Signal transmission competing with noise in model excitable brains

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Abstract. This is a short review of recent studies in our group on how weak signals may efficiently propagate in a system with noise-induced excitation-inhibition competition which adapts to the activity at short-time scales and thus induces excitable conditions. Our numerical results on simple mathematical models should hold for many complex networks in nature, including some brain cortical areas. In particular, they serve us here to interpret available psycho–technical data.

Keywords: complex neural networks; adaptive synapses; stochastic multiresonance; excitable brains.

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INTRODUCTION

Transmission in natural media is sometimes observed to be spontaneously optimized by the system itself, so that weak signals are able to go through without damping while overcoming an apparently predominant noisy environment. Analysis of the relevant situations have in the past associated this outstanding feature of nature with various interesting phenomenologies (see, for instance, [1]-[7] and references therein), including enhancement of dynamic range, stochastic resonance, coherence among noise and signal, nonequilibrium phase transitions, etc.

The actual perspective after three decades of effort suggests that such assorted phenomenology always seems originated in the same basic mechanism, namely, kind of excitability which is in practice due to competition between opposing, say, excitatory/inhibitory tendencies. Such a competition concerns, for example, the biophysical processes driving dynamics of actual synapses in the nervous systems. This significantly influences the transmission of information which, encoded in spike trains or in waves of action potentials generated in a given neuron reaches other neurons. As a matter of fact, the postsynaptic response to incoming stimuli has been demonstrated to be an activity–dependent process in such a way that, for instance, may be enhanced and/or depressed at short time scales depending on the stimuli frequency [8, 9, 10].

We here review some of our recent effort, and also present some new material on this topic as communicated in the 12th Granada Seminar. We first focus on the influence of different possible basic hypothesis on the transmission of weak signals by using simple, familiar partial–differential–equation models [11, 12]. The information thus collected
is then applied to study transmission in complex networks [13], which is relevant to many fields of science [14, 15] including neuroscience [16, 17]. The result is a detailed description of the microscopic mechanisms that seem to originate, and the relevant phenomenology that has been reported to accompany lack of dissipation and resonances during the propagation of signals through diverse excitable media. We report qualitative agreement of our main model with available experimental data.

A FEED-FORWARD MODEL

A simple perceptron type of model will first serve us to correlate different basic hypothesis with emergent behavior. Let us assume a unit, which one may interpret as one of the neurons in a network, acted on by a set of other N units or neurons, as illustrated in Fig. 1A. The relation is via complex links, channels or synapses which induce excitability. Specifically, following [18], for instance, we assume that any link, \( i = 1, \ldots, N \), has \( r_i \) random components —to be interpreted as neurotransmitter emitting vacuoles, for example—and that each is activated with probability \( u \) and stays silent afterwards for a time interval \( \tau \), this being a random variable with exponential distribution \( p_t(\tau) \) of mean \( \tau_{\text{rec}} \) at time \( t \). The activation of \( i \) at time \( t_i \) generates a current, \( I_i(t) \), that evolves according to

\[
\frac{dI_i(t)}{dt} = -\frac{I_i(t)}{\tau_{\text{in}}} + \sum_{\ell=1}^{r_i} J_{i,\ell} \delta(t-t_i),
\]

where \( \tau_{\text{in}} \) characterizes the transmission duration, and \( J_{i,\ell} \) is the change in component \( \ell \) if this is active which occurs with probability \( u[1-p_i(\tau)] \) (\( J_{i,\ell} \) is zero otherwise). The variations with \( i \) of this change as well as those of \( r_i \) may be assumed, for simplicity, to be Gaussian distributed with mean and standard deviation \( (J, \Delta J) \) and \( (r, \Delta r) \), respectively. The total current is then \( I_N(t) = \sum_i I_i(t) \), and the voltage in response to an input signal \( A(t) \) may be written as \( dV/ dt = F(V, I_N, A) \), i.e., a dynamics that depends on the nature of each unit which is determined by function \( F \). A familiar choice is the integrate–and–fire (IF) model with refractory period \( \tau_{\text{refrac}} \) in which \( F \) is linear with \( V \) ([19]; see also, for instance, [20]). However, this means a fixed firing threshold \( \theta \), which is a poor description for most purposes [21, 22]. Therefore, one may alternatively assume that units are of the FitzHugh–Nagumo (FHN) type [23, 24, 25]. It follows, which may be more realistic [26], that the threshold unit adapts to the input current. The resulting dynamics is

\[
\frac{dV(t)}{\varepsilon dt} = V(t)[V(t)-a][1-V(t)] - W(t) + \frac{\rho}{\varepsilon \tau_m}[A(t)+I_N(t)],
\]

where \( \rho \) is a resistance to transform current into voltage, and \( W(t) \) is a slow variable, accounting for the refractory time of the unit, which satisfies \( dW(t)/dt = bV(t) - cW(t) \). The (presumed weak) signal may be chosen as \( A(t) \equiv A_0 \cos(2\pi f_{\text{signal}} t) \) but other choices, including Poissonian trends have been used in our studies [27]. A situation of interest is one in which all the, say, presynaptic neurons are in a steady state in which they fire independently, uncorrelated from each other with certain mean frequency \( f_{\text{noise}} \).
FIGURE 1. (A) Feed-forward, perceptron setting in which $N$ units (full circles) transmit noisy, generally uncorrelated activity to a single unit (empty circle) which simultaneously receives a weak structured signal $A(t)$. (B) Time variation of the input signal (top) and response series at low (a), medium (b) and high (c) levels of noisy, for static links and IF neurons. (C) For the same case, the input-output correlation versus $f_{\text{noise}}$ indicating the corresponding ranges of noise as in the previous graph. (D) The same for dynamic links and FHN neurons as one varies $\tau_{\text{rec}}$. Other details are given in the main text and in [27].

The result is a noisy $I_N$ with a difficult dependence on $f_{\text{noise}}$. The question is then how $A(t)$ of frequency $f_{\text{signal}}$ can go through as one modifies $f_{\text{noise}}$.

A convenient measure of this is the input-output correlation function:

$$C(f_{\text{noise}}) = \frac{1}{\Delta t} \int_{t_0}^{t_0 + \Delta t} m(t) A(t),$$

for small $\Delta t$, where $m(t)$ is the firing rate —mean value of activity; see next section— of the, say, postsynaptic neuron. Figures 1B and 1C illustrate the behavior of the system when links are static, namely, $u = 1$ and $\tau_{\text{rec}} = 0$, in which case $p_i(\tau)$ transforms into a delta function and $J_{i,i}$ is constantly nonzero. The first of these figures shows typical outputs for the voltage at the postsynaptic neuron as one modifies the firing frequency of the presynaptic population, $f_{\text{noise}}$. When this is very small, as in (a), the generated current $I_N$ on the postsynaptic neuron can only induce sub-threshold behavior which is weakly correlated if at all with $A(t)$. Increasing $f_{\text{noise}}$ increases both $I_N$ and its fluctuations so that a condition is reached in which the postsynaptic neuron fires so frequently, as in (c), which obscures $A(t)$. However, there is an intermediate value of $f_{\text{noise}}$, as in (b),
at which the neuron fires strongly correlated with $A(t)$, that is, several action potentials are emitted each time $A(t)$ is at a maximum. This interesting behavior, often known as stochastic resonance, is clearly revealed by the peak of the function $C(f_{\text{noise}})$ in Fig. 1C. The situation is even more interesting when the links have an active dynamic behavior and neurons are of the FHN type as described above. This is illustrated in Fig. 1D showing, for a range of $\tau_{\text{rec}}$ values, that two maxima of the correlation then occur so that the transmission is optimized for two ranges of rather well separated noise frequencies. The same occurs if, in addition to synaptic depression as in these examples, we assume facilitation [12]. The precise location of the high and low frequency peaks depends on the level of depression and facilitation which is adopted at the links. Interesting enough, this indicates one how to get a better design of devices for the controlling of signals, for instance.

A systematic study of emergent behavior using variations of our model above reveals the situation illustrated in Fig. 2. A summary is that, under rather general conditions a weak signal may successfully compete with noise and show stochastic resonance —as in the cases in Fig. 2 corresponding to the three graphs in the upper row and to the center one in the bottom row— while transmission through several different levels of noise requires some special conditions. That is, it is not sufficient to have complex dynamic links but the relevant units need also have adaptive thresholds as, for example, in the FHN neuron model.
A COMPLEX NETWORK

A main question is whether this behavior, namely, undamped transmission of weak signals in some cases, which in the above abstract model is due to kind of local excitability, may spontaneously emerge from cooperation in complex attractor networks. To explore this issue, let us consider next a networked set of binary units, say, \( s = \{ s_i \} \), where \( s_i \) at node \( i \) is assigned either 0 or 1. The links or synapses \( ij \) are of intensity or weight given by \( \bar{\omega}_{ij}(t) = \omega_{ij}x_j(t) \). Here, \( x_i(t) \in [0, 1] \) is a dynamic variable to be determined and \( \omega_{ij} = [Np(1-p)]^{-1}\sum_{\mu}(\xi_i^\mu - p)(\xi_j^\mu - p) \) is the maximum of conductance (\( \omega_{ij} \) is defined to be 0). This choice somewhat modifies the familiar Hebbian prescription [32]; it still involves a set of patterns, e.g., \( \xi^\mu = \{ \xi_i^\mu = 0, 1 \} \) with \( \mu = 1, \ldots, P \), as if previously stored in the links, but we are specifically concerned here with random patterns having a given value for the symmetry parameter of the set, \( p = \langle \xi_i^\mu \rangle_{i,\mu} \).

The resulting network [13], which can sensibly metaphor a brain cortical area, evolves with time as a parallel, cellular automaton, namely, by stochastic changes of the whole set \( s = \{ s_i \} \) at each time according to probabilities:

\[
P_i \{ s_i(t+1) = \sigma \} = \frac{1}{2} + \left( \sigma - \frac{1}{2} \right) \tanh \left[ I_i(t)T^{-1} \right], \forall i,
\]

where \( \sigma = 1 \) or 0, and \( T \) is the temperature of the underlying bath which controls the stochasticity of dynamics. Here, \( I_i(t) = 2[h_i(t) - \theta_i + A(t)] \) stands for the total input on each unit, \( h_i(t) = \sum_j \bar{\omega}_{ij}s_j(t) \) is the net current from others on unit \( i \), \( \theta_i \) are thresholds for firing, and \( A(t) \) is the (weak) external signal; for simplicity, these are taken as \( \theta_i = \frac{1}{2} \sum_j \bar{\omega}_{ij} \) and \( A(t) = A_0 \cos(2\pi ft) \). A simple choice to determine the weights \( \bar{\omega}_{ij}(t) \) consists in assuming that \( x_i(t) \) changes with time according to the map [33]:

\[
x_i(t+1) = x_i(t) + \frac{1-x_i(t)}{\alpha} - \beta x_i(t)s_i(t).
\]

This depicts a sawtooth–shaped time change, with \( \alpha \) and \( \beta \) measuring the teeth width and depth, respectively, which describes a competition of effects in the channels weights associated to their “fatigue”. That is, the link of intensity \( \omega_{ij}x_j \) is debilitated as \( \beta \) is increased, while decreasing \( \alpha \) makes \( x \) to recover its maximum value more rapidly. The channel weight effectively remains constant in practice if such a recovery becomes very fast, so that one sometimes speaks of “\( \alpha = 0 \)” as the limit of static synapses which characterizes the standard Ising and Hopfield cases [34, 32]. The motivation for the ansatz (5) are differential equations —such as the ones we developed in the previous section— trying to account for the fact that electrical stimulation due to local and even spatially extended activity may induce short–term plasticity leading to depression and sometimes also facilitation of the channel transmission [8, 35]. As a simpler minded alternative to (5), one may assume that \( x_i(t) \) changes so rapidly with time that its action may be described in the relevant time scale by means of the stationary distribution

\[
p(x_i) = \zeta(s) \delta(x_i - \Phi) + [1 - \zeta(s)] \delta(x_i - 1).
\]
That is, with probability $\zeta(s)$, which will in general depend on the network activity —in practice, it happens not to be essential whether the model considers either local or global activity here—, the weights are changed by a factor $\Phi$ but remain unchanged otherwise. Depending on the value of $\Phi$, this rule may simulate nodes excitability or potentiation or fatigue of the connections as a function of the degree of order in the system. The standard, Hopfield–Hebb model then corresponds to $\Phi = 1$. A convenient choice here happens to be $\zeta(s) = (1 + P/N)^{-1} \sum_\mu (m^\mu)^2$ defined in terms of the overlap $m^\mu = [np(1-p)]^{-1} \sum_i (\xi^\mu_i - p) s_i$ between the system and each of the stored patterns, $\mu$.

The detailed study of the model using either (5) or (6) shows no essential differences for $A(t) = 0 \forall t$ [36]. A main result in the specific case (6) is that, tuning properly parameter values, it exhibits familiar equilibrium phases, namely, a disordered high-$T$ phase—corresponding to the paramagnetic phase in condensed matter—in which the stationary values of all the overlaps are practically zero, a low-$T$ phase with conventional order—corresponding to ferromagnetism—in which the global activity converges with time towards one of the attractors $\{\xi_i^\mu\}$, so that it is often taken as a model example of associative memory, and a —say, spin-glass— phase in which convergence is towards a mixture of stored patterns. In addition, and most interesting, the system may be tuned to exhibit nonequilibrium phases [34]. Namely, (i) one in which there is a rapid and rather irregular roaming among the attractors —thus closely mimicking, for example, long-time structural changes and oscillations that have been associated with reaction–diffusion phenomena in physics and chemistry, as well as efficient, say, states of attention that are of interest in neuroscience—, (ii) one which is mainly characterized by oscillations between one of the stored patterns and its negative or corresponding antipattern, and (iii) one with quite irregular, apparently chaotic roaming randomly interrupted by pattern–antipattern oscillations [36]. The case (5) induces similar though relatively simpler behavior, e.g., the most involved behavior (iii) does not seem to fully develop in this case.

The relevant order in this system may be described by monitoring the firing rate, explicitly defined as $m(t) = N^{-1} \sum_i s_i(t)$, which is in fact sometimes recorded in laboratory experiments. Though hardly experimentally accessible, also interesting to illustrate in detail the system behavior is the overlap of the actual state with each pattern $\mu$, $m^\mu(t)$ as defined above. Furthermore, we are also interested in the input-output correlation which is defined now as

$$C_f = \lim_{\Delta t \to 0} \frac{1}{\Delta t} \int_{t_0}^{t_0+\Delta t} m(t)e^{if\tau}dt,$$  

i.e., the Fourier coefficient at frequency $f$ of the output firing rate. The relevant correlation, to be denoted $C(T)$ in the following, is signal dependent, e.g., we define it in the cosinus case as the value of $C(f, T) \equiv |C_f|^2/A_0^2$ computed at the frequency of the input signal. Some main results of our study are summarized in Fig. 3 [37].

This confirms occurrence of stochastic resonance in complex networks, and it allows one to associate main features of the phenomenon to details of the system, namely, variations of the network link weights which induce some essential excitability. The simplest situation of a single resonance peak, as in Fig. 3A, is for attractor networks with fixed connection weights. The peak in this case occurs at a relatively large level of noise
FIGURE 3. The input-output correlation $C(T)$ for the complex network model with a single stored pattern having asymmetry parameter $p$. (A) The case with static links and $p = \frac{1}{2}$. (B) Same but with links affected by synaptic depression. Increasing parameter $\alpha$ (different curves) the resonance peak moves towards lower noise levels. A plateau suggests tendency to a new resonance at low $T$. (C) Links here are depressed with $\alpha = 80$. Varying $p$ (different curves) allows for various resonances. (D) Recent data from an experiment concerning eye blinks in the presence of auditory noise are compared here with our prediction for $\alpha = 80$ and $p = 0.45$. See main text and [37] for details. 

(corresponding in this model to the underlying bath temperature), around the familiar second-order transition between memory and disordered phases. The potential barrier separating local minima is not too high in this case, and the noise helps the weak signal in overcoming it thus driving the system activity and producing a maximum of correlation. This is not very realistic, however; networks are generally complex in the sense that connection weights are not homogeneous nor constant with time, often adapting to the activity, in such a way that functional connections have in fact abnormal, often power-law distributions [14]-[17]. Allowing for such situation, as we did above with rather general, still expected realistic activity-dependent links, the interesting behavior illustrated in Figs. 3B and 3C, which includes the so-called stochastic multi-resonance phenomena emerges. For instance, Fig. 3B shows how synaptic depression induces a change of the resonance peak toward lower values of the noise as well as the emergence of a plateau of relatively high activity-signal correlation at an even lower level of noise. Interesting enough, this announces the possibility of having further resonances, which is confirmed when our model is implemented with another realistic feature, namely, when the set of patterns which determines the mean values of the connection weights
are assumed to be asymmetric, as is certainly always expected to be the case in nature (where the symmetry $p = \frac{1}{2}$ is quite difficult in practice). Such asymmetry together with short-term depression of connections induce oscillations of $m(t)$ at low noise levels as in a first-order phase transition resulting in correlation with the signal near the transition point. Even a third peak appears in the plateau for a high degree of asymmetry, e.g., $p = \frac{1}{4}$ in our numerical experiments, as may correspond to many actual situations. Note that simplicity dictated our illustrations to be concerned with just a single stored pattern, but we also checked that the relevant phenomenology remains when increasing the number of patterns and using other types of signals.

Unfortunately, even though the transmission of signals in difficult conditions which we are interested in here bears, both theoretically and from a practical point of view a great interest, and one may think of various related experiments which do not seem to be specially involved, the fact is that there is no much data to contrast with our theory. An exception is a psycho-physical simple experiment on eye blink reflex in the presence of auditory noise [38]. This shows resonance and, as Fig. 3D shows, we are able to fit that data to our theory by transforming the level of auditory noise in dB into our noise parameter $T$ using a nonlinear relationship; we refer to [13] for details.

**CONCLUSION**

We have briefly reviewed some recent results concerning phenomena, including stochastic resonance associated with the transmission of signals competing with noise. Our study involves two types of models, namely, partial differential equations and complex networks, and focus on the effects of assuming time-varying connections which depend on the current activity and transform the system into an excitable one. Though the network model in “A Complex Network” section may appear to be rather different from the simpler one in “A Feed-Forward Model” section, so that they may seem to induce resonances by different basic mechanisms, this is not so; for instance, the concern on the pattern asymmetry in the former influences the firing threshold $\theta$, and therefore the network excitability as it was also the case in the latter. The result in both cases is intriguing emergent behavior that shows varied multi-resonances that may easily be tuned by changing the models parameters. In addition to a well-defined theoretical reference, our study thus opens a way to many applications. We also present a first contact with experimental data. No doubt new related experiments would be very useful at this moment.

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27. The parameter values used for the perceptron-like model in the figures are $f_{\text{signal}} = 5$ Hz, $\tau_m = 10$ ms, $\tau_{in} = 3$ ms and $N = 200$, and we specifically used in Figs. 1B and 1C $A_0 = 10$ pA, static synapses corresponding to $J_e = J = 48$ pA, $u = 1$, $\tau_{rec} = 0$ and $r = r = 0$, and IF neurons corresponding to $\rho = 0.1$ GQ, $\tau_{\text{refrac}} = 5$ ms, $\theta = 10$ mV, and $\epsilon = 1$. Figure 1D is for $u = 0.5$, $J = 3 \pm 1$ pA, $r = 50 \pm 0.1$, $\rho = 0.1$ GQ/mV, $\epsilon = 1000$ ms$^{-1}$ which makes the (dimensionless) voltage $V(t) = 1$ correspond to 100 mV and the time variable to be within the ms range, $a = 0.001$, $b = 3.5$ (ms)$^{-1}$, $c = 1$ (ms)$^{-1}$, and $A_0 = 50$ pA. These values are perfectly consistent with reported physiological ranges; see, for instance, [28, 29, 30, 31].
37. The parameter values used for the complex network model in Fig. 3 are $N = 1000$ and $f_{\text{signal}} = 0.04$ (MCS)$^{-1}$ and, for each specific plot, as follows: $\alpha = 0$ (A), variable (B) and 80 (C and D), $\beta = 0.5$ (B, C and D) and it is not relevant for A, $p = 0.05$ (A and B), variable (C) and 0.45 (D), and $A_0 = 0.005$ (A) and 0.01 (B, C and D).