Report

Responses to Lightness Variations in Early Human Visual Cortex

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Summary

Lightness is the apparent reflectance of a surface, and it depends not only on the actual luminance of the surface but also on the context in which the surface is viewed [1–10]. The cortical mechanisms of lightness processing are largely unknown, and the role of early cortical areas is still a matter of debate [11–17]. We studied the cortical responses to lightness variations in early stages of the human visual system with functional magnetic resonance imaging (fMRI) while observers were performing a demanding fixation task. The set of dynamically presented visual stimuli included the rectangular version of the classic Craik-O'Brien stimulus [3, 18, 19] and a variant that led to a weaker lightness effect, as well as a pattern with actual luminance variations. We found that the cortical activity in retinotopic areas, including the primary visual cortex (V1), is correlated with context-dependent lightness variations.

Results

A rectangular version of the Craik-O'Brien (CO) stimulus [3, 18, 19] was used to investigate the cortical responses to context-dependent lightness variations (Figure 1, Illusory). In the Illusory CO stimulus, the left and right equiluminant flanking regions appear to have different lightnesses due to the presence of a central region composed of a contrast border with oppositely signed luminance gradients on each side. We refer to this illusion as the lightness effect. The lightness effect largely diminishes but does not completely vanish if the stimulus is placed on a gray background (Figure 1, Control) [8, 20]. The set of visual stimuli used in both behavioral and functional magnetic resonance imaging (fMRI) experiments included the Illusory stimulus, the Control stimulus, and a pattern with a real luminance difference between the flanks (Figure 1, Real). In the fMRI experiments, cortical activity was measured in regions corresponding to the flanks of dynamically presented versions of the stimuli. In the case of the Illusory and Control conditions, only the central portion varied; the flanks remained constant in luminance during the dynamic display. Even though the flanks remained constant in luminance, their apparent lightness varied in the

Illusory condition. This lightness effect was much weaker in the Control condition. In the Real condition, the luminance of flanks alternated homogeneously.

Recent studies on human observers, as well as studies on anesthetized animals, have produced mixed results regarding the role of early cortical areas in lightness processing. Several studies provided evidence in favor of lightness responses in these areas [11–15], whereas others found no such evidence [16, 17]. In this study, we address three specific questions: (1) Does the cortical activity correlate with context-dependent lightness variations in regions where the physical stimulus remains locally constant? (2) If so, how does it compare with activity in response to actual physical variations? And (3) do the cortical responses occur without attention directed to the lightness effect?

Behavioral Measurement of the Lightness Effect

In order to compare the cortical activity in response to context-dependent lightness variations with that to actual physical variations, we first determined the contrast of the Real stimulus that is perceptually equivalent to the Illusory stimulus for each observer by using an adaptive (1-up 1-down staircase) two-interval forced-choice procedure and maximum-likelihood techniques [21] (Figure 2). We repeated the same procedure for the Control condition. For the Illusory stimulus, three levels of CO border contrast were investigated: 0.3, 0.6, and 0.9 [Contrast = $(L_{max} - L_{min}) / L_{mean}$, where L is luminance]. For the Control stimulus, only the 0.9 contrast level was tested. We found that the effect gets stronger with increasing contrast and that the Control stimulus leads to a smaller lightness effect consistent with that discussed in previous literature [20] (Table 1). Two experienced observers participated in a dynamic version of the experiment in which the stimuli were dynamically presented with the same temporal characteristics as in the fMRI experiment (see the Supplemental Experimental Procedures in the Supplemental Data available online). We found that the dynamic version of the Illusory stimulus led to a slightly smaller lightness effect for those two observers (Table 1).

Cortical Responses to Context-Dependent Lightness Variations

In the fMRI experiment, the Illusory and Control stimuli with the 0.9 contrast level were used because that level produced the strongest lightness effect for all observers. The contrast of the Real stimulus was set for each observer to perceptually match the Illusory stimulus on the basis of his or her behavioral data, as described above. Each stimulus was first presented statically for 18 s; the same pattern was then presented with a 12 s square-wave-modulated counterphase flicker (0.66 Hz, Figure 3A). Throughout the entire scan, observers were asked to perform a demanding fixation task that required them to detect a target letter ("X") among distracters ("Z," "L," "Q," and "J") during

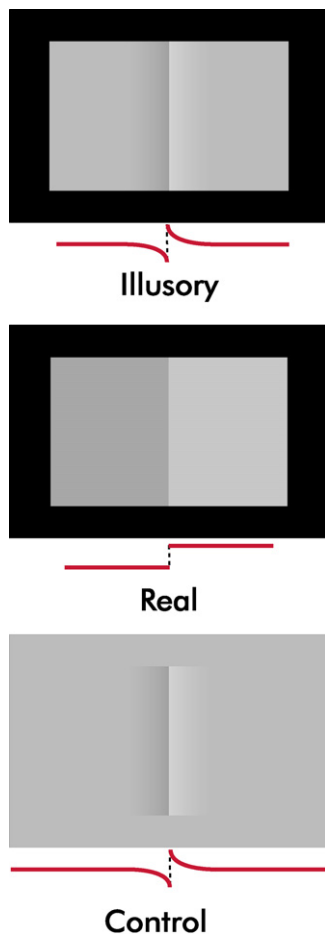*Correspondence: boyac003@umn.edu

Figure 1. Stimuli Used in the Behavioral and fMRI Experiments

Behavioral and fMRI responses to the lightness effect caused by the Illusory Craik-O'Brien (CO) stimulus were measured and compared with responses to the Real condition, in which flanks physically differed. The response to the Illusory stimulus was also compared with that to the Control stimulus, which caused a weak lightness effect. A luminance profile along a horizontal cross-section is shown below each stimulus.

a rapidly changing presentation of these letters (120 to 130 ms for each letter) (Figure 3A). The success rate across observers was 79%, and the mean reaction time was 533 ms.

Regions of interest (ROIs) were defined with square-wave-modulated contrast-reversing (8 Hz) black-and-white checks covering an area of 2 by 2 degrees in observers' periphery (Figure 3B). ROIs were identified by selecting the voxels that respond most strongly to the corresponding checker stimulus with a general linear model [p(corr.) < 10^{-4}]. Because the voxels corresponding to upper ROIs were much closer to the boundaries between the primary visual cortex (V1) and visual area V2, and therefore to the central region of the CO stimuli, we only present the analysis of the signal within the lower ROIs (see Figure S1 for the results in both ROI pairs). With images acquired in a separate scanning session, retinotopic areas were identified with techniques developed by Engel et al. [22] and Sereno et al. [23].

For these ROIs, the magnetic resonance (MR) signal was first normalized by the average of the last two
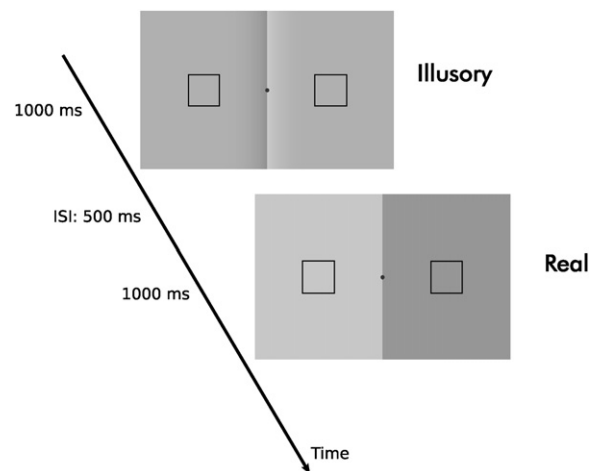

Figure 2. Behavioral Measurement of the Lightness Effect

The contrast of the subjectively equivalent Real stimulus was determined in an adaptive two-interval forced-choice experiment (2IFC). Observers were asked to indicate the interval in which the luminance difference between the flanks, within the square frames, was larger, while maintaining fixation at a central mark. The same measurement method was repeated for the Control stimulus.

time points of all static-presentation blocks in a scan and then event-related averaged according to the type of stimulus (the same baseline was used for all conditions in a scan). The average response from the third through the sixth time points (between 6 and 12 s) of the event-related signal after the onset of the flicker was computed and defined as the cortical response to that condition for each observer and ROI.

What are the possible outcomes? If the cortical activity correlates with the physical properties of the stimulus, we should expect to find no MR signal in the Illusory condition because there was no localized physical variation at the flanks where we measured the activity. Alternatively, if the activity correlates with the lightness variations, we should expect to find a positive signal in the Illusory condition. But this test alone might not be sufficient to prove the activity is in response to lightness variations per se. The activity we find could be a consequence of direct responses (neural or vascular) to the variations in the central portion of the stimulus. Because the luminance profile along a horizontal cross-section is identical in the Illusory and Control conditions, and because the Illusory but not the Control stimulus produces a strong lightness effect, we can test this possibility. If the cortical activity correlates only with the distant contrast and luminance variations, we should expect to find no difference between the activity in Illusory condition and the activity in Control condition. Alternatively, we should expect to find a stronger activity in the Illusory condition because of the lightness effect. Finally, because we used the Real stimulus that was perceptually equivalent to the Illusory stimulus, we can compare the activity to context-dependent lightness variations with the activity to subjectively equivalent actual physical variations.

Figure 4A shows the results averaged across observers in V1, V2, and visual area V3. The average response to the Real condition was significantly higher than that to the Illusory condition in V1 [t(4) = 2.63, p < 0.05] but not in V2 and V3. Critically, the V1, V2, and V3

Table 1. Behavioral Results

| Observer | Illusory | | | Control |
	BC = 0.3	BC = 0.6	BC = 0.9	BC = 0.9
KD: Static	0.20 (0.004)	0.27 (0.006)	0.32 (0.006)	0.15 (0.017)
KD: Dynamic	—	—	0.23 (0.008)	0.14 (0.006)
FF	0.20 (0.003)	0.25 (0.011)	0.24 (0.005)	0.07 (0.020)
HB: Static	0.21 (0.009)	0.33 (0.008)	0.37 (0.006)	0.13 (0.009)
HB: Dynamic	—	—	0.21 (0.006)	0.13 (0.001)
RWS	0.16 (0.005)	0.35 (0.006)	0.39 (0.015)	0.12 (0.008)
ST	0.21 (0.008)	0.29 (0.003)	0.40 (0.010)	0.10 (0.003)

Contrast of the subjectively equivalent Real stimulus reported for all observers (standard errors of the means are reported in parentheses). "BC" denotes the contrast of the central border in Illusory and Control stimuli. Results from the dynamic version of the experiment are shown for the two observers who participated in that experiment (KD and HB).

responses to the Illusory condition were significantly higher than those to the Control condition [t(4) = 6.99, p < 0.01 in V1; t(4) = 4.57, p < 0.01 in V2; and t(4) = 9.8, p < 0.001 in V3]. Therefore, we reject the possibility that the activity in V1, V2, and V3 in the Illusory condition can be explained as a direct response to distant luminance variations.

In V1, individual observer responses to the Real condition tended to be higher than those to the Illusory condition. However, the difference was significant for only two observers (Figure 4B). For all observers except one ("ST"), the response in V1 to the Illusory condition was significantly higher than that to the Control condition. For ST, the difference between the Illusory and

Control conditions was close to significant [t(126) = 1.23, p = 0.053].

We often found negative MR signals in the Control condition (Figure 4). Such negative signals are pervasive in fMRI studies and are usually detected beyond the stimulated regions of visual cortex. The negative signal could be due to either a purely vascular origin (for example, vascular blood steal) or the suppression of neuronal activity [24].

Discussion

The cortical activity correlates with context-dependent lightness variations where locally the physical stimulus
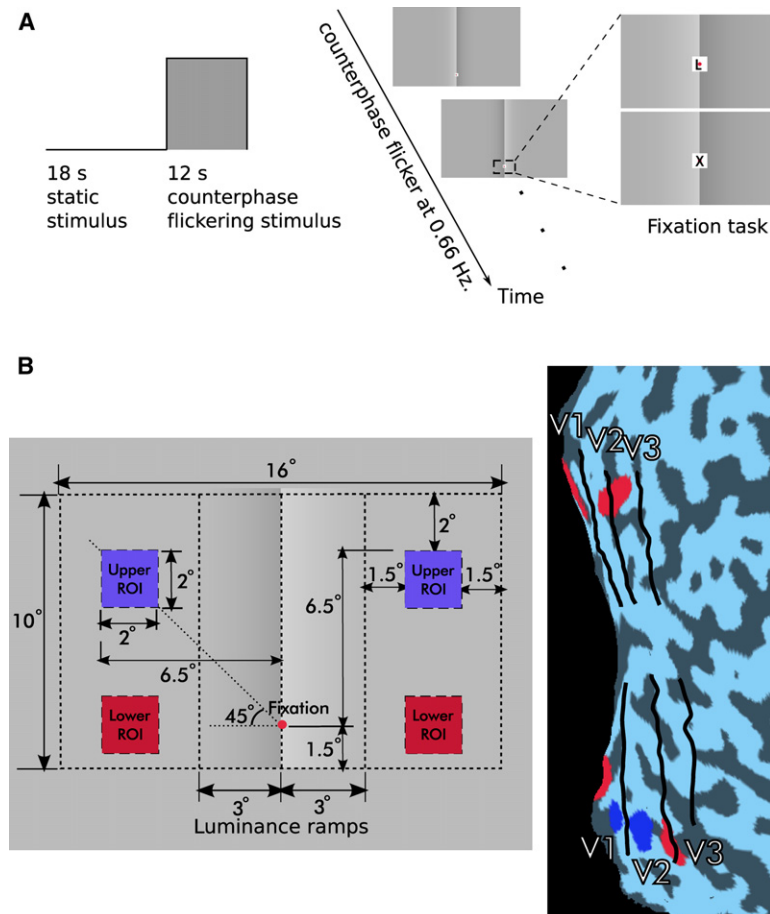

Figure 3. Design of the fMRI Experiment

Cortical responses were measured to dynamically presented versions of the stimuli shown in Figure 1. The contrast of the Real stimulus was adjusted to match the lightness effect for each observer on the basis of his or her behavioral data.

(A) Each stimulus was first presented statically for 18 s; the same pattern was then presented with a 12 s square-wave-modulated counterphase flicker. Throughout the entire scan, observers performed a fixation task that required them to detect a target letter ("X") among distracters during a rapidly changing presentation of these letters.

(B) Region of interest (ROI) definitions. Counterphase-flickering checker patterns were used to localize ROIs. The left panel shows dimensional parameters of the Illusory stimulus and the positions of the ROI localizers. The right panel shows, for one observer, the areas of the visual cortex that were activated by the localizers, [p(corr.) < 10^{-4}]. Red indicates lower ROIs, and blue indicates upper ROIs. Because the cortical areas corresponding to upper ROIs were much closer to the vertical meridian and therefore to the contrast border in the stimuli, only MR data in lower ROI pairs are presented here (see Figure S1 for results from both ROI pairs).
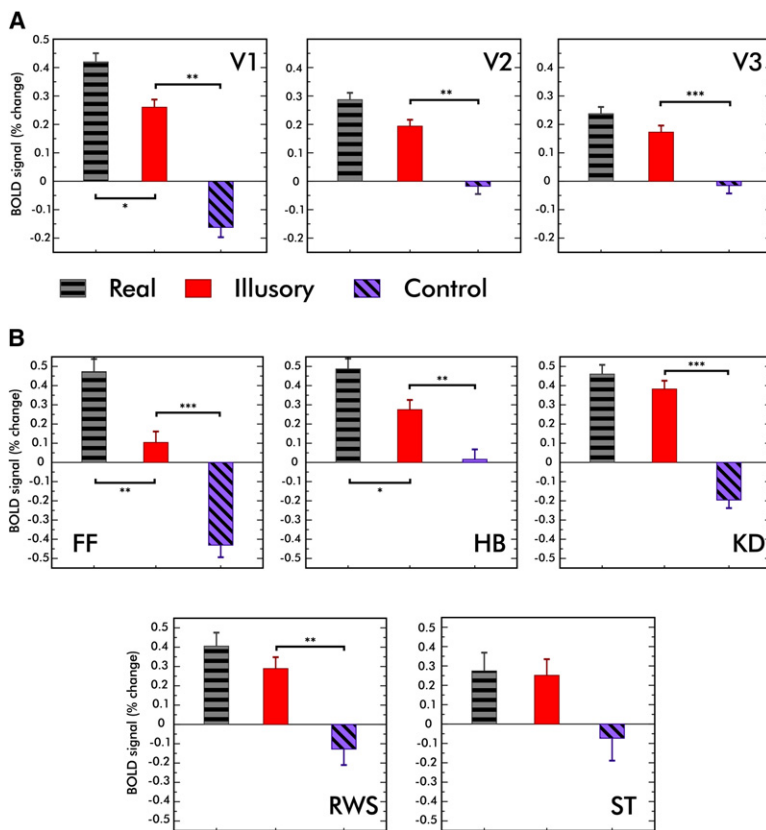
Figure 4. FMRI Results

(A) V1, V2, and V3 responses averaged across observers. The average response to the Illusory condition was smaller than that to the Real condition. However, this difference was statistically significant only in V1. Importantly, the MR signal to the Illusory condition was larger than that to the Control stimulus in V1, V2, and V3. The difference between the MR signals to Illusory and Control conditions suggest that the activity in Illusory condition can not be explained as a direct response (neural or vascular) to distant contrast and luminance variations. (See Figure S1 for the analysis of MR data in both ROI pairs.)

(B) Individual responses in V1. For two out of five observers, MR signals to Real condition was statistically significantly larger than those to the Illusory condition. For all but one observer, the Illusory stimulus evoked a significantly larger MR signal than did the Control stimulus. Error bars represent one standard error of the mean (SEM). Statistically significant differences are indicated ("*" denotes $p < 0.05$, "**" denotes $p < 0.01$, and "***" denotes $p < 0.001$).

remains constant. This finding is consistent with previous studies that provided evidence in favor of lightness responses in retinotopic cortex [11–15].

The response to actual physical variations is larger than that to perceptually equivalent context-dependent lightness variations in V1 but not in V2 and V3. This leaves open the possibility that mechanisms underlying the responses to actual luminance variations, at least in V1, might be different than those to context-dependent lightness variations. In a recent study, Roe et al. [14], using the same CO stimulus and anesthetized monkeys, found that V2 neurons responded to both actual luminance variations and context-dependent lightness variations but V1 neurons responded only to actual variations. Taken together with our results, this might indicate a difference between V1 and V2/V3 in their role in lightness processing. Other than the difference in species, the disagreement between our results and those of Roe et al. [14] in V1 could be a consequence of the anesthesia. Our results in V1 agree with findings of Rossi et al. [13], although one must be cautious in comparing their results with ours because of the differences in the stimuli.

The cortical activity is present when the observers' attention is directed away from the lightness effect. One might be tempted to view our results as supporting the idea that lightness responses in V1 do not involve a top-down flow of information; however, our findings cannot distinguish between the roles of feed-forward and feedback mechanisms. For example, one cannot rule out higher-level feedback, even in the absence of attention [25, 26] or conscious perception [27]. Experimental designs and techniques that are sensitive to the timing of activity are promising candidates to distinguish between these possible explanations and determine how exactly information propagates within V1 [15].

Cornelissen et al. [17] argued that the neural activity in response to context-dependent lightness (or brightness) variations found in previous studies could be explained by a mechanism of so-called "long range edge response," in which contrast-sensitive neurons with large receptive fields respond directly to spatially distant temporal contrast variations (i.e., greater than 1.5 degrees away) and not as a response to lightness variations per se, and they concluded that there is no evidence to support a spatial filling in of lightness in early retinotopic visual cortex. The difference we found between the Illusory and Control conditions argues against such a "direct long-range response" to the central contrast flicker (note that static edges do not contribute to the MR-signal averages reported here because the measurement is done 24 s after the onset of any static edge, and this is sufficiently long for any transient BOLD response to asymptotically converge to its baseline). The disagreement between the studies could be due to differences between the experimental designs. Unlike in our design, Cornelissen et al. [17] could not directly compare the responses to context-dependent lightness variations against those to distant luminance and contrast variations. It is possible that contrast variations evoke a much stronger MR signal that hides the responses to context-dependent lightness variations in the particular stimulus used in their study.

There is a close and subtle relationship between lightness and brightness [5, 28, 29]. Brightness is defined as

the perceived luminance of a surface, and the effect in our Illusory stimulus could be considered a brightness effect, as well as a lightness effect. In fact, often it is not even possible to distinguish between lightness and brightness in simple scenes where information about illumination is not available. Because the reflectance, but not the luminance, of an object is invariant over viewing conditions, it is reasonable to assume that the visual system functions to estimate lightness rather than brightness. Therefore, we described the cortical activity in terms of a response to lightness variations, rather than brightness variations. However, in the behavioral experiments, we used a luminance comparison task as an objective measure of the lightness effect in our stimuli. This task favors low-level mechanisms [5], consistent with the fMRI experiment. With the current design, we cannot say whether lightness and brightness processes are separate or whether one precedes the other.

In summary, our results show that the activity in early visual-cortical areas, including V1, correlates with context-dependent lightness variations, not only with localized luminance variations. We show, for the first time, that the activity in these early cortical areas in response to lightness variations cannot be explained by means of direct responses (neural or vascular) to distant variations in the stimulus alone. These findings are consistent with earlier studies showing that cortical activity in early visual areas correlates with the perceived rather than physical properties of the visual stimuli [30–32].

Supplemental Data

Additional discussion, Experimental Procedures, and two figures are available at http://www.current-biology.com/cgi/content/full/17/11/989/DC1/.

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