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Investigating features of irregular fluctuations of cortical synapse data

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Abstract—We describe results of investigating features of irregular fluctuations of the individual response of an excitatory cortical synapse to stimulation from the viewpoint of dynamical systems. The behaviour of the data is irregular fluctuations (short-term variabilities) and long-term trends. At the first onset we investigate two features of irregular fluctuations. We first apply the small-shuffle surrogate method to investigate whether temporal correlations in irregular fluctuations of the data are absent. Based on the result we then apply the truncated Fourier transform surrogate method to investigate nonlinearity in the irregular fluctuations. The results indicate that the irregular fluctuations have temporal correlations and are linear.

1. Introduction

Although ensemble mean responses of an excitatory cortical synapse to stimulation with variable timing have been studied, the individual response is not well understood, because it has been difficult work to measure the data. Recently it has become easier to obtain sample data. To understand the data we investigate two features of irregular fluctuations. One is whether temporal correlations in irregular fluctuations of the data are absent. The other is whether irregular fluctuations are linear.

As shown in Figs. 1(a) and (b), the synapse data is seemingly not stationary, because the behaviour of the data includes irregular fluctuations (short-term variabilities) and long-term trends. More details concerning the measurement of this data are given in Sec. 2. To investigate irregular fluctuations with long-term trends, a common approach is to separate the irregular fluctuations and long-term trends or to split the time series into segments that can be considered nearly stationary [1]. However, such filtering is not always welcomed because the processed data can lead to spurious results [1]. Hence, it will be preferable, if possible, to investigate features of irregular fluctuations without such pre-processing. Although until recently, no surrogate method has been able to tackle such data, two methods have been proposed recently. One is the small-shuffle surrogate (SSS) method [2] and the other is the truncated Fourier transform surrogate (TFTS) method [1]. Both the methods can investigate features of irregular fluctuations even if they exhibit long-term trends without pre-processing. We show results obtained by applying the SSS and TFTS methods.

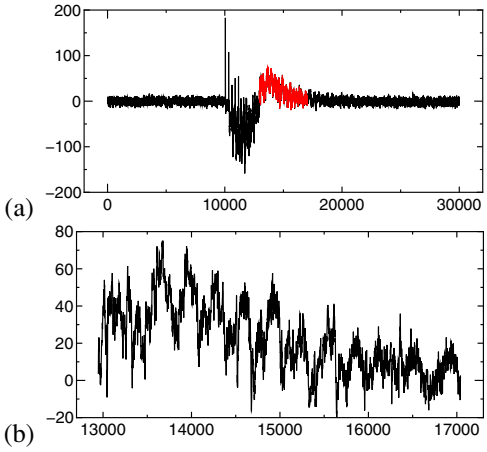

Figure 1: An excitatory cortical synapse time series examined in this paper: (a) whole data in black colour and data used in red colour, and (b) the enlargement of data used.

2. Individual response of an excitatory cortical synapse to stimulation

Data for this study was extracted from cortical slices on multi-electrode arrays from which gamma band (30–80 Hz) oscillations where initiated and recorded. Slices were taken from the somatosensory cortex of mice and electrical stimuli were applied at one or more locations to evoke a gamma band response across the slice. The data analysed in this paper is single scalar time series response to that stimulation. Data is sampled at 20 kHz and stimulation is applied at datum 10 000 (i.e. In Fig. 1 we see the time trace from 0.5 sec. prior to stimulation to 1 sec. post-stumulus). The lower panel depicts 0.2 sec. of data.

3. Methods we apply

In this section we describe methods we apply in this paper, the small-shuffle surrogate (SSS) method and the truncated Fourier transform surrogate (TFTS) method.

3.1. The SSS Method

To investigate whether temporal correlations in data are absent or data are independently distributed (ID) random variables even if it exhibits trends, the SSS method is useful [2]. Moreover, the SSS method does not depend on the specific data distribution. In other words, SSS data have the same probability distribution (rank distribution) as the original data. The SSS method has proven to be effective for tackling data exhibiting short-term variabilities and long-term trends [2].

SSS data are generated as follows; Let the original data be $x(t)$, let $i(t)$ be the index of $x(t)$ (that is, $i(t) = t$, and so $x(i(t)) = x(t)$), let $g(t)$ be Gaussian random numbers and $s(t)$ will be the surrogate data.

(i) Obtain $i'(t) = i(t) + Ag(t)$, where A is an amplitude.

(ii) Sort $i'(t)$ by the rank-order and let the index of $i'(t)$ be $\hat{i}(t)$.

(iii) Obtain the surrogate data $s(t) = x(\hat{i}(t))$.

It has been found that choosing $A = 1.0$ is adequate for nearly all purposes. In the SSS data, local structures or correlations in irregular fluctuations (short-term variabilities) are destroyed and the global behaviours (trends) are preserved. Further details of the method and the mechanism are provided in Refs. [2]. The null hypothesis (NH) addressed by this algorithm is that irregular fluctuations (short-term variabilities) are ID random variables or time-varying random variables (in other words, temporal correlations in data are absent) [2].

3.2. The TFTS Method

To investigate nonlinearity in irregular fluctuations various surrogate data methods have been proposed: the Fourier transform (FT), the amplitude adjusted Fourier transform (AAFT), and the iterative AAFT (IAAFT) algorithms [3, 4]. They are based on a linear process and address a linear null hypothesis. These methods assume that data is stationary. Unfortunately nonstationary data are theoretically incompatible with the assumption of linear surrogate tests and the nonstationarity is therefore very likely to lead to incorrect results [3, 4]. Hence, it is not appropriate to apply these methods to synapse data.

To investigate nonlinearity in irregular fluctuations (especially when they are modulated by long-term trends or periodicities), we want to destroy nonlinearity in irregular fluctuations and preserve the global behaviours. When data exhibit irregular fluctuations and long-term trends the power spectrum is usually like Fig. 2. Figure 2 indicates that the data have large peaks of power in lower frequency domain and power in higher frequency domain is almost white. From this we can consider that the higher frequency domain is probably dominated by irregular fluctuations. This implies that even if we randomize phases in the higher

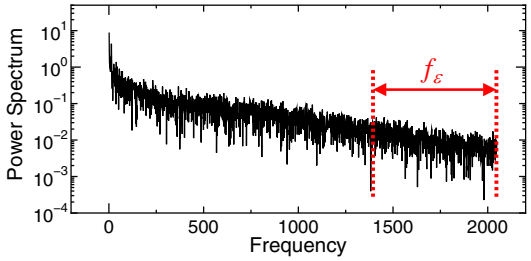

Figure 2: The estimated power spectrum of synapse data shown in Fig. 1(b), where we use 4096 data points. Note the logarithmic scale. We randomize phases in higher frequency domain f_ε and other phases are untouched. The parameter f_ε is the ratio of high frequency domain to the whole frequency domain. For example, when phases with frequency between 1500 and 2000 are randomized (that is, 500 higher frequency domain), f_ε is 500/2000, that is, $f_\varepsilon = 0.25$. We note that when showing power spectrum, these usually correspond to each frequency with unit of hertz (Hz) on the horizontal axis. In this paper, to explain our proposed method more easily we use arbitrary scale which correspond the number of data points.

frequency domain f_ε (see Fig. 2), the influence for long-term trends will not be significant. Hence, we randomize phases only in the higher frequency domain and do not alter low frequency phases. In this way, long-term trends are preserved in these unaltered low frequencies. This approach is in contrast to previously proposed linear surrogate methods, where all phases are randomized [4]. Since some phases are untouched, TFTS data may still have nonlinearity. However, it is possible to discriminate between linear and nonlinear data because the superposition principle is valid only for linear data. The NH addressed by our algorithm is that irregular fluctuations are generated by a stationary linear system [1].

Obviously, the surrogate data generated by the TFTS method are influenced primarily by the choice of frequency domain f_ε (see Fig. 2). The either too narrow or too wide domain is likely to lead to wrong judgement. However, we usually cannot determine an adequate value for f_ε *a priori*. Hence, we increase f_ε to randomize the phases from higher domain to lower domain step by step, for example by every 0.05 or 0.1. We continue until long-term trends are preserved in the surrogate data. In addition to visual inspection, we inspect the auto-correlation (AC) of the original data and the surrogate data at time lag 1 because the AC at time lag 1 must be most sensitive to the nature of the data. When the AC falls within the distribution, we consider that linearity and long term trends are sufficiently preserved in the surrogate data, and then calculate the AMI. When long-term trends are not preserved the AC falls outside the distribution we do not use the data, stop increasing f_ε and adopt the last result. That is, we continue until linearity or long-term trends are preserved in the surrogate data. See more

details on the stopping criterion in [1].

We note that we use the IAAFT algorithm to apply our idea in this paper, however, it is possible to use the FT and AAFT algorithms directly [1].

4. How to reject a null hypothesis

Discriminating statistics are necessary for hypothesis testing. After calculation of the statistic, we need to inspect whether the NH shall be rejected or not. We choose to use the auto-correlation function (AC) and the average mutual information (AMI) as discriminating statistics. The AC; an estimate of the linear correlation in data; and AMI; a general nonlinear version of AC on a time series; can answer the question: on average how much does one learn about the future from the past.

We use both the AC and AMI for the SSS method. This is because we have found that either statistic does not always work for certain test systems [5]. The TFTS method preserves linearity in data. Hence, in this case we use the AMI as a discriminating statistic [6].

To inspect whether a NH shall be rejected or not we employ Monte Carlo hypothesis testing. We check whether an estimated statistic of the original data falls within or outside the distribution of the surrogate data [7]. When the statistics fall within the distribution of the surrogate data, the NH may not be rejected.

In this paper, we generate 99 surrogate data and hence the significance level is between 0.01 and 0.02 for a one-sided test with two non-independent statistics[1].

5. Investigation of synapse data

We apply the SSS and TFTS methods to the synapse data shown in Fig. 1(b). We use 4096 data points for both the investigations.

5.1. Apply the SSS method

We first apply the SSS method to the synapse data to investigate whether temporal correlations in data are absent or data are independently distributed (ID) random variables. If we could confirm that the data have temporal correlations, we expect that the data are due to some kind of dynamical structure.

Figure 3 shows the synapse data and one of the SSS data. Figure 3(a) does not show significantly different behaviour from the synapse data shown in Fig. 1(b), although slight difference can be seen in Fig. 3(b). These figures indicate that the SSS method generates data in which long-term behaviours are preserved and local structures or correlations are destroyed.

[1]When generating 99 surrogate data, if two statistics are identical (dependent), the significance level for the proposed test is 0.01. If the statistics are independent, the significance level for the test is given by $1.0 - 0.99 \times 0.99 = 0.0199$. Hence, the reality should be somewhere in-between.

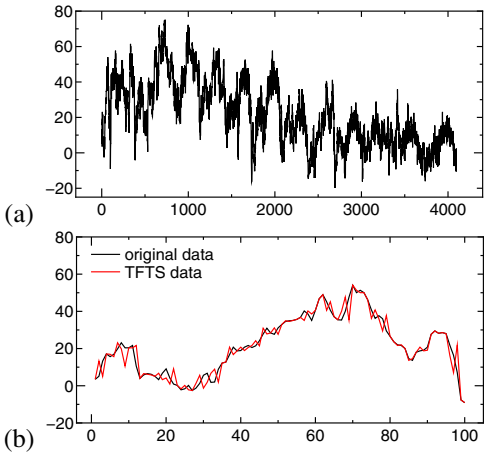

Figure 3: The synapse data and one of the SSS data. (a) SSS data of whole synapse data examined and (b) an enlargement of the synapse data in black colour and SSS data in red colour, where we use $A = 1.0$.

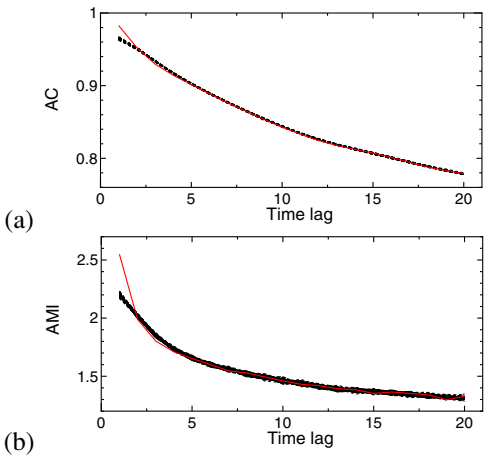

Figure 4: A plot of the AC and the AMI for the SSS data: (a) AC and (b) AMI, where we use $A = 1.0$ and 99 SSS data. The solid line is the synapse data and dotted lines are the SSS data.

Figure 4 shows the result of applying the SSS method. Figures 4(a) and (b) show that the AC and AMI show small difference and both the AC and AMI of the synapse data fall outside the distributions of SSS data[2]. Hence, we consider that the irregular fluctuations of the synapse data would not be ID random variables.

[2]In Figs. 4(a) and (b) some differences between the AC and the AMI of the synapse data and SSS data clearly appear especially when the time lag is relative small. This is because the information in the systems is not retained for longer periods of time. Also, when the time lag is larger, behaviours of statistics of the SSS data are very similar to that of the synapse data. This indicates that the local structures are destroyed and the global structures are preserved in the SSS data.

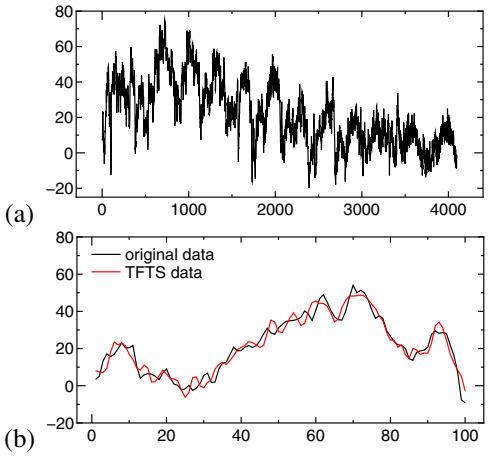

Figure 5: The synapse data and one of the TFTS data. (a) TFTS data of whole synapse data examined and (b) an enlargement of the synapse data in black colour and TFTS data in red colour, where we use $f_\varepsilon = 0.8$.

5.2. Apply the TFTS method

In Section 5.1 we found that there is some kind of dynamics behind the irregular fluctuations of the synapse data. Hence, as the next stage we apply the TFTS method to investigate whether the irregular fluctuations are linear.

To generate TFTS data we increment f_ε in steps of 0.1. We find that long-term trends are preserved in the TFTS data and the AC of the synapse data at time lag 1 falls within the distribution of the TFTS data between $f_\varepsilon = 0.1$ and $f_\varepsilon = 0.8$. However, when $f_\varepsilon = 0.9$ although the AC of the synapse data at time lag 1 falls within the distribution of the TFTS data, long-term trends are not preserved in the TFTS data. As mentioned previously, we adopt the last result (that is, $f_\varepsilon = 0.8$).

Figure 5 shows the synapse data and one of the TFTS data when $f_\varepsilon = 0.8$. Fig. 5(a) shows very similar behaviour to Fig. 1(b), and Fig. 5(b) shows that local structures are different between the two.

Figure 6(a) shows that the AC of the synapse data falls within the distribution of the TFTS data and Fig. 6(b) shows that the AC of the synapse data is almost identical to the TFTS data. From these figures we conclude that linearity and long-term trends are preserved in the TFTS data. Figure 6(c) shows that the AMI of the synapse data falls within the distribution of the TFTS data. Hence, we consider that we cannot detect nonlinearity in irregular fluctuations of the synapse data[3].

6. Conclusion

We describe results of investigating features of irregular fluctuations of synapse data. The results indicate that the irregular fluctuations have temporal correlations and are linear.

[3] Although long-term trends are not preserved in the TFTS data when $f_\varepsilon = 0.9$, the AMI of the synapse data falls within the distribution of the TFTS data.

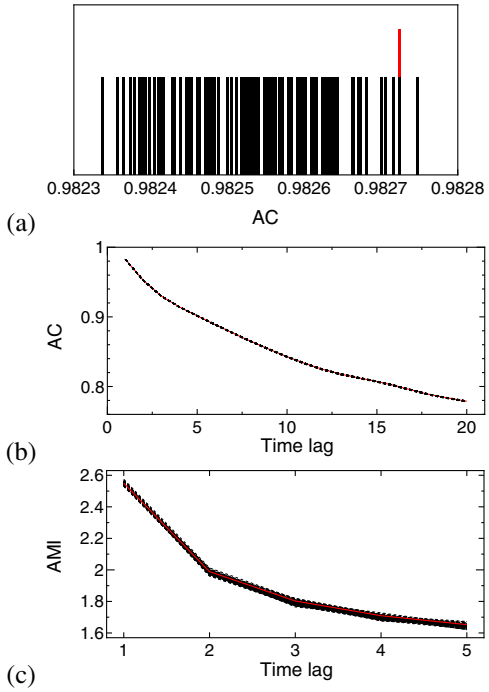

Figure 6: A plot of the AC and the AMI: In (a) the longer and short lines correspond to the AC at time lag 1 of the synapse data and the TFTS data, respectively. In (b) and (c) the solid line is the synapse data and the dotted lines are the TFTS data.

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