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Dynamic Synapse: A New Concept of Neural Representation and Computation

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ABSTRACT: Presynaptic mechanisms influencing the probability of neurotransmitter release from an axon terminal, such as facilitation, augmentation, and presynaptic feedback inhibition, are fundamental features of biological neurons and are cardinal physiological properties of synaptic connections in the hippocampus. The consequence of these presynaptic mechanisms is that the probability of release becomes a function of the temporal pattern of action potential occurrence, and hence, the strength of a given synapse varies upon the arrival of each action potential invading the terminal region. From the perspective of neural information processing, the capability of dynamically tuning the synaptic strength as a function of the level of neuronal activation gives rise to a significant representational and processing power of temporal spike patterns at the synaptic level. Furthermore, there is an exponential growth in such computational power when the specific dynamics of presynaptic mechanisms varies quantitatively across axon terminals of a single neuron, a recently established characteristic of hippocampal synapses. During learning, alterations in the presynaptic mechanisms lead to different pattern transformation functions, whereas changes in the postsynaptic mechanisms determine how the synaptic signals are to be combined. We demonstrate the computational capability of dynamic synapses by performing speech recognition from unprocessed, noisy raw waveforms of words spoken by multiple speakers with a simple neural network consisting of a small number of neurons connected with synapses incorporating dynamically determined probability of release. The dynamics included in the model are consistent with available experimental data on hippocampal neurons in that parameter values were chosen so as to be consistent with time constants of facilitative and inhibitory processes governing the dynamics of hippocampal synaptic transmission studied using nonlinear systems analytic procedures.

KEY WORDS: synaptic dynamics; neural information processing

INTRODUCTION

Electrophysiological recordings in the behaving animal have demonstrated that the hippocampus represents and processes information by the spatio-temporal pattern of neuronal activation (O'Keefe, 1976; Berger et al., 1983; McNaughton et al., 1983; Eichenbaum et al., 1989; Deadwyler et al., 1996). This interpretation is supported by an abundance of additional experimental evidence indicating that hippocampal neurons comprise cellular mechanisms which are exquisitely sensitive to the spatial and temporal convergence of afferent input (Andersen and Lomo, 1967; McNaughton et al., 1978; Wigstrom and Gustafsson, 1983; Kelso and Brown, 1986; Larson and Lynch, 1986; Rose and Dunwiddie, 1986; Yeckel and Berger, 1990; Munoz et al., 1991; Dudek and Bear, 1992; Xie et al., 1992; Mott et al., 1993; Thiels et al., 1994, 1995). Sensitivity of hippocampal neurons to the spatio-temporal distribution of activity is particularly evident with respect to the induction requirements for long-term potentiation (LTP) and long-term depression (LTD), activity-dependent changes in synaptic strength that are widely believed to underlie the recognition memory function of the hippocampus (Zola-Morgan et al., 1986; Eichenbaum et al., 1989; Morris, 1989; Squire et al., 1990; Berger and Bassett, 1992; Cohen and Eichenbaum, 1994). The most prevailing current understanding of this process can be summarized as the following: An action potential originating in a presynaptic neuron generates synaptic potentials in a postsynaptic neuron. These synaptic potentials are integrated at the cell body, where an action potential is generated if the summed potential crosses threshold. The action potential propagates down the axon to all neurons to which it is connected. The temporal patterns of a spike train are defined by the intervals between the action potentials. The spatial pattern of neuronal activation is determined by the spatial distribution of connectivity among neurons. Two important assumptions are common in most neural network models, including those of the hippocampus. First, synaptic strength, i.e., the efficacy of a synapse in generating the synaptic potential, is assumed to be static for the time scale typical for action potential generation of neurons.[1] Second, each neuron is assumed to send the same signal to all neurons

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[1]von der Malsburg (1981) formulated the concept of a rapidly changing synapse as a solution for the combinatorial problem and the binding problem. This concept will be discussed in detail later.

to which it is synaptically connected. In this article, we show that the estimate of the computational power of the nervous system is dramatically increased when these two assumptions are removed.

Although it is well established that there is consistent variation in sequence of action potentials emitted by neurons, it is unclear how information is coded in the spike trains. Two major hypotheses have been proposed, namely, *rate coding* in which information is represented by the average firing rate of neurons and *temporal coding* in which the temporal structure of the spike train carries the information. The high capacity of information coding by spike trains has been noted for some time (MacKay and McCulloch, 1952; Stein, 1967). Many schemes of temporal coding have been proposed (von der Malsburg, 1981; Abeles, 1982; Gray et al., 1989; Richmond and Optican, 1990; Bialek et al., 1991; Hopfield, 1995; Softky, 1995). Despite the potential for a high representational capacity by temporal coding, it has been argued that the noisy nature of the interspike interval precludes such a coding scheme. Instead, the average firing rate which ignores the fine structure of a spike train is proposed to be the primary code used by the nervous system (Adrian and Zotterman, 1926; Shadlen and Newsome, 1994). As a result, the system relies primarily on spatial patterns to code information, with very limited temporal capability. But is the noise that we observe really noise? Or are there statistically significant features hidden in the seemingly noisy temporal patterns? If such features do indeed exist in the spike trains, how can they be extracted and put to use by postsynaptic neurons?

In this article, we illustrate a highly dynamic picture of neural information processing based on experimental observations of events that take place in the synapse. We propose a biologically based concept of a "dynamic synapse"—synaptic strength that is constantly tuned by the temporal pattern of the spike train. The dynamic synapse provides a specific way for transforming the temporal pattern of a spike train into a spatio-temporal pattern of synaptic events. The capability of pattern transformation at the synaptic level gives rise to an exponential computational power at the neuronal level. Such a high representational capacity and the flexibility of dynamically changing synaptic strength allow the extraction of statistically significant features from noisy and variable temporal patterns. This is demonstrated by incorporating dynamic synapse in a simple neural network to perform speech recognition from unprocessed noisy raw waveforms of words spoken by multiple speakers.

DYNAMIC SYNAPSE: MECHANISMS UNDERLYING REPRESENTATIONAL AND COMPUTATIONAL CAPACITY

Neither of the two notions—that a neuron sends identical signals to all neurons that it contacts and that synaptic strength is static—is correct when one examines the events taking place in (chemical) synapses upon the arrival of an action potential. The actual output of a neuron is the neurotransmitter released by the presynaptic terminal, which crosses the synaptic cleft, binds to the postsynaptic receptors, and initiates the synaptic potential. It is well documented that the probability of neurotransmitter release varies significantly upon the arrival of each action potential, owing to various synaptic mechanisms of different time scales, such as facilitation, augmentation, potentiation, and feedback modulation (Magleby, 1987; Zucker, 1989; Berger et al., 1991, 1994). Therefore, synaptic strength, which is determined in part by the probability of release, is dynamically tuned by the temporal pattern of action potential occurrences. Similar to the generation of an action potential, the release of neurotransmitter is a rapid all-or-none event, with a decay time constant of 1–2 ms (Clements et al., 1992). Thus, one may think of the event of neurotransmitter release as an impulse in much the same way as one describes an action potential. That is, at the presynaptic terminal, the sequence of action potentials is transformed into another sequence of release events. A variation in the synaptic mechanisms (which is typical in biological systems) would lead to different release probabilities for different presynaptic terminals (Perkel and Nicoll, 1993; Rosenmund et al., 1993; Stevens and Wang, 1995). The same spike train propagating along the collaterals of a given axon would lead to different temporal patterns of neurotransmitter release events at individual presynaptic terminals (Fig. 1). In other words, the temporal pattern of action potentials generated by a neuron is transformed into a spatio-temporal pattern by dynamic synapses.

The capability of dynamically tuning synaptic strength as a function of the temporal pattern of neuronal activation gives rise to a significant representational and processing power at the synaptic level. Let us consider a neuron which is capable of firing at a maximum of 100 Hz during a 100-ms time window. The temporal patterns that can be coded in this ten-bit spike train range from [0 0 . . . 0] to [1 1 . . . 1], i.e., a total of 2^{10} patterns. Assuming that at most one release event may occur at a presynaptic terminal per action potential depending on the dynamics of the synaptic mechanisms, the number of temporal patterns that can be coded by the release events at a presynaptic terminal is 2^{10}. For a neuron with 100 presynaptic terminals, the total number of temporal patterns that can be generated is $(2^{10})^{100} = 2^{1,000}$. The number would grow even higher if more than one release event is allowed per action potential. The above number represents the theoretical maximum of the coding capacity of neurons with dynamic synapses and will be reduced by several factors such as noise or low release probability. The effect of the most severe factor, noise, will be tested below using real life signals.

PATTERN TRANSFORMATION BY DYNAMIC SYNAPSES

To explore the capability of the temporal pattern transformation function, we used four dynamic synapses to connect an excitatory presynaptic neuron to an inhibitory neuron (Fig. 2A).

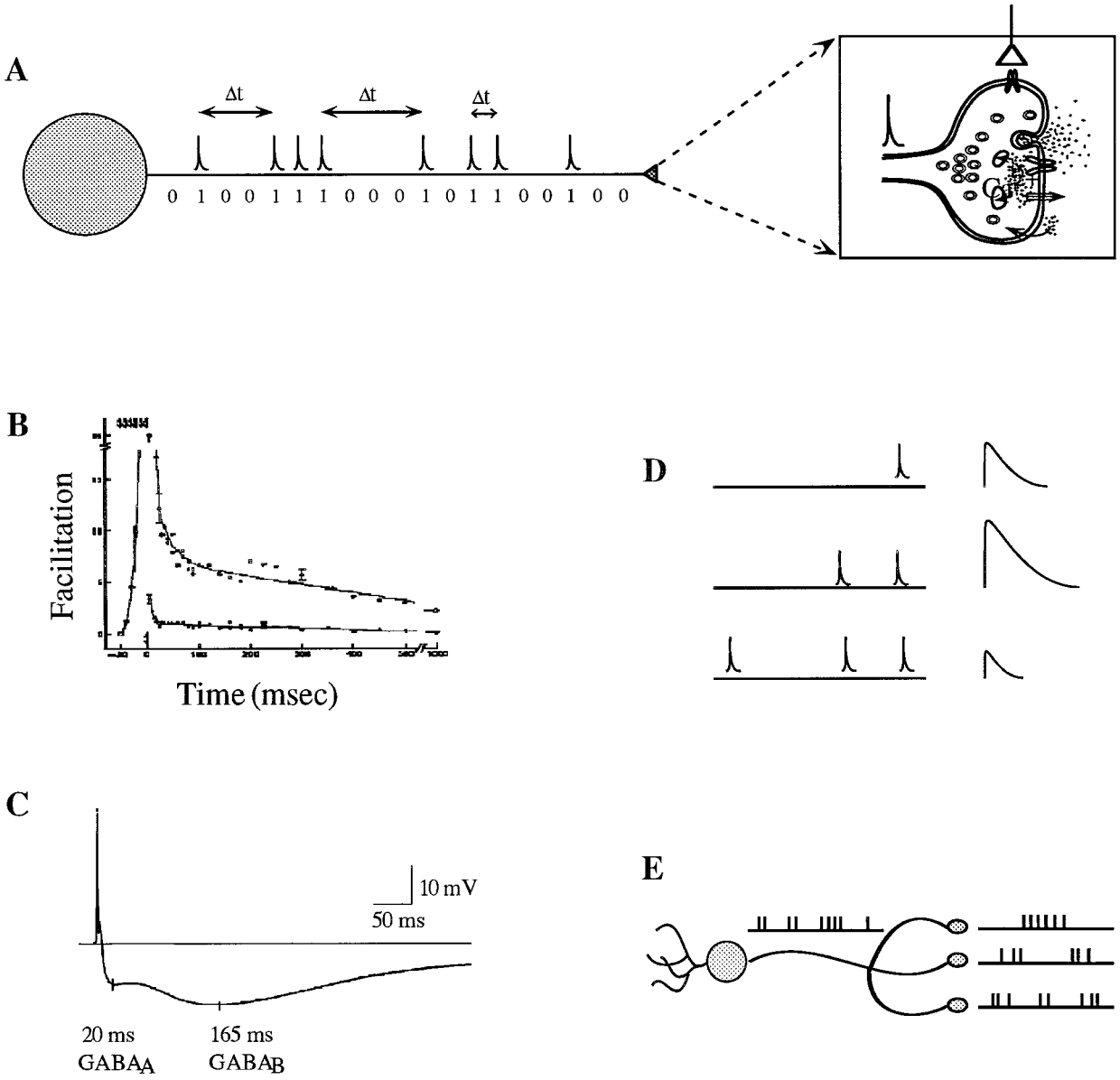

FIGURE 1. Biological mechanisms of dynamic synapse. The probability of release is determined by the dynamical interaction of many synaptic mechanisms and the temporal pattern of the spike train. A: The temporal pattern, defined by the intervals between action potentials, influences the interaction of various synaptic processes. B: A sample of two facilitative processes of different time scales (Zucker, 1974). C: A sample of two inhibitory mechanisms (fast $GABA_A$ and slow $GABA_B$). D: The probability of release is a function of the temporal pattern of a spike train due to the interaction of synaptic mechanisms of different time scales. E: As a result, the dynamic synapses of a neuron transform the temporal pattern of a spike train into a spatio-temporal pattern of the discrete events of neurotransmitter release.

The inhibitory neuron sends feedback modulation to all four presynaptic terminals. The synapse in the model consists of a presynaptic component which determines when a quantum of neurotransmitter is released and a postsynaptic component which scales the amplitude of the excitatory postsynaptic potential (EPSP) in response to an event of neurotransmitter release. The potential of release, P_R, is a function of four factors: action potential (Ap), first and second components of facilitation (F_1 and F_2), and feedback modulation (Mod, assumed to be inhibitory in this example). Parameter values for these factors were chosen so as to be consistent with time constants of facilitative and inhibitory processes governing the dynamics of hippocampal synaptic transmission studied using nonlinear systems analytic procedures (Berger et al., 1991, 1994). More specifically, model parameters were as follows:

$$\tau_R \frac{dR}{dt} = - R + k_R Ap \qquad (1)$$

where τ_R (0.5 ms) is the time constant of R for all presynaptic terminals and $k_R = 10.0$ for the control (presynaptic terminal 1).

$$F_1(t + 1) = F_1(t) + k_{f1} \cdot Ap - dt \cdot \tau_{f1} \cdot F_1(t) \quad (2)$$

where τ_{f1} (66.7 ms) is the decay time constant of the first component of facilitation for all presynaptic terminals and $k_{f1} = 0.16$ for control.

$$\tau_{f2} \frac{dF_2}{dt} = - F_2 + k_{f2} \cdot Ap \quad (3)$$

where τ_{f2} (300 ms) is the time constant of the second component of facilitation for all presynaptic terminals and $k_{f2} = 80.0$ for control.

$$\tau_{Mod} \frac{dMod}{dt} = - Mod + k_{mod} Ap_{Int} \quad (4)$$

where τ_{Mod} (10 ms) is the time constant of feedback modulation for all presynaptic terminals and $k_{Mod} = -20.0$ for control.

Finally, the magnitude of the first and second components of facilitation, and modulation are summed up:

$$P_R = R + F_1 + F_2 + Mod. \quad (5)$$

A quanta ($Q = 1.0$) of neurotransmitter is released if P_R is greater than a threshold ($\theta_R = 1.0$) and there is at least one quanta of neurotransmitter available (N_{total}):

$$\text{If}(P_R > \theta_R \ \& \ N_{total} > Q) \text{ then } N_R = Q \text{ and } N_{total} = N_{total} - Q \quad (6)$$

where N_R is the amount of neurotransmitter released. The neurotransmitter is cleared from the synaptic cleft at an exponential rate ($\tau_{Nt} = 1.0$ ms):

$$N_R = N_R e^{-t/\tau_{Nt}}. \quad (7)$$

Furthermore, there is a continuous process for replenishing neurotransmitter:

$$\frac{dN_{total}}{dt} = \tau_{rp}(N_{Max} - N_{total}) \quad (8)$$

where N_{max} (=3.2) is the maximum amount of available neurotransmitter and τ_{rp} (=0.3 ms^{-1}) is the rate of replenishing neurotransmitter.

The rate of change in the amplitude of an EPSP is proportional to N_R.

$$\tau_{epsp} \frac{dEpsp}{dt} = - Epsp + k_{Epsp} N_R$$

where τ_{epsp} (5.0 ms) is the time constant of EPSP and $k_{epsp} = 0.5$.

The neuron in the model is an "integrate-and-fire" unit consisting of two terms, membrane potential (V), which is the sum of all synaptic potentials, and action potential (Ap):

$$\tau_V \frac{dV}{dt} = - V + \sum_i EPSP_i$$

where τ_v (1.5 ms) is the time constant of V.

Ap = 1 if V is greater then some threshold ($\theta_R = 0.1$ for the presynaptic neuron and 0.02 for the postsynaptic neuron) and the neuron is not in the refractory period ($T_{ref} = 2.0$ ms), i.e., the neuron has not fired within the last 2 ms.

The parameter values for the first (uppermost) presynaptic terminal in Figure 2A is constant in all simulations and is treated as the control for comparison with other presynaptic terminals. In the first simulation, only one parameter is varied per terminal by an amount indicated by the bar chart to the right of the simulation results shown in Figure 2B. For example, the contribution of the current action potential (Ap) to the potential of release is increased by 25% for the second terminal (from top), whereas the other three parameters remain the same as the control. The results are as expected, namely, that an increase in either Ap, F_1, or F_2 leads to more release events, whereas increasing the magnitude of feedback inhibition reduces the number of release events. The transformation function becomes more sophisticated when more than one synaptic mechanism undergoes changes (Fig. 2C). First, although the parameters remain constant in the control, it produces fewer release events. This is due to an overall increase in output from the other three terminals, resulting in higher activation of the postsynaptic neuron, which in turn exerts greater inhibition of the presynaptic terminals. This is a clear example of how synaptic dynamics can be influenced by network dynamics. Second, the differences in the outputs from presynaptic terminals are not merely in the number of release events, but also in their temporal patterns. For example, the second presynaptic terminal responds more vigorously to the first half of the spike train and less to the second half, whereas the third terminal responds more to the second half. In other words, the transform of the spike train by these two presynaptic terminals are qualitatively different.

Next, we examine how dynamic synapses would respond to different temporal patterns of action potentials. We tested this by moving the ninth action potential in the spike train to a point about 20 ms following the third action potential (marked by arrows in Fig. 2C,D). As shown in Figure 2D, the output patterns of all presynaptic terminals are different from the previous ones. There are some changes that are common to all terminals, yet some are specific to certain terminals only. Furthermore, due to the interaction of dynamics at the synaptic and network levels, removal of an action potential (the ninth in Fig. 2C) leads to a decrease of release events immediately, and an increase in release events at a later time.

EXTRACTING INVARIANT FEATURES: A CASE STUDY ON SPEECH RECOGNITION

The above discussion of the computational power of a neural system with dynamic synapses is considered purely based on theoretical grounds, and the actual computational capacity of a given neural system certainly would be limited by realistic biological constraints. For example, the representational capability

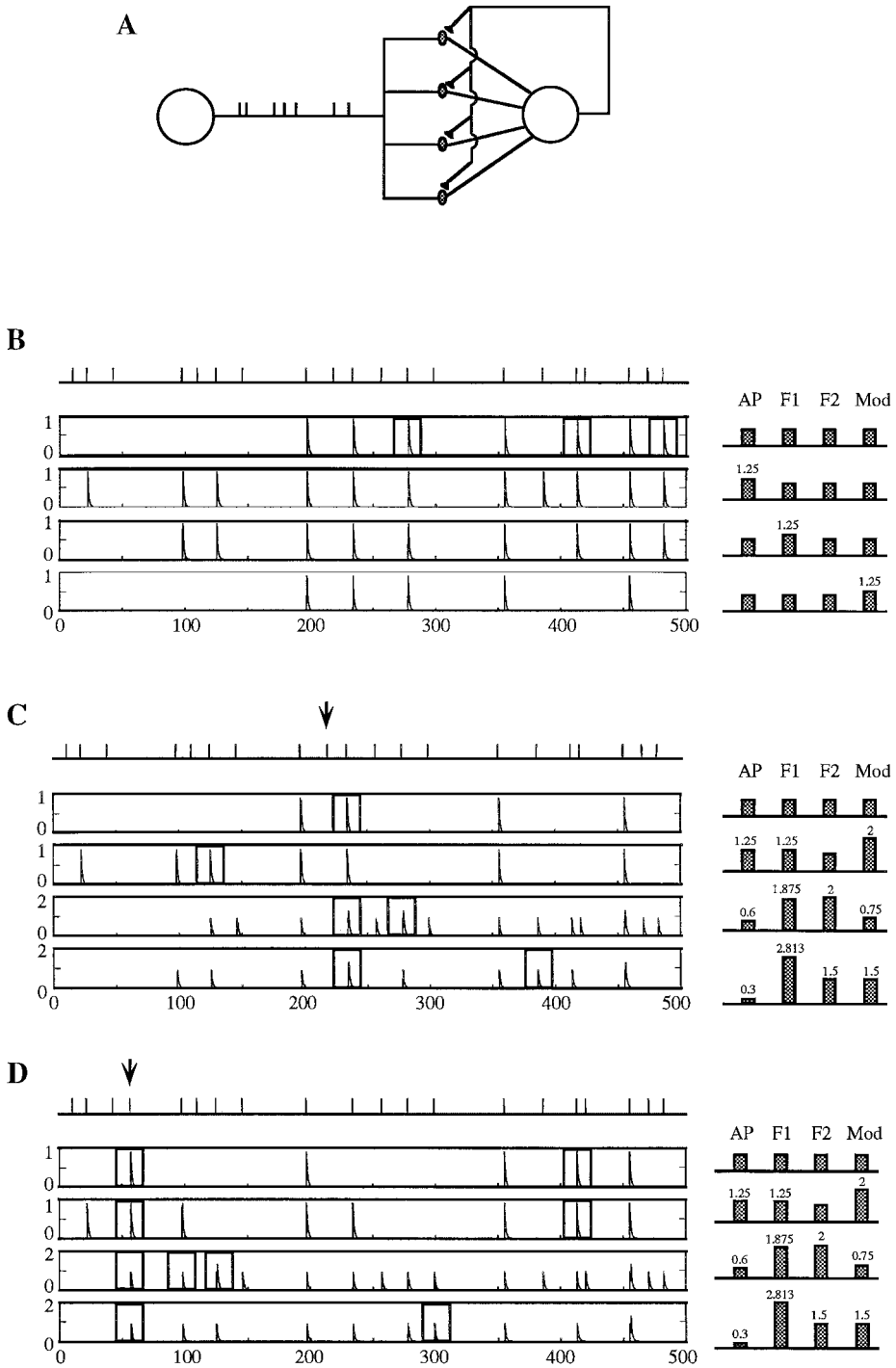

FIGURE 2. **Temporal pattern transformation by dynamic synapses. A: A simple network consists of an excitatory presynaptic neuron which is connected to an inhibitory neuron via four dynamic synapses. The postsynaptic neuron in turn sends inhibitory feedback to all four axon terminals. B–D: The top trace on the left is the spike train from the presynaptic neuron. The other four traces are the events of neurotransmitter release from the four terminals (in the corresponding top-down order as shown in A). The bar chart on the right represents the magnitudes of the presynaptic mechanisms in the corresponding axon terminal. The numbers above the bars indicate the magnitude relative to the control (the uppermost chart in each graph), with the lack of it indicating that the same value is used as in the control. For example, the number 1.25 in graph B, in the third row in the column "F1" means that the magnitude of the contribution of the first component of facilitation for terminal 3 is 25% greater than that of the control. The release events enclosed in a box in B and C highlight those that will disappear in the next graph. For example, the last "spike" of the first terminal shown in B will not be seen in the corresponding trace in C, or the second "spike" in the first trace in C will disappear in D, whereas the boxed "spikes" in D are new ones that do not exist in C.**

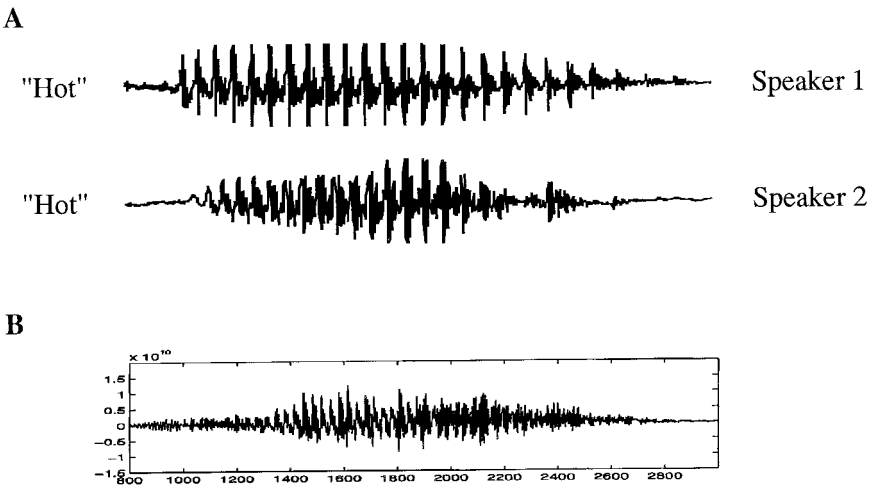

FIGURE 3. Noise and variations in speech waveforms. A: Two raw waveforms of the word "hot" spoken by two speakers. B: The cross-correlation of the waveforms in A is very low, indicating that the two waveforms are not similar.

of $2^{1,000}$ is based on the assumption that a dynamic synapse is sensitive to the occurrence or nonoccurrence of a single action potential (i.e., each "bit") in a spike train. A negative consequence of this assumption is that the synapse also will be very sensitive to corruption of the spike train by noise. The paramount question, then, is whether dynamic synapses are capable of extracting statistically significant features from noisy spike trains. This problem is particular acute in biology given that, to survive, an animal must extract regularities from an otherwise constantly changing environment. For instance, to navigate to its nest or to a food store, a rat must be able to choose from a number of possible routes, including novel ones, and to follow a given route regardless of variations in a wide variety of conditions such as lighting, time of day, a cloud drifting by, a swaying tree, winds, odors, sounds, etc. That is, neurons in the hippocampus must extract invariants from varying input signals. There are very little data available concerning the actual spatio-temporal patterns of input signals to hippocampal neurons. Thus, we need to find some signals with similar characteristics in order to examine how well a system with dynamic synapses can extract invariants.

To this end, one of the most preeminent temporal patterns, speech waveform, was chosen as the test case. The hallmark characteristics of a speech waveform are noise and variability. Two sample waveforms of the word "hot" spoken by two speakers are shown in Figure 3A. There is a high degree of variations in waveforms, as illustrated in their cross-correlation (Fig. 3B). The task is to extract invariant features embedded in the waveforms that give rise to constant perception of the word "hot."

RESULTS

The aim of the study is to recognize words spoken by multiple speakers by a neural network model with dynamic synapses. In order to test the coding capacity of dynamic synapses, two strong constraints were imposed. First, the neural network had to be small and simple. Second, no preprocessing of the speech waveforms was allowed. The speech test is a variant of the standard HVD test (H-voewl-D, e.g., had, heard, hid). The test words are [care, hair, key, heat, kit, hit, kite, height, cot, hot, cut, hut], spoken by two speakers in a typical research office with no special control of the surrounding noises (i.e., nothing beyond lowering the volume of a radio).

The neural network is organized into two layers, an input layer and an output layer, with five neurons in each layer, plus one inhibitory interneuron (Fig. 4A). The input neurons receive unprocessed, noisy raw speech waveforms. Each input neuron is connected by dynamic synapses to all of the output neurons and to the interneuron. There is a feedback connection from the interneuron to each presynaptic terminal. The synapses and neurons are the same as those described in the previous section. The speech waveforms are sampled at 8K Hz. The digitized amplitudes are fed to all the input neurons and are treated as EPSPs.

The objective of training the network is to increase the cross-correlation of the output patterns for the same words while reducing that for different words. The network is trained following the Hebbian and anti-Hebbian rules. During learning, the presentation of the speech waveforms is grouped into blocks in which the waveforms of the same word spoken by different speakers are presented to the network for a total of four times. Within a presentation block, the Hebbian rule is applied, namely, if the postsynaptic neuron fires after the arrival of an action potential, the contribution of excitatory synaptic mechanisms is increased, while that of inhibitory mechanisms is decreased. If the postsynaptic neuron does not fire, then the excitatory mechanisms are decreased while the inhibitory mechanisms are increased. The magnitude of change is the product of a predefined learning rate

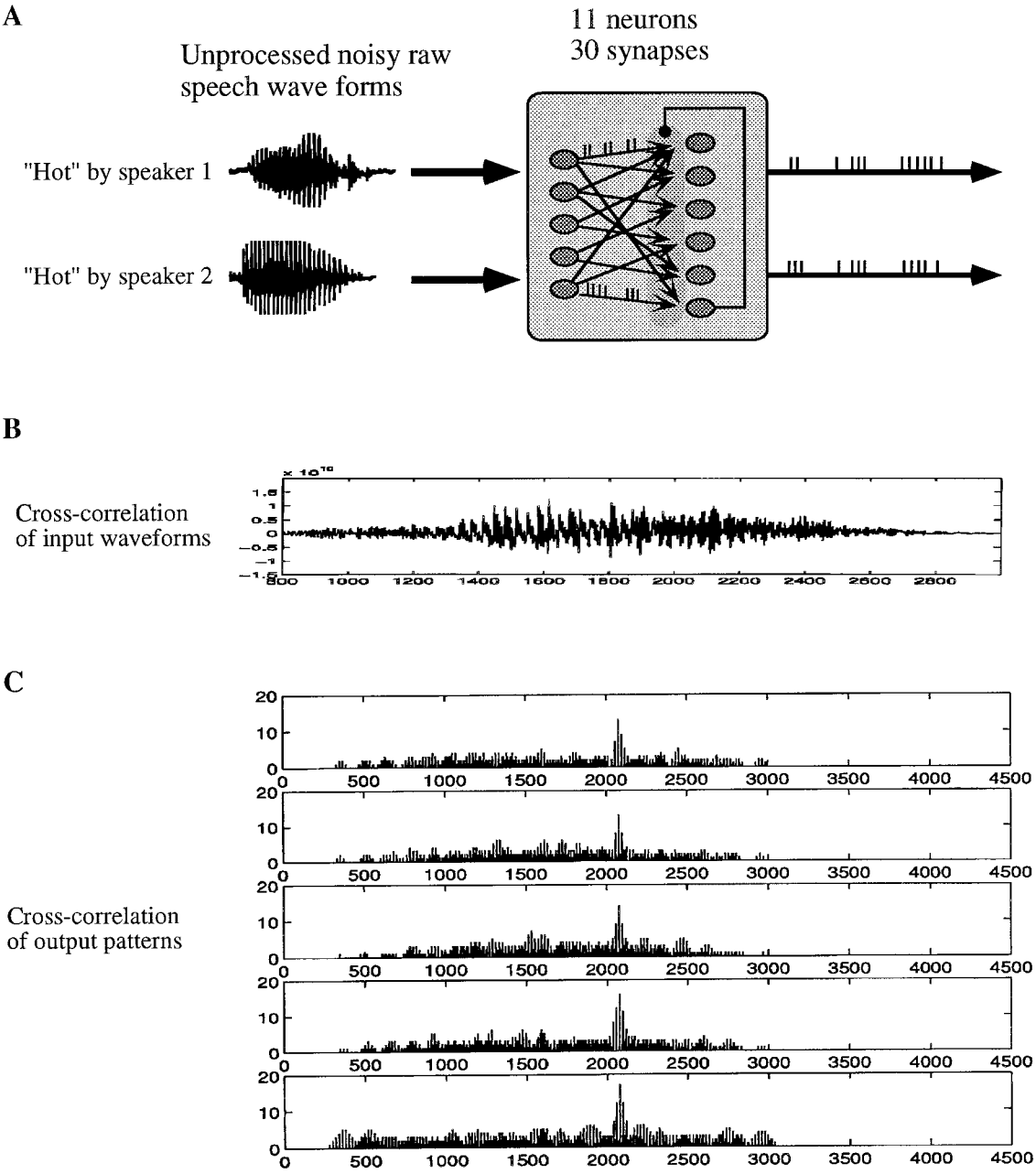

FIGURE 4. Speech recognition by a small network with dynamic synapses. A: The neural network is composed of two layers, an input layer and an output layer, with five neurons in each layer, plus one inhibitory interneuron. Each input neuron is connected to all of the output neurons and the interneuron by dynamic synapses. The interneuron sends an inhibitory signal to each presynaptic terminal. The input to the network consists of unprocessed noisy raw speech wave forms. B: The cross-correlation of the raw wave forms of the same word "hot" spoken by two speakers. C: Each trace shows the cross-correlation of the output patterns produced by an output neuron in response to the two speech waveforms. For all five output neuron, their outputs are highly correlated, showing that each neuron extracts certain invariant features from the input pattern.

and the current activation level of a particular synaptic mechanism. In this way, the responses to the temporal features that are common in the waveforms will be enhanced while that to the idiosyncratic features will be discouraged. When the presentation first switches to the next block of waveforms of a new word, the anti-Hebbian rule is applied. This enhances the differences between the response to the current word and the response to the previous, different word.

The results of training the neural network is shown in Figure 4B and C. There is a high degree of variation in the waveforms of the same words spoken by different speakers. This is apparent in the cross-correlation of the waveforms of the same word "hot" spoken by two speakers, showing almost no correlation at all, indicating that the two waveforms are very different from each other. However, after training, the output neurons generate temporal patterns that are highly correlated with each other. That is, given

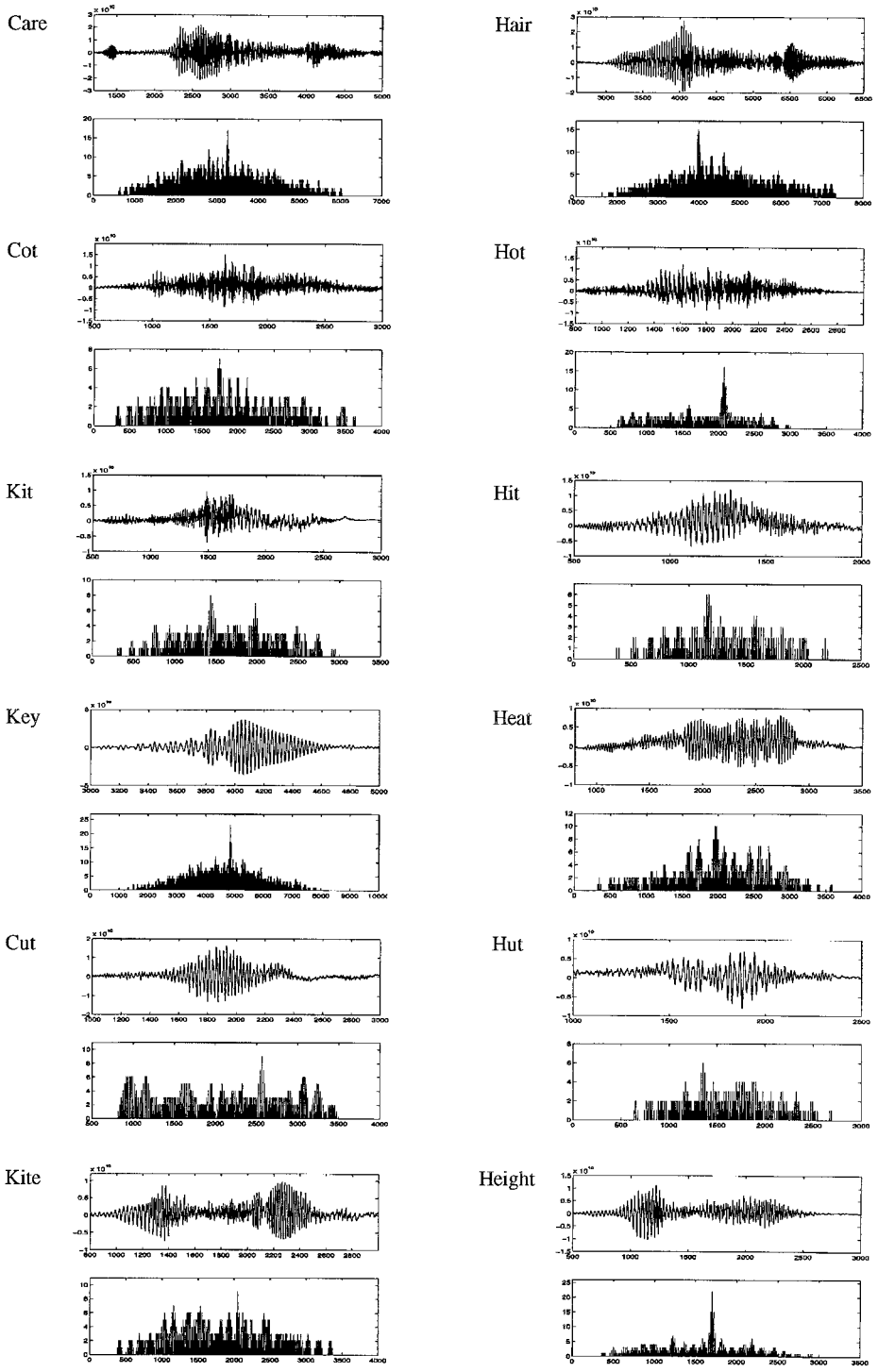

FIGURE 5. Results of testing with 12 words. The network with dynamic synapses are tested with 12 words spoken by two speakers. For each word, the cross-correlation of the speech waveforms (top trace) and that of the output patterns of a representative output neuron (bottom trace) are shown. A significant increase in the correlation is seen in all cases.

two radically different waveforms that nonetheless contain within them a representation of the same word, the network generates temporal patterns that are virtually identical. The extraction of invariant features from all 12 test words are shown in Figure 5. A significant increase in the cross-correlation of output patterns is obtained in all test cases.

DISCUSSION

In this article, we propose a biologically based dynamic synapse which is an emerging property of the interaction of the underlying excitatory and inhibitory synaptic mechanisms of different time

scales. The strength of a dynamic synapse is constantly changing according to the temporal pattern of the spike train. Incorporating dynamic synapses into a neural network model provides a specific way for transforming the temporal pattern of a spike train into a spatio-temporal pattern of synaptic events. A neural network with dynamic synapses possesses an enormous computational power. Dynamic synapses are sensitive only to action potentials occurring with a relatively small time window. Such temporal chunking helps to prevent temporal interference when each dynamic synapse learns to extract a small but statistically significant sub-pattern in the spike train. Such a capability for extracting invariant temporal features allows the transmission of information contained within noisy and variable spike trains. Learning involves not only changing synaptic efficacy (e.g., by tuning postsynaptic receptor/channel kinetics), but more importantly, modifying the presynaptic short-term plasticities. That is, alterations in the presynaptic mechanisms lead to different pattern transformation functions, whereas changes in the postsynaptic mechanisms determine how the synaptic signals are to be combined.

The concept of the dynamic synapse presented here goes beyond the inclusion of realistic synaptic mechanisms in a neural network, which has been implemented previously. For example, Little and Shaw (1975) incorporated facilitation and depression of presynaptic and postsynaptic factors of different time scales to establish short-term memory (on the order of a second) and intermediate- and long-term memory. Edelman and Finkel (1984; see also Edelman and Finkel, 1987) included presynaptic facilitation and depression as a basis for long-term global presynaptic modification that is applied uniformly to all presynaptic terminals of a neuron. More recently, Buonomano and Merzenich (1995) constructed a network of neurons that includes paired-pulse facilitation and slow inhibitory postsynaptic potential. They showed that temporal information (i.e., the length of different interstimulus intervals) can be transformed into a spatial code by a population of neurons. We demonstrated that by identifying that the output of a neuron is the neurotransmitter rather than the action potential and that the probability of its release is determined dynamically based on the temporal pattern of the spike train, each synapse can perform a transformation of such a temporal pattern. Together, dynamic synapses increase the computational power of a neuron exponentially.

von der Malsburg (1981) proposed an idea of a rapidly changing synapse which he termed dynamic link. According to his theory, a synapse can be switched between active and inactive states depending on the correlation of the activity of two neurons in a fraction of a second. He showed that dynamic link provides a theoretical basis for solving both the combinatorial problem and the binding problem. The combinatorial problem refers to the fact that there is almost an unlimited number of possible patterns in the external world. This fact has profound implications for the representational capacity of the nervous system required to distinguish among all of those possible patterns, i.e., the number of neural patterns that the nervous system must learn to recognize must be correspondingly unlimited. Therefore, the combinatorial problem in the external world introduces a corresponding combinatorial problem for the internal, or neural, world. The binding problem refers to the issue that neurons involved in any one representation are grouped separately in different parts of the brain. How, then, can the activity of these different and spatially distinct groups of cells be coordinated?

Since the connections between neurons can be modified rapidly, the same neurons can take part in representing different features, allowing an almost unlimited capability of the nervous system to deal with the combinatorial problem. The strengthening of synaptic connections based on the correlation of neuronal activities binds together those neurons that correspond to the same feature. The most popular mechanism for carrying out neuronal correlation is by synchronizing the firing of neurons (von der Malsburg, 1981; Gray et al., 1989). According to the synchronization hypothesis, neurons that correspond to the same feature fire in synchrony, whereas those that do not fire asynchronously.

There are three major differences between the concept of dynamic synapses that we propose and Malsburg's notion of dynamic links. First, the dynamic link assumes that the role of a synapse is to scale the synaptic signal, whereas the concept of a dynamic synapse assumes that temporal pattern transformation is performed by the synapse. Second, the strength of a dynamic synapse is determined by the temporal structure of a spike train, with no constraint imposed on the structure. The switching of the state of a dynamic link, on the other hand, depends on the correlation of the activity of the presynaptic and postsynaptic neurons. Third, learning with dynamic synapses involves modifications of synaptic plasticity itself, in addition to synaptic efficacy. Each dynamic synapse learns to extract temporal features of a spike train, and the postsynaptic neuron learns the proper way to combine these features.

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