Are Neural Spike Trains Deterministically Chaotic or Stochastic Processes ?

the Dynamics of Spontaneous Neural Interspike Intervals

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Abstract

Before examining neural interspike intervals to see how they might encode information, an essential question that has first to be answered is whether, under the unstimulated condition, the apparent randomness of the neural firing pattern reflects deterministic chaos or a stochastic process. Here, we use short term predictability and the structure of the prediction residual to determine the dynamic characteristics of interspike intervals. As demonstrated in given computer simulations, unlike stochastic processes, deterministic chaos is highly predictable in the short term by linear and / or nonlinear prediction techniques. Interspike intervals recorded from somatosensory cortex and hippocampus were, thus, analyzed by using the same techniques. The results show that the neural spontaneous interspike intervals are poorly predictable in the short term, and the models that best fit the interspike intervals are linear (AR or ARMA) stationary processes. Therefore, the pattern of neural spontaneous firing can be characterized as stochastic rather than deterministically chaotic.

I. Introduction

One of the most pervasive enigmas regarding brain function is how information becomes transmitted from one location to another. In view of the fact that nerve impulses are *per se* more or less all or none in character, attention has been focused on the pattern of interspike, i.e. inter impulse, intervals as the carriers of information. A good deal of evidence has accrued to the effect that in an anesthetized unstimulated brain, the interspike intervals recorded from single neurons in a variety of locations are essentially random in their distribution. Models of the interspike process have therefore been constructed upon the assumption that this randomness reflects a stochastic process. Stochastic resonance models [1, 2, 3] and stochastic resonance with noise models [4] have been especially fruitful in simulating actual data obtained from spike trains. However recording randomness does not in itself insure that a process is stochastic. Recently a surge of interest has developed for the possibility that the behavior of spike trains, though random, could be generated by a deterministic nonlinear process which results in chaos. The current project sets out to test whether deterministically chaotic or stochastic processes best characterizes the patterns

of interspike intervals recorded from hippocampus and from somatosensory cortex in the lightly anesthetized rat.

Deterministic chaos is defined as a process which can be described precisely by a deterministic dynamic function. This deterministic function generates an 'unpredictable' bounded stable state [5]. The 'unpredictability', here, reflects the fact that the system is not periodic, quasi-periodic, or at equilibrium, i.e. converges onto a point attractor. The definition highlights two important considerations: The first is that the generator of the behavior is deterministic, even though the behavior currently displays randomness. The second consideration is that the observed randomness is not due to noise or interference from outside the system under observation; rather, the apparent randomness is due to the internal properties of system, i.e. its internal dynamics. Furthermore, to be chaotic, its randomness must reflect the fact that the system is sensitive to initial conditions, small perturbations, and the numerical errors caused by finite data length.

There is no widely accepted definition for stochastic processes. Any process will be called stochastic if its behavior is unpredictable from available past information. Instead of being generated by a determining function, the randomness of a stochastic system is due to possible interference from outside of the system under observation, improper selection of observations, or lack of knowledge about its coding structure. This ambiguity must not be reducible by improving precision of measurement and / or computation. For example, the trajectory of the orbit of Uranus was confusing before Neptune was discovered. The unpredictability in the trajectory of Uranus could not be reduced by just increasing the precision of measurement and computation. Once the interference from Neptune was taken into account, the trajectory became predictable. Thus, the similarity between chaotic and stochastic systems is that both of them currently display random behavior; the major difference is that chaotic randomness is due to an internally determinable generator while stochastic randomness is not.

Furthermore as a result of the operation of a deterministic generator, the trajectory of a chaotic process is structured while that of the stochastic process is not. The structure imbedded in the trajectory will therefore be reflected in its prediction error (residual). Ideally, this error reduction is unbounded when the frequency and precision of measurement and computation are improved. This unbounded characteristic of the reduction of the residual is one of most important measurements characterizing the chaotic process. In a stochastic system, the autocorrelation function of the residual after all the past information has been removed is a delta function. Also, in a stochastic system the variance of the residual will be much larger than that of the computational error, and can not be significantly reduced by increasing the rate of measurement and improving the prediction techniques.

II. Short term prediction in a chaotic process

According to the above, to distinguish a chaotic process from a stochastic one, the current output of a chaotic process must be predictable from immediately previous observations. This characteristic is called short term forward predictability. The characteristics of the prediction error (residual) is an important measure of the unknown process. Therefore, short term prediction becomes the key to determining whether an unknown process is chaotic or stochastic. When the variance of the residual has been minimized, the structure of the process becomes exposed, thus, whether the autocorrelation function of the residual is bounded or not can help to determine if the process is chaotic or stochastic. This section will describe and discuss some linear and nonlinear techniques used in short term prediction. These techniques will, in subsequent sections, be used in the computer simulations. The purpose of this section and the later computer simulations is to demonstrate, in the final section, that short term prediction is a useful tool in analyzing the dynamic properties of an unknown process such as those displayed by spike trains recorded from brain.

In nonlinear system analysis, the infinite series expansion of a general nonlinear function f(x) is useful. If all the derivatives of the nonlinear function f(x) exist, the function f(x) can be written as the following infinite series (the Taylor expansion), expanded at $x=x_0$.

$$f(x) = f(x_0) + \frac{df}{dx}\Big|_{x=x_0} (x - x_0) + \frac{1}{2!} \frac{d^2 f}{dx^2}\Big|_{x=x_0} (x - x_0)^2 + \dots + \frac{1}{k!} \frac{d^k f}{dx^k}\Big|_{x=x_0} (x - x_0)^k + \dots$$
(1)

where $\frac{d^k f}{dx^k}\Big|_{x=x_0}$ is the value of the kth derivative of nonlinear function f(x) with respect to x

evaluated at the point $x=x_0$. Clearly, if $\Delta x = |x-x_0|$ is small enough, or x is near x_0 , then, $\Delta x^* \approx 0$, for all $k \ge 2$. In equation (1), the sum of the terms of the second-degree and higherdegree of $(x-x_0)$ are negligible compared with the sum of the first two terms, thus, f(x) in the vicinity of x_0 can be represented as following linear form

$$f(x) = f(x_0) + \frac{df}{dx}\Big|_{x=x_0} (x - x_0);$$
(2)

for $\Delta x = |x - x_0| < \delta << 1$.

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Equation (2) is the linear approximation of nonlinear function f(x) within the vicinity of x_0 .

The first derivative $\frac{df}{dx}\Big|_{x=x_0}$, the slope of linear approximation representation of f(x), is a function of x_0 . If x is a function of time t, and t is discretized by a sampling operation, i.e. $t = n\Delta t$, $n = 0, 1, 2, \cdots$, and $x(n) = x(n\Delta t)$, the dynamic trajectory y(t) = f(x,t), at $t = (n+1)\Delta t$, can be derived from equation (2) by

$$y(n+1) = f(x_n, n\Delta t) + f'(x_n, n\Delta t)(x_{n+1} - x_n)$$

= $y(n) + f'(x_n, n\Delta t)(x_{n+1} - x_n)$ (3)

where $x_n = x(n\Delta t)$, and $f'(x_n, n\Delta t) = \frac{df}{dx}\Big|_{x=x_n}$. The derivative $f'(x_n, n\Delta t)$ in equation (3) is time varying. Thus, a nonlinear function y(t)=f(x,t) can be treated as a time varying linear dynamic equation proposed in equation (3).

This approximation usually works if x_{n+1} is close enough to x_n , or, equivalently, if $\Delta x = |x_{n+1} - x_n|$ is small enough in which case higher degree terms can be negligible. Therefor, to get a good approximation, the sample period Δt has to be small enough to satisfy the condition that $\Delta x^* \approx 0$, for all $k \ge 2$.

Equation (3) can be rewritten as a difference equation, i.e.

A Sub-

$$y_{k+1} = y_k + f'_k x_{k+1} + f'_k x_k$$
(4)

which is a first order autoregressive moving average process (ARMA(1,1)) for a one dimensional dynamic system (single variable system). More generally, a nonlinear multidimentional dynamic equation (multivariable dynamic equation) $\Psi = F(X,t)$ can be represented approximately as a linear time varying ARMA(p,q) process. Based on the dynamic model been constructed, the immediately future state y_{k+1} can be predicted by using the present and previous observations.

There are many different linear prediction methods, such as the autoregressive process (AR), the moving average process (MA), and the autoregressive moving average process (ARMA) [6]. Sometimes the "seasonal" model is also useful in predicting the behavior generated by a combination of slow and fast dynamics. All these estimators are called linear parametric estimators; they assume that the unknown system can be described by a linear difference equation, a discrete form of a linear differential dynamic function. The advantage of the linear estimator is its simplicity. These techniques have been well developed and successfully implemented in solving practical problems. The disadvantage of the linear estimator is that chaotic dynamics are strongly nonlinear and thus require a high sampling rate or frequency of observation. Meanwhile, the tracking rate of the linear estimator, known as the convergence rate, must be faster than that of the unknown dynamics.

To handle the above problem, a piecewise linear model can be realized by using a sliding data window for parameter estimation. The narrower the sliding window is, the shorter the linear pieces, and the faster the estimator can track. However, the tracking accuracy of the estimator is related to the variance of estimation, which is related to the total number of samples obtained. If, in a noisy situation, the sliding data window is too narrow, the variance of the estimation will be increased dramatically. The prediction error will contain a great deal of estimation error caused by noise. Therefore, the linear techniques are limited to those slow dynamic processes, mostly continuous cases. For fast chaotic dynamics, especially the discrete chaotic process, nonlinear techniques are needed to get good results. These techniques are usually more sophisticated than the linear techniques and also more computational intensive.

Unlike the linear parametric estimation techniques, the nonlinear methods are usually strongly related to the nonlinear model selected. If the structure of a dynamic function is known, and there are only a few unknown parameters in the function, then the least squares methods can be used to estimate these parameters. However, if the structure of the dynamic function is unknown, the

reconstruction of the dynamics from previous observations will be more difficult than the linear methods.

One of promising nonlinear modeling methods is to assume that the nonlinear dynamic function, y=F(X), can be decomposed as a linear combination of a set of basis functions, i.e.

$$y = F(\mathbf{X}) = \sum_{i=1}^{N} \lambda_i \Phi_i(\mathbf{X})$$
(5)

where $\Phi_i(X)$, i = 1,2,...N, are called basis functions, and λ_i ; i=1,2,...N, are the coefficients or weightings assigned to the basis. The present output of the dynamic is y(t), and the set of previous observations called the input vector becomes $X = \{x_1, x_2, ..., x_n\}$. The function $F(\cdot)$ defines a projection from the input domain to the output domain. Once the basis is selected, given a set of sample input vectors and their outputs, the unknown function can be reconstructed by estimating the parameters in equation (5). The estimated function gives the 'best fit' to the given samples, and a 'reasonable estimation' in the region between samples.

The success of the method is very much dependent on the selection of basis functions. Here, a radial basis function interpolation network (RBF network) [7, 8] is chosen as a nonlinear estimator to predict the behavior of the unknown process. The idea of radial basis function interpolation is to use the radial basis function as the basis in equation (1), such as a Gaussian function defined by

$$\Phi_i(\mathbf{X}) = e^{(\underbrace{\mathbf{X} - \mathbf{C}_i}]_{\sigma_i^2}}$$
(6)

where $C_i = [c_1, c_2, ..., c_n]$ is the center of base $\Phi_i(X)$; σ_i is the expansion parameter of $F_i(X)$; and, $\|X-C_i\|$ is the Euclidean distance from X to the center C_i . To simplify the problem, σ_i , i = 1, ..., N are usually selected as the same constant value for the basis, which are equal to the maximum expansion of the input dynamic region. The center position C_i is selected according to the location of samples. A robust method referred to as orthogonal least square (OLS) [9] can be used to select the center from the input vectors and to compute the weighting coefficients. The interested reader can obtain the details of technique from the listed references.

III. Computer simulations

The computer simulations are designed to demonstrate the performances of linear and nonlinear methods in predicting the chaotic process, especially, to expose the characteristics of the residual, which is important in determining the dynamic properties of an unknown process. The examples are all chaotic processes. One is a continuous dynamic process generated by the Lorenz equation, and the other is the discrete process generated by the Henon equation. Both the linear and nonlinear techniques are tested in the computer simulation.

In the first computer experiment, the Lorenz equation is defined by

$$\frac{dx}{dt} = \sigma(y - x)$$

$$\frac{dx}{dt} = xz + \alpha x - y$$

$$\frac{dz}{dt} = xy - \beta z$$
(7)

where α , β and σ are constants. Chaotic solutions of the Lorenz equation are presented when $\alpha = 28$, $\beta = 8/3$, $\sigma = 10$ [10]. The Lorenz equation is a third order nonlinear differential equation whose phase plane is three dimensional with variables of x(t), y(t), and z(t). Figures (1a) and (1b) give the phase plane plot of the Lorenz equation and the trajectory of x(t).



Figure 1. (1a) the trajectory of the Lorenz equation; (1b) the time waveform of x(t) variable

In the simulation, a third order autoregression (AR) forward estimator was used to perform a one step forward prediction. The parameters of the AR model were continuously estimated by the Burg algorithm [11] with a sliding window of 100 data points. The estimated trajectory shows (Figure 2a) a good match to the real trajectory (Figure 1b). The variance of the prediction error e(t) is about 5.4794×10^{-5} . Studying the prediction error e(t) (Figure 2b), its autocorrelation functions are not a delta function (Figure 3a). It has a relative long tail slowly cut at about a time lag = 40, which indicates that the prediction error contains information about the past which could be further removed by the predictor. Moreover, comparing e(t) with the original dynamic trajectory x(t), we can find that the prediction error shows a structure identical to that in x(t).



Figure 2. (2a) the forward prediction of x(t) by using the Burg algorithm. (2b) the residual of the Burg estimation.

To further explore the structure of the residual, we plot the normalized residual together with the normalized Euclidean distance which is measured from the trajectory position [x(t),y(t),z(t)] to the hyperbolic point of the Lorenz equation (Figure 3b). The diagram shows that the closer the trajectory is to the hyperbolic point, the larger the prediction error will be after immediately passing the vicinity of this special point. The fact that the hyperbolic point is an unstable equilibrium point which separates the attractors and their dynamic basins (in the phase space) brings about the uncertainty of chaos. Like an ideal rigid ball dropping on the top of an ideal needle, the closer the ball approaches to the center of the needle, the more sensitive its trajectory is to its initial conditions and perturbations. To determine exactly a future trajectory, infinite precision of measurement and computation are required. That is, if we can make our estimator infinitely accurate, the prediction error reduction becomes unbounded. As noted, this is important in distinguishing a chaotic from a stochastic process.

The same Lorenz trajectory is used to test the nonlinear prediction model. The total number of bases used in equation (5) is 20. The variance of the prediction error is 3.2485×10^{-6} , which is about 20 times lower than that obtained with a linear predictor. Comparing the residual obtained with the nonlinear estimator (Figure 4a) to that of the linear one(Figure 3a), there are some similarities; however, the residual of the nonlinear estimator is much smaller than that of the linear predictor. Furthermore, the autocorrelation function of the nonlinear prediction error (Figure 4b) shows a long tail, which suggests that the information contained in the residual is still attributable to the history of its processing. This indicates that the prediction error can be further reduced by improving the numerical precision and the performance of the estimation. This also is important evidence that an unknown trajectory is chaotic.



Figure 3. In (3a), the dots are estimated autocorrelation coefficients of the residual by using Burg algorithm, and, the dashed lines are the ± 2 times standard devination of the estimation. In (3b), the solid line is the normalized Euclidean distance from the hyperbolic point of the Lorenz equation to the present trajectory x(t), and the dashed line is the present residual power.

In the second computer simulation, a discrete chaotic dynamic equation is used. The dynamic function is called the Henon equation [5] defined by

$$y(n) = c + ay(n-1) + by(n-2)$$
(8)

By selecting different parameters of $\{a, b, c\}$, the above difference function can demonstrate periodic, unstable, or chaotic behaviors. The parameters are selected in our simulation as c=1, a=-1.4, and b=0.3 to place y(n) into a chaotic region. Figure (5a) and (5b) show the dynamic trajectory y(n) and its input vectors in an input vector space defined by y(n-1) versus y(n-2). In physics, this input vector space is also called a phase space, and the input vector plot in Figure (5b) is called the return map of the Henon equation. In the simulation, a linear forward predictor was used to develop the discrete trajectory y(n). The orders used in the autoregressive model were 2, and 4. Both results demonstrated large prediction errors, whose relative variances were 0.7150, 0.6368 respectively. Here the relative variance is defined by the variance of residual divided by the variance of unknown process y(n), it is a ratio that measures the percentage of unpredictable information. The results indicate that about 72% to 64% information in y(n) is unpredictable, especially, increasing the order of the linear predictor does not improve its performance if the residual is caused by nonlinearty.

Next, a radial basis function nonlinear predictor was used to analyze the dynamic of the Henon equation. The number of the basis used was 11. The original y(n) and its estimation totally overlap. The relative variance of the residual was 9.6623×10^{-10} . Both the residual (Figure 6a) and its autocorrelation function (Figure 6b) show a white noise pattern. The future states of the

y(n) are almost predictable from the past, and the unknown process is deterministic despite the fact that the trajectory itself looks random.



Figure 4. (4a) plots the forward prediction residual e(n) by using RBF network. In (4b), the dots are estimated autocorrelation coefficients of the residual in (4a), and, the dashed lines are the ± 2 times standard deviation of the estimation.



Figure 5. (5a) is the time series of the Henon equation. (5b) shows the input vectors of the Henon equation for training RBF network.



Figure 6.(6a) is the forward prediction residual of the Henon equation by using RBF network. In (6b), the dots are estimated autocorrelation coefficients of the residual in (6a), and the dashed lines are the ± 2 times standard deviation of the estimation.

IV. The analysis of the interspike intervals

In the previous sections, both the linear and nonlinear methods have been delineated for detecting a chaotic process. The computer simulations showed these methods to be promising in modeling chaotic processes. The structure embedded in the prediction error was shown especially useful in testing the low bound of the estimation. This estimation can, then, be further used to discriminate a stochastic process from chaotic dynamics. In this section, these techniques will be implemented in an analysis of interspike intervals. The experiments are designed to model the interspike interval both by linear and nonlinear methods. The questions to be answered are: First, whether or not the interspike interval can be modeled as being generated by a deterministic generator. Such a model would show (or not show) a short term predictability of the unknown process. Second, would such a model be linear or nonlinear? Only those processes which proved to be nonlinear and short term predictable would be classifiable as chaotic.

The raw data were collected from anesthetized (with barbiturate) rat somatosensory cortex and hippocampus. The records are of spontaneously firing neural units (there is no stimulus). Records of raw data were obtained by means of a Grass Model P5 preamplifier with an FET cathode follower. The recorded signal was band limited between 300 and 3000 Hz and amplified with a gain of 20,000. One hundred seconds of continuous voltages were sampled at a rate of 32 kHZ and stored by a BRAINWAVE system onto a PC-486 based computer. The raw data were then transferred for processing to a Silicon Graphics workstation. The units were sorted by a template matching program. The templates are histograms composed of the peak to peak amplitude and descending slopes of all units in a recording. Individual units were matched to one of the several templates obtained in this fashion from each recording.

Records from 12 rats were used. Twenty three units were obtained from 7 hippocampal recording; 12 units were obtained from 5 somatosensory cortex recording. Figure (7a) gives a typical interspike interval record from somatosensory cortex. The mean value of the inter spike intervals is 115 ms, with a standard deviation of 86.65 ms. The interspike intervals appear to occur randomly but they also show a tendency to group at 50 to 125 ms. However, about every 15 to 20 intervals, the interval will suddenly increase to the level of 300 to 400 ms, and to oscillate a few times before returning to the lower base line. The autocorrelation functions (figure 7b) at lag =1, 2 are higher than the 95% confidence level. There are also some seasonal changes although these are below the 95% confidence level. The partial correlation function drops abruptly at lag >1, and and it approximately equals to 95% level at lag 17.

A seasonal autoregressive model was constructed from one recording of the somatosensory spike-trains according to the autocorrelations and partial autocorrelations. The model equation is

$$(1-a_1B)(1-a_2B^{17})y(n) = e(n)$$
(9)

where B^k is a k steps delay operator, e(n) is the excitation noise of the process or residual of the prediction, and $[a_1, a_2]$ are the unknown parameters of the model. The estimated results are

$$(1+0.5092B)(1+0.2924B^{17})y(n) = e(n)$$
(10a)

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$$y(n) - 0.5092y(n-1) - 0.2924y(n-17) + 0.1489y(n-18) = e(n)$$
(10b)

Figures (7c) and (7d) give the one step forward prediction error e(n) and its autocorrelation function. The variance of the residual is 5425.9 (the stand deviation = 73.66). All the autocorrelation functions of the residual are below the 95 confidence level at lag > 0. The T ratio test for the estimated parameters in the equation (10a) are 5.87 and 2.7 respectively. Moreover, a sliding window of 100 interval points was applied to the interspike intervals; the estimated model parameters keep almost the same values as the window moves across the records.

Next, the nonlinear radial basis function estimator was applied to the same record. Fourteen bases were used in reconstructing the recorded interval train; the variance of the residual, and its autocorrelations were identical to the those obtained with the linear estimators.

The rest of the interspike intervals recorded from somatosensory cortex were processed using the same techniques. Most of them can be modeled as a first order autoregression function plus some seasonal effects at seasonal intervals of 7 to 17. Only 3 out of the 12 interval records from somatosensory cortex can be modeled as a first order autoregression model (AR(1)) or first order autoregression and first order moving-average model (ARMA(1,1)) without a seasonal period. The relative variance of the residual and the original interspike intervals was 0.914 in the linear prediction cases and 0.903 in the nonlinear cases, which means that less than 10 percent of the information in the interspike interval can be predicted according to previous observation. The results indicate that the interspike intervals of the somatosensory cortex can be modeled as a time invariant (stationary) linear autoregression process under the condition of no stimulation. Only a very low percentage of the information at any interval can be predicted from previous intervals. Such a process is not chaotic but stochastic.



Figure 7. (7a [top left]) gives an example of interspike intervals recorded from somatosensory cortex. In (7b [top right]), the solid line is the estimated autocorrelation coefficients of interspike intervals in (7a), and dashed lines are the ± 2 times standard deviation of the estimation. (7c [bottom left]) is the residual of forward prediction of interspike intervals, and (7d [bottom right]) is the estimated autocorrelation coefficients of the residual and ± 2 times standard deviation of the estimated autocorrelation of the estimated autocorrelation coefficients of the residual and ± 2 times standard deviation of the estimation of the estimation drawn as solid line and dashed lines respectively.

Figure (8a) gives an example of interspike intervals from hippocampus. As some units fire in bursts, only the first spike in a burst was sorted, so that the interspike interval becomes the inter burst interval (assuming that the unit is related to the burst). The same prediction methods as those used for analyzing the recordings made from somatosensory cortex were applied to the 20 different units obtained from the hippocampal records. The typical autocorrelation function (figure 8b) and partial autocorrelation functions were cut abruptly at lag = 1 or 2, which is almost white noise. There is no seasonal tendency found in any of the hippocampal records. The first order or second order autoregression functions provide excellent models of the processes. The autocorrelations of prediction errors occur also as white noise. The relative variance of the residual and the interspike intervals *per se* are both about 0.974 for the linear estimator and 0.967 for the nonlinear one. These results indicate that the hippocampal interspike intervals are even more unpredictable than those recorded from somatosensory cortex. Both are stochastic.



Figure 8. (8a [top left]) gives an example of interspike intervals recorded from hippocampus. In (8b [top right]), the solid line is the estimated autocorrelation coefficients of interspike intervals in (8a), and dashed lines are the ± 2 times standard deviation of the estimation. (8c [bottom left]) is the residual of forward prediction of interspike intervals, and (8d [bottom right]) is the estimated autocorrelation coefficients of the residual and ± 2 times standard deviation of the estimation drawn as solid line and dashed lines respectively.

V. Conclusion

1 Methods have been presented to distinguish chaotic from stochastic processes. These methods are based on short term predictions and the characteristic patterns of the prediction error. Computer simulations provided evaluations of the techniques when applied to known chaotic processes. When applied to real interspike intervals, the analysis showed that none of the interspike intervals could be modeled as a chaotic process generated by a deterministic function. Instead the results showed almost no predictability in the records, indicating the unstimulated interspike intervals to be essentially stochastic.

2 From an information transmission point of view, the more of a current process that can be predicted from previous observations, the less information can be contained in the current process. As the chaotic process is short term predictable from previous observations, the information obtained from any current sample would be small. If the train of interspike intervals were a carrier of information in the brain, the efficiency of information transmitted would be low in a chaotic mode. Only the less redundant stochastic process, i.e. a white-noise-like process can possible carry and transfer large amounts of information. Our data show spike trains to be open to such large amounts of information transmission.

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