

# Stimulus transmission by tonic and burst responses in a minimal model of thalamic circuit

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## Abstract

Burst and tonic responses are studied in a minimal model of thalamic circuit composed of a retinal spike train, a relay neuron and a reticular neuron. The integrate-and-fire-or-burst model is used to simulate the neurons. Cross-correlation studies show that burst events are more reliable than tonic firings in stimulus transmission to the cortex, and may be capable of scanning the sensory spike train for certain temporal correlations. The implications of these results about the information content of bursts and their possible role in attention mechanisms are discussed.

## Introduction

The thalamic relay cells respond to the sensory stimulus in two distinct modes, known as tonic and burst. When in tonic mode, the relay cell responds to the incoming stimulus by one or more individual action potentials. In the burst mode, the response of the cell to the stimulus is in the form of dense, stereotyped packets of action potentials, called bursts events. Until recently, it was believed that thalamic bursts are only present during certain pathological states and slow wave sleep. However, recent evidences indicate that bursts are also present during normal awake states in Lateral Geniculate Nucleus (LGN: the visual nucleus of thalamus), and may play an important role in the transmission of sensory stimulus to the cortex (see Sherman 2001 for a review). Nevertheless, the nature of information conveyed by bursts in comparison with tonic responses is still a matter of question. This study aims to approach this question by means of numerical simulations of a biologically realistic minimal LGN circuit.

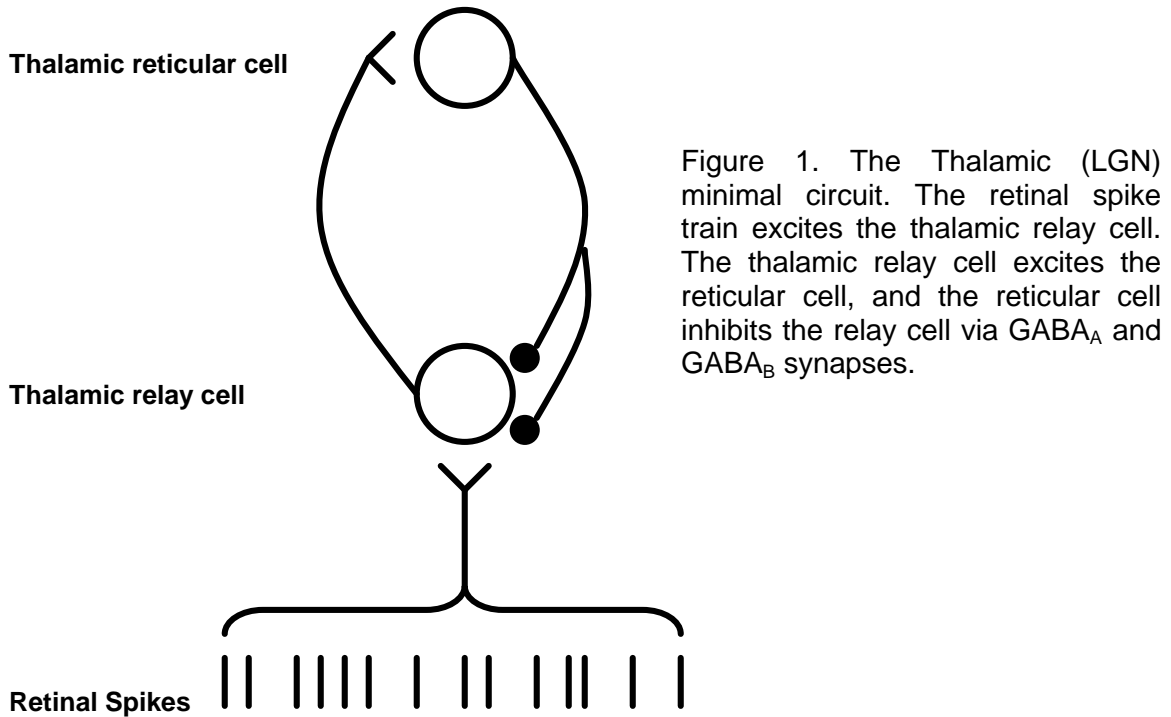
The neurons in the thalamic reticular nucleus densely innervate the thalamic relay neurons with GABAergic inhibitory synapses and provide the major inhibitory input to them (Charles et al 1997). On the other hand, in LGN, as the prototypical thalamic nucleus, individual relay neurons receive very strong excitatory input from a single retinal ganglion cell, which constitutes the main excitatory drive of the relay cell (Hamos et al 1987). Thus, a minimal thalamic (LGN) circuit, which will be studied here, consists of 1) a thalamic relay neuron, 2) a thalamic reticular neuron, and 3) an input spike train

from the retinal ganglion cell. Note that a similar minimal circuit was subject of dynamical clamp experiments in the studies of Le Masson and colleagues (2002).

## Methods

The retinal spike train is modeled as a renewal process with  $g$  distributed intervals. The mean rate of the modeled spike train is  $30\text{ Hz}$  and the order of  $g$  is 3 (Troy & Robson 1992).

For the thalamic relay (TC) and reticular (RN) neurons the integrate-and-fire-or-burst (IFB) model has been used. The IFB model is an extension of the simple integrate-and-fire model by adding a slow variable, which represents the gating parameter of the low threshold calcium current. Although quite simple, the IFB model captures most of the



biological properties of the thalamic cells and its behavior matches properly with the experimental data (for details see Smith et al 2000). The only difference between the TC IFB and the RN IFB is that the threshold for the low threshold calcium current is slightly higher in the RN IBF (Smith & Sherman 2002).

The TC receives the retinal spike train via an excitatory AMPA synapse and sends its spikes to the RN via another excitatory AMPA synapse, with a lower strength. The RN in

turn sends its spikes to the TC via inhibitory GABA<sub>A</sub> and GABA<sub>B</sub> synapses (figure 1). For the AMPA and GABA<sub>A</sub> synapses, conductance changes are modeled by exponentially decaying functions. The decay time constants for the AMPA and GABA<sub>A</sub> synapses are *5 ms* and *10 ms* respectively. For GABA<sub>B</sub> synapse, the conductance changes are modeled by a double exponential function with a rise time constant of *100 ms* and a decay time constant of *200 ms*. The maximal conductance values of the synapses are *0.30 mS* for the retina-TC AMPA, *0.09 mS* for the TC-RN AMPA, *0.18 mS* for RN-TC GABA<sub>A</sub>, and *0.08 mS* for RN-TC GABA<sub>B</sub>. These values are chosen in pilot simulations so that the response properties of the thalamus in awake animals could be reproduced, namely *30 Hz* average firing rate of the TC with 1% of its total spikes in burst mode (Ramcharan et al 2000).

The burst events in the spike train generated by the TC are then identified using the “liberal criteria” proposed by Ramcharan et al (2000). According to this criteria, a burst event is a group of spikes, with first one proceeding a silent period of *>50 ms*, the first inter-spike-interval in the burst being *>6 ms*, and all the following spikes are part of the burst event if their inter-spike-interval increases no more than *2 ms* for each successive spike, up to a maximum allowed inter spike interval of *16 ms*. So that from the original spike train of the TC, two additional spike trains are extracted: 1) the tonic spike train, containing the spikes that do not contribute in bursts, and 2) the burst event train, containing the first spike of each burst event (figure 2). As burst events are highly stereotyped (Reinagel et al 1999), only the first spike of each burst is chosen as a representative for the event.

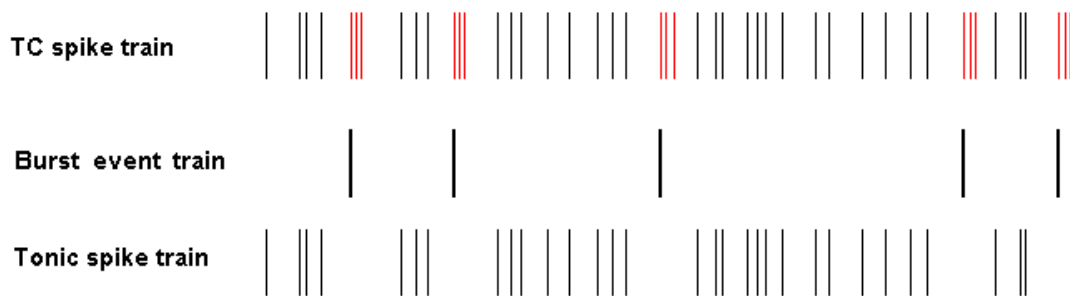


Figure 2. Discriminating burst and tonic responses. Both burst and tonic responses are present in the original spike train of TC (top). Bursts are identified by the “liberal criteria” (see text) and are shown in red. From the original spike train, the burst event train (middle) and the tonic spike train (bottom) are then extracted.

## Results

All the results are obtained by simulating the model thalamic circuit for *1000s* (in neuron time). Figure 3 shows the cross-correlograms of the model TC tonic spike train (3.a) and burst event train (3.b) with the retinal spike trains, binned *1 ms* intervals, normalized by the total number of events (single spikes or burst events) in the TC spike train. The peak of these normalized cross-correlograms are indices of reliability of the TC activity for transmitting the retinal information (Le Masson et al 2002). As can be seen, the peak is higher for the burst event train than the tonic spike train. This suggests that burst events are more reliable in transferring retinal information. Moreover, the cross-correlogram for the burst events (3.a) has two distinct peaks: a lower peak in about *-40 ms* lag, and a higher peak near zero lag. This may suggest that burst events scan the retinal spike train for certain temporal correlations.

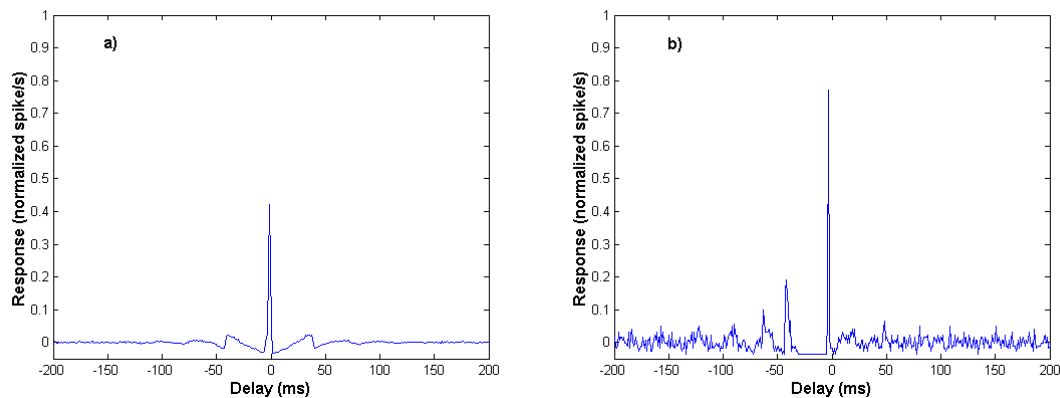


Figure 3. a) Cross-correlogram of tonic spike train and the retinal spike train, normalized by total number of tonic spikes. b) Cross-correlogram of burst event train and the retinal spike train, normalized by total number of burst events. Note that the peak is higher for burst events, and also of two peaks exist for the bursts.

## Discussion

The results confirm that burst events are indeed reliable transmitters of information to the cortex, at least in a minimal circuit of thalamus. Although bursts rare in the spike train of the TC in awake animals, their higher reliability compared to tonic spikes may explain the equal information content of these two modes of activity in LGN, which was reported by Reinagel and colleagues (1999).

The two-peaked cross-correlogram of the burst event may suggest that they are capable of scanning the retinal spike train for some spike-silence-spike temporal sequences. This in turn may be suggested as a possible mechanism for bottom-up attention, as proposed by Crick (1984) for the thalamic bursts.

Although the studied thalamic circuit is highly simplified, it is possible to use the similar methods for more realistic and complex models, and also for simultaneous in vivo recordings of retinal ganglion cells and thalamic relay cells (Hamos et al 1987).

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