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Neurocomputing 32–33 (2000) 1013–1020

NEUROCOMPUTING

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A Bayesian decision approach to evaluate local and contextual information in spike trains

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Accepted 13 January 2000

Abstract

In this study, we applied Bayesian decision theory to evaluate the information contained in neural spike trains. We used the spike statistics from 90% of the labelled trials to classify each of the remaining unlabelled trials. Classification rate were computed at different post-stimulus time within time windows of different durations. This allowed us to visualize and evaluate the information content of the spike trains in a scale-space representation. We found that discrimination of patterns within the receptive fields of the neurons can be accomplished at an early stage of the response within a relatively small time window (5–30 ms), while the discrimination of global contextual information can be accomplished at a later time. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Scale-space; Information; Neural data analysis; Bayes decision

1. Introduction

The average firing rate of a neuron as measured in electrophysiological studies has been considered the most reliable measure in explaining the function and representation of the neuron. However, in ‘real-time’ behavior, the animal typically has to make decisions using the information encoded within a few spikes [7]. How could this be accomplished? Two possible solutions have been proposed: (1) the system could be

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taking the population average of the responses of a group of neurons within a short-time window [2,8], and (2) the exact timing structure of the spikes might carry additional and more precise information [1,3,4,6,9,10].

Here, we examined the continuum between these two extremes by evaluating the information at different time after stimulus onset within windows of different durations. We measured information by asking the question, how well could we discriminate the input stimuli based on the spike counts of an incoming spike train within a specific window, provided the statistics of the responses of the cell to all the conditions are available? Specifically, we wanted to develop a representation that allow us to evaluate the effectiveness of spike count as a neural code systematically.

2. Experiments

The data analyzed in this study was collected from single and multiple units in the primary visual cortex of awake behaving monkeys while they were performing a fixation task, i.e. staring at a red spot on the screen while the test stimulus was presented on the screen 350 ms each trial. Eighty-seven cells from two monkeys were studied (see [5] for details). Ten sessions of multielectrode recording were conducted to evaluate the information encoded in the simultaneous activities of multiple neurons. Two stimuli with a texture figure embedded in a contrasting texture surround are used. In one stimuli, the texture inside the figure is of the preferred orientation of the cell, while in the other, the preferred orientation is in the background. The receptive

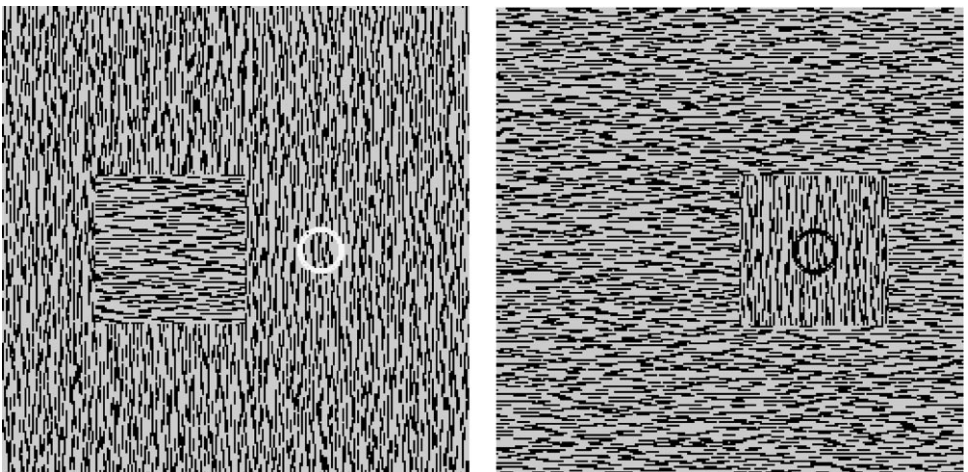


Fig. 1. The two stimuli evaluated in this paper. The actual experiment actually contained 17 pairs of figure-ground stimuli, sampling the response of the cells along the color, luminance and texture dimensions. The width of the texture square was typically 3° to 5° visual angle. The average RF size of the cells was about 0.75° . Pattern discrimination was to discriminate the textures within the RF inside the figure. Contextual discrimination was to discriminate whether the RF was placed inside the figure (black circle in (A)) or outside the figure (white circle in (B)) when the RF was 'seeing' the same vertical texture pattern.

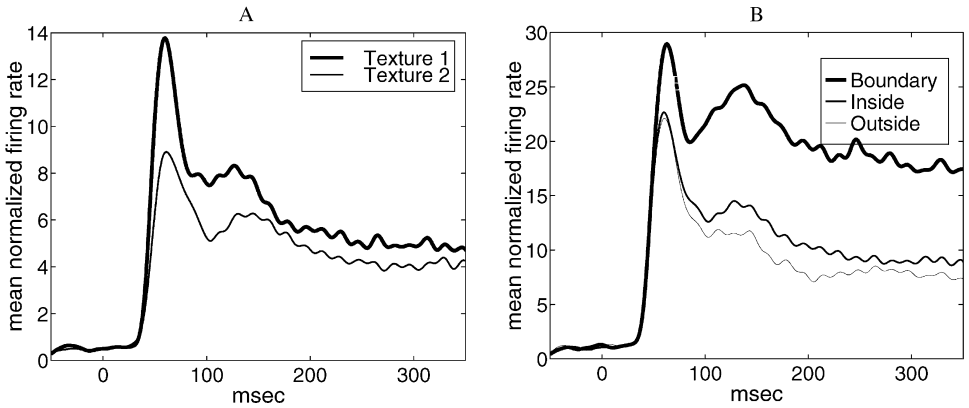


Fig. 2. Population average responses of the 87 tested neurons to different patterns (A) and to the contextual relationship (B), i.e. whether the RF was placed inside the figure or outside the figure. (see [5] for details).

field of the cell was placed in two possible positions in each stimulus image: either inside the figure or outside the figure (Fig. 1).

Earlier experiments [5] have shown that the spontaneous firing rate of V1 neurons carried different kinds of information in different stages of the response. Fig. 2 shows that as a population, the neurons could discriminate the difference between local texture during the initial responses (40–80 ms post-stimulus onset) (2A) and the inside-outside relationship 80–250 ms post-stimulus onset (2B). Here, we ask, how well can an individual neuron discriminate the local stimulus pattern and the global contextual relationship based on the spike count of one spike train within a short time window?

3. Data analysis

In this analysis, the approach we have taken is as follows. For each time window of interest, the statistics of the spike counts within the window for 90% of the trials were compiled, and a classification rule (decision boundary) was determined based on the spike count distributions corresponding to the two conditions being compared. Even though we typically collected 30–80 trials per condition to obtain a reasonable distribution, it is often useful to fit the spike-count distribution with either a Poisson distribution or a normal distribution. The selection between these two distributions is entirely based on empirical fit for each cell. Then, we can use Bayes' rule (Eq. (1)) to determine the conditional probabilities for each condition (the presence of a particular stimulus feature or a perceptual structure) given each possible spike count, where C_i is category or condition i , and x is the number of spikes

$$P(C_i | x) = \frac{P(C_i)P(x | C_i)}{P(x)}. \quad (1)$$

Table 1

Classification rate as a function of post-stimulus time and analysis window duration of a neuron (corresponds to Fig. 3a)

Window\Time (ms)	40	50	60	80	100	150	200
5	0.49	0.80	0.77	0.54	0.52	0.43	0.51
10	0.50	0.81	0.83	0.60	0.52	0.58	0.57
15	—	0.85	0.90	0.73	0.56	0.62	0.53
20	—	0.84	0.88	0.81	0.55	0.63	0.53
25	—	—	0.88	0.88	0.57	0.63	0.50
60	—	—	—	—	0.86	0.56	0.55
100	—	—	—	—	—	0.80	0.60
150	—	—	—	—	—	—	0.73

Using these probabilities, we can design a decision rule to minimize the following probability of error:

$$P(\text{error} | x) = \sum_k P(C_k | x), \quad (2)$$

where the C_k are all the categories that are not chosen.

This decision model was then tested on the 10% of trials not used in the ‘training’ of the model, and a classification rate equal to the percentage of correct classifications relative to the total number of classifications was calculated. This whole process was repeated 10 times to obtain an ‘average’ classification rate for a specific window at a specific time. Windows of various duration and at different time relative to stimulus onset were considered and compiled to produce a table of classification rates for both local pattern and global context discrimination for each neuron. In this particular calculation, we set $P(C_i)$ to be equal for all i , where $\sum_i P(C_i) = 1$. This assumed that the information contained in one window independent of the other windows and the neuron expect to encounter each category with equal frequency, i.e. equal priors. Table 1 shows a sample of two-texture discrimination classification rates of an individual neuron computed within analysis windows of various durations that end at different specific points in time.

4. Scale-space representation

The classification rates table can be displaced as a gray-scale picture, with highest rate the brightest and lowest rate the darkest. We called this the scale-space representation signature of the information content of the spike train. We have similarly used signal detection theory (receiver-operating characteristics curves) and information theory (mutual information) to compute the cell’s scale-space representation signature and found that they are roughly similar qualitatively. In this paper, we will focus our discussion to the Bayesian decision approach.

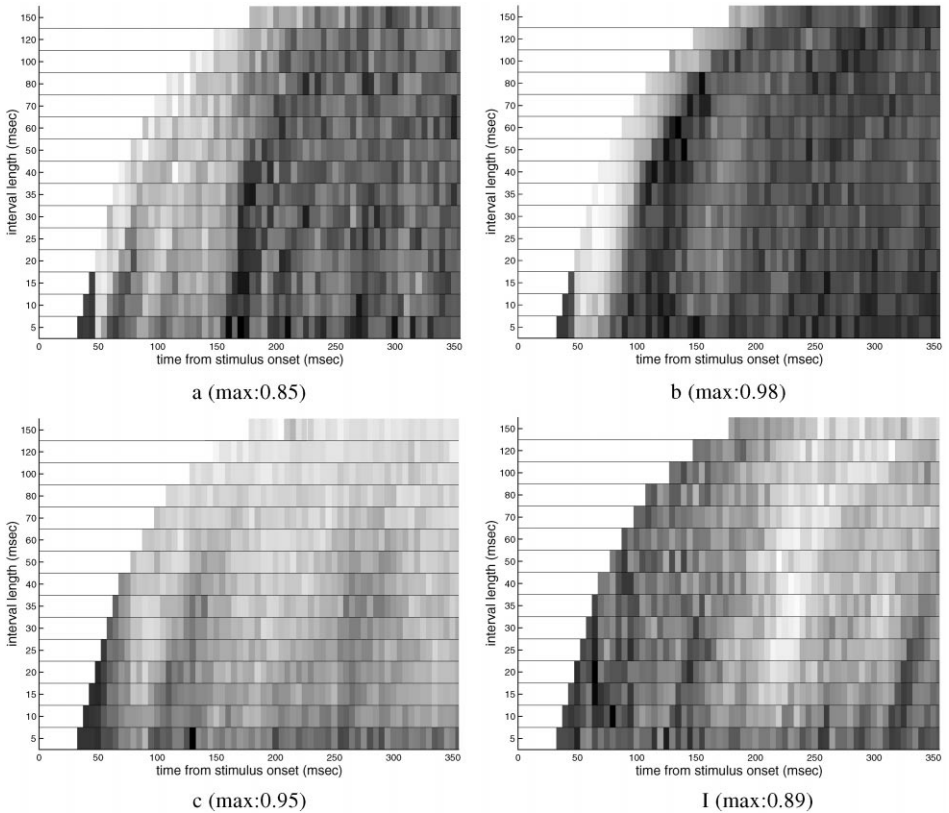


Fig. 3. Typical types of scale-time representation of the information signatures for selected neurons. Each rectangle corresponds to the rate achieved at a given time within an integration window of a particular duration prior to that time, where white represents the maximum rate achieved by the neuron, and black represents chance rate (0.5) for a two-alternative choice discrimination. Texture discrimination classification rates can be divided into five classes: (a) the rate is initially high and gradually falls over time, (b) the rate is initially high, but falls sharply around 80 ms and remains low, (c) the rate is initially high and remains consistently high, (d) (not shown) the rate increases over time, and (e) (not shown) the rate appears to reflect random classification. Figure/ground classification rates are less varied, and neurons tend to fall into either (I) the rates indicate that the neuron detects a figure/ground difference, or (II) (not shown) the rates appears to be random fluctuation about chance.

Typically, pattern discrimination was highest during the initial phase of the response. On the other hand, contextual discrimination improved slowly and often was highest around 80–200 ms post-stimulus onset, and required a much larger window of integration. But the scale-space information signatures are different for different neurons, and different for the same neurons handling different conditions. The signatures can be roughly grouped into six types: two for contextual discrimination and four for pattern discrimination (Fig. 3). The distribution of various combinations of different types of pattern and contextual discrimination signatures is shown in the pie-chart in Fig. 4.

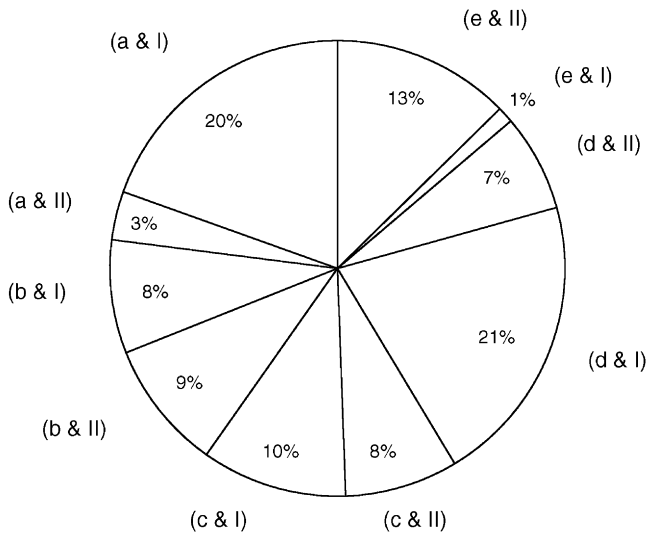


Fig. 4. Pie chart illustrating the distribution of different combinations of information signatures as detailed in Fig. 3.

Using these scale-time information signatures, we can also compute parameters relevant to understanding the necessary timing and the window size for the pattern and contextual discrimination. The earliest time and the smallest windows (defined in Fig. 5) are two such parameters. These parameters are sensitive to performance criteria. For example, the population median earliest time and shortest window to reach 90% performance are 140 and 25 ms for pattern discrimination, 185 and 25 ms for contextual discrimination. The median earliest time and shortest window to reach 80% optimal performance are 98 and 15 ms for pattern, and 160 and 15 ms for context.

When two or more simultaneously recorded neurons' spikes were used to build the Bayesian decision statistics, the classification performance in general was improved, indicating an increase in the information content. However, the recruitment of some irrelevant cells into the decision process could actually undermine the performance.

5. Conclusion

In this study, we analyzed the information of spike trains by looking at the cell's classification rate across a scale space. This gives a more precise measure of the observations that we have made earlier [5]. The basic new findings in this study are: (1) Information of different nature is richest at different specific post-stimulus time, suggesting that multiple perceptual representations might be computed or communicated at different time. (2) A 5–30 ms time window usually contains most of the

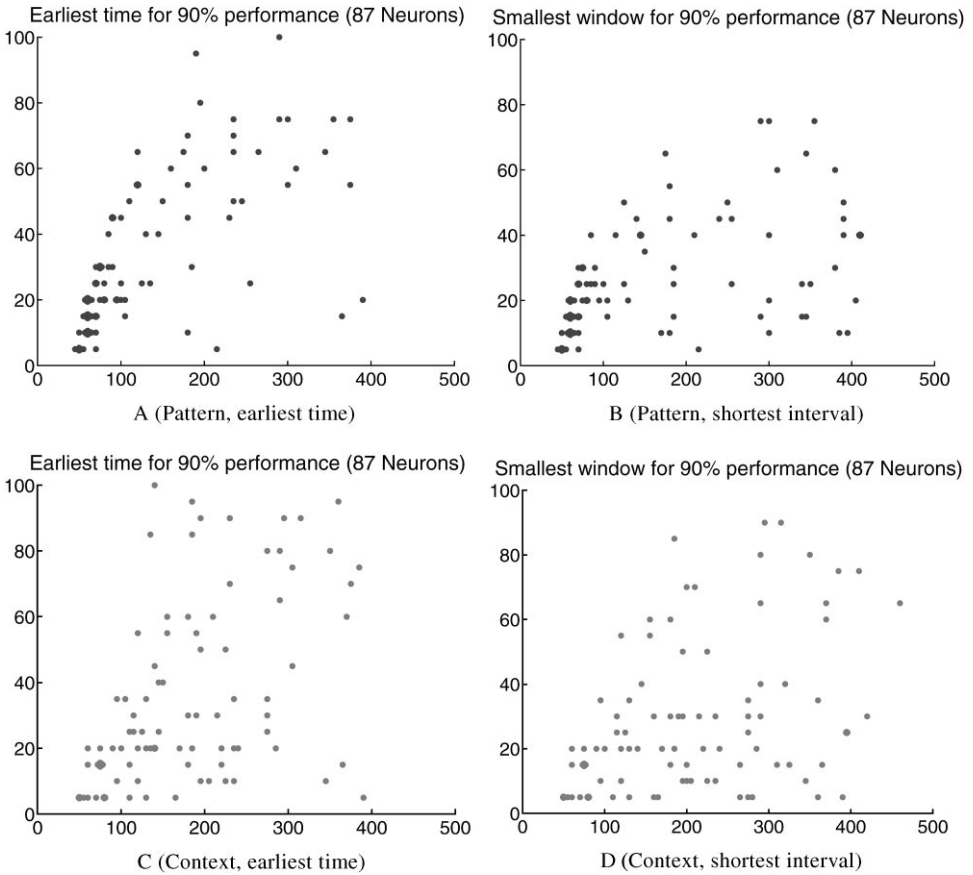


Fig. 5. Distribution histograms of the shortest and earliest intervals. Earliest time was defined as the earliest time post-stimulus onset by which the classification rate has reached 90% of its possible optimal performance, i.e. $0.9(\max - 0.5)$, regardless of window size. Smallest time was defined as the smallest window within which the classification rate has reached 90% optimal performance regardless of the post-stimulus time. We can see the clustering to the early time and small windows for pattern discrimination (A,B) and the more scatter nature of these parameters for the contextual discrimination (C,D).

information of what a cell can offer, suggesting that extensive temporal integration might not be necessary for an organism to extract the relevant information. (3) When multiple neurons are recruited into the decision process, discrimination performance in general is improved.

Acknowledgements

Lee is supported by a grant from the McDonnell-Pew Foundation, and LIS Grant 9720350 from NSF. Yan is supported by American Zhu Kezhen Education

Foundation. The research facility is supported in part by EY 08098 core grant for Vision Research to the Eye and Ear Institute of Pittsburgh.

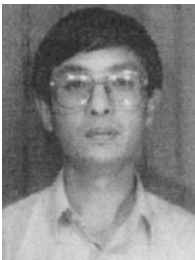
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(Lee's photo can be found in Yu and Lee's paper in the same issue).



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