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Review article

Towards building a more complex view of the lateral geniculate nucleus: Recent advances in understanding its role

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ABSTRACT

The lateral geniculate nucleus (LGN) has often been treated in the past as a linear filter that adds little to retinal processing of visual inputs. Here we review anatomical, neurophysiological, brain imaging, and modeling studies that have in recent years built up a much more complex view of LGN. These include effects related to nonlinear dendritic processing, cortical feedback, synchrony and oscillations across LGN populations, as well as involvement of LGN in higher level cognitive processing. Although recent studies have provided valuable insights into early visual processing including the role of LGN, a unified model of LGN responses to real-world objects has not yet been developed. In the light of recent data, we suggest that the role of LGN deserves more careful consideration in developing models of high-level visual processing.

Contents

Abbreviations: ART, adaptive resonance theory; BOLD, blood oxygen level dependent; Ca^{2+}, calcium; DoG, difference of Gaussians; EEG, electroencephalogram; EPSP, excitatory postsynaptic potential; fMRI, functional magnetic resonance imaging; IT, inferotemporal cortex; K, koniocellular; LFP, local field potential; LGN, lateral geniculate nucleus; M, magnocellular; MEG, magnetoencephalography; MT, middle temporal visual cortex, V5; Na^{+}, sodium; P, parvocellular; PSP, postsynaptic potential; RGC, retinal ganglion cell; TRN, thalamic reticular nucleus; V1, visual cortex area 1, striate cortex; V2, visual cortex area 2; V3, visual cortex area 3; V4, visual cortex area 4.

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1. Introduction

We shall be reviewing the literature on the lateral geniculate nucleus (LGN), with a particular interest in its possible cognitive and computational role in higher vision, such as object recognition. Coming from computational backgrounds, we are interested in including a comprehensive summary of recent advances in LGN neurobiology that may assist those interested in developing more advanced and realistic modeling. As we are not proselytizing a specific theory of LGN function, the range of topics covered will be rather unfiltered and eclectic, with the hopes that this will foster a cross-fertilization in future experimental and theoretical work.

1.1. The lateral geniculate as a relay nucleus

The LGN, interposed between retina and primary visual cortex, has traditionally been characterized as a "relay nucleus" joining the two. What does it mean to be a "relay nucleus" in the brain? Perhaps the concept arose by analogy with 19th century telegraph relay stations that were placed at intervals along the line to boost signal strength attenuated by resistance in the wires. However, the demonstration by Adrian (1926) of the regenerative nature of neural action potentials, which did not attenuate with distance, showed that the brain did not need a "relay nucleus" in that sense. Despite that, the term has continued in use for decades, a vacuous placeholder for lack of a compelling theory of LGN function.

Another more recent concept of a relay, besides being an amplifier, is as a gating device in which a small signal controls a large signal, switching it on and off, as in an electromechanical relay or a transistor switch. We find this second concept of "relay" emphasized in ideas about LGN function developed several decades ago. Specifically, modulatory inputs from brainstem nuclei to LGN are believed to behave as an on/off switch for transmission of signals from retina to cortex during sleep (Burke and Cole, 1978; McCormick and Bal, 1997; Singer, 1977; Steriade et al., 1993).

While the idea of LGN as a gating relay associated with sleep/wakefulness certainly has merit, the elaborate anatomical organization of the LGN together with its known physiological response properties suggest that it also has a role in computationally *transforming* or *non-linearly filtering* visual signals that goes beyond simply *relaying* them. While the purpose of the LGN still remains a mystery, we hope that by emphasizing the literature related to visual functions in the awake state we shall be in a position to clarify and highlight the more central issues that need to be resolved in the future.

People used to think of the LGN as a simple, largely linear, early stage of visual processing whose details we do not have to worry about in the context of higher-level functions, like object-vision and attention. However, recent studies suggest that LGN plays a more active role in visual information processing (e.g. Andolina et al., 2013; Briggs et al., 2013; Cudeiro and Sillito, 2006; Kastner et al., 2004, 2006; McAlonan et al., 2008; O'Connor et al., 2002; Saalmann and Kastner, 2009, 2011; Sillito et al., 2006). This review links between neurophysiological, neuroimaging, and computational studies about the LGN. We also cover modeling studies of LGN neurons and networks, a topic that has not been extensively reviewed before. The modeling part in particular defines a roadmap to be considered for future modeling efforts. It has an impact not only on modeling the early visual processes but also on object-vision models of higher visual areas. We argue how considering more realistic models of LGN can help to boost the performance of high-level object-vision models. In essence, we suggest a general framework in which a computational model of the LGN can be considered as an additional layer before the first layer of biologically inspired hierarchical models of object recognition (Dura-Bernal et al., 2012; Ghodrati et al., 2012; Rajaei et al., 2012; Riesenhuber and Poggio, 1999; Serre et al., 2007a; Wallis and Rolls, 1997).

1.2. Evolutionary constraints affecting LGN organization

Developmental constraints reflecting the evolutionary history of biological structures are likely to be a force for conservatism in their organization (Olson, 2012). Such constraints hinder radical reorganizations of those structures even when arrangements that are more efficient become possible as new contexts arise. The general topology of neural connections between retina, LGN, and cortex currently in mammals appears to have conserved patterns established at least three hundred million years earlier, amongst precursor structures that existed in the common ancestor to all amniotes (Butler, 1994a,b; Hofmann and Northcutt, 2012; Northcutt, 2011). Amniotes originated in the carboniferous era and comprise reptiles, birds, and mammals, all of which have a direct projection from retina to a dorsal thalamic nucleus, which in turn projected to the pallium (from which neocortex originated). The pallium has then sent a reciprocal projection back to the thalamic nucleus, with this feedback likely in existence since at least the