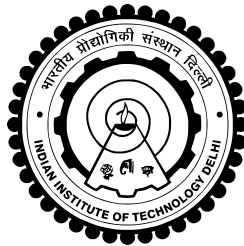


**MODELING OF LAYER 2/3 CELLS
IN PRIMARY VISUAL CORTEX:
MODULATION RATIO AND DISPARITY**

DHANARAJ K. J.



**DEPARTMENT OF ELECTRICAL ENGINEERING
INDIAN INSTITUTE OF TECHNOLOGY DELHI
MARCH 2017**

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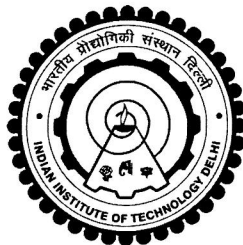
by

DHANARAJ K. J.

Department of Electrical Engineering

Submitted

in fulfillment of the requirements of the degree of Doctor of Philosophy
to the



Indian Institute of Technology Delhi

March, 2017

Dedicated

to

My family and friends

Certificate

This is to certify that the thesis entitled “**Modeling of Layer 2/3 Cells in Primary Visual Cortex: Modulation Ratio and Disparity**”, being submitted by **Mr. Dhanaraj K. J.** for the award of the degree of **Doctor of Philosophy** to the Department of Electrical Engineering, Indian Institute of Technology Delhi, is a record of bonafide work done by him under my supervision and guidance. The matter embodied in this thesis has not been submitted to any other University or Institute for the award of any other degree or diploma.

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DHANARAJ K. J.

Abstract

The combined processing of signals from the left eye and the right eye starts at the primary visual cortex (V1). In the primary visual cortex, Hubel and Wiesel identified two classes of neurons namely simple cells and complex cells. Complex cells are in abundance in layer 2/3 of primary visual cortex. Disparity selective complex cells are present in layer 2/3. In order to model and study the responses of disparity selective complex cells in the primary visual cortex, one needs to model layer 2/3 cells in V1 that receives feedforward input from layer 4 simple cells and incorporate lateral connections within layer 2/3 and feedback contribution from higher cortical areas.

In this thesis, we have presented a model for disparity selective binocular complex cells in the primary visual cortex. A four layer visual pathway model is used to get the response of layer 2/3 cortical cells in the cat primary visual cortex. The first, second, third and fourth layers represent the retinae, the LGN, the layer 4 of V1 and the layer 2/3 of V1 respectively. The competition among neurons for limited resources and the cooperation among neighbouring neurons form the basis of our model. Feedforward connection weights from the LGN to the layer 4 and from the layer 4 to the layer 2/3 were developed using reaction-diffusion equations. The local lateral connections in the layer 2/3 were also developed in a similar manner as that of feedforward connections, with layer 2/3 cells as presynaptic cells as well as postsynaptic cells. The feedback signals were modeled as delayed and scaled version of feedforward signals.

Our reaction-diffusion based feed-forward model of visual pathway captures realistic

complex cell RFs and response properties with similar orientation maps in layer 4 and layer 2/3. The layer 2/3 cells in iso-orientation regions have sharper orientation tuning compared to that of the cells near pinwheel singularities, which agrees with the experimental results of Nauhaus et al. (2008).

As per the criterion of modulation ratio (MR) of spike response, majority of layer 2/3 cells are complex cells, which agrees with the experimental results of Ringach et al. (2002). Quantification of the extent of overlap between ON and OFF subregions of layer 2/3 cells was done. A significant correlation between the modulation ratio of the cells and the ON-OFF subregion overlap in the cells' receptive fields was found. The spiking threshold and the nonlinearity in spiking have a significant effect on the MR of the cells, which agrees with the experimental results of Priebe et al. (2004). It is observed that the simple cells have sharper orientation tuning compared to that of the complex cells. This is in agreement with the experimental studies of Rose and Blakemore (1974).

The 'complex cell like' behaviour of a layer 2/3 cell was found to have no dependence on the cell's location in orientation map. The corresponding experimental results are not yet reported in the literature.

Local lateral connections modulate the response of the cells with an improvement in orientation tuning characteristics. Modulation ratio of layer 2/3 cells decreased when feedback connections were incorporated. The cells with higher modulation ratio showed a larger reduction in the modulation ratio when the feedback connections were incorporated, which is in agreement with the experimental results of Bardy et al. (2006). Feedback con-

nections improved the orientation tuning characteristics of the cells. We report that the cells achieved sharper tuning characteristics while maintaining phase invariance in the response, due to the combined effect of local lateral connections and feedback connections.

We could capture disparity selectivity in layer 2/3 cells. Preferred binocular phase disparity of layer 2/3 cells can be predicted from the knowledge of receptive fields of its layer 4 simple cell subunits. Characterization of disparity preference of layer 2/3 cells was done, and disparity map was obtained for the layer 2/3. The disparity map is weakly clustered. Disparity tuning characteristics of layer 2/3 cells have no relationship with their orientation tuning characteristics. Local lateral connections improve the disparity sensitivity of the cells. Due to feedback, most of the cells achieve the phase invariance property as well as high resolution in orientation detection and disparity detection. Low delay feedback improves disparity selectivity whereas high delay feedback improves phase invariance property of the cells. This prediction of our model needs experimental verification.

सार

बाईं आंख और दाईं आंख से संकेत के संयुक्त प्रसंस्करण प्राथमिक दृश्य कोर्टेक्स (वि-1) में शुरू होता है। प्राथमिक दृश्य कोर्टेक्स में, हूबेल और विजल, न्यूरोन्स अर्थात् साधारण कोशिकाओं और जटिल कोशिकाओं के दो वर्गों की पहचान की। जटिल कोशिकाओं प्राथमिक दृश्य कोर्टेक्स की परत-2/3 में बहुतायत में हैं। असमानता चयनात्मक जटिल कोशिकाओं की परत-2/3 में मौजूद हैं। मॉडल और प्राथमिक दृश्य कोर्टेक्स में असमानता चयनात्मक जटिल कोशिकाओं की प्रतिक्रियाओं का अध्ययन करने के लिए, वि-1 में परत-2/3 कोशिकाओं मॉडल करने की जरूरत है, जो परत-4 साधारण कोशिकाओं से फीडफॉरवर्ड इनपुट प्राप्त करता, और परत-2/3 के भीतर पार्श्व संबंध शामिल करना और उच्च कॉर्टिकल क्षेत्रों से राय योगदान करना है।

इस शोध में, हम प्राथमिक दृश्य कोर्टेक्स में असमानता चयनात्मक दूरबीन जटिल कोशिकाओं के लिए एक मॉडल प्रस्तुत किया है। एक चार परत दृश्य मार्ग मॉडल बिल्ली प्राथमिक दृश्य कोर्टेक्स में परत-2/3 वल्कुटीय कोशिकाओं की प्रतिक्रिया प्राप्त करने के लिए प्रयोग किया जाता है। सबसे पहले, दृष्टिपटल दूसरे, तीसरे और चौथे परतों क्रमशः प्रतिनिधित्व करते हैं, एल. जी. एन., वि-1 की परत-4 और वि-1 की परत-2/3। सीमित संसाधनों के लिए न्यूरोन्स के बीच प्रतिस्पर्धा और पड़ोसी न्यूरोन्स के बीच सहयोग के हमारे मॉडल के आधार फार्म। प्रतिक्रिया-प्रसार समीकरण का उपयोग कर, एल. जी. एन. से परत-4 तक फीडफॉरवर्ड कनेक्शन का भार और परत-4 से परत-2/3 तक फीडफॉरवर्ड कनेक्शन का भार विकसित किए गए। परत-2/3 में स्थानीय पार्श्व कनेक्शन भी फीडफॉरवर्ड कनेक्शन के रूप में एक समान तरीके से विकसित किए गए, जिसमें प्रेस्न्याप्तिक कोशिकाओं के रूप में और पोस्टअन्तर्ग्रथनी कोशिकाओं के रूप में परत-2/3 कोशिकाओं है। प्रतिक्रिया संकेतों देरी और बढ़ाया फीडफॉरवर्ड संकेतों के रूप में मॉडलिंग कर रहे थे।

दृश्य मार्ग की हमारी प्रतिक्रिया-प्रसार आधारित फीड आगे मॉडल परत-4 और परत-2/3 में इसी प्रकार के उन्मुखीकरण के नक्शे के साथ यथार्थवादी जटिल सेल आरएफएस और प्रतिक्रिया गुण को दर्शाता है। परत 2/3 कोशिकाओं जो आईएसओ उन्मुखीकरण क्षेत्रों में हैं, जो कोशिकाओं के पास पिनव्हील विलक्षणता हैं की तुलना में

तेज उन्मुखीकरण ट्यूनिंग है, जो नाहहस एट अल.(2008) की प्रयोगात्मक परिणामों के साथ सहमत हैं।

मॉडुलन अनुपात कील प्रतिक्रिया की (एमआर) की कसौटी के अनुसार, परत-2/3 कोशिकाओं के बहुमत जटिल कोशिकाओं रहे हैं, जो रिंगक एट अल.(2002) की प्रयोगात्मक परिणामों के साथ सहमत हैं । परत-2/3 कोशिकाओं के पर और बंद उपक्षेत्र के बीच ओवरलैप की हद तक की मात्रा का ठहराव किया गया था।कोशिकाओं के मॉडुलन अनुपात और 'कोशिकाओं ग्रहणशील क्षेत्रों में पर बंद छोटा प्रदेश ओवरलैप के बीच एक महत्वपूर्ण संबंध पाया गया था।स्पैकिंग सीमा और स्पैकिंग में गैर रैखिकता, कोशिकाओं के एमआर पर एक महत्वपूर्ण प्रभाव है, जो प्रिडबे एट अल.(2004) की प्रयोगात्मक परिणामों के साथ सहमत हैं। यह देखा गया है कि साधारण कोशिकाओं जटिल कोशिकाओं की तुलना में तेज उन्मुखीकरण ट्यूनिंग है। यह रोस और ब्लैकमोर(1974) की प्रयोगात्मक अध्ययन के साथ समझौते में है।

एक परत-2/3 सेल के व्यवहार 'की तरह जटिल सेल' उन्मुखीकरण नक्शे में सेल के स्थान पर कोई निर्भरता है पाया गया था। इसी प्रयोगात्मक परिणाम अभी तक साहित्य में रिपोर्ट नहीं कर रहे हैं।

स्थानीय पार्श्व संबंध उन्मुखीकरण ट्यूनिंग विशेषताओं में सुधार के साथ, कोशिकाओं की प्रतिक्रिया मिलाना कर सकते हैं। परत-2/3 कोशिकाओं की मॉड्यूलेशन अनुपात में कमी आई है जब प्रतिक्रिया संबंध शामिल थे। उच्च मॉडुलन अनुपात के साथ कोशिकाओं मॉडुलन अनुपात में एक बड़ा कमी देखी गई जब प्रतिक्रिया संबंध शामिल थे, जो बारडी एट अल.(2006) की प्रयोगात्मक परिणामों के साथ समझौते में है। प्रतिक्रिया संबंध कोशिकाओं के उन्मुखीकरण ट्यूनिंग विशेषताओं में सुधार हुआ। हम रिपोर्ट है कि स्थानीय पार्श्व कनेक्शन और प्रतिक्रिया कनेक्शन के संयुक्त प्रभाव के कारण, कोशिकाओं को हासिल तेज ट्यूनिंग विशेषताओं, जबकि प्रतिक्रिये में चरण गैर विचरण बनाए रखने। हम परत-2/3 कोशिकाओं में असमानता चयनात्मकता पर कब्जा कर सकता। परत-2/3 कोशिकाओं की पसंदीदा दूरबीन चरण असमानता इसकी परत-4 साधारण सेल सब यूनिटों के ग्रहणशील क्षेत्रों के ज्ञान से भविष्यवाणी की जा सकती है। परत-2/3 कोशिकाओं की असमानता वरीयता की विशेषता किया गया था, और असमानता नक्शा परत-2/3 के लिए प्राप्त हुई थी। असमानता नक्शा कमजोर क्लस्टर है। परत-2/3 कोशिकाओं की असमानता ट्यूनिंग विशेषताओं के साथ कोई रिश्ता नहीं है उनकी उन्मुखीकरण ट्यूनिंग विशेषताओं। स्थानीय पार्श्व संबंध कोशिकाओं की असमानता के प्रति संवेदनशीलता में सुधार होगा। प्रतिक्रिया के

कारण, कोशिकाओं के सबसे चरण गैर विचरण संपत्ति को प्राप्त, और उन्मुखीकरण का पता लगाने और असमानता का पता लगाने में उच्च संकल्प। जबकि उच्च देरी प्रतिक्रिया कोशिकाओं के चरण गैर विचरण संपत्ति में सुधार कम देरी प्रतिक्रिया असमानता चयनात्मकता में सुधार। हमारे मॉडल की यह भविष्यवाणी प्रायोगिक सत्यापन की जरूरत है।

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