Dynamics of Self-Organized Delay Adaptation

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(Received 7 May 1997)

Adaptation of interaction delays is essential for the functioning of many natural and technical systems. We introduce a novel framework for studying the dynamics of delay adaptation in systems which optimize coincidence of inputs. For the important case of periodically modulated input we derive conditions for the existence and stability of solutions which constrain the set of mechanisms for reliable delay adaptation. Using numerical examples we show that our approach is applicable to more general than periodic input patterns such as Poissonian point processes with coordinated rate fluctuations. [S0031-9007(99)08395-7]

PACS numbers: 87.10.+e, 02.30.Ks, 87.18.Sn

Distributed systems occur ubiquitously in the physical, biological, and social sciences. A fundamental problem concerns how the flow of information from the distinct, independent components can best be regulated to optimize a prespecified performance of the network. For example, in parallel computing machines the asynchronous output of independent processors must be integrated to yield well-defined results [1]. In the brain, time delays arise because interneural distances and axonal conduction times are finite. In several sensory systems, delay lines are essential for coordinating activity, e.g., the auditory system of barn owls, echo location in bats, and the lateral line system of weakly electric fish [2].

Several models for supervised delay adaptation have been developed [3]. However, these are not always applicable since there is no global teacher signal in many systems. There is some evidence that unsupervised activity-dependent adaptation of delays occurs in the nervous system [4]. Here we introduce a novel framework to describe the dynamics of self-organized delay adaptation expressed in the form of integro-differential equations which permit the mechanisms of delay adaptation to be explored in a precise manner. We illustrate our results with a study of delay adaptation in a network of neurons.

Two mechanisms have been proposed for the self-organized adaptation of transmission delays in the nervous system. One mechanism ("delay shift") assumes that the transmission delays are altered [5,6]. This mechanism is possible because transmission velocities in the nervous system can be altered, for example, by changing the length and thickness of dendrites and axons, the extent of myelination of axons, or the density and type of ion channels. The second mechanism ("delay selection") supposes that a range of delay lines are present in the beginning from which, during development, appropriate subsets become selected [7].

Consider a neural network consisting of a large number of presynaptic neurons and one postsynaptic neuron which receives its input via delay lines (Fig. 1a). The kth action potential (spike) at the ith presynaptic neuron occurs at time $t_{i,k}$ ($i = 1, \dots, N$, $k \in \mathbf{Z}$), and after a delay τ_i, the excitatory postsynaptic potential E arrives at the postsynaptic neuron, where it contributes to the membrane potential U according to the synaptic efficacy ω_i. The input I to the postsynaptic neuron then reads $I(t) = \sum_{i,k} \omega_i \delta(t - (t_{i,k} + \tau_i)) \circ E(t)$, where $\circ$ denotes convolution and $\delta(\cdot)$ is the Dirac delta distribution. The postsynaptic neuron is a nonlinear threshold device such as a Hodgkin-Huxely neuron [8] or, more conveniently, an integrate-and-fire neuron [9,10]. At times t_s the postsynaptic neuron fires, depending on this input and its own previous activations.

We employ a local adaptation rule for neural interaction delays which was already proposed by Hebb [11] (p. 63). The Hebbian learning rule depends on correlations between presynaptic and postsynaptic activity within a certain time window. Assume that temporal

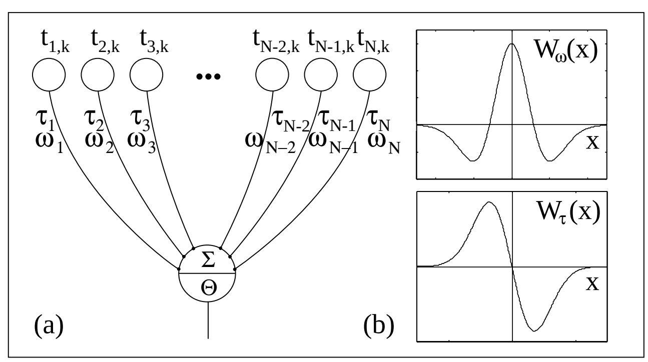

FIG. 1. (a) Overview of the neural network. (b) Schematic examples for the window functions W_ω and W_τ corresponding to weight adaptation (top) and delay adaptation (bottom), respectively. In the case of a finite rise time of the postsynaptic potential, E, both functions have to be slightly shifted to the left on the abscissa [7].

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patterns $\vec{\vartheta} = (\vartheta_1, \ldots, \vartheta_N)^T$ occur at times t_k such that at synapse i there is activation at times $t_{i,k} = t_k + \vartheta_i$. Hebbian adaptation usually corresponds to changes of $\vec{\omega} = (\omega_1, \ldots, \omega_N)^T$ according to the contributions of the corresponding synapses to the occurrence of a postsynaptic spike [7]. In our case, this means that synapses whose contributions arrive simultaneously with the postsynaptic spike become strengthened, while others do not change or even become weakened. The learning rule then reads $\Delta\omega_i \propto W_\omega(t_k + \vartheta_i + \tau_i - t_s)$ $(i = 1, \ldots, N)$, where $W_\omega(x)$ represents a learning window that is maximal just before the time of spiking (Fig. 1b, with a slight shift of W_ω to the left). Intuitively, this rule leads to a selection of delay lines for which the effects align at the soma [7]. A similar Hebbian scheme can be used for delay shift, $\Delta\tau_i \propto W_\tau(t_k + \vartheta_i + \tau_i - t_s)$, where W_τ denotes a learning window for delay adaptation [6]. $W_\tau(x)$ should be positive when the presynaptic contribution precedes the postsynaptic spike, and negative in the other case (Fig. 1b, with a slight shift of W_τ to the left). This rule will adjust the delays such that their effects will align in time at the soma [6].

A common framework of investigating the dynamics introduced by the above learning rules can be obtained by considering a continuous set of input connections described by two functions, $\rho(\tau, t)$ and $\omega(\tau, t)$, for the delays and weights, respectively. $\rho(\tau, t)\, d\tau$ gives the fraction of connections with delays in $[\tau; \tau + d\tau]$, and $\omega(\tau, t)$ is the average weight of connections with delay τ. Assume that ρ and ω change on a slow time scale t such that their temporal development is determined by an average over an ensemble of presynaptic input patterns; the faster time scale of neuronal dynamics is described by the variable τ. This assumption is equivalent to assuming that delays in the nervous system adapt on a developmental time scale, though we do not exclude the possibility of post-ontogenetic changes. Without loss of generality, the input patterns consist of synchronous firing of a portion of the presynaptic neurons such that the activation time offsets of the corresponding synapses vanish ($\vec{\vartheta} \equiv \vec{0}$). Note, however, that other choices are equally possible and mathematically equivalent by transforming τ_i into an effective synaptic delay $\tilde{\tau}_i := \tau_i + \vartheta_i$.

In this continuous description, the input density $J(\tau, t)$ provided by the synapses at time τ after presentation of a pattern has the particularly simple form

$$J(\tau, t) = \omega(\tau, t)\rho(\tau, t) \tag{1}$$

[12]. The general case with explicit postsynaptic potentials will be discussed elsewhere [13].

The input density, $J(\tau, t)$, as a function of τ results in a distribution of spike times of the postsynaptic neuron, $P(\tau, t) \propto \sum_m \delta(\tau - \tau_m^*)$, where τ_m^* denotes the mth spike time. The firing of the postsynaptic neuron in turn acts on the weights $\omega(\tau, t)$ and the delays $\rho(\tau, t)$ via one of the learning rules described in the previous section. The dynamics of the input are governed by two simultaneous equations: a balance equation for the input density,

$$\frac{\partial}{\partial t} J(\tau, t) = -\frac{\partial}{\partial \tau}[J(\tau, t)v(\tau, t)] + Q(\tau, t), \tag{2}$$

and a continuity equation for $\rho(\tau, t)$, indicating the conservation of the number of neural connections,

$$\frac{\partial}{\partial t} \rho(\tau, t) = -\frac{\partial}{\partial \tau}[\rho(\tau, t)v(\tau, t)]. \tag{3}$$

The drift velocity, $v(\tau, t)$, and the source term, $Q(\tau, t)$, will be defined below according to Hebbian principles. While in general, ρ and ω will be modified simultaneously, we consider here the two limiting cases of delay shift and delay selection which serve to illucidate basic mechanisms.

Case 1: Delay shift.—In this case, the weights are not modified and the source term, $Q(\tau, t)$, on the right-hand side of (2) vanishes. The dynamics are governed by (3), where the drift velocity, $v = d\tau/dt$, of the delays realizes the Hebbian adaptation,

$$v(\tau, t) := \gamma_\tau \int_{-\infty}^{\infty} W_\tau(\tau - \tau')P(\tau', t)\, d\tau', \tag{4}$$

and γ_τ denotes the learning rate. For delays τ, where $\rho(\tau, 0) \neq 0$, we assume $\omega(\tau, 0) = 1$ without loss of generality, and (2) and (3) imply that $\omega(\tau, t) = 1$ for all t if $\rho(\tau, t) \neq 0$.

The distribution of spike times, $P(\tau, t)$, of a neuron depends on the input and its statistics. In general, the input patterns appear irregularly and are obscured by random nonsynchronous background activity. The spike generation of the neuron also depends on various parameters as its own firing history, the timing of inputs, and on the dynamics of the synapses. In the following, we consider the firing times of an integrate-and-fire neuron [10] which receives periodic input with period T, $t_k = kT$. In this case the adaptation dynamics can be evaluated by defining a periodic continuation of $\rho(\tau, t)$, $\rho(\tau, t) = \rho(\tau + T, t)$.

For the distribution of spike times we assume a linear neural response, $P(\tau, t) \cong \beta J(\tau, t)$. Whereas an integrate-and-fire neuron receiving periodic input can exhibit phase locking, aperiodic firing, or quenching when firing eventually stops [14], it has been shown that adding a small amount of noise to the input approximately linearizes the behavior [15]. Therefore, our approximation is valid if the input is sufficiently high and if there is some random background activity. Linear neural behavior may also occur even without background noise. A numerical example is shown in Fig. 2.

Equation (3) has two equilibrium solutions. The first is the homogeneous solution $\rho(\tau, t) \equiv \rho_0$ around which a linear stability analysis yields eigenvalues λ_n with $\mathrm{Re}(\lambda_n) = (2\pi)^{3/2}\beta\gamma_\tau\rho_0 n\, \mathrm{Im}[\tilde{W}_\tau(-2\pi n/T)]/T$, where

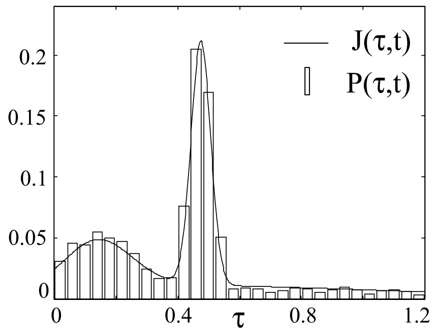

FIG. 2. Example of a firing distribution, $P(\tau, t)$ (histogram), of an integrate-and-fire neuron which is proportional to the input, $J(\tau, t)$ (solid line) for fixed t. In this case, the periodicity of the input implies that the addition of input noise is unnecessary. The histogram is rescaled by a constant factor to facilitate comparison. $\Theta = 1$, $T = 1.2$.

$\tilde{W}_\tau$ is the Fourier transform of the window function W_τ. For an antisymmetric window function such as the one in Fig. 1b at least one of the Re (λ_n) exceeds zero, and the solution is unstable. The second equilibrium solution is given by $\rho(\tau, t) = \delta(\tau - \tau_0)$ provided that $\sum_{n=-\infty}^{\infty} W_\tau(nt) = 0$ which is the case for antisymmetric window functions. The solutions form a one-dimensional manifold described by a parameter $\tau_0 \in [0; T]$ which is a delay offset common to all input neurons. The Liapunov functional $L[\rho] = \int \rho(\tau, t)(\tau - \int \rho(\tau', t)\tau' \, d\tau')^2 \, d\tau$ yields the result that the equilibrium solutions are marginally stable in the τ_0 direction and stable in the other directions provided that $W_\tau(x) > 0$ for $x < 0$ and $W_\tau(x) < 0$ for $x > 0$.

We illustrate our results for the special case where the window function is given by $W_\tau(x) = -x \exp(-x^2/c^2)/c$, where $c > 0$. In this case, the real parts of the eigenvalues are given by $\mathrm{Re}(\lambda_n) = 2\pi^{5/2}\beta\gamma_\tau\rho_0 n^2 c^2 \times \exp(-n^2\pi^2 c^2/T^2) > 0$. Figure 3 shows the dynamics of the change in the distribution of delays, $\rho(\tau, t)$, as the network evolves in time. Starting from an initial uniform distribution perturbed by random noise $\rho(\tau, 0)$ (Fig. 3a), the delay distribution $\rho(\tau, t)$ progressively contracts to a single delta peak (Fig. 3d), as expected from the analysis. During contraction, a bimodal distribution can transiently appear (Fig. 3c).

The above results also hold for the more general case of nonperiodic and unreliable input patterns which are superimposed on background activity. Consider, e.g., the situation where the presynaptic neurons fire according to a Poisson process with a constant background rate, r_b. At certain random times this rate is increased to value r_p for a short time period of length Δ which, e.g., happens in response to an external stimulus. Figure 4 illustrates that also under these conditions, the delay shift dynamics may yield narrow delay distributions.

Case 2: Delay selection.—For pure delay selection, the drift velocity of the delays, $v(\tau, t)$, vanishes and the

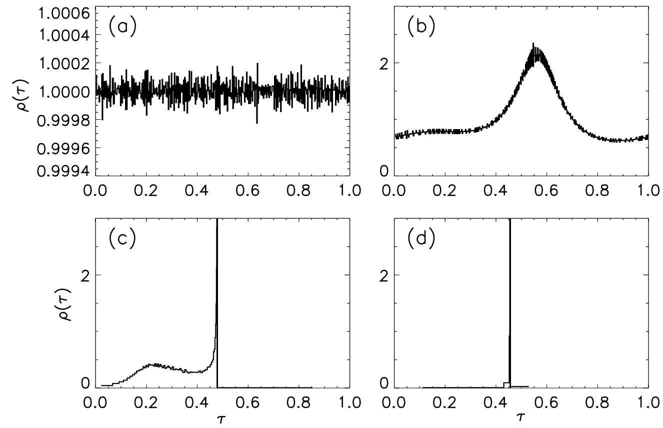

FIG. 3. Numerical iteration of (3) with W_τ as used in Fig. 1b. (a) Initial delay distribution $\rho(\tau, 0) = 1 + \xi(\tau)$, where $\xi(\tau)$ is Gaussian white noise. (b)–(d) $\rho(\tau, t)$ for $t = 12.0$, 18.0, and 20.0, respectively. Two peaks transiently emerge and then merge into a single delta peak which corresponds to the equilibrium solution of the distribution of delays. $T = 1.0$, $\beta\gamma_\tau = 0.1$, $c = 0.2$.

total input of the postsynaptic neuron is not conserved. Equations (2) and (3) result in

$$\rho(\tau, t) \frac{\partial \omega(\tau, t)}{\partial t} = Q(\tau, t) . \tag{5}$$

From a straightforward generalization of the Hebb rule, we obtain the source density

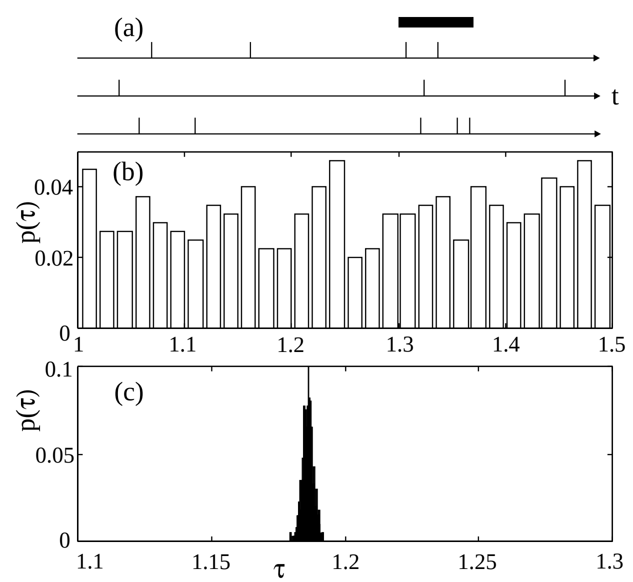

FIG. 4. Delay shift dynamics with Poissonian input. (a) Schematic drawing of the spiking behavior of three presynaptic neurons. Action potentials occur independently in all neurons according to a Poisson point process with rate r_b. During presentation of a stimulus (bar), this rate is increased to r_p. (b) Randomized delay distribution, $p(\tau)$, prior to learning and (c) after 1700 learning steps. $N = 400$, $\Theta = 1$, $\omega_0 = 0.005$, $\gamma_\tau = 0.001$, $r_b = 0.04$, $r_p = 12.0$, and $\Delta = 0.03$.

$$Q(\tau, t) = \gamma_\omega \omega(\tau, t)\rho(\tau, t) \int_{-\infty}^{\infty} W_\omega(\tau - \tau')P(\tau', t)\, d\tau', \quad (6)$$

with γ_ω denoting the corresponding learning rate. In analogy to the previous case, a periodic continuation of $\omega(\tau, t)$ is introduced: $\omega(\tau, t) = \omega(\tau + T, t)$, and without loss of generality we assume $\rho(\tau, 0) \equiv 1$, which implies $\rho(\tau, t) = 1$ for arbitrary t because $v(\tau, t) \equiv 0$.

Equation (5) has an equilibrium solution $\omega(\tau, t) = \omega_0$ provided that $\int_{-\infty}^{\infty} W_\omega(x)\, dx = 0$. The real parts of the eigenvalues are given by $\mathrm{Re}\,(\lambda_n) = \sqrt{2\pi}\,\beta \times \gamma_\omega \omega_0 \tilde{W}_\omega(-n\omega)$, where $\tilde{W}_\omega$ is the Fourier transform of the window function W_ω. For a symmetric window function such as the one shown in Fig. 1b, the homogeneous solution is unstable. In contrast to case 1, there is no stable solution: weight distributions $\omega(\tau, t) = A(t)\delta(\tau - \tau_0)$ retain their shape, but explode in size, i.e., $A(t)$ diverges in finite time. This situation commonly arises in networks with Hebbian learning of synaptic weights [7].

Self-organized delay adaptation in sensory neural systems requires that information carried along separate axons be regulated such that these signals arrive at a postsynaptic neuron simultaneously. Our analysis places constraints that ensure that stable solutions exist for arbitrary temporal inputs. A comparison of our results with recent experimental estimations of Hebbian learning windows [16] indicates that the interactions in cortex, in fact, self-organize the shortest possible set of delays which yield coincident input [13]. However, in other applications, such as those which arise in industry, traffic flow, and parallel computing, such a solution would clearly be disastrous. Here the goal is to have the separate inputs not arrive at the same time, but rather arrive in some staggered manner. We anticipate that it will be possible to incorporate these scenarios into our framework by an appropriate design of the window functions and the neural network architecture. By analogy with other parallel computing devices, the nervous system may also have, as yet undiscovered, mechanisms to regulate temporally staggered information flow based on delay adaptation.

We thank J. Bélair, T. Mundel, and R. Müller for useful discussions. This research was partially carried out while C. W. E. was at The University of Chicago. The research was supported by grants from BASF (C. W. E.), the Max-Planck Foundation (C. W. E., K. P.), the National Institutes of Mental Health (J. M.), the Brain Research Foundation (J. C., J. M.) and the McDonnell-Pew Foundation (J. C.).

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