DOES THE LATERAL GENICULATE NUCLEUS (LGN) PAY ATTENTION?

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Introduction

The dorsal lateral geniculate nucleus (LGNd) of the thalamus has been long regarded as a simple relay station for visual information passing from the periphery to cortex. If true, what advantages does this design impart? Furthermore, why should the brain invest resources in constructing and maintaining a nucleus for visual information if messages transmitted through it are not changed appreciably? We know, for example, that the receptive field (RF) properties of LGNd neurons are very similar to those of their retinal ganglion cell inputs. We also know that the LGNd, like other thalamic sensory relay nuclei, receives input not only from the periphery (the retina), but also from many cortical and subcortical sources. In the case of the LGNd, these other inputs significantly outweigh, in terms of synapse number, the retinal input. In fact, the precise inhibitory circuitry and array of different transmitter receptors that are located on both excitatory relay cells and inhibitory interneurons within the LGNd indicate that signals are modulated in complex ways.

With the exception of changes in firing patterns associated with major changes in an animal's state of arousal (i.e., sleep versus waking), it has been difficult to define behaviorally relevant roles of thalamic nuclei like the LGNd. A number of models have proposed that the various inputs to thalamic nuclei like the LGNd may modulate signals related to task relevance and attention. Additionally, state-dependent modulation has been demonstrated in the main target of the LGNd, the primary visual cortex (V1) as well as in other cortical and subcortical areas that project directly to the LGNd. The few studies that have examined directly the role of attention at the level of the LGNd have yielded conflicting results.

In this study we tested the hypothesis that LGNd cell activity is influenced by attention by examining the firing pattern of single LGNd cells while two monkeys performed three simple visuomotor tasks. In support of our hypothesis we show that LGNd cells change their firing pattern significantly depending upon whether or not attention is paid to a target.

Methods

Subjects: Two awake behaving bonnet macaque (*Macaca radiata*) monkeys

Stimuli: Small, isoluminant, colored squares optimized for each neuron

Detection of eye movements: Search coil

Physiological recordings: Extracellular, single-unit recordings were made via vertical penetrations from all layers of the LGNd (Fig. 1). RFs of recorded cells were located, on average, 10 degrees eccentric to the point of fixation.

Analysis: The timing of significant modulations of activity, including visual response latencies, were examined using a Poisson spike train analysis described originally by Legendy and Salcman (1985) and applied by Hanes et al. (1995) (Fig. 2). Additionally, the mean firing rate of the cell was determined for the period of time the RF was stimulated. Because the tasks involved a saccade, this period of time corresponded to the time between the target response latency (mean = ~40 msec), as reported by the Poisson analysis, and the saccade latency (mean = ~165 msec).

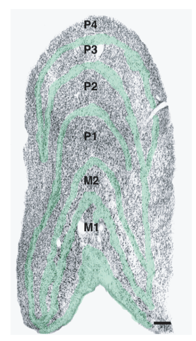


Fig. 1. Coronal section through a macaque monkey LGN showing the location of magnocellular layers (M), parvocellular layers (P) and koniocellular layers (green) (scale bar = 500 microns). Each individual layer of the LGNd receives input from only one eye. P4, P2, and M1 are driven by the eye contralateral to the LGNd while the remaining 3 layers are driven by the eye ipsilateral to the LGNd.

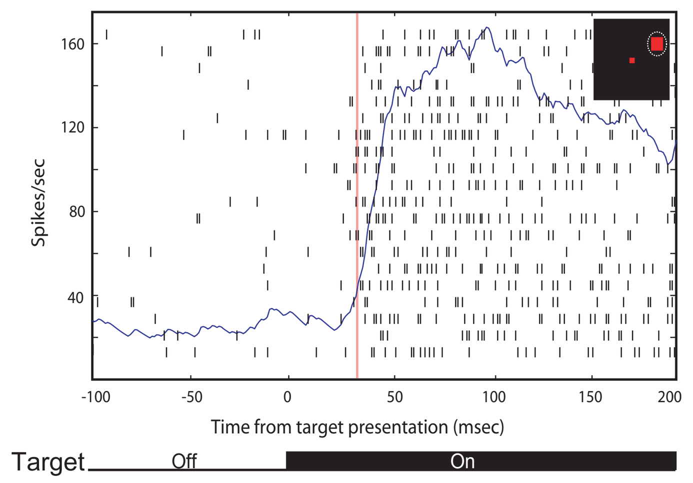


Fig 2. Peristimulus time histogram of an LGNd P cell recorded before and during stimulation of its RF by an optimized colored stimulus while the monkey fixated a single pixel (see inset). The vertical red line denotes the response latency as determined by the Poisson analysis.

Results

LGN Cell Identification

Figures 3-6. LGN cells were classified based on a constellation of criteria including color selectivity, ocular dominance, latency to target onset, and response transience. Figures 3 - 6 are peristimulus time histograms for four LGN cells. Trials are aligned to target onset (vertical column of triangles at 0 msec). The red line indicates the response latency to target onset as determined by the Poisson analysis. Targets were presented inside the mapped LGN cell's RF (see insets) for 350-650 msec while the monkeys fixated a central fixation spot. Target stimuli were isoluminant with each other and were optimized for each neuron tested (eg. color).

Fig. 3

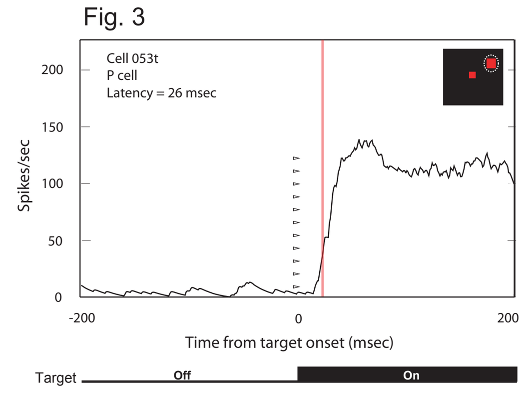


Fig. 4

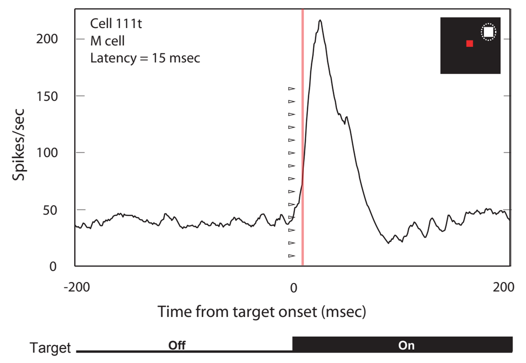


Fig. 5

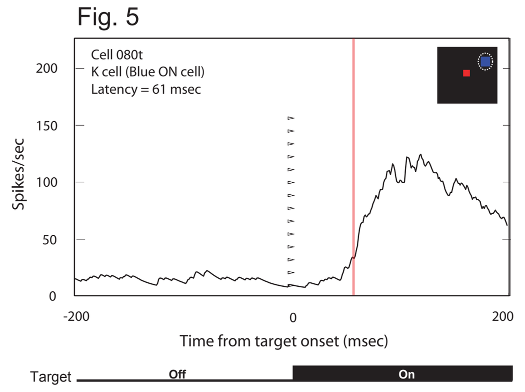
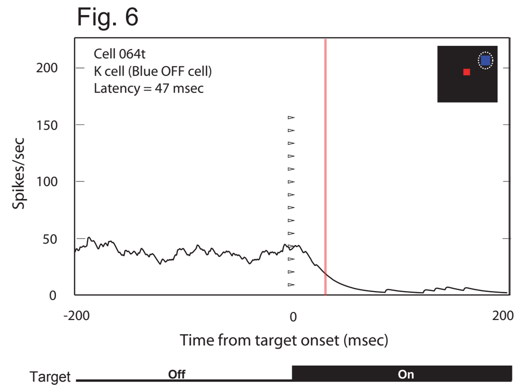


Fig. 6



Two Stimuli: One Hemifield

Trials are blocked into groups of 10-20

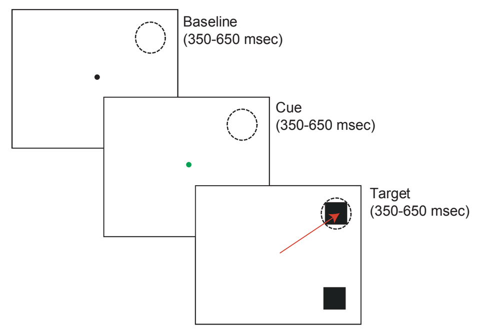


Fig. 7. Two Stimuli, Saccade into RF. Trials begin with the monkeys fixating the fixation point. After a variable period of fixation, the monkeys were cued by a change in color of the fixation point from white to green, indicating to the monkey to prepare to make a saccade to an impending target. Two targets are presented simultaneously, one inside the cell's RF and one outside the RF (within the same hemifield at a position with the same eccentricity but opposite elevation). After a short reaction time, the monkey shifts gaze to the target for a reward. The monkeys use a win-stay/lose-shift strategy to maximize reward as the 'correct' target is unknown on the first trial.

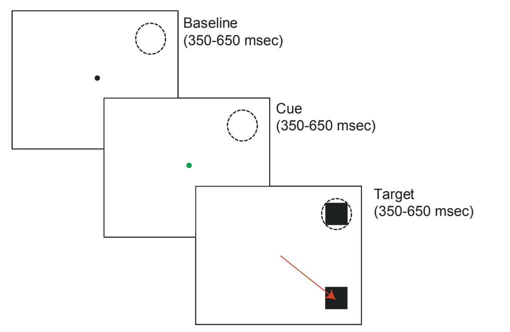


Fig. 8. Two Stimuli, Saccade outside RF. This is an alternative version of the task presented in figure 7. Trial events are identical until the monkey shifts gaze to one of the two targets. Here, the 'correct' target is the target presented outside the LGN's RF. Again, when the first trial begins, the monkeys are unaware as to the 'correct' or 'rewarded' target. Monkeys will employ a win-stay/lose-shift strategy in order to maximize reward.

Figures 9 and 10. Peristimulus time histograms from two LGNd cells that were recorded during the Two Stimuli task described in figures 7 and 8. The blue trace refers to trials where the monkey shifted gaze to the RF and the black dashed trace refers to trials where the monkey shifted gaze to the nonRF location. The red line indicates the cell's response latency to target onset as determined via the Poisson analysis.

It should be noted that the response latencies to target onset were not significantly different between the two tasks for these cells.

The cells' mean firing rate from the time of target onset to the time of saccade initiation was significantly higher when the monkeys made saccades to the RF location.

Fig. 9

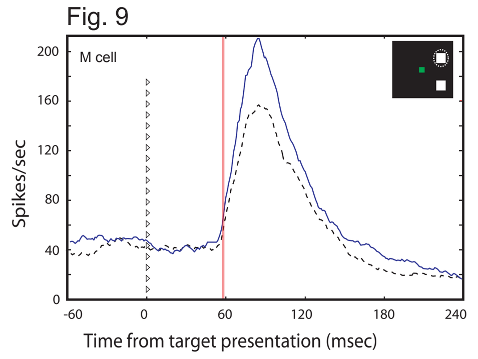
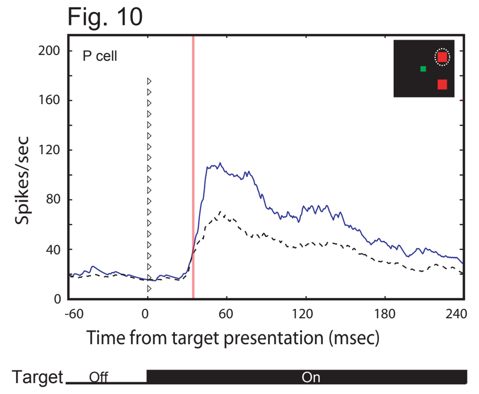


Fig. 10



Two Stimuli: Two Hemifields

Trials are blocked into groups of 10-20

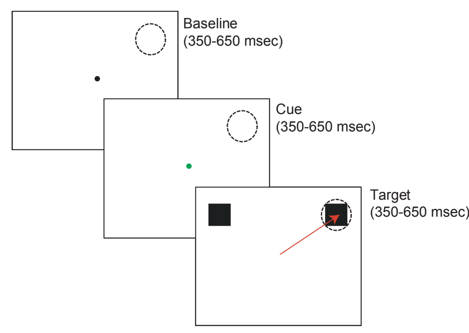


Fig11. Two Stimuli, Saccade into RF

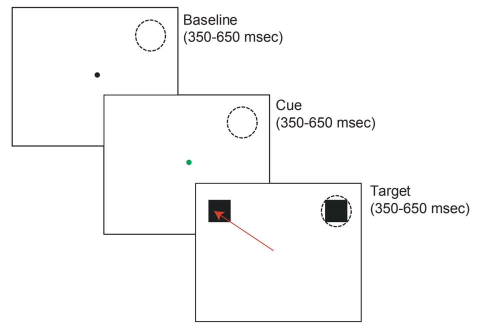


Fig. 12. Two Stimuli, Saccade out of RF

Figures 11 and 12 represent an alternative form of the task outlined in figures 7 and 8. This modification is subtle in design yet quite significant when one considers the connectivity of the LGNd. Each LGNd receives information from only one hemifield, therefore, the previous tasks test the spatial specificity of attentional modulation within a hemifield/ LGNd whereas the tasks outlined above test whether attentional effects cross hemifields.

Trial events are identical to those described for the previous task. Again, when the first trial begins, the monkeys are unaware of the 'correct' or 'rewarded' target. Monkeys will employ a win-stay/lose-shift strategy in order to maximize reward.

Figures 13 and 14. Peristimulus time histograms from two LGNd cells that were recorded during the Two Stimuli task described in figures 11 and 12. The blue trace refers to trials where the monkey shifted gaze to the RF and the black dashed trace refers to trials where the monkey shifted gaze to the nonRF location. The red line indicates the cell's response latency to target onset as determined via the Poisson analysis.

As before, the response latencies to target onset were not significantly different between the two tasks for these cells.

The cells' mean firing rate from the time of target onset to the time of saccade initiation was significantly higher when the monkeys made saccades to the RF location.

Fig. 13

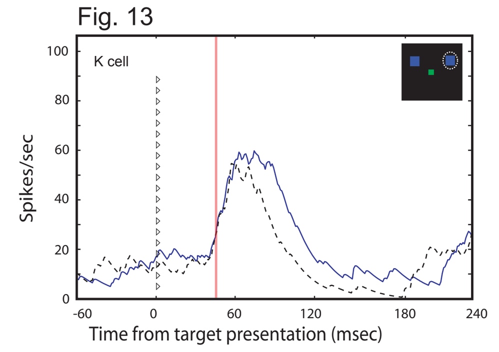
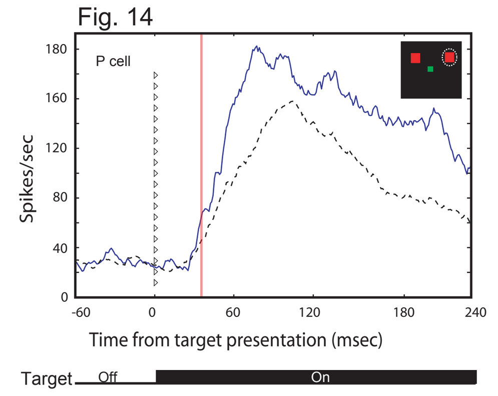


Fig. 14



One Stimulus: Go-NoGo

Trials are interleaved

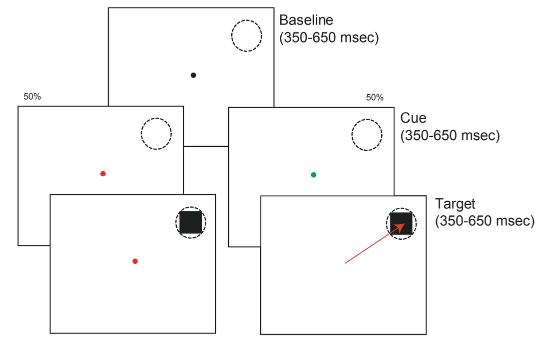


Fig. 15. One Stimulus, Fixate or Saccade into RF based on cue presented at the fixation point. This task differs from the earlier designs in that here, monkeys are required to follow the instructional cue at the fixation point in order to maximize reward - red cue means the monkey is to continue fixating the fixation point (left panels), and a green cue instructs the monkey to shift gaze to the target (right panels). Trials are interleaved, therefore, monkeys must be more vigilant during this task than the previous tasks in order to maximize reward.

Figures 16 and 17. Peristimulus time histograms from two LGNd cells that were recorded during the One Stimulus task described above. The average saccade latency was ~150 msec. Therefore, please note that we have truncated the histograms appropriately.

Similar to the other tasks, response latency to target onset was not affected significantly by the demands of the task. However, unlike the Two Stimuli conditions, the cells' mean rate of firing from target onset to time of saccade initiation did not vary significantly for the single target condition.

Fig. 16

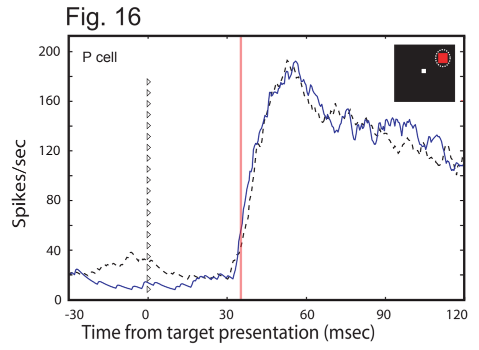
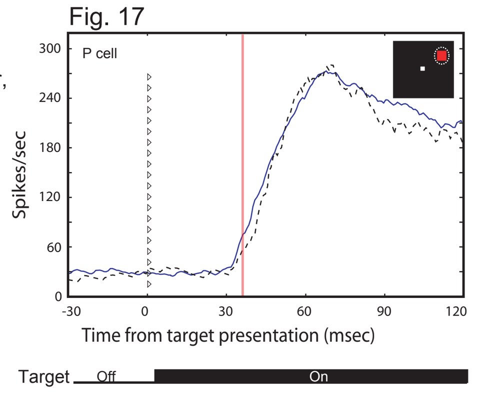


Fig. 17



Results Summary

1. A total of 90 LGNd cells were recorded during the Two Stimulus conditions and a total of 58 LGNd cells were recorded during the Single Stimulus condition. Cells were recorded from all layers of the LGNd.

2. Sixty percent of LGNd cells of all classes demonstrated significant enhancements in peak response magnitude (mean = 28%) and mean activity (mean = 26%) when the correct target was in the RF, regardless of whether the nonRF target location was in the hemifield ipsilateral or contralateral to the RF. Only two cells showed significant enhancement of activity when the nonRF target was correct (in both cases the enhancement was less than 10%).

3. Significant modulation of LGN activity was never observed in the Single Target condition.

Conclusions

1. LGNd cells demonstrated enhancements in peak and mean firing rate during tasks where monkeys were rewarded for choosing a target presented inside the RF over a target presented outside the RF.

2. No changes in LGN activity were seen when monkeys were rewarded for either remaining fixated or making a saccade to the RF based upon a foveal cue.

3. These results suggest that LGN activity is enhanced under conditions where monkeys must allocate spatial attention to a target in the RF.

4. Future studies will require that we demonstrate these changes in LGN cell activity in a task (manual) that does not involve saccadic eye movements.

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