# Neural ensemble coding and statistical periodicity: Speculations on the operation of the mind's eye

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**Abstract** – Statistical periodicity is a statistical property of densities which arises in the description of retarded dynamical systems. This property is particularly attractive as a possible mechanism for the ensemble coding of information in the nervous system because it operates rapidly and has high storage capacity. For a population of neurons which exhibits statistical periodicity, information would not be encoded by the periodicity, but rather by the spatio-temporal distributions of neural activity. Statistical periodicity is discussed in relation to the temporal binding hypothesis and to the occurrence of multistability in neural systems. © 2000 Éditions scientifiques et médicales Elsevier SAS

**coding / ensemble / densities / statistical periodicity**

## 1. Introduction

Watching an action packed movie, participating in a fast moving hockey game, watching children at play. What do these tasks have in common? They all require that the nervous system rapidly acquire, encode, transmit, decode, and act on the ever-evolving information presented to it. Indeed neuro-physiological and neuro-psychological evidence indicates that by 70–80 ms after light-induced neural activity reaches the primary visual cortex faces are recognized [65]; more complex scenes within 100–200 ms [32]. How is this challenge met?

The observation that inter-spike intervals of cortical neurons are typically $\leq 10$–$30$ ms [1, 64] strongly implies that rapid cognitive tasks must involve populations of neurons, rather than single neurons. Population encoding has been demonstrated using a wide range of techniques including simultaneous extra-cellular micro-electrode recordings [97], recordings using subdural EEG electrodes [84], and by the use of a variety of multimodal imaging techniques [83, 87], including fMRI. However, it is one thing to conclude that population encoding occurs; it is yet another to produce a population encoding mechanism that

operates with sufficient rapidity and storage capacity.

Time delays are intrinsic properties of the nervous system and arise because axonal conduction times and inter-neuronal distances are finite [20, 26, 61, 62, 96]. Moreover, neural populations operate in a noisy environment [2, 10]. Thus it is natural to examine the possibilities for encoding mechanisms in terms of the statistical properties of dynamical systems which possess retarded variables. Here we review the current state of the knowledge in this field and draw attention to those results which seem to qualify as potential encoding mechanisms by large populations of neurons.

## 2. Population codes

Although a variety of explanations have been proposed to explain the nature of the coding mechanism in large populations of neurons; e.g. frequency coding [3, 80], temporal coincidence coding [91], and temporal delay of spikes [36, 78], two are particularly relevant to this discussion. In ensemble coding [16], attention is focused on the statistical properties of the neural activity across an entire neural population. In temporal pattern coding [22, 57], it is the actual timing and patterning of neural spikes which is the important variable. For both mechanisms the coding is in the form of the spatio-temporal pattern of neural ac-

tivities. Intuitively one might anticipate that these two notions are not that distinct, but rather lie at opposite extremes of a continuum. Here we briefly summarize those observations which are particularly relevant for our discussion of the statistical properties of dynamical systems with retarded variables.

## 2.1. Ensemble coding

One of the first experimental studies suggesting that neural information might be encoded in a distribution, or density, of activity across an ensemble of neurons is that of Werner and Mountcastle [93]. In their study of the firing of thalamic neurons in monkeys to sensory stimuli they found a relationship between the mean inter-spike interval, $\Delta t$, and the standard deviation, $\delta$, of the instantaneous firing rate, i.e.

$$\delta = 0.5\Delta t$$

They speculated that this relationship might be indicative of the utilization of inter-spike interval density coding mechanism.

Certainly changes in the inter-spike interval histograms of neurons can be readily demonstrated [64], for example, in cortical neurons between sleep and wake [21], and in retinal ganglion cells as the ambient light level changes [76]. However, the clearest evidence for spatio-temporal distribution coding comes from studies which have involved the simultaneous recording from large numbers (70–100) of implanted electrodes in selected neural populations. We cite three examples.

First, Wu et al. [97] studied two different behaviors (gill withdrawal and respiratory pumping) in *Aplysia* while recording from seventy neurons. They discovered that the populations of neurons that were active during the two behaviors were highly overlapping, but that the pattern of activity across the population was quite different during the two behaviors. They interpreted these results to indicate a distributed neuronal organization in which virtually the entire population of neurons participated in the two responses, but with two different densities of activities. Second, Georgolpoulos et al. [28] have shown that the pre-programming of limb movements in monkeys involves a population activity in which the direction of limb movement is coded in terms of the vector calculated from the spatially weighted firing activities of the distributed neurons. Finally, in olfactory cortex it has been shown that odors are encoded in the form of different ensemble responses as manifested by differing oscillatory properties of the electro-encephalogram (EEG) [27, 48].

Intimately connected with the notion of distribution coding has been its association with neuronal oscillations. Werner and Mountcastle [93] found that in both spontaneously firing neurons and neurons firing in response to a constant stimulus the resulting records of neural firing rate (impulses/second) showed a clear and statistically significant 'periodicity' with frequencies ranging from 0.09 to 1.4 Hz. Since that time it has also been demonstrated that the coding of odor in the olfactory cortex is associated with a change in the rhythmicity of the electro-encephalogram (EEG) [27, 48], that the hippocampus exhibits rhythmic oscillatory fields potentials (4–12 and 40–100 Hz) during its activated, exploration-associated state [4, 8], and that the 'temporal binding' of sensory stimuli or perceptions by the involved cortex is accompanied by the appearance of a 40-Hz rhythm in the EEG [30].

## 2.2. Temporal pattern coding

Recently emphasis has been placed on the concept that the actual timing or sequence of action potentials, and therefore the sequence of inter-spike intervals, is important for coding. In a classic series of experiments, Richmond and Optican [74, 75] presented black and white patterns to alert behaving monkeys while recording from a neuron located in the inferior temporal cortex. The stimulus set was based on 64 Walsh functions which can be used to represented any visual pattern. They observed that the neuron exhibited a unique response to each Walsh function, but that the response was not represented by a change in spike count alone. They argued that the temporal modulation of the spike train carried the relevant information and then demonstrated that a temporally modulated code carries more information than a code based on spike frequency alone [68].

More recently emphasis has been focused on studies of certain neurons located in the hippocampus, referred to as place cells [72]. Place cells are activated sequentially while an animal moves about in a structured environment [5, 96, 99]. It has been shown that repeating spike sequences, as detected by template matching and joint probability mapping techniques, are present both in the awake and sleeping animal. The spike sequences recorded in the awake animal appear to be 'replayed' on a faster time scale during sleep which may serve to consolidate information [66, 82, 95].

Middlebrooks et al. [60] examined the firing patterns of single neurons in the auditory cortex of cat in response to different spatial locations of auditory stimuli. They discovered that single neurons can respond to sound locations throughout 360 degrees, and even more interestingly that these individual units responded with patterns of action potentials that varied systematically with the location of the auditory stimulus. They speculated that, in contrast to a place code, an auditory stimulus at nearly every location activates diffuse populations of neurons. Each of the active neurons in this population signals, with its temporal firing pattern, the approximate location of the auditory stimulus, and that the precise location is signaled by the concerted activity of many such neurons. The concept of temporal pattern coding is supported by the demonstration that spike timing in the nervous system can be precise [38, 58], and by the demonstration that recurrent neural loops can readily generate temporally patterned spike trains [24–26].

## 3. Statistical periodicity

It is not particularly surprising, given the extensive convergence and divergence properties of the nervous system as well as the large numbers of neurons involved, that some form of population, or ensemble, coding would be important for the nervous system. If indeed population coding is of importance, then a natural way to describe the ensemble activity is through the density of the distribution of activity in the ensemble. An example of a density is the histogram of inter-spike intervals. Typically one only thinks of density descriptions of systems as being of use in the calculation of static statistical properties. However, much is now known about the evolution of densities (statistical properties) under the action of deterministic dynamics [47], and a number of types of convergence behavior of densities have been described (see Appendix A). From a theoretical point of view one of the most attractive aspects of thinking that the nervous system might operate by computing with densities is that the speed of convergence of a sequence of densities is typically many orders of magnitude larger than one could expect from examining the statistical convergence of a single neural spike train even if the underlying dynamics were ergodic.

The statistical property which we emphasize in this review is referred as to 'statistical periodicity'

and arises in dynamical systems with retarded variables [39, 47, 54]. To illustrate what the term 'statistical periodicity' means we will use the one-dimensional map

$$x_{t+1} = S(x_t) = \begin{cases} ax_t & 0 \leq x_t \leq \dfrac{1}{2} \\ a(1-x_t) & \dfrac{1}{2} \leq x_t \leq 1, \end{cases} \quad (1)$$

where $a$ is a constant, $1 < a \leq 2$, and $x_t$, $x_{t+1}$ are, respectively, the values of $x$ at times $t$ and $t+1$. This map is referred to as the tent map because of its graphical appearance [98]. The variable $x$ could be taken to represent, for example, the instantaneous neural firing rate or the inter-spike interval. Models of the nervous system in which time is discrete arise in the description of pulse-coupled neural networks [26, 41]. The term 'pulse coupling' refers to the fact that when neurons are physically separated, interactions between them are in the form of discrete synaptic potentials driven by spikes. The dynamics of pulse-coupled neural networks are particularly relevant to temporal pattern coding since the critical parameter in these networks is spike timing [26].

We recognize that Eq. (1) is not neuro-physiologically motivated. However, this map is simple enough that it can be readily be programmed into a computer so that the reader can study the phenomena we discuss themselves. More importantly we emphasize that the same types of statistical properties generated by Eq. (1) also occur in other examples of dynamical systems, including discrete maps which incorporate noisy fluctuations [46, 70], in models expressed in terms of continuous time differential delay equations [50, 52, 55, 56], and in neuro-physiologically motivated models of spatially extended excitable systems [53, 62].

Let us pretend that Eq. (1) describes the inter-spike intervals of a neural spike train from a single neuron. It is known from previous studies that this map exhibits statistical periodicity when $a = \sqrt{2}$ [40, 70]. There are two ways that we could plot the data obtained from this artificial neuron. First, we could display the values of $x$ as a function of time. This type of plot is shown in *figure 1a* and corresponds to the same type of information recorded in a neural spike train. The dynamics are obviously complex. A second way that we could plot the data is in the form of a histogram. Here the analogy is to an inter-spike histogram. *Figure 1b* shows the 'inter-spike histograms' prepared from the corresponding time series of *figure 1a*. This

histogram approximates the stationary density of the distribution of $x$ (see Appendix A).

Now let us suppose that instead of monitoring the activity of one neuron, we simultaneously monitor a very large number of non-interacting neurons. We can do this with Eq. (1) by a picking a large number of initial conditions and assigning each initial condition to a separate version of Eq. (1) having the same $a$. At each time step we use the values obtained from the large number of neurons to plot the histogram, or density, of the neural activity and follow this density as a function of time. *Figure 1c* shows the succession of densities calculated in this manner. In contrast to the density obtained from a single neuron (map) (*figure*

*1b*), in this case the density itself cycles with period 2! Moreover, by changing the value of the parameter, $a$, cycling of densities can be observed with periods $2^n$, $n = 1,2,3,...$ [70].

The density shown in *figure 1c* is the density calculated when the observations made from all of the neurons are pooled together. We refer to a density measured in this way as the collapsed density. A collapsed density only accurately captures the dynamics of an ensemble in the special case when all of the neurons are uncoupled. In the general case of a neural ensemble we can expect that there will be coupling between the activity of the different neurons in the network. In this case it is necessary to take into account the spatial-tem-
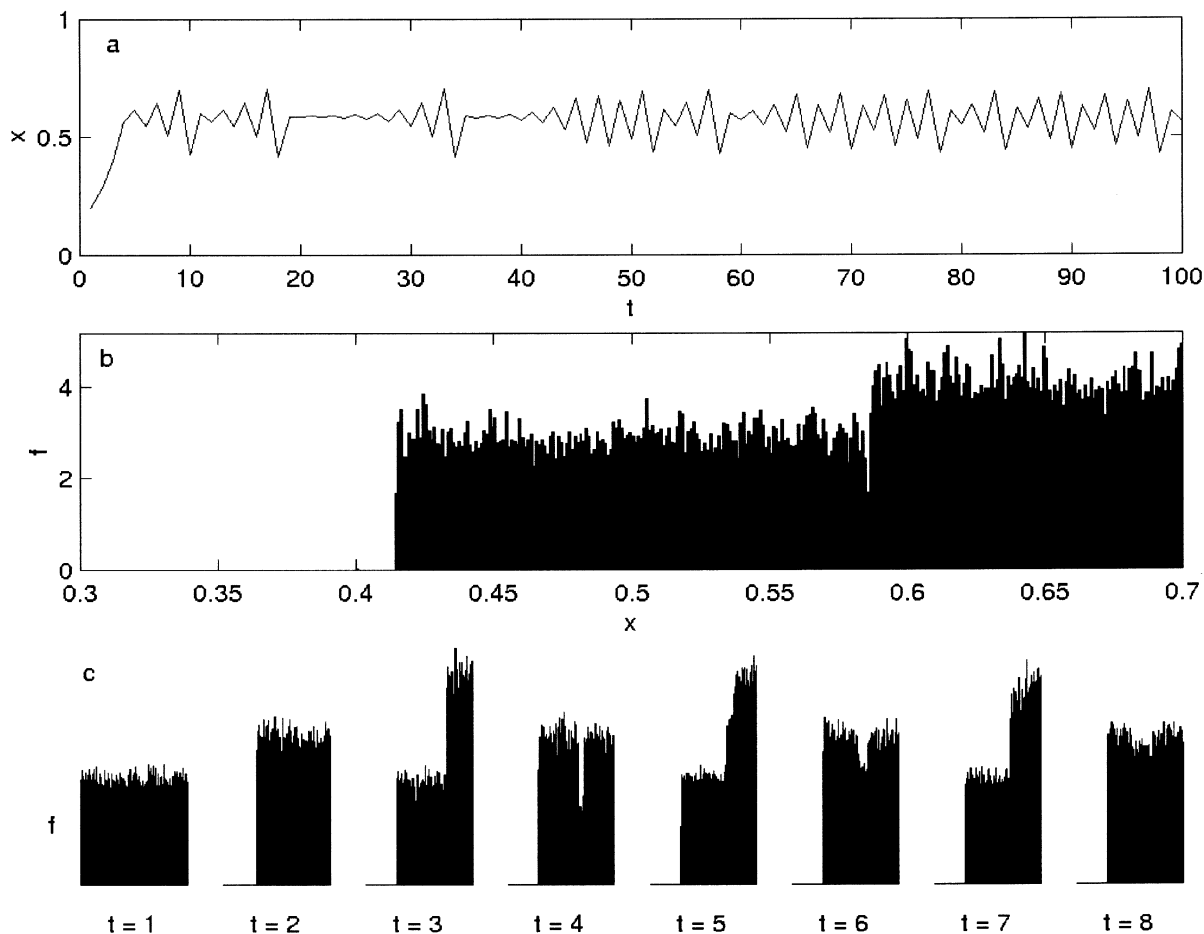


**Figure 1.** Comparison of different representations of the dynamics generated by Eq. (1) for $a = \sqrt{2}$. **(a)** Time series representation obtained for $N = 1$ maps; **(b)** density distribution of the time series shown in (a) obtained by iterating $N = 1$ maps for 40 000 time steps; **(c)** the period 2 cycling of the densities characteristic of statistical periodicity. (c) was prepared by iterating $N = 40 000$ maps and at each time step combining the output of each map to construct the density. The solid horizontal line represents the interval between 0.3 and 0.7. The initial condition for each map was chosen randomly from the initial density distribution shown for $t = 1$ (it is the uniform density on [0.3, 0.7]). Note that for all densities the area is equal to 1.
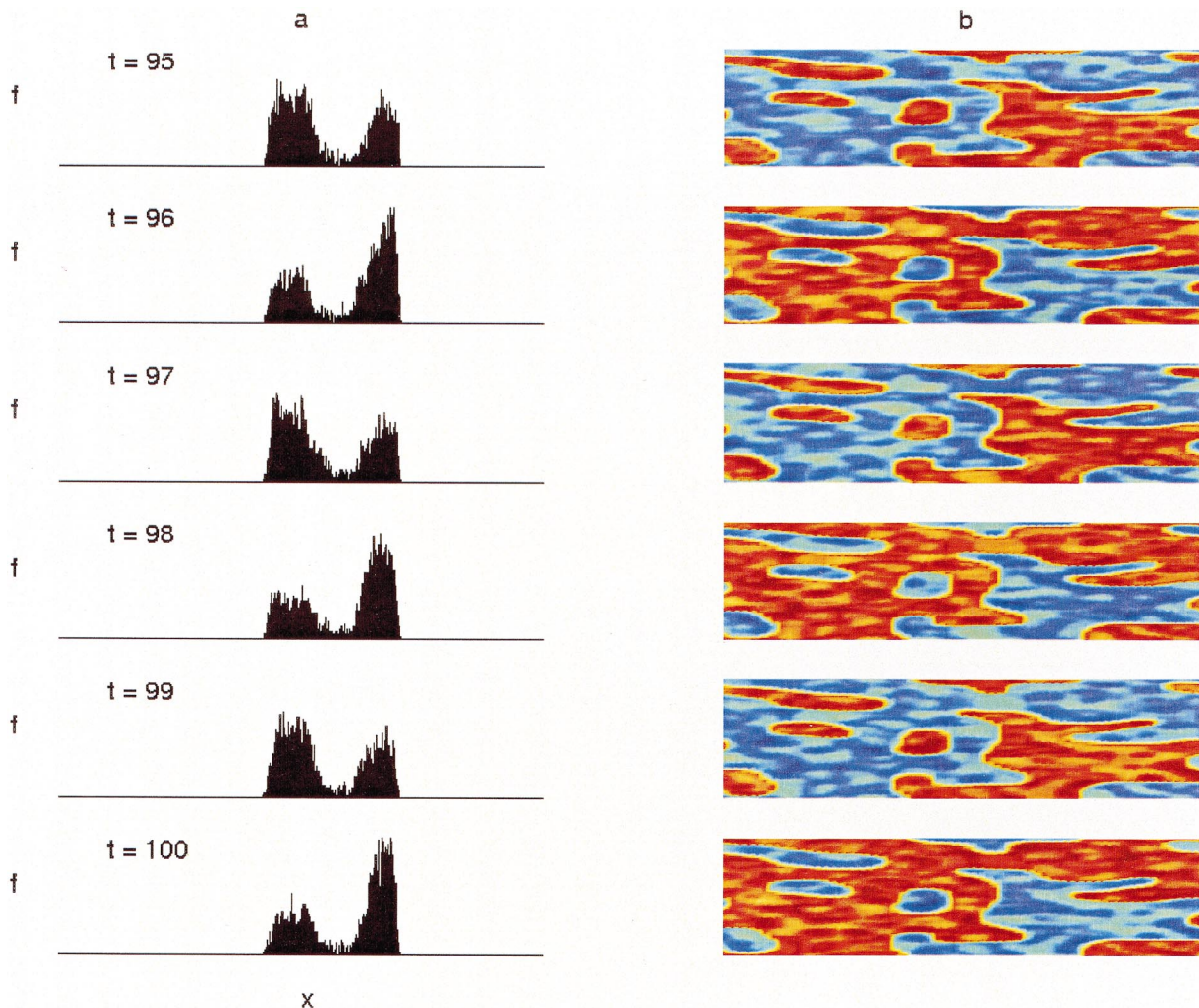
**Figure 2.** Comparison of the (**a**) collapsed density and (**b**) the spatio-temporal distribution of activity for a $60 \times 60$ coupled map lattice of tent maps ($N = 3\,600$). The lattice was iterated for a total of 100 time steps, the densities calculated from the last 6 time steps are shown. In (**a**), the solid horizontal line indicates the interval from 0 to 1. The initial conditions were chosen from a uniform distribution over the interval from 0 to 1. Parameters: $a = \sqrt{2}$, $x = 0.45$. For all densities the area is equal to 1.

poral distribution of the neural activity. To illustrate how these distributions appear in a coupled population which exhibits statistical periodicity, consider the results shown in *figure 2*. This figure shows the dynamics of a 2-dimensional coupled network of tent maps in which the dynamics of each element in the lattice are given by

$$x_{t+1}^{i,j} = (1 - \varepsilon)S(x_t^{i,j}) +$$

$$\frac{\varepsilon}{4}[S(x_t^{i-1,j}) + S(x_t^{i,j-1}) + S(x_t^{i+1,j}) +$$

$$S(x_t^{i,j+1})] \qquad (2)$$

where $i, j = 1, \ldots, N$, $S$ is given by the right hand side of Eq. (1), $\varepsilon$ is the coupling coefficient, and there are periodic boundary conditions. *Figure 2* compares the collapsed density for this 2-D coupled map lattice (*figure 2a*) to the spatio-temporal distribution of activity (figure 2*b*). The coupling coefficient ($\varepsilon = 0.45$) and the value of $a = \sqrt{2}$ are chosen from the range of parameters for which statistical periodicity is known to occur in a lattice of coupled tent maps [51]. The collapsed density reflects the period two cycling of statistical periodicity. However, it is clear on examining the spatio-temporal distribution of activity that there is more going on. In particular, spatio-temporal patterns

are apparent. These patterns arise because of phase transitions [53]. A necessary, but not sufficient condition, for the appearance of these patterns is that the ensemble exhibit statistical periodicity [51, 53].

This cycling of densities is referred to as statistical periodicity [39, 47, 54]. By comparing the observations in *figures 1* and *2*, we see that statistical periodicity is an ensemble property, i.e. its existence can not be easily inferred by measurements of the dynamics of a single element in the ensemble. In the next section we discuss those features of statistical periodicity which make this phenomena particularly attractive as a potential candidate for a neural encoding mechanism. Following this we discuss the relationship between statistical periodicity and multistability and finally possible analo-

gies between statistical periodicity and the temporal binding hypothesis.

## 4. Statistical periodicity and neural coding

From the examples cited in the Introduction it is clear that a plausible mechanism for neural coding must possess two properties: (1) it must be capable of rapid convergence (e.g. $< 70–200$ ms); and (2) it must have high information storage capacity. We discuss these issues from the point of view of statistical periodicity.

*Figure 3* shows the evolution of the collapsed density for a large number of tent maps when $a = \sqrt{2}$. It can be seen that the limiting sequence of densities becomes clearly recognizable within
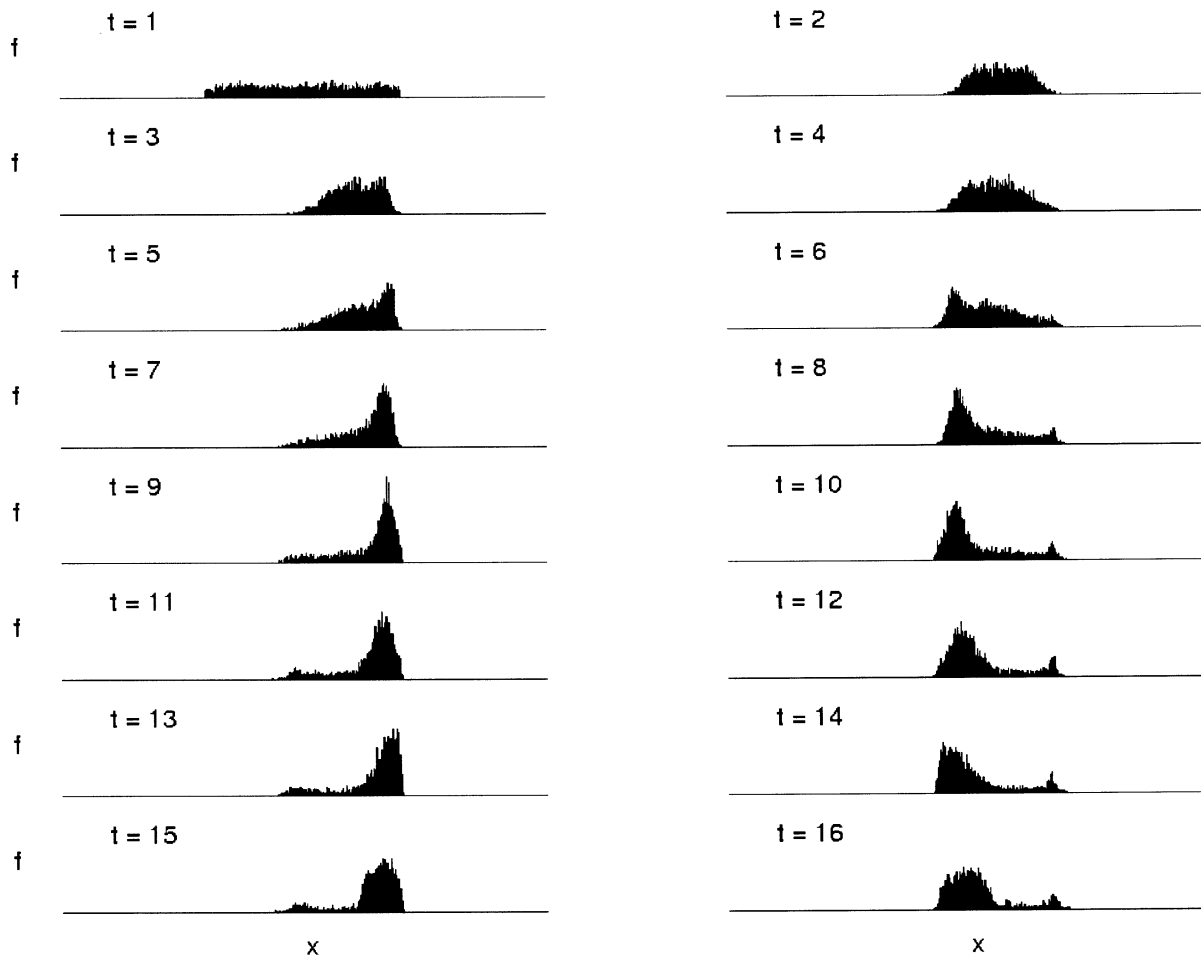


**Figure 3.** Convergence of densities for a $60 \times 60$ lattice of coupled tent maps ($N = 3\,600$) as a function of the time step. The initial distribution ($t = 1$) is the uniform density on [0.3, 0.7]. The solid horizontal line indicates the interval from 0 to 1. Parameters: $a = \sqrt{2}$, $x = 0.45$. For all densities the area is equal to 1.
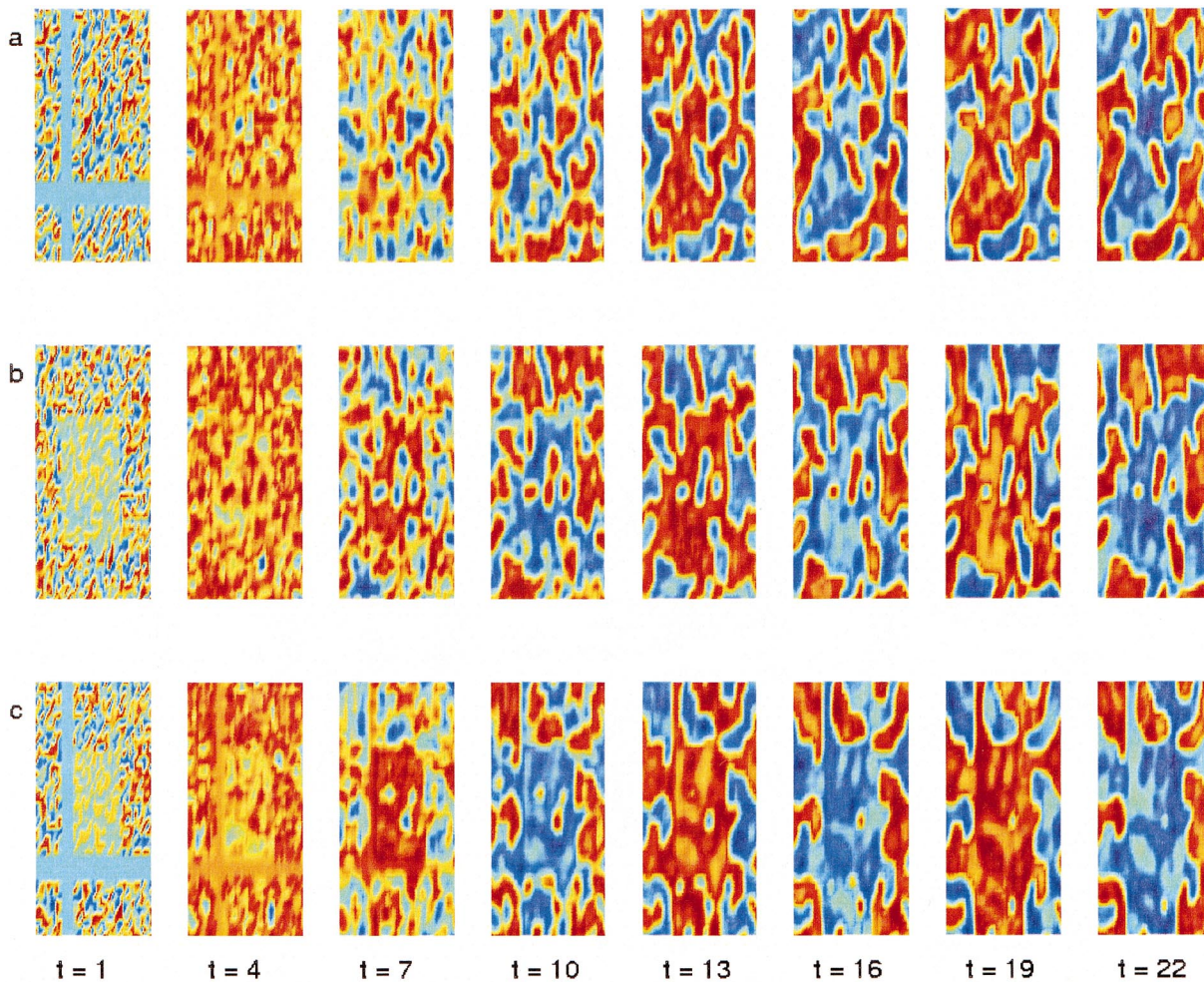
**Figure 4.** Dependence of the limiting spatio-temporal distribution of a $40 \times 40$ coupled map lattice of tent maps ($N = 1\,600$) on the choice of initial spatial patterns (left-hand panel). In all cases the background for the initial pattern was formed from values chosen randomly from a uniform distribution on [0, 1]. In (**a**) the cross is the value $x = 0.3$ and in (**b**) the square was constructed from points chosen randomly from a uniform density on [0.3, 0.7]. The square-cross pattern in (**c**) was formed by constructing the cross ($x = 0.3$) and then randomly choosing values from a uniform density on [0.3, 0.7] to construct the square. As can be seen the limiting spatio-temporal pattern of the lattice obtained for the cross-square pattern is not simply the linear combination of the limiting patterns obtained for cross and square. The values of the parameters for the tent map and the coupling strength are the same as in *figure 3*.

7–8 time steps. The fluctuations in the densities observed for subsequent iterations largely reflect statistical fluctuations since only 3600 neurons are used to estimate the density. This rapid convergence to the limiting densities is seen for most initial densities [54]. Thus ensemble coding mechanisms based on statistical periodicity are fast.

*Figure 4* shows the dependence of the spatio-temporal properties of the 2-D coupled map lattice of tent maps as a function of the initial spatial pattern (left hand side of figure). Clearly each different input leads to a different cycling of spa-tio-temporal patterns. However, in all cases the period of the cycling is two. In general it can be shown that the nature of the limiting oscillations of the densities is continuously dependent on the initial dynamics [39, 54]. Thus if statistical periodicity were used as a dynamic mechanism for storing patterns or memories, one could have a virtually continuous relationship between the ensemble response and the stimulus. The ability to discriminate between the continuous array of responses would be only limited by our ability to discern 'tiny' differences.

## 5. Multistability and statistical periodicity

There is a consensus in the neural network literature that there is an intimate connection between associative memory and multistability [34, 100]. From a mathematical point of view, multistability refers to the co-existence of multiple attractors. This implies that there is a dependence of the eventual behavior on the input that the dynamical system initially received. Moreover it is possible to rapidly switch between two attractors as a result of small perturbations.

There is an extensive theoretical [23] and experimental [31, 37] literature which demonstrates that two attractors can co-exist in isolated neurons; recent work indicates that more than two attractors can co-exist in some neurons [11, 12, 49]. Moreover, there is nearly 25 years of theoretical [33, 35, 42, 79, 94, 100] and experimental [42, 44, 45] work demonstrating that neural populations can exhibit multistability. Finally, evidence obtained from the perception of ambiguous sensory stimuli [45], postural sway [19], and seizures in patients with epilepsy [63] suggest that the human nervous systems exhibits multistability as well.

Multistability can arise in populations of pulse-coupled oscillators with time-delayed inhibitory connections [17, 18, 89]. Recently it has been demonstrated that multistability can arise in a single recurrent inhibitory neural loop simply due to the fact that a conduction delay has become sufficiently long [26]. The multistability in delayed recurrent loops can lead to attractors which take the form of qualitatively different temporal patterns of spiking [24–26]. This observation is of interest given the growing number of observations which have drawn attention to the importance of temporal patterns of spikes for encoding (see Section 2.2).

With respect to neural coding, one of the strengths of multistable dynamical systems is the multiple solutions that exist as a consequence of the dynamics, i.e. they need not be generated by training. However, there is a more important aspect of multistable dynamical systems with 'retarded variables' that is often overlooked. In the multistability that occurs in systems of ordinary differential equations, a single suitably timed stimulus (initial condition) of the proper magnitude and timing is capable of switching between attractors. In contrast, for multistable differential delay equations, an entire history of the stimulus pattern for some finite interval of time is required to determine the eventual behavior. This property of differential delay equations fits in very nicely with experimental observations which indicate that temporal spiking patterns may be important for coding.

The cycling of the statistical properties of a dynamical system which exhibits statistical stability is reminiscent of a multistable dynamical system subjected to noisy fluctuations: each distribution reflects statistical fluctuations in one of the basins of attraction, the cycling reflecting switching between the attractors. It has been shown that a stochastic resonance-like phenomena can arise in dynamical systems with retarded variables and its occurrence depends on the correlation time of the noisy fluctuations [9, 67].

The strongest connection between multistability and statistical periodicity comes from studies of high dimensional coupled map lattices of [52, 53]. On the analytic side [52] and [53] have given sufficient analytical conditions for the existence of statistical periodicity of densities in large $N \times N$ coupled map lattices, so they are in fact high dimensional discrete time dynamical systems of dimension $N^2$. However, on the numerical side they have also shown that starting from two random initial conditions in these $N^2$ dimensional systems the eventual patterns of activity in the system corresponding to the two realizations were different both to the eye, and as evaluated by the less subjective index of the 'collapsed density' which also showed clear behavior indicative of statistical periodicity. Thus there is a clear correspondence in the coupled map lattices between the occurrence of multistability on the one hand, and statistical periodicity on the other.

Similar links between multistability and statistical periodicity are found in the lattice representations for differential delay equations presented in Losson and Mackey [52]. Thus it is highly likely that there is a strong connection between the occurrence of multistability in high dimensional dynamical systems (of which differential delay equations are but one example since they are effectively infinite dimensional) and the property of statistical periodicity.

The nervous system is now well recognized to be a noisy environment. What are the statistics of large populations of multistable elements? We conjecture that these networks may in general exhibit statistical periodicity.

## 6. EEG and statistical periodicity

The demonstration that a large population of neurons exhibits statistical periodicity is problematic since it pre-supposes the existence of technology capable of independently monitoring the activity of a very large number of neurons with a time resolution approaching 1 ms [62]. This approach would be necessary in order to construct the spatio-temporal distribution of neural activity. This is technically not possible at present.

A technique which does record the activity of a large population of neurons is the electro-encephalogram (EEG). The potential measured by a single electrode represents a weighted-average of the synchronous activity of neurons located in a $\approx 6$ cm$^2$ area of cortex located within the solid angle subtended by the scalp electrode [14]. Thus the activity measured by an EEG electrode is related to an average based on the 'collapsed density' of a large neural population. If the underlying population of neurons exhibited statistical periodicity, then this weighted mean should also oscillate periodically.

Classically the background activity of the human EEG is interpreted in terms of the spatial distribution of its frequency content. For example, alpha rhythms (8–12 Hz) are typically recorded from posterior head regions, and theta rhythms (4–8 Hz) are found more anteriorly. There is regional coherence in the EEG [6, 7, 85, 86] and the spatial patterns of coherence change in response to cognitive tasks [29]. Although to an experienced reader the EEG is most easily thought of as a signal composed of distinct bands of periodic components, modern methods of time series analyzes have emphasized that it may have a 'chaotic' structure [69, 77].

It is of interest to interpret these observations from the point of view of populations of neurons which exhibit statistical periodicity. Time-delayed negative feedback dynamical systems amplify frequencies of $0.5/\tau$ and their integer multiples (for positive feedback $1/\tau$ and integer multiples) [73]. In the nervous system time delays range from 1–2 ms at the level of the synapse to 100–200 ms introduced by the very small diameter unmyelinated inter-hemispheric axons [61, 92] to even longer [90, 96]. Since the period of statistical periodicity depends on the delay, this range of time delays would introduce a range of frequencies in the EEG.

Although the regionality of EEG coherence has been interpreted as a reflection of the histological regionality of the human cortex [86], the observations in *figures 2* and *4* clearly demonstrate that this heterogeneity can arise dynamically as a result of phase transitions. Indeed multimodal imaging techniques involving an array of SQUIDs (Superconducting QUantum Interference DeviceS) of subjects performing a syncopation task have shown that the complex changes which occur in the spatio-temporal distributions of neural activity most closely resemble phase transitions [43]. Finally it is likely to be very difficult to distinguish between chaotic dynamics, i.e. dynamics which reflect the co-existence of multiple unstable attractors [13], from the dynamics of a multistable dynamical system in which the noise level is so high that noise-induced switches between attractors occur rapidly. Thus the findings obtained from EEG recordings strongly support the idea that statistical periodicity is occurring in the underlying neural populations.

Recently evidence has accumulated that the temporal binding of sensory stimuli or perceptions by the involved cortical regions is accompanied by the appearance of a 40-Hz rhythm in the EEG [30, 81]. A 40-Hz rhythm would require time delays of the order of 5–20 ms which are consistent with the time delays introduced by the larger axons in the central nervous system. Thus, the observation of a 40-Hz rhythm could reflect a statistical periodicity encoding mechanism. Indeed the observation that the period of this EEG rhythm is independent of the nature of the sensory stimulus that is temporally bound [30, 81] is exactly what would be anticipated if statistical periodicity is involved. In a network which exhibits statistical periodicity, the information is not stored in the period of the cycling, but rather in the spatio-temporal distributions of neural activity.

## 7. Discussion

The complex, intertwined recurrent loop organization of the nervous system has been emphasized previously [26, 62]; the visual system is no exception [59, 88]. Given this anatomical arrangement it is tempting to assume that coding might be related to the dynamics of information flow through and within the layers of organization of the central nervous system [15]. Passing neural information from one level of neural organization to the next (e.g. from retina to lateral geniculate to primary visual cortex and so on) clearly involves the activity of very large numbers of neurons. Since this

information flow must necessarily be associated with a time delay, it is tempting to draw analogies to the evolution of statistical densities of dynamical systems possessing retarded variables. One type of statistical behavior which can arise in this situation is statistical periodicity.

Statistical periodicity has two properties which make it attractive as a potential coding mechanism: (1) it converges rapidly, and (2) it has a high capacity for recognizing the complexity of the external world. The rapidity of the encoding is evidenced by the fact that within a few time steps (say 7–10) the limiting densities are obtained to good approximation. If we choose a delay time of a living neural network as 5–20 ms (i.e. the delay introduced by the larger diameter myelinated axons), this means that a pattern could be dynamically encoded in a recognizable form within 35–200 ms. This time is well within the time estimated from neuro-psychological experiments to recognize a scene. Since there is a continual relationship between the input to a network which exhibits statistical periodicity and the shape of the cycling distributions, the storage capacity is technically infinite. Of course there are limits that arise because of the firing characteristics of the neurons, such as the length of the relative refractory period. However, since the upper limit of neural spiking approaches 500–700 Hz, it is clear that the potential for a time-delayed noisy neural network to serve as a rapid, high capacity pattern recognition device is considerable.

Population encoding mechanisms leave unanswered many intriguing questions. For example, which parts of the nervous system have access to the spatio-temporal distribution of neural activity, what does it mean to read the population code, and how is this done? Clearly there are an equally great number of mathematical and technical questions to be addressed. Can the properties of dynamical systems with statistical periodicity be formulated so that empirical tests of the hypothesis can be made with existing experimental techniques? Can techniques be developed which have the required spatial and temporal resolution?

We anticipate that the thoughts we have expressed in this article will open doors towards exciting new directions in neuroscience and to heated debates! We hope that out of this chaos will emerge a clear understanding of how the human brain rapidly and reliably encodes information. After all, there is always another hockey game to watch!

## Appendix A. Mathematical Details

In this appendix, we briefly review some of the relevant mathematical background that forms the basis of the ideas presented in this paper. These come from modern developments in ergodic theory. We give here only a telegraphic outline of the ideas, and further details along with the precise mathematical formulations can be found in [47, 54].

Central to the notions presented in this paper is that of a 'density'. By density we mean a non-negative normalized function $f$ (i.e. $f \geq 0$ and $\int f = 1$). Common examples are the density of the Gaussian distribution, and inter-spike interval histograms (when normalized).

Though it is clear from Eq. (1) how successive temporal points $x$ are computed to form the trajectory $\{x_t\}_{t=0}^{\infty}$ we must introduce an analogous concept for how densities evolve. Any linear operator $P: L^1 \to L^1$ that satisfies: (1) $Pf \geq 0$; and (2) $\|Pf\| = \|f\|$ for all densities $f$ is called a Markov operator (the notation $\|f\|$ denotes the $L^1$ norm of the function $f$). Any density $f$ that satisfies $P^t f_* = f_*$ for all $t$ is said to be a stationary density of the Markov operator P.

If S is a nonsingular transformation, then the unique Markov operator P defined by

$$\int_A Pf(w)\,\mathrm{d}w = \int_{S^{-1}(A)} f(w)\,\mathrm{d}w$$

is called the Frobenius-Perron operator corresponding to S. The Frobenius Perron operator P describes the evolution of densities under the ac-

tion of a dynamics S. The equation defining the Frobenius-Perron operator has a simple intuitive interpretation. Start with an initial density $f$ and integrate this over a set B that will evolve into the set A under the action of the transformation S. However, the set B is $S^{-1}(A)$. This integrated quantity must be equal, since S is nonsingular, to the integral over the set A of the density obtained after one application of S to $f$. This final density is $Pf$.

We next turn to a consideration of the dynamical properties of maps S as manifested through the behavior of sequences of densities $\{P^t f\}$ where P is the Frobenius Perron operator corresponding to S with stationary density $f_*$.

First, a nonsingular transformation S is said to be ergodic if

$$\lim_{t \to \infty} \frac{1}{t} \sum_{k=0}^{t-1} \langle P^k f, g \rangle = \langle f_*, g \rangle$$

(Here, the scalar product of two functions is denoted in the usual way:

$$\langle f, g \rangle = \int_X f(x)g(x)\delta x$$

where $f \in L^1$ and $g \in L^\infty$.) Ergodicity is completely equivalent to the existence of a 'unique' stationary density $f_*$. Secondly, let S be an $f_*$ measure preserving transformation operating on a finite normalized space. Then S is called mixing if

$$\lim_{t \to \infty} \langle P^t f, g \rangle = \langle f_*, g \rangle,$$

i.e. the sequence $\{P^t f\}$ is weakly convergent to the density $f_*$ for all initial densities $f$.

Third, S is said to be statistically stable if

$$\lim_{t \to \infty} \| P^t f - f_* \| = 0$$

i.e. $\{P^t f\}$ is strongly convergent to $f_*$, for all initial densities $f$. Statistical stability implies mixing which, in turn, implies ergodicity.

Now we turn to a discussion of one of the central concepts of this paper-statistical periodicity. Let P be a Markov operator. Then if there is an integer $r > 0$, a sequence $i = 1,...,r$ of densities $g_i$ and bounded linear functionals $\lambda_i$, and an operator $Q:L^1 \to L^1$ such that for all densities $f$, $Pf$ has the form

$$Pf(x) = \sum_{i=1}^{r} \lambda_i(f)g_i(x) + Qf(x) \qquad (3)$$

we say that the operator P is statistically periodic. The densities $g_i$ and the transient operator Q have the following properties:

– The $g_i$ have disjoint support (i.e. are mutually orthogonal and thus form a basis set), so $g_i(x)g_j(x) = 0$ for all $i \neq j$.
– For each integer $i$ there is a unique integer $\alpha(i)$ such that $Pg_i = g_{\alpha(i)}$. Furthermore, $\alpha(i) \neq \alpha(j)$ for $i \neq j$. Thus the operator P permutes the densities $g_i$.
– $\| P^t Qf \| \to 0$ as $t \to \infty$, $t \in N$

Notice from Eq. (3) that $P^{t+1}f$ may be immediately written in the form

$$P^{t+1}f(x) = \sum_{i=1}^{r} \lambda_i(f)g_{\alpha^t(i)}(x) + Q_t f(x), \ t \in N, \qquad (4)$$

where $Q_t = P^t Q$, $\| Q^t f \| \to 0$ as $t \to \infty$, and $\alpha^t(i) = \alpha(\alpha^{t-1}(i)) = \dots$. The density terms in the summation of Eq. (4) are just permuted by each application of P. Since $r$ is finite, the series

$$\sum_{i=1}^{r} \lambda_i(f)g_{\alpha^t(i)}(x) \qquad (5)$$

must be periodic with a period $T \leq r!$. Further, since $\{\alpha^t(1),...,\alpha^t(r)\}$ is just a permutation of $\{1, ..., r\}$ the summation in Eq. (4) may be written in the alternative form

$$\sum_{i=1}^{r} \lambda_{\alpha^{-t}(i)}(f)g_i(x)$$

where $\alpha^{-t}(i)$ is the inverse permutation of $\alpha^t(i)$.

This rewriting of the summation portion of Eq. (4) makes the effect of successive applications of P completely transparent. Each application of P simply permutes the set of scaling coefficients associated with the densities $g_i(x)$.

One of the interesting interpretations of Eq. (4) is that if $t$ is large enough, which simply means that we have observed the system longer than its relaxation time so $\| Q^t f \|$ is approximately zero, then

$$P^{t+1}f(x) \cong \sum_{i=1}^{r} \lambda_i(f)g_{\alpha^t(i)}(x)$$

Asymptotically, $P^t f$ is either equal to one of the basis densities $g_i$ of the $i$-th pure state, or to a mixture of the densities of these states, each weighted by $\lambda_i(f)$. It is important to also realize that the limiting sequence $\{P^t f\}$ is, in general, continuously dependent on the choice of the initial density $f$ because the $\lambda_i(f)$ are functionals of the initial density $f$.

How would the property of asymptotic periodicity be manifested in a continuous time system? If $t$ is continuous then for every $t$ we can find a positive integer $m$ and a number $\theta \in [0, 1]$ such that $t + 1 = m + \theta$. Then, asymptotically

$$P^{t+1}f(x) = P^m(P^\theta f) \cong \sum_{i=1}^{r} \lambda_{a^m(i)}(P^\theta f)g_i(x)$$

Now, in the continuous time case we expect that there will be a periodic modulation of the scaling coefficients $\lambda$ dependent on the initial density $f$, and the asymptotic limiting density will continue to display the quantized nature characteristic of the discrete time situation. This behavior has been studied in a first order differential delay equation with and without noise [50].

Statistically periodic Markov operators always have at least one stationary density given by

$$f_*(x) = \frac{1}{r}\sum_{i=1}^{r} g_i(x) \tag{6}$$

where $r$ and the $g_i(x)$ are defined above. It is easy to see that $f_*(x)$ is a stationary density, since we also have

$$Pf_* = \frac{1}{r}\sum_{i=1}^{r} g_{\alpha(i)}(x)$$

and thus $f_*$ is a stationary density of $P^t$. Hence, for any Markov operator the stationary density Eq. (6) is just the average of the densities $g_i$. It is important to note that if one were dealing with a statistically periodic system and constructed a density from the iterates along a trajectory, as we have done in *figure 1*, then the resulting density is the 'stationary density' and 'not one of the cycling densities'.

To illustrate these concepts, consider the tent map (Eq. (1)). In [70], the statistical periodicity of the tent map with period $T = n + 1$ has been shown for $2^{1/2^{(1/n+1)}} < a \leq 2^{1/2^{(1/n)}}$. Thus, for example, $\{P^t f\}$ has period 1 for $2^{1/2} < a \leq 2$, period 2 for $2^{1/4} < a \leq 2^{1/2}$, period 4 for $2^{1/8} < a \leq 2^{1/4}$, etc. Further, the Frobenius Perron operator corresponding to the tent map (Eq. (1)) is [71]

$$Pf(x) = \frac{1}{a}\left\{ f\left(\frac{x}{a}\right) + f\left(1 - \frac{x}{a}\right) \right\}$$

When $a = 2$ the stationary density is uniform for all $x \in [0, 1]$, $f_* = 1$ and the tent map is statistically stable, i.e. for all initial densities $f$ we have $P^t f \to f_* = 1$. When $a = \sqrt{2}$ then the stationary density is given by

$$f_*(x) = u 1_{J_1}(x) + v 1_{J_2}(x) \tag{7}$$

where $u = [3 + 2\sqrt{2}]/2$, $v = [4 + 3\sqrt{2}]/2$, and the sets $J_1$ and $J_2$ are defined by

$$J_1 = [\sqrt{2} - 1, 2 - \sqrt{2}], \quad J_2 = [2 - \sqrt{2}, \tfrac{1}{2}\sqrt{2}],$$

respectively. The notation $1_A(x)$ denotes the indicator function defined by

$$1_A(x) = \begin{cases} 1 & x \in A \\ 0 & x \notin A \end{cases}$$

It is easy to show that S maps the set $J_1$ into $J_2$ and 'vice versa'. It is also easy to show analytically that picking $f_*(x)$ given by Eq. (7) as an initial density simply results in a sequence of densities all equal to the starting density.

However, this is quite different from what happens with an initially uniform density

$$f(x) = (2 + \sqrt{2})1_{J_1 \cup J_2}(x)$$

In this case, the first iterate $f_1(x)$ is given by

$$f_1(x) = (1 + \sqrt{2})1_{J_1}(x) + 2(1 + \sqrt{2})1_{J_2}(x)$$

and iteration of $f_1(x)$ leads, in turn to an $f_2(x) = f(x)$ and thus the cycling of densities repeats indefinitely with period two.

This effect of the choice of the initial density on the sequence of subsequent densities can be made even more dramatic, as illustrated by choosing an initial density

$$f(x) = [3 + \sqrt{2}]1_{J_1}(x),$$

totally supported on the set $J_1$. In this case,

$$f_1(x) = Pf(x) = [4 + 3\sqrt{2}]1_{J_2}(x),$$

and $f_2 = f$, $f_3 = f_1, \ldots$, so once again the densities cycle between $f$ and $f_1$ with period 2.

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