Binocular summation in human LGN and visual cortex

Keith A. Schneider[1], Steven A. Engel[2], Hilda M. Fehd[1], Sabine Kastner[1]

[1]Department of Psychology and Center for the Study of Brain, Mind and Behavior, Princeton University
[2]Department of Psychology, UCLA

Introduction

The lateral geniculate nucleus (LGN) is a unique structure in the human visual system in that it contains only monocular neurons segregated into non-interacting, eye-specific layers. These layers are too small to be resolved with the currently available fMRI techniques. The primary visual cortex (V1) contains monocular neurons in its input layers, separated into ocular dominance columns, and binocular neurons in its output layers. Higher visual areas contain only binocular neurons. To investigate the binocular interaction properties of different modules of the visual system, and to investigate the summation of the fMRI signal from disjoint yet unresolved neural populations, we examined the responses of the LGN and a number of functional visual areas in the cortex to a range of contrast stimuli viewed either binocularly or monocularly, with the other eye dark-adapted.

Background

Interactions between the eyes have been investigated psychophysically and physiologically for more than a century. Under conditions of equal illuminance between the eyes, there is little perceptual difference between monocular and binocular viewing. For example, the figure below demonstrates the results of a matching experiment in which a subject manipulated the contrast of a binocular pattern in one hemifield to match the apparent contrast of a monocular pattern in the other hemifield. Likewise, the apparent contrast of a stimulus apparently does not change when you briefly close one eye.
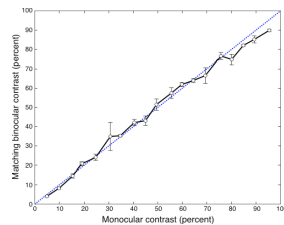
However, differences in monocular and binocular performance may be observed when the overall luminance level is changed between the eyes. For example, in such circumstances, detection thresholds vary between the viewing conditions in a manner that depends on the contrast and spatial frequency of the stimulus, with the binocular advantage typically around a factor of 1.4.

Here, we patch one eye, depriving it of stimulation and causing it to become dark-adapted. The dark-adapted eye exerts a tonic interocular suppression which generally degrades performance relative to binocular viewing. Our primary goal is to test the responses in the LGN, which contains two disjoint populations of monocular neurons. Presumably, given a linear fMRI response and a limited role of any binocular feedback connections, the response in the LGN in the binocular viewing condition should be exactly double that of the monocular response, across the contrast range. Visual cortical areas, subject to interocular interactions and thus the suppression, should exhibit a more complex pattern of responses.

Methods

Four normal subjects were scanned during two separate sessions, with a different eye patched in each in a 3T Siemens Allegra head scanner (gradient-echo EPI, 64x64 matrix, FOV=192mm, 22 interleaved axial 3mm slices, flip angle=90°, TE=30 ms, TR=2 s). During the first half of each session, one of the subjects' eyes was covered with a patch until it was dark-adapted, and the stimuli were viewed monocularly with the other eye. For the second half, the patch was removed for binocular viewing, allowing sufficient time for the patched eye to become light-adapted.

The stimuli consisted of a contrast-reversing checkerboard (flicker frequency = 4 Hz) covering one visual hemifield to an eccentricity of 15°, and a uniform gray background of mean luminance (147 cd/m^2) in the other hemifield. The checkerboard and background alternated hemifields every 16 s. The contrast of the checkerboard was presented at one of three levels, 5%, 25% and approximately 100% contrast (with contrast defined as $(L_1-L_2)/(L_1+L_2)$), with the mean luminance of the checkerboard remaining constant, equal to the luminance of the background. In separate scanning runs, the sequence of stimulus blocks was composed two alternation cycles at each contrast level, with the contrasts presented in increasing or decreasing order, for a total of six stimulus cycles per run. In addition, longer sessions containing ten high-contrast alternation cycles were presented immediately after the patch was removed and at the end of the scanning session. These runs were used to aid in the localization of the LGN and cortical areas but were not analyzed further.

The cortical visual areas were identified through retinotopic mapping obtained in separate scanning sessions. The timecourses of the voxels in each region of interest were averaged, and the baseline, defined as the average response during the troughs of the non-stimulation periods, was subtracted. The timecourses were then converted to percent change by dividing by this baseline. Across runs, the blocks corresponding to the same contrast and viewing conditions were averaged together, and the response amplitude was determined as the area under the hemodynamic response profile. The amplitudes were then averaged across visual hemispheres, and across the two scanning sessions for each subject, since little difference was observed between the two monocular conditions. The group data was then averaged across all subjects. The data from one subject did not exhibit substantial LGN activation was omitted.

Results
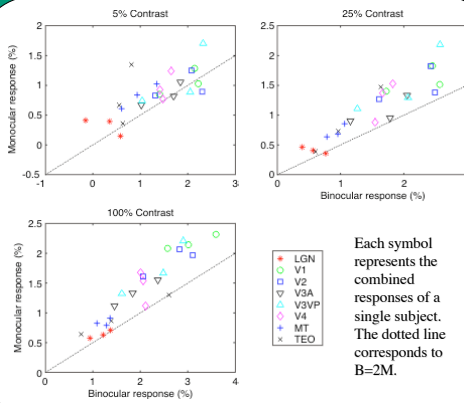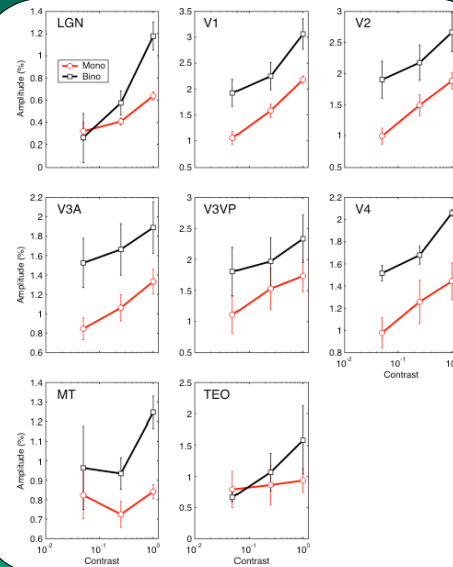
Each symbol represents the combined responses of a single subject. The dotted line corresponds to B=2M.
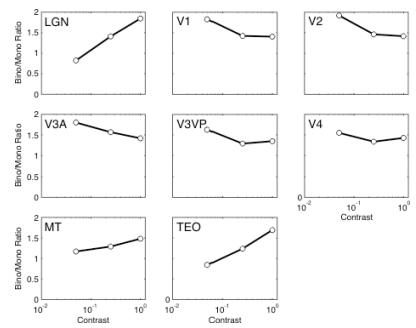
The LGN exhibited a binocular response roughly double that of the monocular response (B=2M) for high contrast stimuli, while the binocular response in the lower cortical areas was double the monocular response for low contrast stimuli. The responses for the early visual areas V1–V4 were very similar to each other, tending towards approximately B=1.5M for high contrasts. The monocular penalty in the cortical areas was roughly constant, independent of the contrast and response level.

Conclusions

As predicted, the binocular fMRI response in the LGN was about twice that of the monocular response, but surprisingly only for high contrast stimuli. The pattern of responses in V1 differed from those of its LGN input and were very similar to those in the other early visual areas. These results demonstrate that it is possible to independently measure responses of distinct neural populations that are spatially unresolved in the functional image.