

## A model for the speed of memory retrieval

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**Abstract.** The memory retrieval process of number problems with external noise is studied with the use of the Bonhoeffer–van der Pol oscillator model. Three cell assembly responses are simulated, coding one true number and two neighboring erroneous. The time of a correct response,  $T_c$ , was averaged over statistical assemblies of numerous trials. It is demonstrated that  $T_c$  takes a minimum value for a certain noise intensity. This result correlates well with experimental data by Usher and Feingold (2000). The location of the minimum as a function of the time delay between two consecutive simulation trials is investigated.

Usher and Feingold (2000) showed experimentally that the speed of memory retrieval depends on external noise nonmonotonically: it is minimal for a certain value of noise intensity. The authors called this phenomenon stochastic resonance.<sup>1</sup> Usher and Feingold (2000) measured the mean time  $T$  of the response of 19 participants to the task of memory retrieval for single-digit arithmetical multiplications at six levels of external noise and determined that it had a minimum. The measurements were taken in such a way that participants were prompted by the software to make a new response if they produced an error until the correct response was produced.

For an explanation of the experimental results Usher and Feingold (2000) suggested a random-walk-type model with an artificial response criterion to determine response time (RT). We suggest a biologically oriented model for the following reason.

Higher brain functions are thought to be based on processing units called cell assemblies. Cell assemblies consist of large groups of neurons with strong reciprocal internal connections and form a randomly coupled

neuronal network where certain sets of neurons simultaneously become active so that their connections become increasing stronger (so-called Hebb's law) (Hebb 1949; Gustafson et al. 1987; Bonhoeffer et al. 1989; Ahissar and Vaadia 1990). Due to strong intraassembly connections, the activation of a certain amount of neurons of an assembly results in the spreading of activation in the local network and, finally, to the ignition of the whole assembly. A special regulatory mechanism guarantees that only one or a limited number of assemblies will ignite simultaneously (Braitenberg 1978). If a cell assembly has strong internal connections, its ignition will occur instantaneously so that all or at least many neurons of this assembly become active almost concurrently. The question is how quickly the activity will spread through the assembly. We consider only fast and slow modes of the activation of all neurons. In the fast mode, after activation of a neuron subset of an assembly, almost all its remaining neurons can be activated synchronously because of a low threshold of activation of all neurons in the network. The low threshold means that a certain neuron can be activated under the action of a very small amount of previously activated neurons. If the activation threshold is high (i.e., when large amounts of previously activated neurons are necessary to activate a certain neuron), a "stepwise" mode of activation will be realized. This means that the activity spreads from one set of neurons to the next only after all neurons of the previous sets have been activated. Obviously, in the "stepwise" mode, much more time is required to activate a whole neuron assembly.

It is known (Lopes da Silva et al. 1997; Nishida et al. 1997) that each neuron has two kinds of inputs: informational input, i.e., neural code for specific informational operations, and irrelevant input, or arousal, which keeps neurons at the appropriated level of excitability. The latter is the slightly correlated noise of the neuron network, which is similar to thermal noise. It is possible that the brain uses this inevitable noise as an energy factor that takes part in the regulation of excitability of neurons. It can be inferred that the level of neural noise depends on the general level of neuronal activity, which

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<sup>1</sup> We believe this term is not as appropriate for the phenomenon indicated and ones like it (Collins et al. 1995; Stemmler 1996) as for the "classical" problem of an overdamped two-well oscillator because the term "resonance" usually indicates some relation between frequencies, which is absent here (see, e.g., Landa 2001).

is determined by internal and external (sensory) events irrelevant to the basic task. Thus in general, the higher noise level, the higher excitability of neurons and the shorter the period of activation of a whole assembly.

It should be noted that external noise makes a partial contribution to neuronal noise. But how does the level of external noise influence the elements of cognitive activity, for example, in recognizing certain symbols, numbers, letters, etc.? For example, if we intend to think about some symbol, e.g., test number “31,” this number must be coded in brain by activation of a specific neuron assembly. We will call this assembly memory item 31. To recall the number 31, i.e., to retrieve it, it is necessary to activate memory item 31 again. This activation should occur through corresponding “informational” input in response to the presented number 31. The faster the activation of the memory item occurs, the shorter the period of number recognition.

It should be noted that some neurons within the cell assembly of memory item 31 can be initially activated by the presentation of an “error” symbol that is graphically similar to the true one, e.g., the number “34” or “81.” As a result, either total activation of the memory item 31 will be delayed or no activation will occur. In the former case, the number 34 or 81 will be falsely recognized as 31, whereas in the latter case, the response will be correct.

But what happens if, in addition to the information input, the noise input is present? It is possible that in the absence of this input the threshold of activation of different memory items may be sufficiently high, so that the signal coming in through an information input is insufficient for the activation of the corresponding memory item. In this case, the presence of noise, supplying additional spikes and thereby lowering the activation threshold, causes the increase in the probability of the recognition of the required symbol. At the same time, the increase of the noise intensity can bring into operation the erroneous identification of symbols similar to the required one.

To explain errors it is necessary to consider the joint operation of the whole pool of memory items coding similar symbols, i.e., 31, 34, and 81. Assume the input is 31; as the noise intensity increases, the probability of the activation of memory items 34 and 81 increases too because the spike flow from the noise input is added to the spikes of the informational inputs partially activated by symbol 31 that correspond to memory items 34 and 81. This results in the increase of the errors caused by the erroneous recognition of the true symbol (31) as a false one (i.e., 34 or 81).

Thus, to explain the observed features of the memory retrieval process with external noise it is necessary to simulate at least three cell assemblies, coding one true number and two graphically similar to it. For the sake of simplicity, we will assume that each of these assemblies functions like one neuron. This assumption can be justified by the fact that neurons comprising the assembly are well synchronized. One model of neuron activation was suggested by Bonhoeffer (Bonhoeffer 1941; Bonhoeffer 1948; Bonhoeffer and Langhammer 1948;

Bonhoeffer 1953) and became known as the Bonhoeffer–van der Pol oscillator (Landa 1996). This model describes oscillations of voltage across the neural membrane taking into account refractoriness. The equations that we simulated describe three coupled Bonhoeffer–van der Pol oscillators with noise sources. They are

$$\begin{aligned}\dot{x}_1 &= x_1 - \frac{x_1^3}{3} - y_1 + I_1 + \xi_1(t), & \dot{y}_1 &= c(x_1 + a - by_1) \\ \dot{x}_2 &= x_2 - \frac{x_2^3}{3} - y_2 + I_2 + \xi_2(t), & \dot{y}_2 &= c(x_2 + a - by_2) \\ \dot{x}_3 &= x_3 - \frac{x_3^3}{3} - y_3 + I_3 + \xi_3(t), & \dot{y}_3 &= c(x_3 + a - by_3)\end{aligned}\quad (1)$$

where  $a = 0.7$ ,  $b = 0.8$ , and  $c = 0.1$  are parameters assumed to be the same for all oscillators,  $I_{1,2,3}$  are the informational inputs that must be different for the oscillator responsible for the correct response and the oscillators responsible for false responses, and  $\xi_1(t)$ ,  $\xi_2(t)$ ,  $\xi_3(t)$  are independent white noises assumed to have the same intensity  $\kappa$  for all oscillators. We designate the first oscillator to be responsible for the correct response and set  $I_1 = 0.3$  and  $I_2 = I_3 = 0.15$ .

In the absence of noise, each of the oscillators is in its equilibrium state because the excitation threshold is equal to  $I_0 \approx 0.341$ , i.e., it is greater than  $I_1, I_2$ , and  $I_3$ . The presence of a small noise results in the appearance of probabilities of excitation of any of these oscillators, but the probability of excitation of the first oscillator, even if very small, is higher than that of the other two. This probability increases with increasing noise intensity, i.e., the mean time of the excitation of the first oscillator decreases rapidly. At the same time, the probabilities of excitation of the two other oscillators grow too, resulting in an increase in the number of errors.

Just as in Usher and Feingold (2000), we took for the time of a correct response  $T$  the total time required for the first oscillator to be excited before the others, assuming that if an error occurs, a new response is required until a correct response is produced. To find  $T$ , for each value of the noise intensity  $\kappa$  ( $\kappa$  is determined by the formula  $\langle \xi_{1,2,3}(t)\xi_{1,2,3}(t + \tau) \rangle = \kappa\delta(\tau)$ ), we performed

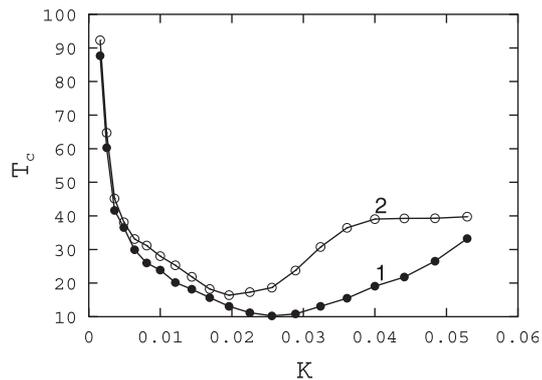
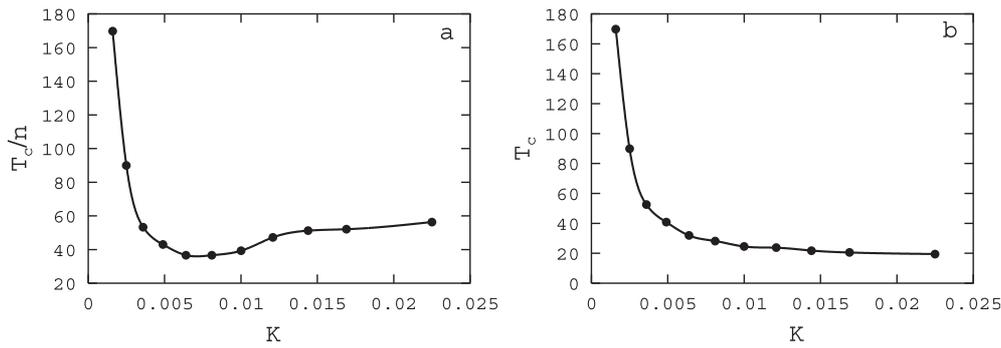


Fig. 1. The plot of  $T_c$  vs.  $\kappa$  for  $T_0 = 15$  (curve 1) and  $T_0 = 30$  (curve 2)



**Fig. 2.** The dependencies (a) of the ratio of the mean correct response time  $T_c$  to  $n$  and (b) of  $T_c$  on noise intensity  $\kappa$

a set of simulation trials until the oscillator responsible for the correct response was excited. If this occurred in the first simulation trial, the corresponding set consisted of a single element and  $T = T_1$ ; otherwise, it consisted of a greater number of elements. Repeating these sets of simulation trials, we obtain a statistical ensemble of the values of  $T$  and can average  $T$  over this ensemble. Thus, the formula that we used for calculation of the mean time of a correct response  $T_c$  is

$$T_c(\kappa) = \langle T \rangle = \left\langle T_1 + T_2 + T_3 + \dots + T_k + (k-1)T_0 \right\rangle \quad (2)$$

where  $T_i$  ( $i = 1 \dots k$ ) is the excitation time of any oscillator in the  $i$ th simulation trial,  $k$  is the number of trials required for a correct response,  $T_0$  is the time delay between the  $i$ th and  $i+1$ -th simulation trials, and angle brackets mean the average operation over the sets of trials. The results are presented in Fig. 1 for two values of  $T_0$ . It is seen that  $T_c$  does have a minimum for a certain value of noise intensity. As  $T_0$  increases, this minimum is somewhat shifted in the direction of smaller values of  $\kappa$ .

It should be noted that similar results can be obtained using a simpler model of two Bonhoeffer–van der Pol oscillators with different excitation thresholds (the oscillator with the smaller threshold (first) is assumed to be responsible for a correct response, and the oscillator with the larger threshold (second) is assumed to be responsible for a false response). As before, we set  $I_0 = 0.3$  ( $x_0 \approx -0.9933$ ) for the first oscillator and  $I_0 = 0.15$  ( $x_0 \approx -1.10432$ ) for the second one. We suppose that the response is correct if the first oscillator is excited first and calculate the ratio of the mean time of a correct response  $T_c$  to  $n$ , where  $n$  is equal to twice the difference between the relative number of the correct responses  $n_c$  and  $1/2$ .<sup>2</sup> The dependence of this ratio on the noise intensity is illustrated in Fig. 2a. We see that this dependence has a minimum. The presence of the minimum can be explained as follows. In accordance with the general theory (Landa and Stratonovich, 1962), as the noise intensity increases, the mean time of the excitation of the first oscillator (as well as the second)

decreases monotonically (Fig. 2b). At the same time, the probability for the second oscillator to be excited first increases, i.e., the relative number of the correct responses decreases. If the latter decreases more rapidly than the former, the minimum appears.

Thus, we have shown that the experimental results by Usher and Feingold (2000) concerning the nonmonotone dependence of the speed of memory retrieval on external noise intensity can be explained in the framework of a more biological model as compared to what has been suggested in Usher and Feingold (2000). The reason for this nonmonotony lies, on the one hand, in the decrease of the threshold of activation of the neuron assembly responsible for the memory retrieval of some symbol, and, on the other hand, in the increase of the number of errors with increasing noise intensity.

## References

- Ahissar E, Vaadia E (1990) Oscillatory activity of single units in a somatosensory cortex of an awake monkey and their possible role in texture analysis. *Proc Natl Acad Sci USA* 87: 8935–8939
- Bonhoeffer KF (1941a) Über die Aktivierung von passiven Eisen in Salpetersäure. *Z Elektrochem* 47: 147–156
- Bonhoeffer KF (1948b) Activation of passive iron as a model for the excitation of nerve. *J Gen Physiol* 32: 69–75
- Bonhoeffer KF, Langhammer G (1948c) Über periodische Reaktionen. IV. Theorie der kathodischen Polarisation von Eisen in Salpetersäure. *Z Elektrochem* 52: 67–72
- Bonhoeffer KF (1953d) Modelle der Nervenerregung. *Naturwissenschaften* 40: 301–311
- Bonhoeffer T, Staiger V, Aertsen AMHJ (1989) Synaptic plasticity in rat hippocampal slice cultures: local “Hebbian” conjunction of pre- and post-synaptic stimulation leads to distributed synaptic enhancement. *Proc Natl Acad Sci USA* 86: 8113–8117
- Braitenberg V. (1978) Cell assemblies in the cerebral cortex. In: Heim R, Palm G (eds) *Theoretical approaches to complex systems. Lecture notes in biomathematics*, vol 21. Springer, Berlin Heidelberg New York, pp 171–188
- Collins JJ, Chow CC, Imhoff TT (1995) Aperiodic stochastic resonance in excitable systems. *Phys Rev E* 52: R3321–R3324
- Gustafsson B, Wigstroem H., Abraham WC, Huang YY (1987) Long term potentiation in the hippocampus using depolarizing current pulses as the conditioning stimulus to single volley synaptic potentials. *J Neurosci* 7: 774–780
- Hebb DO (1949) *The organization of behavior: a neuropsychological theory*. Wiley, New York
- Kramers HA (1940) Brownian motion in a field of forces and diffusion model of chemical reactions. *Physica* 7: 284–304
- Landa PS, Stratonovich RL (1962) On the theory of fluctuational transitions of different systems from one stable state to another. *Vestnik MGU (Physics and Astronomy) No 1*: 33–45 (in Russian)

<sup>2</sup> We note that in the case of a very strong noise, when the probabilities of correct and false responses are equal,  $n_c \rightarrow 1/2$ .

- Landa PS (1996) *Nonlinear Oscillations and Waves in Dynamical Systems*. Kluwer, Dordrecht, The Netherlands
- Landa PS, McClintock PVE (2000) Changes in the dynamical behavior of nonlinear systems induced by noise. *Phys Reports* 323: 1–80
- Landa PS (2001) *Regular and chaotic oscillations*. Springer, Berlin Heidelberg New York
- Lopes da Silva FN, Pijn JP, Velis D, Nijssen PCG (1997) Alpha rhythms: noise, dynamics and models. *Int J Psychophysiol* 26: 237–249
- Nishida S, Nakamura M, Suwasono S, Honda M, Shibasaki H (1997) Estimate of physiological variability of peak latency in single sweep P300. *EEG Clin Neurophysiol* 104: 431–436
- Stemmler M (1996) A single spike suffices: the simplest form of stochastic resonance in model neurons. *Network* 7: 687–716
- Usher M, Feingold M (2000) Stochastic resonance in the speed of memory retrieval. *Biol Cybern* 83: L11–L16