BURST SPIKING AS A NEURAL CODE IN INSECT AUDITORY RECEPTORS

Hugo G. Eyherabide[1,2], Ariel Rokem[2], Andreas V M Herz[2] and Inés Samengo[1]

1: Instituto Balseiro and Centro Atómico Bariloche, San Carlos de Bariloche, Argentina.

2: Institute for Theoretical Biology and Bernstein Centre for Computational Neuroscience Berlin, Germany

SUMMARY

Based on the characteristics of the ionic channels that compose the cellular membrane, some neurons have a tendency to alternate high frequency periods, with silent intervals. This is called burst firing. In order to characterize the type and amount of information transmitted through burst firing in sensory systems, the activity of grasshopper acoustic receptor neurons was recorded, for several stimulating sound waves. The analysis of these data reveals that the probability of generating bursts is strongly influenced by the statistical properties of the acoustic stimulus. Hence, the tendency to burst is not only determined by intrinsic neuronal properties, but also by the way in which those properties interact with the temporal structures in the stimulus.

These findings imply that there is a selective correspondence between specific stimulus features and particular response patterns. We characterized this correspondence, showing that bursts containing a specific number of spikes are usually found shortly after stimulus segments that share common features, and reciprocally, bursts containing different number of spikes are associated with stimuli that are qualitatively different from each other. Hence, the number of spikes in a burst conveys information about specific characteristics of the stimulus. In addition, the time at which a burst is initiated allows one to locate the relevant stimulus in time. In order to provide a quantitative measure of the relevance of burst firing in information transmission, we developed a new method to quantify the mutual information rate between stimuli and responses. We find that bursting grasshopper receptors encode 47% of the total information they transmit in burst-like patterns.

Experiments

were conducted on adult *Locusta Migratoria*. These grasshoppers communicate by means of species-specific songs which are broadband carrier signals, amplitude modulated. The behavioural response of them is related to the shape of the amplitude modulation. The stimuli used in the experiments were low-pass filtered Gaussian noise with different cut-off frequencies and standard deviation. Spike trains in response to these stimuli were recorded intracellularly from the axons of auditory receptor neurons. Each cell was tested with two or more stimuli resulting in a set of 132 experiments.
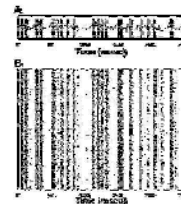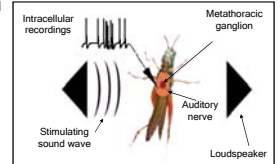

In the figure, both spikes and bursts are often observed shortly after a stimulus upstroke. Moreover, whereas fairly shallow stimulus excursions are followed, at most, by a single action potential, the deflections that are more pronounced (either in height or in width) are often accompanied by short sequences of 2 or 3 spikes. Panel B shows the response of the same neuron in panel A to 165 identical repetitions of the stimulus.

Bursts are highly reproducible across trials, which suggests that burst spiking may play a relevant role in the transmission of sensory information.

Burst classification

was assessed by defining a limit value of the inter-spike interval (ISI). It comes from the analysis of the peak structure of the autocorrelation function show in the figure. The right minimum at the initial peak was set as the limiting ISI, given that it is significantly different from the maxima immediately at both sides. Significance was estimated taking into account the uncertainty due to limited sampling.
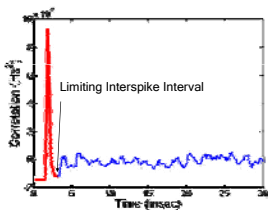
An n-burst is defined as n consecutive spikes which inter-spike intervals are lower or equal to the limiting ISI.

The neural response was segmented into sequences of n-bursts, elicited at the time of the first spike inside them, as we show in the next figure (same neuron from section EXPERIMENTS).

Colour identification
1-bursts=isolated spikes
2-bursts
3-bursts
4-bursts
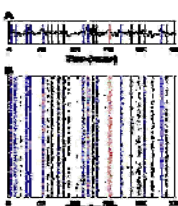
This automatic algorithm gives more power for calculating the limiting ISI than previous work based on naked eye techniques, and a quantitative measure of the significance.

Bursts code stimulus features,

which, for the same neuron and stimulus, depends on the number of spikes of the burst. The figure at the upper left shows the n-BTA (n-burst triggered average) of an example cell, for four different values of n. Thick lines in a particular n-BTA means that at that time, it is significantly different from all the others, assessed by multiple two-tailed t-tests, which shows that n-BTA at significantly different for most of the times inside the central peaks.

Both height and width increase systematically with the order of the burst. The mean latency, defined as the temporal interval between the maximum of the central peak and the time at which the burst is fired, decreases with the order of the burst.

Lower left figure shows the standard deviation of the stimulus distributions that elicit n-bursts. The minima coincides in time for all of them.
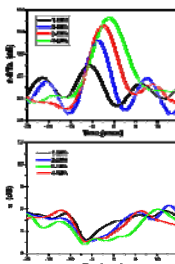
77% of the experiments show n-BTA' significantly different (time to time) from each other, and similar behaviour: increasing height and width, and decreasing mean latency with the order of the burst, while the minimum standard deviation for the stimulus distribution stands at the same time.

The shapes of the n-BTAs indicates an association between up-and-down excursions of the stimulus preceding n-burst and the n-burst generation. Among several possible dependencies of the probability of generating burst, we estimate the probability P(n|h) of generating an n-burst given the previous upward stimulus excursion of height h, shown in the figure at the left. There is a partial segregation between the responses elicited by deflections of different heights.
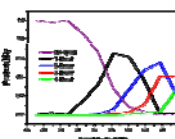
Previous works have considered differences in the messages transmitted by bursts and isolated spikes. What is new here is the evidence that the simple consideration of the number of spikes contained inside a burst leads us to a better description of the messages coded by them.

The stimulus features coded by bursts are associated to the order of the burst (the number of spikes that it contains).

Information coded by bursts

is quantified by a method developed by Brenner et al (2000), calculating the average amount of information transmitted by each individual n-burst. The total information transmitted is the sum of the information transmitted by the individual events, supposing that they are independent from one another. Evidence supporting independence comes from the reduction of the Pearson correlation coeficient when we consider the sequence of n-bursts, as shows the figure at the left.
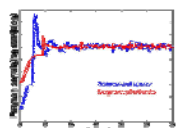
n-Bursts are considered as independent.

Brenner's information per burst is shown in A. The larger the order of the burst, the higher the amount of information (found in all bursting cells). The information per event is large when the event happens rarely (see B), it is reproducible on different trials, and is temporally accurate (the jitter in the trial-to-trial variability is low (see C)). In all the bursting cells, the fraction of n-bursts was a decreasing function of n, and in 80% of them the jitter was not significantly dependent on n.

The information rate of n-bursts (D), assuming independence, is the information carried by each n-burst (A) multiplied by its rate of occurrence (proportional to B). Although isolated spikes (n = 1) are the ones that have highest information rates, 69% of the total information transmitted by this cell was encoded in higher order bursts (n > 1). The population average of this porcentage among all bursting cells is 47%.

The procedure here introduced allows one to calculate mutual information rates between time-dependent stimuli and neural responses in a very simple and straightforward fashion. Two assumptions have been made: the independence of different n-bursts from one another, and the irrelevance of the timing of subsequent spikes inside an n-burst (only the first spike was taken into account). Our results are highly correlated with those of the direct method with the NSB correction for limited sampling.
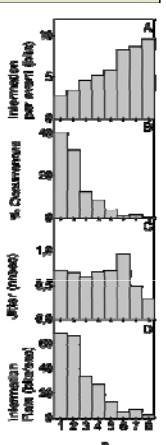
The timing of the first spike and the number of spikes in a burst are the main response features encoding the information about the stimulus.

The two aspects that seem to be relevant to information transmission (namely, the time at which a burst is initiated and the order of the burst) would also be good candidates to represent what in the literature has been distinguished as the *what* and the *when* in the stimulus. Bursts containing different number of spikes are associated to stimulus deflections of different heights and widths. In other words, n provides qualitative information about particular features of the associated stimulus deflections. Also, the time at which an n-burst begins indicates *when* the corresponding stimulus deflection took place. The two aspects, however, are somehow inter-wound, since the latency has a certain dependence on n. That is, in order to decode *when* a given deflection took place, in addition to the time at which the burst began, one also needs to know the order of the burst (which, in turn, implies something about the *what*). In the present system, hence, there is an appreciable number of cells encoding a large fraction of the information about the stimulus in the form of stereotyped packets of action potentials. As a rule of thumb, the temporal location at which a given burst is generated tags a particular point in time when a relevant feature in the stimulus took place, whereas the duration of the burst provides a qualitative description of that feature. We have analyzed those features, and also proposed an approximate method that allows to easily calculate the information rate that is transmitted by each type of burst.