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Toward an interpretation of dynamic neural activity in terms of chaotic dynamical systems

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Abstract: Using the concepts of chaotic dynamical systems, we present an interpretation of dynamic neural activity found in cortical and subcortical areas. The discovery of *chaotic itinerancy* in high-dimensional dynamical systems with and without a noise term has motivated a new interpretation of this dynamic neural activity, cast in terms of the high-dimensional transitory dynamics among "exotic" attractors. This interpretation is quite different from the conventional one, cast in terms of simple behavior on low-dimensional attractors. Skarda and Freeman (1987) presented evidence in support of the conclusion that animals cannot memorize odor without chaotic activity of neuron populations. Following their work, we study the role of chaotic dynamics in biological information processing, perception, and memory. We propose a new coding scheme of information in chaos-driven contracting systems we refer to as *Cantor coding.* Since these systems are found in the hippocampal formation and also in the olfactory system, the proposed coding scheme should be of biological significance. Based on these intensive studies, a hypothesis regarding the formation of episodic memory is given.

Keywords: Cantor coding; chaotic itinerancy; dynamic aspects of the brain; dynamic associative memory; episodic memory; high-dimensional dynamical systems; SCND attractors

1. Introduction

In recent studies in neuroscience, dynamic aspects of the brain have been the subject of a good deal of investigation. There has also been an accumulation of data that cannot be rationally explained within a static framework. Recently, it has been suggested in various contexts that the brain is organized not only in a hierarchical fashion but also in a "heterarchical" fashion. In this context, the word "heterarchy" refers to structure or states existing in reticular networks, in contrast to hierarchical structure or states. According to this point of view, a single neuron or a neuron assembly is represented by a single code and also by a multiple code; the information representation is realized both by the state of neurons and by the *dynamic* relation among states.

In neural network models of biological information processing, it has been assumed that an attractor in phase space (state space) represents external and/or internal information. In other words, it has been assumed that a neural network maps the structure of information contained in the external and/or internal environment into embedded attractors (see, for example, Amari 1974; 1977; Amari & Maginu 1988; Kohonen 1972; 1982; Hopfield 1982). With this assumption, if the static representation of information is universal, the concept of an attractor should be adequate for neural representation (Hirsh 1989).

Recently, however, dynamic modalities of neuroactivities have been observed as, among other types of phenomena, a coincidence of random spikes (for example, Abeles 1991; Aertsen et al. 1994; Fujii et al. 1996; Oliveira et al. 1997; Riehle et al. 1997), as coherent activity in neuron assemblies (Aertsen et al. 1987; Arieli et al. 1996), as the synchronization of oscillatory spike trains (Deppisch et al. 1993; Eckhorn et al. 1988; Engel et al. 1992; Gray & Singer 1987; 1989; Gray et al. 1990; Singer 1994), as chaotic population dynamics in the γ-range (Freeman 1987; 1994; 1995a; 1995b; Kay et al. 1995; 1996), as chaotic interspike intervals giving rise to a chaotic fluctuation of membrane potentials (Hayashi & Ishizuka 1995). We have adopted the framework of chaotic dynamical systems to *interpret* the functions of dynamic neural activity emerging in the brain, which can be regarded as a *hermeneutic device* (Érdi 1996) that can act in a hermeneutic process (Érdi & Tsuda, in press; Tsuda 1984).

The dynamical systems' interpretation of dynamic neural activity with chaos analysis has also been presented (see, for example, Babloyantz & Lourenço 1994; Érdi et al. 1993; Freeman 1987; 1995a; Kaneko & Tsuda 1996; Nicolis 1982; 1991; Nicolis & Tsuda 1985; Tsuda 1984; 1990; 1991a). In these works it has been shown that chaos can be effectively used for biological information processing. Types of com-

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plex dynamical behavior, such as chaos, can be categorized in terms of quantities including topology, measure, and dimension. The functional form of a decay of amount of information also categorizes chaos according to the ability of a chaotic network to store spatial patterns using the dynamic orbits (Matsumoto & Tsuda 1985; 1987; 1988). The forms of chaotic behavior observed in biological systems possess a common feature: a nonuniform probability density and a weak instability. The probability distribution of chaotic dynamics is biased due to excitability and its bifurcation parameter, which is a control parameter, is biased due to biological specificity. The former bias is responsible for the network ability mentioned above, and the latter bias results in a restricted high-dimensional process. From these considerations, it is seen that chaos appearing due to a weak instability cannot be restricted to merely a low-dimensional phase space. Thus transitory dynamics in high dimensions emerge.

Since biological neural networks operate in noisy environments, the interplay between their deterministic model dynamical systems and noise is an important subject for study. Taking into account this issue and those discussed in the previous paragraph, in this paper we study the roles of *critical* chaos in biological information processing with regard to, in particular, the inseparability of dynamic memory and perception. Based on new concepts of high-dimensional dynamical systems, we present a hypothesis on the formation of dynamic memory and perception. This hypothesis accounts for dynamic functional processes such as episodic memory and the itinerant process of perception. This hypothesis clarifies the biological significance of the chaotic activity observed in the hippocampus and in the olfactory system. The hypothesis also suggests a form of the *prototype* of thoughts.

2. Perception and dynamic memory

Studies of neural correlates of memories have developed through investigation of the hippocampus, the olfactory system, the temporal cortex, the prefrontal cortex, and their interacting systems. The working memory (Baddeley 1986; Funahashi et al. 1989; Goldman-Rakic 1987; 1996; Sawaguchi & Goldman-Rakic 1991) as a cognitive modality can be dynamic and is easily destabilized in the state space. In contrast, the episodic memory can be stabilized in state space, but it appears in association with dynamic cognitive processes. Finally, the semantic memory must be described as a stable object. On the other hand, neural activities associated with these kinds of memories seem a highly random spatio-temporal pattern. If these neural activities correspond precisely to memories, it is unlikely that they would be represented by a single attractor in state space, but rather by a more unstable one. This observation leads to the following conclusion: Memories do not emerge entirely from stored information. Rather, the nature of that which emerges is influenced at each instant by "traces" of information resulting from perception and cognition.

Motivated by the above conceptual observation, we have constructed a neural network model of dynamic memory in terms of mathematical objects that are not attractors in the conventional sense (Tsuda 1991b; 1992; 1994; Tsuda et al. 1987). This model is discussed in the next section from another viewpoint.

There are interesting experimental results demonstrating the dynamic relations between perception and memory. In particular, an experiment conducted and a model constructed by Freeman and his colleagues have attracted general attention (Skarda & Freeman 1987). In both Freeman's work (1995a) and Kay's work (Kay 1995; Kay et al. 1995; 1996), it is claimed that odor memories are represented by the chaotic behavior of the collective activity of the olfactory bulb, and that the process of odor perception can also be represented by itinerant motion of local EEGs in the olfactory bulb, in the olfactory cortex, and in the hippocampus. It was found that in the animals' motivated state during the process of learning, which is inevitably associated with the recall and the perception processes, the neural activity is chaotic (Freeman 1995a; Kay et al. 1995; 1996).

The studies of Freeman and Kay suggest that chaos underlies the entire process of odor perception, and this process is inseparable from the dynamic memory process. Among a number of noteworthy findings of Freeman and his colleagues, a key finding was that animals do not respond directly to external stimuli, but rather to internal images created by chaotic dynamics in the olfactory bulb (Freeman 1995a; 1995c). This suggests that the brain is hermeneutic (interpretative) in nature and exhibits chaotic behavior (Tsuda 1984; 1991a). Furthermore, Skarda and Freeman (1987) offer a hypothesis on the role of chaos in the dynamic processes of perception and memory. According to this hypothesis, without chaos animals can neither record nor perceive odor. As described in the next section, the dynamic behavior exhibited by our theoretical model strongly suggests that their hypothesis is correct.

For other modalities of sensation, the dynamic receptive field may be understood as a neural correlate of dynamic perception like a perceptual drift (Freeman 1995a). Dynamic (spatio-temporal) receptive fields have been observed in the retina (Mizuno et al. 1985; Tsukada et al. 1983), the auditory cortex (Eggermont et al. 1981), and the primary visual cortex (Dinse 1990; 1994). It was pointed out that there exist subfields, some of which are activated for only 20–50 msec during a presentation of stimuli; the combination of activated subfields varies even for a stationary presentation of stimuli. In the theory of the dynamic receptive field, a classical receptive field, which is understood as static one, is reinterpreted as a spatio-temporal average of the dynamic receptive field. The spatial average should be taken over an entire receptive field, and the temporal average over a few hundred milliseconds. Since the time scale 20–50 msec is approximately a "unit" of psychological time, we may consider the dynamic receptive field as a neural correlate of internal dynamics for restructuring and/or reorganization of mental space (Dinse 1990), in other words, the presence of a dynamic receptive field suggests the presence of dynamic restructuring due to dynamic interactions between higher and lower levels of information processing (see also Dinse 1994).

Concerning the processing of visual information, Gray and Singer (1987; 1989) and Eckhorn et al.(1988) found neural oscillations of around 40 Hz in the primary visual cortex. These findings followed studies giving evidence for the presence of γ-range oscillations (Bressler & Freeman 1980; Freeman 1987). As an underlying mechanism for these oscillations, the synchronization of neuron spikes may be conjectured. It was actually conjectured that one of the roles of spike synchronization is to extract the invariant continuum as a figure out of diverse stimuli, and consequently to bind different modalities of stimuli (Eckhorn et al. 1988; Gray & Singer 1987). This is reminiscent of Abeles's (1991) synfire chain, proposed to describe how neuron assemblies in the prefrontal cortex can obtain useful information from purely random spike trains through coincident and phase-locked firings.

In the prefrontal cortex, after Abeles's proposition of the synfire chain, Vaadia, Aertsen, and others observed the coincidence of neuron spikes, and Aertsen et al. analysed these data precisely (Aertsen et al. 1994; Vaadia & Aertsen 1992). Aertsen et al. found a new functional representation of neurons, which can be compared with the so-called rate coding. Fujii et al. (1996) has proposed a dynamic cell assembly hypothesis, based on the concepts of coincidence detecting neurons and functional connectivities resulting from coincidence (see also Aertsen et al. 1996). Recently, Diesmann et al. (1999) constructed a neural network model for synfire-chains.

Our main concern here is not formulating a coding scheme at the level of a single neuron. Rather, we cast our description in terms of macro-variables that represent macroscopic behavior observed as collective motion (see the Technical Appendix). These macro-variables can in turn limit the possible types of coding scheme at the level of a single neuron. In this respect, our viewpoint is similar to that of statistical physicists and dynamicists (see, for example, Amit 1989; Amit et al. 1985; 1987; Babloyantz 1986; Haken 1979; 1983; 1991; Mayer-Kress 1986; Sompolinsky & Crisanti 1988; Sompolinsky & Kanter 1986), where the understanding of Haken leads to the idea that *pattern formation is pattern recognition*). A crucial point in the treatment we employ, which distinguishes our treatment from the conventional treatments of statistical physics and dynamical systems, is that the macro-variables we consider do not behave as simple functions, such as a constant function or a function periodic in space and time, and in this sense they are fundamentally different from *order parameters* (see the Technical Appendix). The description of the chaotic behavior in which we are interested necessitates the use of these mathematically more general macro-variables. Such chaotic behavior cannot always be described by a low-dimensional attractor. We thus need a dynamical description that captures the high-dimensional complex dynamics. Another crucial problem is to describe the interplay between the order parameter and the "rest" of the system – that is, the interplay between the deterministic dynamics and the noise. In the next section, we consider these issues in relation to neural dynamics.

We take the view that there exists a neural correlate of cognitive behavior. The inadequacy of the symbolic approach to higher functions of the brain, which has been used in the field of artificial intelligence, was clearly pointed out by Skarda and Freeman, who showed the biological significance of chaotic behavior found in local EEG. Additionally, it should be noted that a sharp distinction cannot be drawn between the molecular-level timescale and the psychological timescale. For instance, one can observe psychological events at some timescale, say 1 sec, and also observe molecular events and electric events over almost the same timescale. Hence there exists an overlap of timescales. In addition, there are overlaps of many other timescales. For these reasons, it is not appropriate to describe cognitive behavior as simply a "macroscopic" behavior. It is thus necessary to study the interplay between macroscopic and microscopic behavior and from this to propose a plausible cognitive interpretation of neural activity. For this purpose, we study the dynamic behavior in non-equilibrium neural networks, which gives a skeleton description of behavior observed in the brain.

In this article we study two kinds of networks. One is a stochastic recurrent network, and the other is a chaos-driven stable network. Based on this study, we present hypotheses on dynamic memory and perception.

3. Dynamical systems with and without noise as a tool for interpretation of neural activity: Changeover of interpretation from low-dimensional attractor to high-dimensional itinerancy

3.1. What is noise in neural systems?

In order to clarify the origin of noise, let us consider a system consisting of many interacting elements. Here an "element" is assumed to obey a deterministic law, so that it entails no unknown component. In cortices, the system in which we are interested consists of on the order of 10^5 to 10^{10} the interacting neurons. Such a system is called deterministic because of the absence of stochastic behavior. The system may, however, be intractable as a deterministic system in the practical sense, because it contains too many degrees of freedom. Then, one may attempt, in the sense of mode-mode coupling theory, to identify collective modes to act as an order parameter. This approach succeeds in the critical regime of equilibrium phase transitions, and it can be extended to bifurcation points in nonequilibrium states (see for example Haken 1983). Here, the collective mode is decoupled from the residual modes, since the collective mode is low frequency, whereas the residual modes are high frequency. In other words, in such a treatment the slow motion on the center manifold is decoupled from the fast motion involved in the convergence to the center manifold. Here, the collective mode can be described by deterministic equations with a few degrees of freedom, and the rest is viewed as *noise.*

Noise is dynamically *generated* in such manner, but it is usually assumed to contain infinite degrees of freedom. Hence, as is shown in Figure 1A, the interaction between the order parameters constituting a deterministic system and noise is unidirectional. However, this condition is broken when order parameters, that is, collective modes, become weakly unstable in a direction normal to the center manifold, as the slow motion begins to interact with fast motion.[1] Then the number of variables behaving like noise changes in time. Figure 1B depicts this situation. An asymptotic theory, in general, provides an effective method to obtain a center manifold. Then, once one obtains the center manifold of interest the stability of states within this center manifold must be investigated. In the situation we study here, however, stability in the direction normal to the center manifold must be investigated, using an index like a normal Lyapunov exponent.

Taking into account the situation as described above, it is plausible to think of a neural network in the brain as existing in a noisy environment even in the absence of thermal

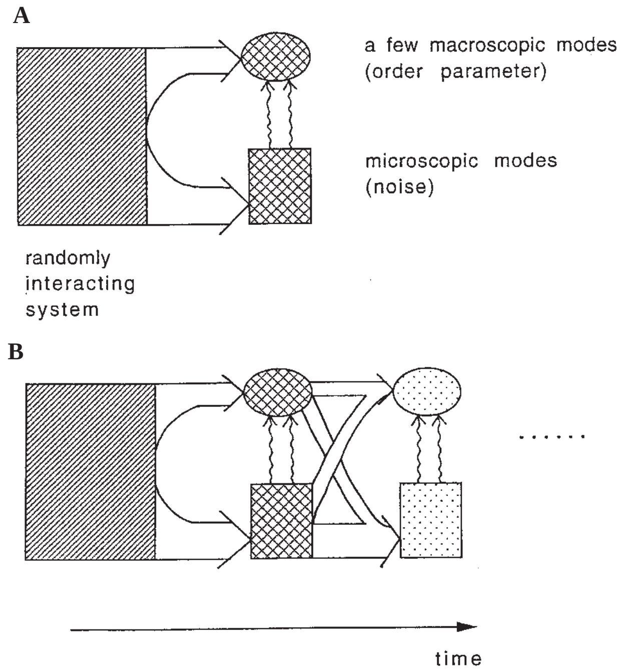

Figure 1. (**A**) Unidirectional interactions between order parameters representing a deterministic system and noise. (**B**) Order parameters and the rest can be varied in a weak instability regime. The components that play the role of noise change with time.

noise and quantum noise. Since neurons can process information even in such a noisy environment, in our model "noise effects" must be taken into account.

An additional type of noise we have not yet mentioned has been observed in neurons. This type of noise differs from that discussed above in that it originates in nondeterministic factors. The following two types of noise can be distinguished. One type results from electric current randomly leaked from neighboring neurons. We refer to this as *dendritic* noise. The second type results from quantal emissions of synaptic vesicles. There are two kinds of quantal emission, spontaneous emission and stimulus-induced emission.

Spontaneous emission is too weak to activate the postsynaptic membrane. Actually, a single such process simply induces a change on the order of several μV to the postsynaptic membrane potential.

For the firing to be effective, emission on the order of 10^4 over all connecting neurons must occur within the decay time of membrane potential. Taking into account the maximal number of synapses per neuron and the average decay time of a membrane potential, this is unlikely to occur. Thus this type of noise cannot in itself represent information. It should, however, be noted that it may influence the subthreshold dynamics.

This kind of noise may play a decisive role in the reduction of the effective dimension when delay-differential equations are used to describe the networks. A system with delay terms is described as an infinite dimensional dynamical system. In such a system, the infinite number of variables generated by the delay allows for highly complex behavior of high dimension. In this case, noise can reduce the complexity of the system, because noise divides a continuous delay time into some finite intervals within which correlations among some finite variables are preserved. Hence the effective dimensionality can be reduced by noise.

On the other hand, stimulus-induced stochastic emission, which is referred to here as *synaptic noise,* can be effective for the firing, since a single such process provides an effect on the order of several mV. Thus here, a coincident emission on the order of only 10 among $\sim 10^4$ synapses is sufficient to cause a firing. In the study of model systems, it will therefore be necessary to consider the effects of dendritic and synaptic noise.

3.2. The interplay between the dynamical system and noise

In this subsection, we highlight the difference between digital and analog computations and the related role of noise. This issue is of importance in order to properly address the role of noise in excitable biological systems, like neural systems. Excitable systems are, in many cases, sensitive to noise, because of the presence of a separatrix between states (i.e., the firing states and resting states) or the presence of an extremely nonuniform vector field. The latter occurs in physiological situations described by the Hodgkin-Huxley equation. Furthermore, an interacting system of such elements often possesses a critical regime of stability.

Some deterministic models with a few degrees of freedom used to describe the Belousov-Zhabotinsky reaction system exhibit only periodic oscillations when studied on digital computers, but the digital simulation of these models with a noise term as well as the analog simulation of the deterministic model exhibit "chaotic" oscillations also (Showalter et al. 1978; Tomita & Tsuda 1979). These oscillations have topologies and probabilistic properties that are similar to those observed in the actual Belousov-Zhabotinsky system (Roux et al. 1981).

Higher-dimensional dynamical systems like the KIII model of Freeman and our model for the dynamic association of memory also is sensitive to noise. The KIII model possesses a tiny basin of attraction whose size is reduced to the size of the digitizing unit (around 10^{-16}) due to attractor crowding as the number of coupled oscillators is increased. Such a situation prevents locally unstable states from appearing. Thus noise is necessary to obtain aperiodic orbits stably (Freeman 1997). Our model, which will be introduced in the next subsection, consists of two components, the deterministic system and two kinds of noise terms. The deterministic part consists of a multi-Milnor attractor system whose stability is critical. Hence, without noise terms, its asymptotic solution is like that of a multi-stable state system in the sense that one of the Milnor attractors is eventually selected, depending on initial conditions. However, the dependence on the initial conditions in the present case may be more complicated than in the case of a multi-stable state system. A Milnor attractor is a kind of generalized attractor that may be neutrally stable, as it can possess unstable directions. For further discussion, see section 3.4, and for a precise definition see the Technical Appendix.

Furthermore, contrary to conventional belief, it is possible that digital computation will create spurious periodic orbits (Yamaguchi 1997).

These points suggest that the digital computation of a high-dimensional dynamical system with an excitable element like a neuron or even a neuron population could lead to fatal error. Apparently, the simulation of excitable biological systems demands careful treatment regarding the interplay between deterministic and stochastic components of the system. In the context we consider, it will be fruitful to study systems in regimes in which chaos does not exist but chaotic behavior generated by noise appears and systems that can be stabilized by noise, as in the case of *noise-induced order* in chaotic systems (Matsumoto & Tsuda 1983) and *stochastic resonance* in multi-stable systems (see, e.g., Liljenström et al. 1996). These studies should be more relevant to neurosciences than studies of low-dimensional deterministic chaos, because the brain seems to employ a mechanism by which it distinguishes ordered motion in noisy signals.

3.3. A model for dynamic associative memory

A nonequilibrium neural network model was proposed (Tsuda et al. 1987) to investigate the neural correlate of the dynamic association of memory and dynamic perception. This network consists of two blocks, one (called block I) containing a recurrent net and positive and negative feedback connections whose strengths are randomly fixed, and the other (called block II) constructed from the same network as in block I except for the addition of a specific negative feedback connection (see Fig. 2).

The skeleton of the model was based on Szentagothai's works (1975; 1983) on the network structure of the cerebral cortex. It is likely that the skeleton possesses a structure seen in the mammalian cerebral cortex. In the cerebral cortex, the existence of a recurrent net is insured by a distribution of axon collaterals of pyramidal cells, though only a few neighboring neurons are connected to any given neuron. A Hebbian synaptic learning can be assumed in the network. The existence of a positive and negative feedback to this network is guaranteed by the distribution of stellate cells and basket cells. These neurons can cause a dynamic change of the collective internal states of pyramidal cells. The specific negative feedback existing only in block II may result from specifically formed inhibitory neurons like the Martinotti cells or the axonal tuft cells.

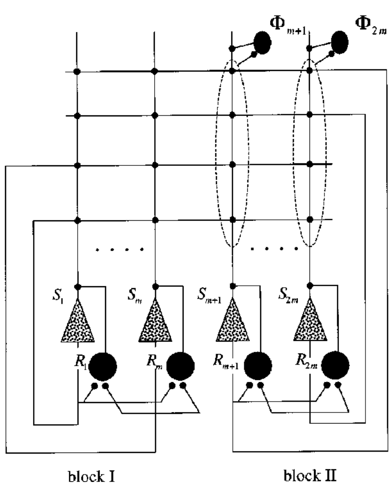

Figure 2. Skeleton network for dynamic associative memory. The network consists of two blocks, I and II. Block I consists of a recurrent network of a pyramidal-type neuron and a network providing global feedback, whose strength is randomly fixed. Block II consists of the same network as in block I with the addition of specific negative feedback connections.

There are several possibilities for the function of the specific inhibitory neurons. We give here three examples.

(1) A pyramidal cell fires, an inhibitory neuron may receive its output and as a result act to reduce the output.

(2) The inhibitory neuron may receive information corresponding to the internal state like the membrane potential of the pyramidal cell and then work to reduce the output of the pyramidal cell with a strength proportional to this internal state.

(3) If the pyramidal cell is in a steady state, the inhibitory neuron may receive such information and then act to inhibit the firing of the pyramidal cell.

In all of these cases, the role of the inhibitory neuron is to temporarily hide the information contained in the state of the pyramidal cell. In our model, the state of the pyramidal cell is reset to the initial state when the information is hidden. The connections between two blocks may mimic intra- and/or inter-cortical connections, where again Hebbian synaptic learning is also assumed.

Two modifications are made in order to see the effects of dendritic and synaptic noise. First, extremely small additive noise terms are introduced to represent dendritic noise. Second, a type of *stochastic renewal of dynamics* is adopted to represent synaptic noise. The second dynamics consists of two independent rules for evolution of which one is selected randomly at each time step. With stochastic dynamics of this type, a neuron does not always output a pulse even if the sum of the inputs exceeds the threshold at a certain time. At a given time, according to pre-determined probabilities, either a particular neurodynamics is selected (i.e., a threshold dynamics is employed), producing some output, or simply the same output as that for the previous time is used. The two maps used here thus constitute a contracting IFS (iterated function system) (Barnsley 1988; Tsuda 1991a). Therefore, the overall dynamic behavior is determined by the parameter that indicates the degree of the instability of the Cantor sets produced by the IFS. This instability is due to the reset caused by the specific inhibitory neurons.

A "chaotic" transition among memories can occur, depending on the values of the assigned probabilities for choice of a specific neurodynamics. If such a probability value is given by the inverse of the number of neurons, then the model is equivalent to the Hopfield model (1982). Thus the existence of steady associative recall is also certain. Increasing the probability, a chaotic transition, (dynamic recall) occurs. This transition in block II is a bit artificial, because of the presence of specific inhibitory neurons, whereas in block I the transition is self-organized (i.e., it is an emergent property of the network), since it occurs even in the case of infinitesimal connection strength between blocks I and II. It should be noted that memories can be represented by an *exotic attractor* in spite of the fact that we use Hebbian learning. If the system is composed of a recurrent net only, then memories are represented by an attractor in the usual sense. The appearance of exotic attractors is due to the introduction of specific inhibitory neurons. In the next subsection, we extend the concept of the attractor. As we will see, the exotic attractor here can be identified with a Milnor attractor.

Choosing an appropriate coordinate, the transition can be described by the critical stage of a circle map, which is known as a typical chaotic map. In Figure 3A and B, we show the one-dimensional map representation of the transition.

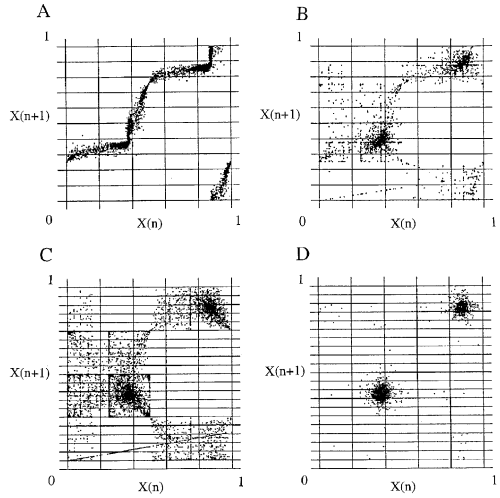

Figure 3. (A) and (B) correspond to a one-dimensional map representation of the chaotic transition among memory traces. (C) and (D) correspond to a one-dimensional map representation of a random transition due to an addition of noise. The abscissa denotes the internal state of the network at a discrete time step n, and the ordinate the internal state at the next time step $n + 1$. In (A) and (C), strongly correlated patterns are learned, and weakly correlated patterns are learned in (B) and (D). The functional relation between the internal states for the present and the next time step is clearly seen, especially in (A). Also, in (B), a skeleton of the one-dimensional map is seen. This is not seen in the case of the random transition ((C) and (D)). The one-dimensional map in (A) provides an emergent dynamic rule for the chaotic transition.

The dimension of the transitions is a decreasing function of the correlation among memories (Tsuda 1992). Compared with this chaotic transition, a random transition among memories occurs in a deterministic network with dendritic noise only, which is depicted in Figure 3C and D. This situation is equivalent to the case of simulated annealing.

Following the study producing Figure 3, a similar chaotic transition has been observed in other network models, for instance, in chaotic neural networks with refractory periods (Adachi & Aihara 1997; Aihara et al. 1990), in neural networks with dynamic masking (Körner et al. 1989; 1991), in associative networks with memory of the limit cycle type (Nara & Davis 1992; Nara et al. 1995), in associative cognitive networks controlling robot movements (Tani 1992), and in a modified Hopfield network for the travelling salesman problem (TSP) (Chen & Aihara 1995; Nozawa 1994; Tokuda et al. 1997). (See also Horn & Opher 1996 as an independent but similar study.)

From these studies, it has been found that such chaotic transitions can be used for problem solving in various fields. We discuss below basic functions of networks exhibiting this type of emergent property.

In this article, we would like to propose several hypotheses regarding dynamic memory and perception, based on the results of our investigation of several model systems. Then, a basic network model is constructed using in one case a modified recurrent net like the one treated in this subsection, and in another case a unidirectional coupling (a skew product) of an unstable network with a stable network, where a chaotic network like the one treated here can be adopted as the unstable network.

Before proceeding to the main topic, the introduction of new concepts of high-dimensional dynamical systems is necessary. The next three subsections are devoted to this. First, in the next two subsections, we discuss the concept of *chaotic itinerancy,* which was proposed in order to capture the essence of complex transitions in high-dimensional dynamical systems.

3.4. Chaotic itinerancy, ruins, and Milnor attractors

We proposed the concept of *chaotic itinerancy* as a universal dynamical concept in high-dimensional dynamical systems (Ikeda et al. 1989; Kaneko 1990; Tsuda et al. 1987; Tsuda 1991a; 1991b). In low-dimensional dynamical systems, which have been adopted as a tool for the interpretation of neural activity, four classes of attractors are known: fixed points, limit cycles, tori, and strange attractors. They are used to represent a steady state, a periodic state, a quasiperiodic state, and a chaotic state, respectively. Chaos can be characterized by the presence of a positive Lyapunov exponent, which represents the orbital instability defined by the exponential increase of separation of nearby orbits on average. With this characterization, chaos can exist also in high-dimensional dynamical systems. One example is hyper-chaos, which is characterized by the presence of more than one positive Lyapunov exponent (Rössler 1983). The chaotic transition among memories discussed above, however, leads us another type of chaotic behavior.

Let us imagine a multi-stable system of high dimension. As long as each of these stable states is represented by an attractor, one attractor is separated from the others by separatrices, forming a basin of attraction. Then, the asymptotic behavior corresponds to one such attractor, depending on the initial conditions. What happens following the destabilization of the system? If the instability is sufficiently strong, many chaotic modes appear, and consequently the system moves toward a turbulent state, that is, a very noisy macroscopic state. In this case, not even a "trace" of the original attractors remains. (The present meaning of the word "trace" is made clear below.)

If, however, the instability is not so strong, an intermediate state between order and disorder can appear. The dynamics of such a state may be regarded as those of an itinerant process, indicating a correlated transition among states. Here, the state of the system before the instability corresponds to an attractor, but after the appearance of the instability this is no longer the case. In this case of weak instability, a crucial characteristic is that a "trace" of the original attractor remains in spite of the generation of unstable directions in the neighborhood of the attractor. Such an itinerant process often becomes chaotic. A destabilized attractor is called an *attractor ruin,* and the corresponding overall behavior is called *chaotic itinerancy* (Fig. 4, see also Technical Appendix). In this situation, an attractor of the destabilized system consists of a collection of attractor ruins and itinerant orbits connecting attractor ruins. We refer to this new type of attractor as an *itinerant attractor.*

Attractor ruins are closely related with Milnor attractors (Milnor 1985). A Milnor attractor is a kind of generalized attractor that may possess unstable directions. A Milnor attractor is defined as a minimal limiting set whose initial points possess positive (Lebesgue) measure, and hence the presence of unstable directions is allowed (see Technical Appendix for precise definition). It should be noted that a Milnor attractor is a limiting set, but dynamical orbits can escape from it due to small (even infinitesimal) perturba-

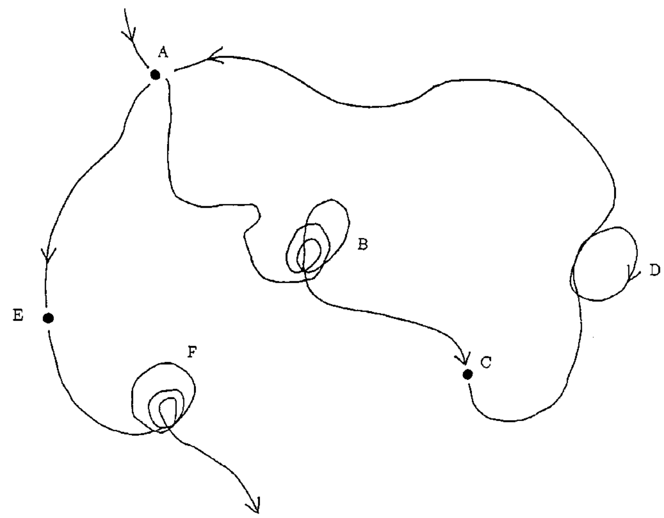

Figure 4. Schematic drawing of chaotic itinerancy. Dynamical orbits are attracted to a certain attractor ruin, but they leave via an unstable manifold after a (short or long) stay around it and move toward another attractor ruin. This successive chaotic transition continues unless a strong input is received. An attractor ruin is a destabilized Milnor attractor, which can be a fixed point, a limit cycle, a torus or a strange attractor that possesses unstable directions.

tions. A trivial but typical example of a Milnor attractor is a fixed point in a map at a tangent bifurcation (i.e., a saddle-node bifurcation). Such a map and point are depicted in Figure 5. In this Figure, the fixed point p is the unique asymptotic state for any starting point. A similar structure of phase space is observed in a one-dimensional map representation of the chaotic association of memories (see Fig. 3A), but in the case of chaotic transitions, the Milnor attractor collapses due to the nonlinear interactions and stochastic renewal of the neurodynamics. Figure 6, which is a two-dimensional representation of the transition, also shows the flow in the neighborhood of degenerate attractor ruin. In this figure both the dynamic inflow and outflow of orbits can be seen.

In the case of neither noise terms nor dynamical interactions among variables, the orbits approach a Milnor at-

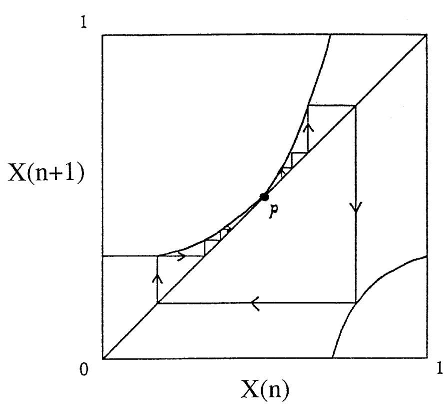

Figure 5. The simplest Milnor attractor in a one-dimensional map. The absissa denotes a state at a discrete time step n, and the ordinate a state at $n + 1$. There is only one fixed point, p, in this map. This fixed point is a unique asymptotic state for any starting point.

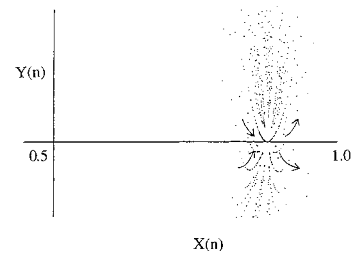

Figure 6. A two-dimensional representation of a chaotic transition. Arrows denote the direction of motion. The dynamical orbits approach a fixed point, but they then escape from it. Hence the fixed point can be regarded as a ruin of a Milnor attractor.

tractor, even if this Milnor attractor is embedded in a higher-dimensional space. Instability due to dynamic interactions or noise is thus necessary for the appearance of chaotic itinerancy. The structure of phase space in the neighborhood of attractor ruins is complex, and this structure may be related to *riddled basin boundaries* often appearing in multi-attractor systems (Grebogi et al. 1987; Kaneko 1997). It is plausible that such a complex boundary is destabilized and comes to chaotic orbits connecting attractor ruins.

A transition through chaotic itinerancy is topologically quite different from a transition resulting from noise in multi-attractor systems. In Figure 7 the schematic drawing clarifying the difference is shown. In the latter, which has been dealt with in previous studies, the external noise is necessary to obtain the transitions. On the other hand, in the former, the entire phase space is decomposed into several subspaces, and in each subspace the system is stable, as characterized by the Lyapunov exponents within each subspace, but in a direction normal to a subspace the system is unstable, as characterized by the "normal" Lyapunov exponents. Since for each subspace the normal Lyapunov exponent is positive, the set representing an asymptotic state of the dynamics restricted to each subspace is unstable, and thus it is not an attractor in the conventional sense. It is, however, a Milnor attractor.

One may think that a Milnor attractor is structurally unstable, as it exhibits such critical behavior as that appearing in saddle-node bifurcations. It is not difficult, however, to construct a model in which a change of parameter values preserves such a critical regime. Actually, only the bifurcation parameter in our neural network model is given by the probabilities determining the renewal process of mappings, and Milnor attractors are preserved through the change of the other system parameters, such as the connection strength of nonmodifiable synapses and input biases. Thus chaotic itinerancy is represented in a quite different manner from stochastic transitions caused by external noise in the attractor landscape. "Pasting" subspaces together (shown in Fig. 7B) on the time axis according to the development of the dynamics, one can understand the concept of an *epigenetic landscape,* proposed by Waddington, in which dynamics are embedded.

3.5. Information structure of chaotic itinerancy

The information structure of chaotic itinerancy may provide foundation for description of dynamic information processing in the brain. Since chaotic itinerancy has actually been observed in animal motivated learning (see for ex-

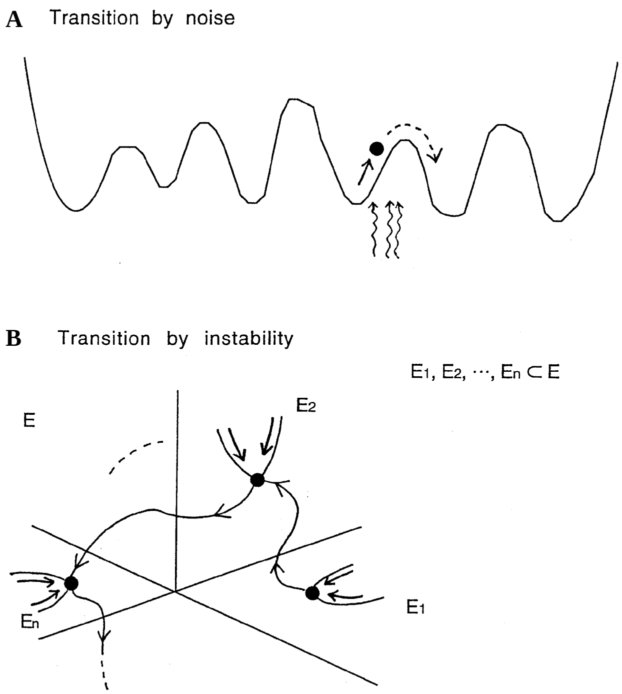

Figure 7. The difference between transitions created by producing chaotic itinerancy and by introducing noise. (**A**) A transition created by introducing external noise. If the noise amplitude is small, the probability of transition is small. Then, one may try to increase the noise level in order to increase the chance of a transition. But this effort is not effective because the probability of the same state recovering is also increased as the noise level increases. In order to avoid this difficulty, one may adopt a simulated annealing method, which is equivalent to using an "intelligent" noise whose amplitude decreases just when the state transition begins. (**B**) A transition created by producing chaotic itinerancy. In each subsystem, dynamical orbits are absorbed into a basin of a certain attractor, where an attractor can be a fixed point, a limit cycle, a torus, or a strange attractor. The instability along a direction normal to such a subspace insures a transition from one Milnor attractor ruin to another. The transition is autonomous. Recently, Komuro constructed a mathematical theory of chaotic itinerancy with the same idea as demonstrated in (B), based on the investigation of itinerant behavior appearing in the coupled map lattices found by Kaneko (Komuro 1999).

ample, Freeman 1995a; 1995c; Kay et al. 1995; 1996), it may be possible to use it for the *dynamical interpretation* of cognitive processes. We investigated the information processing of neural networks in the case that the network exhibits chaotic itinerancy, drawing on the information theory of chaos (Matsumoto & Tsuda 1985; 1987; 1988; Nicolis 1991; Nicolis & Tsuda 1985; Oono 1978; Shaw 1981). We summarize this investigation below.

3.5.1. Dynamic retention of information. *Information is dynamically preserved in the chaotic behavior of a network of nonuniform chaos* (Matsumoto & Tsuda 1987; Tsuda 1992).

There exist neurons whose activity is characterized by the skewness of the distribution of interspike intervals caused by the skewness of the distribution of membrane potentials. The latter skewness stems from the excitability of the membrane. For this kind of system, the amount of information contained in the initial distributions, which is measured by the mutual information between states of the system, slowly decreases in the form of an exponential or power law in time. Here, the mutual information between states indicates the information existing commonly in both states. When information given in the form of probability distributions is fed into a network of such chaotic neurons, it is found that the information propagates in the network without loss. This property has been demonstrated in a general framework.

3.5.2. Learning capability. *The learning capability of neural networks increases in the presence of chaotic itinerancy.*

This proposition is based on a numerical study of Hebbian learning (Tsuda 1992). Since Hebbian learning works locally in phase space, it usually strengthens the stability of learned patterns. Hence, superfluous learning representing learning beyond a critical capacity of memory simply strengthens one particular memory, or destroys most memories. Chaotic itinerancy as a dynamic process of a network endows Hebbian learning with a different feature. Let us define the critical memory capacity of a network as the largest number of memories in the case of usual associative network learning, in which only a single association of memory for a single input occurs. Our model network exhibits successive association represented by chaotic itinerancy as well as this single association, depending on the value of the system's parameter, that is, the probability value for choice of the dynamics. Thus, one can compare the memory capacity in succesive association with that in single association. We found about a fifty percent increase of the capacity in the case with chaotic itinerancy, compared to the case without chaotic itinerancy.

How can chaotic itinerancy save the network from "Hebbian break" described above? Since the state of the network continually changes even under learning so that the dynamical orbits link memory states, the dynamical paths linking memory states are also strengthened in spite of the locality of Hebbian learning. Thus, superfluous learning is possible, implying that the memory capacity is beyond the conventional capacity. This scenario has been verified by another numerical experiment in which random transitions among memory states induced by noise occur, though the orbits become uncorrelated due to noise. Actually, we did not find an increase of memory capacity in this experiment (Tsuda 1992).

3.5.3. Pattern recognition. *Neural networks exhibiting chaotic itinerancy can judge whether or not any input is close to one of the memories.*

Let us assume that a memory is represented by the state of a neural network *independently* of context (this is the vector representation). The closeness between two representations can be expressed, for instance, by their inner product. Numerical simulations have shown that the network outputs a particular memory if the input is close to this memory, whereas it outputs chaotic itinerancy if the input is far from all memories (Tsuda 1992). This characteristic of the network dynamics is independent of the type of embedded patterns and the input patterns.

3.5.4. Pattern search. *Neural networks exhibiting chaotic itinerancy can perform an effective search of memory.*

Distinct from a random search with noise and a simulated annealing with sophisticated noise, a pattern search with chaotic itinerancy is quite effective because of the formation of internal rule linking memories. In chaotic itinerancy, a dynamical rule for linking orbits emerges. This rule gives rise to a causal relation among memories. The numerical calculations demonstrated that the memories close to each other are likely linked. When one wishes to obtain a certain memory state as an output of a network but has only incomplete information regarding this memory, it is necessary to search in memory space with only this partial knowledge. A random search follows chance, and simulated annealing requires sophisticated noise whose amplitude is controlled by both the current state of the network and the potential landscape. A search with chaotic itinerancy, on the other hand, simply follows a dynamically changing rule created in the network, which provides a dynamic relation among memories. Thus the memory in question is output after several linking stages. This characteristic of chaotic itinerancy has actually been used to effectively solve the travelling salesman's problem (Chen & Aihara 1995; Nozawa 1994; Tokuda et al. 1997) and also to provide an effective method for pattern recognition (Nara et al. 1995).

3.5.5. Simultaneous process of learning and recall. *Neural networks exhibiting chaotic itinerancy can simultaneously perform learning and recall.*

In conventional neural network models, the learning phase and the retrieval of memories phase must be split in order to avoid creation of spurious memories. In other words, if these phases are not split, spurious patterns are also memorized. As a result there is serious confusion of "true" memories and "spurious" memories. On the other hand, the presence of chaotic itinerancy permits this simultaneous performance of learning and retrieval. In this case, no confusion results, since spurious memory states inevitably produced during the learning constitute dynamical orbits which link "true" memories (Tsuda 1992; 1994).

3.5.6. Representation by process. *Memory is represented not by a state but by a process.*

Memories formed in a network model via a Hebbian learning algorithm are represented by states. When a neural network is described by a dynamical system, the state can be expresssed as an attractor. As we have shown in studies of such models, however, memory is in general described by a Milnor attractor, which is not always an attractor in the conventional sense. Then a "trace" such as that consisting of an attractor ruin is a representation of memory and the memory trace is manifested through the transition process. Here the transition process, that is, the linking process of ruins, is reasonable. In other words, memories are realized only when they are linked to each other.

3.5.7. Indistinguishability. *Memory and information processing cannot be distinguished.*

Regarding Proposition 3.5.6, in our conscious experience, memories are always manifested in the *current* process of cognition. This view has been proposed by a number of people. Among them, Elman (1990), in discussing dynamic memory in the context of machine learning of language, asserted that memory is inextricably bound up with the rest of the processing mechanism. Goldman-Rakic (1996) also asserted, through her neurophysiological studies, that a *working memory* can be classified as so-called short-term memory, but it cannot effectively be distinguished from the working *process.* Our studies support the plausibility of this indistinguishability.

Let us now discuss the biological significance of the above propositions. The olfactory bulb receives odor input, but the correlation between the bulb's activity and the behavior of the animal in question stems not from external input but from internal input coming from the olfactory cortex, hippocampus, and amygdala (Bressler & Freeman 1980). This feedback information generates chaotic activity of the bulb (Freeman 1987). Thus, the bulb can be regarded as an *interface* between the external odorant world and the internal odor world. Here, dynamic behavior like chaotic itinerancy is likely generated as an interfacial dynamics (Rössler 1987) which facilitates the formation of coordinates where external inputs are compatible with internal images.

Such interfacial dynamics can be seen in other areas where "higher" and "lower" level information meet. The hippocampus-parahippocampus system is one possible such area in the sense that here the neural activity of the frontal cortex meets the sensory inputs. A neuron in the frontal cortex generates only a few spikes per second, and even in the sub-areas directly connected to the motor cortex a neuron exhibits at most a few tens of spikes per second, whereas a neuron in the sensory cortex can usually generate a few hundreds of spikes per second. If a dynamical system or a noisy dynamical system is responsible for the firing mechanism, chaotic itinerancy is expected to exist, because it can also be generated by the interaction of the dynamical system with distinct timescales (Okuda & Tsuda 1994). Furthermore, massive recurrent connections controlled by inhibitory neurons in the CA3 of the hippocampus can act as a dynamic associative network like our model. Thus, we anticipate that chaotic itinerancy facilitates the formation or collapse of memory traces, controlled by a certain marker, generated probably in the frontal cortex, such as "somatic marker" of Damasio (1995; 1996). Actually, chaotic behavior has been found by Hayashi in CA3 neurons (Hayashi & Ishizuka 1995), and it has also been shown that the spatio-temporal representation of information is embedded in at least CA1 (Tsukada et al. 1996). Tsukada et al. found that the information encoded in the higher order statistics (at least 2nd order) of spike sequences can be extended as spatial information of the hippocampus CA1. Taking into account these points, it is likely that Propositions 3.5.1–3.5.5 hold in the hippocampus-parahippocampus system.

Another possible area for interface is the inferotemporal cortex, where a complex figure is represented by neural activity for some short period (Miyashita 1988; 1993; Miyashita & Chang 1988).[2] In order to perform a task, an animal must retain an image of the key figure until the next cue comes. Since retention can be viewed as a concurrent process of storage and recall, it is likely that the experimental conditions themselves force the animal to simultaneously carry out the write-in and the read-out of the information concerning this key figure. From the fact that neural networks with chaotic itinerancy can dynamically preserve an external input and can perform the concurrent process of the write-in and read-out of information, Miyashita's finding suggests that Propositions 3.5.1 and 3.5.5 hold in the inferotemporal cortex. Such a concurrent process can also be observed in a stable network driven by a chaotic network. This point will be discussed in the next subsection.

3.6. SCND attractors and Cantor coding

Our next concern is another type of dynamic behavior that generically appears in a chaos-driven contracting system. Here we treat unidirectionally coupled networks, where an unstable network generating chaotic behavior plays the role of a "driver," and a stable network plays the role of a "receiver." In other words, this system consists of a stable network driven by a chaotic network. This kind of network appears as a unidirectionally coupled network from CA3 to CA1 (CA3 → CA1) in the hippocampus and also as a forward network from the olfactory bulb to the prepyriform cortex. These two systems are our concerns in this article. A unidirectionally coupled network also appears more commonly in, for example, the prefrontal cortex → the motor cortex, and the visual cortex → the temporal cortex. There could be feedback loops in most areas, but it is plausible that the forward pathways (looked at from primary sensory levels toward higher cortices) are used to send a basic code for the information, while the backward pathways are used to send the code for the context. The presence of feedback loops does not lead to a contradiction of the discussion below if the forward system is contractive and the backward system is unstable.

Chaos-driven contracting systems possess another type of attractor called SCND (*s*ingular-*c*ontinuous but *n*owhere-*d*ifferentiable) attractors (see Technical Appendix). It would be particularly interesting to see the information structure embedded in the stable network when the unstable network acting as a driver exhibits a sequence of events via chaotic itinerancy, because such a coding may be related with the formation of "episodic" memory and primitive "thoughts" processes.

The SCND attractor is an attractor represented by a SCND function (Rössler et al. 1992; 1995; Tsuda 1996; Tsuda & Yamaguchi 1998). The precise definition of a SCND function is given in Technical Appendix; here it is enough to think of a fractal image on a discrete set like a *Cantor set* (see Technical Appendix) as a graph of such a function. In chaos-driven contracting systems, no one can see an attractor itself, since it appears in a slow dynamical process in which the discrete set like the Cantor set is generated in some cross-section of a differentiable dynamical system. Only finite subsets, each of which contains a finite number of elements, can be observed.

The dimension of a SCND attractor exceeds its topological dimension[3] by more than 1, whereas the difference between two dimensions in a conventional strange attractor is less than 1. Thus the SCND attractor is "fat," distributed in a wide domain of phase space. This dimensionality insures the robustness of coding on the attractor, which is discussed below.

Rössler found a mechanism for the emergence of this kind of attractor (Rössler et al. 1992). In a simple neural network model, we recently demonstrated the presence of such an attractor (Fig. 8).

The SCND attractor generally appears in a contracting space when contracting dynamics are driven by chaotic dynamics, provided that the speed of contraction in the former is lower than the largest speed of expansion in the latter. It could thus be observed in stable neurons or neuron assemblies that are connected with chaotic neurons or neuron assemblies.

In our study, a SCND attractor generated in the membrane potential of an excitatory neuron is fragile with respect to external noise, but that generated in the membrane potential of an inhibitory neuron is robust with respect to noise. Therefore, it has been predicted that the SCND attractor will be observed in the potential of inhibitory neurons which are driven by chaotic neurons (Tsuda 1996).

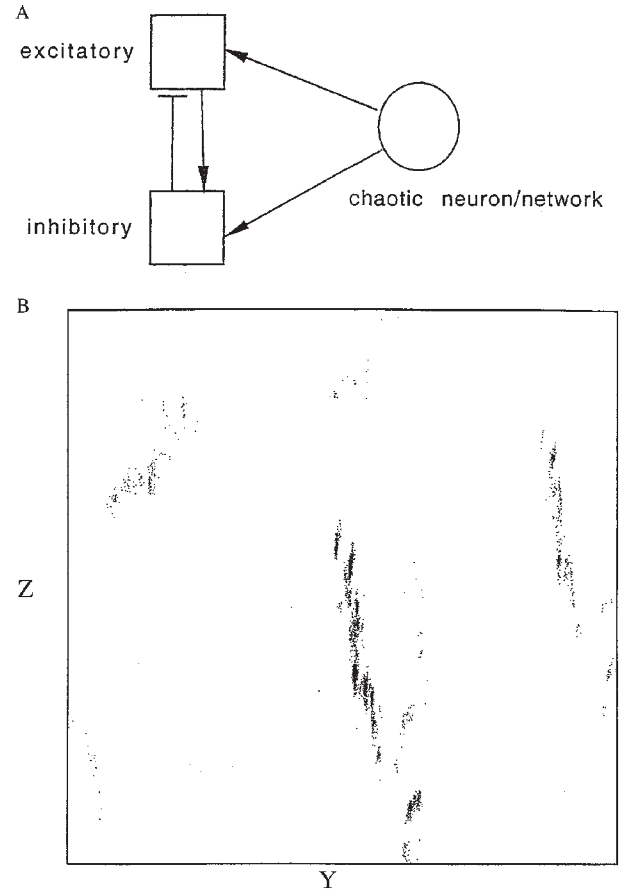

Figure 8. (A) A schematic drawing of the model exhibiting SCND attractors consisting of three neurons/neural networks: one is a chaotic neuron/neural network and the other two are stable excitatory and stable inhibitory neurons/neural networks. The stable neurons/neural networks' activities form a contracting subspace. (B) An example of SCND attractors.

Nearby orbits in phase space become separated due to expanding dynamics and approach each other again due to contracting dynamics. In chaotic dynamics, nearby orbits become separated on average. This results in the presence of a positive Lyapunov exponent. From the information theoretical point of view, expanding dynamics can act as the read-out process of information, and contracting dynamics can act as the write-in process. Because in chaotic dynamics the expanding and contracting phases depend on the position in phase space, the read-out and write-in processes appear successively in the time series. The presence of a positive Lyapunov exponent indicates that the overall dynamics on average represent the read-out process of the information contained in the initial conditions.

On the other hand, in chaos-driven contracting dynamics, the information read out by chaos is written in the contracting subspace by the contracting dynamics. More concretely, symbol sequences created by chaos are encoded as an element of the set in the contracting subspace. A code table is thus formed on the SCND attractor. Actually, the one-to-one correspondence between the symbol sequence generated by chaos and the position of Cantor elements has been elucidated (see Fig. 9).

The coding scheme in this study reminds us of the coding scheme employing a fractal image generated in iterated function system (IFS) (Barnsley 1988), and also of the coding scheme employing the Cantor set in recurrent neural networks (RNN) (Elman 1990; 1991; Kolen 1994a; 1994b; Pollack 1991). The former work presents a method of compressing spatial patterns, whereas the latter works present a method of encoding temporal patterns. According to the *totally disconnected IFS theorem* proved by Barnsley, if and only if there is no overlap in fractal images constructed by any two invertible maps which constitue a contacting IFS, the IFS is totally disconnected, and hence the unique coding. Kolen (1994a; 1994b) proved that a type of second order RNN known as sequential cascaded network is equivalent to the set of affine transformations of an IFS if the transformation function is linear, so that the theorem is applicable to Cantor coding even for temporal patterns.

In our system – a chaos-driven contracting system – a strong contraction can allow the existence of non-overlapping elements of the SCND attractor, but overlapping is determined by the nature of the nonlinearity responsible for the existence of the chaotic behavior in the system under study. Thus it is not easy to quantify this condition. If we do not use chaotic dynamics but simply a random number generator as the driver, this overlapping problem can easily be solved, since the only condition for the existence of a unique coding scheme is the strength of contraction. On the other hand, if a contracting IFS is used as the receiver, the existence of a unique coding scheme is possible even in the case that chaotic dynamics are used as the driver, due to the presence of forbidden symbol sequences resulting directly from the grammatical structure of symbol sequences inherently embedded in the chaotic dynamics. With the same contraction strength as in the above case, the use of uncorrelated random noise, such as white Gaussian noise, may bring about overlapping fractal patterns. In such a case, the coding is only defined up to some finite number of significant digits (Ichinose et al., preprint; Ryeu et al., in press).

In the context of the machine learning of languages, Elman (1990) reconstructed a hierarchical structure embedded in the input word sequences as snapshots of the internal states of some RNN during the process of the input. Pollack (1991) found that a Cantor coding can be realized in recurrent neural networks as a dynamical recognizer. These two studies are within the framework of PDP (parallel distributed processing) (Rumelhart & McClelland 1986). Their noteworthy finding is that the hierarchy of a Cantor set is generated in the phase space of the neural network which can encode a grammatical structure of English sentences.

The noise effects for the SCND attractor can be investigated using physical quantities such as the dynamical entropy and mutual information. These quantities have been computed up to the limit of digital computations, which is demanded to obtain precise values (Tsuda & Yamaguchi 1998). For a small amount of noise (up to $\sim 10^{-4}$ for a system size of 1), it was found that these quantities do not change to a precision of 6 significant figures. On the contrary, these quantities decrease, as increasing the noise level up to $\sim 10^{-3}$. The computations at this noise level reached the computation limit. Although the mechanism responsible for this kind of stability of the attractor with respect to noise is still under study, it is certain that the state corresponding to a Cantor set can be observed even in noisy environments. In dynamical systems without noise, a measure-zero set, like a Cantor set, can be observed as a limiting state if it is dynamically stable. If the contraction rate in a dynamical system with noise is sufficiently large, compared with the amplitude of noise, even a measure-zero set is observable. Furthermore, since the SCND attractor is widely distributed in phase space because of its dimensionality mentioned above in contrast to a conventional Cantor set, the size of the overlapping region due to noise is reduced. This results in a reduction of the ambiguity of the code. These factors account for the effectiveness of the code on a measure-zero set.

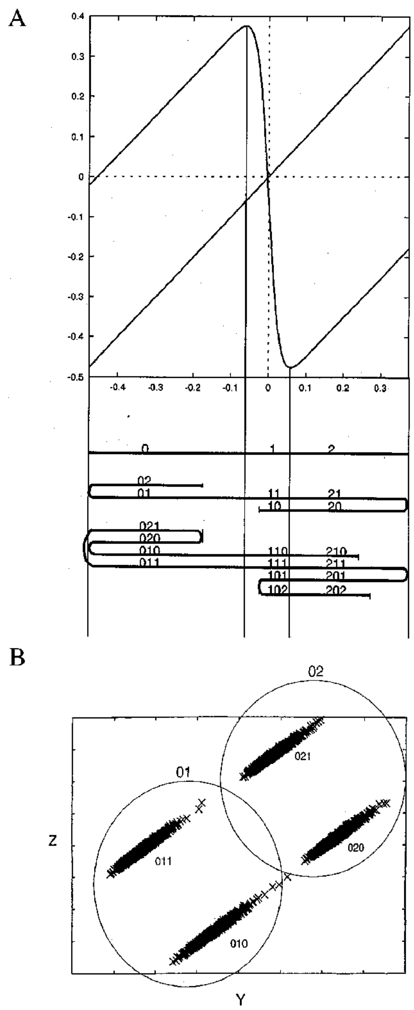

Figure 9. The hierarchical structure of an SCND attractor represented by symbol sequences encoding chaotic orbits. (A) The chaotic neuron map (Aihara et al. 1990) adopted here can produce symbol sequences consisting of, e.g., 0, 1, and 2. The abscissa denotes the states at discrete time steps n, and the ordinate the states at $n + 1$. Thus the figure is a graph of a one-dimensional map which can represent the activity of a chaotic neuron. Below the chaotic neuron map, the first, second and third transformations of the interval are shown, accompanied by the symbol sequences indicating the labeled orbits starting from the points in the respective subintervals. (B) An example of Cantor coding. Each cluster in the Cantor set has a code generated by a chaotic neuron map. Each cluster contains further depths of hierarchy of code. The second depth is shown in the figure by splitting each cluster.

Our concern with regard to robustness is maintenance of the Cantor coding in the presence of external noise. Since the SCND attractors can be sparsely distributed in phase space because of the dimension gap mentioned above, a code that is fragile with respect to noise easily drops in the Cantor gaps (Siegelmann & Sontag 1994), where no code exists. In this sense, one can judge if a perturbed pattern is the correctly encoded one. Furthermore, orbits slightly perturbed by noise promptly return to their original positions where the dynamical orbits possesses a Cantor code due to the effect of contraction. Therefore, one can observe a Cantor code on the cross-section even in a noisy environment if the rate of the impingement of noise on the system is low compared with that of the development of dynamics. The numerical studies of entropy and information mentioned above also indicate the robustness of the coding scheme, as evidenced by the invariance of entropy and information with an addition of a small amount of noise.

4. Hypotheses for dynamic memory and perception

4.1. Dynamic memory and Cantor coding in the hippocampus

Using the concepts of high-dimensional chaotic dynamical systems discussed in the previous section, we would like to propose here a model for the formation of sequences of sensory events that may suggest the neural correlate of episodic memory (Mishkin 1982). For this, we are concerned with the dynamic behavior of hippocampal networks.

The activity of hippocampal CA3 has been analyzed under isolated but close to physiological conditions, and it was concluded that it is highly probable that the CA3 pyramidal neurons can exhibit chaotic activity under physiological conditions (Hayashi & Ishizuka 1995). If the CA1 neurons are stable in the absence of any input and the CA3 neurons are chaotic, the contracting space defined by the CA1 network will be driven by the chaotic CA3 network via the Shaffer collaterals. It was also recently found that the information embedded in the higher statistics of temporal pattern inputs can be encoded in the real space of CA1 (Tsukada 1994; Tsukada et al. 1996).

The situation can be created in which the positions of elements of the Cantor set in phase space indicate the magnitudes of membrane potentials of neurons, that is, the number of spikes, or local EEG. A local difference of magnitudes in real space brings about a global difference in the network activity via the propagation of waves. Hence the Cantor code in phase space can also be embedded in the spatial pattern of the network activity. Since there are recurrent circuits from the CA1 neuron to the CA3 neuron via the neocortex and the parahippocampal area, the dynamics on the recurrent circuits over such a wide range may work cooperatively to accomplish both encoding and decoding in a single process.

Concerning the long-term potentiation (LTP) in CA1, various artificial stimulations applied to the Shaffer collaterals of the CA3 pyramidal neurons have also been investigated. It was found that chaotic input with long autocorrelation (i.e., *intermittent chaos*) are the most effective for LTP (Tatsuno & Aizawa 1997; 1999).

We here use a simple model as a skeleton network. As a model for the CA3 chaotic network, we adopt our model of dynamic associative memories discussed above or modified version of it. Using this kind of model, we characterize the dynamic features of the CA3 network and its functional relation. As a model for the CA1 network, we employ a stable network consisting of excitatory and inhibitory neurons. An excitatory neuron receives CA3 outputs via Shaffer collaterals and also receives the output of a few neighboring inhibitory neurons. An inhibitory neuron, on the other hand, receives the output of each excitatory neuron.

In our framework, the CA3 network is a device for the generation of a sequence of patterns. The existence of such a sequence is insured by the presence of chaotic itinerancy. The distance between (or the closeness of) memories represented by a spatial pattern of neuron activity can be specified in CA3 by the extent of attracting areas in phase space. Defining the distance between sequences is, however, impossible in CA3, because only the states of a network are basic variables in such a phase space. Therefore, it is reasonable to conjecture that such a definition can only be made in CA1. In fact, it can be made by means of the hierarchies embedded in the SCND attractors, in the same way shown in Figure 9. We have verified the existence of such a hierarchical coding in the model CA1 network of *any* temporal sequence given by the stimulations of the Shaffer collaterals. We have also verified the existence of hierarchical coding in the model CA1 network when the model CA3 network produces a temporal sequence of patterns linked by chaotic orbits. The details of this study will be published elsewhere (Tsuda & Kuroda, in press).

4.2. Dynamic memory and Cantor coding in the olfactory system

The hard-wired condition necessary for the presence of SCND attractors could hold in many areas of the brain. Freeman (personal communication) pointed out as a possible such area the prepyriform cortex for olfaction, which receives synaptic connections from the olfactory bulb, where dynamic activities such as chaotic itinerancy appear. In the prepyriform cortex, the network consisting of excitatory and inhibitory neurons could provide stable behavior and thus could form a contracting space. Thus SCND attractors will be observed in the prepyriform cortex.

Memories of olfactory sensation are created in the olfactory bulb. These memories are expressed as chaotic activities of neuron assemblies. Odor memories may be linked with higher level's functions as well as being directly linked with emotion. Thus odor memories could be associated with episodic memories. Since olfactory information is sent also to the entorhinal cortex, olfactory information is likely abstracted, at least at the level of the prepyriform cortex (see also Fig. 10). Olfactory information could be encoded and decoded concurrently by the combination of chaotic activities in the bulb and SCND attractors in the cortex. In this process, the entorhinal cortex, whose activity also exhibits itinerant transitions among attractor ruins, may act as a type of a history-dependent continuous perception (Kay et al. 1996).

4.3. Episodic memory

Based on the above detailed theoretical and numerical considerations, we now propose an interpretation of the formation of episodic memory (Fig. 11).

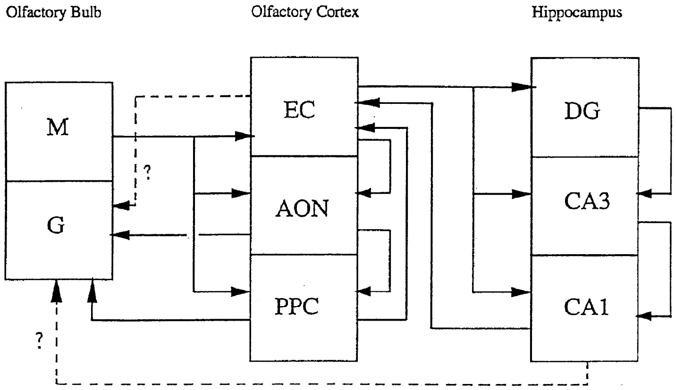

Figure 10. The information flow in the olfactory system (modified from L. Kay 1995). The meaning of the symbols follow. M: Mitral cells, G: Granular cells, EC: Entorhinal cortex, AON: Anterior olfactory nucleus, PPC: Prepyriform cortex, and DG: Dentate gyrus.

Episodic memory is memory concerning the information of individual experiences (Tulving 1972). Here, an "individual experience" is not a series of events which one actually experiences in daily life, but, rather, is identified with the structure of dynamic neural activity created internally that is associated with the sensory input during such events. Thus such an individual experience (or "episode") is dependent on the spatio-temporal context of the individual. It is convincingly argued in reports on H.M. (Scoville & Milner 1957) and R.B. (Zola-Morgan et al. 1986) that the hippocampus is responsible for episodic memory.

In the modeling, it is important to note that the structure of CA3 is very similar to that of the neural network model of associative memory (see, e.g., Amari 1977; Kohonen 1978). Since the work of Marr (1971) there have been many model studies with this structural similarity. These studies are based on the idea that the hippocampus temporarily retains episodic memory as an associative memory (see for example McClelland et al. 1995; Treves & Rolls 1994). Since conventional associative memory models possess attractor dynamics only, an additional mechanism is necessary to create temporal patterns which may represent episodes. As seen in sections 3.3 and 3.4, the presence of inhibitory interneurons satisfies the condition for the generation of temporal patterns. It is known that such inhibitory neurons exist in CA3 (Buzśaki 1996). Taking these points into account, in the present article we further develop the theory of episodic memory.

The situation we consider is that in which a given itinerant chaotic sequence generated by one network gives rise to a unique Cantor coding in another network. Actually, this situation is insured in a certain type of simple neural network model. Furthermore, in our theory for the formation of episodic memory, we associate the above mentioned chaotic network with the CA3 network and the stable one with the CA1 network.

A variety of memory sequences is created in CA3 by means of chaotic itinerancy. In some short period, say on the order of a hundred milliseconds, only a few transitions may occur. For instance, there may be a transition from (semantic) memory P_1 to P_2 via intervening chaotic behavior. We label this transition a_2a_1. This label can be embedded in the Cantor set generated in the space of the membrane potential of CA1. This label is also hierarchically represented by one of the subsets of the whole set. This code is sent to the entorhinal cortex and also to the neocortex. Among the diverse pathways to the neocortex, the pathway to the prefrontal cortex is emphasized here by the property of the close functional relations to the motions, which may be a key to the formation of episodic memory. The connections from CA1 to the entorhinal cortex shown in Figure 10 are used to send this kind of information (see also Tsukada 1992).

It is likely that in the neocortex and also in the entorhinal cortex such a code is stored. Although there must be a difference between the codes of the two cortices – such as

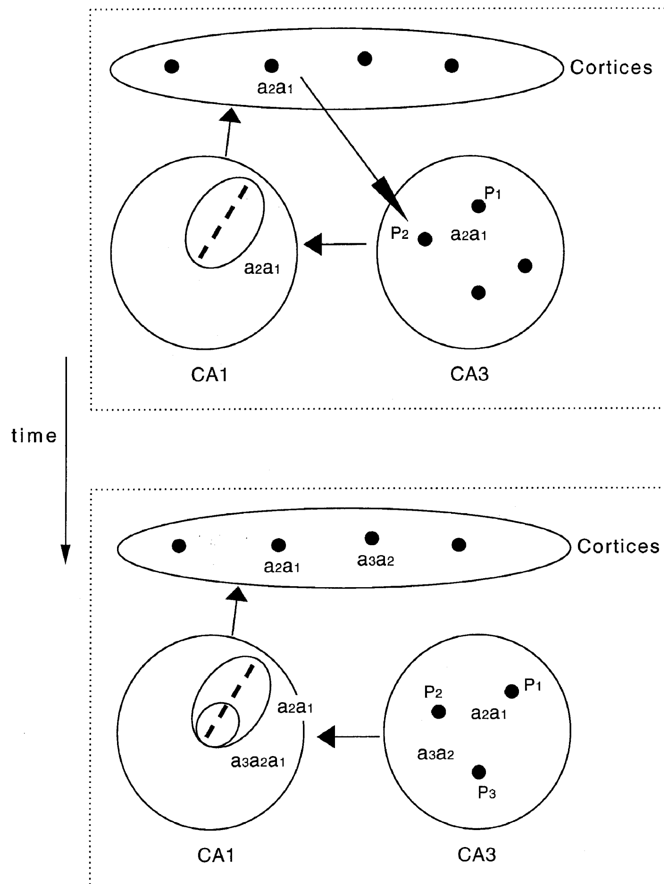

Figure 11. A hypothetical information flow in the formation of episodic memory. Sensory information is temporarily stored as a pattern of the network activity in CA3. However, it is not represented by a conventional attractor, but rather by an exotic attractor, such as a Milnor attractor. The metric in pattern space is measured in CA3 by the extent of the basin of attraction. Because of the instability of Milnor attractors, pattern sequences are generated. These sequences denote the sequence of the experience of sensation. The metric with respect to pattern sequences is defined in CA1 by the Euclidean distance between elements of the Cantor set. This information is sent to the entorhinal cortex and also to the neocortex, where a short sequence of patterns appearing as a result of the transitions during a short period of time (say 100 msec) is represented by, for example, a fixed point of the Milnor type. The transition between these Milnor attractors in the cortices represents a concatination of the transitions. If the most recent pattern appearing in the concatinated sequence is successfully followed by a current pattern in CA3, the correct sequence of sensory experience can be reconstructed.

abstract and inferential in the neocortex and emotional and sensational in the entorhinal cortex – two cortices may play similar roles for the hippocampus, namely giving the *content* of information to the hippocampus (Buzśaki 1996). We thus think that the coding scheme in the two cortices must be similar, though the content, that is the meaning, differs.

Let us assume that the cortices process information temporarily stored in the unstable sub-networks which have structure similar to that of the hippocampus CA3. Then, in the cortices, labels like a_2a_1 can be expressed as a fixed point attractor in Milnor's sense. If an input to hippocampus CA3 with such a label a_2a_1 from the cortices coincides with the instability of P_2 in CA3, then the next transition in CA3 (namely from P_2 to, for example, P_3) is reinforced. If no coincidence between them exists, the input from the cortices to CA3 will disturb the transition process itself in CA3. Another mechanism seems to be necessary in order to avoid the possibility that the matching occurs accidently. A "somatic marker" hypothesized by Damasio (1995; 1996) may provide a mechanism controlling chaos, as mentioned in section 3.5.

The memory sequence $P_1P_2P_3$ is encoded in CA1 in a deeper level of the hierarchy of set than in the sequence P_1P_2. Thus the code $a_3a_2a_1$ embedded in the set in CA1 is sent to the cortices. This stimulation can afford the transition from one fixed point to another, which are expressed by the codes a_2a_1 and a_3a_2, respectively, in the cortices. This transition reinforces the correct sequence of memories. It may provide a mechanism of the formation of *episodic memory.*

We have highlighted so far the Cantor coding of the transition process. One may also propose the Cantor coding of another type, for example, the Cantor coding of memory sequence itself. Then, chaos linking the memories does not manifest in the code sequence itself. We, too, can construct such a model (Tsuda & Kuroda, in press).

In the formation of episodic memory, the relation between pattern sequences in CA3 and the geometory of the Cantor set in CA1 may be flexibly altered, whereas in cortices the alteration of the representation due to structural changes will be slowly varied. In this respect, the hippocampus may be likened to a blackboard: The timing between writing and erasing on this hippocampus "blackboard" and slowly varying transition among symbols in the cortex is a key to the formation of episodic memory. This illustrates the necessity of a long period of time, from a few years to a lifetime, for the complete formation of episodic memory, as can be understood by considering the existence of retrograde amnesia for one to three years as well as anterograde amnesia after hippocampal deprivation (Scoville & Milner 1957), and also after sustainment of a CA1 lesion (Zola-Morgan et al. 1986).

Finally, it is interesting to note the recent work of Tani (1998). Tani found that chaotic behavior appears in the internal states of his recurrent network which controls robot learning when conflicts arise between the bottom-up perception and the top-down prediction. Tani interpreted this chaotic neural activity as an indication of awareness. In our theory, chaos is considered to be a reflection of not only conflicts between the hippocampal and the cortical activity but also of intentionality (Freeman 1999) from the cortex to the hippocampus (also see the Appendix). Furthermore, chaotic itinerancy among semantic memories may reflect a perceptual drift, and therefore it may be the case that the interplay between the cortex and the hippocampus produces episodic memory. If this is true, then the existence of a variety of temporal sequences of semantic memories would be insured in CA3, and the temporal sequences would be encoded hierarchically in phase space of CA1. Also, the Cantor set appearing in CA1 would provide a measure of "distances" between episodic memories.

5. Concluding remarks and outlook

We discussed in this article dynamical models of dynamic associative memory and episodic memory in which chaotic itinerancy and SCND attractors are linked in terms of the Cantor coding. In relation to this, a dynamic mechanism for the concurrent process of the read-out and write-in of information was proposed. The indistinguishability of memory from information processing – thus, perhaps, from cognitive processes – was suggested. This dynamic mechanism and indistinguishability seem to characterize the human cognitive process.

We emphasized the biological significance of chaotically itinerant attractors in high-dimensional systems, but one can raise the criticism that "chaotic" behavior observed to this time in the brain may not be chaotic in the mathematical sense (Freeman 2000; Rapp 1995). Referring to the discussion in sections 3.1 and 3.2, it should be noted that the phenomena we can observe in laboratories can clearly be described as the chaotic behavior of noisy systems, in other words, chaotic behavior in a dynamical system with additive or multiplicative noise or stochastic renewal. Thus it would seem that chaos does exist in the real world in some form, although what we actually observe as chaotic behavior is dependent on our point of view. Also, we note that in an excitable system with sensitive dependence on noise, noisy chaotic behavior can appear due to the interplay between a prechaotic state and noise. Even if mathematical chaos does not exist in such an excitable system, the interplay of the system with the noise may create "chaotic" behavior possessing topology similar to that of some truly mathematically chaotic behavior. For this reason, the model studies are effective to understand the causation underlying chaotic phenomena.

Our theory supports the notion of the dynamic brain, which has been investigated in various contexts, as mentioned in the Introduction. The *chaotic aspects of the brain* described by our theory may change the conventional interpretation of brain functions (see also Freeman & Núnez 1999).

Since Brodmann introduced functional maps of cerebral cortex, it has been believed that it is decomposed into different conceptual areas, each of which is responsible for a specific single function. This belief resulted in the conclusion that the cortical functions can be hierarchically represented by a combination of subfunctions corresponding to these areas (or simply the "sum" of them). This concept of functional localization may lead to another concept that a single neuron is responsible for merely a single representation of information, namely, the concept of "single neuron-single representation."

Although much experimental evidence has been published to support the presence of such a neuron, its existence is still questionable, since other experiments strongly suggest the multiple function of single neurons (Dinse

1990; 1994). The multiple function of an area was also reported for Broca's area (Paulesu et al. 1993). Broca's area has been thought to be related only with writing and articulation of speech, but the activation of the area by inner speech alone has been observed (Inui 1997; 1998; Paulesu et al. 1993). Inui (1997) has pointed out, based on the experimental report of Imamura et al. (1996), that Area 45, a portion of Broca's area, must be responsible not only for the prediction of phonetic sequences but also for the learning and prediction of motor sequences. It can be concluded that the multiple function observed in Broca's area is the result of dynamic interactions between Broca's area and neighboring areas (Inui 1997; 1998).

The notion of hierarchical organization of functional modules and the notion of a direct mapping of the information regarding an environment into the states of a neural net are based on the conventional systems theory, which are summarized as follows:

1. Each function is allocated to a respective element of the system, namely to a neuron or a module. A higher function is obtained by unifying or binding distinct lower functions.

2. A feature of external stimuli (for instance, the orientation of lines, edges, color, etc., for vision) is directly mapped to each neuron or to each module. The processing of information proceeds, taking the combination of such features, which may be realized through synaptic learning.

The dynamic behavior discussed here may, however, lead us to consider aspects of the brain that sharply contrast with those considered within the conventional framework, namely the chaotic aspects of the brain. These can be summarized as follows:

(i) The function of a system's element is dynamically determined so that the entire function of the system is realized. Since this entire function varies in a manner determined by the changing environment and the system's purpose, a function of each element cannot be uniquely determined. Therefore, the functional unit can be varied. Even if a module is organized as a subsystem, the hierarchical structure of modules will not be seen, because the boundary between modules is inevitably altered due to the change of *relations* among elements which depend on the entire function. Thus "heterarchical" structure, referred to as "moiré patterns" by Szentágothai (1978) appears.

(ii) Higher information in the brain is not always represented by the combination of lower information but, rather, represented by dynamic properties emergent via the chaotic activity of neurons and/or the neural network.

Furthermore, if the brain is composed of static functional modules, the organization of distinct pieces of information, or the binding among them (the so-called the binding problem), must be a central issue. If we take the dynamic viewpoint, on the other hand, the binding problem might not be a real problem but simply a *pseudo*-problem, because in this case information representation is dynamically realized as a whole, based on the spatio-temporal organization of the network.

Finally, it is interesting to note the similarity of the chaotic aspects of the brain we have studied with the notion of *dynamic equilibrium* hypothesized by Ramachandran (1998). Ramachandran found evidence of drastic changes of "functional modules," which agree with the concept of a dynamic brain. In a dynamic equilibrium state, there is a time dependence of the states of neurons or neuron assemblies, as determined by the states of neighboring neurons. Consideration of this concept requires that we change the interpretation of a "functional map." The term "dynamic equilibrium" is self-contradictory, since an equilibrium state cannot be dynamic, as no net flow of energy or matters exists. The implication of the term "dynamic equilibrium" is not, however, inconsistent with our assertions.

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Appendix

Chaotic dynamics associated with inference processes

In this appendix, we briefly describe the recent developments in studies on the relation between dynamical systems and logic, in particular the relation between chaotic behavior and deductive inference processes (Basti & Perrone 1992; 1995; Grim 1993; Nicolis & Tsuda 1985).

The dynamical systems studies whose purpose was to relate the neural activity to inference processes have been highlighted since the cybernetics studies of McCulloch and Pitts (1943).[4] They adopted classical logic, and used a so-called "formal neuron," which is now called a "McCulloch-Pitts neuron," as a dynamical device to simulate "thought." A neural network consisting of neurons of this type of can carry out a universal computation in the sense of Turing. In order to capture the complexity underlying inference processes, however, it seems that we need more complex dynamical systems that provide a basis for *analog* computations and also a method of generating "symbols" out of dynamic behavior. For this purpose, we adopted *Tukasiewicz logic,* which is defined on a continuous space of truth values. Using this type of logic, we formulated several dynamical constructs, including a *meta-dynamical system,* which is defined as a set of dynamical transformations of a function whose arguments are dynamical variables. (For further discussion, see below and Tsuda & Tadaki [1997]. Also see Kataoka & Kaneko [2000a; in press b] for a model of meta-dynamics referred to as a [mathematical] functional map.)

We are concerned with neural activity which is assumed to represent mental states. We assume that such neural activity can be represented by vectors. In our theory, "true" and "false" are represented by orthonormal vectors, which thus span a subset of two-dimensional space represented by a unit square. We consider a projection of neural vectors into this two-dimensional space. The component of such a projected vector in the direction of "truth" represents the truth value of the corresponding neural activity (see also Mizraji & Lin 1997). This truth value can be regarded as a dynamical variable in the case of dynamic neural activity.

Taking into account the successive processes of the logical transformation from a *premise* to a *consequence* and the substitution of this *consequence* for the subsequent *premise,* one may describe an inference process as a dynamical system (Grim 1993; Mar & Grim 1991). In the framework employing such processes formulated by McCullogh and Pitts (1945) and recently developed by Mar and Grim (1991), and Grim (1993), a contradictory statement is represented by a limit cycle, while a consistent and self-referential statement is represented by chaos (see also Nicolis & Tsuda 1985). This formulation includes the idea that since a person's capability for self-reference enables him or her to carry out self-reflective action, such a capability seems to guarantee at least the capability of deductive inference. It is reasonable that chaos would emerge in such a process, and this is an assertion of Nicolis and Tsuda, and also an assertion of Grim and Mar. In all theories mentioned above, the direction of scalar projection remains undetermined. In the brain, this direction surely depends on awareness and attention. Its determination is believed to be related to intentionality (Basti & Perrone 1995; Freeman 1995a; 1995b; 1999), but such considerations are beyond the scope of the present theory.

In the manner discussed above, deductive inference processes can be described by a certain class of chaotic dynamical systems. In any given case, this class is determined by the type of presupposed logic. On the other hand, the brain describes the dynamics of the real world surrounding it, and such a description itself must be dynamic. We have attempted to formulate such a description (Tsuda & Hatakeyama 2001; Tsuda & Tadaki 1997). In our formulation, the dynamics of the description are functional dynamics, like those briefly mentioned above. In an extreme case, these functional dynamics possess a fixed point, which implies the existence of a fixed description, independent of the environmental dynamics. This description may be expressed as an "autistic state." In another extreme, unrealistic case, the functional dynamics are identical to the environmental dynamics. In this case, the brain actually copies the dynamics of the environment. The dynamics exhibited by models of machine learning represent such copies.

The actual description generated by the brain should be somewhere between these two extreme cases. If such a description of dynamics follows Lukasiewicz logic, the functional dynamics will be chaotic (Tsuda & Tadaki 1997). Such a functional dynamical system can be compared with the chaotic dynamical system with fuzzy distributions proposed by Grim (1993).

Recently, this manner of thinking has led us to the study of a dynamical description of *syllogism.* (Actually it is better to refer to this as *modus ponens* as it is treated as a separation rule.) We have constructed a theory describing tasks performed in cognitive experiments (Tsuda & Hatakeyama 2001). This theory can also be applied to experiments in which one investigates the correlation between deductive inference processes and internal neuronal dynamics measured as the neural activity at the behavioral level. Interpreting logic in terms of dynamical systems thus should be fruitful as a complement to studies of the emergence of logic from dynamic behavior.

Technical Appendix

1. Order parameters and macro-variables

The term "order parameters" originally appeared in studies of phase transitions in condensed matter physics. These order parameters are used to capture the behavior of a macroscopic ordered state emerging from large fluctuations in a critical regime. For instance, in ferromagnetic materials, in the absence of an external magnetic field the magnetic moment of each atom is randomly distributed above the Curie temperature, so that the net (average) magnetic moment is zero, while below the Curie temperature, a nonzero net magnetic moment appears due to the spontaneous cooperative behavior of atoms. The order parameter used for such a system is defined as the net magnetic moment, which indicate the degree of order. In an equilibrium state, this order parameter is a constant. In relaxation processes from near-equilibrium states, the time evolution of an order parameter is expressed by an evolution equation. The use of such equations can be extended to the case of ordered motion in far-from-equilibrium states and also to the case of many order parameters.

An ordered state can be described by a few degrees of freedom (a few macro-variables), which emerge in the evolution of the system out of many degrees of freedom. These few degrees of freedom are called "order parameters." This concept has been extended to transitions and bifurcations in far-from-equilibrium systems. Haken formulated the slaving mode principle (regarding the behavior of such systems), which is mathematically equivalent to the center manifold theorem. This principle asserts that order parameters (slaving modes) enslave the remaining modes (slaved modes) (see for example Haken 1983). Qualitatively, the manner of thinking employed in this context is that we describe a total system only in terms of its slow motion behavior, eliminating fast motion, and we do this by defining order parameters as the variables governing the slow motion on the center manifold. It should be noted that "slow" and "fast" are used here in a relative sense. In reaction-diffusion systems, for instance, where spatio-temporal organization is taken into account, there is no clear distinction between slow and fast modes. In such a case, by taking into account the diffusion term too as a perturbation, one can extract the macro-variables describing gentle fluctuations.

Because the center manifold theorem (or the slaving mode principle) does not apply to the case of chaotic motion, the macro-variables describing chaotic motion cannot be used as order parameters. In chaotic motion, there exist both "macro-modes," represented by low-frequency components, and "micro-modes," represented by high-frequency components. Hence, it might seem that after rescaling time an "order parameter" would emerge. In chaotic motion, however, there is no clear boundary in frequency space that distinguishes a low-frequency behavior from high-frequency behavior, because of the continuous nature of the spectrum. We note, however, that in chaotic itinerancy, the slow motion exhibited around attractor ruins seems to be distinguishable from the fast motion associated with transitions among ruins. We believe it is important to resolve this conceptual discrepancy.

2. Attractors in the conventional sense and the Milnor sense

Attractors have been defined by using the concept of *attracting sets.* Let X be a compact, or at least finite dimensional, smooth manifold. Let the development of orbits in phase space be given by a continuous map or a diffeomorphism $\phi : X \rightarrow X$. For a set A, the trapping region $N \supset$ A is defined as the region satisfying $A \subset \phi(N) \subset N$. A set A is called an attracting set when

$\bigcap_{i=0}^{\infty} \phi^{(i)}(N) = A$, where $\phi^{(i)}$ is the i-th iteration of ϕ and $\cap$ represents set intersection. An attractor is an attracting set, but an attracting set is not necessarily an attractor. We call a set A an attractor if it is an attracting set and $\phi|A$ is topologically transitive, so that A cannot be separated into subsets by ϕ. Therefore, all points in the trapping region of an attractor are absorbed, or at least approach the attractor. In other words, any point in this neighborhood approaches the attractor as time (or the number of iterations) goes to infinity. Thus an attractor is a topological concept.

Milnor (1985) defined an attractor from another viewpoint, in which both topological and measure-theoretic concepts play roles. Here we give this definition. Let ρ be a measure equivalent to the Lebesgue measure on X. A compact invariant set α is called a (minimal) Milnor attractor if the following hold: (1) The basin of attraction $B(\alpha)$ of α has a positive ρ-measure, that is, $\rho(B(\alpha)) > 0$. (2) There does not exist a proper closed subset α' satisfying

$$\rho(B(\alpha)/B(\alpha')) = 0$$

According to this definition, a Milnor attractor can possess an unstable manifold.

Many definitions of attractors have been proposed from various points of view in which different properties are emphasized. (See Buescu 1997 for detailed discussion on various attractors, including Milnor attractors.)

3. Attractor ruin

We define an attractor ruin as that which remains after the collapse of a Milnor attractor. If there is no such collapse, the asymptotic behavior of the system is not transitory, but rather the behavior corresponding to the Milnor attractor. Thus for the emergence of itinerant behavior another instability is necessary.

4. Chaotic itinerancy

The mathematical study of chaotic itinerancy has only recently begun, and for this reason, its definition has not yet been established. After the present author, together with Ikeda and Kaneko (Kaneko & Tsuda 1996; 2001) found complex but ordered itinerant behavior in a variety of high-dimensional dynamical systems, and we recognized such behavior as possessing common characteristics, we considered the analogy between such behavior and that expected to appear in two interacting subsystems, one of which possesses many more degrees of freedom than the other. In such a situation, it is possible that the smaller subsystem would reach a certain stable state, influenced by the larger subsystem, but through the feedback from the smaller subsystem to the larger one, the state of the larger subsystem may change. As a result, the stability of the smaller subsystem could also change. Such interaction seems to allow the appearance of a slow transition among "quasi-stable states" in the smaller subsystem. Phenomenologically, such transitions are often observed as being history dependent or as process dependent.

Another important characteristic we commonly found is the appearance of many zero- or near-zero-Lyapunov exponents.

I introduced in the text one possible mathematical mechanism of chaotic itinerancy. Through this mechanism, the entire phase space is decomposed into several subspaces, and in each subspace the dynamical orbits are attracted to an attractor ruin, as characterized by the negative tangential Lyapunov exponents defined within each subspace. However, in a direction normal to the subspace the dynamical orbits are repelled from such a ruin, as characterized by the positive normal Lyapunov exponents.

5. Cantor sets

A typical Cantor set, called a "ternary set" or a "middle-third set," can be constructed by repeating the procedure of dividing a closed interval equally into three, and removing the middle open set. Let us consider the construction of such a Cantor set from the unit closed interval $I = [0,1]$. The set removed in the first step of the procedure is the middle open interval (1/3,2/3), and thus the remaining intervals are the closed intervals $I_{11} = [0,1/3]$ and $I_{12} = [2/3,1]$. At the n-th step of the procedure, 2^n closed intervals I_{ni} ($i = 1,2, \ldots ,2^n$) are obtained. Then, the Cantor set C is defined by $C = \bigcap_{n=1}^{\infty} C^{(n)}$, where $C^{(n)} = \bigcup_{i=1}^{2^n} I_{ni}$. The Cantor set can also be represented by a set of points in I whose position is represented by $x = \sum_{n=1}^{\infty} \frac{p_n}{3^n}$ where $p_n = 0$ or 2 for each n, hence comes the name ternary set.

The Cantor set is thus the closure of a set of countably infinite number of endpoints of subintervals. In other words, the Cantor set consists of a countably infinite number of uncountable sets on a bounded interval. If one measures this set with a scale of dimension zero, that is, a point, one concludes it has an infinite "volume." On the other hand, if one measures it with a scale of dimension one, one concludes it has zero "volume." It is thus reasonable to think that there is some appropriate scale in terms of which this set has a finite "volume." If such a scale actually exists, it should have "fractal" (noninteger) dimension. The dimension of this scale is considered the dimension of the set itself. In fact, the Cantor set does have a noninteger dimension. An effective method to intuitively understand such an infinite set is to follow the procedure.

In the main text, we did not restrict ourselves to the above described ternary Cantor set, and actually addressed the Cantor set in a more general sense. The Cantor set is generally defined as a *closed, totally disconnected,* and *perfect* set. When a set does not contain any finite intervals, it is termed *totally disconnected.* When every element of a set is an accumulation point, it is termed *perfect.*

6. The SCND attractor

The SCND (singular-continuous but nowhere-differentiable) attractor can be represented by the graph of a SCND function. The SCND function, first studied by Rössler et al. (1992), was defined by Tsuda and Yamaguchi (1998) in terms of singular continuity, and differentiability on the Cantor set (Tsuda & Yamaguchi 1998), where definitions are given below. The following definitions are given for the ternary Cantor set, but they can be extended to the more general case.

Definition: Singular continuity

For the union of intervals I_{ni} ($i = 1,2, \ldots 2^n$) remaining at each step n in the process of constructing a Cantor set C, one can define a continuous function $h_n(x)$ in each interval I_{ni}, namely for $x \in I_{ni}$ for each i. If the functional series $\{h_n(x)\}$ uniformly converges, then we call its limit h(x), with $x \in C$, a singular-continuous function.

Definition: Differentiability on the Cantor set

*The set of right endpoints C_r and the set of left endpoints C_l of subintervals I_{ni} for every i and n are subsets of the Cantor set. That is, $C \supset C_r \cup C_l$. For each $x \in C$, the quotient $\delta_n(x) \equiv \dfrac{h(y_n) - h(x)}{y_n - x}$ is defined, where the series $\{y_n\}$ consisting of endpoints is a monotonically convergent series to x. Then, since Dini's derivatives always exist, if we allow $\pm\infty$, one can define $D^*(x) \equiv \limsup_{n\to\infty} \delta_n(x)$ and $D_*(x) \equiv \liminf_{n\to\infty} \delta_n(x)$, where * denotes a symbol "plus" or "minus." For $y_n < x$, Dini's left derivatives $D^-(x)$ and $D_-(x)$ are defined for $x \in C_r$. Similarly, for $y_n > x$, Dini's right derivatives $D^+(x)$ and $D_+(x)$ are defined for $x \in C_l$. If for any convergent series, $D^-(x) = D_-(x)$ for $\forall x \in C_r$ and $D^+(x) = D_+(x)$ for $\forall x \in C_l$, then we call h(x), $x \in C$, a differentiable function on the Cantor set.*

If for some function the above condition for differentiability is not satisfied at any value of $x \in C_l \cup C_r$, we say that it is a nowhere-differentiable function on the Cantor set.

7. Contracting map under the Hausdorff metric

We dealt with contracting maps in sections 3.6 and 4. The contraction and expansion of a map are defined in terms of some metric. We adopted the Hausdorff metric. Now, let D be a set, which for our purpose is a phase space. Let $H(D)$ be the collection of all nonempty closed subsets of D. For every A and $B \in H(D)$, the Hausdorff metric is defined as:

$$d_H(A, B) := \inf\{\epsilon > 0 | N_\epsilon(A) \supset B, \text{ and } N_\epsilon(B) \supset A\},$$

where $N_\epsilon(\bullet)$ is an ϵ-neighborhood of $\bullet$.

NOTES

1. If the instability in the normal direction is too strong, the system's overall behavior becomes fully-developed turbulence.

2. These authors used the term "fractal" figures in reference to represent complex figures including concave contours and/or nonsmooth curves, but this name is misleading. The figures they defined are not literally "fractal." Even though a procedure to produce fractal figures was used, the figures they used are produced by using only one or two iteration(s). The fractal, which was defined originally by Mandelbrot, must have a noninteger dimension, so that it contains infinitely many copies with various sizes of reduction of the whole figure or its parts, whose reduction is realized by affine transformations.

3. This is the dimension of the support of the attractor.

4. George Boole is, as far as we know, the first person to notice the deep relation between dynamics (recursive maps) and logic, but he used only fixed points (0 and 1) of the dynamical system, $x_{n+1} = x_n^2$, solving the algebraic equation $x = x^2$. Here, x may represent, for instance, "being blue," and the algebraic equation may imply equivalence between the two expressions "being blue" and "being blue and blue." This equivalence class can be expressed as the fixed points of the above dynamical system (Boole 1854).

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Chaotic neurons and analog computation

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Abstract: Chaotic dynamics can be related to analog computation. A possibility of electronically implementing the chaos-driven contracting system in the target article is explored with an analog electronic circuit with inevitable noise from the viewpoint of analog computation with chaotic neurons.

The target article by Tsuda provides intriguing possible roles of chaotic dynamics with exotic attractors like Milnor attractors and SCND attractors in neural networks. Recently, theory of analog computation has been profoundly developing (Blum et al. 1997; Siegelmann 1999). Deterministic chaos is, on the other hand, closely related to real numbers because complexity of real numbers specifying an initial condition is read out dynamically with time by chaotic transformation as typically demonstrated by the Bernoulli shift map and the tent map. This fact motivated engineers to implement chaotic dynamics with analog circuits rather than digital circuits (Chua et al. 1993; Shimizu et al. 1991).

Electrical behaviour of nerve membranes can be described by such "analog" excitable dynamics as the Hodgkin-Huxley equations (Hodgkin & Huxley 1952). It was shown both electrophysiologically with squid giant axons and numerically with the Hodgkin-Huxley equations that the excitable neurodynamics easily generates chaotic response properties (Aihara et al. 1995; Aihara & Matsumoto 1986). In this meaning, biological neurons can be understood as analog chaotic devices.

Characteristics of the chaotic response in squid giant axons are qualitatively modeled by the following simple one-dimensional map of a chaotic neuron (Aihara & Katayama 1995; Aihara et al. 1990) which is used as the chaotic driver of Figure 9a in the target article (Tsuda & Yamaguchi 1998): where $y(t + 1)$ is the internal state of the chaotic neuron at the discrete time $t + 1$, k is the decay parameter, α is a positive parameter, f is the sigmoidal output function and a is the bias related to the external input and the threshold.

Since noise seems to play functional roles in or have influence

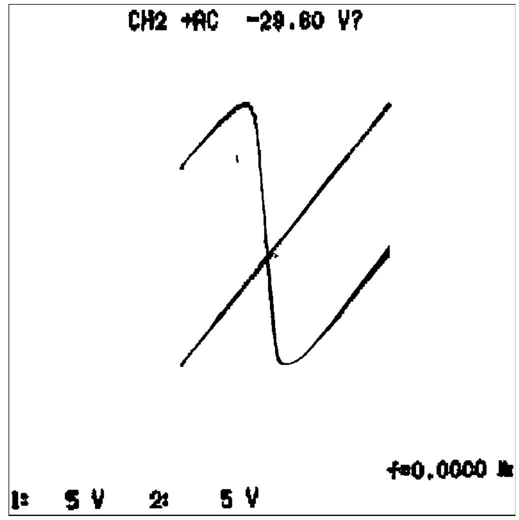

Figure 1 (Aihara & Ryeu). A return plot of a chaotic neuron electronically implemented with an analog electronic circuit.

on generation of the chaotic dynamics with exotic attractors, it may be an interesting problem in implement chaotic neurodynamics with an analog electronic circuit with inevitable noise. Figure 1 demonstrates a return plot of time series generated by an analog electronic circuit implementing the chaotic neuron map with analog discrete devices (Ryeu et al. 2000; Shimizu et al. 1991). Furthermore, several kinds of analog IC with the chaotic neurons have been already designed and fabricated (e.g., Herrera et al. 1999).

Tsuda also pointed out noise tolerance in the Cantor coding in a chaos-driven contracting system (Tsuda & Yamaguchi 1998). Figure 2 demonstrates fractal-like structure observed on the *Y-Z* space in an analog electronic circuit of a chaos-driven contracting system of Figure 3 (Ryeu et al. 2000). The system of Figure 3 is a simplified version of the system shown in Figure 8a of the target article where *EI* is the external input to the chaotic neuron *X* and h_1 *and* h_2 are discontinuous Heaviside transfer functions from the chaotic neuron *X* to the static neurons *Y* and *Z*. *EI* is used to control chaotic dynamics of the neuron *X*. The Heaviside functions h_1

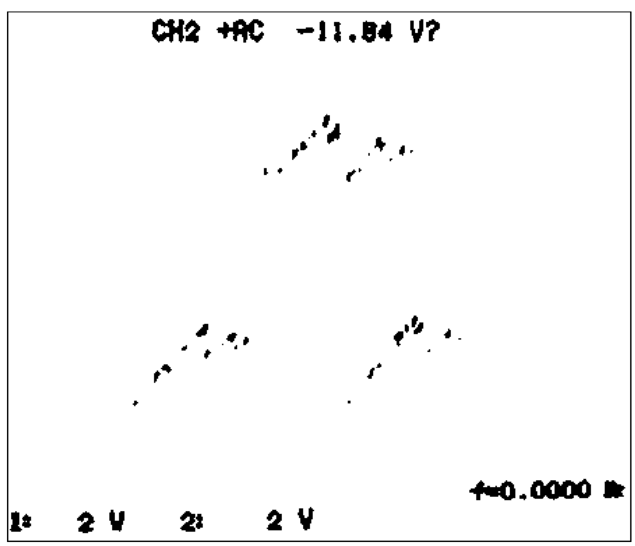

Figure 2 (Aihara & Ryeu). Fractal-like structure observed on the *Y-Z* space in an analog electronic circuit of a chaos-driven contracting system of Figure 3.

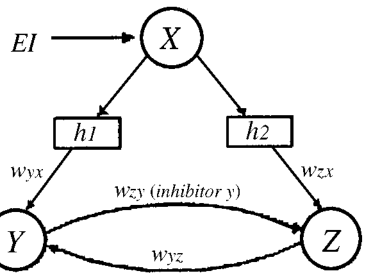

Figure 3 (Aihara & Ryeu). A chaos-driven contracting system with external input *EI* to the chaotic neuron *X* and Heaviside transfer functions h_1 and h_2 from the chaotic neuron *X* to the static neurons *Y* and *Z*.

and h_2, which represent wave-shaping effect of axons with all-or-none thresholds for propagating action potentials (Aihara et al. 1990), make the system simpler by transforming the output of the chaotically forcing neuron *X* from analog values to the digital values of 1 or 0. It may be an important problem to consider whether introducing the discontinuity to the chaos-driven contracting system reinforces stability and robustness of the Cantor coding or not; it is proved that an asymptotically stable attractor for a continuous map on a locally compact, locally connected metric space has finitely many connected components which are cyclically permuted (Buescu 1997). The discontinuity also makes it easier to compare the dynamics of the chaos-driven contracting system with that of iterated function systems (Barnsley 1988; Stark 1991).

It is theoretically found that chaotic neural networks composed of the chaotic neurons (Aihara et al. 1990) can produce spatiotemporal chaotic dynamics with computational ability (Chen & Aihara 1997; 1999; Komuro & Aihara 2000). Although it is a future problem to examine resolution and noise tolerance of the Cantor coding in the chaos-driven contracting system implemented by an analog electronic circuit and explore a possibility to explain mesoscopic and macroscopic patterns of brain activity (Freeman 2000) by the chaotic neural networks, the chaotic dynamics with exotic attractors and the Cantor coding in the target article are quite attractive from the viewpoint of analog computation with the chaotic neural networks in engineering, too.

The roles played by external input and synaptic modulations in the dynamics of neuronal systems

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Abstract: The framework within which Tsuda proposes his solution for transitory dynamics between attractor states is flawed from a neurological perspective. We present a more genuine framework and discuss the roles that external input and synaptic modulations play in the evolution of the dynamics of neuronal systems. Chaotic itinerancy, it is argued, is not necessary for transitory dynamics.

The dynamics of Hopfield networks (Hopfield 1982) are a far cry from that of systems of neurons in the brain. The existence of the energy function ensures that under the guidance of an asynchronous update rule, such networks relax to fixed point attractors. This behavior is not in conformance with that observed in systems of neurons in the brain where limit cycles, let alone stable fixed points, are not encountered. Tsuda's efforts at introducing complex dynamics into such model networks are commendable. His solution, however, is suspect.

Tsuda's system (Tsuda 1991; 1994), an otherwise standard Hopfield network without the symmetric coupling constraint, is endowed with an additional class of specialized nodes that, by his own account, is primarily responsible for the system's unconventional dynamics. It therefore stands to reason that we take a closer look at these nodes.

Roughly speaking, the nodes in the noted class stay dynamically inactive (imparting a constant bias) as the remainder of the system approaches an attractor. If the remainder of the system settles on a fixed point, these nodes spring into action and attempt to dislodge it from that state. The dynamics of the overall system is itinerant when this attempt meets success. Although this constitutes an elegant example of an artificial neural network, the claim of biological relevance seems contrived.

The specialized nodes, in essence, maintain a record of the activity of the system from the most recent instance when it attained a state of equilibrium (however long ago this might have been), and persistently relay this information to the remainder of the network for as long as it takes for it to attain its next state of equilibrium. These are exceptional qualities that cannot be ascribed to any class of neurons in the brain, axonal tuft cells or otherwise.

These observations also throw doubt on the second category of systems that Tsuda proposes (systems that manifest SCND attractors). Both the unstable "driving" network that displays chaotic itinerancy, as well as the multistable "receiving" network that admits multiple fixed point attractors, are untenable from a neurological perspective.

The above arguments are not intended to make a case against chaos in systems of neurons in the brain. On the contrary, our own investigations into the dynamics of systems of spiking neurons (Banerjee 2001a; 2001b) indicate that under normal operational conditions (the state of sparse activity typically observed in the brain), the behavior of such systems is almost surely chaotic; stable periodic, stable quasiperiodic, and stable fixed point behavior almost surely do not occur. Furthermore, analysis of the phase-space structure of these systems has revealed that attractors in such systems are potentially anisotropic (in our framework several Milnor attractors are combined to form one generalized topological attractor, hence the anisotropy).

Our views are, however, diametrically opposed when it comes to the question of *the role of chaos* in neuronal systems. Ingrained in this question is the position that chaos is a likely *remedy* for any of a number of difficult situations that the brain might face during its regular course of activity. This outlook is harmful for it presumes other modes of behavior (such as stable periodic or fixed point behavior) in the brain, all of which remain unsubstantiated after several decades of intensive experimental research (in this regard, the revised views in Freeman & Skarda [1990] are noteworthy). An unfortunate consequence of this outlook has been the creation of several spurious issues with regard to the dynamic aspects of memory. The physical realization of semantic memory is considered different from that of episodic memory based on the erroneous assumption that the former is represented as a fixed point attractor. Although their physical realizations might indeed be different, if such is the case the differences will be found elsewhere.

In what follows, we highlight the profound difficulties that lie before us on the road to a clearer understanding of the dynamics of neuronal systems.

First, any analysis is inherently incomplete should the impact of external input on the neuronal system not be considered. Neuronal systems do not operate in isolation. Whereas the study of an isolated system (or one that receives an initial input following which the dynamics evolves in isolation) does provide insight into the general tendencies of its dynamics, the interplay between the dynamics and the input remains obscure. To illustrate, any cortical column is incessantly bombarded by input from neighboring cortical columns as well as the thalamus. When the impact of this input is taken into consideration, the problem takes on an added dimension of complexity. What was heretofore dynamics in a domain of static attractors, is transformed, at the very least, into dynamics in a domain of evolving attractors. This follows from the observation that input into the system can be regarded as a bifurcation parameter. In this perpetually changing domain, attractors drift, new ones originate, some coalesce, and some disappear. Transition between attractors is effected either by the catastrophic birth of a new attractor around the dynamic state of the system, or by the smooth, albeit relatively fast, drift of an attractor in such a manner that the dynamic state of the system is overtaken by its realm of attraction.

Second, the impact of synaptic modulations on a neuronal system complements the impact of the external input, since it, too, can be regarded as a bifurcation parameter. The deliberations in the previous paragraph, therefore, apply equally well here. Even if the rules that govern synaptic modulations prove to be simple, the corresponding impact on the structures in the phase-space of the neuronal system will, in all likelihood, be nontrivial.

The resultant scenario is therefore one of profound complexity.

The puzzle of chaotic neurodynamics

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Abstract: Experimental evidence and mathematical/computational models show that in many cases chaotic, nonregular oscillations are adequate to describe the dynamical behaviour of neural systems. Further work is needed to understand the meaning of this dynamical regime for modelling information processing in the brain.

Generally speaking, the models of mathematical/computational neuroscience could be categorised into the following sub-classes:

1. Stochastic model. A neural activity is described by a stochastic process. A multi-dimensional stochastic process with interactive components is a typical representative of such models (see, for example, Cottrel & Turova 2000).
2. Deterministic model. This model is based on the axioms of dynamical system (with discrete or continuos time) and time dynamics is completely defined by initial values of the variables and boundary conditions (see, e.g., Ermentrout 1998).
3. Deterministic model with a stochastic component (influence of noise). Usually the noise is eliminated by special filtering or averaging procedures to reduce the model to some deterministic system (see references in the target paper).

The author of the target paper considers the deterministic models with complex behaviour and he has stressed that the oscillatory activity is an important feature of neural activity and experimental evidence confirms this statement. In general, the deterministic (dynamical) system demonstrates the following types of oscillatory dynamics:

(i) Regular oscillations. In this case, a stable limit cycle is the attractor. The system shows one-frequency oscillations nearby this attractor.

(ii) Quasi-periodic oscillations. In this case, a stable torus is the attractor. The system shows two-, three-, or many-frequency oscillations.

(iii) Chaotic (complex, nonregular) oscillations. In this case, a strange attractor exists in the phase space of the system. A power spectrum consists of many frequencies with similar power values.

To generate the chaotic neurodynamic, Tsuda considers the influence of chaotic network on a neural oscillator consisting of excitatory and inhibitory neural populations (see Fig. 8 of the target article). Another natural way to generate chaotic neurodynamics is described by Borisyuk et al. (1995). Irregular chaotic oscillations appear in the system of two coupled neural oscillators with inhibitory to excitatory connections. Strange attractors of different types appear in the phase space under variation of the coupling strength with different scenarios of transition to the chaotic behaviour.

Despite the fact that the importance of complex dynamics for description of neural activity has been recognised in many papers (see the list of the target paper references), the following question is still very actual. "Is the chaotic dynamics an artefact caused by different noise sources in neural tissue or is this kind of dynamics a necessary component for information processing?" If we agree that the chaotic dynamics is not an artefact, then we should put forward some hypothesis about its role in information processing and explain the advantages/disadvantages of such an approach.

The author of target article suggests a new concept of chaotic itinerancy in high-dimensional system that is different from conventional cases with the dynamics described in terms of simple transitions between low-dimensional attractors. However, it is not clear why transitions between strange attractors are more useful for neuroscience than transitions between equilibrium points or between limit cycles. Also, it is not clear what the advantages are (if any) of the Milnor attractor and Cantor coding in comparison to other attractors and coding schemes.

The idea of using transitions between attractors for memorising sequences of events has been exploited by many authors. For example, Baird (1990) has used the bifurcation theory for programming fixed and oscillatory attractors for memorising sequences. Freeman (1991) has suggested a brilliant example of the chaotic dynamics for modelling the olfactory system. The model describes a process of odour recognition as the iterative movement along the strange attractor assembled with many wings relating to different odours. The odour recognition means that the system passes a corresponding wing more often then others. Kryukov et al. (1990) suggested that the attractors of neural dynamics are represented by metastable states that are characterised by stabilisation of average activity and increasing variance to prepare the system for transition to another metastable state. Several applications of this metastability approach to modelling memory, attention, and other brain functions are considered.

From a mathematical point of view, the process of itinerancy of neural activity might be described by a dynamical system with time-dependent coefficients. We can imagine the evolution of the activities from zero time onwards as the movement of some "representing point" (current point) of the system in a multidimensional phase space of the system variables. The representing point travels through the phase space under the influence of neighbouring attractors. Being in the basin of some particular attractor, the representing point begins waltzing along the attractor. The attractor is formed by a sub-set of "principal" variables (usually, the number of principle components is small) which describe the dynamics of the system during a limited time period. The coefficients of the dynamical system depend on time and it is possible that the stability of the attractor will decrease and the attractor will disappear. After that, the representing point moves to another attractor which is governed by another subset of "principal" variables, and so on.

The global dynamical behaviour of the system is non-stationary. Nevertheless, the travelling of a representing point nearby of some attractor might be considered as being more or less stationary during some limited period of time. Thus, the information processing in the nervous system is represented by a complex spatiotemporal dynamics in the multi-dimensional space. At each moment of time, there is a set of principle variables, which form the attractor and govern the system dynamics during some period of time, then new attractors appear and one of them takes the initiative. The crucial point of this consideration is the mechanism for controlling the system behaviour by the variation of coefficients. There are several possibilities of such control: stimulus-dependent control; adaptation of coefficients according to behavioural "goals" or learning rules (cost function optimisation); control from a higher level structure, the central executive, and so on. For example, Kazanovich and Borisyuk (1994; 1999) studied oscillatory networks with a central element and the applications of this network to modelling attention focus formation. The mechanism for controlling the system dynamics is based on synchronisation of neural activity. It has been shown that the regime of partial synchronisation is very promising for the description of neurodynamics. In this regime, some oscillators work synchronously with a central element forming a temporally existing attractor. Makarenko and Llinas (1998) have applied the synchronisation principle to study phase synchronisation of chaotic systems and model the activity of inferior olivary neurons.

Conclusion: The chaotic neurodynamics seems a very intriguing and promising mathematical technique. Further research should be done in mathematics and neuroscience to understand the meaning of chaotic dynamics for modelling of information processing in the brain.

Symmetries and itineracy in nonlinear systems with many degrees of freedom

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Abstract: Tsuda examines the potential contribution of nonlinear dynamical systems, with many degrees of freedom, to understanding brain function. We offer suggestions concerning symmetry and transients to strengthen the physiological motivation and theoretical consistency of this novel research direction: Symmetry plays a fundamental role, theoretically and in relation to real brains. We also highlight a distinction between chaotic "transience" and "itineracy."

Attractor networks and brain-like neural systems: Symmetry is the missing link. Symmetry has been central to the conceptual development of the dynamics of high dimensional nonlinear systems, but is a notable absentee from Tsuda's target article. Basin riddling was first described in the context of dynamical systems with symmetry (Alexander et al. 1992, not Grebogi et al. 1987). Symmetrical systems remain the focus of research into basin riddling (e.g., Heagy et al. 1994) and attractor networks (Buono 2000; Kaneko 1997). Symmetries play the crucial role of enforcing the dynamical invariance of low-dimensional linear manifolds. When these manifolds support chaotic sets, Milnor attractors and basin riddling can arise naturally (unlike the "exceptional" examples that originally motivated Milnor [1985] such as depicted in Fig. 5). Basin riddling occurs when these sets also contain a dense set of periodic orbits which are repelling in the transverse direction. However, typical orbits (of full measure) are transversely attracting. Hence, the "natural" transverse Lyapunov exponent associated with the chaotic set is negative (*not* positive as erroneously stated in para. 6 of sect. 3.4). It is only low-order periodic orbits (that have zero measure) that are associated with positive Lyapunov exponents (and hence "connections" to other attractors). Approaching high dimensional systems from the perspective of symmetry thus permits a clear understanding of the mechanisms of "weak" instability. In addition, it is possible to exploit the different degrees of symmetry exhibited by the attractors to construct a rigorous classification and ordering of the network (e.g., Ashwin et al. 1992). This permits an improvement on the vague notion of attractors arbitrarily distributed throughout phase space, as depicted in Figure 4.

Symmetries arise naturally in systems of coupled nonlinear oscillators (Field et al. 1996). Brain-like neural systems are characterised by networks of coupled nonlinear oscillators – from the scale of the neuron, up to the scale of the macrocolumn. In these systems dense local excitatory and inhibitory interconnections construct individual "nodes," which are coupled into larger ensembles by sparser long-range excitatory connections. Thus, the organisation of the brain motivates a study of coupled nonlinear systems and, hence, symmetry. Moreover, the attractors of symmetrical systems represent synchronous oscillations among clusters of nodes of different sizes (Kaneko 1997) which strengthens this motivation. Attractor networks in symmetrical systems have been used to model normal olfactory perception (Breakspear 2000), visual hallucinations (Bressloff 2001) and animal gaits (Buono et al. 2000). In contrast, systems with skew-product structure (as considered by Tsuda) are not well motivated, because nearly all brain interactions are reciprocal (even the LGN of the thalamus sends many projections to the retina). Symmetry considerations may strengthen the relevance of Tsuda's interesting and original proposals.

Saddles, chaotic transients, and noise: The need for clarity. Tsuda is correct in pointing out that it may be more relevant to study transient or itinerant behaviour rather than attractors in dynamic systems where inputs and parameters change relentlessly (Friston 1997). However, it is important to ensure clarity and consistency in the use of the terms "transience" and "itineracy." Traditionally, the term "chaotic transience" was applied in the following way (Greborgi et al. 1983): A chaotic attractor (A), subject to some parameter perturbation, "collides" with its own basin boundary. Subsequently, orbits on the attractor are mapped into another basin and subsequently onto another attractor. Put another way, A is no longer an invariant of the dynamic. However, a large set of initial conditions will still approach the region of A (now an attractor "ruin") and transiently mimic the behaviour of the former attractor, before collapsing onto the alternative attractor. After this collapse, the transient is not seen again *unless* the system's parameters are tuned back in the opposite direction. If this is the case, attractors may constantly be "ruined" and then "rebuilt." Such relatively rapid changes in attractors may be effected by NMDA-receptor mediated changes in the underlying control parameters (Friston 1997).

On the other hand, the process of chaotic itineracy – which Tsuda exploits – occurs by a different mechanism. A chaotic attractor, A, is subject to a parameter perturbation that weakens its *transverse stability.* At some critical point (the *blowout bifurcation*), the transverse Lyapunov exponent for the attractor (the *natural measure*) becomes positive (Ashwin et al. 1996). A is then a saddle, not an attractor ruin. Note that A is still an invariant of the dynamic, but will attract only a zero measure set of initial conditions. However, if the phase space contains many such saddles, it may be that typical orbits relentlessly shadow these saddles. Hence the evolution of the system is characterised by irregular switching between different types of itinerant chaos corresponding to the shadowing of different saddles. This tuning of the dynamics into a regime of saddle networks may be achieved by enduring monoamine-mediated changes in functional synaptic coupling (Breakspear 2000).

In summary, there are two types of "transient chaos" with potentially distinct neurophysiological mechanisms. "Chaotic transience" induced by dynamically changing control parameters and "Chaotic itineracy" due to an invariant but complex manifold (discussed as engendering type 1 and type 2 complexity in Friston 2000). As brain science calls more upon dynamical systems theory, it is important to keep such distinctions clear.

Summary. The progression from autonomous, low-dimensional strange attractors to systems with noise and many degrees of freedom represents an important advance in the theory of neural systems (Wright 2000). The present paper by Tsuda outlines many potential computational benefits of this progression. Yet, it is critically important that due respect is paid to both neurophysiology and nonlinear theory, before another magic "man in the machine" in cognitive neuroscience research takes shape.

Multiple and variant time scales in dynamic information processing

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Abstract: Single cell receptive field dynamics characterized by highly complicated spatio-temporal activity distributions observable during sensory information processing transforms into much simpler spatio-temporal activity pattern at a population level, indicating a qualitative transformational step of time-variant processing from microscopic to mesoscopic levels. As these dynamics are subject to significant modifications during learning, dynamic information processing is in a permanent state of use-dependent fluctuations.

The target article by Tsuda offers a challenging reinterpretation of time-dependent information processing in the brain. While most of the concept of chaotic itinerancy in high-dimensional dynamical systems is discussed in respect to hippocampal activity related to memory functions, at present little is known about the applicability and consequences of chaotic dynamics for the interpretation of low-level sensory information processing. As argued by Tsuda, the dynamic receptive field (RF) described for early sensory cortical areas may be understood as a neural correlate of dynamic processes reflecting ongoing interactions between higher and lower levels of information processing (cf. Dinse 1994; Dinse et al. 1990).

Our first studies on dynamic RFs, taking up on previous reports of the Nijmegen and the Marburg groups, have been performed in visual cortex and confirmed a substantial time-dependence of cortical information processing. According to these studies, subfields of RFs are active for only 20–50 msec during stimulus presentation (Dinse 1994; Dinse et al. 1990). We have extended these analyses to auditory and somatosensory cortices in order to allow comparison between modalities. Dynamic RFs studied in auditory cortex showed a similar time-dependence, however, the duration of active states was only 3 to 9 msec indicating the existence of significantly different dynamics (Dinse & Schreiner 1996). Similar results were obtained for somatosensory cortex (Dinse 1994; Godde et al. 1993). It has been suggested that RF dynamics represent particular adaptations for processing of inherently time-variant signals specific for each modality. Accordingly, a common feature of cortical signal processing would undergo modality-specific adaptations to match the requirements of the signal space (Dinse & Schreiner 2001).

The question remains then how these highly intricate dynamics observed at a single cell level transform into dynamics at a level of large population of neurons.

From a phenomenological point of view, the idea to analyze entire populations is a rather inescapable consequence of the observation that a huge number of neurons is activated, even after the simplest form of stimulation. We recently introduced a new approach to study population activity in early sensory cortices in the coordinates of the stimulus space (Dinse et al. 1996; Dinse & Jancke, in press; Jancke et al. 1999).

"Dynamic population-RFs" (Jancke et al. 1999) were constructed from the entire temporal structure of neuron responses of nearly 200 single cells recorded in area 17 using a Gaussian interpolation procedure (for technical details see Erlhagen et al. 1999; Jancke et al. 1999). Population dynamics were captured using the time slice technique, frequently used for calculation of single cell dynamic RFs (time-slicing and reverse correlation are identical, given simple stimuli and simple time course of stimulation). However, the temporal evolution of "population RFs" differed in several aspects as compared to visual single cell Rfs. First, the time scale of "population RFs" was much shorter: "Population RFs" were characterized by a gradual build-up and decay of activation within 40 to 50 msec, while single cell dynamics typically extend over much longer periods (Dinse et al. 1990; Eckhorn et al. 1993; Jones & Palmer 1987). Second, activity was quite uniform across the activity distribution as indicated by a remarkable spatial coherence of activity.

Accordingly, the temporal structure of single cell RF dynamics that is characterized by highly complicated distributions of activity in space and time transforms into much simpler spatio-temporal activity pattern when the dynamics of large numbers of neurons are taken into account. A comparable compression in overall dynamics have also been observed for somatosensory cortical populations (Kalt et al. 1996). Consequently, the complex spatio-temporal behavior of single cells is not preserved in the population dynamics. This, however, does not imply that the single cell dynamics are irrelevant. According to one interpretation, the detailed time structure is a consequence of cooperative processes that in turn generates complex time-dependent interaction effects. In this view, idiosyncratic spatio-temporal properties observable at a single cell level are transformed into global, that is, consistent population behavior of time-variant interactions. In fact, recent evidence from our laboratory indicates that moving stimuli are represented as dynamically maintained moving waves of population activity and that these waves emerge as an result of active processes from internal interaction dynamics (Jancke et al. submitted).

Populations of this type have been discussed as reflecting an intermediate, so-called mesoscopic scale of cortical processing (Freeman 1999). As each single neuron is part of a population, its activity is based on the entire network activity, and vice versa, the network activity is depended on the contributing single neuron. It has in fact been shown that the activity of a single neuron reflects the actual state of the entire neural network (Arieli et al. 1996). It is an interesting question whether a population is in fact able to create de novo "qualia" neither explicitly present at the single cell level nor in the input (Lehky & Sejnowski 1999).

While the existence of dynamically organized RFs is now well acknowledged – quite in contrast to the situation about 15 years ago – their characteristic dynamics are often regarded as complex, but rather invariant fingerprints of individual RF properties (McLean & Palmer 1989). However, there is increasing evidence that the time structure of single cells and of populations are subject to significant modifications during learning processes (Dinse 1994; Faggin et al. 1997; Godde et al. 1993; Katz et al. 1999; Ohl & Scheich 1997). Accordingly, one has to acknowledge that the temporal structures of cortical response properties are in a permanent state of use-dependent fluctuations.

These latter experiments are important in bridging aspects of cortical processing dynamics with aspects of learning, thereby providing a fairly direct link between the fast time scale of a few milliseconds reflecting the dynamics of cooperative processes, and the time scale of learning processes. The results also imply that "modules" of cortical processing are in fact rather flexible, showing various degrees of adaptations to rapidly changing requirements in the environment (Dinse & Merzenich 2001). It remains to be seen in how far the results described above can be embedded by new frameworks like that suggested by Tsuda to provide a comprehensive understanding of dynamic brain functions.

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How to construct a brain theory?

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Abstract: Philosophical, dynamical, neural, network-theoretical, and cognitive ingredients of Tsuda's brain theory are discussed and anayzed. The integrative approach emphasized by Tsuda would be a welcome one.

The target article is a step toward a synthetic approaches to cognitive neurosciences (Sporns 2000). Tsuda attempts to integrate different approaches, such as philosophical, dynamical, neurobiological, network-theoretical and cognitive ones. The present review focuses both on the ingredients of the theory, and also on the way these ingredients are integrated.

The philosophical ingredient: The hermeneutical framework. Tsuda adopts hermeneutics, "the art of interpretation" to interpret the dynamic acticvity patterns of the brain. According to his approach (Tsuda 1984), the brain is involved in a hermeneutic process. According to my own argument, the "technical" or "device approach" to the brain and the philosophical approach can be reconciled (Érdi 1996). It was concluded that the brain is a physical structure which is controlled and also controls, learns and teaches, process and creates information, recognizes and generates patterns, organizes its environment and is organized by it. It is an "object" of interpretation, but also it is itself an interpreter. The brain not only perceives but also creates new reality: it is a hermeneutic device.

The dynamical ingredient: Chaos everywhere? Both the structural aspects and the functional significance of the chaotic phenomena in the brain are controversial issues. While Tsuda's main concern is to point out the fundamental importance of chaos in connecting neural and mental phenomena, he does not show too much interest in the neural mechanisms of chaos generation. The occurrence of chaotic temporal patterns has been reported at different hierarchical levels of neural organization. Chaotic patterns can be generated at the single neuron level, due to the nonlinearity of voltage-dependent channel kinetics of the ionic currents, at the multicellular network level, due to the interactions among neurons, and at the global level in consequence of spatiotemporal integration.

Chaotic itinerancy, in any case, is a very nontrivial concept. It gives a new, dynamic mechanism for the time-dependent transition among unstable traces of attractors. Whether or not Tsuda's whole theory works critically depends on the mathematical reliability of the concept. Now it is being evolved from an interesting idea to a well-founded one. As I see now, the notion of the Milnor attractor helps to understand the important concepts of chaotic itinerancy and "attractor ruin."

The neural ingredient: Olfactory system and hippocampus. To demonstrate how his mathematical construction works in specific neural cases, Tsuda mentioned mostly the olfactory system and the hippocampus. I think, there are two ways of supporting the neural plausibility of mathematical constructions. First, it is possible to cite some relavant experimental literature, second, to show that a plausible neural model has the required property. In case of the olfactory system, there are citations to works coming from Walter Freeman's lab. There are however, several interesting structure-based dynamic models for explaining the rhythmogenesis and memory phenomena both in the olfactory bulb and in the olfactory cortex (see, e.g., Arbib et al., Ch. 5). Since I do not clearly see the structural condition of a system leading to chaotic itinerancy, I really do not know, whether or not chaotic itinerancy could be deduced based on these models.

The situation is certainly different concerning the hippocampus. It seems to be convincing that chaos-driven contracting systems may lead to an attractor with the property "singular-continuous but nowhere-differentiable". and believable that hippocampus may exhibit this property. It should be the subject of a more thorough study whether it is true that the feedback system does not work against the scenario. How to prove that the massive feedback connections from the olfactory cortex (and from other central areas) to the olfactory bulb does not contribute to the generation of the code and plays role "only" in the context generation?

The network-theoretical ingredient: Chaos driven networks. Tsuda adopts two types of neural networks, stochastic recurrent networks, and a chaos-driven stable network. Specifically, the latter construction is very interesting. Nowadays there is a lot of controversy about the nature of the neural code. Tsuda's construction is applied to neural centers, while the ongoing debates related to the "rate code" versus "temporal code" speak about the coding strategy applied by a single neuron. It would be interesting to see whether what could be the conditions of applying Cantor coding. Is it possible to imagine any situation when Cantor coding may play a role in coding the information transmitted by a single neuron?

The cognitive ingredient: Memory and perception. There are two different, only slightly interfering approaches to explain the memory function of the hippocampus. First, it has been observed that the anatomical structure of the CA3 region is similar to an abstract network capable of showing associative memory character. Second, hippocampal rhythms have a fundamental role in memory trace formation and consolidation. While Tsuda's dynamic memory hypothesis benefits from both approaches, again, more detailed computational studies should be done to relate the mechanisms of the generation of different hippocampal rhythms and the roles of these rhythms in various memory phenomena, such as memory formation, consolidation, retrieval, and amnesic syndromes.

Integration: An important step. It is not possible to overestimate the need for integrative approaches in neurosciences. Tsuda's theory integrates new concepts of dynamic system theory with data on neural activity patterns. The theory is abstract, as a beautiful theory really should be. The story should be continued, however, both at the level of abstractness as it stands now at the target article, and also on the level of conventional neural modeling.

Cantor coding and chaotic itinerancy: Relevance for episodic memory, amnesia, and the hippocampus?

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Abstract: This commentary provides a critique of Tsuda's target article, focusing on the hippocampus and episodic long-term memory. More specifically, the relevance of Cantor coding and chaotic itinerancy for long-term memory functioning is considered, given what we know about the involvement of the hippocampus in the mediation of long-term episodic memory (based on empirical neuroimaging studies and investigations of brain-damaged amnesic patients).

In this ambitious article, Tsuda applies the mathematical framework of chaotic dynamical systems to the interpretation of high-dimensional complex dynamics of the brain. The focus of this paper is the discovery of chaotic itinerancy in high-dimensional systems with and without a noise term, which is then applied to brain functions, concentrating on high-dimensional transitory dynamics along "exotic" attractors. (Tsuda contrasts this interpretation with the conventional view of dynamic neural activity, which tends to be phrased in terms of simple behaviour on low dimensional attractors.) Tsuda seeks to apply his framework to biological information processing, perception, and memory, proposing a coding scheme of information in chaos-driven contracting systems which he refers to as Cantor coding. It is argued by Tsuda that these systems are found within the brain in the hippocampal system and also in the olfactory system, among other possible candidate brain regions. Subsequently, a hypothesis regarding the involvement of chaos-driven contracting systems in the mediation of episodic memory is proposed.

Tsuda's operating framework specifies that the brain is organized not only in a hierarchical fashion but also in a "heterarchical" manner, according to which a single neuron or neuron assembly is represented by a multiple code (i.e., the information representation is realized both by the state of the neurons and by the dynamic relations among these states). Tsuda does not state in detail how he views these multiple codes operating within and across snapshots of time. (He does state in the piece that "the time scale 20–50 msec is approximately a 'unit' of psychological time," although this assertion is unreferenced.)

Tsuda's view seems to bear some similarity to the consensus viewpoint emerging from cognitive activation studies of brain functioning, whereby – it is argued – regional brain activity should be evaluated within the neural context in which it occurs, rather than in terms of isolated neural activations (McIntosh 1999). More specifically, the general view emerging from these neuroimaging studies is that cognitive functions are the emergent properties of large-scale neural network interactions (so that a common brain region may play a different role across many functions, with its specific cognitive role governed by its interactions with anatomically related regions). One is also reminded of the conceptual framework articulated by E. R. John, who has – over the past several decades – repeatedly emphasized the interactivity of coherent ensembles of neural cell assemblies in mediating cognitive functioning (see John et al. 1997, for a recent review).

The conceptualisation of memory that Tsuda proposes – and, in particular, the interplay between episodic and semantic memory – is not clear. It would be useful if Tsuda provided a clear definition of how he is using terms such as episodic memory, semantic memory, and working memory, and to which specific psychological construct these terms refer. Tsuda appears to adopt a variant of the Bartlettian framework, noting that memory is the product of a complex interplay between what is stored and what is currently being perceived, and later stating that "memory and information processing cannot be distinguished." He additionally states that he is adopting the "hermeneutic" (i.e., interpretive) framework of dynamic neural activity – which presumably extends to the neural basis of episodic long-term memory – although this hermeneutic framework is not explored in detail.

More generally, the paper is pitched primarily from a mathematical perspective, and is somewhat lacking in appropriate psychological and neurological detail and appropriate references to these literatures. The paper may therefore have benefitted considerably from co-authorship with an individual with appropriate expertise in the cognitive and brain sciences. Where neurological information is presented, it is often highly simplified; for example, in the context of regions where "higher" and "lower" level information meet, it is proposed (unreferenced) that "the hippocampus-parahippocampus system is one possible such area in the sense that here the neural activity of the frontal cortex meets the sensory inputs." This statement in one sense captures the excitement of recent findings in the neuroimaging literature linking prefrontal cortical activations to the established role of the medial temporal brain regions in subserving episodic long-term memory. However, given the lack of cognitive detail adduced by Tsuda, one is left wondering to what extent the mathematical concepts employed are indeed neurologically implementable. On a related note, there are a number of logical leaps and non-justified extrapolations requiring considerable tolerance from the reader. For example, in section 2, paragraph 4, we jump from a consideration of the findings of Freeman et al. in their explorations of the olfactory bulb to the statement that "this suggests that *the brain* is hermeneutic (interpretative) in nature and exhibits chaotic behaviour" (my emphasis).

With respect to the computational basis of episodic long-term memory, Tsuda proposes an interplay between (1) a modified recurrent net and (2) the unidirectional coupling of an unstable network with a stable network. He further proposes a 50% increase in the memory capacity in the case of a network manifesting chaotic itinerancy compared with the case without chaotic itinerancy. Taken together, these assertions are most interesting in the context of our own findings (Foster et al. 1997) indicating that the hippocampus modelled as a straightforward recurrent net with some biologically plausible characteristics (Treves & Roll 1992) does not manifest a high enough level of memory retrieval performance to serve as an adequate model of long-term memory. Also appealing is Tsuda's proposal that chaotic itinerancy permits simultaneous learning and retrieval, given the tendency in the hippocampal memory literature to propose models which distinguish between a "learning phase" and a "retrieval phase," without adequately specifying the necessary mechanisms for such a state shift. However, I was not clear from Tsuda's writing on the precise interplay proposed between the hippocampus, the entorhinal cortex, and the neocortex in the consolidation of information into long-term memory and the time course that he wishes to specify for these processes. More explicit comparison with the proposed characteristics of the influential neurally-constrained long-term memory model of McClelland et al. (1995) would also have been useful for the reader interested in the neural basis of episodic long-term memory, specifically the proposed computational mechanisms underlying hippocampal/neocortical interactions.

Noise-driven attractor landscapes for perception by mesoscopic brain dynamics

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Abstract: Tsuda offers advanced concepts to model brain functions, including "chaotic itinerancy," "attractor ruins," "singular-continuous nowhere-differentiable attractors," "Cantor coding," "multi-Milnor attractor systems," and "dynamically generated noise." References to physiological descriptions of attractor landscapes governing activity over cortical fields maintained by millions of action potentials may facilitate their application in future experimental designs and data analyses.

Based on work with the Japanese "gang of five" (Kazuyuki Aihara, Hiroshi Fujii, Shigetoshi Nara, Minoru Tsukada, and Ichiro Tsuda) Tsuda has advanced substantially beyond elementary basin-attractor theory, which has served well because of its intelligibility and communicability, but which is too simple and too rigid to match the richness of new data and the qualities of perception, particularly the nuances of schemata and meanings that inhere in episodic memories. He describes dynamic brain states as trajectories across state space, constituting chaotic itinerancy in analogy to the cyclical visits of itinerant workers to familiar places with seasons and years. Each new site of visitation is governed by an attractor that dissolves into "ruins" even as soon as it is actualized, persisting in its pervasive influence but allowing the brain state to avoid capture and incarceration in some pathological deep well. Tsuda does not use the term "attractor landscape," because he thinks that it denotes rigidity and unchangeability. I view his system as too rigid because, like the loop formed by a chain of water falls in an etching by Escher, it does not admit changes in the structure or sequence of the choice points resembling saddle nodes. In my view, the flexibility of the olfactory system is given by the fact that each time the animal inhales, the attractor landscape is recreated to enable a classification, and with each exhalation the entire landscape collapses, so that the system is freed to make another test. Conceptions are needed of adaptive landscapes subject to modifications by tilting, raising, and lowering to enhance or expunge attractors, enlarging or contracting basins in the manner of tessellated Voronoi diagrams (Okabe et al. 1992) executed by limbic controls (Kay & Freeman 1998) that actualize the processes of intention and attention in the regulation of sensory inflow and motor outflow.

Tsuda conceives nonlinear neural networks as operating far from equilibrium through the collective interactions of neurons in uncountable numbers, hence being capable of reaching and sustaining highly organized stable macroscopic states by sequential phase transitions. He views cognitive functions not simply as macroscopic but as maintained through "the interplay between macroscopic and microscopic behavior." I identify the microscopic with activity of neurons, and the macroscopic with patterns of enhanced metabolic activity in gyri and lobes, which are being observed noninvasively with imaging techniques such as fMRI and PET scans. In order to bridge the "explanatory gap" between these levels I have borrowed from physicists the term of intervening "mesoscopic" domains (Freeman 2000a), in order to give proper place to the fully textured patterns of amplitude and phase modulation of chaotic waves in the EEG gamma range. These spatially coherent "AM patterns" and "PM patterns" manifest the local mean fields of cooperative neural populations that are much larger than cortical columns and barrels but smaller than gyri in human cortex, perhaps comparable in size to Brodmann's areas as they are illustrated in classical texts. The cortical and bulbar EEGs reveal the formation by first order phase transitions (compatible with SCND) of transient and sequential episodes of gamma oscillations (Freeman 1999b). In sensory areas the AM patterns are triggered by sensory stimuli that destabilize cortical populations, select an appropriate basin, and enable the dynamic construction, transmission, and rapid dissolution of neural activity patterns that actualize the meanings of stimuli by incorporating a lifetime of experience and an expectancy of what the stimuli mean for directing future actions by the individual subject (Freeman & Kozma 2000). The attractors governing these mesoscopic patterns mediate between the neurons and the on-going construction of macroscopic patterns in whole brain activity. Each pattern is broadcast through the brain by divergent-convergent axon projections. Simultaneous reception of multiple broadcasts by tuned neural circuits leads to integration of multisensory percepts (Gestalts).

Tsuda uses the oxymoron "singular-continuous nowhere-differentiable" (SCND, Tsuda & Yamaguchi 1998) to denote attractors at the mesoscopic level. I take this to refer to the "point-process" pulse activities of neurons that simultaneously participate in generating cooperative d.c. biases and gamma wave patterns that control the neurons in "circular causality" (Haken 1983), so the mesoscopic attractors are continuous but have derivatives neither in time nor space. His "Cantor set" is an apt descriptor for sparse, seemingly random, continually renewing distributions of action potentials in steady state cortical activity. "Chaos-driven contraction systems" well describes the "Cantor coding" for the prepyriform cortex, the performance of which during partial complex seizures (Freeman 1986) confirms his prediction that "the SCND attractor will be observed in the potential of inhibitory neurons which are driven by chaotic neurons" (Tsuda 1996). It must be noted, however, that the bulb-prepyriform link is not "unidirectional" but reciprocal, and though the prepyriform is "driven" by the bulb, the bulb (M and G) and prepyriform (PPC) combine with the anterior olfactory nucleus (AON in his Fig. 10) to create the chaotic activity of the olfactory system by their mesoscopic interactions. That activity is modulated by the entorhinal cortex (EC), but it persists after isolation of the olfactory system from all central connections (Freeman 2000a). The bulbar EEG reflects activity that is truly mesoscopic and self-organized, and it is modulated but not driven by "internal inputs coming from olfactory cortex, hippocampus and amygdala." Most important, the EEG manifests chaotic attractors of populations and is not due to phase-locking of microscopic chaos of neurons, on which Tsuda and I agree. The reason this is important is that sensory stimuli are converted by receptors to patterns expressed by point processes (trains of action potentials – "units") on a surface (pyramidal cells in an area of cortex), and each pattern is the relation of each point to every other point. This is a mesoscopic property, and classification requires selection of a mesoscopic basin. We agree also that in a contracting system such as the prepyriform cortex, chaotic input serves as a driver.

Tsuda's mathematical description of "dynamically generated noise" fits the way in which each neuron disseminates and randomizes its action potentials into the neuropil to its neighbors (Freeman 2000c) and receives from them by a distributed recurrent axons (Freeman 1996), with a feedback gain that exceeds unity, thus giving rise to sustained background activity at the mesoscopic level called "stochastic chaos" (Freeman 2000b) to distinguish it from low-dimensional "deterministic chaos." This excitatory bias is an order parameter for the induction of state transitions in cortical itinerancy. He comments on the utility of two kinds of noise for associative memory: "dendritic" noise that is "equivalent to the case of simulated annealing," and "synaptic" noise that is essential in chaotic itinerancy. His distinction between "dendritic" and "synaptic" is not useful in physiology, but his identification of multiple roles for noise is crucial. Noise serves to select and stabilize a local domain known as a Milnor attractor (Kaneko 1998) by smoothing the SCND state space resembling mammalian fur to a pockets with fractal boundaries. Noise promotes destabilizing by forcing jumps across separatrices that appear as first order state transitions (Barrie et al. 1996; Freeman & Barrie 2000). Additionally, noise enables Hebbian learning of new attractors rather than reinforcing those existing (Freeman 1991).

A complementary approach should be explored in brain dynamics by treating the AON as a "chaotic controller" (DiBernardo 1996; Pecora et al. 1997; 1998; Pecora & Carroll 1999). Measurement of radially symmetric phase gradients of EEG gamma bursts indicate that the bulb is self-organizing, whereas the prepyriform cortex lacks these and is not (Freeman 2000a; Freeman & Barrie 2000). The chaotic activity of the olfactory system is produced by the interactions of these modules, not by any of them alone, nor by any driving from outside (Kozma & Freeman 1999). Comparable properties should be sought in the dynamics of the entorhinal-dentate-hippocampal relations, and likewise between triads of neocortices.

Control of chaos and memory dynamics

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Abstract: Neurally inspired models of human cognition exude explanatory power without necessarily making predictions that can be verified behaviorally. This is the case for Tsuda's dynamic model. It is suggested that a simpler principle based on the nonlinear dynamic interaction between modules based on control of chaos, can achieve a similar theoretical goal in a cognitively verifiable way.

A sensible strategy for constraining the large number of competing neurally-inspired models for human cognition involves ensuring that such models are both dynamic and based on known brain mechanisms. Tsuda accomplishes this difficult task in the context of episodic memory by considering the neurophysiological and neuroanatomical properties of the prefrontal cortex and the hippocampus. He then extends the fundamental principles of nonlinear dynamics to devise a modular model that purports to solve such problems as the storage and recall of episodic memories. Of particular significance is the proposal that such memories are not simply stored like letters in a mailbox or images distributed throughout a hologram. Instead, they consist of a dynamic representation of the interactions between modules at different levels of the nervous system.

In terms of contemporary memory theory, this is a revolutionary concept. However it is not without precedent. For example, Heath (2000a) presents a modular neural network model involving at least two modules, each of which undergoes spontaneous dynamics at any point in time. Any interactions generated by one module influencing the other are reflected in changes in the qualitative nature of the dynamics occurring at each module. For example, spontaneous chaotic dynamics (see Freeman 2000 for a contemporary account) can be replaced by limit cycles under the influence of strong external stimulation. In Figure 8.7 in Heath (2000a), the input from one module generates quasi-periodic dynamics in the other module. A remnant of this dynamics remains when the external stimulus is terminated, indicating that such models can store episodic memories as dynamics, rather than as static entities. Such systems are quite general and can serve as interesting models for psychological processes such as perceptual segmentation (van Leeuwen et al. 1997).

The modeling strategy adopted by Tsuda is essentially a dynamic reconstruction of a signal in the presence of noise, where the latter can be both beneficial and destructive to adaptive information processing. A large number of processing units ensures that neural processing is high dimensional, yet fundamentally deterministic. Instead of focusing on control of chaos as a general information processing principle, Tsuda employs an itinerant attractor to represent the internalization of transient external events.

The use of an itinerant attractor is an interesting idea. One of the difficulties of applying attractor models from the behavioral point of view is that seldom do such models provide a mechanism for completing one cognitive transaction and readying the system to deal with another. By allowing the neural network to escape from an attractor ruin via an unstable manifold such a process is possible. Alternatively, as Heath (2000b) has shown, control of chaos techniques can be used to achieve the same theoretical goal in a chaotic neural model for stimulus discrimination. Prior to stimulus presentation, the network dynamics consist of nonlinear determinism (possibly chaotic if the attention gain is high) plus superimposed noise. When the stimulus is presented, the system sheds degrees of freedom under control of chaos, information processing occurs, and a psychophysical decision is made. However, once the stimulus terminates, the system reverts to its high dimensional deterministic, noisy dynamics, in readiness for the next stimulus.

From the behavioral perspective, the major difficulty with Tsuda's model is how the basic principles can be incorporated into a cognitive model that can be evaluated experimentally. The fundamental principles expressed in section 3.5 seem reasonable, especially from the perspective of a modular chaotic neural network. However, the assumption that memory can operate independently of context is puzzling, especially since contextual cues play an important explanatory role in several contemporary memory models (Dennis & Humphreys 1998). This relegation of context to the theoretical background is subsequently negated in section 3.6 (as well as in sect. 4.3) when top-down processes provide a dynamic contextual code.

The neurally-inspired model for the formation and use of episodic memories, based on hippocampal information processing, is interesting. However, the mathematical predictions of the model are not clearly stated, as surely would be possible for the storage and retrieval of stimulus sequences. This makes it difficult to compare and contrast the model with competing models for episodic memory. The practical significance of "distances" between episodic memories, presumably facilitated by the Cantor set fractal representation of clustered information storage, is not evident. At no stage does the fractal representation become a critical explanatory concept, simply because its predictions are never contrasted with those of models that do not have such a property.

The challenge for future cognitive research is to translate the principles presented in this paper into predictions that can be evaluated experimentally. The problem of relating neural activity to mental states, a fundamental challenge in neurocognitive modelling, is recognised but not achieved. Nevertheless, a brief account of such an enterprise is presented in the Appendix and perhaps a more detailed account of that project (Hatakeyama & Tsuda 2000) would have been helpful. Otherwise, these ideas will remain floating in a turbulent sea of interesting dynamical principles desperately seeking an attractor within empirically verifiable cognitive theory.

Chaotic itinerancy needs embodied cognition to explain memory dynamics

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Abstract: Memory dynamics need both stable and unstable properties simultaneously. Hence memory dynamics cannot be simulated by chaotic itinerant dynamics alone, with no real world correspondence. Memory dynamics are constrained by both semantics and causalities in the embodied cognition.

We are sympathetic with Tsuda's attempt to invoke dynamical systems ideas to understand cognitive functions, in particular memory dynamics. Because a variety of new phenomena reported in brain systems require a very powerful description system other than natural language, we think it is essentially instructive to consult other powerful systems studies, that is, chaos and dynamical systems. Novel phenomena observed in chaos can give us new ways of understanding complex phenomena, so that we can use them for understanding brain systems. Since we consider the advantage of dynamical systems to be the dynamical interpretation of phenomena, brain systems can be reinterpreted as dynamical processes.

For the past 10 years, a variety of new words and ideas have been accumulated in dynamical systems studies. Chaotic itinerancy (CI), noise induced order (NIO), riddled basins and singular-continous but nowhere-differentiable (SCND) attractors have been concerned in particular with the interplay between dynamical systems and noise phenomena as Tsuda introduced in the first part of the paper. Using these terminologies, we may be able to discuss brain functions without having explicit distinction between memory and information processing. Simultaneous read-out/write-in processes in brains can also be understood as emergent property of some novel dynamic property (e.g., Sato & Ikegami 2000).

On the other hand, the second part of the paper is devoted to the application of CI and SCND attractor to episodic memory, where we find the article needs substantial clarification and improvements. In particular, Tsuda's idea of episodic memory sounds very static against his overall "dynamic" attitudes. From the series of works using recurrent neural networks (RNN), we have the following notions with respect to memory and perception structures, which are mostly neglected in Tsuda's argument.

When we use RNN to study various cognitive tasks ranging from robot navigations (Tani 1998) to game playing situations (Taiji & Ikegami 1999), our basic attitude towards modeling cognition is that it has to deal with two opposite features simultaneously; procedural and nonprocedural memory structures. RNN is often called a dynamical recognizer (Pollack 1991) which recognizes any information of its experience in a time sequence. As a result, one's actions against the external world generate a new set of rules and dynamics as a sequence of transitions among "clusters" in a phase space. This sequence constitutes a so-called context map in a network. Sometimes those rules become explicit and we see a good correspondence between a finite automaton and cluster patterns in the phase space of networks (Elman 1990; Pollack 1991). Here we say that a memory structure is obtained as a procedural-like rule.

Sometimes those memories cannot be explicit and become highly dependent on the on-going interaction between subject and environment (including other subjects). In this case, cluster patterns in the phase space become cloud-like patterns, which often correspond to chaotic attractors in an iterated functional system (IFS). That is, a tiny fluctuation in the states of RNN will completely alter the whole sequential structure of memory. A memory structure is not procedural-like in this case. Thus we cannot make a simple causal relationship among clusters. What we call memory dynamics underlying cognitive function is defined in this itinerant phenomena among procedural- and nonprocedural-like memory structures.

Moreover, what is missing in Tsuda's argument is the semantics and causality that should emerge spontaneously from the memory dynamics. Tsuda only relates each cluster to (semantic) memories and discusses the chaotic transitions among them, but fails to refer to its total causalities among them. Even if we take episodic memory as a combination of given semantic memories, there is no discussion on the emergent structure of the episodic memory itself. We cannot freely reconstruct the memories since we inevitably experience episode sequences under a kind of "continuity axiom" to preserve natural causality. A continuity axiom is requested between successive (semantic) memories (Igari & Ikegami 2000). As well as in the second law of thermodynamics, some paths from one memory to the other are prohibited not by thermodynamics but by cognitive constraints. Without mentioning such cognitive constraints, chaotic itinerary of memory dynamics (with Cantor coding) becomes just a metaphorical statement. The constraint is only explained by the learnability of RNN against the richness of perceptual experience.

Finally we argue that memory dynamics underlying cognition has both stable and unstable nature in some more difficult level. Subjectively a memory structure is stable in the sense that we can draw on our memory structure. We believe that it is stable since memory structures are constrained by both semantics and causalities in the embodied cognition. But objectively, neural activities underlying memory dynamics look very chaotic as Tsuda continuously argued in the article. This apparent paradox should be properly answered. In order to resolve this question, we think that brain systems should have its outside. To study how a brain system is situated in a given environment (including other brain systems) is a necessary condition to understand how it generates memory dynamics. We argue that memory dynamics internalize the externality of its environment by making a distinction between self and nonself actions.

Chaotic itinerancy: Insufficient perceptual evidence

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Abstract: Chaotic itinerancy is useful for illustrating transitions in attractor dynamics seen in the olfactory system. Cantor coding is a good model for information processing, but so far it lacks perceptual proof. The theories presented provide a large step toward bridging the use of chaos as an interpretive tool and hard examination of chaotic neural activity during perception.

Tsuda has presented the idea that itinerant chaos can adequately represent the dynamic brain as a hermeneutic device. The argument is attractive and persuasive. Chaotic itinerancy describes the character of olfactory system dynamics seen during odor discrimination (Kay et al. 1996; Kay & Freeman 1998). In those studies we saw an orderly succession of attracted states in the olfactory-limbic system axis. We concluded there that the entire system is involved in both memory storage and dynamic recall and that centrifugal projections from the limbic system to the olfactory bulb (OB) are important to the evolution of the attracted state through which the OB transits. With these data and others, a chaotic system was hypothesized, but physiological data do not lend themselves easily to proof of mathematical chaos. State transitions are abrupt, and a given state may be as brief as 100 msec. Tsuda's theory comes close to providing a framework in which to evaluate such claims, and he reassures us that it is not necessary to prove chaos. Thus, chaotic itinerancy can be a useful model for interpreting a succession of temporary attracted states, where a global itinerant attractor may contain the temporal order of transitions and represent the perceptual process of learning, memory, and recall. I would also urge Tsuda to include action in the perceptual process. The somato-motor system has been shown to exhibit dynamic properties (Laubach et al. 2000; and others). Following Tsuda's representation of interfacial dynamics, the output mechanism cannot be removed from the process, nor can the motor behavior involved in information seeking (sniffing and whisking in rats). An animal's response is an integral part of the perception and including the method of action via motor cortex and other brain areas in the global itinerant attractor system removes the necessity for a separate "decoding" mechanism to produce the desired output.

Tsuda makes a good argument in favor of dynamical over hierarchical processing. Evidence for this includes dynamic neural cell assemblies, dynamic receptive fields, and dynamically changing system structure. In all of these cases, the appearances of the system support the dynamical hypothesis. However, we should have a compelling reason to choose dynamical over hierarchical processing and chaos over a simpler dynamical system. The discussion of Cantor coding, especially in the hippocampus, is an attempt to address both concerns. However, I am left with some questions.

(1) Is it necessary to "decode" what is stored in the cortex to extract the temporal information, and, if so, how can this be accomplished? One hopes that the system can simply recreate the dynamic set of states, which is the memory, the learning, the recall, and the action. In this case there is no need for decoding or binding.

(2) Can evidence from the isolated hippocampus support a perceptual theory? We have seen that when a brain wakes up and performs a task, what we believed to be simple and static rules, such as receptive fields, are drastically changed (Nicolelis & Chapin 1994). As described in the text, the hippocampus exhibits chaos and in its isolated state produces a stable system driven by chaotic input. Chaos has also been shown to provide a good framework for controlling simulated seizures in the hippocampus (Schiff et al. 1994). When we examine the hippocampus in a perceiving animal, does it follow the same rules? I take the olfactory system as an example. Tsuda describes the OB-prepyriform cortex (PPC) system as another instance of a stable system driven by chaotic input. He argues that feedback connections from the PPC can be seen as contextual information, which can therefore be ignored for the sake of argument. However, it is these connections from the PPC and elsewhere that make possible the putative chaos in the OB (Freeman 1987). Sensory input to an anesthetized or isolated OB may produce non-chaotic activity and relatively sim-

ple odor coding (Gray & Skinner 1988; Mori et al. 1999). On the other hand, odor perception produces sensory activity in OB mitral cells that is strongly modulated by context, to the extent that "odor coding" is difficult to extract (Kay & Laurent 1999). Thus, chaotic and contextual activity seen in the OB may be part of the perceptual reenactment of the itinerant attractor set distributed over at least four olfactory and limbic system structures and several seconds (Kay et al. 1996), not driving by chaotic sensory input. Does the theory hold up under this condition?

I am left with the impression that there remains a large gap between using itinerant chaos as a descriptor of system characteristics during perception and using it to interpret hard physiological data from a behaving animal. The closest the data come to proof of chaos is in the isolated preparation. We still face the issue of statistical nonstationarity in awake animals, but Tsuda's approach may be our best bet for bridging this gap.

The noise of chaos

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Abstract: When theoreticians talk about noise, they frequently forget about the idealization coupled with this term. Another implicit and rarely mentioned assumption is that the tools of mathematics used are idealizations, too. Though some of Tsuda's ideas are similar to mine (e.g., we both believe that nonlinearity is one of the main reasons why the brain works the way it does; Kowalik et al. 1996), some critical remarks are in order.

The brain is an open system. The brain, similar to all other "real" systems, is an open system. That means, the environment's influence on the system is more or less uncontrolled. We can be lucky when our experimental setup provides a well defined, clearly structured object of investigation. However, the human brain *in vivo* never works like that. For instance, in order to observe "clean" evoked responses we need to repeat a stimulation many times and (linearly) average the signals, with the hope that all these uncontrolled influences will vanish due to their random character. That is only a supposition. Where is the border between noise and a high-dimensional dynamics?

It is indisputable that a point or a line are idealized mathematical objects. It is very rare that the same can be said about noise. Noise as an infinite-dimensional signal is an ideal mathematical object. The same can be said about the simple (or more complex) oscillation. Nature is a complex, extremely high-dimensional, nonlinear system and there is no constituting element therein being an ideal object. When looking for dimensionality of subsystems we will find this as 2, . . . 5, . . . , or more dimensions. We will start to believe it is a true value when this number is too large. After that, we will call it "noisy." Thus, there is no strict limit between noisy and deterministic behavior. The same should be said about stochasticity – every time we are not able to write down all the required equations of the system's motion, we will assume its "stochastic character." Tsuda goes still further. He speaks about a deterministic system constituting 10^{15} elements. It requires a definition at least. We met a similar problem while looking for a low-dimensional character in the magnetoencephalogram (Kowalik & Witte 2000). We observed a spatial distribution of local Lyapunov exponents (lLE) in all 122 measured channels, and found that there exist distinct maxima of the lLE. It was a clear proof that low-dimensional chaos occurs transitorily at some brain areas. It does not mean that the rest (of not enough frequently repeated dynamics) had no deterministic character. One should maybe observe further and further, up to dimensional saturation?

Coexisting attractors with a weak barrier. In a simple system of a bouncing ball (Kowalik et al. 1988) we were able to find that coexisting attractors are real. In our experiment, one of these attractors was chaotic and another a quasiperiodic one. It was also possible to observe transitions between them. We called this behavior "self-reanimating chaos," as dominating chaotic state was temporarily disturbed by a quasiperiodic one and could reanimate itself. We postulated then that the main force that allows the jumps between two topologically strongly different structures is "noise." It was indeed impossible to control these jumps, but it is also true that such a change could be involved through simple disturbance of the motion plane (just throwing). While calculated, the "life-time" of the chaotic state was dependent on the adequacy of estimations. An idealization was then that beneath a certain limit, only one of these attractors (depending on initial conditions) would be realized, and only once, and in infinite time.

Brain mixture. The animal models of the brain are very useful. To consider them equal and to suppose that all their properties and parameters can be transferred into a human brain is unacceptable. Why should the 40 Hz oscillations in the cat (Gray & Singer 1987) and in the rabbit (Freeman 1987) be the same nature as gamma-oscillations (Kowalik et al. 2000) in humans? The self-organized context of feature binding is in all cases rather clear, but the fact that one specific of the many spectral components is preferred in different substances sounds amazing and esoteric.

Fragmented attractor boundaries in the KIII model of sensory information processing: A potential evidence of Cantor encoding in cognitive processes

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Abstract: Spatio-temporal neuro-dynamics is a quickly developing field of brain research and Tsuda's work is a significant contribution toward establishing theoretical foundations in this area. It is conceivable that the fragmented attractor landscapes and dynamical memory patterns identified earlier in various K-sets are biologically plausible manifestations of attractor ruins, chaotic itinerancy, and Cantor encoding as applied to sensory information processing.

High dimensional chaos in brain activity. An overwhelming part of chaos studies is directed toward the description of low-dimensional systems. This approach is partly motivated by the success of chaos models in explaining the behavior of physical systems with a few degrees of freedom. The limited interest toward high-dimensional systems is also dictated by necessity, as existing chaos methods have difficulties with describing high-dimensional systems. In fact, it is a wide-spread belief among chaos researchers that high-dimensional systems are outside the realms of chaos studies. Tsuda disagrees with this opinion and outlines a solid mathematical theory of high-dimensional dynamical systems using chaotic itinerancy, attractor ruins, and Milnor attractors. We strongly support Tsuda's point of view, as our studies with the EEG activity in animals also point to the crucial role of high-dimensional dynamical effects in producing higher brain functions.

The models introduced by Tsuda (1992; 1994) are relatively simple. They are useful to demonstrate important aspects of the attractor ruins and chaotic itinerancy. However, they are very far from reflecting realistic high-dimensional behavior related to cognitive functions. We propose that recent results by the KIII model are in fact possible manifestations of Tsuda's attractor ruins in a biologically plausible neural network model (Kozma & Freeman, in press).

Studying fragmented attractor landscapes in the K-models of sensory information processing. Following the work of Freeman et al. (1997) as cited by Tsuda, crucial advances have been made in studying the extremely fragmented attractor landscape of various K-sets and the related phase transitions induced by sensory stimuli. Originally, the KIII model has been introduced as a coupled set of second order ordinary differential equations (ODE) (Freeman 1975; Freeman et al. 1997), where the space-dependence of the dynamical brain processes has been represented indirectly via a system of ODEs with distributed parameters. In an alternative approach (Kozma & Freeman 1999) the space-time dynamics is emphasized by regarding the KIII model as a discrete-space instantiation of coupled nonlinear partial differential equations (PDE). In the latter approach, the topology across cortical areas is directly incorporated and the link with coupled map lattices having intermediate-range (mesoscopic) effects has been established (Freeman & Kozma 2000; Kaneko 1994; Kozma 1998).

In recent studies with the KIII model the spatio-temporal self-organization of neuro-dynamics has been addressed and it has been applied to develop a robust dynamical memory device (Kozma & Freeman 2001). It has been shown that noise not only stabilizes aperiodic orbits, but an optimum noise level also acts as a control parameter to produce a robust pattern recognition device. The observed effect is called chaotic resonance and it is believed to be a typical feature of chaotic self-organization in living systems and, in particular, in spatio-temporal dynamics of sensory cortices.

Noise induced transitions versus noise stabilization. On the surface, the observed effects might resemble stochastic resonance, as Tsuda cites (Liljenstrom et al. 1996). There are however, crucial differences which have to be pointed out (Kozma & Freeman, in press). Chaotic resonance (CR) is a collective effect of neural populations with limit-cycle autonomous dynamics while chaos is present already at the individual level in stochastic resonance (SR). Noise is crucial in both SR and CR, but the role of noise is drastically different in SR and CR, respectively. Noise is used in SR to amplify weak input signal by de-stabilizing chaos, while noise stabilizes chaos in CR. The oscillatory signal in the K-sets experiencing chaotic resonance is not coming from the external world but it is of internal origin. Therefore, there is an intimate interaction between the noise and the oscillatory signal, which is responsible for the development of complex trajectories that resemble Tsuda's chaotic itinerancies. It is very encouraging to see Tsuda's solid mathematical theory of high-dimensional chaos, which is expected to provide a tool for the interpretation of the behavior of sensory cortices.

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How (dis)ordered is our brain?

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Abstract: The dynamical view of the brain that Tsuda presents is thoroughly substantiated by theory and computer simulations, but strong experimental evidence for chaotic brain processes is still lacking. New methods are called for. It is also important to make a distinction between the generating mechanisms and the observed behavior, which is complicated by a mixing of stochastic and deterministic processes.

In the artificial neural network community there has traditionally been a focus on convergence to stable steady states and point attractors corresponding to certain patterns or memories. In contrast, Tsuda has been at the forefront in focusing on the significance of the complex dynamics of neural systems. During the last decade, the interest in neuronal noise and chaos has steadily increased, but lately with a shift in focus toward more high-dimensional, or even "noisy brain chaos" (e.g., Freeman 2000). A broad spectrum of theoretical and experimental perspectives on these problems is given in Århem et al. (2000).

In order for the brain to function properly, it would seem reasonable to assume that its underlying neural processes are ordered and predictable. Ordered processes and signals could easily be used for computations and for prediction. However, exact predictability is not possible, due to the uncertainty provided by intrinsic and external fluctuations. Yet, a certain degree of disorder should provide flexibility to the system, so there must be a balance between order and disorder, determined by microscopic and macroscopic states.

Disorder in brain processes may be described as noise or chaos, usually related to the spatial scales involved. However, the distinction between noise and chaos lies in the mechanisms and the simplicity: chaos is generated by simple, controllable mechanisms, noise by a large number of uncontrollable mechanisms. But the border is not sharp: there is a continuous transition from chaos to noise, when increasing the system complexity. Time scale is also important. At *short time scales,* chaos is predictable, while noise is unpredictable at all time scales. At *long time scales,* chaotic processes seem indistinguishable from noise, when referring to probabilistic properties. What can be considered as short or long time scale is, however, system and level dependent, and not well defined. For neural systems at different organizational levels, this is an important issue if one wants to investigate the underlying mechanisms behind the process irregularities (for further discussions on these issues, see Århem et al. 2000).

Tsuda points out the importance of the interplay between microscopic (noise) and macroscopic dynamics (chaos), but the description of this interplay is not fully developed or described. For example, there can be strong amplifications of microscopic events to macroscopic effects that depend on other aspects of noise than those discussed in the target article. Spontaneous activity (firing of action potentials) in small hippocampal neurons have been associated with single-ion channel openings (Johansson & Århem 1994), and a single-action potential can, under certain circumstances, cause an avalanche of neural activity that is experienced consciously (Ochoa & Torebjörk 1989).

At the same time, the synaptic noise (spontaneous emission of vesicles) that Tsuda refers to, may in the brain (in contrast to peripheral neurons) be well in the order of stimulus evoked events, and thus have much larger postsynaptic effects than claimed by Tsuda (Smetters 2000). It is worth noting that spontaneous neuronal firing can only increase the number of spikes reaching a receiving neuron, whereas the probabilistic nature of synaptic discharges usually seems to reduce this number. The probability of synaptic transmission of an action potential may be as low as 10% in the cortex (Smetters 2000).

In simulations with our own neural network models of the olfactory cortex and hippocampus, we demonstrate how single noisy elements can induce global oscillatory or (pseudo-)chaotic network activity (Liljenström 1991; 1996; Liljenström & Århem 1997). This kind of complex dynamics, which includes oscillations, (pseudo-)chaos, and noise is shown to play a constructive role in associative memory tasks (Liljenström 1995; Liljenström & Wu 1995), thus supporting the view presented in the target article. Specifically, the time for recall of memories can be minimized for optimal noise levels, similar to stochastic resonance phenomena. Transitions between different dynamical states, for example from a stationary to an oscillatory, or from an oscillatory to a (pseudo) chaotic state can result from an increased noise level, or from a change in a control parameter associated with a neuromodulator, such as acetylcholine (Liljenström & Hasselmo 1995; Liljenström & Wu 1995).

The work by Tsuda and other theorists raises a number of questions that call for new theoretical methods and experimental approaches. For example, is there any structure in the observed irregular behaviors found in neural systems, and if so, can this structure tell anything about the generating mechanisms? Can the brain tell the difference between noise and chaos, between stochastic and deterministic processes? How are the different spatial and temporal scales related, and in particular, how can the macroscopic activity exert influence on the processes at a cellular and molecular scale? What is the functional significance of the observed complex dynamics?

Many of the traditional methods to find chaos in irregular time series have proved inadequate, but the method of unstable periodic orbits (UPO) seems promising (Moss & Braun 2000; Pei & Moss 1996). This method appears largely immune to the traditional limitations of biological measurements, the non-stationarity of the process, and the contamination by noise in the recordings. For example, Moss and co-workers have shown that certain sensory receptors exhibit chaotic and stable (limit cycle) dynamics, depending on external stimuli and conditions (Moss & Braun 2000; Pei & Moss 1996).

However, such methods can only give partial answers to some of our questions, the most compelling one concerning the relation between neural processes and consciousness, which may or may not be linked to cognition (Århem & Liljenström 1997). For example, while there is no obvious contradiction, it is unclear how the synchronized 40 Hz oscillations associated with attention (Crick & Koch 1990) relate to the chaotic itinerancy described by Tsuda.

Disorder, in the form of noise or (pseudo-)chaos or both, inevitably exists in the brain, but there is still very little experimental evidence that the brain makes use of this disorder. From an evolutionary point, it seems plausible that the nervous system would have suppressed this disorder if it had negatively affected its functions. It is even likely that the system would have evolved to make use of any type of activity that could result as a side effect of its functional constraints.

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Network stabilization on unstable manifolds: Computing with middle layer transients

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Abstract: Studies have failed to yield definitive evidence for the existence and/or role of well-defined chaotic attractors in real brain systems. Tsuda's transients stabilized on unstable manifolds of unstable fixed points using mechanisms similar to Ott's algorithmic "control of chaos" are demonstrable. Grebogi's order in preserving "strange nonchaotic" attractor with fractal dimension but Lyapounov is suggested for neural network tasks dependent on sequence.

At first glance, a chaotic dynamical system seems an odd choice for the mechanism supporting the work of computational one-to-one (in contrast with chaotic one-to-many and many-to-one) input to output mappings by neural networks. The most commonly used feed forward networks are not dynamical systems, since the network's future state is not a function of its present one. In addition, the generic trio of chaotic dynamical system properties (Devancy 1989): (1) Exquisite sensitivity to initial conditions (How could preparation of a physiological system or model obtain a beginning value that precisely?); (2) Undecomposability, called topological transitivity, (How can the correct and incorrect outputs be disjointly separable?); and (3) Phase space objects filled with a countably infinite number of (unstable) periodic points (How can a sequentially ordered language be mapped by orbits hopping and "mixing" their order?) seem ill suited to the convergent uniqueness of input-output functions of computational networks.

Tsuda evokes what he calls a Milnor attractor. The world class topologist's definitional proof is in essence a story of orbits that enter a boundable region and do not leave it, placing points of positive measure (not *necessarily* fixed or periodic points) in that box (Milnor 1985). However, knowledge of this class of attractors has been around for over half a century (Cartwright & Littlewood 1945; Guckenheimer & Holmes 1983; Levinson 1949; Li & Yorke 1975; Lorenz 1963; Rossler 1976; Ruelle & Takens 1971; Smale 1963; Ueda 1973). They are better known as strange attractors, called "strange" because they attract initial conditions and are composed of neither stable fixed nor periodic points. Their recurrent global phase space motions are both expansive (stretching) and contracting (folding), a process which "mixes" the point sequences on the attractor, destroying sequential regularity while maintaining the attractor's geometry. For neural networks, this suggests weight induced stretching and contractive normalization by the sigmoid squash function (Casey 1996).

The article's motivating experiments in the olfactory system by Skarda and Freeman generate claims of flexibly complex, chaotic searching and lock-up avoiding, electrophysiological background activity, consistent with that time's ideas about the role of chaos in physiological systems (Mandell 1983), and odor evoked, information bearing olfactory bulb limit cycles emerging at an internal-external "interface." Tsuda (and Skarda & Freeman 1987) should not regard the response to stimulation of the olfactory system as typical of these interfaces, because the distribution of olfactory neurons with diverse ligand specificities is unlike those of touch, pressure, pitch, visual fields, and color or taste receptors on the tongue. Unlike these, olfactory receptors and sensory way stations are lacking obvious anatomical order and are diffusely distributed, requiring "coincidence detectors" to put together the elements of behaviorally definable odors (Anholt 1994).

In addition, these experiments and their conclusions fail current standards for statistical or mathematical evidence for either chaotic resting dynamics or the rare inverse bifurcation from chaos to limit cycles. These include the existence of a positive Lyapounov exponent that is sensitive to randomization of the original data and its Fourier coefficients in the first instance (Theiler et al. 1992), and the emergence of complex conjugate eigenvalues of the matrix of partial derivatives characteristic of bifurcations to limit cycles (Marsden & McCracken 1976). It appears that the claim that "Skarda and Freeman showed the biological significance of chaotic behavior found in the local EEG" is a bit overstated. However, Skarda and Freeman can hardly be faulted since, in spite of transient claims to the contrary, it can now be fairly stated that over 30 years of work and the weight of evidence from hundreds of studies relating chaotic dynamics and their statistical, "ergodic," measures to a variety of physiological functions have not yielded much reliably relating the two beyond the observations of Mackey and Glass (1977) that changes in dynamical state in a variety of physiological systems can be associated with the appearance or disappearance of chaotic dynamics.

On the other hand, if one restricts the discussion to computational dynamical systems in the class of neurobiologically realistic, completely connected, recurrent neural networks, RNN, and monitors what Zipser has called the "surprisingly" realistic behavior of middle layer computational neurons (Zipser 1992), then the difference between problem solving computation-associated emergent stable fixed points and/or their bifurcations into stable periodic points and successful computations manifesting transient tangencies to the shadows of erstwhile hyperbolic (orthogonal vector fields going inward and outward) fixed points ("itinerancy among attractor ruins") becomes relevant. Tsuda's Figure 5, a plot of the Manneville-Pomeau Type I intermittency map, which can be used to model the irregularly intermittent time structure of vortex appearances in a turbulent flow (Berge et al. 1984) as well as the intermittent bursting of neurons (Mandell & Selz 1997; Selz & Mandell 1991). This figure shows entrapment of the transient orbit "ironed down" in the channel by the stable manifold in the neighborhood of a destabilized hyperbolic fixed point as it traverses the unstable manifold. It remains trapped there for various times. In light of the way "noise" is regarded as a problem in this article, it is interesting that we have found that noise *increases* dwell times in the neighborhood of unstable points, "saddle sinks," along the unstable manifold in our model and experiments involving hippocampal electrophysiological behavior (Mandell & Selz 1993).

Tsuda's proposition is consonant with the growing "computational control of chaos" literature (e.g., Ott et al. 1990), which has as its underlying mathematical mechanism, the experimenter's adjustment of parameters so that a point escaping from the (sometimes shadow) neighborhood of the hyperbolic fixed point along the unstable manifold is folded back into the field of the stable manifold's iron, so as to return and maintain its tangency to the computationally involved (unstable) fixed point. Adaptive computational RNN's appear to exploit this kind of corrective mechanism autonomously. Tsuda's idea that transient computation is more neurobiologically realistic than fixed and/or periodic point mediated computations is intuitively appealing. Bowen's shadow lemma (Bowen 1978) says that in such situations, reliability is born of orbital travel along the unstable manifold, maintained "on the road" by the vectorial bounds of the stable manifold which keep all orbits, even rather noisy ones, on the unstable manifold's track, close to the real "fiduciary" one. This proof also shows how it is that it takes only a few points to outline a geometrically recognizable attractor. This source of computational stability is a reasonable alternative to that of fixed and/or periodic attractors, because a real neuronal fixed point is likely to mean cell death and stable periodic orbits, focal epilepsy, or Parkinsonian tremor (Mandell 1987).

Some of the difficulties involved with realizing predictable function from transient computation dynamics are evidenced in the bifurcation scenario of Figure 1, phase portraits in the squared unit interval, I(n1) I(n2), representing the activity of two self and other coupled "middle layer" logistic neurons (Paulus et al. 1989). As one coupling strength parameter is increased, the bifurcation scenario (left to right and top to bottom): period two quasiperiodic cycles thickened, stretched "homoclinic budding" of the tori through unstable fixed points to six quasiperiodic orbits their joining into two strange attractors expansive fusion into a single global strange attractor with fractal (Cantor set) point distribution. Contrary to visual intuition, the orbit does not move smoothly along the attractor structure outlining unstable manifolds as in Tsuda's hand drawn schematic in Figure 4, but rather the points hop

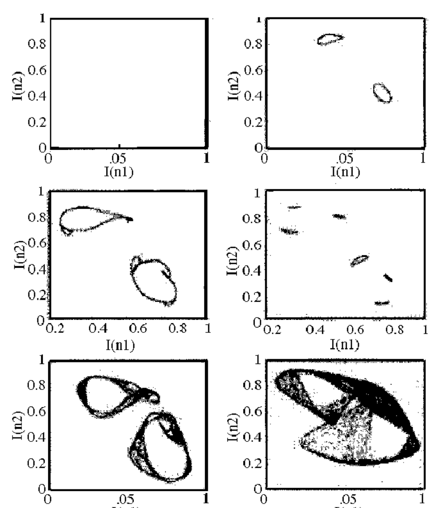

Figure 1 (Mandell & Selz). Phase portrait of two self and other coupled "logistic" neurons as discrete maps.

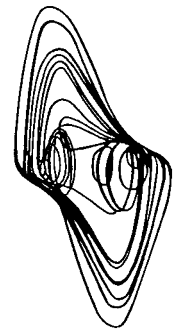

Figure 2 (Mandell & Selz). Phase portrait of Hodgkin-Huxley equivalent forced van der Pol differential equation in the "strange" regime.

among and between structures in an unpredictable way. If the task involves the encoding of sequences, the potential difficulties are obvious. In addition, how difficult must it be to partition the fractal point distributions to allow the definition of the disjoint sets associated with categorizing or match to sample tasks?

In contrast with Figure 1, Figure 2 is a phase portrait of a Hodgkin-Huxley equivalent forced van der Pol differential equation in the "strange" regime that comes closer to the orbital behavior proposed in Tsuda's Figure 4 schematic (Mandell et al. 1987). It demonstrates the unpredictable choice of circling versus crossing made by the orbit in the neighborhood of each of its two hyperbolic fixed points. We have obtained electrophysiological evidence for Grebogi's "strange nonchaotic attractor" (Ding et al. 1989; Mandell et al. 1991), with a fractal structure but no orbital mixing (near zero leading Lyapounov exponents). This dynamic seems better suited for symbol sequence conservation and yet remains consistent with Tsuda's ideas about Cantor coding and the role of itinerancy among destabilized hyperbolic points in attractors of real neural network computation.

Low-dimensional versus high-dimensional chaos in brain function – is it an and/or issue?

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Abstract: We discuss whether low-dimensional chaos and even nonlinear processes can be traced in the electrical activity of the brain. Experimental data show that the dimensional complexity of the EEG decreases during event-related potentials associated with cognitive effort. This probably represents increased nonlinear cooperation between different neural systems during sensory information processing.

In his target article, Tsuda proposes that, in brain functions like memory and perception, high-dimensional chaos has to be introduced to be able to explain the underlying mechanisms. Most of the arguments are based on neural modeling and hypothetical flow-charts.

Nevertheless, the notion of high-dimensional chaos may be welcome by all those investigators who entertain the idea of seeing the electrical phenomena of the brain through the chaoticist's magnifying glass because whether the existence of mathematical chaos in the electroencephalogram (EEG) can be verified or not is seen as a critical aspect in those studies that seem to accept it as an axiom. In other words, if high-dimensional chaos can be proved to exist in brain function (as reflected by its electrical activity), this may appear to be more appealing to those who object to the notion of low-dimensional chaos, maintaining that such a mode of operation would be too simple with respect to the extreme complexity of the brain.

Tsuda refers to Rapp (1995), whose reflections on this issue indicate that "'chaotic' behavior . . . in the brain may not be chaotic in the mathematical sense" (quote from Tsuda's article). More precisely, the very existence of nonlinearity – of which chaos is usually regarded as a possible manifestation – itself was questioned and could not be systematically proved (Pritchard & Stam 2000; and others) in the EEG, although this view is not widely accepted (Fell et al. 2000; and others).

It still seems unclear if the above dilemma is valid at all and if one of these standpoints – the presence or absence of low-dimensional chaos and nonlinearity itself – can be substantiated by available data, which issue is left open by Tsuda. For all those, however, who have to deal with the criticism coming from the "linear side" – who by definition reject the idea of low-dimensional chaos in brain function – the finding of chaos (although high-dimensional, but taken for granted by Tsuda) may come to the rescue, as mentioned above. It should also be noted that this issue is strongly methodologically biased, that is, the most important question is probably not if nonlinearity and chaos can be verified in the EEG but how the methods of analysis applied can or cannot handle this problem. Although most if not all of everyday experience indicates that nonlinearity dominates the features of brain function (for example, doubling the intensity of a stimulus never results in an evoked potential that has twice as large early components, not to speak about the extremely complicated relationship between a stimulus and the longer latency "cognitive" components it may elicit, etc.), the majority of related studies still try to reject the null hypothesis that the analyzed signal is a linearly filtered Gaussian white noise and use different surrogate data, which – nonetheless necessary – testing seem to apply to the method used, rather than to the basic question itself.

A number of available data show that decreasing dimensional complexity may be an essential feature of sensory information processing. It was found that the dimensional complexity of the EEG, as revealed by the calculation of its correlation dimension, decreased with the occurrence of the P3 event-related potential component in a task-dependent and area-specific way (Molnár 1999; Molnár & Skinner 1992; Molnár et al. 1995). The method used for the analysis was the "point correlation dimension" (PD2, Skinner et al. 1994), capable of tracking time-dependent dimensional changes in epochs with nonstationary features. Our interpretation of this phenomenon was that this dimensional decrease reflected increased (nonlinear) cooperativity between different systems working in unison when the evaluation of the meaning of a stimulus and the decision-making about its importance – typically associated with cognitive processing as signalled by the appearance of the P3 wave – was necessary.

This increased cooperativity, causing the degrees of freedom (i.e., the dimensionality) of the system to decrease, may also apply to the increased synchronization in the gamma frequency range, referred to by Tsuda. However, the reader is left in doubt if the two ways of operation (low- and high-dimensional chaos) can or cannot coexist in the brain. Can high-dimensional chaos be also classified as deterministic? Is it possible that both deterministic and stochastic processes can be found in brain function but have different biological significance? The answer to these questions should come from data obtained in real biological experiments, analyzed with appropriate methods not biased toward any extreme viewpoints.

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Learning and control with chaos: From biology to robotics

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Abstract: After critical appraisal of mathematical and biological characteristics of the model, we discuss how a classical hippocampal neural network expresses functions similar to those of the chaotic model, and then present an alternative stimulus-driven chaotic random recurrent neural network (RRNN) that learns patterns as well as sequences, and controls the navigation of a mobile robot.

Introduction. Brain activity fluctuates between an open and closed functional mode as suggested by brain theories, from stimulus-response paradigm of behaviorism to mental representations of cognitivism. Chaos theory of brain activity had also to face this dilemma and evolved from completely autonomous to partially open systems. However, the proposed model does not explicitly address this problem, nor the related adaptability/stability trade-off. The mathematical language used appeals to both neuroscientists and modelers, but sufficiently convincing biologically grounded mathematical justifications are lacking. Most of the functional accounts can also be provided by classical neural network models or stimulus-driven RRNN.

Theoretical and neurophysiological relevance of the model. From a strict mathematical standpoint, mixing stochastic (e.g., noise) and deterministic (e.g., chaos) concepts is confusing, as it becomes difficult to assess the contribution of each of these factors to the system's behavior and does not resolve the nature of biological chaos. Further, the choice of Milnor attractors or Cantor sets is not biologically justified. A biologically constrained differential system (like Hodgkin-Huxley equations) presenting this type of attractor and modeling the desired function properties (sequence learning) would be an improvement.

Nevertheless, *multistable systems* such as Milnor attractors could constitute an advantage for working-short-term memory, but a drawback for LTM. A balance (possibly peculiar to each brain state) must be found between attractor stability and itinerancy. At the limit, should the dynamics actually stay for a while on the attractor (which seems reasonable for memory states), or is the attractor just a "check point" in the state space?

Furthermore, itinerancy provides correlated transitions among states and possibility of path learning. This path learning, a possible advantage over transitions resulting from noise or simulated annealing, could account for the increased memory capacity of the system. However, is not noise necessary for the creation of new attractors when the system is close to a tabula rasa? Furthermore, how a Hebbian rule "shapes" the dynamic landscape so as to associate an attractor ruin with an input remains an unanswered question. Do the ruins pre-exist and are the inputs allocated to one of them according to the initial condition (and learning only increases the attraction basins), or are they created by interaction with the input?

SCND attractors in chaos-driven contracting systems seem to be linked to encoding (CA3) and decoding (CA1) of temporal sequences. In our hippocampal model (Gaussier et al. 2000), similar couplings between associative and categorization nets allow for the emergence of place cells (entorhinal cortex-dentrate gyrus), and then subsequently allow to learn place cell sequences through transitions (CA3-CA1). Our model does not operate a hierarchical embedding of the sequences, yet it learns higher order transitions.

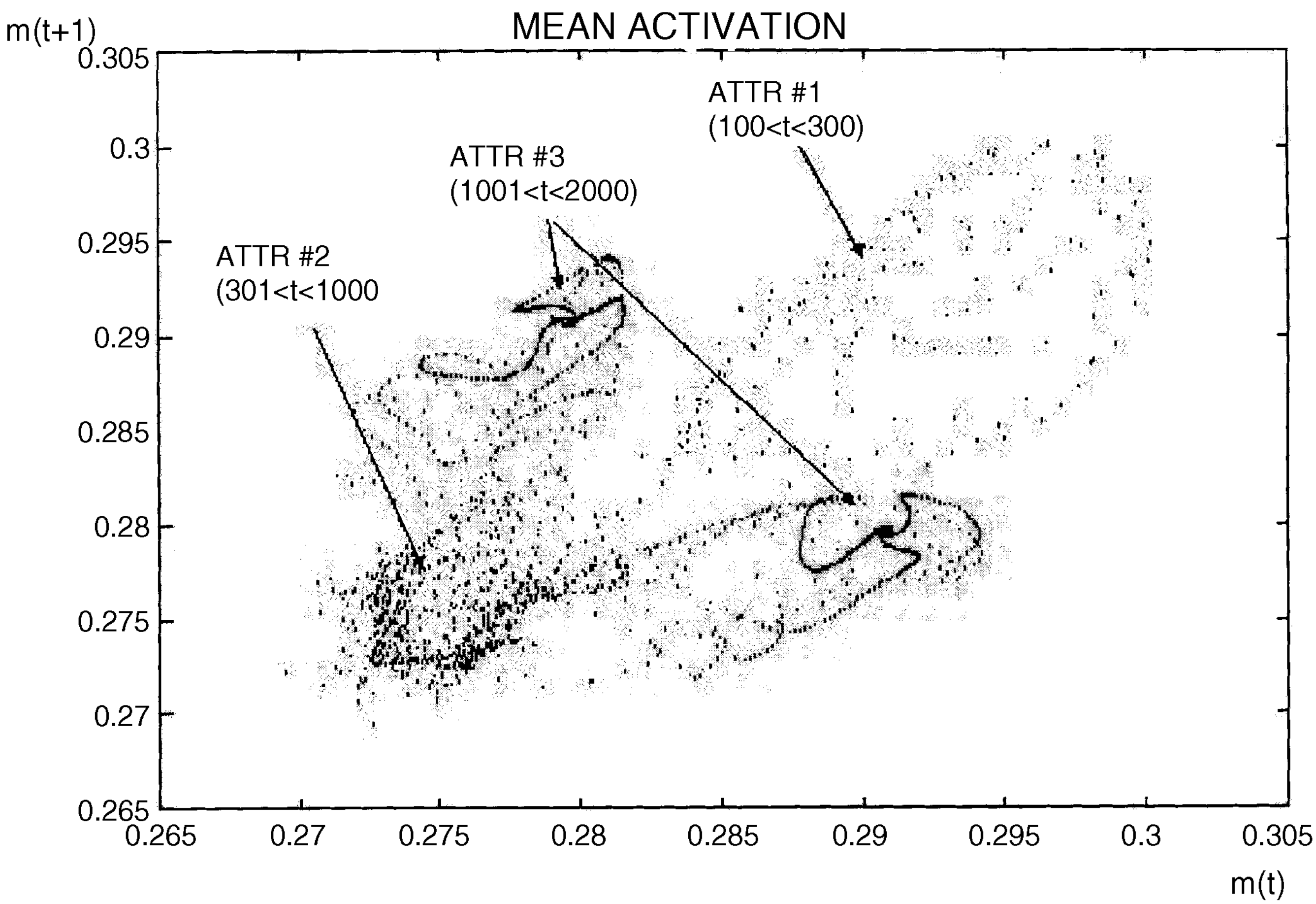

Figure 1 (Quoy et al.). Return map giving the evolution of the mean activation of an RRNN on 2,000 steps, with continuous small changes on input vector. One can distinguish three attractor structures and continuous transitions between them.

Finally, the model attributes the multi-functionality of neurons or brain areas to chaotic itinerancy. Nevertheless, the most illustrative examples of functional adaptation occur in direct relation to changing external conditions, and could also imply *structural reconfiguration.* Among other examples, Ach septal modulation of hippocampus, when confronted with novelty, seems to act by suppressing the expression of learned patterns (attractors) in recurrent CA3 connections, thus, favoring the instantiation of novel patterns through distal, direct entorhinal connections. This kind of structural reconfiguration of the system could imply more than mere chaotic dynamics. Possibly, in more internally driven (cognitive) tasks, the balance could tilt in favor of more autonomous chaotic dynamics.

Links with random recurrent neural networks. RRNN systems with a high degree of freedom can display high dimensional chaos (Cessac et al. 1994). When the network receives no input, it behaves as an autonomous deterministic system possessing a unique strange attractor. At variance with multi-attractor dynamic systems where the input allows choosing one attractor depending on the attraction basin, our system uses inputs as *control parameters* which change the dynamical system and therefore the attractor. Neural fields constitute such a system, where attractors are fixed points. In the absence of simultaneously coexisting attractors, the behavior of an RRNN in constant interaction with inputs may be very close to itinerancy, since a continuous smooth evolution on the input may produce a wandering through several distant attractors (see Fig. 1). In few steps, Hebbian learning stabilizes chaotic attractor orbits into a limit cycle, implying a stronger attractivity and regularity of the associated attractor, in accordance with Freeman's hypothesis on odor recognition. Then, slight input changes may not be sufficient to escape from such a cyclic attractor (Daucé et al. 1998).

A further development of our model combines an RRNN and a stable input/output layer in order to learn *temporal sequences* (Daucé & Quoy 2000). The interplay between the two nets combined with learning increases the congruence of the two dynamics, producing the learned behavior. Like in the target model, write-in (perception) and read-out (recall) constitute interleaved processes corresponding to the same dynamical phenomenon. The chaotic layer acting as a working memory feeds back the input/output layer with a signal that filters the input according to a dynamical context provided by stability of the dynamical attractor for several steps (working memory). Thus, in a mobile robot navigation application, this system learns a sequence of rotative movements associated with images captured by a camera. Each image and associated actions constitute the components chained to build a sequence. Two distinct behaviors were observed, one when a movement-image association corresponds to a component of the sequence (attractor); the other, during erratic search ("itinerancy" produced by a mismatch between input signal and inner signal) for an image belonging to the learned sequence.

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Chaos and neural coding: Is the binding problem a pseudo-problem?

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Abstract: Tsuda's article suggests several plausible concepts of neurodynamic representation and processing, with a thoughtful discussion of their neurobiological grounding and formal properties. However, Tsuda's theory leads to a holistic view of brain functions and to the controversial conclusion that the "binding problem" is a pseudo-problem. By contrast, we stress the role of chaotic patterns in solving the binding problem, in terms of flexible temporal coding of visual scenes through *graded* and *intermittent* synchrony.

Tsuda's article suggests relevant neurodynamic principles and models related to cognitive processes. Specifically, *chaotic itinerancy* is a dynamic property that may plausibly characterize the flexibility of memory and processing operations in cortical and hippocampal networks. Tsuda's notion of a *dynamic memory* based on chaotic itinerancy and exhibiting dynamic retention, as well as representation by process, may enable a deeper understanding of the neural dynamics related to the interaction between perceptual and memory processes. In a related framework, multistable perceptual patterns and a nonstationary interface of perceptual and memory processes, have been modeled in coupled map (CM) systems (lattices and globally coupled maps, see Kaneko 1990) exhibiting chaotic dynamics and Hebbian adaptive coupling on several time-scales (van Leeuwen et al. 1997; van Leeuwen & Raffone, in press).

By stressing the collective properties of neuronal interactions, and thus implying a "global precedence" in brain processing, Tsuda's theory leads to the strong as well as controversial conclusion that the *binding problem* may be a pseudo-problem. This conclusion is based on the idea that "information representation is dynamically realized as a whole," and that the functions of neural elements, such as neurons or cortical sub-areas, are not relevant in themselves, but rather guided by nonlocal dynamic patterns. Hence, it may be observed that Tsuda's theory is a *holistic* theory of brain function.

Although we may agree on the functional relevance of dynamic relations between neural elements in terms of chaotic processes, and on the idea of a functional (dynamic) rather than static modularity in the brain, in our view chaotic dynamic patterns play a complementary role in flexible neural coding and integration processes. *Both* local and global representational patterns in the brain may be coded by chaotic neural assemblies "moving" on several spatial and temporal scales.

The dynamic interplay of local and global processes in visual perception, for example, has been pointed out by van Leeuwen et al. (1998). According to this study, pattern recognition is dominated by *local* features at an early visual stage, whereas *global* structures dominate at a later visual learning stage through a *hologenetic process.* The same representational evolution has been shown in visual classification learning (Goldstone & Medin 1994), in which classification occurs in terms of simple features at early stages, while being based on more complex features in later stages. Thus, the global precedence in perception and in its neurodynamic correlates, may not plausibly be observed over all stages of visual cognition, and it may also be task- and context-dependent. It has been suggested that the neural correlates of hologenesis in visual perception are given by chaotic or intermittent dynamics (van Leeuwen et al. 1997).

Our recent neurocomputational studies (Raffone & van Leeuwen, in preparation) suggest that the flexible synchrony of chaotic neural oscillators may be a more effective code than the stable syn-

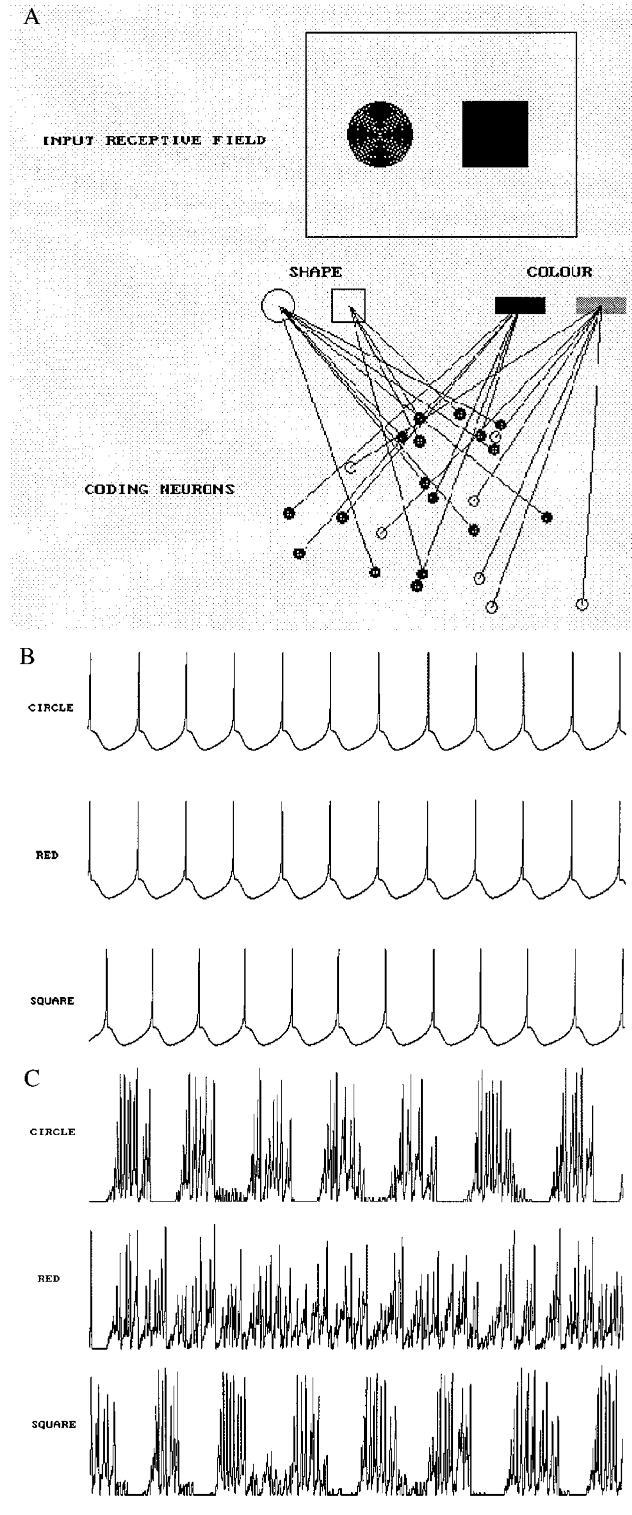

Figure 1 (Raffone & van Leeuwen). "Superposition catastrophes" in terms of both firing rates and stable synchrony of periodic signals when (A) two objects in the same relatively large receptive field of visual neurons share some features, for example, a red square and a red circle. (B) The synchrony of periodic neurons (or assemblies) cannot discriminate the non-shared features of the two objects. (C) By contrast, coupling of chaotic neural assemblies (chaos emerges from within-assembly neuronal interactions) may solve the binding problem with overlapping features in terms of intermittent synchrony, in which *red* assembly is synchronized with assemblies *circle* and *square* at different times. In both cases, excitatory connections are between color and shape neurons, and inhibitory connections between neurons coding the two "competing" shapes.

chrony of periodic oscillators. Specifically, unlike synchrony of periodic signals, dynamic links between chaotic neural elements (neurons or neural assemblies) may enable the flexible unambiguous representation of visual scenes when some features (and the related coding neurons) are shared by separate objects (Fig. 1).

In fact, temporal coding of visual scenes is usually assumed to occur in terms of a *transitive* synchrony among periodic (e.g., sinusoidal) neural oscillators (e.g., Engel et al. 1992). However, this type of synchrony indiscriminately binds even unrelated features when the coded patterns overlap, since if a neuron (or neural assembly) *A* is synchronized with a neuron *B*, and neuron *B* is synchronized with a neuron *C*, neurons *A* and *C* are synchronized as well. According to our *graded synchrony hypothesis* (Raffone & van Leeuwen, in preparation), a superposition catastrophe in terms of synchronous periodic signals is avoided by (non-transitive) *graded* and *intermittent* synchrony patterns among chaotic neural elements, which enable neurons to simultaneously participate in multiple disjoint computations during a psychological time-scale period (Fig. 1). In this functional logic, a flexible population coding in terms of synchrony grades, may take place in neuronal networks, which may also operate in high-level visual processing, for example, in visual working memory (Raffone & Wolters, in press).

Hence, chaotic neurodynamics may operate in solving the binding problem, rather than simply eliding it in terms of holistic neural representation patterns, as Tsuda's view implies. Neural chaos may enable a rich and flexible combinatory repertoire operating on elementary processes. Even if we recognize the plausibility of time-dependent or dynamic receptive fields, which are stressed in Tsuda's article, the remarkable degree of functional or spatial segregation observed, for example, in the visual cortex (e.g., Zeki & Shipp 1988), implies the reality of the binding problem. It may be that the truth lies between a holistic and a localist interpretation of neural systems, based on stable synchrony of periodic signals, may be regarded as "the tip of the iceberg" of more functionally relevant binding dynamics involving chaotic neural elements.

Dynamic neural activity as chaotic itinerancy or heteroclinic cycles?

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Abstract: I question whether chaotic itinerancy is anything new or different to existing research on heteroclinic cycles (cycling-chaos), and blow-out bifurcations (attractor-bubbling) that provide more detailed and better definition for nonlinear phenomena occurring in neural systems. I give a brief description of this research for comparison and expansion, and see it as an important component in dynamical models of neural activity.

I am to focus on Tsuda's concept of chaotic itinerancy which appears very similar to heteroclinic cycles or cycling chaos and associated research that may provide better definition (Armbruster & Guckenheimer 1988; Ashwin 1997; Buono et al. 1999; Field 1980; 1996; Guckenheimer & Holmes 1988). Also, Tsuda's mention of Cantor set is more synonymous with the "simpler" homoclinic cycle (Bevilaqua & de Matos 2000; Guckenheimer & Holmes 1983) rather than chaotic itinerancy. I present a brief description and comparison of cycling chaos and mention its relevance to memory.

A *heteroclinic cycle* is a collection of solution trajectories that connects sequences of equilibria, and/or periodic solutions (Buono et al. 2000), and/or chaotic basins. These cycles persist under small perturbations to preserve symmetry, manifesting in transverse regions of invariant subspace (Ashwin & Rucklidge 1998). They may exist as a coupling of localized attractor networks, typically consisting of Milnor attractor types (as suggested by Tsuda).

Each attractor within the network may display basin riddling where a number of chaotic attractors form within chaotic basins (Glendinning 1999). Riddled basins occur in regions of parameter space where a synchronous chaotic state is attracting on average (i.e., the typical transverse Lyapunov exponent is negative) while orbits embedded in the chaotic state are simultaneously transversely unstable. The basin of the synchronous chaotic state may become a fat fractal (an SCND attractor?) so that neighbouring points belong to basins of another attractor (Maistrenko et al. 1999). Basin riddling may be full, partial or unriddled (Ashwin & Terry 2000). This permits high complexity and variability in the network states. In particular, the networks display trajectories which leave through an unstable invariant manifold but return orbits which are relatively stable and localized, similar to chaotic itinerancy.

In a neural system we may expect that cycling commences or continues in response to internal and external perturbations in an attempt to maintain symmetry. Perturbations result in bifurcations that initiate heteroclinic cycles, that is, the blow-out bifurcation (Ott & Sommerer 1994) or the riddling bifurcation which can give rise to attractor bubbling (Ashwin et al. 1994; 1996).

Different bifurcatory behaviour may occur at blow-out; *Super-critical* or *soft* bifurcations display localised riddling of the attractor basin and dynamics so that trajectories from weaker attractors that come in contact with the absorbing basin boundary are destroyed. This destruction of the weak attractor occurs where the bifurcation takes the form of a *crisis,* although many invariant sets within the previous attractor may still persist at the basin boundary (Ashwin & Terry 2000). In this case, synchronized chaotic states resulting from local riddling will contain an absorbing area from which trajectories starting near a "mixed" absorbing area cannot escape (Maistrenko et al. 1999). This results in the destruction of the Milnor attractor and may form what Tsuda calls an *attractor ruin.* Trajectories may cycle back through this attractor in set-super critical bifurcation, possibly resulting in a chaotic itinerancy. In the *set-super critical* bifurcation the branch of chaotic attractors generated after blow-out still contain the original attractor in the invariant subspace and the fixed points involved in the heteroclinic cycle (Ashwin & Rucklidge 1998). *Sub-critical* or *hard* bifurcations result in global riddling (a Fat attractor?) and new states of activity so that the attractor before bifurcation is no longer contained in the new dynamic structure (Ashwin et al. 1998; Maistrenko et al. 1999).

Sub-critical bifurcations may be analogous to flexible transitions in neural activity. The set-super critical bifurcation may draw some similarities to associative learning mechanisms in the brain resulting in robust heteroclinic cycles. Lyapunov exponents associated with heteroclinic cycling also display transitions through zero at the blow-out bifurcation (Ashwin & Rucklidge 1998), similar occurrences are found in other systems displaying self-organized criticality (Bak et al. 1987; Mendes 1999), Tsuda also found similar occurrences in his experiments.

Noise also presents a crucial element in the dynamics of the nonlinear phenomena (as identified by Tsuda). In systems that operate on the edge of chaos, noise has been shown to be crucial for stable dynamical activity (Freeman 1990; Freeman et al. 1997). White noise activity may be necessary to "fill in" activity that reflects shallow points of local minima preventing the system from settling into spurious attractor states. In simulations of chaotic systems it has been found that noise has the effect of suppressing nonlinear activity (Kuske & Papanicolaou 1998). Some weaker attractor types can be destabilized by the presence of small amounts of noise so that trajectories will converge toward more stable or robust attractor networks (Kaneko 1998). Other types of Milnor attractors in the presence of noise may lead to destabilisations by a type of *bubbling* mechanism (Ashwin et al. 1994).

Therefore, white noise or some diffused activation can become critical for maintaining stability or transitions in systems displaying chaotic properties. It has the effect of maintaining system behaviour within a set of "useful" states, thus placing constraints on the trajectories that the system may explore so that divergent trajectories will tend to disappear, leaving more convergent patterns of activity.

Memory formations here are described in terms of heteroclinic cycles which initiate specific patterns of neural activity in the form of cycling chaos in response to perturbations, in an effort to maintain symmetry. In the absence of appropriate perturbation, complexity or neural states in the system will decompose as attractor ruins through the destabilisation of weak or transient attractors due to blow-out bifurcations or diffused noise.

Summary. There is much literature not mentioned by Tsuda in nonlinear dynamics that bears resemblance to chaotic itinerancy. Whether or not it is the same, or which form of nonlinear activity is occurring within the brain is subject to debate and/or requires further numerical analysis. However, the associated research as described above should serve as an useful adjunct to Tsuda's own formulations or any model of nonlinear dynamics in the cerebral cortex.

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Using experimental data and analysis in EEG modelling

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Abstract: We question the falsifiability of Tsuda's theory and emphasise the need for physiologically based, quantitative models of large scale cortical function that can be validated through experimental data. We outline such a model emphasising its verification through experimental data and possible avenues for testing Tsuda's predictions about nonlinearities in neural behaviour.

Tsuda's dialogue provides a useful metaphor of neural activity but lacks direct comparison with human brain data. There is the added complication of testing such a theory when the brain is a complex nonstationary system. Such systems, due to their complexity and asymmetrical nature, create problems of numerical and analytical tractability so that any nonlinear analysis tends to be indirect and of symmetrical systems (e.g., Buono et al. 2000).

We provide an avenue for testing some of Tsuda's predictions by introducing a model of cortical neural activity (Rennie et al. 1999; Robinson et al. 1997) that provides direct comparisons with human electroencephalographic (EEG) data (Robinson et al., in press). We believe that the information transactions of neurons at a microscopic scale may be approached from the analysis of macroscopic activity, using linear approximations in the first instance. The numerical nature of our model permits such linear analysis in a stationary and controlled system and further analysis of nonlinear dynamics if desired. Other approaches similar to ours include those by Nunez (1995a; 1995b), Lopes da Silva and colleagues (Lopes da Silva & Mesulam 1990; Stam et al. 1999), Frank et al. (2000), and Jirsa and Haken (1996; 1997).

PDE model. Our model provides a structure of intracortical and corticothalamic feedbacks and delays that determine the attractor dynamics exhibited by local neural networks, properties thought to be necessary for chaotic dynamics in neural systems (Freeman 2000). Parameters such as dendritic time constants, synaptic densities, conduction delays and neural gains are compatible with independent physiological measurements (Braitenberg & Schuz 1991; Liley & Wright 1994; Thomson 1997) and are used to constrain model fitting to experimental data.

The model consists of 2-dimensional continuum fields representing averages of firing rate and membrane potential in a macroscopic patch of cortex. This activity is simulated through partial differential equations (PDEs) that embody the nonlinear firing activity of neurons in response to imposed dendritic potentials, the interactive activity of cortical and subcortical neural populations (excitatory and inhibitory), and associated dendritic and axonal delays. Corticothalamic feedback pathways are also incorporated, parameterised with additional nuclei, longer axonal projections, more localized dendritic connections, dendritic filtering and delays. The analytical modelling permits inclusion of other potential feedback loops through nuclei displaying similar characteristics.

Simulations and model fits. Numerical simulations in linear and integral model versions display the emergence of localized oscillations found in the gamma range (~40 Hz) through the interaction of excitatory and inhibitory neurons (Rennie et al. 2000; Wright 2000). Similar behaviour has also been occurred in PDE versions (Rowe 2000; Wright 2000).

In the linear version spatial and temporal domains are transformed via Fourier transforms of PDEs and auxiliary equations. This permits the analysis of a complex spatial and temporal signal within the Fourier domain, while still maintaining all the underlying physics. This level of detail is equivalent to spectral plots of human EEG which are also derived from Fourier transforms of EEG time series.

Our linear model fits have provided neurophysiological information about changing states of arousal and the primary features of the EEG. For example, negative thalamic feedback is concurrent with theta (3–7 Hz) enhancement and sleep spindling (~14 Hz). Cycling cortico-thalamic signals are responsible for the dominant resonant modes in human EEG including alpha (8–12 Hz), beta (16–20 Hz), and so-called beta-2 (24–36 Hz) peaks (Robinson et al., in press).

Coupled neural networks

Chaotic fluctuations in membrane potentials. Our linear model has been shown to be valid for primary features of human EEG when constrained by physiological parameters. The equivalent PDE form presents a unique opportunity to test some of the nonlinear behaviour suggested by Tsuda. An example, is the case of chaotic interspike intervals giving rise to chaotic fluctuation in membrane potentials.

In electro-cortical models membrane potential is typically modelled using an integral function (Nunez 1995a; 1995b; Wright & Liley 1995; 1996), but due to its convoluted form we transform this function into two ordinary differential equations (ODEs) still preserving the original physics (Robinson et al. 1997; 1998). These parameterised functions simulate dendritic rate constants (rise and decay) and peak potential coupled with the arrival of impulses from neighbouring and thalamic neurons. Additional nonlinearities are generated through intracortical and corticothalamic feedback. The analytical form of the model permits analysis of nonlinear relationships.

Coupled ODEs as strange attractors. We have also derived steady state PDE and truncated ODE versions of our model to examine nonlinear dynamics. Our results suggest that basins of attraction can evolve from cortical feedback mechanisms that allow for more complicated patterns, possibly limit cycles or chaotic evolution (Robinson et al. 1998; 2000).

This work provides a basis from which to examine chaotic patterns occurring within the brain. For example, the behaviour of the ODE as a neural signal may follow the pattern of a strange attractor due to the underlying feedback and delay dynamics embedded in the equations. The coupling two ODE sources in attempt to model the behaviour of two coupled neural networks may be observable by examining the phase relationships between the two systems. The Hilbert transform can be used to examine the phase synchrony of the analytic signal, by extracting instantaneous phase and amplitude data. An index based on Shannon entropy is used to characterize the distribution of relative phase between the two attractors. Similar computations can be performed on EEG data permitting direct comparisons between simulations and experimental data (e.g., Breakspear 2000; Pritchard & Duke 1992).

Summary. We find several of Tsuda's arguments compelling but suggest that many need to be addressed in the context of a physiologically based, dynamic theory of cortical behaviour. We have presented such a model that reproduces the primary features of the EEG and has been verified in its linear form. We have also suggested avenues for nonlinear analysis of chaotic dynamics through equivalent PDE and ODE forms.

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Author's Response

The plausibility of a chaotic brain theory

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Abstract: We consider the significance of high-dimensional transitory dynamics in the brain and mind. In particular, we highlight the roles of high-dimensional chaotic dynamical systems as an "adequate language" (Gelfand 1989), which should possess both explanatory and predictive power of description. We discuss the methods of description of dynamic behavior of the brain. These methods have been adopted to capture the averaged or deterministic complexity, and further to allow for discussion of a new approach to capture the complexity of the deviation from such an averaged complexity and also the complexity of interactive modes. We also give arguments in defense of our models for dynamic memory with chaotic itinerancy and Cantor coding. In addition, we discuss the reality that a model of the brain and mind should reflect.

R1. What would a theory of the brain be like?

R1.1. Why hermeneutics?

As **Érdi** correctly points out, the brain is a hermeneutic device in the sense that it interprets the world through sensory information processing, and for us to understand the brain, we must develop some way of interpreting its activity. The brain not only receives and processes external information but also creates a new "reality" and "actuality." According to Bin Kimura (1998; 2000), "reality" is a kind of sensation that can be objectively understood, while "actuality" is a more subjective experience based on sensation relating to action and behavior. With the revolutionary finding of **Freeman** and his colleagues that took place over a period of over 40 years, we now know with certainty the following: Animals do not directly respond to external stimuli but rather respond to internal images they create, and animals' perception is a result of an autonomic interpretation process. In the case of human cognition, a more direct interpretation process must exist. In this case, interpretation is a recursive process evolving in time that acts between pre-understanding and perceived information. A person's pre-understanding should be altered in accordance with perceived signals, while the perceived information will also change in a manner that depends on the change in the pre-understanding.

In order to understand the global function of the brain we must learn how to interpret brain activity. Many people have attempted in the laboratory to find a neuronal representation of information, assuming the existence of neuronal correlates to cognition. However, it is not possible to obtain such a representation without knowing precisely the actual effects experienced by neurons or neural assemblies during the performance of the task in question. On the other hand, such actual effects themselves are the object of study.

In order to observe how an artificial brain creates a new actuality in the sense of Kimura, **Ikegami & Tani** (see also Tani 1998) attempted to interpret with cognitive language the interaction between perception and action manifested in the behavioral self-control of robots. Although it is still controversial whether or not the interpretation provided by Ikegami & Tani regarding the perception and behavior of a robot with recurrent neural network (RNN) is plausible, we consider it to be one study in one possible useful direction. The work of **Quoy et al.** on robot navigation control utilizing random RNN also represents a promising direction. Actually, these works can be viewed as implementation of a hermeneutic theory of the brain (Arbib & Hesse 1986; Arbib et al. 1998; Blomfield & Marr 1970; Érdi 1996; Érdi & Tsuda, in press; Marr 1982; Tsuda 1984; 1991; Winograd & Flores 1986).

Raffone & van Leeuwen criticize our theory as a holistic theory expressing opposition to our statements in our target article that information representation in the brain is dynamically realized as a whole, and that the precise nature of neural elements, such as neurons and cortical sub-areas, is irrelevant. They interpret our theory as a top down theory and thus as a hermeneutic theory. However, as **Érdi** correctly states and as we emphasized above, a hermeneutic theory is plausible and even provides an adequate language system (Gelfand 1989) that is sufficient to express an understanding of the brain function in terms of a relation of physiological phenomena to cognitive and psychological phenomena. A proper theory of the brain must be a hermeneutic theory. It is correct for Raffone & van Leeuwen to point out what their model suggests: In early vision, the dominance of local features processing and the later processing of global structure. This local dominance, however, exists only under the condition of tabula rasa in the sense of Locke. After the development of learning, the processing of global structure can become dominant. This situation is clearly seen in the cognitive process of inference in a certain language game that I introduced previously (Kaneko & Tsuda 2001; Tsuda 1991) as a Shannon test. Shannon invented this game when he estimated the information content (the number of bits) contained in one (English) word. In this game, there are two people, *A* and *B*. In the beginning, *A* has a sentence in mind, of which *B* has not been informed. *B* attempts to determine this sentence and does so by first attempting to determine the first word, and hence the successive letters. This is done by asking a series of questions to which *A* can give only Yes and No answers. Early in the game, *B* can only ask questions randomly, in a bottom-up form of processing. As *B*'s knowledge increases, however, a top-down form of processing that relies on *B*'s context-dependent judgment becomes increasingly effective.

Let us further discuss briefly the uncertainty regarding the understanding of neural elements. **Dinse** has described recent developments in the study of dynamic receptive fields (dynamic-RFs). Population level activity in early sensory cortices expressed with respect to coordinates of the stimulus space has been studied, and dynamic population-RFs have been constructed (Jancke et al. 1999). Dinse has discussed the possibility that these two types of RFs play a functional role, influenced by the structure and function of surrounding neural networks in early sensory cortices. In other words, the difference between spatio-temporal dynamics in dynamic-RFs and those in dynamic population-RFs clearly reflects the dependence of the identity of the neural element or functional unit on the nature of the information processing. We would also like to mention Sakurai's series of studies on the flexible coding and decoding of cortical neurons (Sakurai 1996; 1998; 1999) as well as the work of Arieli et al. (1996) which both **Dinse** and we (in the target article) cite. These studies clearly show the dependence of neuron activity on the activity of the system as a whole or at least of the surrounding networks on a large scale. Sakurai found that the type of activity displayed by individual neurons is correlated with global behavior, which was characterized according to different tasks performed by the experimental subject. Both **Kay**'s comment and **Freeman**'s finding on the olfactory bulb support the existence of such a relation, although **Foster** argues against it. The fundamental fact underlying our point of view is that the identity of the neuronal element cannot be known a priori.

In addition to the points raised above, adult neurogenesis (Eriksson et al 1998; Kempermann et al. 1997; Pincus et al. 1998; Sakakibara & Okano 1997) in wide areas of the brain, in particular the olfactory system, the hippocampus, and even the neocortex may support the hypothesis of the variability of neural representation due to dynamic reorganization of neural networks. The term "as a whole" that we use in the target article expresses the variability of the nature of the functional unit in the sense that what acts as the "unit" may change in a manner that depends on interrelations within the surrounding network and also the process of functional manifestation. Therefore, the word "holistic" is not appropriate to characterize our theory. A term like "relationally dynamic" would be more appropriate.

R1.2. The method of description

Freeman has proposed a mesoscopic level description in order to identify the level at which functional dynamics emerge. Through his own studies and other evidence, he has found that this level is not that of a single neuron level, that is, the microscopic level. In conventional phase transitions studied in physics, many degrees of freedom at a microscopic level begin to become correlated with each other in some critical regime of the system's parameter(s), and as a result macroscopic order that can be described by a few degrees of freedom emerges. These few degrees of freedom are represented by so-called order parameters. However, in some complex systems, the dynamics of these order parameters can be complex and even chaotic, though chaotic behavior in this case is confined to a low-dimensional attractor. In more complex systems, the identity of the quantities that act as the order parameters may change in space and time. In this case, the macroscopic description loses its descriptive power. It is natural to consider an intermediate level between the microscopic and the macroscopic levels as a level of description where dynamically complex behavior can be captured. Physicists call this level the "mesoscopic" level. **Freeman** borrows this idea. **Freeman**'s use of the term "mesoscopic" in the description of inputs-driven chaotic behavior in the olfactory system is appropriate, because in the brain, dynamically transient motion is generic, as **Breakspear & Friston, Dinse, Freeman, Heath,** and **Kay** correctly point out in their commentary.

Several methods have been employed in the construction of scientific theories. Before discussing the method we propose in the modeling of the brain, we give some general discussion. It should be noted, though, that the following distinction between such methods described below might be controversial, and many other ways of distinguishing such methods based on different philosophical viewpoints are possible. However, since we believe there is a difference between the methods of constructing theories in the study of the brain and the study of physics, we feel that the manner of thinking we use here is useful.

One method employed in the construction of theories is that which begins from "first principles." Here, by a "first principle" we mean a hypothesis or an axiom on which a theory is based. An example of a theory obtained using this method is Newtonian dynamics formalism. However, in the situation that proper first principles cannot be identified or when a theory based on first principles is not feasible, a "phenomenological" method is adopted. The description of fluid using Navier-Stokes equations is a typical such method. Thermodynamics is also such a "phenomenological" theory. By "phenomenological" theory we here mean that a theory is based on experiential rules. In neural systems, a useful method of modeling that seems to be based on something very different from both a method of first principles and a phenomenological method has been proposed. This method consists of modeling in terms of the Hodgkin-Huxley equations (Hodgkin & Huxley 1952). The distinguishing characteristic of this method is that it includes a set of inductively derived equations that explicitly include experiential equations. We call this type of model a "semi-experiential model." **Banerjee**'s model of spiking neurons is at this level. Also, **Aihara & Ryeu** have studied chaotic neuron model constructed by Aihara et al. (1990, see also Fig. 9 in the target article). This chaotic neuron model is a kind of abstraction of periodically forced Hodgkin-Huxley equations.

It is probably true that among models which possess a physiological background there is no generic model found up to now other than the Hodgkin-Huxley equations. **Freeman's** population model simulates many types of dynamic behavior in the olfactory system, as described by **Freeman** and **Kozma** in their commentaries. Through studies of population models like the KIII model, one can extract the essence of the dynamics that might be embedded in various areas of the brain. Whether this type of model can be directly applied also to cortical systems other than the olfactory system is still unclear. Therefore, it is still not known if we can use a KIII-type model as a generic model applicable to all areas of the brain. Nevertheless, we believe that population models, rather than types of models such as coupled Hodgkin-Huxley equations, are more suited to describe (macroscopic) functional manifestations, such as perception and cognition. It is important to determine the proper variable at a mesoscopic level which can be used to make a bridge between the physiological level and the psychological level. In other words, it is important to determine the "adequate language." It should be noted that an electric potential or a sequence of impulses as such cannot be considered a proper variable for the description of cognition.

Instead of a direct use of a KIII-type model, we have considered another mesoscopic description in the target article. This description is based on the realization of self-organization in memory through chaotic dynamics.

We have also investigated a general method of study for complex dynamical systems, which will, we believe, provide a high-power description also for the study of the brain and mind (see sect. R2). The basic steps of this method are as follows (Kaneko & Tsuda 2001): (1) find structural changes of complex behavior from both static and dynamic viewpoints by means of dissecting phase space; (2) find universality, reconstructing structures and relationships, immanent in various types of complex phenomena; (3) construct an artificial system, based on the fundamental conceptual elements of the universal properties; (4) construct a model that describes both top and bottom levels from an intermediate level which is neither macroscopic nor microscopic; (5) construct an adequate language system sufficient to describe complex systems, based on a mathematical theory for treating the complex dynamics and processes; (6) acquire new intuition by formulating a contra-intuitive situation and by observing the simulated variety of complex phenomena.

In the above described procedure, the method of modeling mentioned in (4) corresponds to the mesoscopic description discussed by **Dinse** and **Freeman**. The present attempt to construct a theory of the brain and the modeling given in the target article represent a realization of this generic method. The above steps (5) and (6) are deeply related to hermeneutics. It is important to realize the existence of a dual purpose regarding the predictive and the explanatory power of a model (Gernert 1998). The above described generic method possesses such a duality. This dual purpose, proposed by Gernert, is also alluded to by **Ikegami & Tani**. They correctly assert the importance of dynamical systems as a tool or descriptive language, which is thought to possess a stronger descriptive power than natural language. We agree with Ikegami & Tani, in particular with regard to the point that high-dimensional dynamical systems including IFS may provide an appropriate descriptive language for the brain. Certainly physiological terminology itself cannot be considered as possessing explanatory power regarding cognitive phenomena, as psychological terminology itself cannot be considered to possess predictive power regarding the physiological phenomena. We wish to obtain a third language, a language system that is capable of thoroughly describing brain and mind. At this time, of course, our chaotic dynamical systems terminology is still primitive to realize such a goal.

Quoy et al. suggest a similar perspective, inquiring about the standpoint of chaos theory concerning behaviorism (stimulus-response) and cognitivism (mental representation). For the modeling of animal experiments involving higher functions, most of which consist of a type of stimulus-response, we have attempted to interpret the internal states of the brain as mathematical functions or distributions by observing the stimulus-response relations. We employ high-dimensional chaotic dynamical systems for this inferred internal representation. In order to decrease the ambiguity of an interpretation of this type of animal experiment, we have constructed (Tsuda & Hatakeyama 2001) a formal theory of the structure of task-related functional manifestation. We have applied this theory to a series of experiments conducted by Sakagami et al. (Sakagami & Niki 1994; Sakagami & Tsutsui 1999). The theory was able to predict all possible types of discrimination of stimuli and conditions that can be represented by neurons found in the prefrontal cortex. We believe that chaotic dynamical systems can be used to represent the neural correlates of cognitive processes that can be detected by mesoscopic level measurements, such as f-MRI, optical recordings, and (local) electroencephalograph. If a neuronal dynamical system possesses point attractors and limit cycles only, this neural system lacks adaptability to varying environments. Thus it will inevitably become destabilized if we attempt to use it to model a full range of animal behavior. The emergent dynamics capable of providing this adaptability should possess a moderate stability that may be a global stability. Our idea is to use chaotic itinerancy as a means of guaranteeing both stability and adaptability.

R2. Reality of the model

R2.1. Falsifiability of the theory

In our attempt to find a new method of understanding the brain and mind at a mesoscopic level, we face several difficult problems. First, a hermeneutic theory seems to lack the falsifiability property demanded by Popper as a minimum condition that a scientific theory must possess, since this theory can develop self-consistently through the evolution of the pre-understanding, allowing for a self-consistent interpretation to be reached. A hermeneutic theory consists of components, each of which could itself consist of a quantitative model and its predictions, and these, rather than the theory as a whole, can possess falsifiability. From another standpoint, we could construct a theory – something that could be termed a "qualitative model" – for the purpose of providing a plausible story of neurons or neuron assemblies. Such a theory should be constructed to allow us to carry out a more proper and deeper understanding of the brain and mind. Thus, as **Rowe & Wright** state, a quantitative model like theirs can lead to elemental models supplying such a qualitative theory. For example, the PDE and coupled ODEs which constitute an elemental level of Wright's theory (2000) of the brain activity and its cognitive function can possess falsifiability, while the whole theory can be justified as a hermeneutic theory.

In biology, it has been asserted that the correspondence between structure and function is crucial (Li & Hopfield 1989; Szentágothai & Érdi 1989). Following this assertion, we have attempted to construct a structure-based model of biological function. Actually, we constructed a skeletal model, based on anatomical data that were collected in detailed studies over thirty years by Szentágothai. In the modeling, we hypothesized that a type of structure that is common to various areas possesses a common function, and a structure specific to a given area possesses a specific function (see also Li & Hopfield 1989). Both models presented in the target article were constructed according to such a principle, and thus these models are examples of a kind of skeletal model.

Heath has proposed a cognitive model consisting of dynamic neural networks, which could possess a predictive power. He also discusses the possibility of converting the principles given in section 3.5 of the target article into predictions that can be verified.

One of the characteristics observed in chaotically itinerant behavior is a long time tail of the time-dependent mutual information. This tail often exhibits an algebraic damping. This characteristic exist even when noise is present, because the frequency of stagnant motion in the vicinity of an attractor ruin cannot be decreased by such a perturbation. The presence of a long time tail indicates the presence of recurrence of similar dynamic behavior in the evolution of the system, and hence it may provide a mechanism capable of producing short-term memory, like working memory. Nicolis and Tsuda (1985) proposed a feasible mechanism of magic number seven plus minus two with chaotic dynamics with large fluctuations, and further demonstrated (Nicolis & Tsuda 1989) that these long-range correlations may lead to a universal power law known in the study of natural languages as the Zipf law. The presence of recurrence of similar dynamic behavior can work effectively when an episode is embedded in the CA1 region by the use of Cantor coding. During a period of approximately 100–200 msec cortical-hippocampal loop time, only a few events in an episode will be able to be embedded in a Cantor set. This loop time would not be sufficient for the transformation of episode from a short-term memory to a long-term memory. Some kind of recursive dynamic behavior may facilitate this type of transformation.

At this point, we must consider the fact that a memory is not independent of its cortical context, as **Heath** points out. Therefore, taking into account context cues in studying the process of memory dynamics and formation is essential. It is certain that our present model lacks this feature. Although the significance of context cues has been emphasized by many authors, no mathematical model that is capable of incorporating them has yet been proposed, as far as we know. We believe that such context cues are input into other lower cortical areas in the more abstract form of codes rather than raw sensory information. Usually, this input corresponds to a feedback signal. For proper modeling, cortical neural activity representing codes must differ from that representing raw sensory information. In our hippocampal model, CA3 activity consists of chaotic itinerancy, but CA1 activity does not. This is because Cantor coding is carried out in the cross section on which CA3 chaotic activity is constant. Coding hierarchy is generally limited only by the nonlinearity of the chaos that provides a grammar of chaotic motion. This limitation can be observed in the present model (see also **Aihara & Ryeu**). If code signals strongly affect the chaotic behavior in CA3, the Cantor coding will be fragile, and this calls into question its realism, as pointed out by **Érdi, Freeman** and **Kay** in the case with feedback. We believe that the feedback signal is generally different in quality from the feedforward signal. Thus we doubt that the feedforward and the feedback connections can be thoroughly described in the same form as in coupled oscillators.

It would be very useful for further development of the study of dynamic memory to identify those features of our model with stochastic renewal and **Heath**'s model with chaos control that are similar and those features that are different, since they have a similar structure of the interacting "modules" (see also Heath 2000a).

R2.2. Could inputs and modifiable synapses be a bifurcation parameter?

The brain is an open system in both energetic and informatic senses. With respect to energy, the brain is a far-from-equilibrium system, since it is maintained in a high energy state by the influx and outflux of energy and matter. With respect to information, the brain receives external information and dictates action on the environment in response to this information. However, contrary to **Banerjee**'s claim, we assert that such inputs should not take the form of bifurcation parameters.

Banerjee's observation concerning transitory dynamics made with regard to his treatment of spiking neurons is correct. This observation is that the attractor created in any cortical "column" is continually influenced by neighboring "columns," subcortical areas, and the environment. For this reason, this attractor changes or disappears, and a new attractor is created. This is the nature of the transitory dynamics characterizing the system. Through this observation, Banerjee studied these transitory dynamics using a treatment in which the inputs are represented by a bifurcation parameter. **Quoy et al.** also consider inputs as bifurcation parameters. Although we appreciate the models proposed by Banerjee and by Quoy et al., we are skeptical of their assumption that inputs can be treated as bifurcation parameters.

We now consider the situation in which a system receives inputs from other systems. In the case that invariant sets like attractors are present in phase space, the change of such invariant sets in parameter space can be described as a bifurcation. To treat an input as a bifurcation parameter is equivalent to assuming the presence of such invariant sets, and hence this treatment becomes feasible only when the inputs change extremely slowly, compared with the system's dynamics. This is not a valid assumption in a dynamic system like the brain or any of its subsystems in which the input rapidly varies. It is crucial for understanding a brain of this nature to investigate it as a dynamical system influenced by varying inputs that may be produced by other dynamical systems either with or without noisy perturbations. By viewing inputs as originating from other system, rather than as bifurcation parameters internal to the system, the dynamic behavior of the model can be better characterized.

When considering inputs as variables controlled by other systems, rather than as bifurcation parameters, a total system can be viewed as an IFS. Pollack (1991) used recurrent neural networks for the system under study and incorporated the external world in the form of varying inputs. In a dynamic memory model, we used recurrent neural networks with inhibitory neurons for the model brain system and modeled probabilistic synapses as varying inputs. This model appears to contain a Hopfield spinglass-like model, since it is essentially reduced to a Hopfield net when the probability characterizing these synapses approaches the inverse of the system size. Even in the neighborhood of this value, our net is dynamically equivalent to the Hopfield net, as **Banerjee** points out. Despite this fact, there are dynamics embedded in our model that are essentially different from any dynamics exhibited by the Hopfield net. In particular, our model exhibits a chaotic transition between far-from equilibrium quasi-stationary states. (It should be noted that this is not a transition from an equilibrium state.) Increasing the probability to a certain value, chaotic itinerancy appears. In our chaos-driven contracting system, the model brain is a stable network and varying inputs are provided by a chaotic dynamical system which exhibits high-dimensional chaotic itinerancy or low-dimensional chaos with a restricted grammar. This grammar is restricted in the sense that it possesses forbidden symbol sequences. We regard this as a skeletal mathematical model of the olfactory system and the hippocampus. Other studies in which inputs are treated as variables controlled by other dynamical systems have recently been published by Gohara and colleagues (Gohara & Okuyama 1999a; 1999b; Gohara et al. 2000; Sato & Gohara 2000; Yamamoto & Gohara 2000).

As an important factor other than inputs that can influence the system, **Banerjee** discusses synaptic modulation. For a reason similar to that in the case of inputs, it is not feasible to model this as a bifurcation parameter when one wishes to understand the mechanism of nonstationary and itinerant behavior. Only if one tries to understand the system's dynamics as consisting of the change undergone by invariant sets can inputs and synaptic modulation be treated as bifurcation parameters.

R2.3. Landscape lacks a reality

Freeman claims that attractor landscapes in the olfactory system are recreated in each inhalation period. Freeman identified this recreation as the olfactory flexibility. He criticizes our model as being too rigid and not allowing for the change of phase space structure. A similar criticism is also made by **Ikegami & Tani**. However, despite this criticism, we assert that our memory dynamics model does indeed exhibit structural change of phase space under the Hebbian learning. With regard to this point, **Quoy et al.** questioned how the dynamic landscape changes via Hebbian learning. We now briefly explain this process. The learning of new patterns alters the transition of memories in such a way that new memories are incorporated into a sequence of memories which appear dynamically to display chaotic itinerancy. In this way, a new sequence of memories is created.

Hebbian learning classifies the closeness of input patterns in the following way. In a conventional associative memory model, a new input pattern is placed within the basin of a certain attractor. Here, some attractors are a memory representation and others are a parasitic one. If that pattern is learned, the basin structure becomes complex due to the formation of a new basin (see also Amari & Maginu 1988). In our dynamic memory model, there is no conventional (geometric) attractor, and hence no conventional basin is present. In place of such a basin, at least one hole is present, which links each memory representation to all the others. We have not obtained a mathematical proof of whether riddled basins appear in the present model. We have not found symmetry in our model like that which **Breakspear & Friston**, and **Rowe** have discovered. It is, however, certain that a similar structure to that of riddled basins has been observed in numerical studies. Because, in the situation that the transition of memories is allowed, Hebbian learning acts along the transition paths also; that is, the transition paths are also reinforced. The closeness of input patterns can thus be defined in terms of temporal order, since the transition occurs between patterns with a large overlap. In this way, as more patterns are learned, the phase space structure becomes more complex.

In the manner of **Freeman**, here we would like to use a metaphor. Imagine we are observing a stream at a fixed position. Then, we always observe different water molecules at each time, even in Escher's waterfall chain. For this reason, we cannot find invariance at such a level. On the other hand, a river possesses certain structures at different levels – from mesoscopic to macroscopic – as a flow of water. We may be able to find some invariance at such levels and we may recognize universality within the continually changing behavior. In contrast to Freeman's intended demonstration in his allusion to Escher, we think Escher's chain demonstrates a method of representing the creation of new "quality," even though the structure appears static. Geometric impossibility embedded into this static structure forces us to change the viewpoint from which we consider the picture and enables us to find new "quality" hidden in the structure, for instance, the waterfall chain may provide us with a hint about the four-dimensional "qualia" of the scene. New "qualia" at a mesoscopic or a macroscopic level, which is not manifested at a microscopic level, might be created in the same way, as **Dinse** discussed.

Freeman and **Quoy et al.** both use the term "landscape." Freeman in the expression "attractor landscape" and Quoy et al. in the expression "dynamic landscape." We think the use of this word is misleading with regard to both our model and the KIII model, and maybe also with regard to other far-from equilibrium dynamic systems. Concerning this point, we give the following discussion from the general theory of nonlinear dynamical systems (Kaneko & Tsuda 2001). If there are at least two extremely different time scales characterizing the system in question, then the system's behavior can be described by dynamics on a static landscape and its dynamic modulation. Here, the landscape can appear to be a rugged landscape. Such an extreme separation of time scales is often observed in nonlinear systems. However, no evidence for such a separation of time scales has been found in the very flexible system like the olfactory system that Freeman studies. In such flexible systems, the "landscape" cannot exist. Thus the statement that the "landscape is recreated" is misleading. If we interpret Freeman's intention correctly, we may be able to describe this as something like "epigenetic landscape" proposed by Waddington. However, this cannot be described by anything that could be considered a "landscape." (Although, when considering the dynamic behavior of the entire process of development, it might be possible *a posteriori* to account for this development in terms of a landscape.) Describing a system with a landscape is inconsistent with the flexibility of the system, and the concept of a landscape does not apply to the flexible brain.

R2.4. Action is contained implicitly in probability terms

Kay points out that our model lacks an action term, and for this reason she suggests that we introduce a somatosensory system. She asserts that by doing this, interfacial dynamics may emerge. This is closely related to the causality problem considered by **Ikegami & Tani**, context cues considered by **Heath**, and falsifiability considered by **Rowe & Wright**. Kay is right that our model does not explicitly contain an action term. However, the model implicitly contains such a term. A typical mathematical model in which an action term exists implicitly is given by Samuel Karlin (1953). He formalized the situation in which a living system with internal state that can be expressed by a variable x must make a decision to choose a certain action i among many possibilities at a certain time. Let $pi(x)$ be the probability of choosing an action i, where x is the state of the living system. We consider this process to be described by a dynamical system. That is, the state of the system is determined by a dynamical system. As the result of the choice of an action, the state must change in accordance with this action. Thus the state evolves as a parametrized dynamical system, $F_{pi(x)}(x)$. Since $pi(x)$ depends on the state x, a change in the state causes the probability for the choice of the succeeding action to change also. This Karlin's formulation gives the first example of IFS.

The system described above exhibits a stochastic renewal of dynamics, since the dynamical system governing the development of the state depends on the action chosen. If the probability function for the choice of the action is described by a certain chaotic dynamical system, this type of decision making can be described by a skew product transformation. In this case, the feedback effect of the action on the state of the system is implicitly taken into account. We believe that the feedback from the environment as influenced by system's action is thus implicit. As stated in section R2.1, this framework yields "coupled" systems with characteristics that differ from those typically seen in what **Breakspear & Friston** present as symmetrically coupled nonlinear oscillators. There may be a level at which brain activity can be described by coupled nonlinear oscillators, but it is doubtful that a symmetric coupling system would be useful in the modeling of actual brain activity. In general, the forward connections in the brain are related to a sensory information processing, while the backward connections are related to the context, that is, the intention, motivation, situation, condition, and so on. The context may appear to be a cue code for sensory information. The key factor is the existence of a type of "connection." In the brain, the type of connections between feedforward and feedback differs. For this reason, it is important to study the effects of skew product transformations.

Because the chaotic behavior found in the olfactory bulb (OB) is caused by the feedback connections from the prepyriform cortex (PPC) possessing contraction dynamics, the presence of physical coupling is likely, as **Kay** mentions. We would like to know what the feedback is in such a case. Damped oscillations are enhanced and then become chaotic in the OB. According to **Freeman**, this happens only in a motivated condition like in the hunger state of an animal. Hence, the feedback to the OB is a motivational signal. This situation of the "coupling" can be realized in the following dichotomy. The input-output function of the OB is chosen to be *F1* in the presence of motivation, and chosen to be *F2* in the absence of motivation, where chaos is assumed not to exist. Then, the main dynamics in the PPC appear as the process of chaos-driven contraction dynamics.

Taking into account the stimulus-induced stochastic release of synaptic vesicles, whose physiological significance is correctly pointed out by **Liljenström**, contrary to the claims of **Freeman** and **Breakspear & Friston**, we considered the metaphor of "neuronal decision making." One can extend the present model to include the state dependence of the probabilities for the choice of action. This is a topic for future study. Karlin investigated ergodicity and the convergence of the distribution, assuming a simple form for the state dependence of the probabilities, and showed as a special case that the limiting distribution is a singular distribution on the Cantor set. Later, Norman (1968) demonstrated a convergence theorem in stochastic learning models. Bressloff and Stark applied Norman's idea to the dynamics and learning in neural networks in a series of works (Bressloff & Stark 1992; Stark 1991). Thus, our model can be viewed as a model of action-driven (though yet uniform) dynamic memory and perception.

R2.5. What is the relation between the model and reality?

One common type of criticism was made by **Foster**, among others. Essentially, this criticism is that the theory is mathematical, but neither psychological nor physiological. This is why we present our theory for a dynamic brain from a different viewpoint. As we emphasized above, especially in section R1, it is important to seriously consider the levels of a model. Most commentators neglect this point. Modeling from an overly physiological point of view results in a theory that lacks explanatory power for cognition, and modeling from an overly psychological point of view results in a theory that lacks predictive power for the mechanism of cognitive processes that should be related to brain activity, as long as we consider the mind to be a physical phenomenon. At a certain time in scientific history, those in the field of artificial intelligence neglected brain activity, especially neurophysiological facts. Perhaps they believed that the physiological nature of the brain need not be studied for a full understanding of cognition. On the other hand, people who have studied neural network models have tended to neglect symbol manipulation. Perhaps they did/do not realize how something expressed symbolically could possess a neurophysiological basis. Then, the connectionist approach proposed neural networks that can treat symbol manipulation through its dynamics. This was epoch-making. However, it seems that connectionists have not yet found an adequate language system, whose importance we emphasized in section R1.

In the situation that most approaches do not provide an adequate language system to make a bridge between psychological and physiological levels for understanding of the brain and mind, we have chosen a mathematically interpretative direction of study. In particular, we have chosen in this article a high-dimensional chaotic dynamical system as one possible explanatory and predictive language.

Recently, psycho-physiological experiments have been conducted on various areas of the brain. In these experiments, a cognitive task is performed by an animal or a person, and while it is being performed the activity of neurons or neural assemblies is monitored. Then, neural correlates are investigated. This represents a promising direction of study, but has the serious weak point that neural correlates must be interpreted in terms of natural language, taking into account the meaning of the task and the neural activity. Moreover, there might be an "experimenter effect." This is not surprising, since the object of experiment is a very complex system.

We have proposed a mathematical formal theory to analyze the task performed in these experiments itself (Tsuda & Hatakeyama 2001). We are now studying the establishment of a formalism for such experiments and attempting to construct a method of extracting the immanent chaotic dynamics of neural systems exhibiting cognition. We point out that Descartes' principles of thoughts (Descartes 1701) should still be useful in our attempt to gain a deeper understanding of the brain and mind.

The Lorenz model for atmospheric unpredictable and nonperiodic motion is also relevant to the present discussion (Lorenz 1963; 1991). Following Saltzman's observation (Saltzman 1962), Lorenz derived three-dimensional ordinary differential equations for the purpose of describing atmospheric circulations, and he found chaotic motion resulting from the instability of convective solutions. However, the chaotic motion he found, which is called Lorenz chaos, has never been observed in real atmospheric motion. Apparently, therefore, his model does not simulate real turbulent motion of atmosphere. Then, why did the Lorenz model impart such a strong scientific impact (much stronger than that of conjecturing of the "butterfly effect," which alleges that a butterfly flapping its wings in China can drastically change the weather in New York)? It should be noted that this impact does not stem from falsifiability nor from provability of this model. In fact, this impact is not due to the ability of this model to correctly simulate physical phenomena. Rather, this impact is due to the fact that his chaotic model displays the essence of atmospheric motion, its immanent chaotic dynamics. A similar type of modeling is seen in Kaneko's series of studies of complex phenomena in terms of coupled map lattices (CML) and globally coupled maps (GCM) (Kaneko & Tsuda 2001 and references cited therein). We believe this way to capture certain features of reality (or it might be better to use the term "actuality" in place of "reality," according to Bin Kimura), some of whose features may be hidden but can emerge in observation with an adequate language, is effective and possesses an explanatory and predictive power at a level that differs from that of physiologically realistic models, like the KIII model that **Kozma** recently developed. The underlying important point in this discussion is that we believe strong evidence that chaotic dynamics exist in living brains, as **Liljenström, Mandell & Selz,** and **Rowe & Wright** have suggested.

Given the present situation with regard to a theory, **Liljenström's** suggestion that the mechanism of emergent properties should be discriminated from observed behavior itself is crucial for maintaining the reliability of theory. If an effect of macroscopic activity on activity at the cell level and/or molecular level emerges, through the mechanism of macroscopically emergent properties, a qualitative theory could be directly tested in the laboratory. As **Molnár** suggests, the discovery of an unbiased method to describe the potential functional significance of high-dimensional chaotic or stochastic behavior will help to further the development of a qualitative theory.

R3. Poor man's chaotic itinerancy and chaotic code

R3.1. Mechanism of chaotic itinerancy

Many commentators have reported dynamic behavior similar to chaotic itinerancy (CI). (**Rowe** supplies many references on chaotic dynamical systems which generate phenomena similar to chaotic itinerancy. Komuro has investigated a possible mechanism of CI in some mathematical framework (Komuro 1998; 1999). We have described CI as chaotic transition dynamics resulting from a weak instability of Milnor-type attractors, that is, a chaotic transition among attractor ruins, and before such an instability arises, a certain complex phase space structure similar to a riddled basin appears. **Érdi, Breakspear & Friston** and **Rowe** inquired about the structural conditions of the emergence of CI. Breakspear & Friston particularly emphasize the significance of symmetry in the emergence of Milnor attractors and a riddled basin. (They corrected our citation of works on the riddled basin. As they point out, the first paper on the riddled basin is that of Alexander et al. 1992. The paper by Grebogi et al. 1987, which we cite in the target article is concerned with fractal basin boundaries multidimensionally intertwined on arbitrarily fine scales.) Since symmetrically coupled systems like globally coupled maps (GCM), possess certain symmetries, such systems have been studied thoroughly. As Breakspear & Friston point out, studies of the Milnor attractor have been carried out most actively in the context of symmetrical systems. Typical such studies are reported in a series of works by Ashwin and his colleagues (Ashwin & Terry 2000). However, as Kaneko showed (1998), symmetrical coupling is not a necessary condition for the emergence of Milnor attractors, since they also appear in GCM systems without such symmetry.

Let us assume that a dynamical system f: $M \to M$, where M is the phase space, commutes with a certain group action q:$M \to M$ on M; that is $fq = qf$. Let $S(q)$ be an invariant set under the action q: $S(q) = \{x|qx = x\}$. Then, $f(S(q)) = S(q)$, because $f(qx) = f(x)$ and $q(fx) = f(qx) = f(x)$. When a dynamical system possesses this type of symmetry, its effective dimensionality can be drastically reduced, and as a result the detailed structure of its invariant sets can be investigated. In this respect, the assertion concerning symmetry made by **Breakspear & Friston** is very relevant with regard to the mechanism responsible for Milnor attractors and riddled basins. However, such symmetrical systems are not characteristic of the brain, as networks of neurons in the brain are asymmetrically coupled. Nevertheless, the questions of what type of symmetry could be present in our asymmetrically coupled neural network and how, if it exists, could this symmetry affect the potential invariant sets are interesting to consider. Also, we note that the noise effect is crucial in CI-like transitions, since neural systems in the brain exist in a noisy environment. As **Rowe** points out, it is important to note that depending on the type of Milnor attractor in question, the stability with respect to noise differs. In relation to this, it should be noted that noise can induce basin riddling even after a blowout bifurcation, that is, even in the presence of a transversely positive Lyapunov exponent (Lai & Grebogi 1996).

Feudel et al. found a CI-like phenomenon in the double rotor system with small amplitude noise (Feudel et al. 1998). In this system many periodic orbits coexist. Among these, the higher periodic orbits possess very tiny basins which disappear under the influence of noise, leaving only the low periodic orbits. This situation is similar to that in the KIII model, which **Kozma** and **Freeman** found. Due to fractal basin boundaries, long chaotic transients appear before the system falls into a periodic orbit. Orbits are trapped for some time in the vicinity of periodic attractors, but eventually are kicked by noise into the fractal boundary region.

Figure 5 in the target article shows the presence of the simplest Milnor attractor and also presents a model to describe our simulation results, empirically determined quasi one-dimensional return maps. **Mandell & Selz** treat the situation shown in Figure 5 in the target article as a bifurcation point of tangent bifurcations. In this treatment, for a parameter a, in the case $a < ac$, where ac is a bifurcation point, there exist a pair of stable and unstable fixed points (this resembles a saddle-node pair), and for $a > ac$ no fixed points exist and chaotic behavior appears, so that the system at $a = ac$ is structurally unstable. This is not the case we consider. In our case, this one-dimensional map representation is a projection of high-dimensional dynamics. All fixed points, each representing a different memory, are reduced to two critical points. Furthermore, in our dynamic memory model, this critical situation is robust with respect to changes of the system's parameters, such as the strength of synaptic connections, the steepness of the input-output function of the neurons, and assigned probabilities, within the regions that chaotic itinerancy occurs. We have found evidence through network simulations that suggests the possibility of such a critical system becoming structurally stable. One such possibility is realized through the appearance of structurally stable heteroclinic cycles (Chawanya 1995; 1997; Guckenheimer & Holmes 1988; May & Leonard 1975; Nishiura & Ueyama, in press). Because the appearance of structurally stable heteroclinic cycles requires differentiable vector fields that are equivariant with respect to a symmetry group, whether our case corresponds to such an ideal case is unknown. Our assertion is that the essential dynamics may be due to indifferent fixed points, not hyperbolic fixed points. The appearance of non-hyperbolicity yields characteristics of nonstationary statistics, such as a long time tail of the correlations (Yuri 2000, and references cited therein).

From the result of studies on several types of neural networks with different structures (Körner et al. 1987; 1991), the empirically determined conditions for CI are as follows. (1) The presence of networks, such as recurrent neural networks, which guarantees the coexistence of attractors. (2) The presence of a mechanism causing the neutral stability of attractors. It is by this mechanism that Milnor attractors are generated. (3) The presence of perturbations that weakly destroy such an attractor. These conditions are not well-suited for the appearance of CI, and for this reason, mathematically detailed studies are needed for a deeper understanding of this mechanism.

R3.2. Ubiquitous chaotic itinerancy

Many commentators discussed transition phenomena similar to that of CI. Many CI-like phenomena other than those we consider in the target article have been studied. **Breakspear & Friston** assert the significance of chaotic transience. **Rowe** suggests the possibility of heteroclinic cycles in CI-like phenomenon, and emphasizes the significance of heteroclinic cycles in neural networks. **Banerjee** discusses a topological attractor as representing the overall dynamics of coupled Milnor-type attractors in his spiking neuron model. This topological attractor is identical to an itinerant attractor. **Kowalik** applies the name, "self-reanimating chaos," to a transition between weakly barriered chaos and quasi-periodic oscillations. **Borisyuk** hypothesizes that CI-like activity in neural assemblies may be describable as behavior of a dynamical system with a time-dependent coefficient. In relation to Borisyuk's idea, we constructed a simple model consisting of unidirectionally coupled chaotic systems with distinct time scales (Okuda & Tsuda 1994). When a fast system forces a slow system, the slow system usually becomes simply noisy. This could be used to simulate the motion in a dynamical system with noise. Conversely, when a slow system forces a fast one, CI-like behavior often appears. This may correspond to the slow modulation of a certain parameter of a dynamical system. It might also be similar to the CI-like behavior observed by **Mandell & Selz** in neural systems.

Among other systems, CI-like phenomena in random recurrent neural networks, which were discovered by **Quoy et al.**, are very interesting. Their system used for robot navigation control can learn both patterns and pattern sequences. CI-like phenomena appear in this system when the input signal and the inner signal are mismatched. This behavior and function of chaos and CI-like high-dimensional activity are very similar to those Tani found in his robot control system (Tani 1998). On a related note, **Breakspear & Friston** suggest the involvement of NMDA channels in the neural mechanism causing the relatively rapid change of attractors. They further predict that if the phase space includes many saddles, "typical orbits" will shadow a saddle and that this may be realized in monoamine-mediated changes of functional synaptic coupling. This prediction is worth checking. However, one question arises: Does the phenomenon of irregular transitory orbits accompanied by a saddle network that can be shadowed by typical orbits belong to the same class of statistical behavior as CI orbits? **Mandell & Selz** (1993) found that the effect of noise increases the residence time of orbits in the neighborhoods of unstable states, and they actually reported the observation for it in the hippocampus. Since NMDA channels in the hippocampus are responsible for LTP, this noise effect might guarantee the structural stability of transitory dynamics through the noise-induced shadowing.

As described above, CI-like phenomena have been found in many neural systems. Most researchers are mainly concerned with the topological similarity of these phenomena, but what we have asserted as their important characteristics are as follows. (1) The appearance of many approximately zero Lyapunov exponents, but with large fluctuations. (2) It possesses nonstationary statistics, and hence convergence theorem might not hold. These observations regarding the statistics of the CI in our network model indicate the non-existence of shadowing of both individual orbits and attractors. Sauer has identified this CI characteristic and proposed this non-existence as a definition of CI (Dawson et al. 1994; Grebogi et al. 1990; Sauer 2000; Sauer et al. 1997).

R3.3. Chaotic code

In the target article, we stressed the functional significance of a certain class of chaos and networks. The required characteristic for the functional significance is information mixing due to large fluctuations of information flow (Matsumoto & Tsuda 1985; 1987; 1988; Nicolis & Tsuda 1985; 1989). This class of chaos should appear as intermittent activity. A network displaying this class of chaos can preserve input information in its dynamic activity. Thus, such a network may provide a dynamic mechanism of working memory, which should be arbitrarily long term. CI possesses the same characteristic. Furthermore, as proposed in the target article, CI consists of high-dimensional transitory dynamics which may provide a dynamic mechanism for linking memories. The linking of memories is necessary for categorization and perceptual drifts. Here let us recall the criticism made by **Ikegami & Tani** that since memory dynamics should be restricted by semantics and causalities under "embodied conditions" through behavior, it is not possible to simulate memory dynamics only with CI, which does not have a clear correspondence to the real world. This criticism seems to be worth considering. In thinking "embodied conditions," studies with machines, like robots, are very important. However, we should not overlook the fact that the world robots are experiencing is not real, but man-made, in which the experimenter's intention has been built in advance. A theory based on such biased experience of robots leads us to over-interpretation.

It is important to inquire into the nature of the neural mechanism of chaotic activity, as **Érdi** points out. In this regard, we identified three distinct situations (Tsuda 1991): (1) chaotic activity at one level results from chaotic activity existing at a lower level; (2) chaotic activity at one level is independent of that at the lower levels, and rather it results from damped oscillations enhanced by feedback from activity at higher levels; (3) chaotic activity at one level results from a self-organization at the lower level.

A representative model for each of the above situations has been investigated: Kaneko's CML and GCM for case (1), **Freeman's** KIII model for (2), and our dynamic memory model for (3).

Contrary to the assertion of **Mandell & Selz**, chaotic dynamical systems can be viewed as computation machines. In general, the expanding dynamics can be used to "read" the information given initially or as an input. For instance, let us consider the discrete dynamics defined by the function $f(x) = 2x$, where x is a real number. Here, the variable x is represented by a binary expansion. This type of dynamics is equivalent to a shift dynamics in which the decimal point is shifted one place from left to right per iteration of the dynamics. In contrast, contracting dynamics can be used to "write" the information. For instance, the discrete dynamics defined by the function $g(x) = x/2$, where x is a real number represented by a binary expansion, is equivalent to shift dynamics in which the decimal point is shifted one place from right to left per iteration. Usually, in chaotic dynamics these two types of dynamics appear alternately, and on average the process of "readout" of the information given in the initial distribution is dominant. This situation corresponds to the presence of a positive Lyapunov exponent. The function of chaotic dynamics as a computation machine can be realized in the case that the expanding and contracting dynamics are embedded by cut and paste operations in each eigen-direction, as is seen in Moore's generalized shift (Moore 1990; 1991), and also in the case that these two kinds of dynamics are well separated along each eigen-direction, as is seen in Smale's horseshoe map (Smale 1967). In particular, in the former case, a Turing machine can be embedded at each point in the phase space of a generalized shift map. In this respect, a generalized shift can be viewed as a universal Turing machine.

An essential feature of the horseshoe map as a chaotic dynamical system is described by the transformations $f(x, y) = (2x, ay)$ (for $0 < x < 1/2$) and $f(x, y) = (2 - 2x, 1 - ay)$ (for $1/2 < x < 1$), where $0 < a < 1/2$. Here, the dynamics of x are expanding, chaotic dynamics that are independent of y, and the dynamics of y, which consists of two types of contracting dynamics, depends on x. A horseshoe map is the simplest example of a chaos-driven contracting system. The x variable is responsible for reading the information provided by the initial conditions, and the read-out of this information is written in the dynamics of y direction. Actually, in the contracting case, $0 < a < 1/2$, a Cantor set is generated along the y direction. This observation led us to the study of Cantor coding in chaos-driven contracting systems. In neural systems, unidirectional coupling usually produces overlapped IFS. In a totally-disconnected IFS, this loss of information does not exist, and thus in this case coding and decoding have a one-to-one correspondence (see also **Aihara & Ryeu**).

Borisyuk and **Érdi** asked the advantage of chaotic coding. As mentioned in the target article, the advantage of Cantor coding is the ability for encoding and decoding a large amount of information hierarchically in some finite region of phase space, that is, with a restricted activity level. In other words, a set of temporal patterns with infinite length can be hierarchically embedded, in principle. This coding is robust with respect to noise to some depth. In the hippocampus, embedding of a large amount of information with an extremely long code for a short period is not necessary, and hence this coding is realistic, even in a noisy environment. Hierarchical embedding in terms of Cantor coding in the hippocampus may represent the emergence of a grammar concerning the time order of events. In CA1 or PPC, the neural activity changes in a short time, on the order of 100 msec. This implies that Cantor sets can only be observed by the superposition of snapshots of activity during an interval of approximately 100 msec. The functional significance of the metric of Cantor coding, about which **Heath** inquires, lies in the identification of the closeness of episodes as the closeness of codes. Through the introduction of such a metric, we can realize that any code in a code sequence can be a cue signal for the association of episodes.

Raffone & van Leeuwen demonstrated one merit of chaotic coding by showing that a flexible synchrony of chaotic neural activity is more effective than a stable synchrony of periodic activity. They propose to use this effectiveness to solve the binding problem. Friston (1997) also discussed the significance of transient coding, which is associated with a transient motion, and he confirmed its existence in some functional-MEG data. These are a nice realization of our idea that the dynamic link of memories in terms of chaos and CI may provide a means of flexible information processing in perception (Kaneko & Tsuda 2001;

Tsuda 1993; 1996). The "binding" of features shared by different objects through the synchrony of chaotic oscillations should inevitably generate an alternation of synchronized and desynchronized states. This alternation activity should be CI-like transitory dynamics. The strengths of interactions among oscillations determine synchronization. In opposition to this, chaos is effective for causing rapid desynchronization, because of its characteristic exponential divergence of nearby orbits. Contrary to the assertion of **Raffone & van Leeuwen**, we still think that the binding problem is only a pseudo-problem. To solve the binding problem, people have used spike coincidence and neural oscillations, that is, temporal information, because rate coding fails for this problem. It is not yet clear if the cause of this problem is spike coincidence or neural oscillations. This is something of a chicken-and-egg problem. If an oscillation is periodic, or binding is created by the coincidence of feature-detecting neurons, nonflexible operations, and even combinatorial explosion cannot be avoided. Ironically, in such a nonflexible case, the concept of "binding" is appropriate. In order to avoid this difficulty, and to make "binding" functional, we must abandon the concept of bound feature(s). If we use chaotic oscillations, a flexible synchrony can appear. In such a case, the "binding" process will proceed in the neural dynamics without a help of feature-detecting neurons. The term "binding" cannot be an element of an adequate language system.

R3.4. Real chaos?

Borisyuk, Freeman, Kowalik, Liljenström and **Molnár** point out the difficulty to discriminate high-dimensional chaos from noise. With regard to this, we first note that the chaos analysis of experimental data is still at an immature level. We believe that there will be great development of chaotic dynamical systems analysis in the future. Before the discovery of deterministic chaos, the analysis of random phenomena was commonly carried out by first finding the probability distribution of an appropriate random variable and then calculating average values and fluctuations of observables using this distribution. The true fluctuations can be approximated by calculating the second, third, and (if necessary) higher order moments of the distribution. Also, in time-series analyses, the autoregression method has been used in linear prediction theory. Recently, Okabe et al. proposed a new statistical method that includes nonlinear filters, which has proved to be effective when the data is stationary (Okabe & Inoue 1994; Okabe & Kaneko 2000; Okabe & Nakano 1991; Okabe & Yamane 1998). However, because the discovery of deterministic chaos implies that a certain class of random phenomena can be described by a deterministic rule, such as that provided by a dynamical system on some smooth manifold, it has come to be believed that many types of random phenomena result from deterministic chaos and their randomness originates from a nonlinear transformation of phase space, and further a random time series can be considered projections of orbits on a manifold on to the real axis. Unfortunately, however, chaos analysis in its present form, and especially the embedding technique, is feasible only for relatively low-dimensional dynamical systems. It is ineffective for extremely high-dimensional cases and also in the presence of nonstationarity.

Given the present situation of our understanding of chaos, **Kowalik** states that there is no strict limit between noise and high-dimensional deterministic chaos in the sense that we are not able to clearly distinguish between these. However, before jumping to a conclusion in this regard, it is prudent to note **Liljenström's** observation that chaos is predictable over short time scales, while noise is unpredictable over any time scale, but no discrimination can be made over long time scales. Concerning this point, it is also important to note that in statistical physics, the hypothesis of molecular chaos at a microscopic level is necessary to derive the velocity distribution of an ideal gas as a macroscopic quantity. The presence of molecular chaos guarantees the ergodicity of the system. With respect to this velocity distribution, physical properties of a gas can be expressed as an average plus a variance. This method is very often formally applied to other stochastic phenomena. Usually in such treatments, the average term is viewed as a deterministic component and the variance term as a noise, equivalent to molecular chaos. Since a biological system is not a Hamilton system but a dissipative system, we are concerned with far-from equilibrium conditions. To maintain such a system in a far-from equilibrium state, an external source of energy is necessary. Therefore, generally a far-from equilibrium system is caused to be in high energy level. Under such conditions, aperiodic and unpredictable behavior of the averaged deterministic component is often observed. In order to discriminate this deterministic random behavior from the molecular chaos, physicists have referred to the former as "deterministic chaos" or "macroscopic chaos." Since these chaotic states appear in a far-from equilibrium system, deterministic chaos should have a much greater power than noise. During the early stage of the study of deterministic chaos, the indicator of such chaos used in experiments was the power spectrum. There are two merits of using the power spectrum to discriminate chaos from noise. First, while both chaos and noise have continuous spectra, the power of chaos is much greater than that of noise, which is almost negligible. Second, since chaos appearing in dynamical systems is generated by bifurcations, one can insure the existence of chaos through the change of control parameters. At this standpoint, enhanced noise can be interpreted as resulting from chaos.

It should be further noted here that most common methods of experimental data analysis are problematic. In order to determine whether the neural activity observed in any given case is described by CI, the measurement of neural activity over a long time is necessary. Interestingly, the data found in long-term measurements of neural activity usually exhibit nonstationarity. This is in contrast to the case of shadowing of an entire attractor, that is, a set of orbits, in which the long-term nature of a measurement implies stationarity. When we wish to study nonstationary neural phenomena experimentally, is it possible to use conventional methods of measurement and analysis? When we wish to observe the neural mechanism corresponding to a single act, are data obtained as the average of neural activity measured over many trials, such as a firing rate or correlation coefficients, meaningful? If so, what is the assumed condition? To use statistical quantities under the assumption of a stationary process reflects the belief that a single time series of neural activity is meaningless or that such time series possesses ergodicity. However, ergodicity does not likely exist for behavior-related neural activity. Therefore, people who attempt to use (stationary) statistical quantities in effect deny the meaningfulness of a single time series of neurons or neuron assemblies. But a single time series of neural activity has been observed to be associated with a single act in the laboratory, and hence it is known that such an activity is indeed meaningful. It would thus seem that we have to invent a new dynamical systems analysis which is able to treat high-dimensional and/or nonstationary data.

R4. Dynamic brain revisited

R4.1. Multiple codes

As **Dinse** points out, a cortical "module" is flexible enough to be able to adapt to rapid changes in the environment, allowing for the link between fast time scales on the order of msec and time scales of learning. Here, the alternation of synchronization and desynchronization of the activity of neuron assemblies often appears, associated with this adaptation process. This chaotic alternation between synchronization and desynchronization could be described by CI. In this case, the output resulting from an input is determined by the internal dynamics, which are not fixed as a rigid input-output relation or a stimulus-response relation, but change flexibly, in a manner that depends on the outputs (see **Freeman, Kay,** and **Kozma**). Thus there is a feedback of the action from the environment to the system that generates internal dynamics. Our idea is that any feedback represents code at some level. We think that this might be one origin of multiple codes in neurons or neuron assemblies. In general, there cannot be a feedback process existing in a hierarchical information processing system. If there were some feedback an originally hierarchical structure would be broken, resulting in multiple codes. **Foster** introduced John's works on the interactions of coherent ensembles in neural cell assemblies. Here we briefly introduce Sakurai's series of works (Sakurai 1996; 1998; 1999) on multiple codes based on neural cell assemblies.

Sakurai studied the hippocampal and temporal cortical neuron activity exhibited during the performance of simple auditory, simple visual, and configural auditory-visual discrimination tasks. He found behavior-correlated activity of neurons, which emerged as task related. It was found that approximately one third of the task-related neurons overlap. A single neuron's activity represents the difference between stimuli to be memorized and stimuli to be discriminated in a given task. However, cell assemblies that arise through functional connections between neurons are necessary in order to represent the difference between kinds of tasks. He called this sharing of roles between individual neurons and neuron assemblies "dual coding." From this viewpoint of cell assemblies, the function of a single neuron is not fixed, but changes flexibly depending on its relations with other neurons. A single neuron can belong to many different cell assemblies, and for this reason, a single neuron can represent different functions in manners related to task, purpose, the functions of other neurons, and so on.

We believe that by taking into account macro-action, as **Kay** suggests, the existence and function of multiple codes will become clearer. There is a work of Iwamura and Tanaka (1978) that reports the discovery of active touch-related neurons in the somatosensory cortex of monkey. These neurons become active only when a monkey holds an object that it has come to possess through its own action; that is, such neurons do not respond when an object is placed in its hands.

These findings show that the presence of feedback from behavioral levels to individual neurons and neuron assemblies generates multiple codes at neuronal levels. We emphasize again that feedback signals carry codes corresponding to action, not action itself.

R4.2. Dynamic memory

We have proposed a dynamic memory model for episodic memory and also for olfactory perception. Here, for the first time, following Foster, we present the definitions of episodic memory, semantic memory, and working memory, which we envisage in the target article. Our definitions of semantic and episodic memories basically follow Tulving (1972), but we have added a new perspective. Declative memory is classified into two categories, semantic memory and episodic memory. Semantic memory is memory consisting of general knowledge. Semantic memory is apparently separated from the spatio-temporal causality of events occurring in our daily experience. The database in a computer is similar to semantic memory in this sense. However, since knowledge is essentially internal (Gernert 1996), semantic memory may be represented in a manner that depends on the internal dynamics, and hence can change, while a database is external and fixed.

Episodic memory is that concerning individual experience in the spatio-temporal context. This individual experience includes "future memory" consisting of plans for future actions (Meacham & Leiman 1982; Tsukada 1992). Meacham and Leiman call this "prospective remembering." Individual experience is, in general, memorized chronologically, but it can be memorized according to causality if a mechanism, in which the prefrontal cortex participates and by which the hippocampal dynamics can be influenced, that precedes consistency in experienced events operates. In our dynamic memory model, we treated this type of causality using a chaotic rule generated through the interactions between internal dynamics and external information (acquisition of knowledge). Generated CI provides a flexible grammar for linking memories of events, in which highly correlated memories are linked. In order to develop the theory and the model in the manner in which **Ikegami & Tani** suggest, introducing an explicit state dependence of the assigned probabilities and a mechanism of learning probabilities should be helpful (see also sect. R2.4).

We follow Baddeley's definition (1986) of working memory. According to Baddeley, working memory consist of a conscious-related system providing a procedure of obtaining knowledge and a temporal storage of knowledge, which is necessary for performing complex cognitive tasks. For this reason, Baddeley calls this "active memory."

In the target article, semantic memories are assumed to be represented as disperse spatial patterns in the network. We represent them by dynamical fixed points of the Milnor type. A weakly collapsed Milnor attractor can form an attractor ruin. Since we assume that a chain of knowledge associated with experienced events forms an individual episode, we consider episodic memory to consist of a chain of semantic memories. We have cited two possibilities: that in which a code sequence representing chaotic orbits which link events is embedded in Cantor sets, and that in which a series of events is embedded in Cantor sets. In either case, the Cantor coding of a chain of knowledge is equivalent to the decoding of an episode.

Ikegami & Tani addressed an important question concerning a seemingly paradoxical feature of memory structure. On one hand, memory structure appears stable, but on the other hand memory dynamics are chaotic. We do not think that this is a paradox. Dynamics that are unstable in the usual sense are not always unstable from the information theoretical point of view. In chaos with non-uniform invariant measure that is absolutely continuous w.r.t. the Lebesgue measure, and in transitory dynamics like CI, there exist quantities that remain stable in the unstable dynamics of orbits. One such quantity is the difference between the Kullback information before and after applying the Perron-Frobenius operator. In the case with uniform invariant measure, this quantity is equivalent to the maximum Lyapunov exponent but in the case with non-uniform invariant measure, it is related to the fluctuations of Lyapunov exponents. In the latter case, the time-dependent mutual information provides an appropriate quantification of such fluctuations. The slow decay of the mutual information in time reflects an information mixing, which ensures the conservation of information content through the dynamics in coupled non-uniform chaos (see also sect. R3.3). This implies that input information repeatedly appears and disappears in each local element but is globally maintained. A coupled system can then be viewed as an information channel, though its dynamics are chaotic. In other words, the inputs can be extracted as outputs, even though the state of the channel is chaotic. We believe that the appearance and disappearance of the information in places over the system carries meaning.

Many theories and models of learning and memory have been proposed. However, in general, models lack an explicit coding scheme and a description of its relation to neurodynamics. McClelland et al. (1995) have discussed the details of a possible mechanism for the consolidation of memory. For this reason they are concerned with temporally graded retrograde amnesia, which typically appears in patients with hippocampal lesions like H.M. The presence of temporally graded retrograde amnesia indicates a consolidation of memory based on a continual interaction between the hippocampal system and the neocortical system. We have constructed a model for a CA3-CA1 interacting system, which we present in a separate paper (Tsuda & Kuroda, in press). In this model, cholinergic and GABAergic innervations are introduced, and Cantor coding is found. The new point in such models is that the phase of theta rhythms may control whether the dynamics in CA3 become CI-like dynamics or stable attractor dynamics. In connection with the comments of **Foster** and **Heath**, we wish to consider the method by which a stimulus sequence is recalled by use of Cantor codes. There could be two types of recall, direct and indirect. When a person experiences some events, sensory stimuli enter CA3 from the entorhinal cortex, with the influence of internal dynamics, and as a result, CA3 begins to display the associative dynamics, such as CI. Then, a Cantor code is retrieved from this partial sequence of events in a manner that depends on the length of the sequence of events. In this way, the recall of an episode from partial information is possible. This is the usual situation in the recall of a stimulus sequence. Another type of recall that can occur is here called the "Proust phenomenon." In *A la recherche du temps perdu,* by Marcel Proust, the character Marcel suddenly recalled a forgotten episode when he put a madeleine dipped in black tea into his mouth. We all experience this type of recall of episodes in our daily life. We offer a hypothesis about the mechanism of "Proust phenomenon" in which we employ Cantor coding. The distinguishing characteristic of "Proust phenomenon" is that a specific stimulus, which previously had no relation to any episodic memories, triggers a complete recall of some episode. In this situation, CA3 cannot be stimulated directly by such a stimulus, but rather it must be the case that CA1 receives direct stimulation from the entorhinal cortex. A direct perforant path from the entorhinal cortex to CA1 allows for this. Since in CA1 a code sequence is embedded in a cluster of a Cantor set, a certain level of this Cantor cluster contains a single code corresponding to a stimulus which is created in the sensory cortices or the entorhinal cortex. Then, at such a level, a code sequence can be evoked in CA1 or in the neocortex through the temporal evocation of a trace of the code sequence in CA1. This hypothesis is consistent with hypothesis 2 in Treves and Rolls (1994), where they state that the perforant path may be involved in the carrying of a cue signal that can initiate the retrieval of an episode.

We here emphasize that a feedback signal in the brain should consist of a code, so that anatomical couplings do not imply the usual formalization of synaptic connections, nor the usual formalization of oscillation couplings. What we envisage is as follows. We believe that the above described situation holds in the connections from the prepyriform cortex to the olfactory bulb, and also in those from CA1 to CA3 through the neocortex and the entorhinal cortex, in both of which we hypothesize the formation of Cantor coding, described by $dx/dt = F(x) + c\,hy$, $dy/dt = G(y) + w\,x$, where $hy = 0$ if y is included in a certain level of cluster, and $hy = 1$ otherwise.

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Letters "a" and "r" appearing before authors' initials refer to target article and response, respectively.

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