A Spiking Thalamus Model for Form and Motion Processing of Images

Suhas E. Chelian, Narayan Srinivasa

Abstract—The thalamus, far from being a simple relay, supports several functions including attention and awareness. Recent spiking models of the thalamus tend to focus on abstract thalamocortical features such as rhythms and synchrony. Here a new spiking reinto-thalamic model is presented that reproduces several aspects in visual processing including distinct form and motion processing pathways. Using test and natural image sequences, differences between parvocellular and magnocellular relay neurons are studied. In line with several experimental results, parvocellular neurons are found to be more sensitive to changes in color (necessary for form processing) than temporal frequency (necessary for motion processing) and conversely for magnocellular neurons. This model can in turn be used as input into subsequent cortical models or as a tool to aid in experimentation. Future extensions could include modeling brainstem or cortical influence on thalamic processing, as well as the control of virtual agents.

I. INTRODUCTION

The thalamus was once thought to represent a simple relay between sensory input and cortical processing. However, there is growing evidence that the thalamus supports several functions including attention and awareness (e.g., [1], [2]). Although there have been several recent spiking models of the thalamus (e.g., [3], [4], [5], [6]), these tend to focus on abstract thalamocortical processing features such as rhythms and synchrony without modeling modality specific qualities. Here, a new spiking reinto-thalamic model is presented that reproduces several aspects in visual processing including distinct form and motion processing channels.

We now review the relevant anatomy from [7] and [8]. Retinal ganglion cells (RGCs) can be broadly grouped into parvocellular and magnocellular types both of which can be either ON-center OFF-surround or OFF-center, ON-surround. Ninety percent of RGCs project to the lateral geniculate nucleus (LGN) of the thalamus; some RGCs connect to the pretectum and superior colliculus to help control pupillary reflexes and eye movements.

Light from the left visual hemifield falls on the right hemiretina of each eye, which in turn projects to different layers of the right LGN (and conversely for the right visual hemifield). Layers 1 and 2 of the LGN receive both ON and OFF magnocellular inputs while layers 3 through 6 receive both ON and OFF parvocellular inputs [9]. Some neurons of both parvo- and magno- cellular types have delayed responses [10], [11]. Parvocellular lag neurons are likely to be more numerous than magnocellular lag neurons simply because there are more parvocellular layers. Layers 1, 4, and 6 (2, 3, and 5) receive inputs from the contralateral (ipsilateral) visual field. From there, layers 1 and 2 (3 through 6) project to layer 4Cα (4Cβ) of primary visual cortex. This is summarized in Fig. 1.

Fig. 1. Primary connections between retina, thalamus, and primary visual cortex. Parvo- and magno- cellular retinal ganglion cells from each eye, representing the ipsilateral visual hemifield, project to different layers of the contralateral LGN. LGN layers in turn project to different layers of primary visual cortex. Here, yellow (green) represents the left (right) visual hemifield. (Adapted from [7].)

Each LGN layer can be decomposed into three main subpopulations [12]: interneurons, relay neurons, and reticular neurons as diagrammed in Fig. 2. (Reticular neurons form a sheath around the whole thalamus.) Thalamic interneurons (TIs) provide feed forward inhibition to thalamocortical relay neurons (TCs), while thalamic reticular neurons (TRNs) provide feedback inhibition to relay neurons. Relay neurons transform and transmit RGC inputs to visual cortex.
In terms of function, parvocellular relay neurons support form processing along the ventral pathway while magnocellular relay neurons support motion processing along the dorsal pathway. Table I lists the main sensitivity differences between parvo- and magno-cellular relay neurons as derived from [8].

<table>
<thead>
<tr>
<th>Stimulus feature</th>
<th>Parvocellular</th>
<th>Magnocellular</th>
</tr>
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<tbody>
<tr>
<td>Color contrast</td>
<td>Higher</td>
<td>Lower</td>
</tr>
<tr>
<td>Spatial frequency</td>
<td>Higher</td>
<td>Lower</td>
</tr>
<tr>
<td>Luminance contrast</td>
<td>Lower</td>
<td>Higher</td>
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<tr>
<td>Temporal frequency</td>
<td>Lower</td>
<td>Higher</td>
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TABLE I – PRIMARY DISTINCTIONS IN SENSITIVITY BETWEEN PARVO- AND MAGNO-CELLULAR RELAY NEURONS

II. METHODS

In the descriptions below, we focus on the left hemiretina which projects to the right LGN although other combinations (e.g., right hemiretina, right LGN; left hemiretina, left LGN, etc.) can be easily accommodated. Plasticity between the retina and thalamus and within the thalamus was not modeled as it is a primarily prenatal process [13].

A. Retinal ganglion cells (RGCs)

Retinal input was provided by a recent spiking model [14] that leverages GPU-based image convolution [15]. This model exhibits several functionalities including space variant sampling (image regions in the fovea are more densely sampled than those outside the fovea), gain control, habituative dynamics, and cone opponency. In the model, magnocellular neurons have larger receptive fields and more transient responses than parvocellular neurons which agrees with several studies of neurophysiology [7]. It also has greater scaling performance than other retinal models (e.g., [16], [17]).

For simplicity, parvo- and magno-cellular cell responses for both ON and OFF channels were interpolated to full image resolution and fed into their respective interneurons and relay neurons in the thalamus. As an example, magnocellular RGCs feed into layer 1 (Fig. 1). Connections to relay neurons were one to one following the seminal work of [10], which has been recently supported by the use of adaptive optics [18]. (To our knowledge, a similarly detailed study of other connections or weights within the thalamus has yet to be conducted.) Furthermore, RGC inputs to layer 6 were temporally delayed with respect to inputs in layer 4 to simulate lagged relay neurons [10], [11]. RGC connections and weights were controlled using 2D Gaussian patterns. The Appendix lists parameter values.

B. Thalamic Interneurons (TIs)

Thalamic interneurons (TIs) often exhibit rebound spiking after hyperpolarization [19] but no prominent burst mode. To fully leverage the speed of the HRL SyNAPSE simulator [20], this behavior was fit using the 4 parameter Izhikevich neuron model [21]. The equations for this models are:

\[ \dot{v} = 0.04v^2 + 5v + 140 - u + I \]
\[ u = a(bv - u) \]
\[ \text{if } v \geq 30, \dot{v} = c, \dot{u} = u + d \]

where \( v \) is the membrane potential, \( u \) is a recovery variable, \( I \) is the input current, and \( a, b, c, d \) are parameters chosen for each neuron type. The values for each neuron type are listed in the Appendix. Fig. 3a illustrates the tonic and rebound dynamics of TI neurons.

![Fig. 3. Tonic and rebound dynamics of (a) thalamic interneuron (TI), (b) thalamocortical relay (TC), and (c) reticular (TRN) neurons respectively.](image)

The proportion of TIs to TCs varies across thalamic region. We conservatively use 5% to derive the number of TIs for each layer. Each interneuron probabilistically and topographically projected to both ON and OFF relay neurons within its layer using a 2D Gaussian pattern; connection strengths were similarly modulated.

C. Thalamocortical Relay Neurons (TCs)

Thalamocortical relay neurons (TCs) display both tonic and burst firing patterns, with the latter apparent after hyperpolarization [19]. This behavior was modeled with the

![Fig. 2. Primary neuron subpopulations within each LGN layer and their connections. Thalamic interneuron (TI), thalamocortical relay (TC), and reticular (TRN) neurons process and convey retinal inputs to the visual cortex. Neuromodulatory projections from the parabrachial (PBR) region of the brainstem also affect thalamic processing. Here blue (pink, green) represents primarily excitatory (inhibitory, modulatory) connections. (Adapted from [12].)](image)
4 parameter Izhikevich model for the HRL SyNAPSE simulator. Fig. 3b illustrates the tonic and rebound dynamics of TC neurons.

Using a conservative estimate of the proportion of TIs to TCs as 5%, we derive the number of TCs for each layer. Two-dimensional Gaussian patterns were used to probabilistically and topographically connect each relay neuron to the thalamic reticular layer as well as to assign weights.

Because distinct RGC channels feed distinct thalamic layers (Fig.1), several of the functional differences between parvo- and magno-cellular RGCs are evident in thalamic relay neurons as well. Parvocellular relay neurons, for example, often exhibit center-surround cone opponency [23] which helps detect changes in color contrast (Table I). A red ON-center, green OFF-surround neuron, for example, would be excited by a red spot, produce an intermediate response for a red spot in a green annulus, and be inhibited by a green annulus. Fig. 3 demonstrates this order of response magnitudes from an ON parvocellular relay neuron in layer 4 as well as the model’s stochastic spike generation. For each input, we also measured the change in the number of spikes relative to the neuron’s baseline firing rate. It was found it to be 97.72%, -8.75%, and -23.95% in that order suggesting the surround of this neuron is slightly stronger than its center.

D. Thalamic Reticular Neurons (TRNs)

Thalamic reticular neurons (TRNs), like TCs, exhibit both tonic and burst firing patterns, although their firing rates tend to be slower than that of TCs [22]. The HRL SyNAPSE simulator was used to simulate this behavior with the 4 parameter Izhikevich neuron model. Fig. 3c illustrates the tonic and rebound dynamics of TRN neurons.

The number of TRNs relative to the number of TCs or TIs is not known [4]. The number of TRNs was set equal to the number of TIs within a single layer. Each thalamic reticular neuron projected probabilistically and topographically to all relay neurons using a 2D Gaussian pattern; connection strengths were similarly modulated.

E. Test and Natural image sequences

Both test and natural image sequences were used to study retino-thalamic processing. Test image sequences are simplistic but help distinguish form and motion processing. Natural image sequences taken from a recent YouTube action recognition dataset [26], on the other hand, represent realistic inputs which multiplex form and motion.

For test image sequences, form and motion processing were demonstrated with changes in color and temporal frequency respectively. Parvocellular neurons are more sensitive to changes in color than temporal frequency and conversely for magno-cellular neurons (Table I). For color, images like Fig. 3a were created using 6 equinorm colors uniform and static and hence both parvo- and magno-cellular neurons would respond poorly [8].

Fig. 4. Motion sensitivity in a magnocellular relay neuron. Habituation dynamics in RGCs detect changes in intensity which can be detected and amplified in relay neurons. Given a drifting sinusoidal grading (a, b, c) cycled with increasing temporal frequency, the neuron fires with increasing intensity (d, e, f). For this simulation, 5 frame input sequences with two additional frames not shown—the white bar shifted to the far left and between the far left and middle of the image—were presented at 1.33, 2, or 4 Hz (or 150, 100, and 50 ms. per frame respectively). Average firing rates using a 25 ms. window were recorded during each input sequence. The average firing rate in the 1st input presentation was 12.72, 13.56 and 14.67 Hz respectively. The red vertical line denotes the end of each 5 frame input sequence.
on the corners of RGB color cube—red, yellow, green, cyan, blue, and magenta. Each image was presented for 12 frames at 50 ms. per frame (or 0.6 Hz for each color). For temporal frequency, the image in Fig. 4a and two copies with intensities reduced by factors of 2 and 4 created a 3 frame image sequence that looks like a flickering pattern of bars. This image sequence was then presented at 2.22, 3.33, or 6.66 Hz (or 150, 100, and 50 ms. per frame respectively).

If a neuron is selective to a particular feature—color for example—it’s firing rate relative to its average firing rate would increase in response to its preferred stimuli. However, a neuron that is broadly tuned to a feature would not significantly increase or decrease its firing rate to any particular stimuli. To quantify the degree to which a neuron was responsive to a particular feature, we use the Weber contrast ratio (c):

\[ c = \frac{x_{\text{max}} - \mu}{\mu} \] (4)

where \( x_{\text{max}} \) is the maximum average firing rate over all inputs, and \( \mu \) is the average firing rate over all inputs. If \( c \) is close to zero (\( x_{\text{max}} \approx \mu \)), the neuron does not raise or lower its firing rate relative to its average firing rate, meaning it is not sensitive to changes in that particular feature. Large values of \( c \) reflect greater response modulation to changes across that feature. (Other contrast measures such dynamic range, standard deviation, or Michelson contrast are also possible. However, with sinusoidal inputs and response profiles as shown in Fig. 4, for example, Michelson contrast equals Weber contrast [27].)

\( c \) was measured for 10 parvocellular and 10 magnocellular relay neurons. For each population, half were ON neurons and half were OFF neurons. For parvocellular relay neurons, half were from layer 4 and half were from layer 6. Images were presented across the visual field to parvo- and magno- cellular neurons with overlapping receptive fields. This is a worst-case scenario for differentiating between parvo- and magno- cellular relay neurons due to overlapping RGC inputs. For example, to be sensitive to a particular color, a parvocellular neuron must selectively draw from cones representative of that color (e.g., L cones for red). However, the corresponding magnocellular neuron would also be somewhat sensitive to color because of partially overlapping RGC inputs. This protocol was used to thoroughly test the capabilities of the current model.

For the natural image sequence, a video clip of a gymnast performing on a balance beam (v_BalanceBeam_g17_c01, seconds 3 to 7 in [26]) was chosen because of its uncluttered but dynamic content. After removing the letterbox matte from each frame, each frame was resized to be 64 x 64 pixels and presented at 50 ms. per frame (or 20 Hz). For parvo- and magno- cellular channels, Weber contrast was measured using the maximum and average firing rates across all neurons on a per frame basis. Large values of \( c \) for each type of neuron reflect large deviations (\( x_{\text{max}} > \mu \)) for that frame. These values were then averaged across all frames. For each type of relay neuron, large average values of the Weber contrast ratio across all frames reflect large deviations and consequently more change or salience in that channel.

III. RESULTS

A. Test image sequences

In Fig. 5a, parvocellular relay neurons are roughly 1.8 times more sensitive to changes in color than magnocellular neurons (0.29 v. 0.16), a result that is statistically significant (t-test, p < .05). Conversely, in Fig. 5b, magnocellular neurons are approximately 2.3 times more sensitive to changes in temporal frequency than parvocellular neurons (0.035 v. 0.015), a result which is also statistically significant (t-test, p < .05).

![Fig. 5. Mean Weber contrast for parvo- and magno- cellular neurons using changes in (a) color and (b) temporal frequency.](image)

In the case of temporal frequency, the smaller overall contrast values are likely due to the use of oriented bars to which LGN neurons are only weakly tuned [24].

B. Natural image sequences

Fig. 6a shows the gymnast swinging her arms behind her back on a balance bar. Fig. 6b shows parvo- and magno- cellular results for the retina after averaging firing rates over each frame. In both channels, detail drops off as a function of eccentricity, which is indicative of space variant sampling in the retina. Parvocellular results represent the intensity contrast of the gymnast’s skin against the black curtain along the entirety of this boundary—her legs and arms. Magnocellular results are strongest where there is motion—around the gymnast’s hips where her hands were—and weakest in relatively static portions of the image—the curtain. In the video clip, the camera also pans from left to right (following the gymnast along the length of the balance bar) and thus there is some motion in the background as well. Lastly, since magnocellular cells are also somewhat responsive to changes in intensity (Table I), the balance bar also creates a large response in the retina.
Fig. 6. Input image (a) and average firing rates on a per frame basis for retinal ganglion cells (b) and thalamic relay neurons (c). For retina results, proceeding clockwise from the upper left, the channels are magnocellular ON and OFF and parvocellular OFF and ON. For thalamus results, proceeding clockwise from the upper left, the channels are magnocellular ON and OFF in layer 1, parvocellular OFF in layer 4 and 6, and parvocellular ON in layer 6 and layer 4.

For thalamic relay neurons, the results are similar: parvocellular neurons respond to areas of changes in intensity while magnocellular neurons respond to areas of motion. The “ringing” pattern of light and dark spots throughout all channels is caused by TI and TRN neurons suppressing homogenous image regions through feed forward and feedback inhibition respectively. Thus local contrast is enhanced relative to respective retinal responses. Distinct color responses of individual neurons are not apparent at this stage of processing due to spectral mixing and spatial pooling (e.g., there are no pure red spots in Fig. 6a as in Fig. 3a). As illustrated in Fig. 7, Weber contrast for parvocellular neurons is about 1.9 times less than that of magnocellular neurons (0.27 v. 0.51), a difference that is statistically significant (t-test, p < .05). This corresponds to the intuition that the video has more changes in motion than form.

In addition, Weber contrasts for each channel are statistically different for the natural image sequence when compared to the contrasts for the test image sequences (ANOVA, p < .05). Contrasts were also higher than the average contrast across test image sequences (parvocellular 0.27 v. 0.15, magnocellular 0.51 v. 0.08) because of the larger number of neurons recorded from and the greater information content in this image sequence.

IV. DISCUSSION

The current model reproduces several functional distinctions in retino-thalamic processing including distinct form and motion processing pathways. Using test image sequences, thalamic parvocellular neurons were found to be more responsive to color than temporal frequency and conversely for magnocellular neurons. This finding is also present in the natural image sequence. There, parvocellular neurons represented areas of high intensity contrast while magnocellular neurons represented areas of high temporal contrast.

Although the current model does not model intralaminar neurons [23] or a large range of lagged responses [11] which can help sharpen form and motion processing respectively, it can be used as input into subsequent cortical models or as an experimental tool. Future extensions could include modeling brainstem or cortical influence on thalamic processing, as well as the control of virtual agents.

APPENDIX

Relatively little is known quantitatively about the radii and strength of connections across the thalamus (e.g., [4], [18]). Following the work of [12], however, we maintain the qualitative distinction between those connections which are “drivers” (e.g., RGCs to TCs) and those which are “modulators” (e.g., RGCs to TIs). Connection parameters were also adjusted to ensure functional properties such as the balance of feed forward and feedback inhibition.

All radii are specified in terms of post-synaptic neurons. For example, the radius of each RGC to TI connection is 1 x 1 neuron, which means several RGCs can synapse onto the same TI neuron.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
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<tr>
<td><strong>Retina</strong></td>
<td></td>
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<tr>
<td>Size of each interpolated retina channel (ganglion cells, rows by columns)</td>
<td>64 x 64</td>
</tr>
<tr>
<td>Radius of RGC to TI connections (neurons, rows by columns)</td>
<td>1 x 1</td>
</tr>
<tr>
<td>Probability of connection between an RGC and a TI neuron given distance (symmetric normal distribution)</td>
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<tr>
<td>Weight of connection between an RGC and a TI neuron</td>
<td>μ=0.25, σ=0.001</td>
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### REFERENCES


