Neural activity in human V1 correlates with dynamic lightness induction

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Two circles of the same luminance will appear to have different lightness if one is embedded in a dark and another in a light surround. Known as simultaneous lightness contrast, this phenomenon demonstrates that our perceptions are not simply a reflection of the input from the retina but instead an inference about surface properties. Using functional magnetic resonance imaging (fMRI), we investigated whether the response in primary visual cortex (V1) more closely follows retinal information or perception. We induced illusory lightness changes of a disk by temporally modulating the surround luminance. In addition, we varied the luminance of the disk in order to disambiguate the fMRI response to perceived lightness modulation from the response to luminance contrast at the border of the disk. Perceptually, the disk with the lowest luminance (and the highest border contrast) had little or no induced lightness change while the disk with luminance equal to the time-averaged luminance of the surround (and the lowest border contrast) had the strongest induced lightness change. We found that neural activity in V1 strongly correlates with perceived lightness changes of the disk, suggesting significant involvement of early visual areas in processing surface lightness information.

Keywords: V1, brightness perception, lightness perception, fMRI

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Introduction

Lightness (or apparent reflectance) of a surface is strongly affected by the luminance of surrounding surfaces. For example, two circles of the same luminance will appear to have different lightness if one is embedded in a dark and another in a light surround. This phenomenon is called *simultaneous lightness contrast* and is a dramatic demonstration of the potential disconnect between the amount of light arriving at the retina and our perception of that light. Despite extensive research on various aspects of simultaneous lightness contrast, no agreement has been reached on the mechanisms governing this property of the visual system (Adelson, 1993; Gilchrist, 2005), but there is considerable evidence indicating significant involvement of cortical mechanisms (Boyaci, Fang, Murray, & Kersten, 2007; Hung, Ramsden, & Roe, 2007; Kinoshita & Komatsu, 2001; MacEvoy & Paradiso, 2001; Roe, Lu, & Hung, 2005; Rossi & Paradiso, 1999; Rossi, Rittenhouse, & Paradiso, 1996; Sasaki & Watanabe, 2004).

Recently, fMRI has been used to attempt to localize the cortical areas that more closely follow changes in lightness (our perception) rather than just changes in luminance (retinal input) (Boucard, van Es, Maguire, & Cornelissen, 2005; Boyaci et al., 2007; Cornelissen, Wade, Vladusich, Dougherty, & Wandell, 2006; Haynes, Lotto, & Rees, 2004). In particular, two recent studies found that the fMRI signal in early retinotopic visual areas, starting as early as V1, correlates with lightness perception (Boucard et al., 2005; Boyaci et al., 2007; but see Perna, Tosetti, Montanaro, & Morrone, 2005).

However, a recent fMRI study by Cornelissen et al. (2006) posed a strong challenge to the idea that early visual cortex contributes to lightness perception. This study induced illusory flicker in a disk of constant luminance by temporally modulating the luminance of the region surrounding the disk (De Valois, Webster, De Valois, & Lingelbach, 1986; Krauskopf, Zaidi, & Mandler, 1986; Zaidi, Yoshimi, Flanigan, & Canova, 1992). This stimulus can potentially uncouple neural sensitivity to changes in luminance from neural sensitivity to changes in lightness. Specifically, if a particular visual area is sensitive only to physical changes in luminance, there should be no increase in neuronal activity in the retinotopic region corresponding to the disk. However, if that cortical area is sensitive to changes in perceived lightness, the illusory flicker in the disk should generate an increase in neuronal activity.

In Cornelissen et al. (2006), the fMRI signal was measured in small regions-of-interest (ROIs) corresponding to different retinotopic locations within the stimulus. Of particular importance was whether the fMRI signal increased in regions of V1 that represented the retinotopic

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space containing the disk with illusory flicker. No significant fMRI signal was measured in the ROI that represented the centermost position of the disk, though a strong fMRI signal was measured in the ROI corresponding to the edge between the disk and surround. These results were used to suggest that previous effects of lightness changes on neural responses can be explained by long-range border effects—the neural signal induced by luminance contrast spreading to other neighboring retinotopic regions. According to Cornelissen et al. (2006), it is luminance contrast—and not lightness—that results in the increases in activity, which have been measured in previous lightness experiments.

In the current study, we tested this idea directly by using a stimulus that juxtaposed luminance contrast and induced lightness. Similarly to Cornelissen et al. (2006), a circular disk with constant luminance was embedded in a luminance-modulated surround. On different trials, the luminance of the disk could be one of four different values, ranging from mid-level gray (as in Cornelissen et al., 2006) to black. This simultaneously changed the amount of time-averaged contrast at the edge (black = high contrast, gray = low contrast) and the amount of illusory change in lightness of the disk (black = little change, gray = much change). If the fMRI signal in ROIs corresponding to the interior of the test disk is driven solely by luminance contrast, then the gray disk should result in the smallest fMRI signal and the black disk should result in the largest signal. On the other hand, if lightness is the primary factor, then the opposite result is expected: the largest signal is expected for the gray disk and the smallest signal is expected for the black disk. Our results clearly show that the cortical activity in V1 is strongly correlated with perceived lightness induction in the disk, rather than with just border contrast.

Methods

Subjects

The subjects were graduate students and faculty of the University of Washington, aged 24 to 40 years. They had normal or corrected-to-normal visual acuity according to self-report. Five subjects participated in fMRI testing. Four of these subjects took part in the follow-up behavioral testing; one was not available and so an additional subject was recruited for the behavioral study. All subjects gave informed written consent in accordance with the University of Washington Human Subjects Institutional Review Board.

Stimuli

The stimulus spatial configuration is shown schematically in Figure 1. The stimuli were achromatic disks presented in the center of an achromatic surround. The surrounds were either temporally luminance modulated (in the behavioral experiment and in the "induction" condition of fMRI experiment), or static (in the "real flicker" condition of fMRI experiment, depicted in detail in the description of fMRI experiment, below). For simplicity, we will specify stimuli in instrument luminance, or IL, defined as 100% * (L − Lmin)/(Lmax − Lmin), where L is the stimulus luminance, Lmin is the black level of the monitor, and Lmax is the maximal available luminance of the display.

The time-average luminance of the surround was 50% IL. When the surround was modulated, it was modulated

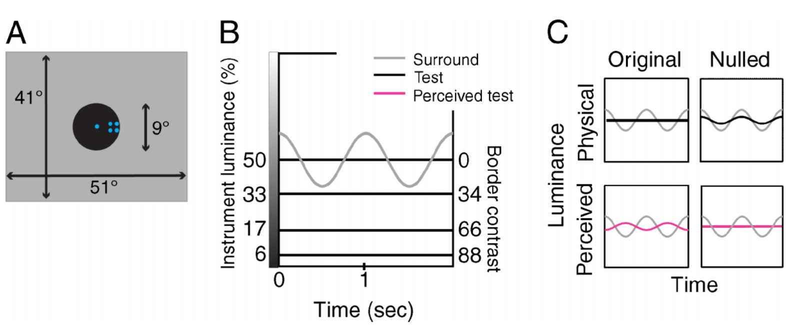

Figure 1. Behavioral experiment. A "test" disk was shown in the center of the screen with a central fixation dot. In addition, 4 blue dots defined a patch at 0, 2, or 4 degrees eccentricity (within the test disk) that directed where subjects were to attend (panel A, 4 deg case shown). On a particular trial, the test disk was one of four different luminance values (50, 33, 17, and 6 percent instrument luminance, shown in panel B), which defined one of four different modified Weber luminance contrasts between the disk border and the surrounding region (0, 34, 66, 88 percent). The region surrounding the disk ("surround," depicted as gray in panel A) was modulated in luminance over time, causing the central disk to appear to change luminance over time. Subjects were asked to "null", or cancel, this perceived flicker by adding luminance modulation to the central disk until the test patch appeared to be static (panel C). The amount of luminance modulation that needed to be added to the disk to make the patch appear static was used as the measure of the strength of lightness induction.

sinusoidally (as a cosine, always starting at the highest luminance point), at 1 Hz. The amplitude of surround modulation was 12.5% IL, from 37.5% to 62.5% IL. Disks of 4 different time-average luminance levels were used: 6%, 17%, 33%, or 50% IL. The disks were either static (induction condition), or temporally modulated at 1 Hz, with the amplitude of 5% IL: from 1% to 11% IL, from 12% to 22% IL, from 28% to 38% IL, and from 45% to 55% IL, respectively (real flicker condition).

Contrast specifications

Because stimulus luminance was modulated in time, it was difficult to find an appropriate contrast measure. For simplicity, and because it explicitly reflects the average luminance differences at the border, we used a modified variant of Weber contrast, defined as 100% $\frac{S_{av}-T_{av}}{S_{av}}$, where S_{av} and T_{av} are the time-average instrument luminances of the surround and the test. The modified Weber contrasts were 88%, 66%, 34%, and 0% for the disks of 6%, 17%, 33%, or 50% IL levels, respectively.

We also calculated the contrast energy, defined here as the integrated square contrast of Michelson contrast function (Pelli, 1981; Watson, Barlow, & Robson, 1983). The contrast energy values in the induction condition were calculated using the following formula:

$$\sqrt{\int_0^1 \left(\frac{S_{av} + S_{amp} * \sin(2 * \pi * x) - T}{S_{av} + S_{amp} * \sin(2 * \pi * x) + T}\right)^2 dx}, \qquad (1)$$

where S_{av} is the time-average instrument luminance of the surround; T is instrument luminance of the test, and S_{amp} is the amplitude of the surround modulation, expressed in IL units.

The contrast energy values in the real flicker condition were calculated using the following formula:

$$\sqrt{\int_0^1 \left(\frac{T_{av} + T_{amp} * \sin(2 * \pi * x) - S}{T_{av} + T_{amp} * \sin(2 * \pi * x) + S}\right)^2 dx}, \qquad (2)$$

where T_{av} is the time-average instrument luminance of the test, S is the instrument luminance of the surround, and T_{amp} is the amplitude of the test modulation, all expressed in IL units. The resulting contrast energy values for the disks of respective 6%, 17%, 33%, and 50% IL levels were: 87%, 55%, 25%, and 9% for static disks embedded in modulated surrounds (induction condition) and 80%, 50%, 21%, and 4% for modulated disks embedded in static surrounds (real flicker condition).

Behavioral experiment

The purpose of this experiment was to establish the size of brightness induction effect under conditions similar to those used in the fMRI experiment. Using a perceptual nulling procedure, we measured the amplitude of luminance modulation that was required to cancel the perceived lightness modulation in the central test disk. This was done for the four different luminance levels used in fMRI experiment, as well as for three positions in the test disk: center, middle, and border.

Apparatus and stimulus specifications

The stimuli were presented on a Dell 1905FP Digital on NVIDIA Quadro FX 1400 color graphics display monitor controlled by a Dell Precision PWS380 Intel Pentium 4 PC and calibrated with a PR 650 spectroradiometer (Photo Research, CA). The monitor subtended 51 × 41 deg of visual angle at a viewing distance of 43.5 cm and had a peak luminance of 210 cd/m^2 and a black level of 0.26 cd/m^2. The stimuli had a diameter of 9 deg; and the surrounds subtended 51 × 41 deg.

Each stimulus presentation was preceded by an adaptation screen, during which a static disk of one of the four luminance levels was presented in a static surround. The adaptation screen lasted for 3 s and was followed immediately by a test screen. During the test period, a small blue fixation point and four blue dots designating the corners of an imaginary 1 deg square test "patch" were presented in different locations of the disk, and the temporal modulation was introduced in the surround. Three different locations were tested: center, 2 degrees, and 4 degrees eccentricity. The stimuli were presented in pseudo-randomized blocks of 24 trials. Five blocks were run per session, for the total of 10 trials per condition.

The luminances of the disks could be adjusted from temporally static to temporally modulated at 1 Hz, in phase with the surround modulation, with the maximal amplitude of modulation equal to 48% of the surround modulation for the 6% IL disk and to 100% of surround amplitude for other disk luminance levels (17, 33, 50 IL). (The difference was simply due to the limited range allowed in the 6% IL condition.)

Procedure

The subjects' task was to adjust the amplitude of the test modulation in a way such that the perceived lightness of the test "patch" was as constant as possible. Once the optimal amplitude was reached, the subject pressed the space bar, recording the amplitude and initiating a new trial. The subjects were asked to only pay attention to luminance of the test "patch" and ignore the perceived brightness flicker in all other areas of the disk. This was necessary because when the amplitude of the disk was adjusted to eliminate the perceived flicker in a particular patch, subjects reported flicker in the other areas of the disk. In order to establish a perceptual analogy to different eccentricities in the fMRI experiment, subjects were asked to fixate at the fixation point in the middle of the disk at all times so that the patch was presented in different retinotopic locations.

fMRI experiment

Apparatus and stimulus specifications

The stimuli were presented on a DLP back-projection display controlled by a Dell Precision PWS380 Intel Pentium 4 PC and calibrated with a PR 650 spectroradiometer (Photo Research, CA). The projector had maximal luminance output of 2746 cd/m^2 and a black level of 0.05 cd/m^2. The stimuli had a diameter of 9 deg; and the surrounds subtended 34 × 25 deg at the viewing distance of 68 cm.

The order of stimulus presentation is shown schematically in Figure 2. The stimuli were blocked by instrument luminance of the disk. The sequences of stimulus presentation within each block, as well as the order of block presentation, were pseudo-randomized throughout the experiment to avoid possible order effects. Each block (shown schematically in Figure 2B) consisted of an adaptation screen (described below), followed either by an induction or real flicker stimulus, followed again by an adaptation screen, and then by a real flicker or induction stimulus. Each component of a trial lasted 10 s. The blocks were separated by a 10-s presentation of a blank static gray screen (50% IL).

The adaptation screen consisted of a static disk of one of the specified luminance levels (6%, 17%, 33%, or 50% IL), embedded in a static surround. During the induction stage (highlighted in yellow in Figure 2B), the surround was modulated in luminance from 37.5% to 62.5% IL, sinusoidally, at 1 Hz, while the disk remained static, with the same luminance level as during the adaptation stage. During the real flicker stage, the surround was static and the luminance of the *disk* was modulated sinusoidally, at 1 Hz with an amplitude of 5% IL.

The induction condition was the primary experimental condition designed to assess whether the observed pattern in the fMRI signal would correlate with the lightness induction effect (measured in the behavioral experiment), or with luminance contrast differences at the border. The purpose of the adaptation condition was to serve as a baseline for which percent signal change was calculated. The adaptation condition also helped to ensure that the fMRI signal measured in the induction condition was not reflecting transient changes in activity caused by the change in the disk luminance at the start of a trial.

The purpose of the real flicker condition was to determine the effect of luminance flicker at the disk/surround border for different disk luminance levels. We reasoned that if just the presence of physical border flicker—and *not* just perceived lightness modulation—determines the fMRI signal, the effect as a function of disk luminance should be similar for the induction and real flicker conditions. Alternatively, if the pattern of fMRI signals in the induction condition was found to be different from that in the real flicker condition, it would serve as additional evidence for a process distinct from purely physical luminance flicker at the border driving the fMRI signal in the induction condition. We hypothesized that lightness perception was this process. The choice of amplitude modulation in the real flicker condition was a trade-off between two conflicting requirements. One was to use a disk that was as dark as possible in the induction condition to limit lightness induction. The second was to make the amplitude of the luminance change in the real

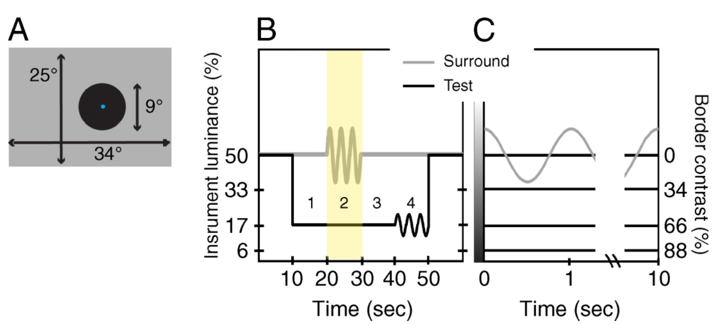

Figure 2. fMRI experiment. The stimulus configuration (panel A) was similar to the behavioral experiment where a central test disk could be one of 4 different luminance values. Panels B and C show two different timescales of the stimulus presentation. A particular "trial" (defined as the presentation of a particular luminance value of the test disk) lasted 40 s and comprised 4 different components: (1) an adaptation period with a static test disk in a static surround, (2) static test disk in a temporally modulated surround ("induction"), (3) another adaptation period, and (4) modulated test disk in a static surround ("real flicker"). These components are numbered in panel B. The adaptation periods served as baselines for which percent signal change was calculated. Panel C shows all possible test/surround luminance profiles for the selected region, highlighted in yellow (induction condition) in the middle panel. It also presents the detailed characteristics of the sinusoid, including the phase, cycles, and amplitude.

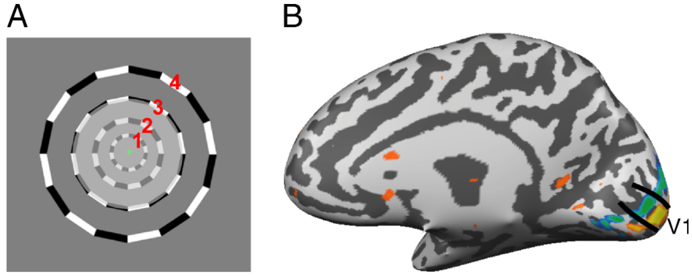

Figure 3. Counterphase flickering rings of four different sizes were used to localize four non-overlapping ROIs within V1. Panel A superimposes all of the rings and the test disk to show their relative sizes. Panel B shows the activation maps resulting from Ring 2 (yellow/red) and Ring 3 (blue/green) for a single subject. These activations were used for defining the ROIs.

flicker condition as large as possible to evoke brain activity. Our specific choice was a compromise between these two requirements. However, it should also be noted that the contrast energy values were very similar in the real flicker and the induction conditions (see Methods section).

Procedure

Subjects viewed stimuli while performing a demanding fixation task that occurred continuously throughout the duration of the scan. The task was to report subtle chromatic changes in a fixation point. The changes were reported by a button press. On average, subject performance on the fixation task was 59%, with a mean reaction time of 600 ms. The testing session lasted from 40 to 90 min and was terminated when either a desired number of trials was obtained or per subject's request. Eye movements were not monitored in the scanner. However, all of the subjects were experienced psychophysical observers and were told about the importance of maintaining eye fixation. In addition, the behavioral task was difficult and required constant fixation so subjects were well motivated to maintain fixation.

Data collection and analysis

The fMRI experiments were performed on a 3T Phillips-Achieva MRI scanner at the University of Washington. fMRI data were processed with BrainVoyager QX software (Rainer Goebel, 2001–2006) and further analyzed with statistical applications written in MATLAB (MathWorks, 1984–2007). The differences between fMRI signals in adaptation conditions and in stimulus presentation conditions in retinotopically defined regions of interest were averaged across like trials. We analyzed retinotopic visual areas in V1, using multiple regions-of-interest corresponding to different portions of the visual stimulus.

Retinotopic mapping and ROI identification

High-contrast counterphase checkerboard wedges and concentric rings (shown in Figure 3A) were used to identify subregions within V1. We defined subregions that corresponded to the center, border, and surround of stimulus in each retinotopic visual area using standard retinotopic mapping techniques (Engel, Glover, & Wandell, 1997; Sereno et al., 1995). A disk with schematically depicted checkerboard rings superimposed over it is shown in panel A, to demonstrate how the size of the checkerboard rings corresponds to the stimulus.

Rings 1 and 2 defined locations within the disk. Ring 3 defined the region at the border between the disk and surround and Ring 4 defined a region in the surround. Thus, we are able to precisely define multiple retinotopic regions in V1 that correspond to the center, border, and outside regions of the stimulus. Rings 1–4 subtended 2, 4, 9, and 12 deg of visual angle (in diameter), respectively. An example of the pattern of neural activity produced by Ring 2 (in red and yellow) and Ring 3 (in green and blue) in V1 is shown in Figure 3B.

Results

Behavioral experiment

The results of behavioral experiment averaged for 5 subjects are summarized in Figure 4. In panel A, each curve represents the amplitude of the nulling flicker (the flicker added by subject to the test disk to make the region defined by the "patch" appear static) as a function of the patch eccentricity (shown on the abscissa) for a test disk of a given luminance. The nulling amplitude, expressed in percent of surround modulation amplitude, is plotted along the ordinate.

We performed a repeated-measures ANOVA (eccentricity $\times$ test-disk luminance) on the nulling amplitudes. There was a significant main effect of luminance ($p < 0.0001$), a significant main effect of eccentricity ($p < 0.0001$), as well as a significant interaction ($p < 0.\ 0001$). The main effect of luminance was expected—a decrease in the luminance of the test disk (which increases the contrast at the border of the disk and the surround) significantly reduced the amount of perceived illusory flicker. To emphasize this point, we averaged the nulling amplitudes from the middle two regions of the test disk ("center" and "middle") and plotted their values as a function of test disk luminance in Figure 4B.

The second main effect, the influence of eccentricity, was not expected. For every contrast level at which induction was observed (i.e., >6% luminance level), the induction effects were strongest near the border and gradually diminished near the center. This is the first

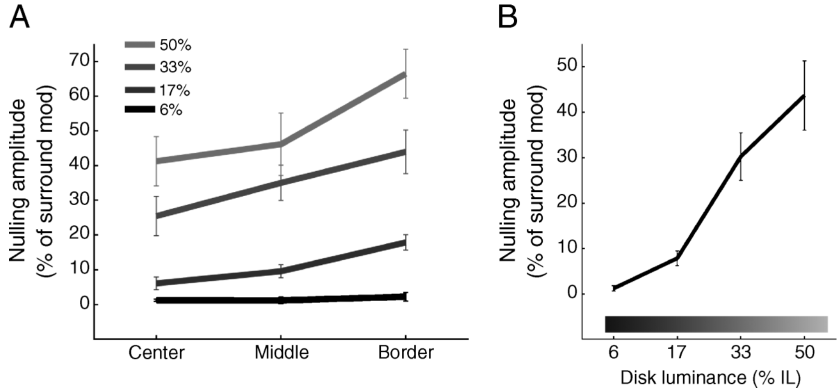

Figure 4. Behavioral results. (A) The magnitude of the perceived lightness induction as a function of spatial position for each of the four luminance levels. Regions near the border of the test disk had the highest perceived illusory flicker. (B) The average magnitude of the center and middle patch positions as a function of test-disk luminance/border contrast. The highest induced illusory flicker occurred for high-luminance/low-contrast test disks.

evidence that we are aware of for spatial non-uniformity of lightness induction from temporally modulated luminance surrounds.

fMRI experiment

The fMRI experiment examined the relationship between the fMRI signal in V1 with perceived lightness induction. The behavioral results demonstrated that as the luminance of the test disk was decreased from 50% IL to 6% IL, there was a significant reduction in the amount of perceived lightness modulation of the central, static test disk. Importantly, this manipulation simultaneously *increased* the amount of contrast energy at the border of the test disk and the surround (i.e., the black, 6% IL test disk has the highest luminance difference with the surround). If the fMRI signal in ROIs corresponding to the interior of the test disk is driven solely by luminance contrast at the border of the disk and the surround, then the black test disk should result in the largest fMRI signal and the gray test disk the smallest signal. On the other hand, if perceived lightness modulation is the primary factor, then the opposite result is expected: the largest signal is expected for the gray test disk and the smallest signal is expected for the black test disk.

The results averaged over five subjects in area V1 are shown in Figure 5. Figure 5A plots the fMRI signal from the ROI defined by Ring 2 ("middle" of the test disk) as a function of time from the onset of surround modulation. Each curve represents a luminance value of the test disk. The gray "window" from 6 to 14 s shows the period of time over which peak fMRI measurements were calculated and takes into account the hemodynamic delay of the fMRI signal.

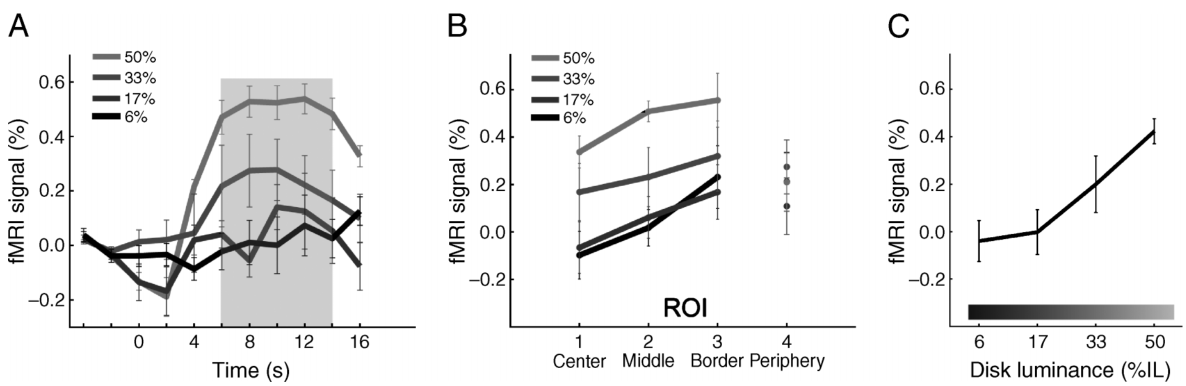

Figure 5. fMRI results. (A) The average time course of fMRI activity in ROI #2 (corresponding to the middle position of the test disk) for each of the four luminance levels. Time = 0 corresponds to the onset of the luminance modulation of the surround. The gray region shows the time points that were averaged to calculate the peak responses shown in (B) and (C). (B) Peak fMRI responses as a function of eccentricity for each of the four luminance levels. Responses were larger near the border of the test disk. (C) Peak fMRI responses averaged across ROIs 1 and 2 (center and middle of the test disk) as a function of test-disk luminance/modified Weber border contrast. The highest fMRI responses were observed for the lowest contrast (gray) test disk.

Figure 5B plots the peak fMRI signal for each luminance value of the test disk as a function of eccentricity. A repeated-measures ANOVA on the peak responses (eccentricity × test-disk luminance) revealed a main effect of test disk luminance ($p < 0.002$) and a main effect of eccentricity ($p < 0.007$), and no significant interaction. Similar to the behavioral results, there was a significant increase in the fMRI signal with increasing luminance of the test disk. In other words, the gray test disk resulted in the largest fMRI signal and black test disk resulted in the smallest fMRI signal. This means that the largest fMRI signals were observed with the smallest luminance contrast between the test disk and the surround. To emphasize this point, Figure 5C plots the fMRI signal averaged across ROIs 1 and 2 as a function of test disk luminance. The highest fMRI signals were observed with luminance values that minimized the contrast between the test disk and the background and closely follow the perceptual data plotted in Figure 4B. The effect of eccentricity (Figure 5B) also follows a similar pattern as the perceptual data. Specifically, higher fMRI signals were observed at the border as compared to the center of the test disk. Finally, as a control, there were no significant differences in the fMRI signal for the different luminance values in ROI 4 corresponding to the surrounding region of the test disk.

The results of the real flicker condition are summarized in Figure 6. The figure shows the activity in V1 associated with the low amplitude luminance flicker in the disk embedded in a static surround. All the conventions are as in Figure 5B. The real flicker condition addressed the possibility that at different luminance levels of the disk, border flicker could result in different fMRI signals in the border ROIs. If present, the differential effect of disk luminance on the border fMRI signal could potentially complicate the interpretation of results in the induction condition. It is clear, however, that there is little or no difference in fMRI signal at the border.

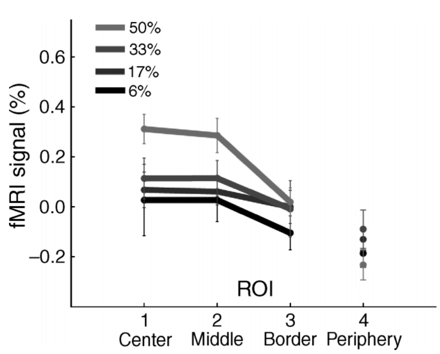

Figure 6. fMRI results. Real flicker condition: Peak fMRI responses as a function of eccentricity for each of the four luminance levels. All conventions are as in Figure 5B. Responses near the border of the test disk are very similar for different luminance levels.

A repeated measures ANOVA (test disk luminance × eccentricity) did not reveal a main effect of luminance ($p = 0.20$). There was, however, a main effect of eccentricity ($p < 0.03$). The eccentricity effect was in the opposite direction as the lightness induction stimulus with the smallest fMRI signal observed at the border. Despite the lack of a main effect of luminance, there does appear to be a trend with slightly higher fMRI signals observed for higher luminance values of the test disk in the ROIs corresponding to the locations within the disk. We talk about the possible reasons in the Discussion section. Most importantly, however, the fMRI signals at the border were very similar for all luminance levels of the disk. This finding further supports the suggestion that the observed differences in fMRI signal in the induction condition were not due to the purely physical effects of the combined luminance flicker/luminance difference at the borders, but rather to perceived lightness modulation in the disk.

Discussion

The role of V1 in the processing of surface lightness is a subject of ongoing debate. The evidence for the role of early cortical processing comes from two main sources: animal single-cell physiology and human fMRI studies. Rossi et al. (1996), using extracellular recordings from individual cells in cat primary visual cortex, found that a significant percentage of the neurons correlated with perceived lightness rather than with the light level in the receptive field. This finding was further confirmed by Rossi and Paradiso (1999) and by MacEvoy and Paradiso (2001). In addition, in areas 17 and 18 of cat visual cortex, Hung et al. (2007) have demonstrated the similarity between border-to-surface interactions of neurons responding to changes in real luminance and to changes in lightness. In monkeys, Roe et al. (2005) did not find a correlation with lightness perception earlier than in thin stripes of V2. All of the above studies, however, were done with anesthetized animals, which could have affected the outcome. Using recordings from V1 neurons in awake-behaving monkeys, Kinoshita and Komatsu (2001) found that the activity in a relatively large group of neurons correlates with lightness perception rather than luminance. These studies raise the possibility that the neural mechanisms underlying lightness perception can be operating at the earliest stages of cortical visual processing, in V1 or V2.

There is, however, little agreement between the findings of different human fMRI studies. Using a Craik-O'Brien-Cornsweet brightness illusion, Boyaci et al. (2007) observed an increase in neural activity in areas V1–V3, correlating with lightness perception. However, another study (Perna et al., 2005), using the same illusion in a different spatial configuration, showed an increase in neural activity in higher order visual areas, including the caudal region of intrapariatal sulcus and lateral occipital sulcus, but no increase in activity in areas V1–V4. Conversely, Boucard et al. (2005) showed activation in early retinotopic cortical areas in response to induced illusory lightness modulation in a circular test field of constant luminance. The lightness modulation in that experiment was obtained by varying the luminance of the surrounding area at a rate of 1 Hz. However, in a later study (Cornelissen et al., 2006), after the luminance contrast effects from the border of the test field were carefully taken into account, the increase in neural activity in V1, V2, and V3 was no longer observed. This study raises the possibility that some of the previous findings of neural activity correlated with lightness perception in early retinotopic visual areas were caused by a distant luminance border artifact rather than perceived lightness change.

We addressed this problem by juxtaposing the predictions of the border luminance contrast account and the lightness perception account and showed that the fMRI signal in V1 correlates with lightness perception rather than just physical luminance contrast at the border. The highest fMRI activity was observed in the ROIs corresponding to the static test disk when the luminance of the disk was equal to time-average luminance of the surround (and thus the border luminance contrast was minimal). By parametrically adjusting the luminance of the test disk, we observed a close relationship between the fMRI signal and the amount of perceived lightness induction.

Our findings are, in part, consistent with the results of Cornelissen et al.'s (2006) study in that the strongest fMRI signal for each disk luminance level was at the border, rather than in the center of the disk. Cornelissen et al. (2006) used this result to substantiate their argument that fMRI signal in the ROIs corresponding to the disk reflects the neural activity caused by physical contrast at the border. However, they overlooked the possibility that perceptual lightness induction also increases at the border, which could lead to an increase in fMRI signal.

Interestingly, both our behavioral and fMRI data showed spatial non-uniformity. The behavioral results showed that the perception of lightness induction is strongest near the border and weakest in the center of the disk. This finding is consistent with that of Cornsweet (1970) and Davidson (1968), who have reported similar perceived spatial non-uniformities in *static* setups. The fMRI signal was also the highest at the border and smallest in the center. This observation further supports the idea that activity in V1 correlates with lightness perception. However, our results do not completely exclude the possibility that the decrease in fMRI signal toward the center reflects, at least in part, the spread of neural activity caused by luminance contrast at the border (Cornellissen et al., 2006). The spatial non-uniformity that we observed is unlikely to be task specific. Since subjects were asked to maintain fixation in the behavioral experiment, the difference in nulling amplitudes across disk position could potentially be explained by different temporal sensitivities at different eccentricities. We have addressed this issue in a separate behavioral study (Pereverzeva and Murray, in preparation) and found that changing the location of fixation does not affect the nulling amplitude in the patches. These findings lend further support to the non-uniformity of lightness induction perception. It also should be noted that most subjects reported that during the free viewing, the perceived induced flicker in the static disk was stronger near the border than at the center.

We were surprised to find elevated fMRI signal in the ROIs corresponding to the center and the middle regions of the disk at 50% IL in the real flicker condition. These results, however, may be explained by the fact that our study did not attempt to disambiguate the border contrast and absolute luminance of the disk. There is some evidence that, independently of contrast, luminance can affect the firing rate of neurons in primary visual cortex. A recent single-unit study of cat primary visual cortex showed that for many neurons, there is a contrast/luminance trade-off in the firing rate (Geisler, Albrecht, & Crane, 2007). The neurons described in this study could achieve the same firing rate when exposed to the stimuli of lower contrast and higher overall luminance as when exposed to stimuli of higher contrast but lower luminance. The trade-off was nonlinear, so a group of similarly behaved neurons could be more active at higher luminance even though the contrast has decreased. If these findings extend to neurons in human visual cortex, they may be responsible for the elevated fMRI signal at higher luminance in the real flicker condition.

In summary, we have demonstrated that neural activity in V1 correlates with lightness perception. However, it is important to emphasize that in order to arrive at an estimate of surface reflectance the visual system uses multiple cues, such as the range of luminances present in the image (Brainard & Maloney, 2004; Webster & Mollon, 1995), as well as 3-dimensional interpretations of the scene, illuminant cues, object cues, and shadows (Adelson, 1993; Gilchrist, 1977; Knill & Kersten, 1991; Lotto, Williams, & Purves, 1999). Further research is needed to examine how these other cues contribute to the neural processing of lightness information.

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