SPATIAL ATTENTION IN THE LATERAL GENICULATE NUCLEUS (LGN): ARE EFFECTS ACROSS HEMIFIELDS THE SAME AS WITHIN A HEMIFIELD?

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Introduction

The functional role of the LGN remains quite controversial. Traditionally, the LGN in primates has been viewed as the lowest level of a set of feedforward parallel visual pathways to cortex. These feedforward pathways are pictured as connected hierarchies of areas designed to construct the visual image gradually - adding more complex features as one marches through successive levels of the heirarchy. In terms of synapse number and circuitry, the anatomy suggests that the LGN can be viewed also as the ultimate terminus in a series of feedback pathways that originate at the highest cortical levels. One role that has been proposed for the LGN is in the regulation of attention. Support for such a role comes from recent fMRI studies (Conners et al., 2003; Kastner et al., 2004). Here we ask whether such a role can be demonstrated at the single-cell level in awake behaving monkeys.

Two types of task were used in this study: 1) A GO-NOGO task where the monkey was instructed by a change in the fixation spot color to either make a saccade (GO) to a target in the receptive field (RF) or to continue fixating (NOGO), 2) A WIN STAY-LOSE SHIFT task where two targets were presented simultaneously equidistant from the fixation point (one target in the RF and the other outside the RF) either in the same or opposite visual hemifields. The GO-NOGO task was presented either in blocks or with trials interleaved. The WIN STAY-LOSE SHIFT task was presented in blocks. In the latter task, the monkey did not know which of the two targets was correct on the first trial in the block but thereafter could predict that the same target would be rewarded for the next 20+ trials (WIN STAY). No reward indicated to the monkey that he should switch to the other target (LOSE-SHIFT).

Methods

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

Stimuli: Single LGN cell receptive fields were mapped with red, green, blue and grey isoluminant stimuli. All cells were tested with stimuli of preferred color that covered both the center and surround of the cell's receptive field.

Detection of eye movements: Search coil (250 Hz sampling rate).

Physiological recordings: Extracellular, single unit recordings (1kHz sampling rate) were made via vertical penetrations from all layers of the LGN (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 onset response latency (mean = ~40 msec) as reported by the Poisson and the saccade latency (mean = ~165 msec).

Fig. 1. Coronal section through a macaque monkey LGN showing the location of both magnocellular layers (M), parvocellular layers (P) and koniocellular layers (green) (scale bar = 500 microns). Each individual layer of the LGNd receives input from only 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.

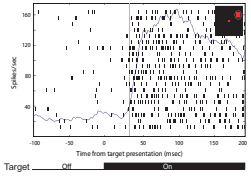

Fig. 2. Peristimulus time histogram of an LGNd P cell recorded before and during stimulation of its RF by an optimized colored stimulus while the monkey fixated a single pixel (see inset). The vertical red line denotes the response latency as determined by the Poisson analysis. Curve was smoothed using a rise constant of 1 ms and a decay constant of 20 ms.

Results

Result 1

Our first task investigated whether shifts in gaze to either the RF location or to a location equidistant from the RF but in the opposite hemifield impacted LGN firing rates (see Fig. 3 for task description). Trials were run in blocks of 20. An analysis of data collected on 53 LGN cells suggested that firing rates of a percentage of LGN cells were enhanced when the animal had prepared to shift gaze to the RF location. Blocks, however, were not interleaved in this condition (see Result 4)

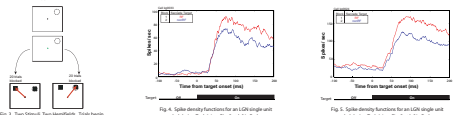

Fig. 3. Two Stimuli, Two Hemifields. Trials begin with the monkey fixating the fixation point. After a variable period of fixation, the monkeys are cued by a change in the fixation point from white to green, indicating to the monkey to prepare to shift gaze to an impending target. Two targets are presented simultaneously, one inside the cell's RF and one outside the RF (in the opposite hemifield at the same eccentricity and elevation). After a short reaction time, the monkey shifts gaze to the target for reward. The monkey use a win-stay/lose-shift strategy to maximize reward as the 'correct' target is unknown on the first trial.

Fig. 4. Spike density functions for an LGN single unit recorded during Task 1 (see Fig. 3 at left). Red curve represents the mean activity recorded during those trials where the monkey produced a saccade to the RF target and the blue curve represents the mean activity recorded during those trials where the monkey produced a saccade to the nonRF. Trials are aligned on target onset. The time of the earliest saccade during these trials and conditions was outside the scale shown.

Fig. 5. Spike density functions for an LGN single unit recorded during Task 1 (see Fig. 3 at left). Red curve represents the mean activity recorded during those trials where the monkey produced a saccade to the RF target and the blue curve represents the mean activity recorded during those trials where the monkey produced a saccade to the nonRF. Trials are aligned on target onset. The time of the earliest saccade during these trials and conditions was outside the scale shown.

Result 2

Our second task investigated whether the effects outlined above were evident when the monkeys produced saccades to RF and nonRF targets within the same visual hemifield. An analysis of data from 17 LGN cells showed that the firing rates of some LGN were larger when the animal prepared to shift gaze to the RF location. Again, the two conditions were practiced in only two blocks, without order counterbalance.

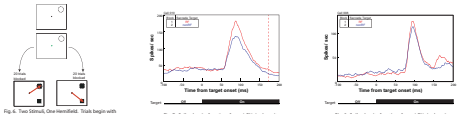

Fig. 6. Two Stimuli, One Hemifield. Trials begin with the monkeys fixating the fixation point. After a variable period of fixation, the monkeys are cued by a change in the fixation point from white to green, indicating to the monkey to prepare to shift gaze to an impending target. Two targets are presented simultaneously, one inside the cell's RF and one outside the RF (in the same hemifield at the same eccentricity but opposite elevation). After a short reaction time, the monkey shifts gaze to the target for reward. The monkeys use a win-stay/lose-shift strategy to maximize reward as the 'correct' target is unknown on the first trial.

Fig. 7. Spike density functions for an LGN single unit recorded during Task 2 (see Fig. 6 at left). Red curve represents the mean activity recorded during those trials where the monkey produced a saccade to the RF target and the blue curve represents the mean activity recorded during those trials where the monkey produced a saccade to the nonRF. Trials are aligned on target onset. Red dashed line indicates the shortest saccade latency across both conditions.

Fig. 8. Spike density functions for an LGN single unit recorded during Task 2 (see Fig. 6 at left). Red curve represents the mean activity recorded during those trials where the monkey produced a saccade to the RF target and the blue curve represents the mean activity recorded during those trials where the monkey produced a saccade to the nonRF. Trials are aligned on target onset. The time of the earliest saccade during these trials and conditions was outside the scale shown.

Result 3

Our third task investigated whether this enhancement was evident when the monkey was required to either continue fixating or shift gaze to a target presented with the LGN cell's RF based upon a colored cue. To increase the task's level of difficulty and avoid block order effects, these two conditions were interleaved randomly. An analysis of data collected on 54 LGN cells suggests that firing rates of LGN cells were not modulated in a systematic manner.

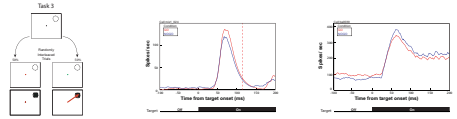

Fig. 9. One Stimulus, Fixate or Saccade into RF based on cue presented at the fixation point (interleaved). This task differs from the earlier designs in that here, monkeys are required to perform a saccade into the RF when instructed in order to maximize reward - red cue means the monkey is to continue 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.

Fig. 10. Spike density functions for an LGN single unit recorded during Task 3 (see Fig. 4 at left). The red curve represents the mean activity recorded during those trials where the monkey produced a saccade to a target presented inside the cell's RF. The blue curve represents the mean activity recorded during those trials where the monkey continued to fixate the fixation point while a target was presented inside the cell's RF. Trials are aligned on target onset. The red dashed line indicates the shortest saccade latency across both conditions.

Fig. 11. Spike density functions for an LGN single unit recorded during Task 3 (see Fig. 4 at left). The red curve represents the mean activity recorded during those trials where the monkey produced a saccade to a target presented inside the cell's RF. The blue curve represents the mean activity recorded during those trials where the monkey continued to fixate the fixation point while a target was presented inside the cell's RF. Trials are aligned on target onset. The time of the earliest saccade during these trials and conditions was outside the scale shown.

Result 4

Result 3 was unexpected considering the effects demonstrated by Results 1 and 2. To investigate the issue further, we modified Task 1 and 2 to include many more trials recorded across multiple, alternating blocks to ensure we were not faced with a 'block order' phenomenon or simple non-stationarities in cellular activity or recording. Preliminary analysis of data collected on 23 LGN cells has thus far failed to yield clear results.

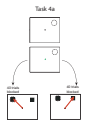

Fig. 12. Two Stimuli, Two Hemifields, Multiple Blocks. This task is nearly identical to Task 1 (Fig. 3) except here the number of trials within each block was increased from 20 to 40. Additionally, multiple blocks were run.

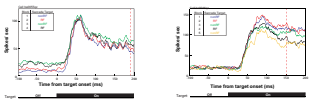

Fig. 13. Spike density functions for an LGN single unit recorded during Task 4a (see Fig. 12 at left). Colored curves represent the mean response of the same LGN single unit to the presentation of a stimulus inside the cell's RF. The curves are color-coded indicating the order in which the blocks of trials were run. Trials are aligned on target onset. The red dashed line indicates the shortest saccade latency across both conditions.

Fig. 14. Spike density functions for an LGN single unit recorded during Task 4a (see Fig. 12 at left). Colored curves represent the mean response of the same LGN single unit to the presentation of a stimulus inside the cell's RF. The curves are color-coded indicating the order in which the blocks of trials were run. Trials are aligned on target onset. The red dashed line indicates the shortest saccade latency across both conditions.

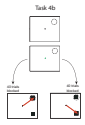

Fig. 15. Two Stimuli, One Hemifield, Multiple Blocks. This task is nearly identical to Task 2 (Fig. 6) except here the number of trials within each block was increased from 20 to 40. Additionally, multiple interleaved blocks were run.

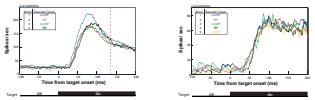

Fig. 16. Spike density functions for an LGN single unit recorded during Task 4b (see Fig. 15 at left). Colored curves represent the mean response of the same LGN single unit to the presentation of a stimulus inside the cell's RF. The curves are color-coded indicating the order in which the blocks of trials were run. Trials are aligned on target onset. The red dashed line indicates the shortest saccade latency across both conditions.

Fig. 17. Spike density functions for an LGN single unit recorded during Task 4b (see Fig. 15 at left). Colored curves represent the mean response of the same LGN single unit to the presentation of a stimulus inside the cell's RF. The curves are color-coded indicating the order in which the blocks of trials were run. Trials are aligned on target onset. The time of the earliest saccade during these trials and conditions was outside the scale shown.

Result 5

To examine our data further for evidence of non-stationarities, we implented a version of Task 3 (see Fig. 9 for more information) where the monkey was required to shift gaze to a target presented in the LGN cell's RF or continue fixating the fixation point in blocks of 20 trials. Analysis of 38 cells from two monkeys revealed a result similar to Results 1 and 2. That is, an enhancement in LGN cell activity was observed when the monkey shifted gaze to the target presented inside the LGN cell's RF. Blocks were not counterbalanced.

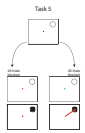

Fig. 18. One Stimulus, Fixate or Saccade into RF based on cue presented at the fixation point (blocked). This task is similar to task 3 (see Fig. 9 at left) except the monkey is required to follow an instructional cue to decide whether to continue fixating of shift gaze following the presentation of a target stimulus. The new element to this task is that trials are run in blocks of 20.

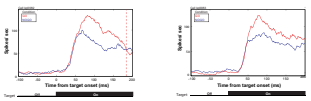

Fig. 19. Spike density functions for an LGN single unit recorded during Task 5 (see Fig. 18 at left). The red curve represents the mean activity recorded during those trials where the monkey produced a saccade to a target presented inside the cell's RF. The blue curve represents the mean activity recorded during those trials where the monkey continued to fixate the fixation point while a target was presented inside the cell's RF. Trials are aligned on target onset. The red dashed line indicates the shortest saccade latency across both conditions.

Fig. 20. Spike density functions for an LGN single unit recorded during Task 5 (see Fig. 18 at left). The red curve represents the mean activity recorded during those trials where the monkey produced a saccade to a target presented inside the cell's RF. The blue curve represents the mean activity recorded during those trials where the monkey continued to fixate the fixation point while a target was presented inside the cell's RF. Trials are aligned on target onset. The time of the earliest saccade during these trials and conditions was outside the scale shown.

Results Summary

1. A total of 81 LGN cells were recorded during the two target conditions and a total of 92 LGN cells were recorded during the single target conditions. Cells were recorded from all layers of the LGN.

2. In one monkey, 47% of LGNd cells (N = 53 cells) of all classes exhibited enhancements in peak response magnitude (mean = 20%) 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. When multiple interleaved blocks were presented to a second monkey, however, there did not appear to be any consistent response differences between blocks where the RF or non-RF were correct (N = 28 cells). This suggests that the first result may have been a result of block order or the fact that our second monkey uses a different strategy to complete the two target saccade tasks.

3. In the single target condition, no differences in response magnitude to target onset were seen between the GO and NOGO tasks when these tasks were interleaved, however, when these tasks were presented in blocks, 79% of cells recorded (N = 38) demonstrated enhancements in peak response activity (mean = 35%) in the GO task.

Conclusions

1. Potential enhancement of response to the RF target was seen in some conditions and not others. At present, it is unclear if this enhancement reflects shifts in attention or other factors.

2. We are currently testing monkeys with more challenging tasks to determine if the attentional effects reported using fMRI can be detected at the level of the single cell in the LGN.

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