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Measuring ensemble consistency without measuring tuning curves

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Abstract

An important question in information processing is the extent to which neural firing patterns remain consistent while processing representations. Transient changes in representational consistency can provide clues to the dynamics of neural processing. We present a generalized framework for measuring the consistency of a neuronal representation that does not require explicit knowledge of the parameters encoded by the ensemble. It requires only neuronal ensembles and a training set of neuronal activity that samples behavioral parameters equally. This will be useful in structures where the behavioral parameters signalled by the neural activity are controversial or unknown.

Keywords: Distributed representation; Neural ensemble; Reconstruction; Kernel density estimation (KDE)

1. Introduction

Neural representations are distributed. Therefore, to address questions about encoded behavioral parameters, recordings from neural ensembles are needed. Although such recordings are becoming commonplace, analysis methods for those ensembles remain underdeveloped. In quantifying the dynamics of neural information processing, two questions might be asked: "What value is encoded by the neural activity?", and "How consistent is the neural activity?".

A number of methods have been developed to address the first question (*reconstruction* [3,4,17]). Given the expected neural firing pattern and the current neural firing pattern, these methods attempt to infer the value of the stimulus from the ensemble

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activity. However, these reconstruction methods do not assess how well the activity supports this value. Subsets of the ensemble could be consistent with different values, yet these reconstruction methods would still report a single value regardless of the representational quality.

For example, the well-known *population vector* reconstruction method reports the represented direction of an ensemble of direction-tuned neurons as the weighted vector sum of the unit-vectors corresponding to each neuron's preferred direction, weighted by their firing rates [4]. Recognizing that this reconstruction method reports a value even with random data, Smyrnis et al. [14] applied the modified Rayleigh test to compare the values reconstructed from their ensemble firing patterns against randomness. This test only works on circular data sets and tests only for non-randomness of the distribution.

Later, Redish et al. [10] developed a more generalized measure of representational quality, which compared the weighted sum of the tuning curves (weighted by current firing rate), with an expected weighted sum (weighted by expected firing rate, for a given represented value). This measure, termed *coherency*, was capable of detecting when hippocampal ensembles realigned between two coordinate systems to an accuracy of approximately 1 s [10]. However, this measure was not mathematically or statistically justified.

In order to overcome these limitations, Jackson and Redish [5] presented a modified method based on [10] that redefined coherency to be the probability of seeing a larger difference than observed in a training set. This statistically justified approach overcame the drawbacks of the earlier method [10], but still required an explicit knowledge of the parameters encoded by the neurons. That is, the approach required that neuronal responses be completely described by classical tuning curves.

In this paper, we present a framework for measuring the consistency of a neuronal representation that overcomes the limitations imposed by requiring explicit knowledge of the parameters encoded by the ensemble. We term this measure *ensemble consistency* (EC). While the examples used in this paper all derive from a standard network model, the EC measure itself is very general. It requires only neural ensembles and a training set of neuronal activity that samples behavioral parameters and stimuli equally.

2. The network model

An attractor network made up of 75 excitatory Wilson–Cowan neurons [7,8,15] was used to generate neural data for the development of the EC method. Excitatory neurons had strong connections to other excitatory neurons with similar preferred stimuli and weak connections to neurons with different preferred stimuli. All neurons had equal projections to an inhibitory interneuron which provided uniform inhibition to the entire network. The stable state of this network is a "bump" of activity where only neurons consistent with the represented value fire maximally. This is a well-studied type of attractor network [1,6,8,15] that has been used to model a variety of neural structures, including the rodent head direction system [9,16].

This network enabled the exploration of issues in neural encoding. It allowed us to test (1) if EC could detect the difference between random and coherent network states; and (2) if EC could detect transient incoherent network states. For example, when this network is started in a random noise state, a stable bump of activity soon forms [6,8,15]. The use of simulation allowed tighter control over the dynamical states of the network, thus allowing a better test of the EC measurement. For example, with this network, a smooth rotation can be effected by chaining together a series of slightly offset inputs starting near a stable representation [8,9,11,16]. This can be contrasted with a sharp, transient instability produced by a strong input far from a stable representation [6,8,11]. Once the EC measurement is understood in the context of well-understood simulations, it can then be applied to real neural ensemble recordings.

3. Ensemble consistency

The novel coherency method presented in this paper relies on the assumption that if neurons in an ensemble are working together to represent some behaviorally relevant parameters, their firing rates will maintain the same relationships under similar conditions. Define the N-dimensional firing rate vector $\mathbf{f}(t)=\{f_1(t), f_2(t), f_3(t), \ldots, f_N(t)\}$, where $f_i(t)$ is the firing rate of neuron i at time t, and N is the number of neurons in the ensemble. If the firing rates maintain the same relationship for similar conditions, these points should be grouped in the same region of firing-rate-space.

To test the similarity of an ensemble firing pattern to firing patterns previously recorded, one has only to test the likelihood of observing that point given the previously recorded firing patterns. In this way, one can measure how consistently an ensemble responds to stimulus and behavioral conditions. We term this measure EC.

In order to measure the likelihood of observing a sample point relative to an expected distribution, we estimate the density of the distribution at the sample point. EC thus measures the probability density of the expected (i.e. previously recorded) firing patterns at the N-dimensional point defined by the ensemble firing pattern at time t.

This density estimation is commonly carried out by dividing a space into bins and estimating the average density in each bin. This method has two major problems: its memory usage can be enormous, and the resolution is limited by bin size. For example, a data set consisting of just 15 simultaneously recorded neurons at a 15-bin resolution would require 3.5 exabytes of memory (3.5 billion GB).

To overcome this limitation, we adopted the method of kernel density estimation (KDE) [13]. In this method, each point in the group is assigned Gaussian parameters to spread out its contribution to the overall density. Normalizing this distribution gives an estimate of the joint probability density distribution. The local density of the sample point can be calculated by evaluating the density contributed by each individual Gaussian in the group and summing the result. Thus, the group of training set points is transformed into a continuous estimate of the local density at the sample point. Fig. 1 shows an example for a two-cell ensemble taken from our training set.

Mathematically, we write

$$C_t = \sum_{i \in \mathscr{S}} \beta_i \exp\left(\frac{-\|\mathbf{f}(t) - \mathbf{f}_i\|^2}{\sigma_i^2} \right), \tag{1}$$

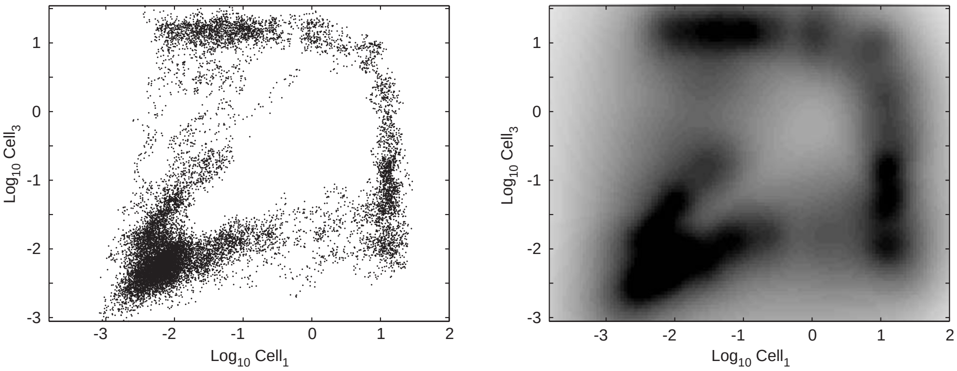

Fig. 1. Density distribution of a two-cell ensemble taken from our training set. Firing rate of cells 1 and 2 are represented by the x and y coordinates, respectively. (Left) the set of observed firing patterns $\mathbf{f}_i$. (Right) the probability density distribution resulting from variable-width Gaussian kernel density estimation on $\mathbf{f}_i$. Black represents maximum density and white represents zero probability of observing a firing pattern. Note: plot is shaded by the logarithm of the density.

where $\mathbf{f}(t)$ refers to the ensemble firing pattern of the point of interest at time t and $\mathbf{f}_i$ refers to the ith firing pattern of the expected distribution $\mathscr{S}$, also called the *training set*. β_i is the constant of normalization for the Gaussian associated with $\mathbf{f}_i$:

$$\beta_i = \frac{(\sigma_i^2)^{-(N/2)}}{\sqrt{2\pi}\; N_{\mathscr{S}}}, \tag{2}$$

where N is the number of neurons in the ensemble, $N_{\mathscr{S}}$ is the number of samples in the training set $\mathscr{S}$, and σ_i is the standard deviation associated with the ith sample of $\mathscr{S}$. Finally, we call C_t the EC since it is a measure of how consistent $\mathbf{f}(t)$ is with $\mathscr{S}$.

To improve our estimate of the density, we let β_i depend on the nth-nearest neighbor distance of $\mathbf{f}_i$. First, the nth-nearest neighbor distance $D_i^{(n)}$ is found for each training set point i using the Euclidean distance measure. The standard deviation σ_i of the Gaussian associated with $\mathbf{f}_i$ was defined as $\sigma_i = k \cdot D_i^{(n)}$. For this data set, $k = 4$ provided a good overlap between neighboring Gaussians. The order of the nearest neighbor distance, $n = 10$ was selected because the average nth-order nearest neighbor distance is very noisy for low n, rises quickly as n increases, then temporarily plateaus. The beginning of this plateau represents how closely the points in the training set are packed and serves as a good reference for choosing the order, n, of the nearest neighbor. For our simulations, $n = 10$ provided a robust density estimation.

In summary, EC is the local probability density of the N-dimensional firing rate vector at a point in time. Low probability densities represent firing patterns unlikely to occur under the conditions of the training set, and high probability densities represent firing patterns that were often seen in the ensemble under training-set conditions.

4. Statistical justification of EC

As stated before, EC measures density not probabilities. Transforming these density measurements into a probability of seeing a density less than or equal to the observed density is complicated by the fact that these densities are unlikely to be unimodal, as can be seen in Fig. 1. This multi-modality occurs because neurons have overlapping tuning curves: the firing of one cell may occur either with or without the firing of the other cell. We therefore, estimated the likelihood of observing a particular density through a "leave-one-out" approach. For each sample $\mathbf{f}_i$ in the training set $\mathscr{S}$, the density at $\mathbf{f}_i$ was measured using Eq. (1) summing over all samples in $\mathscr{S}$ except for $\mathbf{f}_i$. This provided a set of densities found in the ensemble under normal (training) conditions. These densities were used to construct a CDF of expected log-density values for one-sided significance testing. A stringent significance threshold of $\alpha = 0.001$ was used to reduce the false-alarm rate. This still provided for robust detection of inconsistent firing patterns within the ensemble.

5. Results

The training set was created by forcing a rotation of the network through the full range of directions for three revolutions and then a reverse rotation through the same number of revolutions. This sampled the parameter space evenly.

Figs. 2–4 show the results of a 15-neuron ensemble taken from the population of 75 excitatory neurons in the attractor network simulation. The cells are ordered by

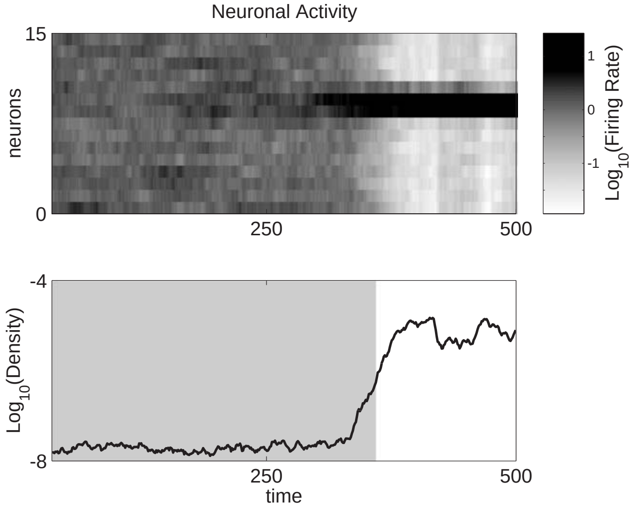

Fig. 2. A simulation started with random input to the network settles to a stable state. (Top) the neural activity. Time is shown in ms on the x-axis. Neurons ordered by their preferred direction along the y-axis, shaded according to their firing rate. (Bottom) EC. During the random state, the probability density, or EC, is low ($p < 0.001$, gray zone). Upon reaching the stable state, the EC rises ($p > 0.001$).

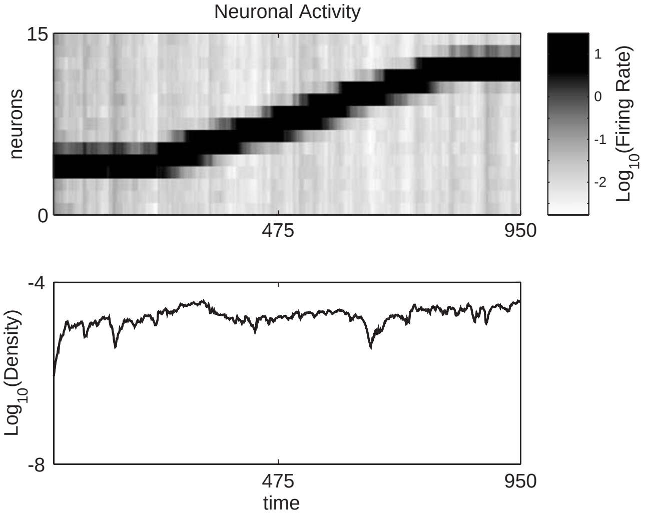

Fig. 3. EC is stable throughout a rotation. (Top) the neural activity rotates smoothly. Time is shown in ms on the x-axis. Neurons are ordered by their preferred direction along the y-axis and shaded according to their firing rate. (Bottom) EC shows a high probability density throughout the rotation ($p > 0.001$).

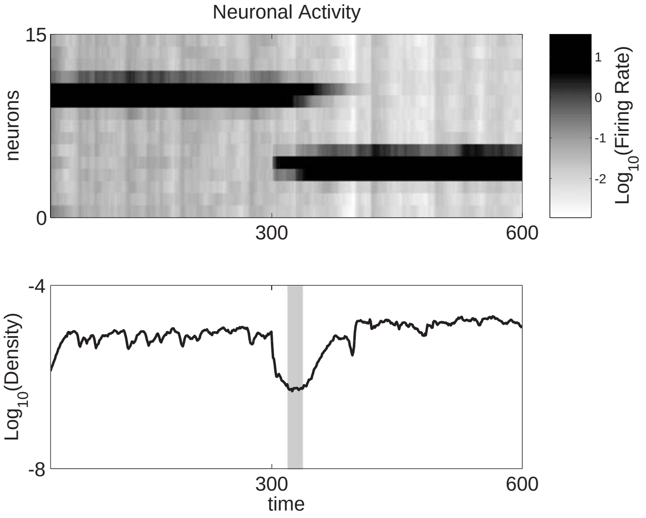

Fig. 4. EC detects a discontinuity. (Top) the neural activity jumps during a dynamic instability. Time is shown in ms on the x-axis. Neurons are ordered by their preferred direction along the y-axis and shaded according to their firing rate. (Bottom) EC shows a low probability density during the jump ($p < 0.001$, gray zone). EC is high during the stable state, before and after the jump ($p > 0.001$).

their preferred direction with the preferred direction of each neuron being 24° from its neighbor. Similar results were obtained with randomly sampled ensembles as long as the component tuning curves spanned the parameter space. Smaller ensembles were particularly dependent on fortuitous choices of the component neurons in the ensemble to span the parameter space.

Fig. 2 shows a simulation started with random activity. However, this network favors a single "bump" of activity, and soon settled to a stable state with only a few neurons in an excited state. While the network was in the random state, EC was very near zero ($p < 0.001$), but transitioning to the stable state resulted in higher densities. Thus, EC differentiated between random and stable activity.

EC was stable during a smooth rotation of the network activity (see Fig. 3). However, when the representational state jumped discontinously, EC detected the period of discontinuity (see Fig. 4). Thus, EC differentiated between a jump in the representation and a stable rotation of the network firing pattern. EC remained stable throughout the rotation (Fig. 3). During the jump, EC was near zero ($p < 0.001$, gray zone, Fig. 4), signifying a group of firing patterns far from the distribution of training set values (i.e. a dynamic instability that did not occur during training).

6. Discussion

Like the coherency measures described previously [5,10,14], ensemble consistency (EC) can be used to measure the quality of a neural representation within an ensemble. However, the EC method has two specific advantages: it does not require explicit knowledge of the neuronal response parameters (the tuning curves), nor does it require a hypothesis of the encoded value. In other words, EC makes fewer assumptions about what the neurons are encoding. Thus, it is possible to measure the consistency of the dynamic relationship between neurons in an ensemble with little or no knowledge about what they encode.

Instead of making assumptions about the encoding, EC measures the dynamic relationship between neurons by using a density estimate to measure how similar the current firing pattern is to other firing patterns observed in the training set. In this way, EC is like an abstracted method of generalized template matching. This density measure is sensitive enough to detect critical changes in state, so as to differentiate between a rotation and a jump or between a stable representation and random noise.

EC is limited, however, by its sensitivity to the training set. Because there is no normalization for the number of training set points collected for each stimulus, EC requires an even sampling of parameter spaces. Otherwise, densities of some firing patterns could be over- or underestimated. But, it is important to note that many behavioral tasks can be constructed such that the animal evenly samples the entire parameter space on every trial. For example, Schmitzer-Torbert and Redish [12] use a continuous $\top$ maze which requires the animal to make a series of $\top$ choices before receiving food reward along a return ramp without turning around. This required the animal to sample each portion of the task equally on each lap. Averbeck et al. [2] recorded ensembles from monkeys copying geometric shapes. Each component of the shape was sampled equally on each trial. Finally, this restriction only applies to the training set. Thus, a rat running a circular track will sample all head directions equally. Using the circular track as a training set, EC could be used with ensembles of head-direction cells to examine questions in an open-field in which directions are not sampled equally.

Our examples in the results section were based on 15-cell ensembles. The key to smaller ensembles is how well the neuronal responses span the parameter space. EC is not dependent on uniformity of the neuronal responses. Thus, an ensemble with tuning curves that span the space of potential stimuli, but are not uniformly distributed will provide a sufficient basis for the EC method.

In summary, the EC method can assess the consistency of an ensemble with little or no knowledge of the neural encoding. This is a powerful method for examining learning in structures that have complex representations of cognitive function and may be especially useful for examining deep brain structures where the behavioral parameters signalled by the neural activity are controversial or unknown.

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