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Random iterative networks

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A general framework for introducing noise into binary networks is developed using random iterative maps. The dynamics of these random iterative networks is written in terms of Markov chains and notions of ergodicity discussed. Generic features of the statistical dynamics of such networks are explored and a path-integral formulation of macroscopic dynamics derived. Two examples are used for illustration. First, the Little model is shown to be equivalent to a random iterative network with threshold noise, and this is used to derive the mean-field equations for a network with random dilution. Second, mean-field equations are derived for networks with synaptic noise, whose form depends crucially on how the thermodynamic limit is defined.

I. INTRODUCTION

Recently there has been a great deal of interest in attractor networks of the Hopfield[1] and Little[2] form. Much progress has been made in applying spin-glass techniques from statistical mechanics to the study of these networks, in the context of associative memory (Refs. 3 and 4 and references therein). However, there are a number of features of the original models which are nonbiological. Firstly, the connection weights J_{ij} are symmetric, $J_{ij}=J_{ji}$, which underlies the fact that a Hamiltonian may be ascribed to such systems. Moreover, the networks are fully connected. Biological synapses, on the other hand, are one way, and neurons are, on average, connected to a fraction 10^{-6} of other neurons. Secondly, memory recall corresponds to an attractor of the dynamics in which some neurons are essentially firing at every time step, whereas others remain inactive. If the fundamental unit of time is taken to be the refractory period, $\tau=2$ ms, then the active neurons have a firing rate of 500 s^{-1}. Empirically, active neurons in the cortex are observed to have firing rates in the range 30–100 s^{-1}.[5] Also note that spatial firing patterns are much more sparse in biological systems.

All the above features can be dealt with by modifying the Little and Hopfield models. Asymmetric and dilute networks may be obtained using random dilution in which a connectivity matrix is introduced, whose elements are random variables with values 0 or 1.[6-9] Low spatial firing rates may be achieved by storing biased patterns in either undiluted[10-12] or diluted networks.[13-14] Finally, a solution to the low temporal firing rate has been found by reducing a network of excitatory and inhibitory neurons to an effective model of excitatory neurons alone.[15] An alternative solution[16] uses the outer-product matrix of Willshaw, Buneman, and Longuet-Higgins.[17]

A third discrepancy between theory and experiment is the nature of the learning rules adopted. The Hopfield learning rule is unrealistic as pairs of neurons which are inactive in a stored pattern have an enhanced synaptic efficacy. Furthermore, it violates Dale's principle,[18] which basically states that each neuron is either excitatory or inhibitory, but not both. These issues have also been considered in Refs. 15 and 16 in which the Hebbian learning rules[19] are used. However, there is growing evidence that the synaptic modification mechanisms of biological neurons are much more complicated than the simple Hebbian form. There appear to be multiple processes occurring at the same synapse, both pre- and postsynaptic, which differ in time scales and in the nature of chemicals involved.[20]

In this paper we shall be concerned with another difference between present attractor networks and their biological counterparts. This relates to the fact that all such models only consider threshold noise, which corresponds to noise at the axon hillock of a neuron. They completely ignore the more biologically significant source of noise arising from the stochastic and quantal nature of the release of chemical transmitters into the synapses.[20-22] Synaptic noise has been modeled by Shaw and Vesudevan[23] and by Taylor.[24,25] However, the dynamical behavior of these models in terms of the storage and retrieval of memories has not been developed. We shall, therefore, set up a general framework for analyzing the dynamical behavior of attractor networks in the presence of either synaptic or threshold noise. Moreover, parameters introduced into the theory will correspond more directly to biological features such as postsynaptic efficacy and the distribution functions of vesicular release.[22] This will then allow more general learning rules to be studied, although we will not consider such issues here.

In Sec. II we discuss a general scheme for introducing noise into binary networks based on random iterative maps.[26] We show how the dynamics of these random iterative networks may be described by a homogeneous

Markov chain. One consequence of this is that for a class of finite networks, including the Little and Taylor models, there exists a unique equilibrium probability distribution for the states of the network. This ergodic behavior is undesirable for applications such as associative memory. Therefore, in Sec. III we consider the statistical dynamics of random iterative networks, and discuss the possible breakdown of ergodicity in the thermodynamic limit. We define the notion of a macroscopic variable and derive associated deterministic, dynamical equations, following Amari, Yoshida, and Kanatani.[27] These equations are reformulated in terms of path integrals by introducing a generating functional for statistical correlations along the lines of de Dominicis and Peliti.[28]

In Sec. IV we consider the Little model as a random iterative network with threshold noise. We then use the path integrals of Sec. III to derive the mean-field equations for a diluted network with biased patterns.[13,14] Finally, in Sec. V we discuss networks with synaptic noise, such as the Taylor model, and derive mean-field equations which, depending on the definition of the thermodynamic limit, correspond to either the nondiluted or the diluted spin-glass equations at zero temperature. Moreover, a new class of mean-field equations are identified related to presynaptic, rather than postsynaptic storage.

II. RANDOM ITERATIVE NETWORKS

Consider a network of N binary neurons and denote the activity of the ith neuron by $a_i \in \{0,1\}$. The state of the network is specified by the vector $\mathbf{a}=(a_1,a_2,\ldots,a_N)$. Assume that the system develops in discrete time according to the stochastic difference equations

$$a_i(t+1)=\Theta\left[\sum_j^N J_{ij}\omega_{ij}(t)a_j(t)+\phi_i(t)-V_i\right], \tag{2.1}$$

where Θ is the step function

$$\Theta(x)=\begin{cases}1 & \text{if } x>0\\ 0 & \text{if } x<0\ .\end{cases} \tag{2.2}$$

The connection weights are taken to be the product $J_{ij}\omega_{ij}(t)$, where J_{ij} is fixed and $\omega_{ij}(t)$ is a random variable generated from the time-independent probability distribution $\rho_{ij}(\omega_{ij})$. At each time step ω_{ij} is selected randomly from its distribution such that

$$\begin{aligned}&\langle\omega_{ij}(t)\rangle_\omega=\bar{\omega}_{ij}\ ,\\ &\langle[\omega_{ij}(t)-\bar{\omega}_{ij}][\omega_{i'j'}(t')-\bar{\omega}_{i'j'}]\rangle_\omega=\delta_{ii'}\delta_{jj'}\delta_{tt'}\sigma^2_{\omega_{ij}}\ ,\end{aligned} \tag{2.3}$$

where $\bar{\omega}_{ij}$ and $\sigma^2_{\omega_{ij}}$ are, respectively, the mean and variance of the distribution $\rho_{ij}(\omega_{ij})$. Similarly, $\phi_i(t)$ is a random external field generated from $\rho_i(\phi_i)$ such that

$$\begin{aligned}&\langle\phi_i(t)\rangle_\phi=\bar{\phi}_i\\ &\langle[\phi_i(t)-\bar{\phi}_i][\phi_{i'}(t')-\bar{\phi}_{i'}]\rangle_\phi=\delta_{ii'}\delta_{tt'}\sigma^2_{\phi_i}\ .\end{aligned} \tag{2.4}$$

The ϕ_i act as random modulations of the deterministic thresholds V_i.

Equation (2.1) may be interpreted as a random iterative map.[29] Define the function f_{α_i} by

$$f_{\alpha_i}(\mathbf{a})=\Theta\left[\sum_j J_{ij}\omega_{ij}a_j+\phi_i-V_i\right], \tag{2.5}$$

where α_i denotes collectively the connection weights and thresholds of the ith neuron. Introduce a probability measure μ_i on the space of maps

$$\Xi_i=\{f_i \mid f_i\colon\ \{0,1\}^N\to\{0,1\}_i\} \tag{2.6}$$

given by

$$\mu_i(f_i)=\int\prod_j d\omega_{ij}\rho_{ij}(\omega_{ij})\int d\phi_i\rho_i(\phi_i)\delta(f_i-f_{\alpha_i})\ . \tag{2.7}$$

Use Eq. (2.7) to define a measure μ on the product space

$$\Xi=\{f \mid f\colon\{0,1\}^N\to\{0,1\}^N,\ f=(f_1,f_2,\ldots,f_N)\} \tag{2.8}$$

by taking the product of measures μ_i,

$$\mu(f)=\prod_i\mu_i(f_i)\ . \tag{2.9}$$

Then Eq. (2.1) may be rewritten as the random iterative map

$$\mathbf{a}(t+1)=F^t(\mathbf{a}(t))=F^tF^{t-1}\cdots F^0(\mathbf{a}(0))\ , \tag{2.10}$$

with F^t chosen randomly, at each time step, from the probability distribution μ. General aspects of random maps on networks, such as entropy, are discussed elsewhere.[26] We shall refer to a network whose dynamics is described by Eq. (2.1), or equivalently (2.10), as a random iterative network.

The above formulation of random iterative networks could equally well have been written in terms of spin states $s_i=\pm1$, with the step function in Eq. (2.1) replaced by the sign function. Note that random iterative networks should be distinguished from the random nerve nets introduced by Amari, Yoshida, and Kanatani.[27] They consider an ensemble of similar networks and define a probability measure on this ensemble using the distributions $\rho_{ij}(\omega_{ij})$ and $\rho_i(\phi_i)$. For each sample of the ensemble, the weights and thresholds are chosen at random from their distributions and are then held fixed during the time evolution of the system. Similar to random nerve nets are the netlets analyzed by Anninos *et al.*[30]

The dynamical evolution of a random iterative network may be described by a homogeneous Markov chain. This follows from the fact that the random map F^t of Eq. (2.10) is reselected at each time step from the same probability distribution μ. In other words,

$$\begin{aligned}&\mathrm{Prob}[\mathbf{a}(t+1)=\mathbf{b}\mid\mathbf{a}(t)=\mathbf{a},\ \mathbf{a}(t-1),\ldots,\mathbf{a}(0)]\\ &\quad=\mathrm{Prob}[\mathbf{a}(t+1)=\mathbf{b}\mid\mathbf{a}(t)=\mathbf{a}]\\ &\quad\equiv Q_{\mathbf{ba}}\ ,\end{aligned} \tag{2.11}$$

where $Q_{\mathbf{ba}}$ is the time-independent transition probability of going from state $\mathbf{a}$ to state $\mathbf{b}$ in one time step, and is defined by

$$Q_{\mathbf{ba}}=\sum_{f\in\Xi}\mu(f\,|\,f(\mathbf{a})=\mathbf{b})\ . \tag{2.12}$$

Introducing the probability $P_{\mathbf{a}}(t)$ that the state of the network at time t is $\mathbf{a}$ leads to the homogeneous Markov chain

$$P_{\mathbf{b}}(t+1)=\sum_{\mathbf{a}} Q_{\mathbf{ba}}P_{\mathbf{a}}(t)\ . \tag{2.13}$$

Since the activities a_i only take the values $\{0,1\}$, Eq. (2.12) may be rewritten as

$$Q_{\mathbf{ba}}=\left\langle \prod_{i=1}^{N}[f_i(\mathbf{a})]^{b_i}[\hat{f}_i(\mathbf{a})]^{\hat{b}_i}\right\rangle_{\mu}\ , \tag{2.14}$$

where $\langle\ \rangle_{\mu}$ denotes expectation with respect to μ, and

$$\hat{f}_i(\mathbf{a})=1-f_i(\mathbf{a}),\quad \hat{b}_i=1-b_i\ . \tag{2.15}$$

Using Eqs. (2.7) and (2.9), the transition matrix takes the form

$$Q_{\mathbf{ba}}=\prod_{i=1}^{N}[p(i\,|\,\mathbf{a})]^{b_i}[\hat{p}(i\,|\,\mathbf{a})]^{\hat{b}_i}\ , \tag{2.16}$$

where

$$\begin{aligned} p(i\,|\,\mathbf{a})=\langle f_i(\mathbf{a})\rangle_{\mu_i}&=\int\prod_{j}d\omega_{ij}\rho_{ij}(\omega_{ij})\int d\phi_i\rho_i(\phi_i)\Theta\left[\sum_j J_{ij}\omega_{ij}a_j+\phi_i-V_i\right]\\ &=\mathrm{Prob}\left[\sum_j J_{ij}\omega_{ij}+\phi_i>V_i\right] \end{aligned} \tag{2.17}$$

Having formulated the dynamics of a random iterative network in terms of the Markov chain, Eq. (2.13), we may now consider features of the dynamics such as ergodicity in terms of the properties of the transition matrix Q. We begin with a number of definitions.[31] Introduce the n-step transition probability $P_{\mathbf{ba}}(n)$,

$$P_{\mathbf{ba}}(n)=\mathrm{Prob}[\mathbf{a}(n)=\mathbf{b}\,|\,\mathbf{a}(0)=\mathbf{a}]\equiv Q^{n}_{\mathbf{ba}}\ . \tag{2.18}$$

Then the period of state $\mathbf{a}$ is defined to be

$$T(\mathbf{a})=G(\{n\,|\,P_{\mathbf{aa}}(n)>0\})\ , \tag{2.19}$$

the greatest common divisor G of the times at which return to $\mathbf{a}$ is possible. That is, $P_{\mathbf{aa}}(n)=0$ unless n is a multiple of $T(\mathbf{a})$. We call a state $\mathbf{a}$ periodic if $T(\mathbf{a})>1$ and aperiodic if $T(\mathbf{a})=1$. If all states of the network are aperiodic, the Markov chain is said to be aperiodic. Define a Markov chain to be irreducible if every state may be reached, after a finite number of steps, from every other state. In other words, for each $\mathbf{a},\mathbf{b}\in\{0,1\}^N$, there exists $m\geq 0$ such that $P_{\mathbf{ba}}(m)>0$. We shall only consider, in the following, random iterative networks described by irreducible, aperiodic, homogeneous Markov chains. When N is finite, and since the number of states of the network is 2^N, the chains are also finite. We may then use the result[31] that all states of a finite, irreducible, aperiodic, homogeneous, Markov chain are ergodic. This means that the state-occupation probability $P_{\mathbf{a}}(t)$ converges, as $t\rightarrow\infty$, to a limiting distribution $P^{\infty}(\mathbf{a})$,

$$\lim_{t\rightarrow\infty}P_{\mathbf{a}}(t)=P^{\infty}(\mathbf{a})\ , \tag{2.20}$$

which is independent of the initial distribution $P_{\mathbf{a}}(0)$. Equation (2.20) implies that time averages are independent of initial conditions and may be replaced by ensemble averages over the limiting distribution $P^{\infty}(\mathbf{a})$. Therefore, for any state variable X

$$\lim_{T\rightarrow\infty}\sum_{t=0}^{T}\frac{X(\mathbf{a}(t))}{T}=\sum_{\mathbf{a}}P^{\infty}(\mathbf{a})X(\mathbf{a})\ . \tag{2.21}$$

Note that in practice time averages are considered over a finite time $T=\tau_{\mathrm{obs}}$. These averages may still be replaced by ensemble averages provided $\tau_{\mathrm{obs}}\gg\tau_{\mathrm{max}}$, the maximum relaxation time characterizing the rate of fluctuations of the system.

General techniques for analyzing P^{∞} have been developed by Schnakenberg[32] and applied to the Little model[2] by Clark.[33] Expressions for P^{∞} tend to be very complicated except for the special cases in which the transition matrix Q satisfies, for some function f,[34]

$$\frac{Q_{\mathbf{ba}}}{Q_{\mathbf{ab}}}=\frac{f(\mathbf{b})}{f(\mathbf{a})}\ . \tag{2.22}$$

Then equation (2.13) becomes

$$P_{\mathbf{b}}(t+1)=\sum_{\mathbf{a}}Q_{\mathbf{ab}}P_{\mathbf{a}}(t)\frac{f(\mathbf{b})}{f(\mathbf{a})}\ , \tag{2.23}$$

which has the stationary solution

$$P^{*}(\mathbf{a})=\frac{f(\mathbf{a})}{\sum_{\mathbf{a}}f(\mathbf{a})} \tag{2.24}$$

Since the limiting distribution is unique, and hence equal to $P^{*}(\mathbf{a})$, we have the Gibbs distribution

$$P^{\infty}(\mathbf{a})=\frac{e^{-\beta H(\mathbf{a})}}{\sum_{\mathbf{a}}e^{-\beta H(\mathbf{a})}}\ , \tag{2.25}$$

where $H(\mathbf{a})=-\beta^{-1}\ln f(\mathbf{a})$ is an effective Hamiltonian and $\beta^{-1}=\kappa$ is a "temperature" parameter for the theory (see below). An example of a random iterative network satisfying (2.22) is the Little-Hopfield model (see Sec. IV). However, most network models, including those with synaptic noise (Sec. V), are effectively non-Hamiltonian.

One of the consequences of Eq. (2.20) is that, strictly speaking, aperiodic, irreducible, random iterative networks cannot display any long-range order in time. For any injection of new information, from external sources, say, can only produce fluctuations about the limiting distribution $P^{\infty}(\mathbf{a})$, and eventually disappear. This is undesirable for applications such as content-addressable memories. One possible solution is to operate the network near the deterministic limit. This involves introducing a "temperature" parameter κ into the theory so that

$$\lim_{\kappa\to 0}\rho_{ij}(\omega_{ij})=\delta(\omega_{ij}-\bar{\omega}_{ij}) , \qquad \lim_{\kappa\to 0}\rho_{i}(\phi_{i})=\delta(\phi_{i}-\bar{\phi}_{i}) . \tag{2.26}$$

Equations (2.7) and (2.26) imply that

$$\lim_{\kappa\to 0}\mu_{i}(f_{i})=\delta(f_{i}-f_{\bar{\alpha}_{i}}) \tag{2.27}$$

and Eq. (2.1) reduces to the deterministic Caianello equations,[35]

$$a_i(t+1)=\Theta\left[\sum_j J_{ij}\bar{\omega}_{ij}a_j(t)+\bar{\phi}_i-V_i\right] . \tag{2.28}$$

The dynamics of these equations consists of many fixed points and cycles and hence corresponds to a reducible Markov chain. By taking κ sufficiently small, $\tau_{\max} \gg \tau_{\text{obs}}$ and the stationary solutions of the Caianello equations persist for practically meaningful lengths of time.

An alternative to the low-noise limit is a large-N limit, in which a breakdown of ergodicity may occur.[36] In such a situation the time averages of Eq. (2.21) are equivalent to ensemble averages over a nonergodic measure $\tilde{P}$. Thus, the state space decomposes into disjoint invariant subsets Ω_m of positive measure, i.e., $\tilde{P}(\Omega_m)>0$, such that

$$\Omega=\bigcup_m \Omega_m, \quad \Omega_m \cap \Omega_n=\phi, \quad \Lambda_t\Omega_m \subseteq \Omega_m , \tag{2.29}$$

where Λ_t is the generator of time translations by t. Moreover, $\tilde{P}$ may be written as the convex sum

$$\tilde{P}=\sum_m \alpha_m P^m, \sum_m \alpha_m=1 \tag{2.30}$$

where each P^m is a time-invariant measure on Ω_m. Hence,

$$P^m(\Omega_m)=1, \quad P^m(\Lambda_t\Omega_m)=P^m(\Omega_m), \quad \tilde{P}(\Omega^m)=\alpha_m . \tag{2.31}$$

The corresponding time averages now depend upon initial conditions with

$$\lim_{T\to\infty}\left[\lim_{N\to\infty}\sum_{t=0}^{T}\frac{X(\mathbf{a}(t))}{T}\right]=\sum_{\mathbf{a}}P^m(\mathbf{a})X(\mathbf{a}) \tag{2.32}$$

for all $\mathbf{a}(0)\in\Omega_m$. Note the ordering of the limits in Eq. (2.32). In general, the long-time dynamics of the network is not equivalent to the equilibrium situation characterized by the ensemble averages

$$\lim_{N\to\infty}\sum_{\mathbf{a}}P^{\infty}(\mathbf{a})X(\mathbf{a}) . \tag{2.33}$$

It is the dynamical, rather than equilibrium, properties of networks that is important for the storage and retrieval of memories. The behavior of random iterative networks in the thermodynamic limit is discussed in Sec. III.

III. STATISTICAL DYNAMICS

In Sec. II we discussed two equivalent descriptions of random iterative networks, one in terms of random maps and the other in terms of Markov chains. The random map formulation is more useful for setting up a statistical dynamics of networks. In particular, it may be used to construct a generating functional for all statistical correlations of the system, and to derive macroscopic dynamical equations in terms of path integrals.

We begin by defining more precisely the limit $N\to\infty$, in terms of the N dependence of the means and variances of the connection weights and external fields. Assume that the distributions of the ϕ_i are N independent. Then, for the limit $N\to\infty$ to be well defined (and assuming the network is fully connected), we require that the product $\bar{\omega}_{ij}J_{ij}$ is $O(1/N)$. Consistent with this are the two alternative conditions

$$\bar{\omega}_{ij}=O(1/N), \quad J_{ij}=O(1) \tag{3.1}$$

and

$$\bar{\omega}_{ij}=O(1), \quad J_{ij}=O(1/N) \tag{3.2}$$

Note that Eqs. (3.1) and (3.2) should be distinguished from the weak and strong dilution conditions of randomly diluted networks.[7] For the random weights ω_{ij} are taken to be annealed rather than quenched. Therefore, if we were to view ω_{ij} as a connectivity matrix, the connections between neurons are broken and reassembled at every time-step. Randomly diluted nets[6-9] correspond to taking quenched weights such that

$$\rho_{ij}(\omega_{ij})=\delta(\omega_{ij}-1), \quad J_{ij}=C_{ij}\tilde{J}_{ij} , \tag{3.3}$$

with C_{ij} a quenched random variable. We may then define strong or weak dilution conditions on the connectivity matrix C_{ij} in the usual way (see Sec. IV).

Taking the limit $N\to\infty$ to be defined by either (3.1) or (3.2), we introduce the notion of a macroscopic variable, along the lines of Amari, Yoshida, and Kanatani.[27] A finite collection of state functions, $\mathbf{X}(\mathbf{a})=\{X_r(\mathbf{a}), r=1,\ldots,R\}$ is said to be a closed set of macroscopic variables if there exists a set of functions Φ_r, $r=1,\ldots,R$ such that for arbitrary $\mathbf{a}$,

$$\lim_{N\to\infty}\langle X_r(f_\alpha(\mathbf{a}))\rangle_\rho=\Phi_r(\mathbf{X}(\mathbf{a})) , \tag{3.4}$$

$$\lim_{N\to\infty}\operatorname{var}_\rho[X_r(f_\alpha(\mathbf{a}))]=0 , \tag{3.5}$$

where $\langle\ \rangle_\rho$ and var_ρ denote respectively, the mean and variance with respect to the distributions of the weights and external fields. The mapping f_α has components f_{α_i} as defined in Eq. (2.5). Thus

$$\langle X_r(f_\alpha(\mathbf{a}))\rangle_\rho=\int\prod_j d\omega_{ij}\rho_{ij}(\omega_{ij})\int d\phi_i\rho_i(\phi_i)\sum_{\mathbf{a}'}X_r(\mathbf{a}')\prod_{k=1}^{N}\delta\left[a_k'-\Theta\left[\sum_l J_{kl}\omega_{kl}a_l+\phi_k-V_k\right]\right] . \tag{3.6}$$

Equations (3.4) and (3.5) imply that

$$\lim_{N\to\infty} |X_r(f_\alpha(\mathbf{a}))-\langle X_r(f_\alpha(\mathbf{a}))\rangle_\rho|=0 \ . \tag{3.7}$$

Hence, in the large-N limit, the probability that in a given trial, $X_r(f_\alpha(\mathbf{a}))=\langle X_r(f_\alpha(\mathbf{a}))\rangle_\rho$, approaches 1. In other words, for N sufficiently large, a good approximation to Eq. (3.4) is

$$X_r(f_\alpha(\mathbf{a}))=\Phi_r(X(\mathbf{a})) \ . \tag{3.8}$$

Equation (3.8) still holds if $\mathbf{a}$ is replaced by the dynamical variable $\mathbf{a}(t)$ satisfying Eq. (2.1). This follows from the fact that the weights and external fields are reselected at random at each time step. Since $f_\alpha(\mathbf{a}(t))=\mathbf{a}(t+1)$, and defining $X_r(t)=X_r(a(t))$, we obtain the deterministic dynamical equations

$$X_r(t+1)=\Phi_r(\mathbf{X}(t)), \quad r=1,\ldots,R \tag{3.9}$$

Equation (3.9) contains information about the long-time dynamical behavior of the network in the limit $N\to\infty$. Suppose, for simplicity, that the set $\{X_r,\ r=1,\ldots,R\}$ completely characterizes the macroscopic dynamics of the system. Moreover, assume that there are stationary solutions of (3.9) which are stable fixed points, denoted $X^{(\alpha)}$. Each such solution satisfies

$$X_r^{(\alpha)}=\Phi_r(\mathbf{X}^{(\alpha)}) \tag{3.10}$$

and the eigenvalues λ_r of the Jacobian

$$\Delta_{rs}=\left.\frac{\partial\Phi_r}{\partial X_s}\right|_{X^{(\alpha)}} \tag{3.11}$$

satisfy the stability criterion, $|\lambda_r|<1$. Then, assuming that $\mathbf{X}(0)\in\Lambda_\alpha$, where Λ_α is the basin of attraction for $\mathbf{X}^{(\alpha)}$, the time average of $\mathbf{X}(t)$ is given by

$$\lim_{T\to\infty}\left[\lim_{N\to\infty}\sum_{t=0}^{T}\frac{\mathbf{X}(t)}{T}\right]=\mathbf{X}^{(\alpha)} \tag{3.12}$$

for all initial states $\mathbf{a}$ such that $\mathbf{X}(\mathbf{a})\in\Lambda_\alpha$. We see that the breakdown of ergodicity is reflected by the existence of more than a single fixed point of Eq. (3.8). In practice, the dynamics may be much more complicated with cycles and chaotic regimes.[37]

We now turn to the general formulation of statistical dynamics in terms of path integrals. To achieve this we set up a stochastic generating functional along the lines of de Dominicis and Peliti.[28] That is, we replace Eq. (2.1) by

$$Z_{\omega,\phi}[l]=\prod_t\int d\tilde{\mathbf{u}}(t)d\mathbf{u}(t)\exp\left[i\sum_{t,i}l_i(t)u_i(t)\right]\exp\left\{i\sum_{t,i}\tilde{u}_i(t)\left[u_i(t+1)-\Theta\left[\sum_j\omega_{ij}(t)J_{ij}u_j(t)+\phi_i(t)-V_i\right]\right]\right\} . \tag{3.13}$$

Taking the average over the ϕ_i, ω_{ij} yields the functional which generates correlation functions for the stochastic variables $a_i(t)$,

$$Z[l]=\prod_{t,i,j}\int d\omega_{ij}(t)\rho_{ij}(\omega_{ij})\prod_{t,i}\int d\phi_i(t)\rho_i(\phi_i)Z_{\omega,\phi}[l] \ . \tag{3.14}$$

For example,

$$\begin{aligned}\langle u_i(t)\rangle &= -i\left.\frac{\delta}{\delta l_i(t)}Z[l]\right|_{l=0}\\ &=\sum_{\{a(t),a(t-1),\ldots,a(1)\}}[Q_{\mathbf{a}(t)\mathbf{a}(t-1)}Q_{\mathbf{a}(t-1)\mathbf{a}(t-2)}\cdots Q_{\mathbf{a}(1)\mathbf{a}(0)}a_i(t)] \ . \end{aligned}\tag{3.15a}$$

Note that there are no contributions from $Z[l]$ for times $t'>t$ since $\sum_{\mathbf{b}}Q_{\mathbf{ba}}=1$. We are taking the boundary condition that $\mathbf{a}(0)=\mathbf{a}_0$, where $\mathbf{a}_0$ is fixed. Similarly,

$$p(i|\mathbf{a})=\langle u_i(t+1)\delta(\mathbf{u}(t)-\mathbf{a})\rangle \ , \tag{3.15b}$$

$$Q_{\mathbf{ba}}=\langle\delta(\mathbf{u}(t+1)-\mathbf{b})\delta(\mathbf{u}(t)-\mathbf{a})\rangle \ , \tag{3.15c}$$

To write Eq. (3.13) in a more useful form introduce the identity

$$1=\prod_t\int d\mathbf{h}(t)d\tilde{\mathbf{h}}(t)\exp\left[i\sum_{t,i}\tilde{h}_i(t)\left[h_i(t)-\sum_j\omega_{ij}J_{ij}u_j(t)-\phi_i\right]\right] , \tag{3.16}$$

so that $Z[l]$ becomes,

$$\begin{aligned}Z[l]=\prod_t\int d\mathbf{u}(t)d\tilde{\mathbf{u}}(t)d\mathbf{h}(t)d\tilde{\mathbf{h}}(t)\\ \times\prod_{t,i,j}\int d\omega_{ij}\rho_{ij}(\omega_{ij})\prod_{t,i}\int d\phi_i\rho_i(\phi_i)\exp\left[i\sum_{t,i}l_i(t)u_i(t)\right]\\ \times\exp\left[i\sum_{t,i}\{\tilde{h}_i(t)h_i(t)+\tilde{u}_i(t)[u_i(t+1)-\Theta(h_i(t)-V_i)]\}\right]\\ \times\exp\left[-i\sum_{t,i}\tilde{h}_i(t)\left[\sum_j\omega_{ij}(t)J_{ij}u_j(t)+\phi_i(t)\right]\right] .\end{aligned}\tag{3.17}$$

The connection weights now appear linearly in the exponential of the generating functional. This will enable quenched averages to be performed in Sec. IV.

Equation (3.17) can be used to construct a path-integral form for Eqs. (3.9). Firstly rewrite (3.17) as

$$Z[l]=\int D(u,\tilde{u},h,\tilde{h},\omega,\phi)e^{iS}\ , \tag{3.18}$$

with S considered as an action. Then, introducing the identities

$$1=\int D(\mathbf{m},\tilde{\mathbf{m}})\exp\left[iN\sum_{t,r}\tilde{m}_r(t)[m_r(t)-X_r(\mathbf{u}(t))]\right]\ , \tag{3.19}$$

where the X_r are macroscopic variables, as defined by Eqs. (3.4) and (3.5), we obtain

$$Z[l]=\int D(\mathbf{m},\tilde{\mathbf{m}})e^{i\tilde{S}[\mathbf{m},\tilde{\mathbf{m}}]} \tag{3.20}$$

Here, $\tilde{S}$ is the action

$$\begin{aligned}\tilde{S}=&N\sum_{t,r}\tilde{m}_r(t)m_r(t)\\&+\ln\left\{\int D(u,\tilde{u},h,\tilde{h},\omega,\phi)\right.\\&\left.\times\exp\left[i\left[S-N\sum_{t,r}\tilde{m}_r(t)X_r(\mathbf{u}(t))\right]\right]\right\}\ .\end{aligned} \tag{3.21}$$

We may now take the thermodynamic limit of Eq. (3.20). Then Eq. (3.9) is obtained by finding the path that minimizes the action (3.21). Explicit examples will be given in Secs. IV and V.

IV. NETWORKS WITH THRESHOLD NOISE: THE LITTLE MODEL

Consider the random iterative network defined by

$$a_i(t+1)=\Theta\left[\sum_j J_{ij}a_j(t)+\phi_i(t)-V_i\right]\ , \tag{4.1}$$

where J_{ij} is fixed and ϕ_i is a random variable with probability distribution

$$\rho_i(\phi_i)=\frac{\partial}{\partial\phi_i}(1+e^{-\beta\phi_i})^{-1}=\frac{\beta e^{-\beta\phi_i}}{(1+e^{-\beta\phi_i})^2}\ . \tag{4.2}$$

Here β^{-1} is a temperature parameter. The conditional firing probability of Eq. (2.17) is

$$\begin{aligned}p(i|\mathbf{a})=&\int_{-\infty}^{\infty}d\phi_i\left[\frac{\partial}{\partial\phi_i}(1+e^{-\beta\phi_i})^{-1}\right]\\&\times\Theta\Big(\sum_j J_{ij}a_j+\phi_i-V_i\Big)\ .\end{aligned} \tag{4.3}$$

Integrating by parts and using the identity $\partial\theta(x)/\partial x=\delta(x)$,

$$p(i|\mathbf{a})=(1+e^{-\beta(\sum_j J_{ij}a_j-V_i)})^{-1}\ . \tag{4.4}$$

This is precisely the updating rule for the Little model.[2] Hence the Little model is a specific example of a random iterative network with threshold noise.

Equation (4.4) may be substituted into Eq. (2.16) and the dynamics described in terms of the Markov chain (2.13). Solutions for the limiting distribution $P^\infty(\mathbf{a})$ may then be discussed along the lines of Clark.[33] In particular, for symmetric connections, $J_{ij}=J_{ji}$, the matrix Q satisfies condition (2.22) so that $P^\infty(\mathbf{a})$ is a Gibb's distribution. This allows spin-glass techniques to be used to study the long-time dynamics of the network for $N\to\infty$.[3,4] More recently, statistical-dynamical formulations of the Little model have been developed in which asymmetric weights are incorporated using randomly diluted networks.[6–9] We shall consider an alternative approach to such networks using the statistical dynamics of random iterative networks developed in Sec. III.

We begin by showing that the variables

$$X_i=\sum_j J_{ij}a_j \tag{4.5}$$

form a closed (infinite) set of macroscopic variables. We shall take the limit $N\to\infty$ following Eq. (3.2) with $\rho_{ij}(\omega_{ij})=\delta(\omega_{ij}-1)$ and $J_{ij}=\tilde{J}_{ij}/N$, $\tilde{J}_{ij}$ independent of N. Using Eq. (3.6)

$$\langle X_i(f_\alpha(\mathbf{a}))\rangle_\rho=\frac{1}{N}\sum_j\tilde{J}_{ij}p(j|\mathbf{a})\ . \tag{4.6}$$

For the Little model $p(j|\mathbf{a})>0$ and hence Eq. (4.6) is well-defined and nonzero in the limit $N\to\infty$. Combining (4.4), (4.5), and (4.6) we obtain

$$\langle X_i(f_\alpha(\mathbf{a}))\rangle_\rho=\frac{1}{N}\sum_j\tilde{J}_{ij}(1+e^{-\beta[X_j(\mathbf{a})-V_j]})^{-1}\ . \tag{4.7}$$

Hence condition (3.4) is satisfied. Moreover,

$$\mathrm{var}_\rho[X_i(f_\alpha(\mathbf{a}))]=\frac{1}{N^2}\sum_j\tilde{J}_{ij}^{\,2}\mathrm{var}_\rho[f_{\alpha_j}(\mathbf{a})]\ . \tag{4.8}$$

We have used the fact that each ϕ_i is independently distributed. Since $\mathrm{var}_\rho[f_{\alpha_j}(\mathbf{a})]$ is finite for each j, condition (3.5) is also satisfied and the X_i form a complete set of macroscopic variables. Thus we have the set of deterministic equations, for large N,

$$X_i(t+1)=\frac{1}{N}\sum_j\tilde{J}_{ij}(1+e^{-\beta[X_j(t)-V_j]})^{-1} \tag{4.9}$$

Note that the N original stochastic equations have been replaced by N deterministic equations (4.9). However, this still leaves a large (infinite) number of equations to solve. To make further progress, it is necessary to put restrictions on the weights J_{ij} so that the macroscopic dynamics may be described by a finite number of variables. In other words, a learning rule should be specified. For comparison with spin-glass techniques, we shall consider a Hopfield[1] form for the J_{ij} corresponding to the storage of R biased patterns,[11]

$$J_{ij}=\frac{1}{N}\sum_{\mu=1}^{R}(\eta_i^\mu-p)(\eta_j^\mu-p)\ , \tag{4.10}$$

where η_i^μ denotes the value of the ith neuron in the μth nominated pattern. The bias of the patterns is p such that the quenched random variables η are generated from the distribution

$$\rho(\eta)=p\delta(\eta-1)+(1-p)\delta(\eta) \, . \tag{4.11}$$

We may then define a finite set of macroscopic variables (for finite R) given by

$$M^{\mu}=\frac{1}{N}\sum_{i=1}^{N}(\eta_i^{\mu}-p)a_i \, , \tag{4.12}$$

$$M=\frac{1}{N}\sum_{i=1}^{N}a_i \, . \tag{4.13}$$

The corresponding macroscopic dynamical equations are

$$M^{\mu}(t+1)=\frac{1}{N}\sum_{i}(\eta_i^{\mu}-p)K\left[\sum_{\nu}(\eta_i^{\nu}-p)M^{\nu}(t)-V_i\right] , \tag{4.14}$$

$$M(t+1)=\frac{1}{N}\sum_{i}K\left[\sum_{\nu}(\eta_i^{\nu}-p)M^{\nu}(t)-V_i\right] , \tag{4.15}$$

with $K(x)=(1+e^{-\beta x})^{-1}$. The analysis so far is limited as it may only be applied to the storage of a finite number of patterns. Letting $R\rightarrow\infty$ still gives an infinite number of equations to solve. We wish to consider cases in which a finite number of patterns are marked for condensation with the remaining infinite number acting as background noise.[3] To achieve this we may use the path-integral techniques of Sec. V. For the Little model, Eq. (3.17) becomes

$$\begin{aligned} Z[l]=\prod_{t}\int d\mathbf{u}(t)d\tilde{\mathbf{u}}(t)d\mathbf{h}(t)d\tilde{\mathbf{h}}(t)\prod_{t,i}\int d\phi_i\rho_i(\phi_i)\exp\left[i\sum_{t,i}l_i(t)u_i(t)\right] \\ \times\exp\left[i\sum_{t,i}\{\tilde{h}_i(t)h_i(t)+\tilde{u}_i(t)[u_i(t+1)-\Theta(h_i(t)-V_i)]\}\right] \\ \times\exp\left[-i\sum_{t,i}\tilde{h}_i(t)\left[\sum_{j\neq i}J_{ij}u_j(t)+\phi_i(t)\right]\right] , \end{aligned} \tag{4.16}$$

where $\rho_i(\phi_t)$ satisfies Eq. (4.2). The connection weights appear linearly in (4.16). Therefore, since $Z[0]=1$, we may perform quenched averages over the weights to take into account an infinite number of patterns. To illustrate this we shall consider a randomly diluted network.[6,7] Take the modified connection rule[13,14]

$$J_{ij}=\frac{C_{ij}}{C}\sum_{\mu=1}^{R}(\eta_i^{\mu}-p)(\eta_j^{\mu}-p)\equiv C_{ij}\tilde{J}_{ij} \, , \tag{4.17}$$

where C_{ij} is a quenched random variable given by the distribution

$$\rho(C_{ij})=\frac{C}{N}\delta(C_{ij}-1)+\left[1-\frac{C}{N}\right]\delta(C_{ij}) \, . \tag{4.18}$$

Assume that $C/N\rightarrow 0$ as $N\rightarrow\infty$. Then

$$\langle Z[l]\rangle_{C_{ij}}=\prod_{t}\int d\mathbf{u}(t)d\tilde{\mathbf{u}}(t)d\mathbf{h}(t)d\tilde{\mathbf{h}}(t)\prod_{t,i}\int d\phi_i(t)\rho_i(\phi_i)e^{iS_0}\prod_{ij}\left[1-\frac{C}{N}+\frac{C}{N}e^{-i\sum_t\tilde{J}_{ij}\tilde{h}_i(t)u_j(t)}\right] \tag{4.19}$$

where

$$S_0=\sum_{t,i}\{h_i(t)\tilde{h}_i(t)+\tilde{u}_i(t)[u_i(t+1)-\Theta(h_i(t)-V_i)]+l_i(t)u_i(t)-\tilde{h}_i(t)\phi_i(t)\} \, . \tag{4.20}$$

We may now proceed in exact analogy to Refs. 7 and 13 to obtain

$$\langle Z[l]\rangle_{C_{ij}}=\prod_{t}\int d\mathbf{u}(t)d\tilde{\mathbf{u}}(t)d\mathbf{h}(t)d\tilde{\mathbf{h}}(t)\prod_{t,i}\int d\phi_i(t)\rho_i(\phi_i)e^{i\hat{S}} \, , \tag{4.21}$$

with $\hat{S}=S_0+\bar{S}$, where

$$\bar{S}=-\sum_{i,t}\sum_{\mu=1}^{S}M^{\mu}(t)(\eta_i^{\mu}-p)\tilde{h}_i(t)+\frac{i}{2}\sum_{i,t,t'}\alpha\tilde{p}^{\,2}\tilde{h}_i(t)C(t-t')\tilde{h}_i(t') \, , \tag{4.22}$$

and $\alpha=R/C$ and $\tilde{p}=p(1-p)$. The quantities $M^{\mu}(t)$ and $C(t-t')$ have to be calculated self-consistently:

$$M^{\mu}(t)=\frac{1}{N}\sum_{i=1}^{N}(\eta_i^{\mu}-p)\langle u_i(t)\rangle_L \, , \tag{4.23}$$

$$C(t-t')=\frac{1}{N}\sum_{i=1}^{N}\langle u_i(t)u_i(t')\rangle_L \, . \tag{4.24}$$

The contributions of random overlaps with most patterns vanishes as R/N, whereas a finite number of marked patterns

$M^1, M^2, \ldots, M^S$ could be of order 1. The last term in (4.22) corresponds to an additional noise $\sqrt{\alpha}\tilde{p}y(t)$ which has a Gaussian distribution with zero mean and correlation function

$$\langle y(t)y(t')\rangle = C(t-t') . \tag{4.25}$$

Hence, Eq. (4.21) becomes

$$\langle Z[l]\rangle_{C_{ij}} = \prod_t \int d\mathbf{u}(t)d\tilde{\mathbf{u}}(t)d\mathbf{h}(t)d\tilde{\mathbf{h}}(t) \prod_{t,i} \int d\phi_i(t)\rho_i(\phi_i) \prod_{i,t,t'} \left[\int dy_i(t)dy_i(t')e^{(1/2)y_i(t)C(t-t')^{-1}y_i(t')}\right] e^{-L} \tag{4.26}$$

with

$$L = \sum_{t,i} \tilde{h}_i(t) \left[h_i(t) - \sum_{\mu=1}^{S} M^{\mu}(t)(\eta_i^{\mu}-p) - \sqrt{\alpha}\tilde{p}y_i(t) - \phi_i(t) \right] + \sum_{t,i} \tilde{u}_i(t)[u_i(t+1) - \Theta(h_i(t)-V_i)] + \sum_{t,i} l_i(t)u_i(t) . \tag{4.27}$$

We note that $\sqrt{\alpha}\tilde{p}y(t)$ acts as an additional contribution to the external random field. To evaluate (4.23) we perform the integration over the fields $u(t)$, $\tilde{u}(t)$, $h(t)$, and $\tilde{h}(t)$ first and then integrate over $\phi(t)$. This yields the result

$$M^{\mu}(t) = \frac{1}{N}\sum_i (\eta_i^{\mu}-p) \int \frac{dy}{\sqrt{2\pi}} e^{-y^2/2} K \left[\sum_{\nu=1}^{S} (\eta_i^{\nu}-p) M^{\nu}(t-1) + \sqrt{\alpha M(t-1)}\tilde{p}y - V_i \right] , \tag{4.28}$$

$$M(t) = \frac{1}{N}\sum_i \int \frac{dy}{\sqrt{2\pi}} e^{-y^2/2} K \left[\sum_{\nu=1}^{S} (\eta_i^{\nu}-p) M^{\nu}(t-1) + \sqrt{\alpha M(t-1)}\tilde{p}y - V_i \right] , \tag{4.29}$$

which are the mean-field equations previously found in Refs. 13 and 14. Similarly for the correlation $C(t-t')$.

We have shown that the spin-glass-type models of Little-Hopfield are equivalent to random iterative networks with a non-Gaussian threshold noise and quenched connection weights. In fact, we could have taken any distribution $\rho_i(\phi_i)$ for the thresholds and applied the same techniques. However, it is not clear that threshold noise, whatever its distribution, is an important feature of most biological neurons. Alternative sources of noise are considered in Sec. V.

V. NETWORKS WITH SYNAPTIC NOISE

The Little model discussed in Sec. IV introduces noise into a network via a random modulation of the threshold V_i. Thus, it is only concerned with noise at the axon hillock of a neuron. It does not take into account other more biologically significant sources of noise arising from the quantal release of chemical transmitters into the synapses.[20-22] Such transmitter release provides a mechanism for converting incoming axonal signals into changes in membrane potential of a postsynaptic neuron. We shall model such synaptic processes as follows.

(a) There are N binary neurons with activities $a_i = 0,1$.

(b) Time is discretized in terms of the smallest unit of time τ, related to the refractory periods, synaptic time delays, etc., of the neurons. (For simplicity set $\tau = 1$).

(c) The arrival of a nerve impluse from the jth neuron causes the release of $n_{ij}^{(d)}$ packets of transmitter substance into synapse (ij).

(d) In the absence of an incoming signal there is the spontaneous release of $n_{ij}^{(s)}$ packets of transmitter substance into synapse (ij).

(e) The packet size is q_0, which may vary from synapse to synapse. We shall take q_0 to be a positive constant.

(f) The contribution to the postsynaptic membrane potential at time $t+1$ is

$$V_i(t+1) = \sum_j \epsilon_{ij}[q_0 n_{ij}^{(d)} a_j(t) + q_0 n_{ij}^{(s)} \hat{a}_j(t)] , \tag{5.1}$$

where ϵ_{ij} is a postsynaptic efficacy and $\hat{a}_j = 1 - a_j$. Here $|\epsilon_{ij}| \leq 1$ with negative ϵ_{ij} corresponding to inhibition.

(g) If the postsynaptic potential exceeds the threshold V_i, the neuron fires. Thus

$$a_i(t+1) = \Theta\left[\sum_j \epsilon_{ij}[q_0 n_{ij}^{(d)} a_j(t) + q_0 n_{ij}^{(s)} \hat{a}_j(t)] - V_i \right] . \tag{5.2}$$

(h) The $n_{ij}^{(d)}$ and $n_{ij}^{(s)}$ are independent random variables selected at each time step from the distributions $\rho_{ij}^{(d)}$ and $\rho_{ij}^{(s)}$.

Comparing Eqs. (5.2) and (2.1) we see that the above models of synaptic noise are random iterative networks with

$$\omega_{ij}(t) = q_0 n_{ij}^{(d)}(t) - q_0 n_{ij}^{(s)}(t), \quad J_{ij} = \epsilon_{ij} \tag{5.3}$$

$$\phi_i(t) = q_0 n_{ij}^{(s)}(t)\epsilon_{ij} . \tag{5.4}$$

The distributions $\rho_{ij}^{(d)}$ and $\rho_{ij}^{(s)}$ are taken to be of the same form, but with $\bar{n}_{ij}^{(s)} \ll \bar{n}_{ij}^{(d)}$. For simplicity, we shall drop the spontaneous activity in the following discussion. If n_{ij} is generated by a Poisson distribution

$$\rho_{ij}(n_{ij}) = \frac{\mu_{ij}^{n_{ij}}}{n_{ij}!} e^{-\mu_{ij}} , \tag{5.5}$$

with $\mu_{ij} = \bar{n}_{ij}$, we obtain the Taylor model.[24,25] A more biologically realistic distribution is a binomial of size M, where M is the maximum possible number of vesicles released. For lower animals and the peripheral nervous system $M \approx 10^3 - 10^4$ and $M \approx 1-10$ for the central nervous system. The case $M = 1$ is the one-vesicle model

$$\rho_{ij}(n_{ij}) = \mu_{ij}\delta(n_{ij}-1) + (1-\mu_{ij})\delta(n_{ij}) , \tag{5.6}$$

which is an annealed version of random dilution [cf. Eq. (4.18)].

To derive mean-field equations for networks with synaptic noise, it is first necessary to specify the limit $N\to\infty$ according to either Eq. (3.1) or (3.2). If we take

$$\bar{n}_{ij}=O(1),\quad \epsilon_{ij}=\frac{\tilde{\epsilon}_{ij}}{N},\quad \tilde{\epsilon}_{ij}\ \text{independent of}\ N \tag{5.7}$$

then the central limit theorem applies to each of the random variables $\sum\tilde{\epsilon}_{ij}n_{ij}a_j$, allowing their replacement by their mean value, the white-noise term vanishing as $N^{-1/2}$. Equation (5.2) reduces to the deterministic Caianello equations

$$a_i(t+1)=\lim_{N\to\infty}\Theta\left[\frac{1}{N}\sum_j q_0\tilde{\epsilon}_{ij}\bar{n}_{ij}a_j(t)-V_i\right]. \tag{5.8}$$

Thus the synaptic noise is eliminated in the large-N limit defined by Eq. (5.7). To apply the central limit theorem we have assumed that $\tilde{\epsilon}_{ij}$ is $O(1)$. If we take ϵ_{ij} to satisfy the Hopfield learning rule, Eq. (4.10), then this assumption corresponds to taking the number of patterns R to be finite. We may consider the storage of an infinite number of patterns by using the functional techniques of Sec. III. The resulting mean-field equations are those of nondiluted spin-glass models at zero thermodynamic temperature.[3] Thus the synaptic noise is still eliminated, the remaining Gaussian noise being due to the crosstalk of unmarked patterns.

Alternatively, consider

$$\bar{n}_{ij}=O(1/N),\quad \epsilon_{ij}=O(1)\,. \tag{5.9}$$

In the following we shall only consider distributions $\rho_{ij}(n_{ij})$ for which, to leading order in N, the higher moments are of comparable size to the mean $\bar{n}_{ij}$ in Eq. (5.9). Hence, $\sigma^2_{n_{ij}}=O(1/N)$, etc. Such distributions include the Poisson and binomial distributions. Then the Mth moment of the random field $q_0\sum_j\epsilon_{ij}n_{ij}a_j$ is $O(q_0^M)$. Note that q_0 is the size of postsynaptic potential due to the release of a single packet of transmitter substance and is much smaller than the thresholds V_i. Taking units defined by $V=1$, where V is a typical neuronal threshold such that, for all i, $V_i\approx V$, then q_0 is a dimensionless parameter with $q_0\ll 1$. Introduce the partition function

$$\begin{aligned}Z[l]=\int D(\mathbf{u},\tilde{\mathbf{u}},\mathbf{h},\tilde{\mathbf{h}})\sum_{\{n_{ij}(t)\}}\prod_{t,i,j}[\rho_{ij}(n_{ij}(t))]\exp\Big[i\sum_{t,i}l_i(t)u_i(t)\Big]\\ \times\exp\left[i\sum_{t,i}\{\tilde{h}_i(t)h_i(t)+\tilde{u}_i(t)[u_i(t+1)-\Theta(h_i(t)-V_i)]\}\right]\\ \times\exp\left[-iq_0\sum_{t,i,j}\tilde{h}_i(t)n_{ij}(t)\epsilon_{ij}u_j(t)\right]\end{aligned} \tag{5.10}$$

along similar lines to Eq. (3.17). In general, the summation over the random variables n_{ij} leads to terms in the action of Eq. (5.10) which are highly nonlinear. To make further progress we shall use a Gaussian approximation by expanding in the small parameter q_0. Note that we are effectively expanding in the dimensionless parameter q_0/V. Performing the Gaussian expansion, Eq. (5.10) reduces to

$$\begin{aligned}Z[l]=\int D(\mathbf{u},\tilde{\mathbf{u}},\mathbf{h},\tilde{\mathbf{h}})\exp\left[i\sum_{t,i}l_i(t)u_i(t)\right]\exp\left[i\sum_{t,i}\{\tilde{h}_i(t)h_i(t)+\tilde{u}_i(t)[u_i(t+1)-\Theta(h_i(t)-V_i)]\}\right]\\ \times\exp\left[-iq_0\sum_{t,i,j}\tilde{h}_i(t)\bar{n}_{ij}\epsilon_{ij}u_j(t)\right]\exp\left[-\frac{1}{2}q_0^2\sum_{i,j,t}\tilde{h}_i^2(t)\sigma^2_{n_{ij}}\epsilon^2_{ij}u_j(t)\right]\end{aligned} \tag{5.11}$$

To obtain (5.11) we have used the approximation that at each time step

$$\begin{aligned}\left\langle\exp\left[iq_0\tilde{h}_i\sum_j n_{ij}\epsilon_{ij}a_j\right]\right\rangle_\rho&=\exp\left[iq_0\tilde{h}_i\sum_j\bar{n}_{ij}\epsilon_{ij}a_j\right]\left\langle\exp\left[iq_0\tilde{h}_i\sum_j(n_{ij}-\bar{n}_{ij})\epsilon_{ij}a_j\right]\right\rangle_\rho\\ &\approx\exp\left[iq_0\tilde{h}_i\sum_j\bar{n}_{ij}\epsilon_{ij}a_j\right]\exp\left[-\frac{1}{2}q_0^2\tilde{h}_i^2\sum_j\sigma^2_{n_{ij}}\epsilon^2_{ij}a_j\right].\end{aligned} \tag{5.12}$$

The conditional firing probability of equation (2.17) becomes

$$\begin{aligned}p(i\,|\,\mathbf{a})&=\langle u_i(t)\delta(\mathbf{u}(t-1)-\mathbf{a})\rangle\\ &=\frac{1}{2}\left[1+\operatorname{erf}\left[\frac{q_0\sum_j\bar{n}_{ij}\epsilon_{ij}a_j-V_i}{\left[q_0^2\sum_j\sigma^2_{n_{ij}}\epsilon^2_{ij}a_j\right]^{1/2}}\right]\right].\end{aligned} \tag{5.13}$$

The average in Eq. (5.13) is with respect to the partition function of Eq. (5.11). A similar equation was derived by Shaw and Vesudevan,[23] but in a more specific context. Note that the Gaussian approximation corresponds to dropping the higher moments of the random field $q_0\sum n_{ij}\epsilon_{ij}a_j$, which is valid for small q_0, since these moments are $O(q_0^3)$. [See discussion below Eq. (5.9).] Using Eq. (5.13) it may be shown that, analogous to Eq. (4.5), the variables

$$X_i=\sum_j q_0\epsilon_{ij}\bar{n}_{ij}a_j,\quad Y_i=\sum_j q_0\epsilon_{ij}^2\sigma_{n_{ij}}^2 a_j \tag{5.14}$$

form a closed set of macroscopic variables as defined by Eqs. (3.4) and (3.5). The corresponding macroscopic dynamical equations are

$$X_i(t+1)=\frac{1}{2}\sum_j q_0\bar{n}_{ij}\epsilon_{ij}\left[1+\mathrm{erf}\left[\frac{X_j(t)-V_j}{\sqrt{q_0Y_j(t)}}\right]\right], \tag{5.15}$$

$$Y_i(t+1)=\frac{1}{2}\sum_j q_0\sigma_{n_{ij}}^2\epsilon_{ij}^2\left[1+\mathrm{erf}\left[\frac{X_j(t)-V_j}{\sqrt{q_0Y_j(t)}}\right]\right]. \tag{5.16}$$

As with the Little model, Eq. (4.9), to make further progress it is necessary to specify a learning rule for the connection weights. However, now both their mean and variance must be determined. Suppose, for simplicity, that

$$q_0n_{ij}=q_0\sigma_{n_{ij}}^2=\frac{A}{N},\quad A=O(1)\ . \tag{5.17}$$

Note that taking the mean and variance in Eq. (5.16) to be equal is valid for the Poisson distribution and, when N is large, for the binomial distribution. Furthermore, impose the Hopfield-type learning rule similar to Eq. (4.10)

$$\epsilon_{ij}=\frac{1}{A}\sum_{\mu=1}^{R}(\eta_i^\mu-p)(\eta_j^\mu-p) \tag{5.18}$$

with the quenched variables η generated from Eq. (4.11). When A is large, we may replace ϵ_{ij}^2 by $\alpha\bar{p}^{\,2}/N$, where α and $\bar{p}$ are defined below Eq. (4.22). Then, in terms of the macroscopic variables M^μ and M of Eqs. (4.12) and (4.13), Eqs. (5.15) and (5.16) reduce to the mean-field equations of a randomly diluted Little network in the zero temperature limit $\beta\to\infty$ [cf. Eqs. (4.28) and (4.29)],

$$M^\mu(t+1)=\frac{1}{2}\sum_i(\eta_i^\mu-p)\left[1+\mathrm{erf}\left[\frac{\sum_{\nu=1}^{S}M^\nu(t)(\eta_i^\nu-p)-V_i}{[q_0\alpha\bar{p}^{\,2}M(t)]^{1/2}}\right]\right], \tag{5.19}$$

$$M(t+1)=\frac{1}{2}\sum_i\left[1+\mathrm{erf}\left[\frac{\sum_{\nu=1}^{S}M^\nu(t)(\eta_i^\nu-p)-V_i}{[q_0\alpha\bar{p}^{\,2}M(t)]^{1/2}}\right]\right] \tag{5.20}$$

As in the treatment of randomly diluted networks, Sec. IV, we are marking $\mu=1,\dots,S$ patterns for condensation.

We conclude that the thermodynamic limit defined by Eq. (5.9) leads to mean-field equations similar in form to spin-glass models with quenched random dilution at zero temperature. Synaptic noise may then lead to the enhancement of pattern retrieval by removal of spurious states, since the term $\sqrt{q_0Y_i(t)}$ acts as an effective temperature. Such a temperature is both space and time dependent. Shaw and Vesudevan[23] suggested taking some space-time average of this temperature, so that Eq. (5.13) becomes

$$\begin{aligned}p(i\,|\,\mathbf{a})&=\frac{1}{2}\left[1+\mathrm{erf}\left[\beta q_0\sum_j\bar{n}_{ij}\epsilon_{ij}a_j-\beta V_i\right]\right]\\ &\approx\left[1+\exp\left[-\beta q_0\sum_j\bar{n}_{ij}\epsilon_{ij}a_j+\beta V_i\right]\right]^{-1},\end{aligned} \tag{5.21}$$

which is the updating rule for the Little model. Shaw and Vesudevan concluded that the Little model may be derived in terms of synaptic noise. However, we have found that the statistical dynamics of networks with synaptic noise depend crucially on how the thermodynamic limit is taken. If the limit is defined using Eq. (5.7), then the synaptic noise is eliminated and Eqs. (5.13) and (5.21) are no longer valid.

Moreover, it is possible to obtain a different class of mean-field equations by taking pattern storage on the means $\bar{q}_{ij}=q_0\bar{n}_{ij}$. For example, consider the Hebbian learning rule

$$\bar{q}_{ij}=\frac{1}{N}\sum_{\mu=1}^{R}\eta_i^\mu\eta_j^\mu,\quad \epsilon_{ij}=1 \tag{5.22}$$

where the η are restricted to be 0 or 1, since $\bar{q}_{ij}\geq 0$. For the Taylor and binomial models, Eq. (5.22) leads to the mean-field equations

$$\begin{aligned}M^\mu(t+1)=\sum_i\eta_i^\mu\sum_{n\geq 0}\frac{1}{n!}[\boldsymbol{\eta}_i\cdot\mathbf{M}(t)/q_0]^n e^{-\boldsymbol{\eta}_i\cdot\mathbf{M}(t)/q_0}\\ \times\Theta(nq_0-V_i)\ ,\end{aligned} \tag{5.23}$$

where M^μ is the overlap with the μth pattern. The derivation of Eq. (5.23) does not require any Gaussian approximation but it is necessary to assume that ϵ_{ij} is synapse independent. Taking ϵ_{ij} to be unity corresponds to a purely excitatory network. This is consistent with Dale's principle[18] which requires that, for a given neuron, efferents are either all excitatory or all inhibitory. In other words, for a given j, $\epsilon_{ij}>0$ for *all i* or $\epsilon_{ij}<0$ for *all i*. Note that the learning rules of Eqs. (4.10) and (5.18) violate Dale's principle since ϵ_{ij} has an equal probability of being positive or negative. One of the consequences of taking a purely excitatory network is that the simple Hebbian rule, Eq. (5.22), leads to mean-field equations (5.23) which do not have Mattis-type solutions and retrieval of memories is not possible. However, it has recently been shown by Amit, Wong, and Campbell[38] that it is possible to define a learning rule which allows pattern storage in a purely excitatory network. They extend this to networks with a mixture of excitatory and inhibitory neurons satisfying Dale's law. Such networks may be incorporated into the framework of random iterative networks. Denote the activities of the excitatory and inhibitory neurons, respectively, by a_i, $i=1,\ldots,N_E$, and b_i, $i=1,\ldots,N_I$. Then Eq. (2.1) becomes

$$a_i(t+1)=\Theta\left[\sum_j J_{ij}^{aa}\omega_{ij}^{aa}(t)a_j(t)+\sum_j J_{ij}^{ab}\omega_{ij}^{ab}(t)b_j(t)+\phi_i-V_i\right], \tag{5.24}$$

$$b_i(t+1)=\Theta\left[\sum_j J_{ij}^{ba}\omega_{ij}^{ba}(t)a_j(t)+\sum_j J_{ij}^{bb}\omega_{ij}^{bb}(t)b_j(t)+\phi_i-V_i\right]. \tag{5.25}$$

We could now proceed as in Secs. II and III. For example, the transition matrix of Eq. (2.16) becomes

$$Q_{\mathbf{b}'\mathbf{a}',\mathbf{ba}}=\prod_{i=1}^{N_E}[p_a(i|\mathbf{a},\mathbf{b})]^{a_i'}[\hat{p}_a(i|\mathbf{a},\mathbf{b})]^{\hat{a}_i'}\times\prod_{i=1}^{N_I}[p_b(i|\mathbf{a},\mathbf{b})]^{b_i'}[\hat{p}_b(i|\mathbf{a},\mathbf{b})]^{\hat{b}_i'}, \tag{5.26}$$

where p_a and p_b are, respectively the conditional firing probabilities of the excitatory and inhibitory neurons. Note that the dynamical equations of the inhibitory neurons may, in principle, be solved in terms of the excitatory neurons provided $J_{ij}^{bb}=0$. Thus it may be possible to store patterns on $q_0\bar{n}_{ij}$ by introducing inhibition via Eqs. (5.24) and (5.25) or by considering alternative learning rules to (5.22). This will be considered elsewhere.

VI. DISCUSSION

In summary, a general framework has been presented in Sec. II which allows the incorporation of various stochastic effects, such as synaptic quantal transmission, both stimulated and spontaneous, and threshold variability. This structure is that of random iterative networks, which has been used to analyze the dynamical evolution of network activity at the microscopic (single neuron) and macroscopic levels. In particular, a path-integral formulation of a generating functional was constructed in Sec. III to allow full expression of the dynamics. These techniques were applied in the Secs. IV and V to the Little model (threshold noise) and to networks with synaptic noise, to deduce mean-field equations. A new derivation was given in the former case of the known mean-field equations for a randomly diluted network with biased patterns.

The conclusions of the analysis are presented here.

(1) The general framework of random iterative networks is a natural dynamical approach to the study of known sources of neuronal stochasticity. The dynamics of such networks may be formulated in terms of generating functionals.

(2) Noise enters neuronal activity in at least two different manners, viz., due to synaptic transmission variability and from threshold fluctuations. However, biological measurements indicate at most a few percent fluctuation of the threshold in central nervous system neurons, so that a temperature of <0.1 is to be expected.[39] This seems to be below the cutoff value of 0.46 for which Mattis states can be retrieved without the problem of spurious states.[3] However, threshold noise may be important for neurons operating near zero threshold, such as the CA2 region of the hippocampus. Under certain circumstances, the retrieval of stored pattern may be aided by synaptic noise. This follows from the mean field equations of Sec. V, which were similar in form to either diluted or nondiluted spin-glass models at zero temperature. In the former case synaptic noise has an effective thermodynamic temperature which is space-time dependent and which may eliminate spurious states. The size of this temperature depends on parameters such as the size of packets of chemical transmitter and the variance of the number of packets released.

(3) A new class of mean-field equations are possible for networks with synaptic noise by taking pattern storage on the mean number of transmitter packets released. This requires alternatives to the simple Hebbian rule and leads naturally to a more realistic incorporation of inhibition which obeys Dale's law.

Extensions of the above analysis are possible along the following lines.

(a) Analysis of the approach to asymptotic dynamics by means of Liapunov exponents, etc., as discussed by Kifer.[29] There is a natural metric (Hamming distance) on the state space, so such techniques may be applicable.

(b) Analysis of alternative learning rules such as the Hebbian learning rule of Willshaw, Buneman, and Longuet-Higgins.[17] Moreover, short-term synaptic effects are known[20] to occur which are purely postsynaptic, and hence non-Hebbian. These also need to be investigated.

(c) Evaluation of Hebbian and non-Hebbian storage without going to the large-N limit, by taking a reducible Markov chain, Eq. (2.13). Such reducibility occurs in the training of probabilistic logical nodes (PLN's)[40] and probabilistic random access memories[41] (PRAM's) to obtain asymptotic states depending on the initial probability distribution. It may be possible that nonergodicity also arises by inclusion of refractory periods and extended summation, although it is not yet possible to analyze this in detail.[42]

(d) Extensions to analog networks. The introduction of noise using random maps may be applied to any neural network, analog or digital, whose operation is described by relaxation dynamics. Stochastic dynamical equations are obtained by taking the connection weights and thresholds to be random. The major difference for analog models is that state space is no longer discrete or finite.

More general questions also need to be answered. Many neurophysiologists have asked whether there is any value in neuronal noise. Conclusion (2) above indicates that synaptic noise may help the retrieval of stored patterns under certain circumstances. Independently of this, noise may have other uses, such as introducing "dither" to prevent phase locking. It may also be important to interfere with incipient chaotic activity arising from long summation periods.[43] More generally, are fixed points at all used by the brain in the storage of patterns? There is not, as yet, conclusive evidence that any parts of the brain act as content-addressable memories. An alternative picture may be developed which uses only feedforward nets which have local endogenous bursters to preserve learned activity or to phase-lock distant features of a common object.[44]

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