

Emerging phenomena in neural networks with dynamic synapses and their computational implications

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October 2, 2012

Abstract

In this paper we review our research on the effect and computational role of dynamical synapses on feed-forward and recurrent neural networks. Among others, we report on the appearance of a new class of dynamical memories which result from the destabilisation of learned memory attractors. This has important consequences for dynamic information processing allowing the system to sequentially access the information stored in the memories under changing stimuli. Although storage capacity of stable memories also decreases, our study demonstrated the positive effect of synaptic facilitation to recover maximum storage capacity and to enlarge the capacity of the system for memory recall in noisy conditions. Moreover, the dynamical phase described above can be associated to the voltage transitions between up and down states observed in cortical areas in the brain. We studied then the conditions in which the permanence times in the up state are power-law distributed, which is a sign for criticality, and concluded that the experimentally observed large variability of permanence times could be explained as the result of noisy dynamic synapses with large recovery times. Finally, we report also recent results concerning how short-term synaptic processes can transmit weak signals throughout more than one frequency range in noisy neural networks by kind of *stochastic multi-resonance*. This is consequence of the competition between changes in the transmitted signals as neurons were varying their firing threshold and adaptive noise due to activity-dependent fluctuations in the synapses.

1 Introduction

In the last decades many experimental studies have reported that transmission of information through the synapses is strongly influenced by the recent presynaptic activity in such a way that the postsynaptic response can decrease (that is called *synaptic depression*) or increase (or *synaptic facilitation*) at short time scales under repeated stimulation [Abbott et al., 1997, Tsodyks and Markram, 1997]. In cortical synapses it was found that after induction of long-term potentiation (LTP), the temporal synaptic response was not uniformly increased. Instead, the amplitude of the initial postsynaptic potential was potentiated whereas the steady-state synaptic response was unaffected by LTP [Markram and Tsodyks, 1996].

Under a biophysical point of view it is well accepted that short-term synaptic plasticity including synaptic depression and facilitation have their origin in the complex dynamics affecting trafficking, release and recycling of neurotransmitter vesicles at the synaptic buttons [Pieribone et al., 1995]. In fact, synaptic depression occurs when the arrival of presynaptic action potentials at high frequency does not allow an efficient recovering at short time scales of the available neurotransmitter vesicles to be released near the cell membrane [Zucker, 1989, Pieribone et al., 1995]. This causes a decrease of the postsynaptic response for successive action potentials. Other possible mechanisms responsible for synaptic depression have been described including feedback activation of presynaptic receptors and from postsynaptic processes such as receptor desensitisation [Zucker and Regehr, 2002]. On the other hand, synaptic facilitation is a consequence of the positive effect that the residual cytosolic calcium - that remains inside the synaptic buttons after the arrival of the firsts action potentials - has to favour the release of more neurotransmitter vesicles for the next arriving action potential [Bertram et al., 1996]. This increase in the concentration of the released neurotransmitters causes a potentiation of the postsynaptic response or synaptic facilitation. It is clear than strong facilitation causes a fast depletion of available vesicles so at the end it also induces a strong depressing effect. Other possible mechanisms responsible for short-term synaptic plasticity include, for instance, glial-neuronal interactions [Zucker and Regehr, 2002].

In the two seminal papers [Tsodyks and Markram, 1997] and [Abbott et al., 1997] a simple phenomenological model has been proposed based in these biophysical principles which nicely fits the evoked postsynaptic responses observed in cortical neurons. A particular mathematical formalization of the model assumes that during information transmission through the synapses in terms of trains of action potentials the state of each synapse j is characterised by three variables $x_j(t), y_j(t), z_j(t)$ that follow the dynamics

$$\begin{aligned}\frac{dx_j(t)}{dt} &= \frac{z_j(t)}{\tau_{rec}} - U_j \cdot x_j(t) \cdot \delta(t - t_{sp}^j) \\ \frac{dy_j(t)}{dt} &= \frac{-y_j(t)}{\tau_{in}} + U_j \cdot x_j(t) \cdot \delta(t - t_{sp}^j) \\ \frac{dz_j(t)}{dt} &= \frac{y_j(t)}{\tau_{in}} - \frac{z_j(t)}{\tau_{rec}}\end{aligned}\tag{1}$$

where $y_j(t)$ is the fraction of neurotransmitter which are released into the synaptic cleft after the arrival of an action potential (AP) at time t_{sp}^j , $x_j(t)$ is the fraction of neurotransmitters which are recovered after previous arrival of an AP near the cell membrane and $z_j(t)$ is the fraction of inactive neurotransmitters. The model assumes conservation of the total number of neurotransmitter resources in time so one has $x_j(t) + y_j(t) + z_j(t) = 1$. The released neurotransmitter inactivates with time constant τ_{in} and the inactive neurotransmitter recovers with time constant τ_{rec} . The synaptic current received by a postsynaptic neuron from its neighbours is then defined as $I_i(t) = \sum_j A_{ij} y_j(t)$ where A_{ij} represents the maximum synaptic current evoked in the postsynaptic neuron i by an AP from presynaptic neuron j which in cortical neurons is around $40 pA$ Tsodyks et al. [1998].

For constant release probability U_j , the model describes the basic mechanism of synaptic depression. The model is completed to account for synaptic facilitation by considering that U_j increases in time to its maximum value U as the consequence of the residual cytosolic calcium that remains after the arrival of very consecutive APs, and follows the dynamics

$$\frac{dU_j(t)}{dt} = \frac{[U - U_j(t)]}{\tau_{fac}} + U \cdot [1 - U_j(t)] \cdot \delta(t - t_{sp}^j) \quad (2)$$

Short term synaptic plasticity has profound consequences on information transmission by individual neurons as well as on network functioning and behaviour. Previous works have shown this fact on both feed-forward and recurrent networks. For instance, in feed-forward networks activity-dependent synapses act as nonlinear filters in supervised learning paradigms [Natschläger et al., 2001], being able to extract statistically significant features from noisy and variable temporal patterns [Liaw and Berger, 1996].

For recurrent networks, several studies revealed that populations of excitatory neurons with depressing synapses exhibit complex regimes of activity [Bressloff, 1999, Kistler and van Hemmen, 1999, Senn et al., 1996, Tsodyks et al., 1998, 2000], such as short intervals of highly synchronous activity (population bursts) intermittent with long periods of asynchronous activity, as is observed in neurons throughout the cortex [Tsodyks et al., 2000]. Related with this, it was proposed [Senn et al., 1996, 1998] that synaptic depression may serve as a mechanism for rhythmic activity and central pattern generation.

All these phenomena have stimulated much research to elucidate the effect and possible advantages of short term synaptic plasticity on the behaviour of neural networks. In this paper we review our own efforts over the last decade in this research field. In particular, we have demonstrated both theoretically and numerically the appearance of different non-equilibrium phases in attractor networks as the consequence of the underlying noisy activity in the network and of the existence of synaptic plasticity (see section 2). The emergent phenomenology in such networks includes a high sensitivity of the network to changing stimuli and a new phase in which dynamical attractors or dynamical memories appear with the possibility of regular and chaotic behaviour and rapid 'switching' between different memories [Pantic et al., 2002, Cortes et al., 2004, Torres et al.,

2005, Cortes et al., 2006, Torres et al., 2008, Marro et al., 2007]. The origin of such new phases and the extraordinary sensibility of the system to varying inputs - even in the memory phase - is precisely the “fatigue” of synapses due to heavy presynaptic activity competing with different sources of noise which induces a destabilisation of the regular stable memory attractors. One of the main consequences of this behaviour is the strong influence of short-term synaptic plasticity on storage capacity of such networks [Torres et al., 2002, Mejias and Torres, 2009] as we will explain in section 3.

The switching behaviour is characterised by a characteristic time scale during which the memory is retained. The distribution of time scale depends in a complex way on the parameters of the dynamical synapse model and are the result of a phase transition. We have investigated the conditions for the appearance of power-law behaviour in the probability distribution of the permanence times in the Up state, which is a sign for criticality (see section 4). This dynamical behaviour has been associated [Holcman and Tsodyks, 2006] to the empirically observed transitions between states of high activity (Up states) and low activity (Down states) in the mammals cortex [Steriade et al., 1993b,a].

The enhanced sensibility of neural networks with dynamic synapses to external stimuli could provide a mechanism to detect relevant information in weak noisy external signals. This can be viewed as a form of *stochastic resonance* (SR), which is the general phenomenon that enhances the detection by a non-linear dynamical system of weak signals in the presence of noise. Recent experiments in auditory cortex have shown that synaptic depression improves the detection of weak signals through SR for a larger noise range [Yasuda et al., 2008]. In a feed-forward network model of spiking neurons, we have modelled these experimental findings [Mejias and Torres, 2011, Torres et al., 2011]. We demonstrated theoretically and numerically that, in fact, short-term synaptic plasticity together with nonlinear neuron excitability induce a new type of SR where there are multiple noise levels at which weak signals can be detected by the neuron. We denoted this novel phenomenon by *bimodal stochastic resonances* or *stochastic multiresonances* (see section 5). We further showed that stochastic multi-resonance not only occurs in feed-forward neural networks but also in attractor networks [Pinamonti et al., 2012].

2 Appearance of dynamical memories

In this section we review our work on the appearance of dynamical memories in attractor neural networks with dynamical synapses as originally reported in [Pantic et al., 2002, Torres et al., 2002, 2008, Mejias and Torres, 2009]. For simplicity and in order to obtain straightforward mean-field derivations we have considered the case of a network of N binary neurons [Hopfield, 1982, Amit, 1989]. However, we emphasise that the same qualitative behaviour emerges in networks of integrate and fire (IF) neurons [Pantic et al., 2002].

Each neuron in the network, whose state is $s_i = 1, 0$ depending if the neuron is firing or not an action potential (AP), receives at time t from its neighbour

neurons a total synaptic current, or local field, given by

$$h_i(t) = \sum_j \omega_{ij}(t) s_j(t) \quad (3)$$

where $\omega_{ij}(t)$ is the synaptic current received by the postsynaptic neuron i from the presynaptic neuron j when this fires an AP ($s_j(t) = 1$). If the synaptic current to neuron i , $h_i(t)$, is larger than some neuron threshold value θ_i , neuron i fires an AP with a probability that depends on the intrinsic noise present in the network. The noise is commonly modelled as a thermal bath at temperature T . We assume parallel dynamics (Little dynamics) using the probabilistic rule

$$\text{Prob}(s_i(t+1) = \sigma) = \frac{1}{2} + \left(\sigma - \frac{1}{2}\right) \tanh[2T^{-1}(h_i(t) - \theta_i)] \quad (4)$$

with $\sigma = 1, 0$.

To account for short-term synaptic plasticity in the network we consider

$$\omega_{ij}(t) = \bar{\omega}_{ij} D_j(t) F_j(t) \quad (5)$$

where $D_j(t)$ and $F_j(t)$ are dynamical variables representing synaptic depression and synaptic facilitation mechanisms. The constants $\bar{\omega}_{ij}$ denote static synaptic weights that contain information concerning a number P random patterns, or memories, $\xi^\mu \equiv \{\xi_i^\mu = 1, 0; i = 1, \dots, N, \mu = 1, \dots, P\}$ previously stored in the network. For concreteness, we assume that these weights are the result of a Hebbian-like learning process that takes place on a time scale that is long compared to the dynamical time scales of the neurons and the dynamical synapses. The Hebbian learning takes the form

$$\bar{\omega}_{ij} = \frac{1}{Na(1-a)} \sum_{\mu=1}^P (\xi_i^\mu - a)(\xi_j^\mu - a) \quad \bar{\omega}_{ii} = 0, \quad (6)$$

also known as the *covariance learning rule*, with $a = \langle \xi_i^\mu \rangle$ representing the mean activity in the patterns.

To model the dynamics of the synaptic depression $D_j(t)$ and facilitation $F_j(t)$, we simplify the phenomenological model of dynamic synapses described by (1-2), taking into account that in actual neural systems such as the cortex $\tau_{in} \ll \tau_{rec}$, which implies that $y_i(t) = 0$ for most of the time and only at the exact point at which the AP arrives has a non-zero value $y_j(t_{sp}) = x_j(t_{sp})U_j(t_{sp})$. Thus, the synaptic current evoked in the postsynaptic neuron i by a presynaptic neuron j every time it fires is approximatively $I_{ij}(t) = A_{ij} x_j(t_{sp}^j) U_j(t_{sp}^j)$ which has the form given by (5) identifying $\bar{\omega}_{ij} = A_{ij}$, $D_j(t) \equiv x_j(t)$ and $F_j(t) \equiv U_j(t)$. We set $U = 1$ without loss of generality in order to have $D_j(t) = F_j(t) = 1 \forall j, t$ for $\tau_{rec}, \tau_{fac} \ll 1$, that corresponds to the well know limit of *static synapses* without depressing and facilitating mechanism. In this limit, in fact, one recover the classical Amari-Hopfield model of associative memory when one chooses the neuron thresholds as

$$\theta_i = \frac{1}{2} \sum_j \bar{\omega}_{ij}.$$

It is important to point out that due to the discrete nature of the probabilistic neuron dynamics (4) together with the approach $\tau_{in} \ll \tau_{rec}$, only discrete versions of the dynamics for $x_i(t)$ and $U_i(t)$ (see for instance Tsodyks et al. [1998]) are needed here, namely

$$\begin{aligned} x_j(t+1) &= x_j(t) + \frac{1-x_j(t)}{\tau_{rec}} - U_j(t) \cdot x_j(t) \cdot s_j(t) \\ U_j(t+1) &= U_j(t) + \frac{[U-U_j(t)]}{\tau_{fac}} + U \cdot [1 - U_j(t)] \cdot s_j(t) \end{aligned}, \quad (7)$$

Eqs. (4-7) completely define the dynamics of the network. Note, that in the limit of $\tau_{rec, fac} \rightarrow 0$ the model reduces to the standard Hopfield model with static synapses.

To numerically and analytically study the emergent behaviour of this attractor neural network with dynamical synapses, it is useful to measure the degree of correlation between the current network state $\mathbf{s} \equiv \{s_i; i = 1, \dots, N\}$ and each one of the stored patterns ξ^μ by mean of the overlap function

$$m^\mu(\mathbf{s}) = \frac{1}{N a(1-a)} \sum_i (\xi_i^\mu - a) s_i$$

Monte Carlo simulations of the network storing a small number of random patterns (loading parameter $\alpha \equiv P/N \rightarrow 0$), each pattern having 50 % active neurons ($a = 0.5$), no facilitation ($U_j(t) = 1$) and an intermediate value of τ_{rec} is shown in fig. 1. It shows a new phase (O) where dynamical memories characterized by quasi-periodic switching of the network activity between pattern (ξ^μ) and anti-pattern ($\mathbf{1} - \xi^\mu$) configurations appear. For lower values of τ_{rec} the network reduces to the attractor network with static synapses and shows the emergence of the traditional *ferromagnetic* or memory phase (F) at relatively low T , where network activity reaches a steady state that is highly correlated with one of the stored patterns, and a *paramagnetic* or non-memory phase (P) at high T where the network activity reaches a highly fluctuating disordered steady state.

The bottom panel of figure 1 shows simulation results of a network with $P = 10$ patterns and $a = 0.1$, demonstrating that switching behaviour is also obtained for relatively large number of patterns and sparse network activity. Fig. 2 top right shows that the switching behaviour is not an artefact of the binary neuron dynamics and is also obtained in a network of more realistic networks of spiking integrate-and-fire neurons. All time constants, such τ_{rec} or τ_{fac} are given in units of Monte Carlo steps (MCS) a temporal unit that in actual systems can be associated, for instance, with the duration of the refractory period and therefore of order of 5ms.

In the limit of $N \rightarrow \infty$ and $\alpha \rightarrow 0$ The emergent behaviour of the model can be analytically studied within a standard mean field approach (see for details [Pantic et al., 2002, Torres et al., 2008]) in the thermodynamic limit ($N \rightarrow 0$) and finite number of patterns ($\alpha \rightarrow 0$). The dynamics of the system then is driven by a $6P$ -dimensional discrete map

$$\mathbf{v}_{t+1} = \mathcal{F}(\mathbf{v}_t) \quad (8)$$

where $\mathcal{F}(X)$ is a complex $6P$ -dimensional non-linear function of

$$\mathbf{v}_t \equiv \{m_+^\mu(t), m_-^\mu(t), x_+^\mu(t), x_-^\mu(t), U_+^\mu(t), U_-^\mu(t); \mu = 1, \dots, P\}$$

that represents a set of order parameters defined as averages of the microscopic dynamical variables over the sites that are active and quiescent, respectively, in a given pattern μ , that is

$$c_+^\mu(t) \equiv \frac{1}{Na} \sum_{i \in Act(\mu)} c_i(t), \quad c_-^\mu(t) \equiv \frac{1}{N(1-a)} \sum_{i \notin Act(\mu)} c_i(t),$$

with $c_i(t)$ being $m_i(t)$, $x_i(t)$ and $U_i(t)$, respectively.

Local stability analysis of the fixed point solutions of the dynamics (8) shows that, similarly to the Amari-Hopfield standard model and in agreement with Monte Carlo simulation described above, the stored memories ξ^μ are stable attractors in some regions of the space of relevant parameters, such as T , U , τ_{rec} and τ_{fac} . Varying these parameters, there are, however, some critical values for which the memories destabilise and an oscillatory regime, in which the network visits different memories, can emerge. These critical values are depicted in figure 2 in the form of transition lines between phases or dynamical behaviours in the system. For instance, for only depressing synapses ($\tau_{fac} = 0, U_j(t) = 1$), there is a critical monotonic line $\tau_{rec}^*(T^{-1})$, as in a second order phase transition, separating the non-memory phase (P) and the oscillatory phase (solid line in panel top(left) of the figure 2) where oscillations start to appear with small amplitude as in a supercritical Hopf bifurcation. Also there is a transition line $\tau_{rec}^{**}(T^{-1})$, also monotonic, between the oscillatory phase (O) and the memory phase (F) which occurs sharply as in a first order phase transition (dashed line in panel top(left) of the figure 2). When facilitation is included, the picture is more complex, although similar critical and sharp transitions lines appear separating the same phases. Now, however, the lines separating different phases are non-monotonic and highly non-linear which shows the competition between a priori opposite mechanisms, depressing and facilitating, as is depicted in the two bottom panels of figure 2. In fact, among other features, synaptic depression induces fatigue at the synapses which destabilises the attractors and synaptic facilitation allow to a fast access to the memory attractors and to stay there during a shorter period of time [Torres et al., 2008]. As in figure 1, τ_{rec} and τ_{fac} are given in units of the typical duration of the refractory period ($\sim 5ms$).

The attractor behaviour of the recurrent neural network has the important property to complete a memory based on partial or noisy stimulus information. In the previous section we have seen that the memory attractors that are stable with static synapses become meta-stable with dynamical synapses. This provides the associative memory with a natural mechanism to dissociate from a memory in order to associate with a new memory pattern. With static synapses, the network would stay in the same pattern of activity forever.

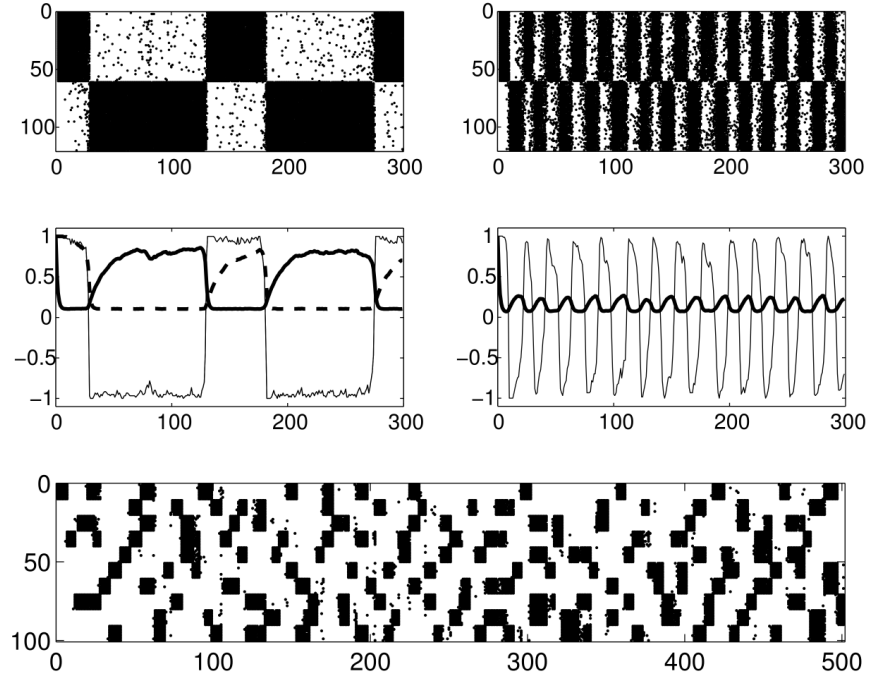


Figure 1: Emergence of dynamic memories in attractor neural networks. Top panels: raster plots showing the switching behaviour of the network neural activity between one activity pattern and its anti-pattern for $\tau_{rec} = 18$ and $T = 0.05$ (left) and for $\tau_{rec} = 30$ and $T = 0.05$ (right), respectively. Middle panels: the behaviour of the overlap function $m^\mu(\mathbf{s})$ (thin line) and the mean recovering variable x_+^μ of active neurons in the pattern (solid thick line) are plotted for the two cases depicted in the top panels. Bottom panel: raster plot that shows the emergence of dynamic memories when 10 activity patterns are stored in the synapses for $\tau_{rec} = 75$. In all cases the network size was $N = 120$. (from [Pantic et al., 2002]).

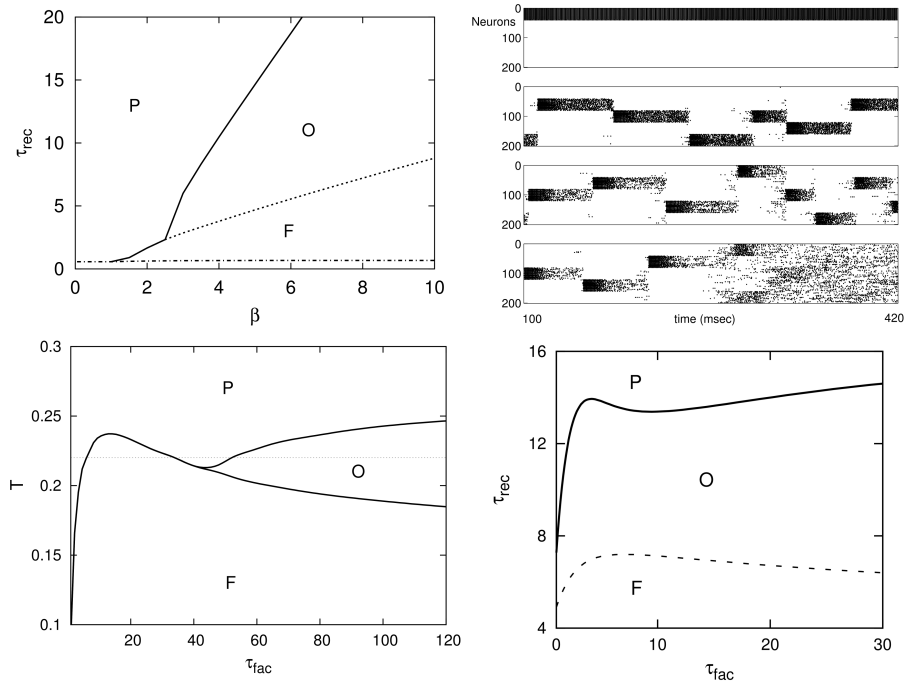


Figure 2: Top: The left panel shows the phase diagram ($\tau_{rec}, \beta \equiv T^{-1}$) of an attractor binary neural network with depressing synapses for $\alpha = 0$. This shows a new phase in which dynamical memories appear (phase O) with the network activity switching between the different memory attractors, between the traditional memory (F) and non-memory (P) phases characterising the behaviour of attractors neural networks with static synapses. The right panel shows that this behaviour is robust when a more realistic attractor network of IF neurons and more stored patterns are considered (5 in this simulation). The panel depicts, from top to bottom, the behaviour of the network activity for $\tau_{rec} = 0, 300, 800$ and 3000 ms, respectively, and clearly shows that for a given value of noise level the activity of the network pass from the memory phase (F) to the dynamical phase (O) and from this to the non-memory phase when τ_{rec} is increased. Bottom: Phase diagrams (T, τ_{fac}) for $\tau_{rec} = 3$ and $U = 0.1$ (left panel) and (τ_{rec}, τ_{fac}) for $T = 0.1$ and $U = 0.1$ of an attractor binary neural network with short-term depression and facilitation mechanisms in the synapses for $\alpha = 0$. Both diagrams depict the appearance of the same memory, oscillatory and non-memory phases than in the case of depressing synapses, but the transition lines between different phases show here a clear non-linear and non-monotonic dependence with relevant parameters consequence of the non-trivial competition between depression and facilitation mechanisms. This is very remarkable in the phase diagram in left panel where for a given level of noise, namely $T = 0.22$, the increase of facilitation time constant τ_{fac} induces the transition of the activity of the network from a non-memory state to a memory state, from this one to a non-memory state again, and finally from this last to an oscillatory regime (from [Pantic et al., 2002]).

3 Storage capacity

It is important to analyse how short-term synaptic plasticity affects the maximum number of patterns of neural activity the system is able to store and efficiently recall, that is, the so called *maximum storage capacity*. In a recent paper we have addressed this important issue using a standard mean field approach in the model described by Eqs. (3-7) when it stored $P = \alpha N$ activity patterns with $\alpha > 0$ and $N \rightarrow \infty$, and in the absence of noise ($T = 0$). The resulting mean-field equation which gives the maximum number of pattern that the system is able to store and retrieve is given by (see mathematical details in [Mejias and Torres, 2009])

$$y \left[\sqrt{2\alpha \left(\frac{1 + \gamma\gamma' - \gamma'}{\gamma'} \right)^2} + \frac{2}{\sqrt{\pi}} \exp(-y^2) \right] = \text{erf}(y) \quad (9)$$

where $y \equiv m / \sqrt{\left(2\alpha r + 2\alpha \left(\frac{1 + \gamma\gamma' - \gamma'}{\gamma'} \right)^2 \right)}$ with m being the overlap of the current state of the network activity with the pattern that is being retrieved, and $\gamma \equiv U\tau_{rec}$, $\gamma' \equiv \frac{1 + \tau_{fac}}{1 + U\tau_{fac}}$. The equation (9) has a trivial solution $y = 0$ ($m = 0$). Non zero solutions (with non-zero overlap with the pattern the system is trying to recall) exist for α less than some critical α , which defines the maximum storage capacity of the system α_c .

An complete study of the system by means of Monte Carlo simulations (in a network with $N = 3000$ neurons) has demonstrated the validity of this mean field result and is depicted in figure 3. In the left panels the behaviour of α_c obtained from equation (9) is shown (collor solid lines), when some relevant parameters of the synapse dynamics are varied, and compared with the maximum storage capacity obtained from the Monte Carlo simulation (different collor symbols). The most remarkable feature is that in the absence of facilitation the storage capacity decreases when the level of depression increases (that is, large release probability U , or large recovering time τ_{rec}); see red curves in the top and middle panels on the left side of the the figure. This decrease is caused by the loss of stability of the memory fixed points of the network due to depression. Facilitation (see green and blue curves) allows to recover the maximal storage capacity of static synapses, which is the well know limit $\alpha_c \approx 0.14$ (dotted horizontal line) in the presence of some degree of synaptic depression. In general the competition between synaptic depression and facilitation induces a complex nonlinear and non-monotonic behaviour of α_c for different synaptic dynamics parameters as is shown in the right panels of figure 3. In general, large values of α_c appear for moderate values of U and τ_{rec} , and large values of τ_{fac} . These values qualitatively agree with those described in facilitating synapses in some cortical areas, where U is lower than in the case of depressing synapses and τ_{rec} is several times lower than τ_{fac} [Markram et al., 1998]. Note, that facilitation or depression never increases the storage capacity of the network above the maximum value $\alpha_c \approx 0.14$.

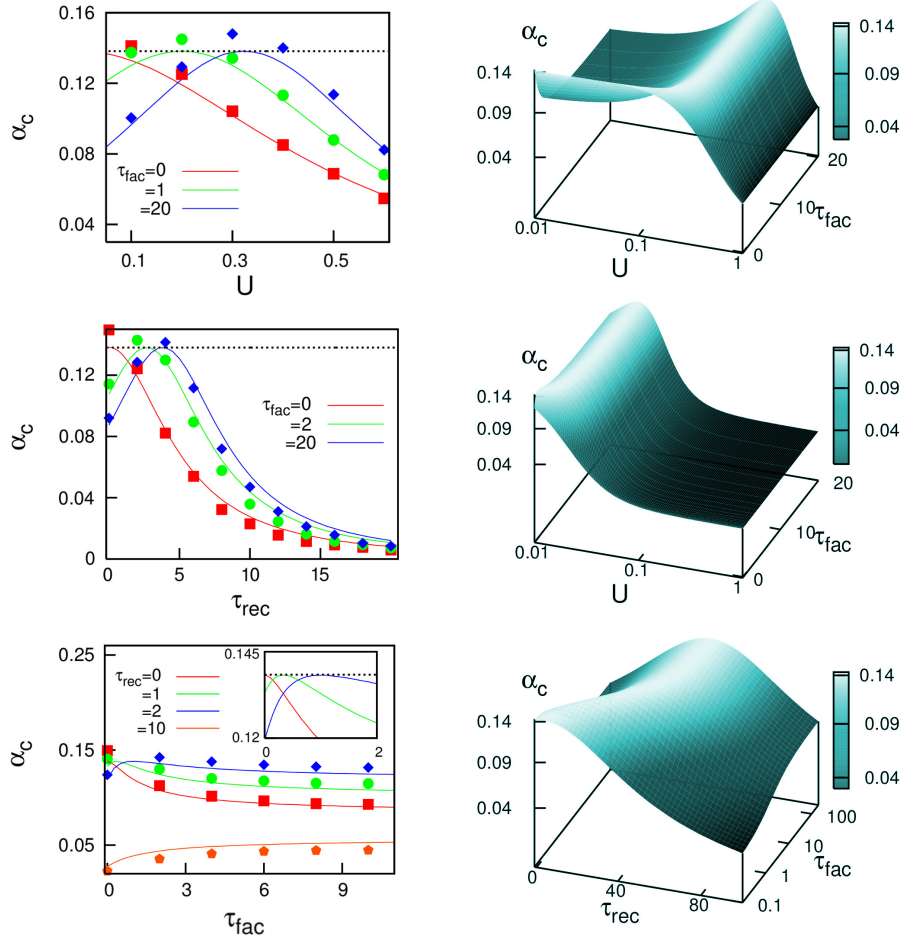


Figure 3: Maximum storage capacity obtained in attractor neural networks with dynamic synapses with both depressing and facilitating mechanisms. Left panels shows the behaviour of α_c as a function of U_{SE} , τ_{rec} and τ_{fac} . The lines correspond the theoretical prediction from the mean field Eq. (9) and symbols are obtained from Monte Carlo simulations. From top to bottom it depicts $\alpha_c(U_{SE})$ for $\tau_{rec} = 2$ and different values of τ_{fac} , $\alpha_c(\tau_{rec})$ for $U_{SE} = 0.2$ and different values of τ_{fac} and $\alpha_c(\tau_{fac})$ for $U_{SE} = 0.2$ and different values of τ_{rec} , respectively. The dotted lines correspond to the static synapses limit $\alpha_c \approx 0.138$. Right panels show mean-field results from Eq. (9) for the dependence of α_c for different combinations of relevant parameters. This corresponds - from top to bottom - to the surfaces $\alpha_c(U_{SE}, \tau_{fac})$ for $\tau_{rec} = 2$, $\alpha_c(U_{SE}, \tau_{fac})$ for $\tau_{rec} = 50$ and $\alpha_c(\tau_{rec}, \tau_{fac})$ for $U_{SE} = 0.02$. In all panels, τ_{rec} and τ_{fac} are given in MCS units that can be associated to a value of 5ms if one assumes that a MCS corresponds to the duration of the refractory period in actual neurons.(from [Mejias and Torres, 2009])

4 Criticality in up/down transitions

In a recent paper [Holcman and Tsodyks, 2006], the emergent dynamic memories described in section 2 that result from short-term plasticity have been related to the voltage transitions observed in cortex between a high-activity state (the Up state) and a low-activity state (the Down state). These transitions has been observed in simultaneous individual single neuron recordings as well as in local field measurements.

Using a simple but biologically plausible neuron and synapse model similar to the models described in sections 1 and 2, we have theoretically studied the conditions for the emergence of this intriguing behaviour, as well as their temporal features [Mejias et al., 2010]. The model consists of a simple stochastic bistable rate model which mimics the average dynamics of a population of interconnected excitatory neurons. The neural activity is summarised by a single activity $\nu(t)$, whose dynamics follows a stochastic mean field equation.

$$\tau_\nu \frac{d\nu(t)}{dt} = -\nu(t) + \nu_m \mathcal{S}[J\nu(t)x(t) - \theta] + \zeta(t)$$

where τ_ν is the time constant for the neuron dynamics, ν_m is the maximum synaptic input to the neuron population, J is the (static) synaptic strength and θ is the neuron threshold. The function $\mathcal{S}[X]$ is a sigmoidal function which models the excitability of neurons in the population.

The synaptic input from other neurons is modulated by a short-term dynamic synaptic process $x(t)$ which satisfies the stochastic mean field equation

$$\frac{dx(t)}{dt} = \frac{1 - x(t)}{\tau_r} - U x(t)\nu(t) + \frac{D}{\tau_r} \xi(t) \quad (10)$$

The parameters τ_r , U and D are respectively the recovery time constant for the stochastic short-term synaptic plasticity mechanism, a parameter related with the reliability of the synaptic transmission (the average release probability in the population) and the amplitude of this synaptic noise. The explanation of each term appearing in the rhs of equation (10) is the following: the first term accounts for the slow recovery of neurotransmitter resources, the second term represents a decrease of the available neurotransmitter due to the level of activity in the population and the third term is noise term that account for all possible sources of noise affecting transmission of information at the synapses of the population and that remains at the mesoscopic level.

A complete analysis of this model, both theoretically and by numerical simulations, shows the appearance of complex transitions between high (up) and low (down) neural activity states driven by the synaptic noise $x(t)$, with permanence times in the up state distributed according to a power-law for some range of the synaptic dynamic parameters. The main results of this study are summarized in figure 4. On the top panel left, a typical time series of the temporal behaviour of the mean neural activity $\nu(t)$ of the system in the regime in which irregular up-down transitions occur is depicted. In the right top panel,

the histogram of $\nu(t)$ shows a clear bimodal shape corresponding to the two only possible states for $\nu(t)$. The middle panels of the figure shows how the parameters τ_r and D that control the stochastic dynamics of $x(t)$, also control the appearance of power law distributions $P(T)$ for the permanence time in the up or down state T . As is outlined in [Mejias et al., 2010], the dynamics can be approximately described in an adiabatic approximation, in which the neuron dynamics is subject to an effective potential Φ . The left bottom panel shows how Φ changes for different values of the mean synaptic strength x . For relatively small x (dashed green line) all synapses in the population have a strong degree of depression and the population has a small level of activity, that is, the global minimum of the potential function is the low-activity state (the down state). On the other hand, when synapses are poorly depressed and x takes relatively large values (dashed blue line) the neuron activity level is high and the potential function has its global minimum in a high-activity state (up state). The right bottom panel shows the complete phase diagram of the system and shows the regions in the parameter space (D, τ_r) where different behaviours emerge. In the phase (P) no transition between a high-activity state and low-activity state occurs. In phase (E) transitions between up and down state are exponentially distributed. The phase (C) is characterised by the emergence of power-law distributions $P(T)$, and therefore is the most intriguing phase since it could be associate to a critical state. Phase (S) is characterized by a highly fluctuating behaviour of both $\nu(t)$ and $x(x)$. In fact, $\nu(t)$ is behaving as an slave variable of $x(t)$ and, therefore, it presents the dynamical features of the dynamics (10), which has some similarities with those of colored noise for U small. In fact for $U = 0$, and making the change $z(t) = x(t) - 1$ the dynamics (10) transforms in that for an Ornstein-Uhlenbeck (OU) process [Mejias et al., 2010].

From these studies, we can conclude that the experimentally observed large fluctuations in up and down permanence times in the cortex can be explained as the result of sufficiently noisy dynamical synapses (large D) with sufficiently large recovery times (large τ_r). Static synapses ($\tau_r = 0$) or dynamical synapses in the absence of noise ($D = 0$) cannot account for this behaviour, and only exponential distributions for $P(T)$ emerge in this case.

5 Stochastic multiresonance

In section section 2 we mentioned that short-term synaptic plasticity induces the appearance of dynamic memories as the consequence of the destabilisation of memory attractors due to synapse fatigue. The synaptic fatigue in turn is due to strong neurotransmitter vesicle depletion as the consequence of high frequency presynaptic activity and large neurotransmitter recovering times. Also, we concluded that this fact induces a high sensitivity of the system to respond to external stimuli, even if the stimulus is very weak and in the presence of noise. The source of the noise can be due to the neural dynamics as well as the synaptic transmission. It is the combination of non-linear dynamics and noise that causes the enhanced sensitivity to external stimuli. This general phenomenon is

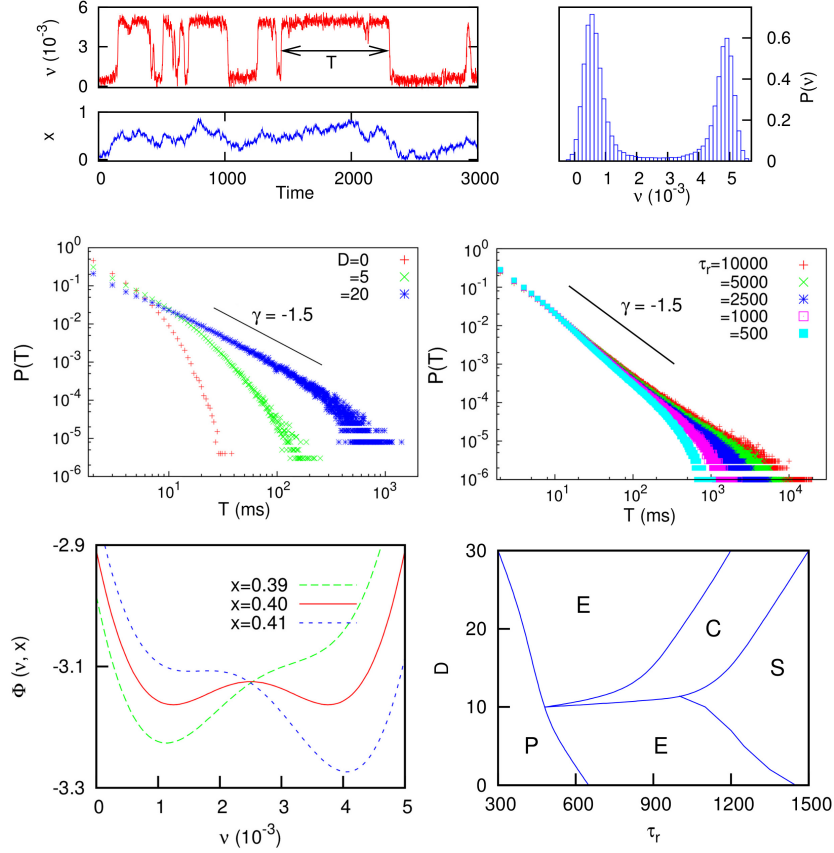


Figure 4: Criticality in up/down transitions: Top left panel shows a typical time series for the neuron rate variable $\nu(t)$ and the depression variable $x(t)$ in a regime where irregular up-down transitions emerge. Parameter values were $J = 1.2V$, $\tau_r = 1000 \tau_\nu$, $U = 0.6$, $D = 0$, $\delta = 0.3$ and $\nu_m = 5 \cdot 10^{-3}$. Top right panel depicts the histogram of the same time series for $\nu(t)$ which present bimodal features corresponding to two different levels of activity. Middle panels show transitions from exponential to power law behaviour for the probability distribution for the permanence time in the up or down state $P(T)$ when parameters D and τ_r are varied. Model parameters were the same than in the top panels except that $J = 1.1V$ in the left panel and $U = 0.04$ and $D/\tau_r = 0.02/\tau_\nu$ in the right panel. Bottom left panel depicts how a variation of $x(t)$ induces a change in the potential function driving the dynamics of the rate variable $\nu(t)$ which is responsible for the transitions between the up and down states. Parameters were the same than in the top panels except that $J = 1.1V$. Bottom right panel shows the complete phase diagram (D, τ_r) , for the same set of parameters than in the bottom left panel, where different phases characterise different dynamics of $\nu(t)$, $x(t)$ (see main text for the explanation). (from [Mejias et al., 2010])

the so called *stochastic resonance* (SR) [Benzi et al., 1981, Longtin et al., 1991].

In a set of recent papers we have studied the emergence of SR in feed-forward neural networks with dynamic synapses [Mejias and Torres, 2011, Torres et al., 2011]. We considered a post-synaptic neuron which receives signals from a population of N presynaptic neurons through dynamic synapses modelled by Eqs (1-2). Each one of these presynaptic neurons fires a train of Poisson distributed action potentials with a given frequency f_n . In addition the postsynaptic neuron receives a weak signal $S(t)$ which we can assume sinusoidal. We assume a stationary regime, where the dynamic synapses have reached their asymptotic values $u_\infty = \frac{U+U\tau_{fac}f_n}{1+U\tau_{fac}f_n}$ and $x_\infty = \frac{1}{1+u_\infty\tau_{rec}f_n}$. If all presynaptic neurons fire independently the total synaptic current is a noisy quantity with mean \bar{I}_N and variance σ_N^2 given by

$$\begin{aligned}\bar{I}_N &= Nf_n\tau_{in}I_p \\ \sigma_N^2 &= \frac{1}{2}Nf_n\tau_{in}(I_p)^2\end{aligned}$$

with $I_p = Au_\infty x_\infty$ and A the synaptic strength. To explore the possibility of SR, we vary the firing frequency of the presynaptic population f_n . The reason for this choice is that varying f_n changes the output variance σ_N^2 and f_n can also be relatively easily controlled in an experiment.

To quantify the amount of signal that is present in the output rate we use the standard input-output cross-correlation or *power norm* [Collins et al., 1995] during a time interval Δt and defined as:

$$C_0 = \langle S(t)\nu(t) \rangle = \frac{1}{\Delta t} \int_t^{t+\Delta t} S(t)\nu(t)dt,$$

where $\nu(t)$ is the firing rate of the post-synaptic neuron. The behaviour of C_0 as a function of f_n for static synapses is depicted in panel A of figure 5 which clearly shows a resonance peak at certain non-zero input frequency f_n . The output of the postsynaptic neuron at the positions in the frequency domain labeled with “a”, “b” and “c” is illustrated in the panel B and compared with the weak signal. This shows how stochastic resonance emerges in this system. For low firing frequency (case labeled with “a”) in the presynaptic population the generated current is so small that the postsynaptic neuron only has sub-threshold behaviour weakly correlated with $S(t)$. For very large f_n (case labeled with “c”) both \bar{I}_N and σ_N^2 are large and the postsynaptic neuron is firing all the time, so it can not detect the temporal features of $S(t)$. However, there is an optimal value of f_n at which the postsynaptic neuron fires strongly correlated with $S(t)$; in fact it fires several action potentials each time a maximum in $S(t)$ occurs (case labeled with “b”).

This behaviour dramatically changes when dynamic synapses are considered, as is depicted in panels C and D of figure 5. In fact, for dynamic synapses there are two frequencies at which resonance occurs. That is, short-term synaptic plasticity induces the appearance of stochastic multi-resonances (SMR). Interestingly, the position of the peaks is controlled by the parameters that control the synapse dynamics. For instance, in panel C it is shown how for a fixed value

of facilitation and increasing depression (increasing τ_{rec}) the second resonance peak moves toward low values of f_n while the position of the first resonance peak remains unchanged. On the other hand, for a given value of depression, the increase of facilitation time constant τ_{fac} moves the first resonance peak while the position of the second resonance peak is unaltered (panel D of figure 5). This clearly demonstrate that in actual neural systems synapses with different levels of depression and facilitation can control the signal processing at different frequencies.

The appearance of SMR in neural media with dynamic synapses is quite robust: SMR also appears when the post-synaptic neuron is model with different types of spiking mechanisms, such as the FitzHugh-Nagumo (FHN) model or the integrate and fire model (IF) with an adaptive threshold dynamics [Mejias and Torres, 2011]. SMR also appears with more realistic stochastic dynamic synapses and more realistic weak signals such as a train of inputs with small amplitude and short durations distributed in time according to a rate modulated Poisson process [Mejias and Torres, 2011].

The physical mechanism behind the appearance of SMR is the existence of a non-monotonic dependence of the synaptic current fluctuations with f_n due to dynamic synapses together with the existence of an adaptive threshold mechanism in the postsynaptic neuron to this incoming synaptic current. In this way, the distance in voltage between the mean post-synaptic sub-threshold voltage and the threshold for firing remains constant or decrease very slowly for increasing presynaptic frequencies. This implies the existence of two values of f_n at which current fluctuations are enough to induce firing in the post-synaptic neuron (see [Mejias and Torres, 2011] for more details).

In light of these findings, we have reinterpreted recent SR experimental data from psycho-physical experiments on human blink reflex [Yasuda et al., 2008]. In these experiments the neurons responsible for the blink reflex receive inputs from neurons in the auditory cortex, which are assumed to be uncorrelated due to the action of some external source of white noise. The subject received in addition a weak signal in the form of a periodic small air puff into the eyes. The authors measured the correlation between the air puff signal and the blink reflex and their results are plotted in figure 6 top panel (square error bar symbols). They used a feed-forward neural network with a postsynaptic neuron with IF dynamics with fixed threshold to interpret their findings (dashed line). With this model, only the high-frequency correlation points can be fitted. Using instead a FHN model or an IF with adaptive threshold dynamics, we were able to fit all experimental data points (solid line). The SMR is also observed with more realistic rate-modulated weak Poisson pulses (open circles) instead of the sinusoidal input (solid line). Both model predictions are consistent with the SMR that is observed in this experiments. In figure 6 bottom we summarize the conditions that neurons and synapses must satisfy for the emergence of SMR in a feed forward neural network.

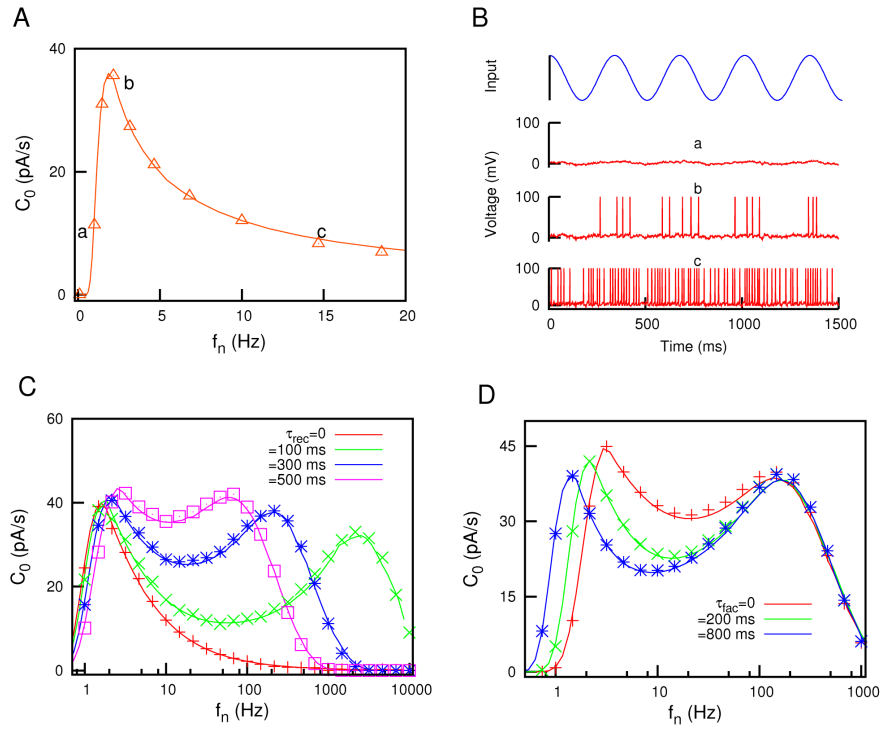


Figure 5: Appearance of stochastic multiresonances in feed forward neural networks of spiking neurons with dynamic synapses. Panel (A) shows the phenomenon of stochastic resonance for static synapses, where the temporal behaviour of the postsynaptic neuron at each labeled position of the resonance curve for C_0 - defined in (5)- is depicted in panel (B). Bottom panels illustrate the changes in the resonance curve for C_0 when dynamic synapses are included. The most remarkable feature is the appearance of a two-peak resonance in the frequency domain, with the position of high and low frequency peak controlled by the particular value of τ_{rec} (panel C) and τ_{fac} (panel D) respectively.

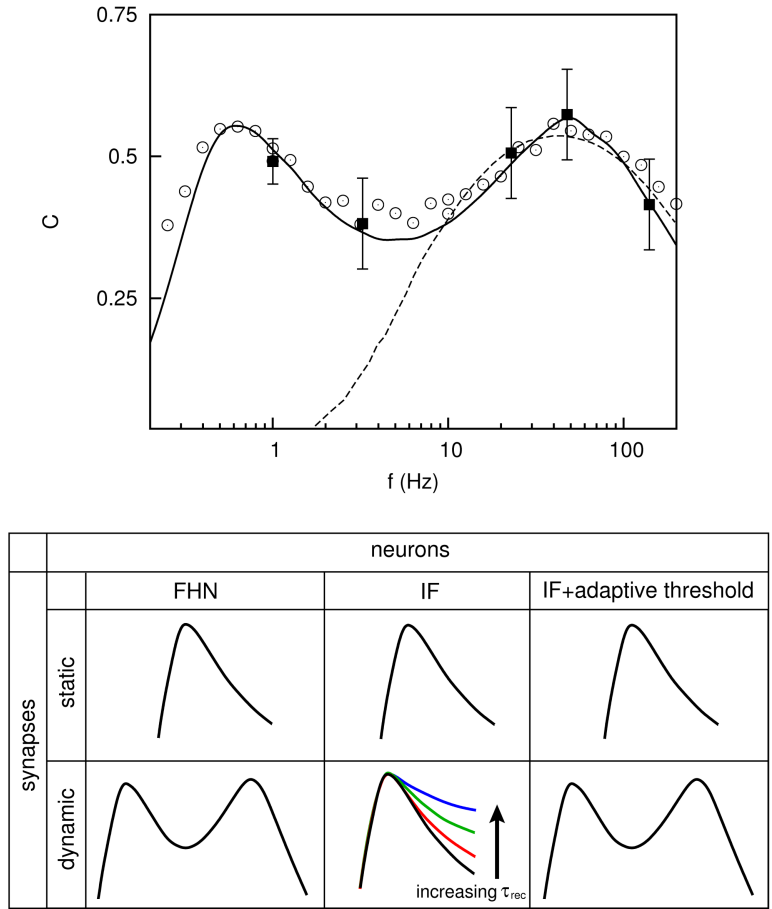


Figure 6: (Top) Appearance of stochastic multi-resonance in experiments in the brain. Square black symbols represent the values of C_0 obtained in the experiments performed in the human auditory cortex. Dashed line corresponds to best model prediction using a neuron with static threshold [Yasuda et al., 2008]. Solid line correspond to our model consisting of a FHN neuron and depressing synapses. Open circle symbols shows C_0 when the weak signal is a train of (uncorrelated) Poisson pulses instead of the sinusoidal input (solid line). (Bottom) Schematic overview showing the neuron and synapse mechanisms needed for the appearance of stochastic multi-resonances in feed-forward neural networks.

6 Conclusions

It is well accepted that during transmission of information synapses show a high variability with a diverse origin, as for instance, the stochastic trafficking and release of neurotransmitter vesicles, variations in the Glutamate concentration through synapses or the spatial heterogeneity of the synaptic response in the dendrite tree [Franks et al., 2003]. The cooperative effect of all these mechanisms is a noisy post-synaptic response which depends on the pre-synaptic activity. The strength of the postsynaptic response can decrease or increase and can be modelled as dynamical synapses.

In a large number of papers, we have studied the effect of dynamical synapses in recurrent and feed-forward networks, the result of which we have summarised in this paper. The main findings are the following:

Dynamic memories: Classical neural networks of the Hopfield type, with symmetric connectivity, display attractor dynamics. This means that these networks act as memories. A specific set of memories can be stored as attractors by Hebbian learning. The attractors are asymptotically stable states. The effect of synaptic depression in these networks is to make the attractors lose stability. Oscillatory modes appear where the network rapidly switches between memories. Instead, the permanence time to stay in a memory can have any positive value and becomes infinite in the regime where memories are stable. Thus, the recurrent network with dynamical synapses implement a form of dynamical memory.

Input sensitivity: The classical Hopfield network is relatively insensitive to external stimuli, once it has converged into one of its stable memories. Synaptic depression improves the sensitivity to external stimuli, because it destabilises the memories. In addition, synaptic facilitation further improves the sensitivity of the attractor network to external stimuli.

Storage capacity: The storage capacity of the attractor neural network, i. e. the maximum number of memories that can be stored in a network, is proportional to the number of neurons N and scales as $p_{max} = \alpha N$ with $\alpha = 0.138$. Synaptic depression causes a decrease of the maximum storage capacity but facilitation allows to recover the capacity of the network with static synapses under some conditions.

Up and down states: The emergence of dynamic memories has been related to the well-known up/down transitions observed in local-field recording in the cortex. We demonstrated that the observed distributions of permanence times can be explained by a stochastic synaptic dynamics. Scale free permanence time distributions could signal a critical state in the brain.

Stochastic multiresonance: Whereas static synapses in a stochastic network give rise to a single stochastic resonance peak, dynamical synapses produce a double resonance. This phenomenon is robust for different types

of neurons and input signals. Thus, dynamic synapses may explain recently observed SMR in psychophysical experiments. SMR also seems to occur in recurrent neural networks with dynamic synapses as it has been recently reported [Pinamonti et al., 2012]. This work demonstrates the relevant role of short-term synaptic plasticity for the appearance of the SMR phenomenon in recurrent networks, although the exact underlying mechanism behind it is slightly different than for the case illustrate here for feedforward networks.

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