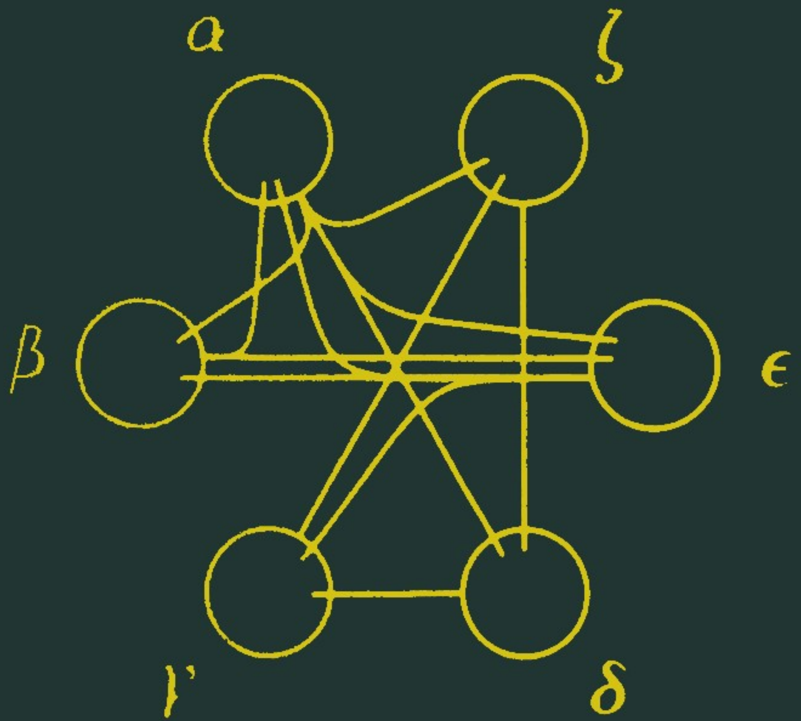
A. Aertsen V. Braitenberg (Eds.)

Information Processing in the Cortex

Experiments and Theory



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Reconstruction and Characterisation of Neuronal Dynamics: How Attractive is Chaos?

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During the last years there has been a great emphasis on the possibility of characterising neuronal dynamics with methods from non-linear dynamical system theory. These new methods, especially the determination of the correlation dimension of time series, were applied to continuous activity as measured by the EEG and also to pulse train activity of single neurons. We could show that the calculation of the correlation dimension leads to incompatible results for a continuous process and for a pulse train generated from that process. This result has implications not only for neuronal data but also for other fields in biology and physics, where one deals with these two types of data.

Recent years have shown a growing interest in the description of dynamics in complex systems, both at a theoretical and experimental level. It was shown that one can distinguish between stochastic and deterministic, non-periodic ('chaotic') processes; various measures for the characterisation were developed and applied in such different fields as ecology, climatology, fluid dynamics, quantum physics and life sciences (for example see the contributions in Mayer-Kress 1986; and Pool 1989).

One goal of electrophysiology and theoretical neuroscience is a better understanding of the dynamics of processes taking place in brain during information processing. In the context of our studies of the dynamics of activity and connectivity in the Neocortex (Preißl and Aertsen 1991), we decided to investigate the applicability of methods for dynamical system theory, in particular the dimension analysis, to the characterisation of these physiological processes. As we will

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demonstrate, one has to be aware of severe limitation when interpreting results of this approach.

Non-linear dynamics and chaos

A dynamical system can be defined by a set of differential equations

$$\dot{x} = F_\mu(x) \tag{1}$$

where x is in general an n-dimensional vector $(x_1,...,x_n)$ The components of this vector are functions of an independent variable, usually of the time t. The vector $(x_1,...,x_n)$ is called state vector and F_μ is a function of it. In the context of deterministic, dynamical systems this function only contains non-stochastic elements. The parameter μ usually stands for another vector $(\mu_1,...,\mu_m)$, the components of which are called control parameters; these parameters determine the dynamic behaviour. One can distinguish two main classes of functions F_μ:

- F_μ is linear in each component of the state vector, these systems are called *linear*
- F_μ contains non-linear combinations of the single components of the state vector, e.g. squares or products, these systems are called *non-linear.*

Up to now we have described systems which are continuous in time, but there are also many dynamical systems which evolve in discrete time steps. In that case Equation (1) changes to $x_{t+1} = F_\mu(x_t)$, where the variable x_t is the state vector at time t. The concepts which will be presented below are also applicable to such discrete dynamical systems.

The main interest in the investigation of a single dynamical system is the determination of the *trajectories.* These are the curves in the n-dimensional state space which the system traverse in the course of time, i.e. which specify the value of the state vector for a time $t = t_1$, if the system was in the state $(x_1(0),...,x_n(0))$ at time $t = 0$. For linear systems there is a well-established theory on how to go about to solve such equations and describe the dynamical behaviour (Hirsch and

Smale 1974). In the non-linear case, however, it is more difficult to get the solutions. In general, it is not possible to solve a non-linear system and get explicit formulas $x_i(t) = f_\mu(t,(x_1,...,x_n)$ for all $i \in \{1,...,n\}$, from which one could calculate the state vector $(x_1,...,x_n)$ for an arbitrary time t. For the characterisation of the dynamics, one has to calculate the trajectories for that system with specified control parameters.

A special class of dynamical systems are the *dissipative* systems. These are characterised by the fact that the volume of an arbitrary cell in state space goes to 0 as time proceeds. These systems have a so-called *attractor* which is reached for t approaching infinity, i.e. the attractor is the asymptotically reached state of the dynamical system, and all trajectories are drawn to this attractor after a transient time. The simplest example is the damped pendulum which has its resting point as the attractor, but there are systems with more complex attractors e.g. limit cycles. By definition, dissipative systems have an attractor with a dimension lower than that of the state space.

In the study of non-linear systems special interest was given to this kind of systems. An important observation was made by Lorenz (1963) when he calculated the trajectories of a non-linear 3-dimensional system as a simple model for the dynamics in the atmosphere. The system is definded by the following differential equation:

$$\frac{d}{dt}\begin{pmatrix} x \\ y \\ z \end{pmatrix} = \begin{pmatrix} -\sigma x + \sigma y \\ -zx + Rx - y \\ xy - bz \end{pmatrix} \tag{2}$$

For the control parameter he chose the following values $\sigma = 10$, $b = 8/3$ and $R = 28$. In that case the system is dissipative and, hence, the asymptotic dynamics are restricted to an attractor. This attractor looks like a two-dimensional surface. However it is impossible that the dimension is two or lower, since in a deterministic system two trajectories can never intersect. It also can not be three, because the system is dissipative. This leads to a new concept for the description of attractors by a non-integer dimension, called *fractal* dimension. This term goes back to the work of Mandelbrot (for an introduction to this concept see Mandelbrot 1983; and Falconer 1990). An attractor with a fractal dimension is called a *strange attractor*.

Another finding was the effect of *sensitive dependence on initial conditions*. In some non-linear dynamical systems the following observation can be made: if we follow the time development of two vectors

x and x' that were initially lying within a small disc of radius ϵ it turns out that their distance will grow exponentially with time. This dynamic behaviour can be characterised by the so called Lyapunov exponents. A system with at least one positive Lyapunov exponent is called *chaotic.*

The resume of Lorenz was the following:
'A finite set of ordinary differential equations representing forced dissipative flow often has the property that all of its solutions are ultimately confined within some bounds. [...] Our principal results concern the instability of nonperiodic solutions. A nonperiodic solution with no transient component must be unstable, in the sense that solutions approximating it do not continue to do so.'

It is obvious that these two measures reflect two different aspects of a system: the fractal dimension of the attractor characterises the asymptotic state, while Lyapunov exponents describe the dynamics. It was, however, shown that these two measures are not independent, and that one can, in fact, calculate the fractal dimension if one knows the Lyapunov exponents. After all, one has to distinguish between chaotic systems and systems with a strange attractor, in most cases these two properties go hand in hand. For a more extensive discussion on these topics see Eckmann and Ruelle (1985) and Bergé et al. (1984).

In view of this theoretical background, there are some important questions regarding the applicability of these concepts:

1. What can be said about an experimental system of which not all state vector components are known and not all components can be observed at the same time?
2. How can the fractal dimension and Lyapunov exponents actually be measured?

Reconstruction and correlation dimension

In most experimental situations the differential equations for the system under investigation and, consequently, the state variables are unknown. The experimenter usually has only access to consecutive measurements of a single scalar observable $z(t)$. A considerable step forward was made when it was shown that the attractor of the underlying system can be reconstructed from such a time series by a procedure known as *embedding* (Packard et al. 1980; Takens 1981). A vector in an m-dimensional *pseudo state space* is defined from the measurements by taking an appropriately spaced comb of values ($z(t)$, $z(t+\tau),\ldots,z(t+(m-1)\tau)$); different values of t correspond to different vectors in that space. For the two-dimensional case this means that the time series: $(z(t),z(t+\tau),\ldots,z(t+(m-1)\tau))$ is represented by the following vectors for reconstruction in a two-dimensional pseudo state space: $\{(z(t),z(t+\tau)\},\{(z(t+\tau),z(t+2\tau)\},\{(z(t+2\tau),z(t+3\tau)\}$.

The *embedding theorem* (Takens 1981) states that if z is the result of a smooth function, mapping the original attractor to the space of real numbers, and if $m \geq 2n+1$ (where n is the dimension of the attractor), the reconstructed attractor in pseudo state space is diffeomorphic to the original attractor: both have the *same dimension*.

This finding gave a possible way for a sufficient reconstruction of an attractor. Grassberger and Procaccia (1983a, b), building on considerations of Renyi (1962), developed an algorithm for determining one special kind of fractal dimension, the so-called *correlation dimension* (G-P algorithm). This dimension measures the density of sample points in the state space by calculating the *correlation integral* $C(\epsilon)$, which determines the number of state vectors x which fall in a region with size smaller than ϵ:

$$C(\epsilon) = \lim_{N\to\infty} \left(\frac{1}{N^2}\right) \sum_{i=1}^{N} \sum_{j\neq i=0}^{N} \theta(\epsilon - |x_i - x_j|) \tag{3}$$

In this formula θ is the so-called Heaviside function, which is 1 if the argument is larger than 0 and 0 otherwise. The indices i and j mark state vectors at different time steps. For small ϵ, $C(\epsilon)$ behaves like a power of ϵ: $C(\epsilon) \sim \epsilon^{\sigma}$, where σ is called the *correlation dimension*. From the correlation integral (3) one can obtain the correlation dimension very simply:

$$\sigma = \lim_{\epsilon\to 0} \frac{\log C(\epsilon)}{\log \epsilon} \tag{4}$$

Thus the correlation dimension can be determined as the slope of the log $C(\epsilon)$ vs. log ϵ curve in the so called *scaling region* (sr), i.e. where this curve is linear.

The embedding theorem and the G-P algorithm now provide the means to analyse the dynamics of a system under experimental observation: a time series is recorded, the data are embedded in an m-dimensional space (usually starting with $m = 1$) and a dimension d is determined with the G-P algorithm. This procedure is then repeated with increasing m. Initially the dimension d will increase with embedding dimension m. However if the underlying system has a low-dimensional attractor with a correlation dimension σ, the dimension d will saturate at this value for increasing m. In the scaling region the log $C(\epsilon)$ vs. log ϵ curves for different m will consequently become parallel.

It is important to realize that the correlation dimension is a geometric characterisation of the attractor. If the observed trajectory is long enough the attractor will be densely covered by it and the exact value of the correlation dimension can be calculated.

However, serious problems may arise when using this procedure. The first is the determination of the time delay τ from a certain time series. If the time delay is too short, the correlation integral is dominated by the data points which are too close to the reference point, which leads to so-called 'spurious dimensions' (Theiler 1986). If, on the other hand, the time delay is too large, consecutive data points are independent. In the experimental situation there are basically two methods to determine an appropriate time delay: the first is based on the auto-correlation function, the second, and the one to be preferred, is based on mutual information (e.g. Fraser and Swinney 1986).

The second problem is the *number of data points*, which should be taken for the calculation. One method is to vary the number of data points and to compare the results of different runs (for example see Dvorak and Siska 1986; Layne at al. (1986). From such studies it was concluded that it is necessary to use only stationary time series, the length of which can be determined experimentally. In addition, theoretical analysis considering the length of the time series required to obtain reliable results provided the following rule of thumb (Smith 1988): for a dynamical system with a correlation dimension of κ one should have at least $42^{\kappa_{int}}$ data points, where κ_{int} is the largest integer less than the correlation dimension.

The product of these two parameters, the time delay and the number of data points, determines the duration of the time series, necessary to obtain a reliable estimate of the correlation dimension.

Correlation dimension and neuronal signals

During the last years there have been several attempts by different groups applying the G-P algorithm to neuronal signals. It was shown, that finite correlation dimensions can indeed be calculated from this data (for example, see Rapp et al. 1985 and the papers in Basar 1990). These studies were done on single neuron spike trains as well as on more global electrophysiological measurements such as the EEG. Since, however, it is not obvious how to apply these methods to the analysis of a distributed system like the brain, we decided to focus on the description of single neuron dynamics.

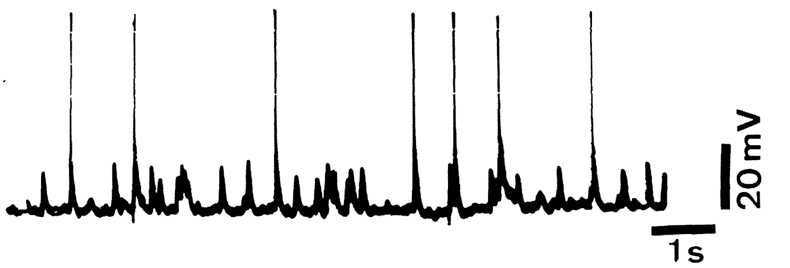

Fig. 1. The membrane potential of a single cell with clearly visible action potentials. Two types of data can be obtained from such a measurement: the continuous time course of membrane potential, and a point process, specified by the time intervals between successive action potentials

The dynamics of a single neuron can in principle be determined from two different experimental observations: the membrane potential, which is a *continuous* signal, and the train of action potentials (spikes), described as a *point process* (c.f. Fig 1). It is not clear beforehand whether a choice of either the continuous signal or the pulse train might possibly influence the outcome of the analysis. Therefore we decided to investigate this question in more detail (Preißl et al. 1990). To this end we analysed several well-known dynamical systems (Lorenz, Rössler, Henon), each one with a strange attractor and chaotic dynamics. In addition we studied the membrane potentials and spike trains derived from a neural network simulator which employs a pseudo-random generator (Boven and Aertsen 1990). In each case we focused on the issue of continuous versus discrete time series observations.

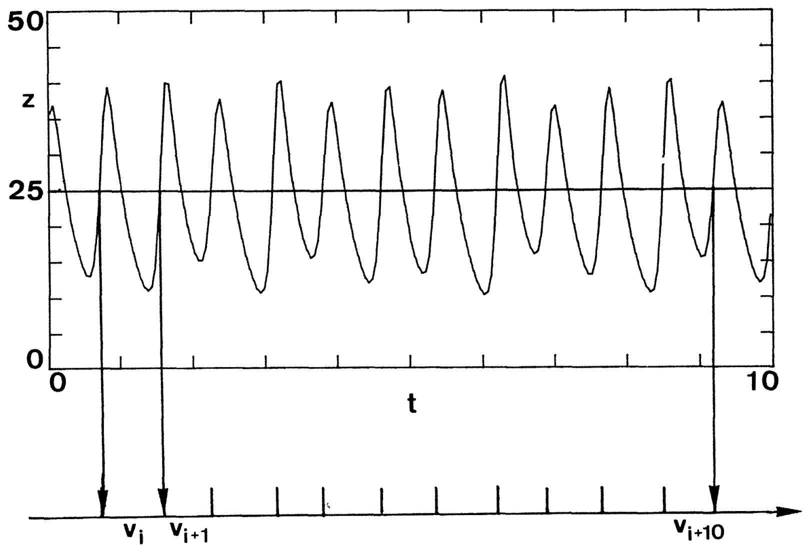

Fig. 2. Generation of the pulse train observations from the z-component of the Lorenz system: the dynamic variable for the reconstruction procedure is the sequence of time intervals between successive, positive-going level crossings at a fixed threshold value Z=25. Note that in this case the vectors are defined by taking sequences of adjacent intervals

In order to obtain the two types of data for each of the various systems, we recorded the time course of one of the system variables (continuous signal) as well as the series of time intervals between successive, positive-going level-crossings of a fixed amplitude threshold (pulse train) (c.f. Fig 2). In the latter case these time intervals were regarded as the variable of the dynamical system.

Here we present results obtained for the Lorenz system (simulation parameters as in Caputo and Atten 1987). We recorded the z component of the Lorenz system, and used 5000 data points with an time delay of 0.2. We embedded these data points in a pseudo state space with a dimension ranging from 1 to 6, and calculated the correlation integral (for the algorithm see Parker and Chua 1989; Grassberger and Procaccia 1983a). From the continuous measurement we obtained the correct correlation dimension of 2.06.

In the case of pulse-train measurements, we used a time series v_i, where v_i is the time between two i^{th} and $(i+1)^{th}$ positive going level-crossings of the z-component with a certain threshold. This time series was regarded as a discrete dynamical system, e.g. the $(i+1)^{th}$-interval is a function of one or more preceeding intervals. The length of this time series was again taken to be 5000. The embedding-dimension ranges

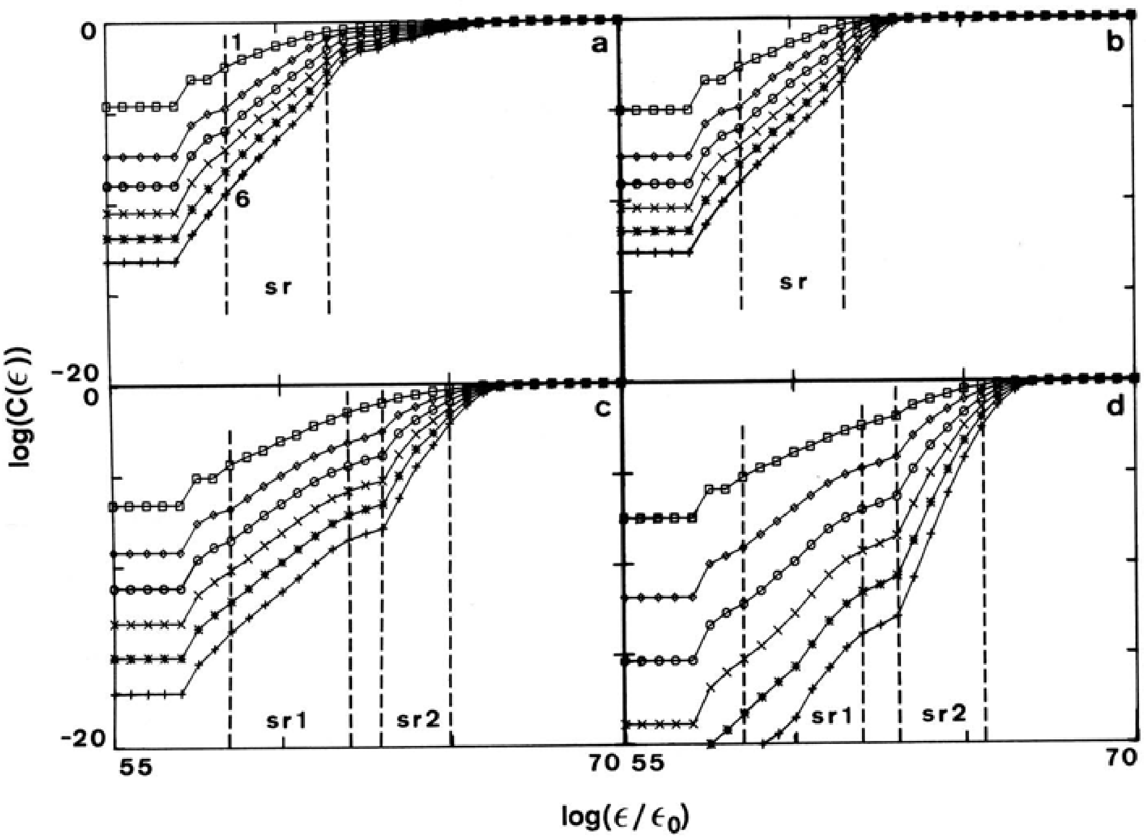

Fig. 3. Results of dimension analysis for pulse trains obtained with different thresholds Z on the z-component of the Lorenz system: Z=35 (a), Z=25 (b), Z=15 (c) and Z=12 (d). In each case the reconstruction was performed with 5000 intervals; the embedding ranges from 1 to 6.

from 1 to 6. In neurophysiology the embedding in the two-dimensional pseudo-state space is usually called scatter plot (Rodieck et al. 1962).

Rather to our surprise, however, the pulse train measurements gave quite different results as compared to the continuous signals. Moreover, the results depended on the threshold level Z used to generate the pulse trains (c.f. Fig 3). For Z=35 and Z=25 we were indeed able to determine a correlation dimension: for Z=35 it was 1.92, whereas for Z=25 it amounted to 1.79. Clearly these two values differ from each other as well as from the correlation dimension of the continuous system. With a threshold at Z=15 or at Z=12 one obtains two scaling regions (sr1, sr2). For Z=15 the correlation dimension equals 1.52 in sr1, whereas in sr2 it could not be determined at all; for Z=12 neither of the two scaling regions allowed to determine a correlation dimension. We made similar observations on the other (x and y) components of the Lorenz-system, as well as for the Rössler- and the Henon-system. In addition, we considered other types of pulse train generation mechanisms, e.g. the sequence of intervals between maxima in a selected component, and the sequence of intervals between consecutive points of entry into an arbitrarily selected box in pseudo state space. In *none* of these cases was it possible to obtain the correct correlation dimension of the attractor from an analysis of pulse train measurements. Finally we analysed both the continuous membrane potential and the simultaneously recorded spike train from a neuronal network simulator. Again, the two different types of measurements gave different results for the correlation dimension.

Discussion

From our observations on the behaviour of the correlation dimension for different types of measurements we are forced to conclude that there exists a fundamental discrepancy between the outcome of an analysis of a continuous process and of pulse trains generated from the same process. Consequently, correlation dimension analysis in its present form is not an appropriate tool for the characterisation of the dynamics underlying spike sequences. The reason is that the pulse train measurement is not the result of a smooth mapping of the underlying continuous process, as is required in the embedding theorem (Takens 1981). This fact also influences other methods for determining dynamical system parameters, such as the Lyapunov exponents. All these methods essentially rely on the assumption that the reconstruction process results in a diffeomorphic attractor. In addition, a point process, by its very nature, induces a description in terms of intervals between events. This dynamical variable does not generate a proper Poincare map of the underlying system. Consequently, this approach of making qualitative statements regarding the systems dynamics seem to be precluded too.

In addition to the above described problems, the concept of correlation dimension faces further, as yet unsolved questions in the field of neurophysiology. The first was already mentioned: the question of stationarity of time series with an very large number of data points. Adopting the boundary of Smith (1988), this implies that an attractor with a correlation dimension between 3 and 4 one needs some ten thousands of data points. This, of course, is not a trivial requirement to be met, especially in a working brain with continuously changing levels of activity.

However there is a second, even more fundamental problem. In the last years it was recognized that spatially extended systems with many interacting components, of which the brain surely is an example, may exhibit dominating long transients (Crutchfield and Kanenko 1988). This makes it impossible for the system to reach the attractor during a reasonable observation interval. Moreover, such systems may have multiple, coexisting attractors (Mayer-Kress and Kaneko 1989). This means that the spatio-temporal dynamics of a spatially extended system cannot possibly be characterised by means of an attractor reconstructed from the measurement of a single variable, irrespective of it concerns a single-neuron pulse train or a continuous signal such as a membrane potential or some other form of spatio-temporal summation like the EEG. Consequently, attractor characteristics such as fractal dimensions and Lyapunov exponents would be of little value here (see also Chate and Manneville 1987; and Lorenz 1991).

This, obviously, directly affects the question whether the concept of attractors, be they fractal or not, may be useful in the study of information processing in the brain. In our opinion, cortical information processing is not governed by attractors. Rather it seems more plausible to us that the dynamics are governed by transient state transduction, perhaps between different attractor states (Skarda and Freeman 1987). Consequently, although the calculation of a correlation dimension can be done on any time series, one has to be very careful in interpreting the results functionally.

Methods from dynamical system theory may possibly lead to new insights in various fields, including neuroscience. However, one should be aware of the fact that fractal dimension analysis is not an appropriate tool for the characterisation of pulse train (or interval) measurements, nor does it seem to be an adequate descriptor for the dynamics of a distributed system like the brain. In this context, concepts that are currently being developed for measuring complexity and prediction of time series seem to be more promising (see e.g. various contributions in Atmanspacher and Scheingraber 1991).

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