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MAXIMUM DECODING ABILITIES OF TEMPORAL PATTERNS AND SYNCHRONIZED FIRINGS: APPLICATION TO AUDITORY NEURONS RESPONDING TO CLICK TRAINS AND AMPLITUDE MODULATED WHITE NOISE

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ABSTRACT

Simultaneous recordings of an increasing number of neurons have recently become available, leading to a renewed interest in cell assemblies. However, so far few methods have been proposed to handle multiple-neuron activity. In this paper, we extract and investigate all the possible temporal neural activity patterns based on synchronized firings of neurons recorded on multiple electrodes, or based on bursts of single-electrode activity in cat primary auditory cortex. We apply this to responses to periodic click trains or amplitude modulated (AM) noise by obtaining for each pattern, comprising both overall firing rate and synchronized rate, its temporal modulation transfer function. An algorithm that maximizes the mutual information between all patterns and stimuli subsequently leads to the identification of patterns that optimally decode the stimulus repetition rate or modulation frequency (MF). We show that temporal stimulus information contained in multi-electrode synchronized firing or spike bursts is not redundant with single-electrode firings and leads to improved efficiency of MF decoding. We also show that the combined use of firing rate and temporal (phase-locking) codes leads to a better discrimination of the MF, mostly because firing rate is able to code higher MFs (>16Hz) than the temporal code. Spike bursts might be more efficient than synchronized firings to discriminate low MFs. Finally, we show that even the combined use of firing rate and phase-locking leads to poor MF coding, which implies that other codes may be actually used by the brain for processing temporal stimulus features.

KEY WORDS

Cell assembly, multiple-neuron activity, neural code, mutual information, temporal modulation transfer function

1. Introduction

According to Donald Hebb, stimuli, objects, but also more abstract psychological entities like concepts, contextual relations, ideas, are represented in the brain by simultaneous activation of groups of neurons that he referred to as cell assemblies [1]. The

neurophysiological substrate from such a strong hypothesis ensues from the fact that “neurons are natural recognizers of synchrony” [2], favoring coincident presynaptic events over asynchronous ones to generate an action potential [3, 4]. As a consequence of this behavior, it also appears that synchronized firings from several neurons feeding the same postsynaptic neuron have a higher probability to activate it, leading subsequently to the propagation of synchronous spiking [5, 6]. However, one single neuron may possibly belong to several cell assemblies, each of them involving an unknown number of neurons, not to speak of the unclear role that shared inputs play in the observed synchronization between neurons. Thus, the probability to identify, observe and describe a full neural network in the brain with only at most a few dozen of extracellular recordings is extremely low. Moreover, studying even a small set of neurons requires the analysis of thousands of possible combinations.

There have been numerous proposed analysis methods for multiple (>2) spike-train recordings in the past thirty years. At first, some studies proposed to identify the most relevant assemblies among simultaneous recordings, mainly by extracting subsets of neurons whose simultaneous firings happen significantly more or less often than if these neurons were independent. Gerstein firstly introduced such a method [7] based on an accretion process: after selecting pairs of functionally related neurons, a χ^2 test is used to add a third neuron to each pair, then the process is iterated as long as the test raises significant relationships. Amazingly, this study found little response and was not cited by Gerstein himself or Brown et al. in their recent reviews about neural assemblies [8, 9]. It is likely that a straightforward interpretation of the properties of such extracted neurons groups was not as easy or relevant as initially expected, but the basic tenets remain interesting. Spike-pattern classification methods can be considered as modern versions of Gerstein’s algorithm [10-14]: n parallel spike trains are binned as a sequence of 1s and 0s if there is a spike or no spike in the bin. A pattern is then defined as a vector of channels composed of 0s and 1s at a given time. The patterns that occur significantly

more often than when the spike trains are independent are retained.

Decoding algorithms are also used to study the neural representation of an external stimulus: typically, a group of neurons is supposed to have encoded part of the external stimulus (for instance through spectro-temporal receptive fields); mathematical functions predicting at best the stimulus from the neural recordings are then searched. Such approaches mainly focused on representation or prediction of movements, localizations or visual analysis [15-21].

The purpose of this paper is to propose a methodology for theoretically estimating the amount of information about a set of stimuli, in the Shannon sense, contained in single-neuron spikes, single-neuron spike bursts, and synchronized firings. Our method, which is both a spike-pattern classification method and a decoding algorithm, focuses on the time dynamics of the synchronized firings through use of their PSTH. We apply this method to the ability of small (< 32) neuronal groups in cat primary auditory cortex (AI) to code the temporal properties of periodic click trains and amplitude modulated (AM) noise.

With this method, we show that most of the information about repetition rate or amplitude modulation is contained in single-unit spike bursts, or in the firings of at most two or three synchronized units, suggesting that multiple spike train analysis methods should mainly focus on pairs or triplets of neurons. We also found that the information carried by synchronized multi-channel activity or single-neuron spike bursts is not redundant with information carried by single channel firings. We show that the activity that is phase-locked with the stimulus carries on average more information about the modulation frequency (MF) than firing rate, even if this information does not involve the same range of MFs.

2. Methods

2.1 Analysis of neural assemblies

The Fig. 1 synthesizes the framework for analysis of neural assemblies based on coincident firing.

Step 1: from P stimuli and N spike-trains, we first extract all the temporal patterns of channels that are synchronously activated (frequent episodes in event sequences, APRIORI algorithm [22-24]). Three rules are applied to limit the combinatorial explosion:

- 1) a pattern must appear more than $d1$ times per second;
- 2) the pattern must not last more than $d2$ ms;
- 3) the same channel must not appear more than $d3$ times in the same pattern.

Step 2: the purpose of this step is to extract parameters characterizing the average temporal response of patterns (extracted in Step 1) to individual stimuli. In the case of click trains or AM noise, we use the modulation transfer function (MTF) which is the strength of the response of a single channel or pattern, as a function of the MF. In order to compute MTFs for each pattern, we form its Peri-Stimulus Time Histogram (PSTH), which is the temporal response of the pattern triggered by the stimulus. We then define two types of MTFs for each pattern: 1) based on the firing rate (FR) at each MF, i.e. the PSTH average: rMTF, and 2) based on the strength of phase-locked response to the stimulus: tMTF. To estimate the tMTF, we compute, for each MF f_j , j being the stimulus number, the absolute value of the Discrete Fourier Transform (DFT) of the PSTH, evaluated at frequency f_j . This is the Synchronized Firing Rate (SR).

Step 3: we then compute the matrix of each parameter as a function of the 21 different stimulus click-repetition rates or amplitude-modulation frequencies, concatenated for all patterns. In our case, this is the matrix of temporal modulation transfer functions

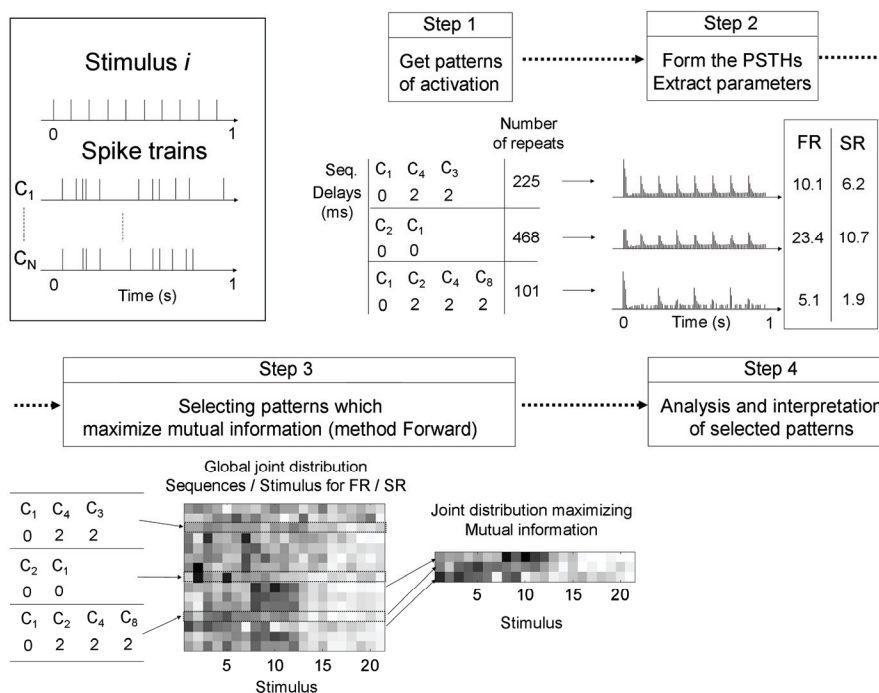


Fig. 1: framework for analysis of neural assemblies based on coincident firing (see methods).

(MTFs) based on FR and/or SR for all patterns available. This matrix allows computing the Mutual Information (MI) between the patterns and the stimuli. We then use a Forward method to select the patterns maximizing the MI.

Step 4: the maximum MI as well as the patterns selected can suggest interpretations about how the neural assembly may decode the stimuli.

2.2 Materials

We use 87 sets of multi-electrode recordings obtained from the primary auditory cortex (AI) of 47 ketamine-anesthetized cats. Each set of recordings was obtained with either two arrays of 8 microelectrodes, arranged in a 4x2 pattern with 0.5 mm separation between electrodes, or two arrays of 16 microelectrodes, arranged in a 8x2 pattern with 0.25 mm electrode separation within the row and 0.5 mm separation between rows. The arrays were independently inserted into the auditory cortex. The depth of recording was between 600 and 1,200 μm and thus the electrodes were likely in deep layer III or layer IV. Finally, we have 87 sets of at most 16 or 32 spike trains obtained in response to both periodic click trains and AM noise (broadband Gaussian noise with sample frequency 97.7kHz).

3. Results

We choose $d1$ as the maximum of 0.5 per second and 15% of the average firing rate of all channels. We also choose $d2 = 10$ ms and $d3 = 4$.

3.1 Global results: patterns analysis

Several parameters may affect the number of patterns found for each electrode array. At first, the average FR is obviously positively correlated with the number of patterns found (Fig. 2A). The number of patterns is also proportional to the number of channels considered (Fig. 2B), at least up to 16 channels. The MF has less influence on the number of patterns (Fig. 2C). Interestingly, more patterns are generally found under evoked conditions (click trains or AM noise) compared to the silence condition, a concatenation of the 21 two-second silent periods following each click train or AM noise burst.

The patterns found during silence constitute at most 85% of those found during stimulation, and the number is independent of the MF. For any MF, click trains and AM noise generate the same patterns only in 60% of the cases (unshown results).

Surprisingly, the patterns found during stimulation with AM noise are larger than during stimulation with click trains (Fig. 2D), i.e. are frequently composed of more channels or more repetitions (bursts) of the same channels.

The proportion of patterns that are only composed of contributions from different channels decreases with the size of the pattern (Fig. 2EF). In other words, large patterns tend to be mainly composed of repeated activity from the same channels. This indicates that temporal sequences with activity from more than 3 recording sites out of 16 or 32 channels are not occurring consistently. The typology of patterns is also not very different for click trains and AM noise.

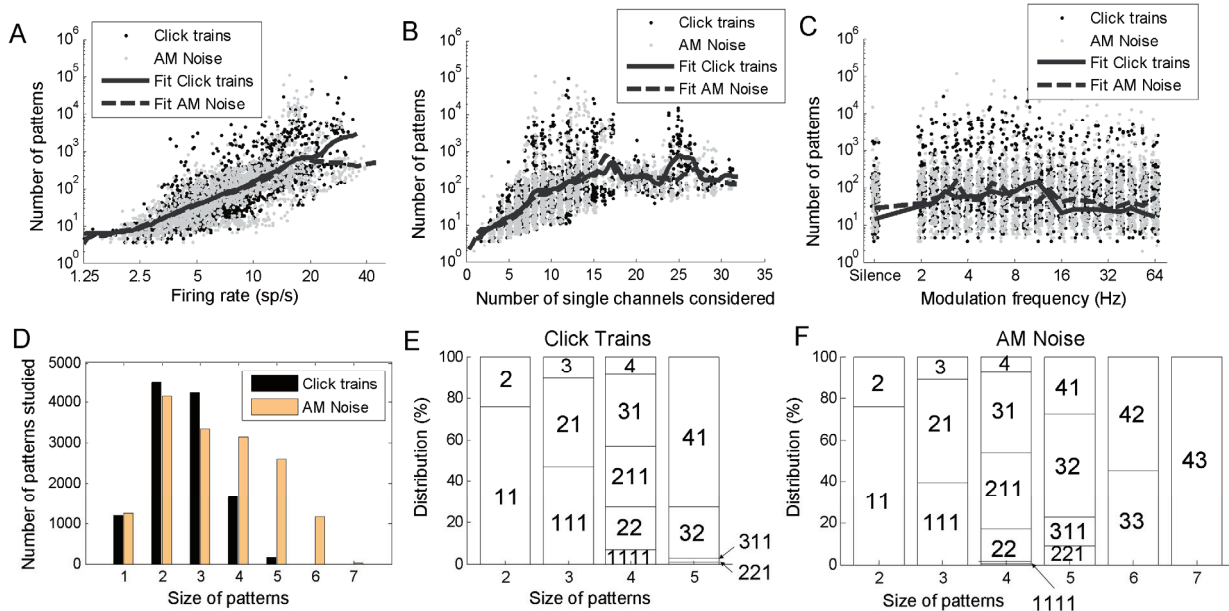


Fig. 2: statistical analysis of patterns extracted. (A,B,C): Influence on the number of patterns found for each set of recordings of (A) average single channel firing rate, (B) the number of single channels considered, and (C) the MF of the click trains or the AM noise as well as for silence. In (A), all MFs are included. (D): Number of patterns studied as a function of their size for click trains and AM noise. (E,F): Distribution of the channels contributing to each pattern as a function of the size of the pattern in response to (E) click trains and (F) AM noise. All the MFs for click trains and AM noise, as well as silence are included. The sequence of numbers represents the number of repeats of one or several channels within the pattern. As an example, 221 stands for a pattern of size 5 that is of the type (Ci,Ci,Cj,Cj,Ck), i.e., with channel Ci contributing twice, channel Cj contributing twice, and channel Ck contributing once in any sorting.

3.2 Global results: Modulation Transfer Functions

Most Best Modulation Frequencies (BMFs, peak frequency of the MTF) obtained from either rMTF (FR of the pattern as a function of the modulation frequency) or tMTF (same for SR) for click trains or AM noise are within the interval [4-16] Hz (Fig. 3AB). For the FR condition, more than 20% of patterns show a $BMF > 32$ Hz in response to AM noise compared to 5% in response to clicks. Moreover, there are no patterns showing a best synchronization rate at $MF > 16$ Hz in response to either clicks or AM noise. Consequently, 16 Hz can be considered as a cut-off frequency for the phase-locked response in primary auditory cortex of anaesthetized cats. Finally, BMFs found in response to clicks are slightly higher than those found under AM noise (Mann-Whitney test, $p < 0.05$).

The degree of phase-locking or synchronization (estimated by the vector strength equal to the SR divided by the FR) reaches a peak around a MF of 8 Hz for neural response to click trains (Fig. 3C) and this peak is sharper for larger patterns. This means that complex patterns appear more likely at the time of the click, i.e. are stimulus triggered. The triggering effect of the stimulus is less visible for AM noise than for click trains.

3.3 Global results: Optimal patterns

Optimal patterns are those for which rMTF or tMTF was selected by the Forward Selection algorithm, i.e. the most informative ones. The simplest patterns, composed of, possibly repeated, activity of a single channel, represent 77.1% (click trains) and 81.4% (AM noise) of the total number of optimal patterns. No pattern size larger than 5 or including more than 3 different channels generates an optimal MTF (Fig. 4A).

The increase in MI decreases with the size of patterns (Fig. 4B). The increase in MI obtained when including patterns of size > 3 never exceeds 10% at most.

The average of optimal MTFs (Fig. 4CD) reveals that FR-based code is more efficient to discriminate high MFs than SR-based one.

Generally, SR (tMTFs) contains more information about the MF than FR (rMTFs), whatever the stimulus (Fig. 4E). Similarly, the association of tMTF and rMTF, i.e. using both types of codes, allows an even better discrimination of the MF (Fig. 4F).

The number of optimal MTFs is little correlated with the number of MTFs considered (Fig. 4GH). In most cases, less than eight optimal MTFs are needed to reach the maximum MI. Given the similar properties of MTFs in general and given that unselected patterns represent 95 to 99% of total patterns, this suggests that there is a huge redundancy among the responses to temporal modulations (click trains or AM noise).

The optimal MTFs are not the same for stimulation with click trains and AM noise: only 11.6% of the optimal MTFs are shared by both stimuli (unshown result).

We have no way of knowing how the optimal MTFs or even all the MTFs, which describe the sensitivity of associated patterns to periodic sounds, are actually used in the process of categorizing a sound as a function of its temporal features. However, the values of MI after maximization (Fig. 4BEF) indicate that MF is at best poorly coded by FR and SR even when all single channels or combinations between channels are used.

Generally, the fact that some parameters are more efficient than some others to code a given stimulus (like

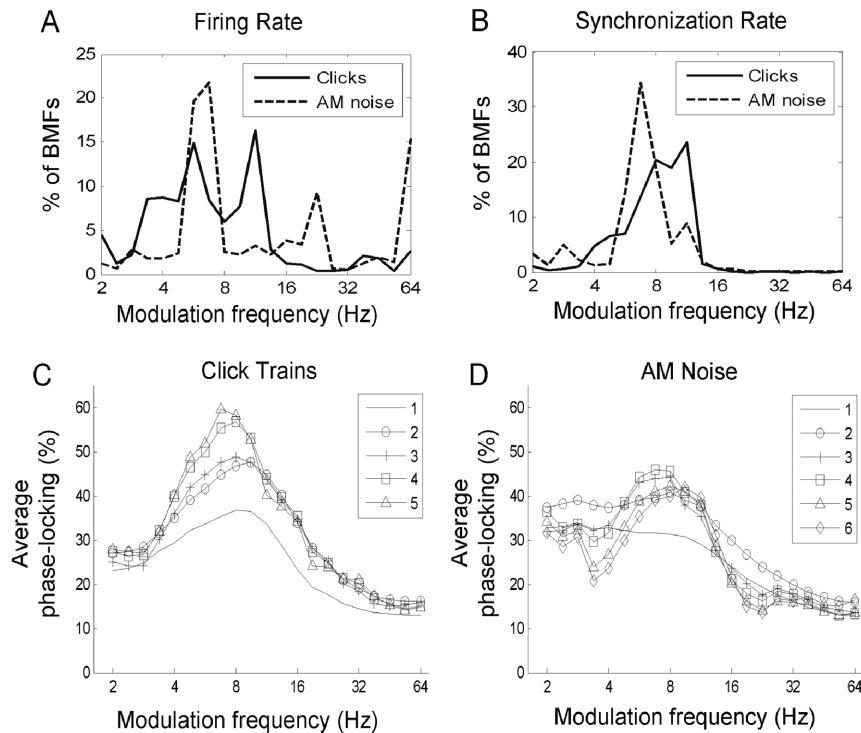


Fig. 3: statistical analysis of MTFs extracted. (A,B): Best Modulation Frequencies (BMFs) of each MTF obtained from (A) firing rate and (B) synchronization rate in response to clicks (solid line) and AM noise (dash line). (C,D): Mean of the percentage of spikes phase-locked to (C) the click train and (D) the AM noise as a function of the MF, for patterns

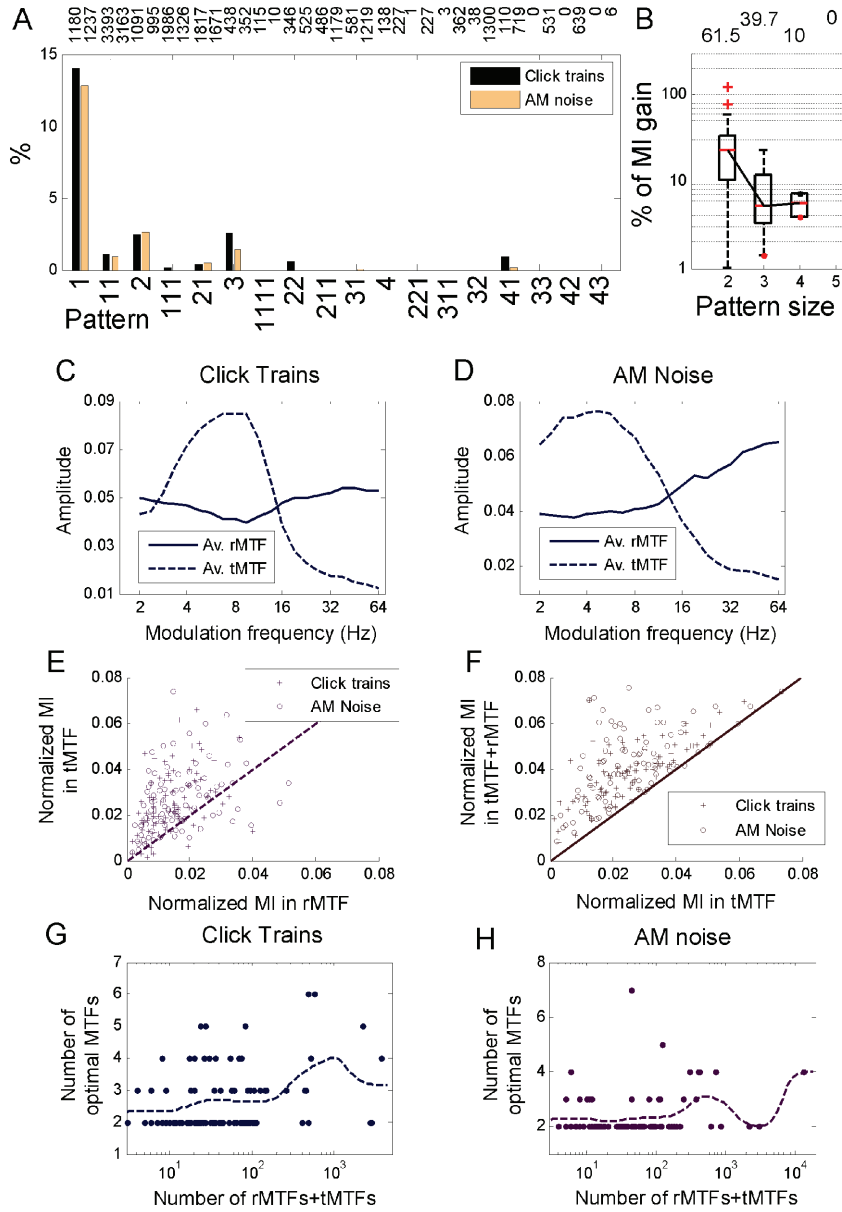


Fig. 4: statistical analysis of optimal patterns. (A): percentage of optimal patterns of each type relative to the number of initial MTFs indicated on the top of each bar. The types of the patterns are the same as those considered in Fig. 2. (B): Boxplots of increase of MI when patterns of size $\leq s$ are included compared to the MI reached when patterns of size $\leq s-1$ are only considered. (C,D): average optimal MTFs for (C) click trains and (D) AM noise. Each optimal MTF had been rescaled such that its sum over the MFs is equal to 1. (E,F): Maximal MI decoded by FR or SR based codes. (E): MI contained in tMTF as a function of MI contained in rMTF. (F): MI contained in tMTF and rMTF as a function of MI contained in the only tMTF. The dashed line is the diagonal. (G,H) number of MTFs maximizing the MI with the stimuli as a function of the number of MTFs (FR and SR taken into account) considered for (G) click trains and (H) AM noise. The dotted line represents a nonlinear regression of logarithm of data in abscissa (window=0.5). A logarithmic scale is used in the abscissa.

SR compared to FR in our study) may lead to the extrapolation that the brain might be using a version of this parameter, even modified, to actually code the stimulus. The result may give a direction to future investigations, but is not a physiological proof of the actual mode of processing in the brain.

4. Conclusion

In our study, the use of PSTHs constructed from temporal patterns involving one or more recording channels provides an insight in the statistics of temporal dynamics among sets of neurons. The combinatorial explosion is a problematic issue but for now it remains the main way to investigate real brain processing. Our results indicate that the information carried by pairs of neurons or short bursts is not completely redundant with that carried by single neurons. There is no clear

evidence that the synchronized firings of more than two or three channels are more efficient to discriminate MFs than single channels or pairs of channels, at least between isolated neuron groups sampled by recording arrays.

We believe that the four-step framework described here (pattern extraction, PSTHs computation, parameters estimation, MI maximization) is not specific to our study and can be applied to other auditory stimuli like vocalizations or tones, or other types of sensory stimuli, maybe by using other parameters in addition to FR or SR. This may lead to potential identification of crucial parameters efficiently coding sensory stimuli.

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