

# Retinal and Nonretinal Contributions to Extraclassical Surround Suppression in the Lateral Geniculate Nucleus

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Extraclassical surround suppression is a prominent receptive field property of neurons in the lateral geniculate nucleus (LGN) of the dorsal thalamus, influencing stimulus size tuning, response gain control, and temporal features of visual responses. Despite evidence for the involvement of both retinal and nonretinal circuits in the generation of extraclassical suppression, we lack an understanding of the relative roles played by these pathways and how they interact during visual stimulation. To determine the contribution of retinal and nonretinal mechanisms to extraclassical suppression in the feline, we made simultaneous single-unit recordings from synaptically connected retinal ganglion cells and LGN neurons and measured the influence of stimulus size on the spiking activity of presynaptic and postsynaptic neurons. Results show that extraclassical suppression is significantly stronger for LGN neurons than for their retinal inputs, indicating a role for extraretinal mechanisms. Further analysis revealed that the enhanced suppression can be accounted for by mechanisms that suppress the effectiveness of retinal inputs in evoking LGN spikes. Finally, an examination of the time course for the onset of extraclassical suppression in the LGN and the size-dependent modulation of retinal spike efficacy suggests the early phase of augmented suppression involves local thalamic circuits. Together, these results demonstrate that the LGN is much more than a simple relay for retinal signals to cortex; it also filters retinal spikes dynamically on the basis of stimulus statistics to adjust the gain of visual signals delivered to cortex.

**Key words:** corticogeniculate; receptive field; spatial; temporal; thalamus; V1

## Significance Statement

The lateral geniculate nucleus (LGN) is the gateway through which retinal information reaches the cerebral cortex. Within the LGN, neuronal responses are often suppressed by stimuli that extend beyond the classical receptive field. This form of suppression, called extraclassical suppression, serves to adjust the size tuning, response gain, and temporal response properties of neurons. Given the important influence of extraclassical suppression on visual signals delivered to cortex, we performed experiments to determine the circuit mechanisms that contribute to extraclassical suppression in the LGN. Results show that suppression is augmented beyond that provided by direct retinal inputs and delayed, consistent with polysynaptic inhibition. Importantly, these mechanisms influence the effectiveness of incoming retinal signals, thereby filtering the signals ultimately conveyed to cortex.

## Introduction

Visual information is transmitted from the retina to the cerebral cortex via relay neurons in the lateral geniculate nucleus (LGN) of the dorsal thalamus. Although the retina provides only 5–10% of the synapses made with LGN neurons (Hamos et al., 1987),

retinal ganglion cells (RGCs) are the primary drivers of LGN activity (Sherman and Guillery, 2009). Accordingly, it has been suggested that nearly all LGN action potentials are triggered directly by retinal spikes (Kaplan and Shapley, 1984; Sincich et al., 2007). The functional dominance of the retina on the LGN is further indicated by the high degree of similarity between the classical receptive fields of synaptically connected RGCs and LGN neurons (Usrey et al., 1999; Rathbun et al., 2010). With these features of retinogeniculate communication in mind, it is important to emphasize that not all retinal spikes are transmitted to visual cortex because the LGN filters incoming spikes on the basis of prior activity, statistics of the visual environment, and behavioral state (Livingstone and Hubel, 1981; Mastrorade, 1987; Usrey et al., 1998; Lesica and Stanley, 2004; Alitto et al., 2005; Denning and Reinagel, 2005; Rathbun et al., 2007, 2010; Weyand,

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