

Further study on $1/f$ fluctuations observed in central single neurons during REM sleep

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Received: 9 January 1992/Accepted in revised form: 15 July 1992

Abstract. Recently, $1/f$ fluctuations have been discovered in the single-unit activity of mesencephalic reticular formation (MRF) neurons during REM sleep. In a previous paper, such behavior could satisfyingly be interpreted on the basis of the clustering Poisson process. The question of applicability of this model to other MRF neurons remained unanswered. The present paper reports on $1/f$ fluctuations in 12 MRF neurons all of which can satisfyingly be modeled by the clustering Poisson process.

1 Introduction

In previous papers, evidence of $1/f$ fluctuations in single-unit neurons of the mesencephalic reticular formation (MRF) of the cat during REM sleep was reported (Yamamoto et al. 1986; Kodama et al. 1989a,b). Recently, the $1/f$ spectrum of one specially selected MRF-neuron could very well be modeled by the clustering Poisson process (CPP) (Grüneis et al. 1989, 1990).

In the present paper, we present a more elaborate analysis of 12 MRF-neurons all of which exhibit $1/f$ -like spectra over about 2 decades. Spectral shapes can satisfyingly be modeled by the CPP.

The single-unit activity of neuronal outputs can be regarded as a stochastic point process. However, its statistical properties have not yet been clarified. Clearly, the appearance of $1/f$ fluctuations in single unit neurons is suggestive of a complicated stochastic process that cannot be characterized by a single rate or time constant. It is expected that a great deal of biological information can be obtained once the underlying stochastic process has been identified (Wise 1981).

The phenomenon of $1/f$ fluctuations in various physical systems is one of the most widely discussed topics in statistical physics (Weissman 1988). Recent

experiments revealed evidence of $1/f$ fluctuations also in biological systems: besides the MRF-neurons investigated by us, it has been discovered in nerve membranes (Verveen and Derksen 1968), impulses of a squid giant axon (Musha et al. 1981), heart beat rhythm (Kobayashi and Musha 1982), spike trains of giant snail neurons (Musha et al. 1983) and in the lower auditory pathway of cat (Teich 1989; Teich et al. 1990).

The origin of $1/f$ fluctuations in both physical and biological systems is still a mystery. Nevertheless, several mathematical models have been proposed to describe $1/f$ fluctuations: superposition of Lorentzian spectra (Bernamont 1937), fractal Brownian motion (Mandelbrot 1982), scaling Brownian noise (Kiss and Hajdu 1989), the clustering Poisson process (Grüneis 1984; Grüneis and Musha 1986) and fractal shot noise (Lowen and Teich 1989) to name only a few.

In this paper, the clustering Poisson process (CPP) is applied for modeling output of 12 MRF-neurons. Data recording of spike trains, estimation of spectra and the fitting procedure have been described for one specially selected neuron in a previous paper (Grüneis et al. 1989) and apply also for the 12 MRF-neurons investigated here. Spectral properties of the CPP has been discussed in previous papers (Grüneis and Baiter 1986; Grüneis and Musha 1986; Grüneis et al. 1989).

All 12 MRF-neurons show $1/f$ characteristics which are most significant during REM-sleep; we found a dynamical transition of single neuronal activities of the MRF from an almost flat spectrum during SWS (slow-wave sleep) to a $1/f$ -like spectrum during REM-sleep (Yamamoto et al. 1986a). $1/f$ neuronal dynamics is expected to underly physiological functions of REM such as dreaming. Possible generation mechanisms of $1/f$ fluctuations in neuronal spike trains have been investigated in applying pharmacological techniques (Mushiake et al. 1988; Kodama et al. 1989a,b) and computer simulations (Nakao et al. 1990).

The purpose of this paper is twofold: first, to emphasize evidence of $1/f$ fluctuations in MRF-neurons and secondly, to demonstrate applicability of the cluster model for modeling neuronal spike trains.

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The paper is organized as follows: Chapter 2 summarizes methods applied. In Chap. 3, $1/f$ characteristics in spike trains of 12 neurons are demonstrated in applying spectral analysis. Empirical findings are interpreted on the basis of the CPP which is dealt with in Chap. 5. A fitting procedure is described in Chap. 6 which is followed by a chapter with discussion and summary of results.

2 Methods

Detailed description on the experimental procedure appeared in our previous paper (Yamamoto et al. 1986a). Briefly, adult cats were prepared for chronic unit recording, in which recording electrodes were implanted to monitor the cortical EEG, LGN EEG, hippocampus activity, EOG, EMG signals from the neck and orbicularis oculi muscles. In order to record single-unit activity from the MRF, bundles of 35 micro-meter wire electrodes were inserted bilaterally to the target regions. Single-unit activity of MRF neurons as well as other activities such as EEG, EMG and EOG were recorded during 2–3 SWS and REM ultradian cycles. Recorded neurons were located in the central tegmental field, A2.0 to 4.0, L2.0 to 3.5, D0.5 to –3.5 in the atlas of Jasper and Ajmone-Marson (1954). The histology of those neurons is presented in our previous paper (Yamamoto et al. 1986a).

Data segments were selected based on polygraphic assessment of sleep-waking states. Sleep states were classified into one of the two following states which continues for a relatively long period (several 100 s):

- (1) slow-wave sleep (SWS), characterized by the low-frequency and high-amplitude cortical EEG with fewer spindle bursts;
- (2) REM sleep, by cortical EEG desynchronization, continuous hippocampal theta-wave activity and complete abolition of tone in neck muscles.

3 Evidence of $1/f$ fluctuations in neuronal spike trains

The output of neurons generates a spike train which can be represented by a point process as

$$y(t) = \sum_n \delta(t - t_n). \quad (1)$$

t_n is the random occurrence time of the n -th spike. Spectral analysis has been applied to neuronal spike trains of 12 MRF-neurons. Weakly stationary spike trains have been selected by the side test (Bendat and Piersol 1971).

Power spectral density of neuronal spike trains has been estimated by Blackman-Tukey algorithm (Bendat and Piersol 1971) and is shown in Fig. 1a-l. All of them reveal a spectrum $G_y(f)$ proportional to $1/f^{b_e}$ over about 2 decades with $0.8 < b_e < 1.38$. In almost all cases (except in Fig. 1j) a plateau appears at frequencies below 10^{-1} Hz. A distinct minimum is found in the

frequency range between 6–20 Hz. In the high frequency range a white noise plateau is observed; this white noise plateau is due to the overall occurrence of events.

4 Fractal character of neuronal spike trains

Occurrence of neuronal spike trains can be represented by (1). One may also describe these events by cumulative number of events $N(\tau)$ which occurred during a time period from t_0 to $t_0 + \tau$. $N(\tau)$ can be expressed by

$$N(\tau) = \int_{t_0}^{t_0 + \tau} y(t') dt'. \quad (2)$$

Fractal point processes are characterized by self-similarity: scaling of the time axis results on the average in an amplitude-scaled version of the same signal. Define a scaling region which ranges from t_{\min} to t_{\max} . Then, for t_{\min} to t_{\max} , $N(a\tau)$ and $a^H N(\tau)$ have the same distribution functions. The scaling exponent H is the so-called Hurst-exponent (Mandelbrot 1982). From this it follows that the variance of counts in an interval of length τ is

$$\text{var}[N(\tau)] \propto \tau^{2H}. \quad (3)$$

It can be shown (Grüneis et al. 1991) that (3) is giving rise to

$$G_y(f) \propto \alpha 1/f^{2H'-1} \quad \text{for } f_{\min} \text{ to } f_{\max} \quad (4)$$

whereby $H' \geq H$, H' being a function of t_{\min} , t_{\max} and H . $f_{\min} \approx 1/t_{\max}$ and $f_{\max} \approx 1/t_{\min}$. For a well extended scaling region (more than about 6 decades) $H \approx H'$.

For $H = 1/2$, the process is characterized by totally uncorrelated spikes which can be modeled by the Poisson process. For $1/2 < H < 1$, the process is characterized by long-term correlations, indicating some clustering or correlations between spikes. Such a behavior can be modeled by the CPP discussed below.

Scaling properties can also be expressed by fractal dimension D . D can be determined from the sample path of $N(\tau)$ in applying box-counting method. It can be shown that $D = 2 - H$ (Mandelbrot 1982).

Neuronal spike trains investigated reveal a spectrum as $G_y(f) \propto 1/f^{b_e}$ which has the same form as (4) with $b_e = 2H' - 1$. Neuronal spike trains investigated in this paper can thus be identified as fractal point processes.

5 Review of the clustering Poisson process

The clustering Poisson process (CPP) consists of a random sequence of clusters; for an illustration see Fig. 2. There is a random series of primary events which trigger a secondary series of events, called clusters. The clusters are assumed to be independent of one another and constitute finite renewal processes. The complete process is the superposition of events originating from different clusters and can be represented by

$$y(t) = \sum_i \sum_{j=1}^{N_k} \delta(t - t_i - t_{ij}). \quad (5)$$

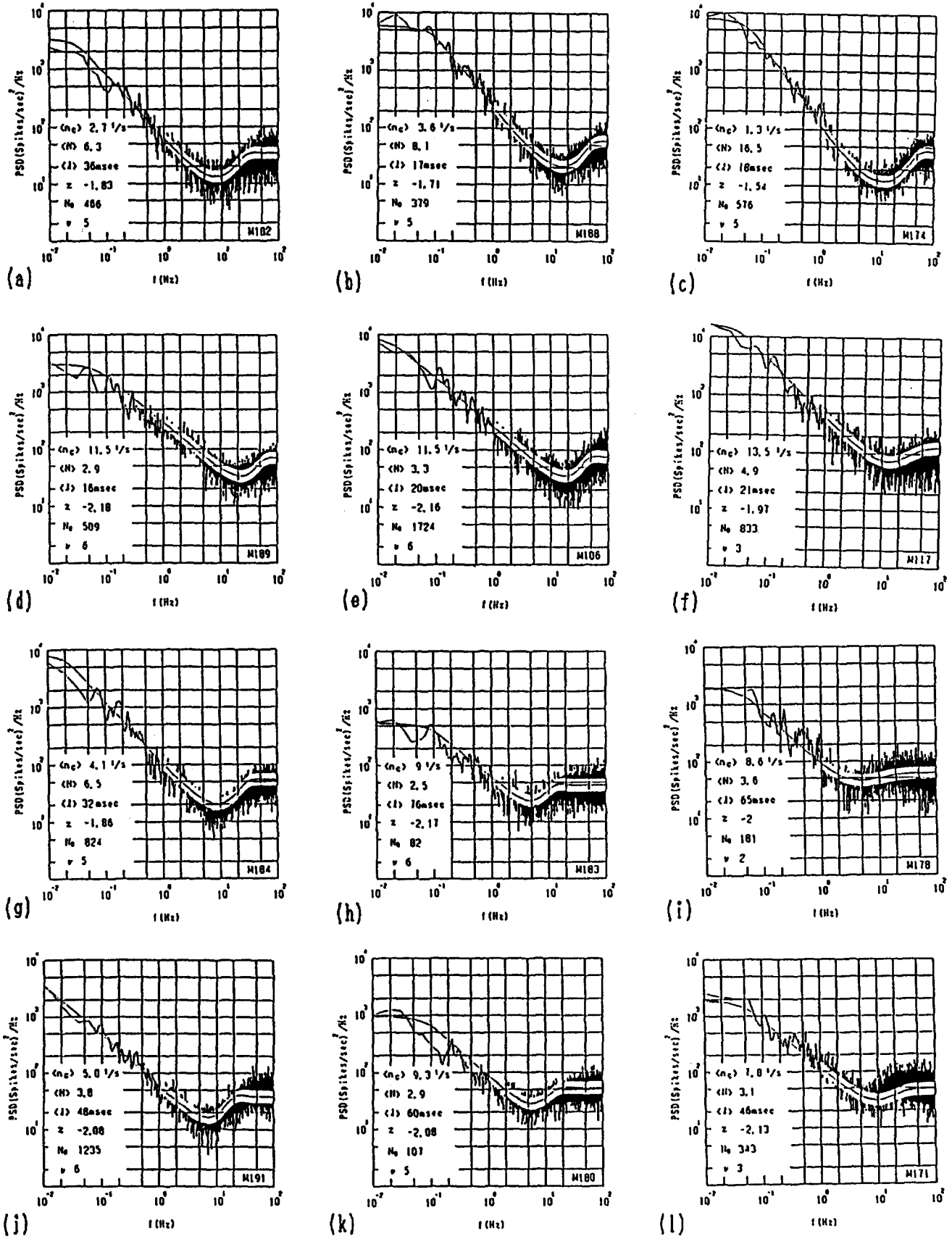


Fig. 1a-l. Power spectral density (PSD) versus frequency in a double-logarithmic scale of 12 MRF-neurons and best fit spectrum (bold lines) with parameters characterizing the CPP

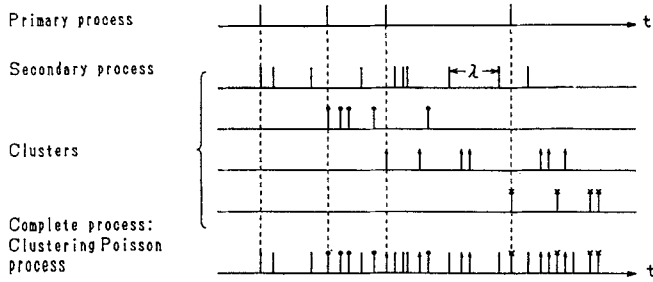


Fig. 2. Illustration of the clustering Poisson process

Herein, t_i are time points of the primary process and i ranges from minus to plus infinity. t_{ij} are time points of the secondary process and N_k is the number of events in the k -th cluster. The complete process $y(t)$ consists of an indistinguishable series of events, whereby the cluster formation may no longer be obvious. Such a situation is illustrated in Fig. 2 where point events originating from different clusters are strongly overlapping. The occurrence of events in the complete process can be expressed in the form of (1) whereby t_n is in a complicated manner dependent on the parameters of the cluster model.

The primary process is a Poisson process with mean rate $\langle n_c \rangle$. The secondary process is a renewal process; intervals λ are assumed Γ -distributed with index ν . A plot of this distribution functions for several values of ν can be found in Grüneis et al. (1989). $\langle N \rangle$ is the mean number of events in the cluster (in our previous paper (Grüneis et al. 1989) the mean cluster size was denoted $\langle m \rangle$; all other notations have been left unchanged). Thus, the mean overall rate of events is $\langle n_{\text{tot}} \rangle = \langle n_c \rangle \langle N \rangle$.

The number of events within the clusters is a statistical variable N with distribution function $p_m = \text{prob}\{N = m\}$ which is called cluster-size distribution. m can take on values $1, 2, \dots, N_0$; N_0 is a maximum cluster-size.

The spectrum of the CPP can be described by five parameters: $\langle n_c \rangle$ for the primary process; z , N_0 , $\langle \lambda \rangle$ and ν for the secondary process.

5.1 Conditions for $1/f$ fluctuations in the CPP

When the clusters are distributed according to a power-law with cluster-size distribution $p_m \propto m^{-z}$, the cluster model was shown to exhibit a $1/f^b$ spectrum whereby $b = z + 3$ with $-3 < z < -1$ (Grüneis and Baiter 1986). Long-term correlation length of the cluster model is given by the duration of the shortest and longest cluster of length $t_{\text{min}} \approx \langle \lambda \rangle$ and $t_{\text{max}} \approx N_0 \langle \lambda \rangle$. The scaling region in the time and frequency domain is given by $t_{\text{max}}/t_{\text{min}} \approx f_{\text{max}}/f_{\text{min}} \approx N_0$. The spectrum can be derived analytically and can in the scaling region be expressed by

$$G_y(f) \propto 1/f^b \quad \text{for } 0 \leq b \leq 2. \quad (6)$$

A schematic plot of $G_y(f)$ is shown in Fig. 3; numerically computed spectra can be found in a previous paper (Grüneis et al. 1989). Below f_{min} , $G_y(f)$ shows a

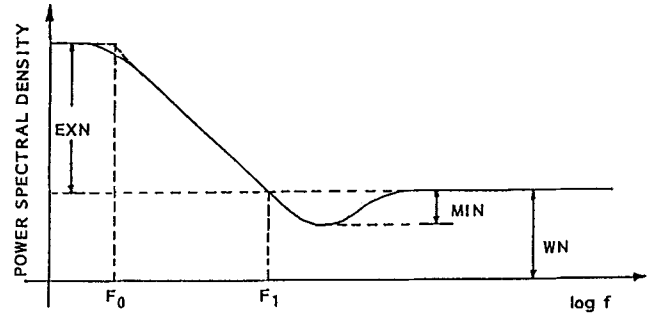


Fig. 3. Schematic plot of power spectral density and parameters which can be derived from the spectrum

plateau; for moderate values of ν a minimum is observed which is followed by a white noise plateau. Comparing (6) with (4), the clustering Poisson process can be identified as a fractal point process; scaling exponents are related by $b = 2H' - 1$.

Thus, the CPP shows spectral behavior which is characteristic for all of the MRF-neurons investigated and appears appropriate for fitting.

6 Fitting procedure

Empirically found spectra of neuronal spike trains of Fig. 1 are characterized by 5 parameters: the white noise level WN , the depth of the minimum below the white noise level MIN , an upper and lower limit F_0 and F_1 to $1/f$ -like shape and the noise plateau in excess to white noise EXN ; for an illustration see Fig. 3. A fit of the spectrum of the CPP to empirically found spectra can be achieved in varying the five free parameters of the CPP.

A fitting procedure described in (Grüneis et al. 1989) has also been applied here. The results can be found in Fig. 1 which shows the best fit spectra (bold line) and the five parameters characterizing the CPP. The agreement between empirical and fitted spectra is satisfying.

7 Summary of results and discussion

In this paper, single-unit activities of 12 MRF-neurons of cat during REM-sleep have been investigated by means of spectral analysis. All spectra reveal $1/f$ -like fluctuations.

Empirical findings can be modeled by the clustering Poisson process (CPP); it consists of a primary process with triggers a secondary series of events called clusters. $1/f$ characteristics are due to fluctuating clusters.

Spectra of all 12 MRF-neurons can satisfyingly be fitted by the CPP. The CPP suggests that at least 5 parameters are needed to adequately model neuronal spike trains investigated: $\langle n_c \rangle$ for the primary process and z , N_0 , $\langle \lambda \rangle$ and ν for the secondary process. It is concluded, that simple stochastic models, like Poisson or renewal processes, cannot adequately model empirical findings.

Recently, a fractal doubly stochastic Poisson point process (FDSPP) has been discussed in context with the cochlear neuronal spike train (Teich et al. 1990). The FDSPP is like the cluster model also a complicated stochastic process which may adequately model neuronal activities.

In accordance with a complicated stochastic process is also analysis of spike trains by a method which was introduced by (Nakahama and Yamamoto 1983). Based upon a higher order Markov process, a new measure dependency D_m is introduced: it is a most compressed measure for expressing the higher order statistical properties of a time series. This method was applied to spike trains in MRF-neurons during REM-sleep; it clearly revealed that occurrence of a spike is strongly dependent on the occurrence of spikes in the past (Yamamoto et al. 1986). This is also expressed by a $1/f$ -like spectrum which is characteristic for a spike train with long-term correlations showing correlation between occurrence of spikes. Thus, the occurrence of neuronal spikes can in general no longer be regarded as purely random because this would give rise to a white spectrum only.

Relation to the cluster model is suggestive and can be explained as follows: the cluster model consists of the superposition of randomly occurring clusters, which are composed of randomly occurring events. Thus, doubly randomly occurring events compose the clustering process. Obviously, successive events may originate from different clusters. Thus, unlike for a purely random process, the cluster formation introduces a new property: the occurrence of an event can be addressed to a certain cluster which originated prior to that event and thus is dependent on its past.

Description on the cross correlation analyses were performed on neuronal pairs which were arbitrarily distant (Yamamoto et al. 1986b). The results showed that the MRF neuronal activities during REM were almost mutually independent, as concerns the limited number of pairs investigated. Although some cross correlations were statistically significant, the pattern of cross correlogram could not be easily generalized, and no synchronously firing pairs of units were observed especially in such an extremely low frequency band. In this context, our further study will include the application of a new measure, the transinformation (Pawelzik 1991), which may give insight into possible synchronous activities as observed in visual cortex of cat (Gray et al. 1989).

In summary, it is concluded that appearance of $1/f$ fluctuations in neuronal spike trains are indicative for correlation between spikes. This property may have implications for dynamic information processing in the neural system. In this context, the CPP is a powerful tool for characterizing neurons.

Acknowledgements. The authors are very grateful to the Toyota foundation for their support of this research. All computations were carried out by using the VAX-8350 VMS system in the Education Center for Information Processing of Tohoku University in Sendai. We are also gratefully indebted to Dr. Barbara Herzberger for reading the manuscript.

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