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Recording site dependence of the neuronal spiking statistics

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Abstract

Spiking characteristics of neurons in the middle temporal (MT) area and the medial superior temporal (MST) area in the visual cortex of a monkey are compared with the ones in the principal sulcus (PS) area in the prefrontal cortex. The comparison is based on the basis of three inter-spike interval statistical measures: the coefficient of variation (CV), the skewness coefficient (SK) and the correlation coefficient of consecutive intervals (COR). Even for the spike sequences recorded from the same neuron, three coefficients computed from 100 intervals do not always exhibit similar values, but distribute rather widely. The distribution of three coefficients obtained from a single neuron in the MST area does not largely deviate from the distribution obtained from multiple neurons in MT and MST areas. Those distributions, however, largely deviate from the distribution obtained from neurons in the PS area. In this way, the distribution of those statistical coefficients reflects the nature of the recording site.

Keywords: Coefficient of variation; Skewness coefficient; Correlation coefficient; Cortical area

1. Introduction

The cerebral cortex is divided into discrete areas on the cytoarchitectural basis. The cytoarchitecturally divided areas turned out to have distinct physiological functions. In addition to the difference in cytoarchitectures and the physiological functions, neurons in different cortical areas may exhibit different spiking characteristics. The difference may even be seen in gross spike rate. For instance, when a visual flow to some direction is shown to a monkey, neurons in the middle temporal (MT) and the medial superior temporal (MST) areas in the visual cortex can exhibit high spike rate, of several tens of spikes per second, or even higher. On the other hand, neurons in the prefrontal cortex do not exhibit such high spike rate, in response to external stimuli as well as internal memory contents. Therefore, if we are to attempt to infer the source of the spike train received, the gross spike rate may become a clue to the inference. In the present paper, we are concerned with higher order non-dimensional statistical measures such as the coefficient of variation (CV), the skewness coefficient (SK), and the correlation coefficient of consecutive intervals (COR) to see if they may supply firmer clues to that inference of the recording site.

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We analyzed the spike sequences recorded from the distinct areas: the MT and the MST areas in the visual cortex and the principal sulcus (PS) area in the prefrontal cortex. It is found that the distributions of the non-dimensional statistical measures evaluated from the recorded data are largely dependent on the recording site.

2. Materials and method

The spiking characteristics may depend not only on the recording site, but also on the animal's behavioral conditions. In order to extract the recording site dependence of the spiking characteristics from multiple experiments, other conditions have to be made as similar as possible. For this reason we required the experiments using same kind of animals. All the following experiments are performed by using macaque monkeys. We also require the animals to take behaviorally steady condition. The first two experiments are performed using an anesthetized monkey, and the steady conditions are naturally satisfied. The third experiment used awake, behaving monkeys but the spiking data, which are used for the analysis, are taken from the period in which the monkey is staying still, as explained later.

1) 'MT/MST'(experiment carried out by Hiroshi Ohno, Tamagawa University): computer generated random dots uniformly moving to a fixed direction were shown to an anesthetized macaque monkey whose eyes are still. Spike sequences were recorded from multiple neurons sampled from the MT and the MST areas, which are known to exhibit selective response to motion of visual objects. Recording neuronal activities was carried out with the standard single extracellular recording method. Twelve directions of motion mutually different with 30 degree in angle were tested with respect to a single neuron. Moving random dots to one direction are shown for 10 s, respectively. It is known that the response latency of this area is less than 50 ms (see Kawano et al., 1994). From each 10-s record, the initial 0.5 s is removed from analysis, regarding those 500 ms as initial transients. If the spike sequence of the remaining 9.5 s contain more than 100 intervals, we take the central 100 intervals to compute the three statistical coefficients CV, SK and COR. The spike records, which do not contain 100 intervals, are dismissed. About 20 neurons sampled from the MT and the MST areas were recorded and we obtained 73 spike sequences with 100 intervals, which were subsequently used to compute the statistical coefficients.
2) 'MST-1' (experiment carried out by Hiroshi Ohno, Tamagawa University): spike sequences were recorded from a single neuron in the MST area of a macaque monkey. Experimental circumstances are same as above. The direction of random dots is chosen so as to result the largest response of the neuron (so called preferred direction). The optimal visual flow is shown for a period of 5 s repeatedly (97 times) with rest intervals of a several seconds. From each spike record, we also removed the initial 0.5 s, regarding the period as initial transient. We linked the multiple spike records according to the prescription, which we called 'L1' in Shinomoto et al. (1999), Sakai et al. (1999). That is to link the segments of different trials directly. We keep the last fragmental interval of one 4.5-s segment and the first fragmental interval of the next 4.5-s segment to compose one interval. From the long sequence, made up by linking the records, spike sequences of 100 intervals are taken out one by one. Eventually we got 55 spike sequences of 100 intervals, from each of which we compute a set of the three statistical coefficients.
3) 'PS' (by courtesy of Shintaro Funahashi, Kyoto University): spike sequences are recorded from multiple neurons sampled from the PS area of alert macaque monkeys performing a delay response task of Funahashi and Inoue (2000). Recording neuronal activities was carried out with the standard extracellular recording method. Recorded spike rate of a prefrontal cortical neuron is found typically ten spikes per s. The behavioral

steady state we could obtain in this case is the delay period of 3 s in a delay response task, in which a monkey is required to keep the cue memory, which is necessary for the correct delayed response. From those 3 s, the initial and final 0.5 s are removed as transients and the spike sequence left for analysis is only 2 s. As the number of intervals obtained from this fragment of time does not serve 100, we linked the records of different trials of the same cue stimulus by the method of linkage L1 explained above, by assuming that the neuron has been subject to the same statistical condition when the monkey was exposed to the same cue information. About 233 neurons in the PS area were recorded and we obtained 666 spike sequences with 100 intervals.

3. Three statistical coefficients

In comparing characteristics of multiple spike sequences, it is desirable to standardize the length of the spiking data. We fix the number of intervals to 100. From the sequence of 100 intervals $\{T_1, T_2, \ldots, T_{100}\}$ prepared accordingly, we compute three statistical coefficients: the CV, the SK, and the COR, respectively, defined below.

The CV is a measure of randomness defined as the ratio of the standard deviation to the mean,

$$\mathrm{CV} = \frac{\overline{(T-\bar{T})^2}^{1/2}}{\bar{T}}, \tag{1}$$

where and hereafter $\overline{\cdots}$ represents an averaging operation over the number of intervals, such that $\bar{T} = 1/n\Sigma_{i=1}^{n} T_i$.

The SK is a coefficient of the asymmetry of the interval distribution, defined as

$$\mathrm{SK} = \frac{\overline{(T-\bar{T})^3}}{\overline{(T-\bar{T})^2}^{3/2}}. \tag{2}$$

The COR is a coefficient of mutual dependence of consecutive interspike intervals, defined as

$$\mathrm{COR} = \frac{(\overline{T_i T_{i+1}} - \bar{T}^2)}{\overline{(T-\bar{T})^2}}, \tag{3}$$

where, T_i and T_{i+1} denote a pair of the consecutive intervals.

4. Two-sample test

Fig. 1 depicts distributions of three statistical measures CV, SK and COR, computed from the above-mentioned three kinds of spike data sets. Fig. 2 depicts the corresponding normalized histograms. In order to quantify the statistical significance of the mutual difference of those distributions, we employ here the two-sample test, which measures the sample mean difference. The t measure for the two-sample test is given by

$$t = \frac{\overline{x_A} - \overline{x_B}}{s}\sqrt{\frac{n_A n_B}{n_A + n_B}}, \tag{4}$$

where x_A or x_B stand for the statistical measures computed for the respective two groups A and B, n_A and n_B are the number of ISI sequences of 100 intervals and

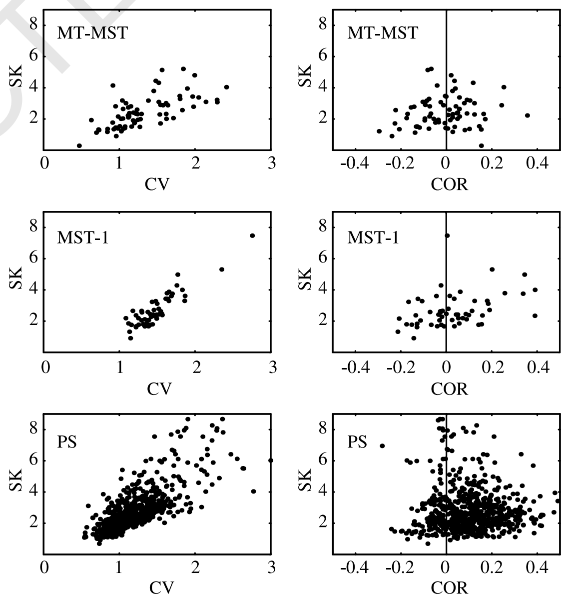

Fig. 1. Distribution of (CV, SK) and (COR, SK) values, respectively, taken from MT/MST, MST-1 and PS. Each dot represents the pair of statistics computed from100 ISIs.

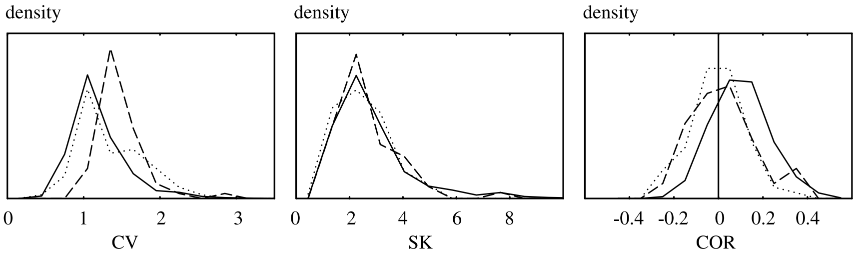

Fig. 2. Normalized histograms of three statistical measures CV, SK, and COR. Histograms of the spike data sets 1 (PS), 2 (MST-1) and 3 (MT/MST) are, respectively, shown in the solid line, broken line and dotted line.

$$\overline{x_A} = \frac{1}{n_A}\sum_{i=1}^{n_A} x_A^i, \tag{5}$$

$$\overline{x_B} = \frac{1}{n_B}\sum_{j=1}^{nB} x_B^j, \tag{6}$$

$$s^2 = \frac{\sum_{i=1}^{n_A}(x_A^i - \overline{x_A})^2 + \sum_{j=1}^{n_B}(x_B^j - \overline{x_B})^2}{n_A + n_B - 2}. \tag{7}$$

If two data sets are drawn from the same distribution, this t measure is expected to obey Student's t-distribution of the degree of freedom $n_A + n_B - 2$. In any pair of the data sets MT/MST, MST-1 and PS, the degree of freedom $n_A + n_B - 2$ is larger than 100. In such a large degree of freedom, the t-distribution is close to the standard normal distribution $N[0, 1]$. Table 1 summarizes the t values with respect to the statistical measures, CV, SK and COR, evaluated for all pairs chosen from the three kinds of data sets MT/MST, MST-1 and PS. Those t values should be compared with reference two-sided percentiles: $t = 1.7$, 2.6, and 3.3, respectively, for 10, 1 and 0.1%.

Table 1
The t-values with respect to CV, SK and COR evaluated for all pairs chosen from the three kinds of data set, MT/MST, MST-1 and PS

	CV	SK	COR
MT-MST vs. MST-1	2.40	1.20	1.61
MT-MST vs. PS	1.98	1.91	6.86
MST-1 vs. PS	4.42	0.54	3.81

For t-distribution with the degree of freedom larger than 100, two-sided percentiles for 10, 1, and 0.1% are, respectively, $t =$ 1.7, 2.6 and 3.3.

5. Discussion

By considering the t measures of entire three statistics, the pairs (MT/MST and PS) and (MST-1 and PS) can hardly be considered as drawn from a single population. In other words, PS is clearly distinct from either MT/MST or MST-1. In this way the spiking characteristics measured on the basis of CV, SK and COR reflect the nature of the recording site. The major cause of the difference is that the PS neurons exhibited large positive COR values in comparison with those of the other two areas. The positive COR is considered to reflect the slow modulation of the spike rate (see Shinomoto and Tsubo, 2001). In addition to this, it is interesting to see that mean CV values of MT/MST and MST-1 are larger than that of PS. Neurons in the MT and the MST areas exhibited higher spike rate than that of the PS areas. Though smaller CV values are naturally expected for higher spike rate, the result turned out to be opposite. This interesting result may reflect the intrinsic nature of the neurons, which constitute each area: difference of the neuronal characteristics or difference in their circumstances.

MT/MST and MST-1 are barely considered as drawn from the same population. The major cause of the difference is due to the deviation of mean CV values. But they are relatively similar with each other in comparison with the other pairs (MT/MST and PS) and (MST-1 and PS). This fact implies that a single neuron may represent the ensemble characteristics of the area, which should be determined from spike sequences of a number of neurons in the same area. In this neuron's case, we can conclude that the MST-1 statistics are definitely different from the ensemble statistics of the PS area. The problem of whether the single neuron spiking statistics represent the ensemble spiking statistics should be examined thoroughly by obtaining more sequences of multiple neurons.

The spiking characteristics may depend not only on the recording site, but also on the tasks performed, and also individual animals. In order to extract the recording site dependence of the spiking characteristics from multiple experiments, we sought the data whose experimental conditions are mutually similar. The points in common are the fact that the subject animals are same macaque monkeys and animals were in behaviorally stationary during recording. The major difference would be that the monkey is anesthetized in experiment 1 and 2 while the monkeys are alert in experiment 3. In order to determine what is the essential cause of the difference of spiking characteristics observed here, we have to lead a new experiment in which different areas are recorded from a single animal, which is repeating the same task.

6. Uncited reference

Ohno, 2002.

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