Contrast adaptation in human early visual cortex as measured with event related BOLD imaging

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Abstract

We have used event-related BOLD imaging to ask how adaptation to the contrast of a visual stimulus changes contrast response functions of early human visual areas. Changes in BOLD signal to brief changes in stimulus contrast were measured for three different contrast adaptation levels. From these measurements we constructed contrast-response curves for the BOLD signal. We found that adaptation resulted in primarily horizontal shifts of contrast response curves. These horizontal shifts are thought to underlie an adaptive mechanism allowing the brain to efficiently encode and process stimuli over a wide range of average contrast levels. Furthermore, we unexpectedly found that while early visual areas show transient decreases in BOLD signal to decreases in stimulus contrast, V4v predominantly shows increases in BOLD response to both contrast increases and decreases. This suggests that V4v may encode stimulus salience rather than faithfully represent contrast.

Introduction

Adaptation of neuronal responses is thought to underlie the astounding ability of the brain to process sensory stimuli over many orders of magnitude of stimulus strength. For the cortical visual system, contrast is the attribute of stimuli that is most directly related to stimulus strength. Indeed, increasing stimulus contrast makes stimuli more visible, and many fMRI experiments have found that the BOLD signal from early visual cortical areas directly encode stimulus contrast, i.e. the BOLD response increases monotonically with stimulus contrast [1, 2]. Prolonged exposure to a single contrast selectively reduces visual sensitivity to that stimulus and correspondingly, fMRI studies have noted that the BOLD signal decays over several seconds [3]. However, it is unclear whether the reduction in fMRI signal itself is the result of a detrimental or beneficial neural function. That is, as responses to sustained stimuli decrease over time this could represent a decrease in signal from the visual cortex over all contrasts, or a horizontal shift of the contrast-response curve which serves to re-center the most sensitive portion of the contrast-response curve around the current ambient contrast level, a potentially beneficial process that has been demonstrated in cat V1 [4]. We provide evidence for the latter, beneficial process.

Methods

General: We studied the occipital visual cortex of four healthy male subjects, two of which are authors (ages 27-39). All procedures were approved in advance by the RIKEN Functional MRI Safety and Ethics Committee and subjects gave prior written informed consent. Scans were conducted on a 4T whole-body MRI system with a Varian Unity Inova console using a quadrature surface coil. Head motion was restrained by a bite-bar system and heart rate, respiration and head motion were monitored. Stimuli were presented via fiber-optic goggles (800x600 resolution, 60 Hz refresh rate) equipped with an infrared eye position monitor (Avotec Inc).

MRI parameters: We collected eight four mm thick coronal slices perpendicular to the calcarine sulcus. Anatomical images were collected with a four segment FLASH sequence. Functional images were acquired with a two segment centric ordered EPI sequence which contained navigator echoes and had a volume TR of 0.8 seconds (100 ms per slice) and a TE of 25 ms. Functional images had an in-plane resolution of 3.75 x 3.75 mm (FOV = 24x24 cm, matrix size = 64x64).

Task: We used an event-related paradigm to determine contrast-response curves for the BOLD response at different levels of contrast adaptation. Imaging sessions began with 30 seconds of baseline measurements where a uniform gray screen was presented and subjects had to maintain fixation at a central cross. We then presented a 7.5Hz contrast-reversing checkerboard stimulus at a single contrast (adaptation contrast) for 60 seconds to adapt subjects to one of three contrast levels (6.25, 12.5 and 25%). After this initial adaptation phase, we presented brief (3 second) test contrasts that were one or two octaves above or below the adaptation contrast level. These test contrasts were presented in random order, interspersed with 8-12 seconds of "top-up" adaptation contrast to maintain the adaptation state. Subjects were required to maintain fixation throughout the approximately 15 minute long imaging session during which at least 16 repeats of each test contrast was presented. Subject attention was controlled by asking subjects to report brief (1/30 sec) changes in the color of the fixation cross with a button press.

Data Analysis: Functional data was first preprocessed by removing physiological fluctuations due to heart rate and respiration via a retrospective correction, applying motion correction and filtering out low frequency signal drifts. We obtained unbiased estimates of hemodynamic response functions to each one of the test contrasts by standard methods [5]. We used the amount of variance accounted for by the estimated hemodynamic responses to identify activated voxels. We fit hemodynamic responses with gamma functions whose exponent was fixed at five, but whose amplitude, tau and latency were adjusted to minimize the least squared error between the fit and the data. Visual areas were identified by reference to functional images acquired separately for each subject that defined the horizontal and vertical meridians.

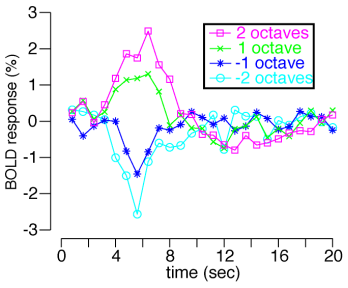

Figure 1. Response of an example voxel to increases and decreases in stimulus contrast.

Results

We observed voxels in retinotopically defined area V1 that showed transient increases in BOLD signal to increases in contrast which scaled with stimulus contrast (magenta boxes and green x's, Figure 1). Decreased stimulus contrast resulted in transient decreases in BOLD signal which also scaled with stimulus contrast (blue stars and cyan open circles). We used the peak of the fit of these responses to construct contrast response curves for V1 by plotting the average peak over all subjects (Figure 2). The mean BOLD response level during the experiment was taken to be the response to the adaptation contrast and was added on to all of the other values. Contrast response curves constructed in this way showed that the BOLD response to contrast was systematically shifted by adaptation. The most apparent change in the contrast response curve was a horizontal shift such that contrast response curves were systematically shifted rightwards as adaptation contrast was changed from 6.25% (cyan curve) to 12.5% (red curves) to 25% (black curve) contrast. There was also a tendency for curves to be shifted slightly downward with higher baseline contrasts and have slightly larger dynamic range, though these effects did not always reach statistical significance. Voxels retinotopically identified in V2 and VP showed mostly similar tendencies as V1. Unexpectedly, however, we found that the majority of V4v voxels did not show signal decreases to decreases in contrast, but instead showed increases in BOLD response just as they did for increases in contrast.

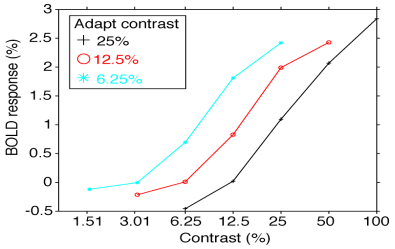

Figure 2. Contrast response curves for V1 voxels at three adaptation contrast levels

Discussion

Our results demonstrate that human visual cortex shows similar adaptation properties to cortical neurons recording from cat cortex. Horizontal shifts of adaptation curves can have a beneficial effect for perception in that it shifts the most sensitive part of the contrast-response curve to the mean ambient contrast, thus insuring that vision is most sensitive to current contrast levels. Our results indicate that while V2 and VP also show contrast response curve shifts mostly similar to V1, V4v behaves fundamentally differently to decreases in contrast level by showing an increase rather than a decrease in BOLD signal. This difference suggests that V4v encodes the contrast of stimuli differently from earlier visual areas, perhaps representing the salience of a stimulus rather than its contrast directly.

References:

[1] Tootell, R.B., et al., J Neurosci, 1995. **15**(4): p. 3215-30. [2] Logothetis, N.K., et al., Nature, 2001. **412**(6843): p. 150-7. [3] Tolias, A.S., et al., J Neurosci, 2001. **21**(21): p. 8594-601. [4] Ohzawa, I., G. Sclar, and R.D. Freeman, Nature, 1982. **298**(5871): p. 266-8. [5] Dale, A.M., Hum Brain Mapp, 1999. **8**(2-3): p. 109-14.

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