A Burst Duration Code in the Thalamus

Adam Kepecs*, S. Murray Sherman† and John E. Lisman*

* Volen Center for Complex Systems, Brandeis University, Waltham, MA
02254-9110, USA; † Department of Neurobiology and Behavior, SUNY at
Stony Brook, Stony Brook, NY 11794 - 5230, USA
E-mail: kepecs@brandeis.edu

Many types of neurons fire brief high-frequency bursts of action potentials. Bursts are not entirely sterotyped and it has been proposed that burst duration may be a neural code. We tested this hypothesis by analyzing *in vivo* recordings from thalamic relay neurons, which have well characterized intrinsic burst mechanisms. Our results show that burst duration, the number of spikes per burst and the interspike structure of bursts all systematically depend on the visual input, demonstrating the existence of burst duration coding. We also show the interspike structure of this burst code allows differential decoding at different cortical layers. Based on these findings we propose that short bursts (< 20ms) of spikes are useful for rapid discontinuous signalling, in contrast to the continuous encoding provided by tonic, single spikes.

Intoduction

Thalamic relay cells can fire in either burst or tonic mode [18]. Here we examine thalamic relay cell signalling in the burst mode. We analyzed data obtained from the lateral geniculate nucleus of anaesthetized cats using extracellular electrodes [16]. Receptive fields were localized and stimulated with stationary sinusoidal gratings having randomly modulated contrast. Figure 1a shows an example of the contrast modulation and the simultaneously recorded spike train. Thalamic bursts are generated by T-type calcium currents, which require hyperpolarization of the membrane to become deinactivated [10]. Based on this requirement for thalamic burst generation,

1

previous studies established criteria to differentiate extracellularly recorded bursts from groups of single spikes [7, 11]; bursts can be recognized as high-frequency clusters of spikes (interspike intervals below 6 ms) preceded by at least 100 ms of silence. The number of spikes in each burst varied from 2 to 6, while the duration varied from 3 to 20 ms (Fig.1b,c).

Multiple encoding of burst duration

We analyzed the interspike interval structure within bursts and found that bursts have a rich and stereotyped substructure. During a burst, the progressive interspike intervals (ISIs) get longer (Fig 2a). This is shown for 5 spike bursts, but the trend was present for all bursts. Furthermore, the first ISI decreases as the number of spikes in the burst increases (Fig.2b) and this was also true for other ISIs when present. However, this relationship inverted for the last ISI, which increases for long bursts (Fig.2c). Therefore longer bursts have both higher and lower frequency components than shorter bursts. Overall, this results in a burst duration that is directly proportional to the number of spikes in the burst (Fig.2d). Similar patterns of burst substructure were observed in all cells (Fig.2e). Taken together these findings show that the burst generation mechanism produces a correlation between the interspike intervals, the number of spikes in the burst and the total burst duration. Throughout the rest of this paper these properties are referred to simply as *burst duration.*

Encoding visual stimuli with burst duration

To determine whether burst duration encodes the visual stimulus, we performed reverse correlation analysis. Figure 3a shows examples of the mean preceding visual stimuli that triggered bursts of different durations. To examine whether these average waveforms vary systematically we determined the peak contrast for each burst duration and the slope of the contrast at the time where the stimulus variance was minimal. Both of these measures vary monotonically with burst duration (Fig.3b,c), consistent with a burst duration code. We quantified these differences across a population of 20 neurons and 102 trials using discriminant and ROC analyses. We found that in all cases, the signal preceding the burst is predictive of the burst duration

and the more different the compared burst duration were, the greater was their predictability (not shown). These findings demonstrate that bursts of different durations systematically encode different stimuli.

Synaptic decoding of a burst duration code

Essential to any neural code is the ability of postsynaptic neurons to read it out (i.e. postsynaptic response should vary systematically with coding attributes of the spike train). A simple way is for the postsynaptic neuron to integrate the response to each spike of a burst. *In vivo* experiments have established that the integration time window of layer 4 cells to thalamic input is approximately 15 ms [**?**], which is well matched to the observed burst duration distribution (Fig.1c). Interestingly, we have found that burst duration is multiply encoded within the interspike structure of bursts (Fig 2). These multiple correlates provide further flexbility in reading the code. For example, the short-term plasticity of thalamocortical synapses (facilitation and depression) [1] makes synapses sensitive to the pattern of interspike intervals within bursts.

Here we use a spike train recorded from a thalamic relay cell to investigate the decodability of the thalamic burst duration code. For our simulations we used a published model [20] that includes facilitation and depression processes, constrained by in vitro measurements [12]. Our results demonstrate that the rich short-term dynamics of synapses can be tuned to differentially respond to specific burst durations. We construct synaptic tuning curves showing the response of a synapse as a function of the burst duration. Changes in synaptic parameters: the initial release probability and the facilitation and depression time constants result in different synaptic tuning curves. The peak of these tuning curves can occur for short, medium or long duration bursts (Fig.4).

1 Conclusions

Initially it was thought that thalamic bursts might only be present during the sleep state, but more recent work indicates that bursts are likely to have a role in stimulus encoding in awake animals [8, 15, 5, 19] and in humans [14]. It has been suggested that in this state, bursts generated due

to feed-forward excitation may be a sign of an "attentional searchlight" [2], serve as a "wake-up call" [17] or optimize signal detection [13]. In each case, rapid information transmission is required of bursts. Burst duration coding greatly enhances the capacity of thalamocortical pathways for rapid signalling by endowing bursts with an ability to carry graded information and thus serve as a "wake-up message". More generally, a burst duration code may be particularly useful for rapid, discontinuous signalling, in contrast to the continuous transmission provided by rate-modulated single spikes. We propose the these dichotomous signalling modes can preferentially activate different cortical layers due the differential short-term dynamics of thalamo-cortical synapses.

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Figure 1: **Variability of LGN bursts during visual stimulation** (a) Time-varying visual contrast and the recorded spike train. The stimulus has an 8Hz cutoff, mean of 0.4 with σ=0.2. Red asterisks mark bursts. (b) Variability of spike count per burst across the entire population of neurons and trials. (c) Each color histogram shows the time duration of bursts of a particular spike count from all the neurons recorded.

Figure 2: **Internal structure of bursts** (a) Histograms of intersike intervals (1st, 2nd, ...) for a 5 spike burst shows strong adaptation. (b) First ISI histograms for different spike counts shows a systematic relationship. Notice, that five spike bursts (B5) are completely distinguishable from two spike bursts (B2) based on the length of the first interspike interval. (c) Last ISI histograms. Longer bursts have longer last interspike interval. (d) The time duration of bursts as a function of spike count (mean +/- SE). Data from the same cell shown in (a-c). (e) Population data for burst substructure. The correlation coefficients between the spike count and the first ISI are on the x-axis and between the burst duration and the last ISI on the y-axis. The cell shown previously is marked with the red circle.

Figure 3: **Example of burst duration code** (a) Burst triggered stimuli for bursts of different durations. Blue, red, green and black curves are for bursts containing 2-5 spikes respectively. (b) Peak contrast as a function of spike count with standard errors. (c) Contrast slope at the time point of minumum variance (as determined from panel a) as a function of spike count.
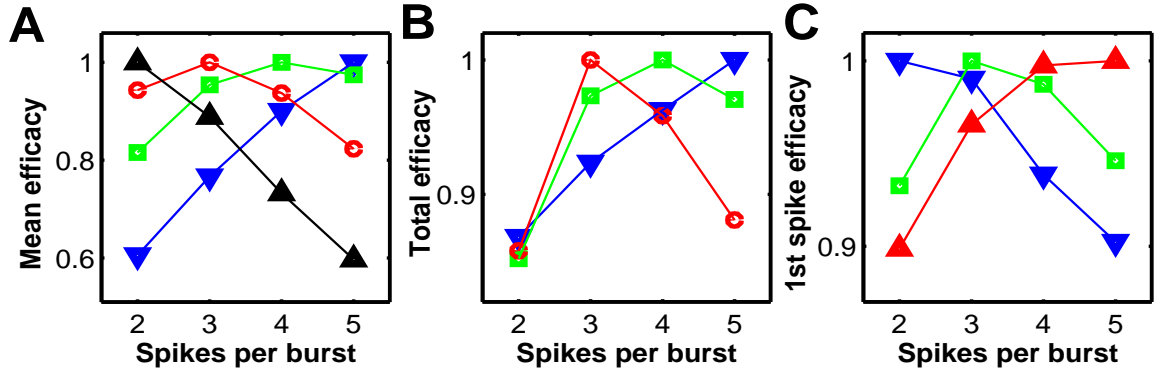
Figure 4: **Synaptic tuning curves for LGN bursts A** Response is measured as the mean efficacy. Synaptic parameters are $\tau_F = 30$, $\tau_D = 30$ ms and $U = \{0.05, 0.1, 0.2, 0.4\}$. **B** Response is measured as the total efficacy of each burst. Synaptic parameters are $U = 0.9$, $\tau_F = 10$, $\tau_D = \{100, 700, 4000\}$ ms. **C** Tuning curve for the efficacy of the first spikes of bursts. Synaptic parameters (U, τ_F, τ_D) are $(0.1, 20, 1000)$ for the blue; $(0.4, 200, 1000)$ for the green; and $(0.7, 20, 200)$ for the red curve.