Review Paper

Mapping the primate lateral geniculate nucleus: A review of experiments and methods ☆

Ailsa M. Jeffries [1], Nathaniel J. Killian [1], John S. Pezaris *

Department of Neurosurgery, Massachusetts General Hospital, Harvard Medical School, 55 Fruit Street, Boston, MA 02114, USA

ABSTRACT

Mapping neuronal responses in the lateral geniculate nucleus (LGN) is key to understanding how visual information is processed in the brain. This paper focuses on our current knowledge of the dynamics the receptive field (RF) as broken down into the classical receptive field (CRF) and the extra-classical receptive field (ECRF) in primate LGN. CRFs in the LGN are known to be similar to those in the retinal ganglion cell layer in terms of both spatial and temporal characteristics, leading to the standard interpretation of the LGN as a relay center from retina to primary visual cortex. ECRFs have generally been found to be large and inhibitory, with some differences in magnitude between the magno-, parvo-, and koniocellular pathways. The specific contributions of the retina, thalamus, and visual cortex to LGN ECRF properties are presently unknown. Some reports suggest a retinal origin for extra-classical suppression based on latency arguments and other reports have suggested a thalamic origin for extra-classical suppression. This issue is complicated by the use of anesthetized animals, where cortical activity is likely to be altered. Thus further study of LGN ECRFs is warranted to reconcile these discrepancies. Producing descriptions of RF properties of LGN neurons could be enhanced by employing preferred naturalistic stimuli. Although there has been significant work in cats with natural scene stimuli and noise that statistically imitates natural scenes, we highlight a need for similar data from primates. Obtaining these data may be aided by recent advancements in experimental and analytical techniques that permit the efficient study of nonlinear RF characteristics in addition to traditional linear factors. In light of the reviewed topics, we conclude by suggesting experiments to more clearly elucidate the spatial and temporal structure of ECRFs of primate LGN neurons.

© 2013 Elsevier Ltd. Published by Elsevier Ltd. All rights reserved.

Contents

* Corresponding author. Address: Massachusetts General Hospital, 55 Fruit Street, THR-425, Boston, MA 02114, USA. Tel.: +1 617 643 5313.
   E-mail address: pezaris.john@mgh.harvard.edu (J.S. Pezaris).
[1] These authors contributed equally to this work.

1. Introduction

The dorsal lateral geniculate nucleus (LGN) of the thalamus is a small, bi-lateral structure that accepts input from each eye representing the contralateral half of the visual field and projects to the primary visual cortex (see Fig. 1). In higher primates, the structure comprises six laminae with associated inter-laminar structures that macroscopically segregate the magno-, parvo-, and koniocellular visual streams originating in the anatomically ipsi- and contralateral eyes. The LGN receives input that originates at the retina, passes through the optic nerves, continues to the optic chiasm where signals from the two eyes are shuffled into the two visual hemifields, then courses along the optic projection to the LGN. The LGN, in turn, sends its output along a projection to primary visual cortex (Area V1) via the optic radiation.

Cells in the LGN respond to small, well-defined regions of visual space that are called visual receptive or response fields (RFs), much like those found in the ganglion cell layer of the retina (RGC). The typical RF can be thought of as a spatio-temporal differentiator that responds best to highly local changes in visual contrast (see Fig. 2 and discussed in Section 2 below). Changes can be either spatially or temporally expressed, with cells largely falling into one of two categories, those that respond to either focal increases (*on* cells) or decreases (*off* cells) of luminance. There is nearly a one-to-one anatomical mapping from retina to LGN in the cat (Hamos et al., 1987) and evidence for similarly high anatomical specificity in primates (Conley and Fitzpatrick, 1989). In addition, there is a nearly one-to-one functional mapping in cats (Cleland et al., 1971) and primates (Kaplan et al., 1987; Lee et al., 1983; Sincich et al., 2009b) from ganglion cell output to LGN cell input, so the close matching of RF characteristics between RGCs and LGN neurons is perhaps not surprising. And, like those found in RGCs, responses in LGN are adapted by luminance and contrast at a larger spatial scale than the RF.

The standard conceptual framework that partitions visual receptive fields into a smaller classical receptive field (CRF) and a larger modulatory extra-classical receptive fields (ECRFs) was established by Hubel and Wiesel (Hubel and Wiesel, 1962, 1961, 1959) a half-century ago. In this paper we will use RF to indicate the entirety of the response field in all of its aspects, CRF to indicate just the classical, small center-surround structure, and ECRF for any parts of the RF that extend beyond the CRF in either space or time, reflecting common usage in the literature.

In this paper we review recent CRF/ECRF studies of the lateral geniculate nucleus of the thalamus. The focus of this review is on the primate LGN and we will frequently cite studies in other species such as cats that serve as points of reference for work in primates. With a growing body of knowledge about RFs in the
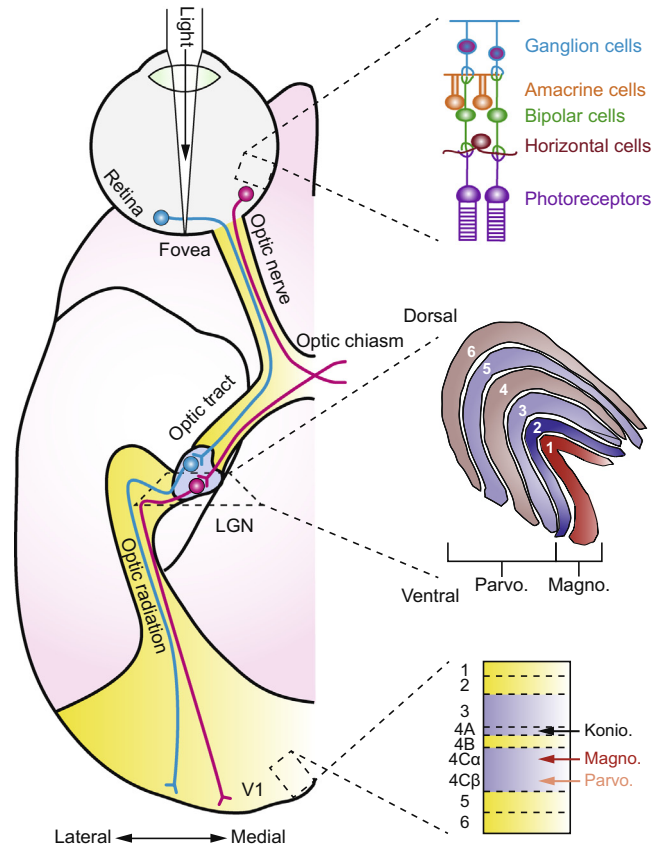

Fig. 1. Early visual system pathways of the macaque monkey. The figure on the left shows the pathway of visual information imaged on the retina as it passes through the LGN and arrives at the primary visual cortex (V1). The anatomical schematic represents a ventral view of the right hemisphere. The visual scene is imaged by photoreceptors in the retina and information is passed through bipolar cells to retinal ganglion cells whose axons exit the back of the eyeball forming the optic nerve. Information from the contralateral part of the scene reaches the LGN with input from the two eyes arriving at separate layers of the LGN: layers 2, 3, and 5 receive input from the ipsilateral eye and layers 1, 4, and 6 receive input from the contralateral eye. The magnocellular layers (1 and 2) receive input that originated from rod photoreceptors and the Parvocellular layers (3–6) receive input that originated from cone photoreceptors. Koniocellular cells in the LGN are interspersed between the magnocellular and parvocellular layers and receive information arising from short-wavelength cones. Cells in the LGN project mainly to layer 4 of the primary visual cortex through a formation called the optic radiation. Adapted from Solomon and Lennie, 2007 with permission.

primate early visual pathway, it is now clear that the ECRF is an important part of LGN RFs in primate, and that the functional im-
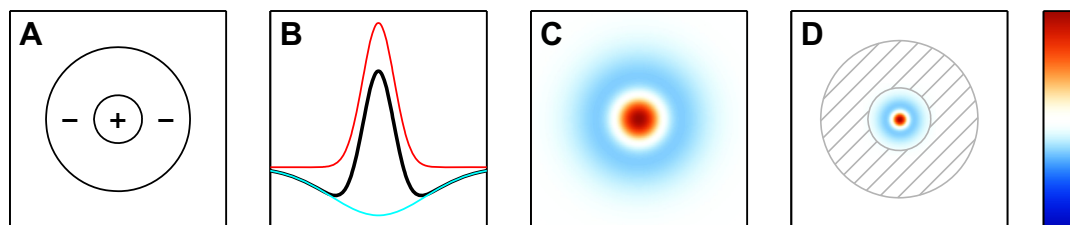

Fig. 2. Classical and Extra-Classical Receptive Fields in the LGN. (A) The classical receptive field (CRF) comprises a central *on* or *off* region and a surrounding ring having the opposite sign. For *on*-center cells, light in the center excites the cell and light in the surround inhibits the cell; the reverse is true for *off*-center cells. Firing rate is approximately linearly determined by weighting the light in the center and surround regions. (B) The CRF can be modeled as the sum of two Gaussians, shown in section through the center of the field, a narrower excitatory region shown in red and a broader inhibitory one shown in blue for the example *on* cell here. The sum of the two is in black, and forms the well-known Mexican Hat profile. (C) The same difference of Gaussians is shown in a full two dimensional plot where color ranges from deep red for excitatory, through white for indifferent, and deep blue for inhibitory. Since the inhibitory field is not as strong as the excitatory field, it does not reach into deep blues, but remains at lighter ones. (D) The ECRF is an as-yet poorly defined region that is larger than the CRF, and is shown here in hatched gray. The reader should note that the ECRF may also extend through the area of visual space in which the CRF resides. Stimuli in the ECRF modulate the response to stimuli in the CRF, but without being able to directly generate spikes. Current thought holds that the ECRF provides contrast-dependent gain control on CRF sensitivity.