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Finite signal transmission times and synaptic memory in neural networks

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We discuss the influence of delayed synaptic signal transmission and memorizing prior synaptic activity on the static and the dynamical properties of attractor neural networks. We find a significant reduction of the system's random response and a considerable enhancement of the response to stimuli with frequencies proportional to the inverse delay or memory time scale.

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I. INTRODUCTION

Biological neural networks exhibit a broad spectrum of delay times in intraneural and interneural signal transmission [1]. Their origin is well understood in the framework of the physiological Hodgkin-Huxley model [2] for a single neuron. Several simplified versions of this model have been proposed that focus on the question of delayed information transport and incorporate either discrete [3] or distributed delays [4]. A system consisting of several such neurons has the associative properties of the standard attractor neural network with instantaneous signal transport [5], which was extensively studied over the past years [6], but is, in addition, capable of learning and memorizing sequences of patterns [7].

Previous investigations of neural networks with realistic signal transmission times focused on single- or few-neuron systems [8] or many-neuron systems with symmetric synaptic couplings [9]. These couplings guarantee the existence of a Lyapunov functional that completely determines the intrinsic dynamics [10]. It was also shown that such systems are dynamically stable, if there are not too many inhibitoric synaptic couplings [9]. A many-neuron network with synaptic memory and rather *special* asymmetric synaptic couplings capable of memorizing sequences was investigated in [11].

In this work we study a many-neuron system with *arbitrary* asymmetric couplings and a generalized synaptic transfer function similar to that used in [11]. It accounts for the history of neural activity via an *a priori* arbitrary memory function and thus allows for the treatment of the dynamical properties of a whole class of neural networks. Delayed intraneural and interneural signal transmission corresponds to a specific choice for this memory function.

We assume that neural activity is governed by Langevin dynamics and extract global properties of the network from a functional integral approach [12]. Thus our investigations extend former studies of asymmetric attractor networks with instantaneous signal transport [13–15].

The outline of the paper is as follows. In Sec. II we present the generalized postsynaptic potential, which memorizes prior synaptic activity. Several possible choices for the memory function are discussed. Neural (Langevin) dynamics is studied in Sec. III and the postsynaptic potential is derived in mean-field approximation. In Sec. IV spectral functions for the case of a nontrivial memory function are compared to those for instantaneous signal transmission. In Sec. V we consider the analytically solvable spherical model. This section is subdivided into two parts. In the first part, we define the model, derive general relationships, and consider static properties. In the second part, we analyze the frequency dependence of the response function of the system, thus providing the complete dynamical solution of the spherical model. Section VI concludes this work with a summary of our results.

II. GENERALIZED NEURAL SIGNAL TRANSMISSION

We consider a system of N neurons, characterized by their state σ_i. The value of σ_i at time t, $\sigma_i(t)$, is determined by the postsynaptic potential $h_i(t)$, which arises from the interactions with the other neurons:

$$h_i(t)=\sum_{j\neq i} J_{ij}w_j([\sigma_j],t) \ . \tag{1}$$

Here J_{ij} is the strength of the interaction exerted by neuron j on neuron i and is in general (i.e., for asymmetric networks) different from J_{ji}. The generalized synaptic transfer function w_j of neuron j is defined as

$$\begin{aligned} w_j([\sigma_j],t) &= \int_{-\infty}^{t} dt' f(t-t')\sigma_j(t') \\ &= \int_0^\infty dx\, f(x)\sigma_j(t-x) \ , \end{aligned} \tag{2}$$

which physiologically corresponds to the synaptic output of neuron j, integrated over all times prior to t with a weight function f, the so-called memory function, which is normalized as

$$\int_{-\infty}^{t} dt' f(t-t') = \int_{0}^{\infty} dx\, f(x) = 1 \; . \tag{3}$$

Note that $w_j([\sigma_j],t)$ is a functional of σ_j in the sense that it depends on all values of σ_j at times prior to t. For the sake of brevity, we will subsequently no longer denote this functional dependence explicitly. Equation (2) defines a class of neural networks with generalized synaptic signal transmission. In the following, we discuss specific choices for the memory function f.

(i) If

$$f(x) = \delta(x) \tag{4}$$

we obtain the case of instantaneous signal transfer [14,15].

(ii) Delayed signal transmission corresponds to

$$f(x) = \delta(x-\tau) \; , \tag{5}$$

where $\tau > 0$ is the delay time [16].

(iii) If

$$f(x) = \tau^{-1}\exp\{-x/\tau\} \tag{6}$$

the past is exponentially forgotten with characteristic time τ [17].

(iv) The case

$$f(x) = \frac{2}{\sqrt{\pi}\tau}\exp\{-(x/\tau)^2\} \tag{7}$$

corresponds to "Gaussian oblivion."

(v) Constant memory back to a time $t-\tau$ in the past is parametrized by

$$f(x) = \tau^{-1}\Theta(\tau - x) \; . \tag{8}$$

The above choices for f are the most simple ones in the sense that they contain no more than one free parameter, parametrizing the scale of delay or oblivion of the neural network.

III. LANGEVIN DYNAMICS AND MEAN-FIELD APPROXIMATION

We assume the dynamics of each neuron i to be governed by a Langevin equation, coupled to the other $N-1$ neurons via the postsynaptic potential (1),

$$\Lambda_i(t) \equiv \Gamma_0^{-1}\partial_t\sigma_i(t) - h_i(t) - h_i^0(t) - \xi_i(t) + \frac{dH_{r,\lambda}(\sigma_i(t))}{d\sigma_i(t)} = 0 \; . \tag{9}$$

Here Γ_0^{-1} is the time scale of changes in neural activity, h_i^0 is an external field, and ξ_i is white noise with variance

$$\langle \xi_i(t)\xi_j(t') \rangle = 2T\Gamma_0^{-1}\delta(t-t')\delta_{ij} \; . \tag{10}$$

The angular brackets denote the "thermal" average, i.e., the average with respect to the white noise ξ. Since each σ_i may assume values $-\infty < \sigma_i(t) < +\infty$, one introduces the potential

$$H_{r,\lambda}(\sigma) = \frac{r}{2}\sigma^2 + \lambda\sigma^4 \tag{11}$$

in (9), which restricts the neural activity to the physiologically realized range of values via an appropriate choice of r and λ.

The interaction matrix J_{ij} entering the postsynaptic potential (1) can be decomposed into a completely symmetric and completely asymmetric part,

$$J_{ij} = J_{ij}^{s} + kJ_{ij}^{\mathrm{as}} \; , \quad k \geq 0 \; , \tag{12}$$

where k is the degree of asymmetry [15]. The case $k=0$ corresponds to the fully symmetric model [5], whereas $k=1$ corresponds to a fully asymmetric model [15]. For the sake of simplicity and since we want to focus on the effects of finite signal transfer times and the history of synaptic activity rather than on realistic learning rules [18], we consider J_{ij}^{s} and J_{ij}^{as} to be random Gaussian variables with zero mean and variance

$$[(J_{ij}^{s})^2] = [(J_{ij}^{\mathrm{as}})^2] = \frac{J^2}{N}\frac{1}{1+k^2} \; . \tag{13}$$

Here the brackets denote the "quenched" average, i.e., the average with respect to the distribution $\mathcal{P}[J]$ of the couplings J_{ij}. In Appendix C of [15] it was shown how the above case is related to a dilute network [14,19,20].

The stochastic equation (9) leads to a generating functional of the form [12,13]

$$Z[l;J,\xi] = \int \mathcal{D}\sigma\, \mathcal{J} \exp\left\{ \int dt \sum_i l_i(t)\sigma_i(t) \right\} \times \prod_{i,t} \delta[\Lambda_i(t)] \; , \tag{14}$$

with $\mathcal{D}\sigma \equiv \prod_{i,t} d\sigma_i(t)$. The Jacobian $\mathcal{J}$ ensures proper normalization of $Z[l;J,\xi]$. Employing

$$\delta[\Lambda_i(t)] = \int \frac{d\hat{\sigma}_i(t)}{2\pi}\exp\{-i\Lambda_i(t)\hat{\sigma}_i(t)\} \tag{15}$$

and averaging over white noise and random couplings [13] we arrive at the generating functional

$$Z[l,\hat{l}] = \int \mathcal{D}\sigma\, \mathcal{D}\hat{\sigma} \exp\{L_0[\sigma,\hat{\sigma}]\} \times \exp\left\{ \frac{J^2}{2N}\int dt\, dt' \sum_{\substack{i,j \\ i\neq j}} \left[i\hat{\sigma}_i(t)w_j(t)i\hat{\sigma}_i(t')w_j(t') + \frac{1-k^2}{1+k^2} i\hat{\sigma}_j(t)w_i(t)i\hat{\sigma}_i(t')w_j(t') \right] \right\} \; , \tag{16}$$

where $\mathcal{D}\hat{\sigma} = \prod_{i,t}[d\hat{\sigma}_i(t)/2\pi]$ and

$$L_0[\sigma,\hat{\sigma}]\equiv\ln\mathcal{J}+\int dt\sum_i\left[l_i(t)\sigma_i(t)+\hat{l}_i(t)i\hat{\sigma}_i(t)+i\hat{\sigma}_i(t)\left\{-\Gamma_0^{-1}\partial_t\sigma_i(t)+h_i^0(t)+T\Gamma_0^{-1}i\hat{\sigma}_i(t)-\frac{dH_{r,\lambda}(\sigma_i(t))}{d\sigma_i(t)}\right\}\right] . \tag{17}$$

The functional (16) generates average neuron-neuron correlation functions, e.g., the neuron autocorrelation

$$C(t-t')=[\langle\sigma_i(t)\sigma_i(t')\rangle]=\left.\frac{\delta^2\ln Z[l,\hat{l}]}{\delta l_i(t')\delta l_i(t)}\right|_{l=\hat{l}=0} , \tag{18}$$

and average response functions, e.g., the local single-neuron response

$$G(t-t')=\left.\frac{\delta[\langle\sigma_i(t)\rangle]}{\delta h_i^0(t')}\right|_{h^0=0}=\left.\frac{\delta^2\ln Z[l,\hat{l}]}{\delta\hat{l}_i(t')\delta l_i(t)}\right|_{l=\hat{l}=h^0=0} , \quad t\geq t' . \tag{19}$$

Since in general the single- or multiple-unit activity is the experimentally relevant observable and not the synaptic output [21], σ itself enters the definition of these quantities and not the quantity w of Eq. (2) [22].

The calculation of (16) simplifies considerably in the mean-field approximation (see Ref. [13] for details). The result is

$$Z_{\mathrm{MFA}}[l,\hat{l}]=\int\mathcal{D}\sigma\,\mathcal{D}\hat{\sigma}\exp\{L_0[\sigma,\hat{\sigma}]\}\exp\left\{\frac{J^2}{2}\int dt\,dt'\sum_i\left[\mathcal{C}(t-t')i\hat{\sigma}_i(t)i\hat{\sigma}_i(t')+2\frac{1-k^2}{1+k^2}\mathcal{G}(t-t')i\hat{\sigma}_i(t)w_i(t')\right]\right\} , \tag{20}$$

where

$$\begin{aligned}\mathcal{C}(t-t')&\equiv[\langle w_i(t)w_i(t')\rangle]\\&=\int_0^\infty du\,dv\,f(u)f(v)C(t-u-(t'-v)) ,\end{aligned} \tag{21}$$

$$\begin{aligned}\mathcal{G}(t-t')&\equiv[\langle i\hat{\sigma}_i(t')w_i(t)\rangle]\\&=\int_0^{t-t'}du\,f(u)G(t-u-t') .\end{aligned} \tag{22}$$

The upper boundary of the integration in Eq. (22) is due to the causality requirement for the response function (19).

A mean-field equation of motion for σ_i is obtained by defining a Gaussian effective noise field $\phi_i(t)$ with zero mean and variance

$$\langle\phi_i(t)\phi_j(t')\rangle=\delta_{ij}(2T\Gamma_0^{-1}\delta(t-t')+J^2\mathcal{C}(t-t')) . \tag{23}$$

Then one removes averaging over the noise field ϕ in $Z[l,\hat{l}]$ via

$$Z[l,\hat{l}]\equiv\int\mathcal{D}\phi\,\mathcal{P}[\phi]Z[l,\hat{l};\phi] , \tag{24}$$

with

$$\begin{aligned}Z[l,\hat{l};\phi]\equiv\int\mathcal{D}\sigma\,\mathcal{D}\hat{\sigma}\,\mathcal{J}\exp\Bigg\{\int dt\sum_i[&l_i(t)\sigma_i(t)\\&+\hat{l}_i(t)i\hat{\sigma}_i(t)\\&-i\hat{\sigma}_i(t)\bar{\Lambda}_i(t)]\Bigg\} ,\end{aligned} \tag{25}$$

$$\begin{aligned}\bar{\Lambda}_i(t)\equiv{}&\Gamma_0^{-1}\partial_t\sigma_i(t)-\bar{h}_i(t)-h_i^0(t)-\phi_i(t)\\&+\frac{dH_{r,\lambda}(\sigma_i(t))}{d\sigma_i(t)} ,\end{aligned} \tag{26}$$

$$\bar{h}_i(t)\equiv J^2\frac{1-k^2}{1+k^2}\int dt'\,\mathcal{G}(t-t')w_i(t') . \tag{27}$$

Applying Eq. (15) to (25) (and setting $\hat{l}\equiv0$) implies the mean-field equation

$$\bar{\Lambda}_i(t)=0 \tag{28}$$

for σ_i. The postsynaptic potential in the mean-field approximation is given by (27). As usual, the mean-field approximation has changed spatial nonlocalities in $h_i(t)$ to a temporal nonlocality in $\bar{h}_i(t)$, Eq. (27).

IV. SPECTRAL PROPERTIES OF THE POSTSYNAPTIC POTENTIAL

The spectral representation of the mean-field equation of motion (26) reads

$$\begin{aligned}\bar{\Lambda}_i(\omega)={}&-i\omega\Gamma_0^{-1}\sigma_i(\omega)-\bar{h}_i(\omega)-h_i^0(\omega)\\&-\phi_i(\omega)+H'_{r,\lambda}[\sigma_i(\omega)]=0 ,\end{aligned} \tag{29}$$

where, according to Eq. (11),

$$\begin{aligned}H'_{r,\lambda}[\sigma_i(\omega)]={}&r\sigma_i(\omega)+4\lambda\int\frac{d\omega_1}{2\pi}\frac{d\omega_2}{2\pi}\sigma_i(\omega_1)\sigma_i(\omega_2)\\&\times\sigma_i(\omega-\omega_1-\omega_2)\end{aligned} \tag{30}$$

and

$$\bar{h}_i(\omega)=J^2\frac{1-k^2}{1+k^2}\mathcal{G}(\omega)w_i(\omega) . \tag{31}$$

Here

$$\mathcal{G}(\omega)=g(\omega)G(\omega) , \tag{32}$$

$$w_i(\omega)=g(\omega)\sigma_i(\omega) , \tag{33}$$

and

$$g(\omega)=\int_0^\infty dx\,f(x)e^{i\omega x} . \tag{34}$$

The variance of the noise field reads in Fourier representation

$$\langle \phi_i(\omega)\phi_j(\omega')\rangle = 2\pi\delta(\omega+\omega')[2T\Gamma_0^{-1}+J^2\mathcal{C}(\omega)]\delta_{ij} \ , \tag{35}$$

where

$$\mathcal{C}(\omega)=g(\omega)g(-\omega)C(\omega) \ . \tag{36}$$

The effect of finite signal transmission times and memorizing the prior synaptic activity is now obvious from Eqs. (32), (33), and (36): in the spectral representation they result in multiplying the quantities $G(\omega)$ and $\sigma_i(\omega)$ entering the postsynaptic potential with the Fourier transform of $f(x)\Theta(x)$, Eq. (34), and the quantity $C(\omega)$ appearing in the variance of the noise field with the corresponding absolute amount squared [$f(x)\Theta(x)$ is real; hence $g(-\omega)=g^*(\omega)$]. Thus the rather complicated integration over the synaptic history in time representation corresponds to the simple multiplication with a frequency-dependent dimensionless factor in Fourier representation [23].

For the class of neural networks considered in this work, the complete information concerning synaptic delay and memory is contained in the function $g(\omega)$. In the following we list the functions $g(\omega)$ corresponding to the different choices for f presented in Sec. II and discuss their effects.

(i) For instantaneous signal transfer we simply have

$$g(\omega)=1 \ , \tag{37}$$

recovering the case discussed in [14,15].

(ii) For signal transfer after the delay time τ we obtain

$$g(\omega)=e^{i\omega\tau} \ . \tag{38}$$

There is no effect on the variance of the noise field $\phi_i(\omega)$, but the postsynaptic potential acquires an additional oscillatoric factor $e^{2i\omega\tau}$ in comparison to case (i). Its static part is obviously not affected.

(iii) Exponential oblivion yields

$$g(\omega)=\frac{1+i\omega\tau}{1+(\omega\tau)^2} \ . \tag{39}$$

The part of the variance of $\phi_i(\omega)$ proportional to $C(\omega)$ thus acquires a factor $[1+(\omega\tau)^2]^{-1}$, suppressing frequency components of the noise generated by the autocorrelation, which are much larger than the rate of oblivion $\omega \gg \tau^{-1}$. On small time scales, where synaptic memory still persists, the noise is therefore purely thermal and neither affected by static correlations nor, for $k\neq 0$, by "dynamical excess noise" [15]. The postsynaptic potential is modified by the factor $(1+i\omega\tau)^2/[1+(\omega\tau)^2]^2$, introducing a more complicated frequency dependence on the real and imaginary parts of the response function, but leaving the static part unchanged. Details will be discussed for the spherical model (see Sec. V).

(iv) "Gaussian oblivion" corresponds to

$$g(\omega)=\exp\left\{-\left[\frac{\omega\tau}{2}\right]^2\right\} \times\left\{1+i\frac{\omega\tau}{\sqrt{\pi}}\,{}_1F_1\left[1;\frac{3}{2};-\left[\frac{\omega\tau}{2}\right]^2\right]\right\} . \tag{40}$$

The effects on the variance of ϕ and the postsynaptic potential are technically more intricate but physically similar to case (iii), wherefore we do not discuss them in detail.

(v) A constant memory up to time $t-\tau$ in the past yields

$$g(\omega)=\frac{e^{i\omega\tau}-1}{i\omega\tau} \ . \tag{41}$$

This has similar effects as in case (iii) in the static and the high-frequency limit. In addition, for frequencies which are multiples of $2\pi/\tau$, $g(\omega)$ vanishes. This renders the variance of ϕ purely thermal and eliminates the corresponding Fourier components from the spectrum of the mean-field potential $\bar{h}_i(2n\pi/\tau)\equiv 0$, $n=1,2,\ldots$.

V. THE SPHERICAL MODEL

In this section we discuss the analytically solvable spherical model for the class of neural networks presented above and explicitly compare cases (ii) and (iii) of Secs. II and IV with the case of instantaneous signal transfer. First, the model is defined and static properties such as the susceptibility, the Edward-Anderson parameter, and the temperature of a possible spin-glass transition are discussed. In the second part, we present the complete dynamical solution for the response function.

A. The model and its static properties

The spherical model is defined by the choice $\lambda=0$ in Eq. (11) and the global constraint [13]

$$1=\lim_{N\to\infty}\frac{1}{N}\sum_{i=1}^{N}\sigma_i^2(t)\equiv[\langle\sigma_i^2(t)\rangle]\equiv C(t=0) \ . \tag{42}$$

This determines the value of r in (11), which would otherwise be a free parameter. Note, however, that the restriction (42) on the neural activity $\sigma_i(t)$ has, from the neurophysiological point of view, the same effect as the model with r fixed and $\lambda>0$: in both cases there is a certain energetically favored value σ_i^*, $|\sigma_i^*|<\infty$, for the neural activity. The difference is that this value may be *a priori* chosen to be finite for free parameters r,λ, while in the spherical model it is completely determined by the intrinsic dynamics.

In the absence of nonlinear terms we write the mean-field equation (29) in the form [13]

$$G^{-1}(\omega)\sigma_i(\omega)=\phi_i(\omega)+h_i^0(\omega) \ , \tag{43}$$

where

$$G^{-1}(\omega)=-i\omega\Gamma_0^{-1}+r-J^2\frac{1-k^2}{1+k^2}g^2(\omega)G(\omega) \ . \tag{44}$$

In the following we will measure frequencies in units of Γ_0 and times in units of Γ_0^{-1}, allowing us to set $\Gamma_0\equiv 1$. Moreover, we define

$$\kappa\equiv J^2\frac{1-k^2}{1+k^2} \tag{45}$$

and consider $h_i^0=0$. From Eq. (44) we obtain

$$G^{-1}(\omega)=\tfrac{1}{2}[r-i\omega+\sqrt{(r-i\omega)^2-4\kappa g^2(\omega)}] \tag{46}$$

and

$$\mathrm{Re}G(\omega)=\frac{r[|G(\omega)|^{-2}-A(\omega)]+\omega B(\omega)}{|G(\omega)|^{-4}-[A^2(\omega)+B^2(\omega)]}\ , \tag{47}$$

$$\mathrm{Im}G(\omega)=\frac{\omega[|G(\omega)|^{-2}+A(\omega)]+rB(\omega)}{|G(\omega)|^{-4}-[A^2(\omega)+B^2(\omega)]}\ , \tag{48}$$

where

$$A(\omega)\equiv\kappa\,\mathrm{Re}g^2(\omega)\ , \tag{49}$$

$$B(\omega)\equiv\kappa\,\mathrm{Im}g^2(\omega)\ . \tag{50}$$

$|G(\omega)|^{-2}$ is the physical root of

$$\begin{aligned}0=\{|G(\omega)|^{-4}-[A^2(\omega)+B^2(\omega)]\}^2-|G(\omega)|^{-2}\\ \times\{(r^2+\omega^2)[|G(\omega)|^{-4}+A^2(\omega)+B^2(\omega)]\\ -2[(r^2-\omega^2)A(\omega)-2r\omega B(\omega)]|G(\omega)|^{-2}\}\ .\end{aligned} \tag{51}$$

For further use we give the real and the imaginary part of $g^2(\omega)$ and the absolute amount squared of $g(\omega)$ for the three cases (i)–(iii) of Secs. II and IV:

$$\mathrm{Re}g^2(\omega)=\begin{cases}1\ , & \text{(i)}\\ \cos 2\omega\tau\ , & \text{(ii)}\\ [1-(\omega\tau)^2]/[1+(\omega\tau)^2]^2\ , & \text{(iii)}\ ,\end{cases} \tag{52}$$

$$\mathrm{Im}g^2(\omega)=\begin{cases}0\ , & \text{(i)}\\ \sin 2\omega\tau\ , & \text{(ii)}\\ 2\omega\tau/[1+(\omega\tau)^2]^2\ , & \text{(iii)}\ ,\end{cases} \tag{53}$$

$$|g(\omega)|^2=\begin{cases}1\ , & \text{(i)}\\ 1\ , & \text{(ii)}\\ [1+(\omega\tau)^2]^{-1}\ , & \text{(iii)}\ .\end{cases} \tag{54}$$

From Eq. (35), Eq. (43) (for $h_i^0\equiv 0$), and

$$\langle\sigma_i(\omega)\sigma_i(\omega')\rangle=2\pi\delta(\omega+\omega')C(\omega) \tag{55}$$

one obtains

$$[|G(\omega)|^{-2}-J^2|g(\omega)|^2]C(\omega)=2T\ . \tag{56}$$

Decomposing this equation into its zero- and finite-frequency parts with $C(\omega)=\tilde{C}(\omega)+2\pi\delta(\omega)q$ (cf. [13]), where q is the Edward-Anderson parameter, one obtains

$$\tilde{C}(\omega)=\frac{2T}{|G(\omega)|^{-2}-J^2|g(\omega)|^2} \tag{57}$$

and

$$q=J^2|g(0)|^2\chi^2 q\ , \tag{58}$$

with the susceptibility $\chi=G(\omega=0)$. From this equation and $|g(0)|^2=1$ for *all* cases under consideration, we draw the following conclusion: *no matter whether there are synaptic delay or memory effects, below* the temperature T_g, where the Edward-Anderson parameter becomes finite, the susceptibility is

$$\chi\equiv J^{-1}\ . \tag{59}$$

Therefore, below T_g, the parameter r is always constant and can be simply obtained from Eq. (47) for $\omega=0$:

$$r\equiv\frac{2J}{1+k^2}\ . \tag{60}$$

Obviously, synaptic delay and memory do not influence results involving the static part of the response function. This is by far nontrivial: although one would naively expect no effect on *any* static quantity according to the explicit form of $g(\omega)$ (see Sec. IV), this does not hold for the Edward-Anderson parameter,

$$q\equiv 1-\tilde{C}(t=0)=1-\int\frac{d\omega}{2\pi}\tilde{C}(\omega)\ . \tag{61}$$

The value of the integral depends on the actual form of $g(\omega)$ [cf. Eqs. (51) and (57)]. Of course, a definite value can be obtained only after solving (51) for $|G(\omega)|^{-2}$. The solution of this equation also provides the complete frequency dependence of $G(\omega)$ and $C(\omega)$ through Eqs. (47), (48), and (57); see also below.

Above T_g the explicit solution of the problem is more complicated: one has to solve Eq. (51) simultaneously with the r-fixing constraint

$$1\equiv\int\frac{d\omega}{2\pi}\tilde{C}(\omega)=\int\frac{d\omega}{2\pi}\frac{2T}{|G(\omega)|^{-2}-J^2|g(\omega)|^2}\ . \tag{62}$$

Equation (62) also serves to determine T_g: the low-frequency behavior of $\tilde{C}(\omega)$ decides whether this equation can be fulfilled for finite T_g or only for $T_g=0$, for the former, $\tilde{C}(\omega)$ must have an integrable infrared divergence $\tilde{C}(\omega)\sim\omega^{-\alpha}$, $\alpha<1$ [13]. To explicitly calculate the infrared behavior one considers (46) at T_g, i.e., where (60) may be employed,

$$\begin{aligned}G^{-1}(\omega)=\frac{J}{1+k^2}-\frac{i\omega}{2}\\ +\left[J^2\frac{1-(1-k^4)g^2(\omega)}{(1+k^2)^2}-i\frac{J\omega}{1+k^2}-\frac{\omega^2}{4}\right]^{1/2}\ .\end{aligned} \tag{63}$$

For the low-frequency limit of this equation, in both cases (ii) and (iii) we may write $g^2(\omega)\simeq 1+2i\omega\tau+O(\omega^2)$, including case (i) as the special case $\tau\equiv 0$. One now readily obtains the low-frequency expansion

$$G^{-1}(\omega)\simeq\begin{cases}J+\sqrt{-iJ(1+2J\tau)}\,\omega^{1/2}+O(\omega)\ , & k=0\\ J-i\omega[1+k^2+2J\tau(1-k^2)]/2k^2+O(\omega^2), & k>0\ .\end{cases} \tag{64}$$

This implies

$$|G(\omega)|^{-2}-J^2|g(\omega)|^2\sim\begin{cases}\omega^{1/2}\ , & k=0\\ \omega^2\ , & k>0\ ,\end{cases} \tag{65}$$

which leads to the conclusion that only in the symmetric case a spin-glass phase may exist at finite temperatures [13]. This result is again independent of the delay or memory effects. Most of the global properties of the network are thus unaffected by finite signal transmission times and the possibility of memorizing prior synaptic activity.

B. Dynamics of the response function

All dynamical quantities, e.g., (47), (48), and (57), depend on the solution of Eq. (51). In the following, we restrict our investigations to $T=T_g$, since in this case r is simply given by (60). As mentioned above, for arbitrary T one would have to solve (51) simultaneously with (62) to obtain a self-consistent value for r. For the sake of simplicity, we only consider the case $J=1$.

In general, Eq. (51) has four (complex) roots, but only one has the property that $|G(\omega)|^{-2}$ is both real and larger than one. This is the physical solution, since it leads to a finite, real value for $G(t)$. For the fully asymmetric case ($k=1$ and consequently $\kappa=0$) the solution is particularly simple [13],

$$|G(\omega)|^2=\frac{1}{r^2+\omega^2}\,, \tag{66}$$

independent of delay or memory effects. Since for $k=1$ all neurons are mutually decoupled [the mean-field averaged potential $\bar{h}_i$ vanishes; see Eq. (27)], the dynamics of such a network is completely governed by "random response."

In Fig. 1 we show (66) together with $|G(\omega)|^2$ for $k=0$ and 0.5 as a function of the frequency ω (in units of Γ_0) in the case (i) of instantaneous signal transmission [13]. One observes that different degrees of asymmetry influence only the domain of small ω: the more symmetric a network, the less the long-wavelength "random" response. However, above $\omega \simeq 10\Gamma_0$ the frequency spectrum rapidly approaches that of white noise ($\sim\omega^{-2}$) in all cases.

Figure 2 shows the effect of delayed signal transmission, case (ii), for a fully symmetric network, $k=0$ [Fig. 2(a)], and a partially asymmetric network with $k=0.5$ [Fig. 2(b)]. The solid line corresponds to instantaneous signal transmission or vanishing delay time τ (cf. also Fig. 1). The dashed and the dotted lines correspond to a delay time of $\tau=\Gamma_0^{-1}$ and $2\Gamma_0^{-1}$, respectively.

One clearly observes two features: (a) the delay considerably suppresses long-wavelength random response and (b) it superimposes an oscillatory structure on top of this reduced random background. As one would expect, the period of the oscillation is proportional to $\pi\tau^{-1}$ [cf. Eqs. (49)–(53)]. The longer the delay time, the more suppressed the long-wavelength random response, the more pronounced the peaks of the oscillations, and the larger the number of oscillatoric peaks.

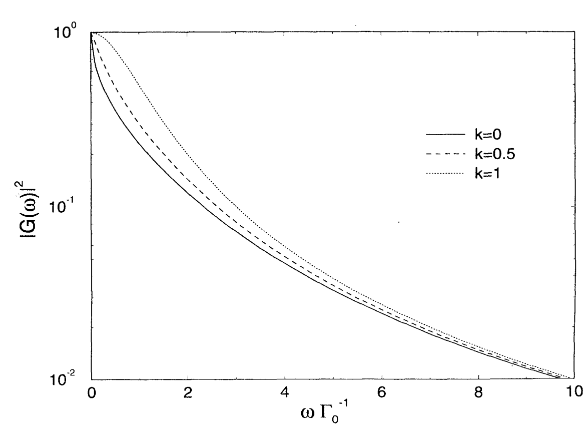

FIG. 1. Fourier spectrum of the absolute amount squared of the response function $|G(\omega)|^2$, for the case of instantaneous signal transfer and various degrees of asymmetry: $k=0$ (full line), $k=0.5$ (dashed line), and $k=1$ (dotted line).

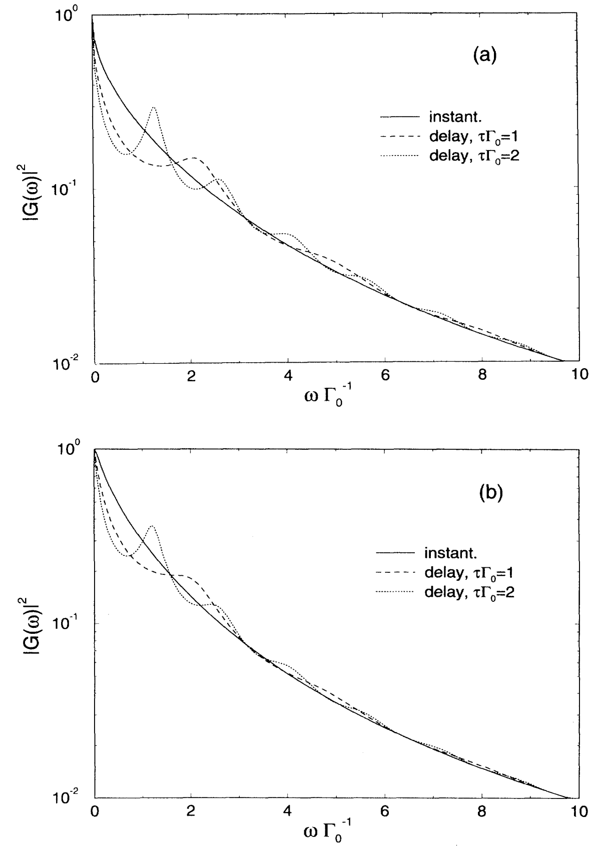

FIG. 2. $|G(\omega)|^2$ for the case of finite discrete delay time $\tau=\Gamma_0^{-1}$ (dashed line) and $\tau=2\Gamma_0^{-1}$ (dotted line) in comparison to instantaneous signal transfer (full line) for (a) $k=0$ and (b) $k=0.5$. The fully asymmetric case $k=1$ is identical to the full line in Fig. 1.

We note that such oscillatoric structures are generic to delay dynamics; see, for instance, the Mackey-Glass equation [24] or the dynamics of graded-response neurons with discrete delay [10]. Solutions include fixed points, periodic limit cycles [9], and chaotic trajectories. Such a diversity of temporal phenomena is possible, since due to the discrete delay the underlying set of equations describes an infinite-dimensional dynamical system. As has been shown by Farmer [25], in the chaotic state the corresponding power spectrum gives rise to motion on very different time scales and exhibits a curious modulation that is quite similar to the shape observed in Fig. 2.

Figure 2 can be interpreted in the sense that the response of the neuron to external stimuli is no longer more or less random, as in the case of instantaneous signal transfer, but will be enhanced, if the stimuli's time dependence is "in resonance" with the system's intrinsic delay time τ. This property could imply that the system is capable of self-organization.

The oscillatoric structures in the frequency spectrum are less pronounced for increasing ω and k. For $\omega \geq 10\Gamma_0$ they are negligible for all k: stimuli that are too rapidly oscillating only generate a white-noise response from the neuron. In the limit $k \rightarrow 1$ they vanish completely for all ω: a fully asymmetric network responds only with "random activity."

In Figs. 3(a) and 3(b) we present the results of the corresponding investigation for "exponential oblivion," case (iii). In this case, the long-wavelength noise is more suppressed the longer the system is able to memorize prior synaptic activity. However, instead of an oscillatory structure there is only a slight and rather broad enhancement of the response function above the reduced random background. Again, these effects vanish for large ω and are less pronounced when k is increased towards the limit of complete randomness $k=1$. We conclude that delayed signal transfer and memorizing prior synaptic activity has no major influence on the static properties of the class of networks under consideration, but drastically changes their dynamical behavior.

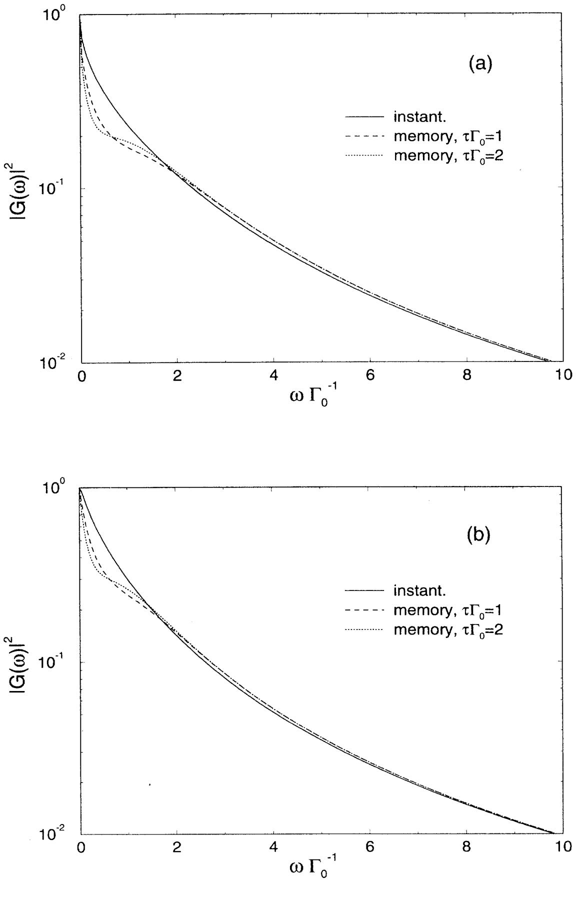

FIG. 3. $|G(\omega)|^2$ for the case of exponential oblivion with time $\tau=\Gamma_0^{-1}$ (dashed line) and $\tau=2\Gamma_0^{-1}$ (dotted line) in comparison to instantaneous signal transfer (full line) for (a) $k=0$ and (b) $k=0.5$. The fully asymmetric case $k=1$ is identical to the full line in Fig. 1.

VI. SUMMARY AND CONCLUSIONS

In this work we have investigated the effects of delayed signal transmission and synaptic memory on static and dynamical properties of a neural network with random and, in general, asymmetric synaptic couplings. We have generalized the standard, instantaneous synaptic signal transfer to account for signal delays and memorizing prior synaptic activity. The dynamical equation for the activity of a single neuron in the network was solved in the mean-field approximation. We found that the modification introduced by delay and memory effects on the frequency spectrum of the mean-field potential and the autocorrelation function simply amounts to a multiplication with the square or the absolute amount squared, respectively, of the Fourier transform of the memory function. An explicit solution was obtained in the framework of the spherical model. It was found that static properties of the network, such as the susceptibility or the transition temperature to a spin-glass phase, are, in general, not affected by delay or memory effects.

On the other hand, the qualitative behavior of dynamical quantities is essentially changed. Our analysis of the response function of the system leads to the following result: the amount of long-wavelength random response is considerably reduced and the response of the system to organized, nontrivial stimuli enhanced. In particular, delayed signal transfer converts a system that exhibits a more or less random response to external stimuli for instantaneous signal transfer into a system responding particularly strongly to stimuli that are in resonance with the intrinsic delay time. Such a feature seems to be a necessary prerequisite for systems capable of self-organization.

So far, our investigations focused on the case of random synaptic couplings, a simple, one-parametric memory function, and the spherical model at $T=T_g$. This leaves a broad spectrum for future, more detailed, and, eventually, neurophysiologically more realistic investigations.

(a) In general, i.e., for $k \neq 0$, the spin-glass transition temperature T_g vanishes and thus the autocorrelation is completely static [cf. Eq. (57)]. At finite temperatures, however, $C(t)$ should, for the case of delayed synaptic transfer, exhibit oscillatoric behavior very similar to the one observed in the visual cortex of the cat [26].

(b) For the general, nonlinear case with the potential (11) there might be qualitative changes of our results obtained in the spherical model. As shown for Ising spins, the existence of a spin-glass phase at $T=0$ depends also on the value of the asymmetry. For $0 \leq k \leq k_{c,1} \simeq 0.31$, spins may at least partially freeze, while for larger values of k one observes random or "chaotic" spin motion [27]. Also, the length of transients (the time the system needs to relax onto an attractor) grows like a power with the system size for $k \leq k_{c,2} \simeq 1/\sqrt{3}$, but exponentially for larger values of k [28]. It remains an open question how these results change under inclusion of delay or memory times.

(c) Our simple choices for the memory function could be considerably improved, for example, by combining the aspects of memory and delay or by introducing several delay time scales.

(d) The synaptic couplings should be chosen according to a learning algorithm capable of pattern recognition [18].

Finally, our rather general treatment opens the possibility to apply it also to other, dynamically coupled, stochastic systems.

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