2 + K)(n - 1) \ . \tag{2}$$

The prediction of this equation was verified using the numerically computed values of T_1, T_2, and n at different noise levels (Fig. 3, bullets). Moreover, Eq. (2) allows us to derive an analytic approximation of the dependence of RT on the parameters of the model (see Appendix).

Computer simulations demonstrate that SR-type behavior also takes place in models with more than two competing accumulators corresponding to multiple distractors. In this case, one observes a faster increase in RT at the high-noise end that is due to the increase in the error rate with the number of distractors.

4. The effect of the difficulty level

Using the analytical approximation formulas derived in the Appendix [Eqs. (A3, A4)] we put to the test a few of the model's predictions involving the effect of noise on RT as a function of the difficulty of the questions. The model indicates that the SR effect will be larger, that is, a deeper minimum, for easy questions (where $I_1 - I_2$ is

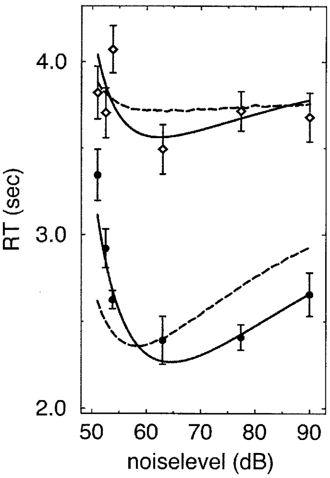

Fig. 4. Effects of task difficulty on RT performance. *Error bars* represent the average RT data pooled over the 19 participants (*bullets* easy, *diamonds* difficult). The *solid lines* result from fitting the analytical approximation of Eqs. (A3, A4) and the *dashed lines* are obtained from the model simulation with the parameters of the fit. Increased difficulty corresponds to a lower value of $I_1 - I_2$ (0.89 for easy condition and 0.32 for difficult condition; Easy: $I_1 = 1, I_2 = 0.08$; Difficult: $I_1 = 1, I_2 = 0.68$; for both cases $K = 74, \lambda = 1.2, \theta = 1.38$)

high) than for difficult questions (where $I_1 - I_2$ is low; see Fig. 4). To test this prediction we first classified the data in our experiment into two categories of difficulty established in a control experiment in which separate groups of participants performed the same experiment in the absence of noise. The mean RTs as a function of noise for the "easy" (bullets) and the "difficult" (diamonds) conditions are shown in Fig. 4. For questions that were classified as easy there is a strong reduction in RT with noise levels up to 63 dB [RT(63 dB) = RT(50 dB); t(18) = 3.73, $P < 0.001$) followed by an increase between 77 dB and 90 dB (RT(90 dB) = RT(77 dB); t(18) = 1.49; $P < 0.08$]. No significant variation between the RT values at different noise levels was found in the case of the difficult questions. Second, we used the analytical formula of Eqs. (A3, A4) to fit the data for the two conditions. The fit is done using a Metropolis-type optimization algorithm that varies the model parameters in order to minimize the χ^2 function, that is, the sum of squared distances between the data and the theory divided by the squares of the corresponding standard errors. Moreover, we assumed that the noise SD in the simulation is linearly related to the level of noise in the experiment, noiselevel (dB) $= a_x + b_x * \sigma$, and that the experimental RT is linearly related to the RT of the model, RT(s) $= a_y + b_y \cdot$ RT(iterations). The linear scaling parameters were varied together with those of the model to minimize the χ^2 function. A single parameter, I_2, was varied to account for the difference between the easy and the difficult conditions.

We observe (Fig. 4) that the analytic fits (solid lines) closely reproduce the experimental data, namely, a deeper minimum is obtained for the easy questions and a relatively flat behavior for the difficult ones. The computer simulation for the corresponding parameters shows similar behavior. Although better agreement between the computer simulation of Eq. (1) and the experimental data could have been obtained for slightly different values of the parameters, it is impractical to obtain a systematic fit between the two. We therefore choose to determine the parameters of the model that correspond to the experiment via the approximate RT formula of Eqs. (A3, A4). The fit allows us to obtain the relation between the variables of the model and those in the experiment. We find that the corresponding scaling parameters are $a_x = 27.57$, $b_x = 33.61$, $a_y = 0.62$, and $b_y = 0.04$. This allows us to characterize the outcome of the experiments in terms of the parameters of the model. We find that the value of the I_2 parameter for the fitted RT curve is higher for the difficult questions (0.68) than for the easy ones (0.08). Since I_2 corresponds to the input received in incorrect responses with a partial match, this result can be interpreted in the framework of the model. Specifically, difficult questions are likely to be those that relate to single-digit representations with wider, less localized activation profiles that should then generate more input for the partial match competitors.

An important feature of the RT data for the easy tasks is that the strength of the SR effect, namely, the depth of the minimum, is significantly larger than that observed in the experiment of Fig. 1. This is a consequence of the fact that the data of that experiment represent a mixture of two different processes, one which displays a pronounced SR minimum and the other which is relatively flat.

The inspection of Eq. (2) allows us to understand the enhancement of the SR effect in the case of easy tasks. On one hand, $T_i(\sigma)$ is a monotonically decreasing function. For a fixed value of σ, both T_i and $dT_i/d\sigma$ grow as I_i decreases. Therefore, $T_i(\sigma)$ goes down faster for the easy tasks than for the difficult ones. On the other hand, the average number of errors, $(n-1)(\sigma)$, is a sigmoidal function that grows at larger σ for larger $I_1 - I_2$ differences. Therefore, for the easy tasks, RT(σ) will display a sharper decrease at low σ due to the mean arrival times, T_i, and a slower increase at larger σ due to the errors, $(n-1)$, leading to an overall more pronounced minimum. In other words, the SR effect is stronger for easy tasks due to enhanced sensitivity of the response times to noise and lower error rates.

5. Discussion

The model we presented here is highly simplified. Future work should address in greater detail the dynamics of neural populations (Eggert and van Hemmen 2000). Moreover, one could extend the model to include the effect of varying difficulty in the experiment by allowing the $I_1 - I_2$ difference to take values from a distribution.

Nevertheless, we believe that our simplified scheme captures the essential features of the process we set out to measure. In particular, the parameterization of the experimental curves on the basis of the model indicates that we observed a novel mode of SR. Unlike in previous studies in which SR improves the perceived quality of a transmitted signal, for example, effective signal to noise ratio, here, SR results from the competition between two opposed factors that characterize many aspects of cognitive performance: speed and accuracy. Since task performance often depends on a combination of speed and accuracy, this is a generic type of SR that operates at the cognitive level and should have important implications for optimizing the efficiency of information processing in this domain. Further investigation within this framework may shed light on the adaptive role played by stochastic processes in cognition (Oaksford and Chater 1998).

6. Appendix

Since an analytic solution for the arrival time of an OU process to threshold is difficult (Ricciardi 1977), in this appendix we present a simple analytical approximation for this process. As illustrated in Fig. 4, this approximation provides results that are close to those obtained from the simulation of the model.

The basis for the analytical approximation is an assumption similar to the principle of *probability summation over time* (Watson 1978), which has been successfully used in computational models of visual threshold detection. Accordingly, the time axis is partitioned into windows of width Δt. The activations of the response units in each window are represented by two random variables, x_1 and x_2, that are independent, uncorrelated, and distributed according to $P_1(x_1)$ and $P_2(x_2)$, respectively. To satisfy the lack of correlations across successive windows, the width of the time window should satisfy $\Delta t > 1/\lambda$. The distribution of activations, $P_i(x_i)$, for each unit is, according to the OU diffusion process, a Gaussian with mean and variance determined by the OU process with drifts I_i (Ricciardi 1977),

$$< x_i > (t) = \frac{I_i}{\lambda}[1 - \exp(-\lambda t)] \ , \tag{A1}$$

$$\mathrm{Var}_{x_i}(t) = \frac{\sigma^2}{2\lambda} \ [1 - \exp(-2\lambda t)] \ , \tag{A2}$$

where Var_{x_i} is the variance of x_i and $x_i(0) = 0$. A simple approximation can be obtained by neglecting the transients, namely, assuming that the accumulators are reaching the steady state equilibrium instantaneously such that neither the means nor the variances of the OU process are time dependent. This assumption leads to constant probabilities for the correct and the incorrect unit to reach the threshold during a time window Δt , P_1 and P_2, respectively,

$$P_i = \frac{1}{2} \ \mathrm{erfc}\left(\frac{\theta - \frac{I_i}{\lambda}}{\frac{\sigma}{\lambda}}\right) \ , \tag{A3}$$

where $\mathrm{erfc}(x)$ is the complementary error function, defined as $\frac{2}{\sqrt{\pi}}\int_x^\infty \exp(-y^2)\mathrm{d}y$. The mean T_1, T_2, and n can be estimated with the following assumptions: [1] The time for a correct response corresponds to the first time window where the discretized trajectories, $x_1, \ x_2$, satisfy $x_1 > \theta; x_2 < \theta$. [2] If during a time window preceding the one in [1] $x_1, \ x_2$ satisfy $x_1 < \theta; x_2 > \theta$, then the process is restarted after a time delay K; [3] If during a time window preceding the one in [1] both accumulators are above threshold ($x_1 > \theta; \ x_2 > \theta$), then a tie is declared and therefore with probability 0.5 the window is considered to render the correct RT and with probability 0.5 the process is reset as in [2]. Summing the series of all possible paths to a correct answer and using Eq. (2), we obtain

$$RT = \frac{\Delta t}{P_1 + P_2 - P_1P_2} + \left(\frac{\Delta t}{P_1 + P_2 - P_1P_2} + K\right) \frac{2P_2 - P_1P_2}{2P_1 - P_1P_2} . \tag{A4}$$

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References

Ahmed B, Anderson JC, Douglas RJ, Martin KAC, Whitteridge D (1998) Estimates of the net excitatory currents evoked by visual stimulation of identified neurons in cat visual cortex. Cereb Cortex 8: 462–476

Amit DJ, Tsodyks M (1991) Quantitative study of attractor neural network retrieving at low spike rates: I. Substrate – spikes, rates and neuronal gain. Network 2: 259–273

Anderson JR, Matessa MP (1996) A production system theory of serial memory. Psychol Rev 104: 728–748

Collins JJ, Chow CC, Imhoff TT (1995) Aperiodic stochastic resonance in excitable systems. Phys Rev E 52: R3321–R3324

Collins JJ, Imhoff TT, Grigg P (1996a) Noise-enhanced information transmission in rat SA1 cutaneous mechanoreceptors via aperiodic stochastic resonance. J Neurophysiol 76: 642–645

Collins JJ, Imhoff TT, Grigg P (1996b) Noise-enhanced tactile sensation. Nature 383: 770

Dehaene S, Changeux JP (1993) Development of elementary numerical abilities: a neuronal model. J Cognitive Neurosci 5: 390–407

Douglass JK, Wilens L, Pantazelou E, Moss F (1993) Noise enhancement of information transfer in crayfish mechanoreceptors by stochastic resonance. Nature 376: 337–340

Eggert J, van Hemmen JL (2000) Unifying framework for neuronal assembly dynamics. Phys Rev E 61: 1855–1874

Ferster D, Spruston N (1995) Cracking the neuronal code. Science 270: 756–757

Grice GR (1972) Application of a variable criterion model to auditory reaction time as a function of the type of catch trial. Percept Psychophys 12: 103–107

Hanes DP, Schall JD (1996) Neural control of voluntary movement initiation. Science 274: 427–430

Levin JE, Miller JP (1996) Broadband neural encoding in the cricket cercal sensory system enhanced by stochastic resonance. Nature 380: 165–168

Luce DR (1986) Response times. Oxford University Press, New York

Oaksford M, Chater N (1998) Rationality in an uncertain world. Psychology Press, Hove, UK

Ratcliff R (1978) A theory of memory retrieval. Psychol Rev 85: 59–108

Ricciardi LM (1977) Diffusion processes and related topics in biology. Lecture Notes in Biomathematics. Springer, Berlin Heidelberg New York

Russell D, Wilkens L, Moss F (1999) Use of behavioral stochastic resonance by paddlefish for feeding. Nature 402: 219–223

Shadlen MN, Newsome WT (1994) Noise, neural codes and cortical T organization. Curr Opin Neurobiol 4: 569–579

Simonotto E, Riani M, Seife C, Roberts M, Twitty J, Moss F (1997) Visual perception of stochastic resonance. Phys Rev Lett 78: 1186–1189

Smith PL (1995) Psychophysically principled models of visual simple reaction-time. Psychol Rev 102: 16–32

Softky W, Koch CJ (1993) The highly irregular firing of cortical cells is inconsistent with temporal integration of random EPSPs. J Neurosci 13: 334–350

Stemmler M (1996) A single spike suffices: the simplest form of stochastic resonance in model neurons. Network 7: 687–716

Stemmler M, Usher M, Niebur E (1995) Lateral interactions in primary visual cortex: a model bridging physiology to psychophysics. Science 269: 1877–1880

Usher M, McClelland JL (2000) On the time course of perceptual choice: the leaky competing accumulator model. Psychol Rev, in press

Usher M, Niebur E (1996) Modeling the temporal dynamics of IT neurons in visual search: a mechanism for top-down selective attention. Journal of Cognitive Neuroscience 8: 311–327

Watson AB (1978) Probability summation over time. Vision Res 19: 515–522

Wiesenfeld K, Moss F (1995) The benefits of background noise. Nature 373: 33–36

Wilson H, Cowan J (1972) Excitatory and inhibitory interactions in localized populations of model neurons. Biol Cybern 12: 1–24