Lightness constancy in primary visual cortex

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When the illumination of a visual scene changes, the quantity of light reflected from objects is altered. Despite this, the perceived lightness of the objects generally remains constant. This perceptual lightness constancy is thought to be important behaviorally for object recognition. Here we show that interactions from outside the classical receptive fields of neurons in primary visual cortex modulate neural responses in a way that makes them immune to changes in illumination, as is perception. This finding is consistent with the hypothesis that the responses of neurons in primary visual cortex carry information about surface lightness in addition to information about form. It also suggests that lightness constancy, which is sometimes thought to involve "higher-level" processes, is manifest at the first stage of visual cortical processing.

The lightness of a surface is a perceptual quantity indicating the fraction of light that the surface appears to reflect. Presumably because this fraction, termed reflectance, is a fixed physical property, we perceive the lightness of objects to be constant across large changes in the level of illumination. Because surface qualities such as lightness provide clues important in object recognition, the capacity of the visual system to generate lightness representations immune to changes in illumination is of considerable behavioral significance. Indeed, lightness and color would be of little use if they were not largely perceptually constant. However, it is not clear how the visual system extracts information about object reflectance because the amount of light entering the eye confounds reflectance with the level of illumination—an increase in either reflectance or illumination will raise the light level entering the eye, but only the former should make the surface appear lighter. A number of heuristics have been proposed to solve this dilemma (1–7), but little is known about the neurophysiological basis of perceived lightness constancy. One point that many models have in common is that lightness perception achieves constancy by integrating information over a large portion of the visual field.

To investigate the neural basis of lightness constancy, we examined the activity of neurons in primary visual cortex (V1). There are several reasons for studying visual cortex rather than earlier visual structures. Although the retina adapts to light level, processes such as dark adaptation are much slower than constancy, which adjusts instantaneously to changes in illumination. Also, we are perceptually aware of the level of illumination despite lightness constancy, suggesting that the effects of illumination changes are not filtered out early in visual processing. Finally, lightness perception is influenced by higher-level factors assumed to be based on cortical processing such as the interpretation of lighting (1, 8, 9) and the arrangement of objects in depth (10, 11).

Consistent with the inferences above, recent research suggests that V1 is the first stage in the mammalian visual pathway at which neurons explicitly represent information about the lightness of surfaces (12–14). Moreover, within V1 the responses of many neurons are influenced by the arrangement and intensity of light over a spatial scale comparable to the integration range involved in visual perception (13, 15–18). Human psychophysical experiments have demonstrated that lightness is not always perceived in a constant manner—some experimental stimulus configurations give rise to perceptual lightness constancy and others do not. Thus, we were interested in examining whether neurons in V1, which represent lightness, are also lightness constant and inconstant in the same situations as human perception.

Methods

Physiological Preparation. Experiments were performed on 14 adult cats, weighing between 2 and 4 kg. All procedures were approved by Brown University's institutional animal care and use committee and were in accordance with the National Institutes of Health *Guide for the Care and Use of Laboratory Animals*. Animals were anesthetized, placed in a stereotaxic apparatus, and paralyzed by continuous infusion of atracurium besylate (1–2 mg/kg/h). During the experiments, they were artificially respirated through a tracheal cannula with a mixture of 50% O_2 and 50% N_2O to which 1–2% isoflurane was added. End tidal CO_2 and rectal temperature were monitored and maintained at 3.5% and 37.5°, respectively. ECGs and electroencephalograms (EEGs) were monitored continuously, and the amount of isoflurane was increased if there was any indication of insufficient anesthesia.

Nictitating membranes were retracted with a 10% ophthalmic solution of phenylephrine, and pupils were dilated with 1% ophthalmic atropine sulfate. The eyes were refracted, and contact lenses of appropriate correction were fit to focus the eyes on a tangent screen and computer monitor at a distance of 57 cm.

A craniotomy was centered at Horsley–Clarke coordinates P3.0 and L2.0, providing access to neurons representing the central visual field in area 17.

Recording Procedures. The cortex was stabilized by filling the craniotomy with agar. Recordings were made with insulated tungsten electrodes with an impedance of about 1 MΩ. After amplification, a window discriminator was used to isolate action potentials of individual neurons on the basis of spike waveform. Receptive field (RF) properties were determined initially with a manually controlled bar of light projected on a tangent screen. Preliminary estimates were made of ocular dominance, orientation selectivity, direction selectivity, presence of on or off subregions, and side or end inhibition. The RF was defined as the area on the screen that could be stimulated by hand with either drifting or flashing bars of light to elicit a response from the neuron (i.e., the minimum response field).

Visual Stimuli. After preliminary studies with a hand held stimulator, the nondominant eye was occluded by an opaque patch, and the response of the neuron to stimulation of the dominant eye was explored. Stimuli were presented on a 27-inch monitor with 640 × 480 pixel resolution. The stimulus on the computer display simulated patches of paper under various lighting conditions. A black-fabric shroud surrounded the visual display and extended to the animal so that nothing but the display was in the animal's field of view. The stimulus was composed of a quasi-random array of overlapping monochromatic gray patches (Fig.

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Abbreviations: RF, receptive field; V1, primary visual cortex.

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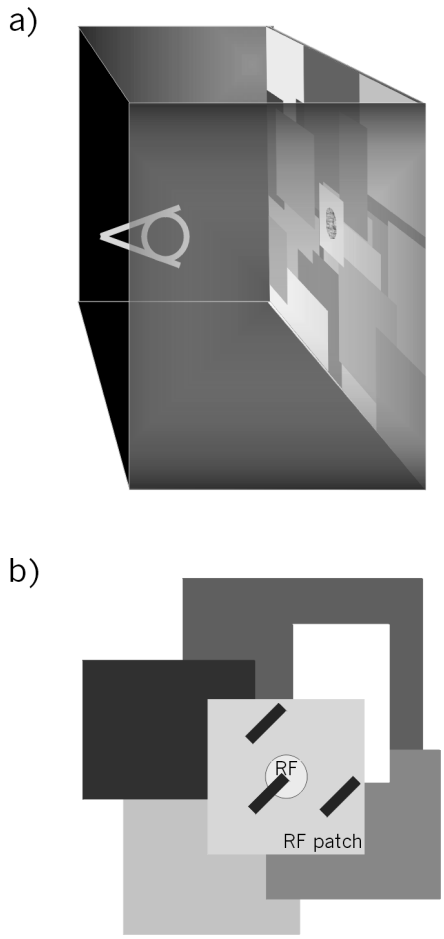

Fig. 1. Schematic arrangement of the Mondrian visual stimulus. (*a*) Stimuli were generated on an RGB monitor (640 × 480 resolution) 57 cm in front of the animal, and a cloth shroud limited the field of view. (*b*) The stimulus consisted of a Mondrian pattern, each element of which was assigned a reflectance value to mimic a piece of paper. Small optimally oriented bar patches drifted through the RF to raise the firing rate. The reflectance of the Mondrian patches ranged from 0.03 to 0.95, the RF-patch reflectance was 0.75, and the bar-patch reflectance was 0.25. To simulate changes in illumination, the luminance of every patch was changed in a manner consistent with its reflectance. For each cell, the stimulus was adjusted to ensure the central patch (RF-patch) completely covered the RF. The full Mondrian stimulus subtended 50° horizontally and 38° vertically.

1*a*), similar to "Mondrian" patterns used in psychophysical studies known to elicit lightness-constant percepts in human observers (5, 19). Each patch in the Mondrian was assigned a reflectance value as if it were a piece of paper. Once a cell was isolated, its classical RF was determined by using bars of light and basic tuning properties were measured (13). For each cell, the Mondrian stimulus was positioned and the central patch (RF patch) was sized (typically 3 times the RF size) so that the RF fell entirely within the central patch (Fig. 1*b*).

To increase the firing rates of the neurons, small bars optimized for orientation, speed, and size were superimposed and drifted across the RF patch. These small bar patches were assigned reflectance values just like the larger patches in the Mondrian. One can think of the central stimulus as simulating, under different levels of illumination, a piece of gift paper that had a bar texture on it. Because the contrast between the bar patches and the larger RF patch was always fixed and their luminances were always changed together, their lightness levels were correlated. The motion of the bar patches should not have had an effect on the lightness constancy of the bar patches and the RF patch. The situation is analogous to moving the textured gift paper mentioned above or watching the leaves of a tree fluttering in the wind—motion *per se* does not disrupt lightness constancy.

In "illumination" conditions, changes in illumination were simulated by adjusting the luminance of each patch (including the bar patches) in a manner consistent with its fixed reflectance. Across conditions, the luminance values of various patches changed by different amounts, but all contrast ratios between patches were constant (including the small oriented bar patches on the RF patch), just as they would be for patches of paper under varying illumination. Luminance settings and contrast ratios were verified by photometer measurements. The Mondrian was presented for 5 sec at each of 5 randomly intermixed illumination intensities. Psychophysical studies using similar stimuli have shown that human observers perceive the lightness of the patches to be constant when the simulated illumination is changed (19).

In control conditions, the RF patch and the bar patches were varied across exactly the same luminance settings as in the illumination conditions (i.e., with fixed contrast between them). However, the rest of the patches in the Mondrian were fixed at the mean values used in the illumination conditions. Consequently, the average contrast of the RF patch on the Mondrian reversed sign as RF-patch luminance increased. The luminance settings in the control conditions were inconsistent with overall changes in illumination.

Results

By analyzing the responses of neurons across the illumination and control conditions, we compared the way responses varied when changes in the luminance of the bar patches and the RF patch could or could not be accounted for by changes in overall illumination. Fig. 2*a* (*Bottom*) shows response histograms for one cell in control conditions across 5 increasing values of luminance within the RF. The neuron's response progressively increased as the luminance of the RF patch and bar patches in the RF increased. Note that in these control conditions, the lightness of both the RF patch and bar patches was correlated with their luminance. Fig. 2*a* (*Top*) shows the response of the same neuron to identical stimuli within the RF in conditions in which the overall Mondrian changed in a manner consistent with varying illumination. In this situation, the responses were considerably more similar across the same range of intensities.

To test statistically any apparent difference between a neuron's responses to illumination and control conditions, we first plotted the average firing rate at each luminance during the first 2 sec of each stimulus. (We limited our analysis to an epoch shorter than the full 5-sec presentation period because the responses often declined significantly after the first 2 sec.) Separate linear regressions then were performed for each set of conditions and a *t* test was used to examine the significance of the slope difference between the illumination and control conditions. Fig. 2*b* illustrates this procedure for the same cell shown in Fig. 2*a*, confirming that the effect of changes in the luminance of the bar patches and the RF patch was reduced greatly in the illumination conditions. For this and the other cells studied, it is important to note that the graphs of the illumination condition data were flat despite significant activation by the stimulus.

We recorded at least 20 trials at each of 12 stimulus conditions (5 illumination conditions, 5 control conditions, plus additional controls) from 57 neurons. Fig. 3*a* plots the illumination and control slopes obtained from each cell. Solid symbols are plotted for neurons that had significantly different illumination and control slopes, and open symbols are plotted for those that did not. When the slopes were significantly different, they almost always differed in the same direction: for 33 of the 39 cells

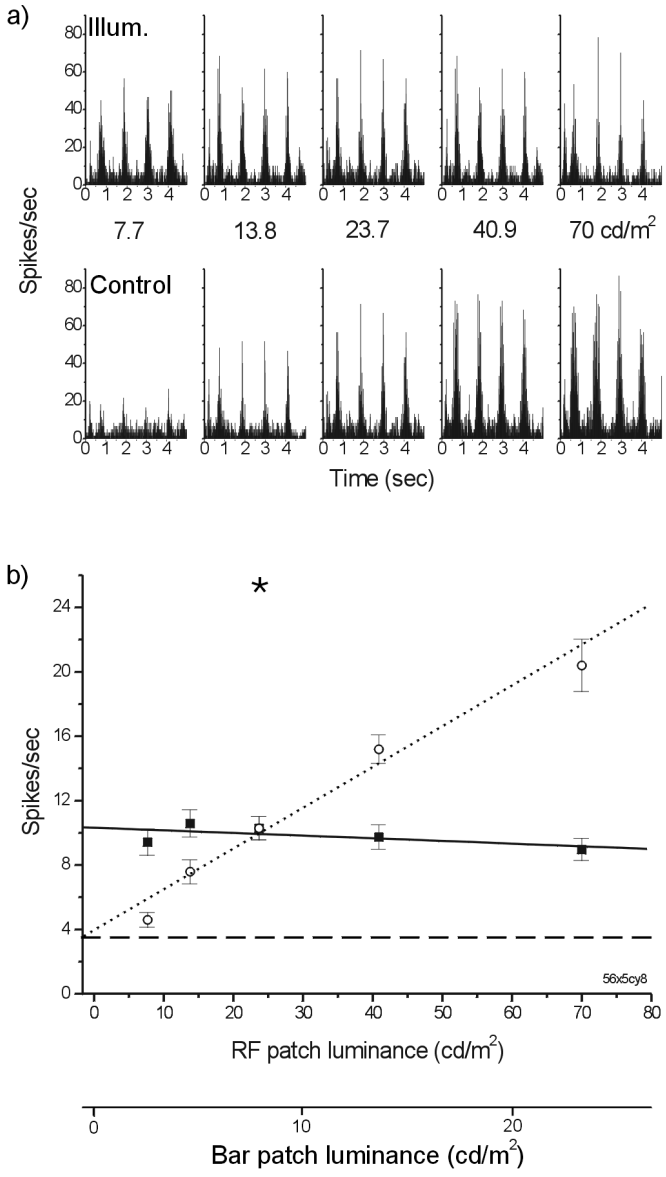

Fig. 2. Response of one neuron in illumination and control conditions. (*a*) Histograms in the upper row show responses in illumination conditions with the RF-patch luminance indicated between the control and illumination histograms. Histograms in the lower row are from control conditions with the same luminance settings for the patches in the RF. As the luminances of the patches in the RF were raised, the response progressively increased in control conditions but was relatively constant in illumination conditions. Periodic peaks in firing rate correspond to the passage of moving bar patches through the RF. (*b*) Average firing rate in illumination (solid symbols) and control conditions (open symbols). Linear regression lines for illumination and control conditions are shown by solid and dotted lines, respectively. The slopes of these lines are significantly different ($P > 0.01$). The asterisk at the top of the figure shows the response of this neuron to the middle RF- and bar-patch luminance values with a solid-black surround rather than the usual Mondrian. As in this example, the effect of adding the Mondrian in most cells was to suppress the neuron's response. The horizontal dashed line indicates the cell's rate of spontaneous activity. This neuron had a simple RF of 1.2 × 1.2 degrees and the RF patch was 3.5 × 3.5 degrees.

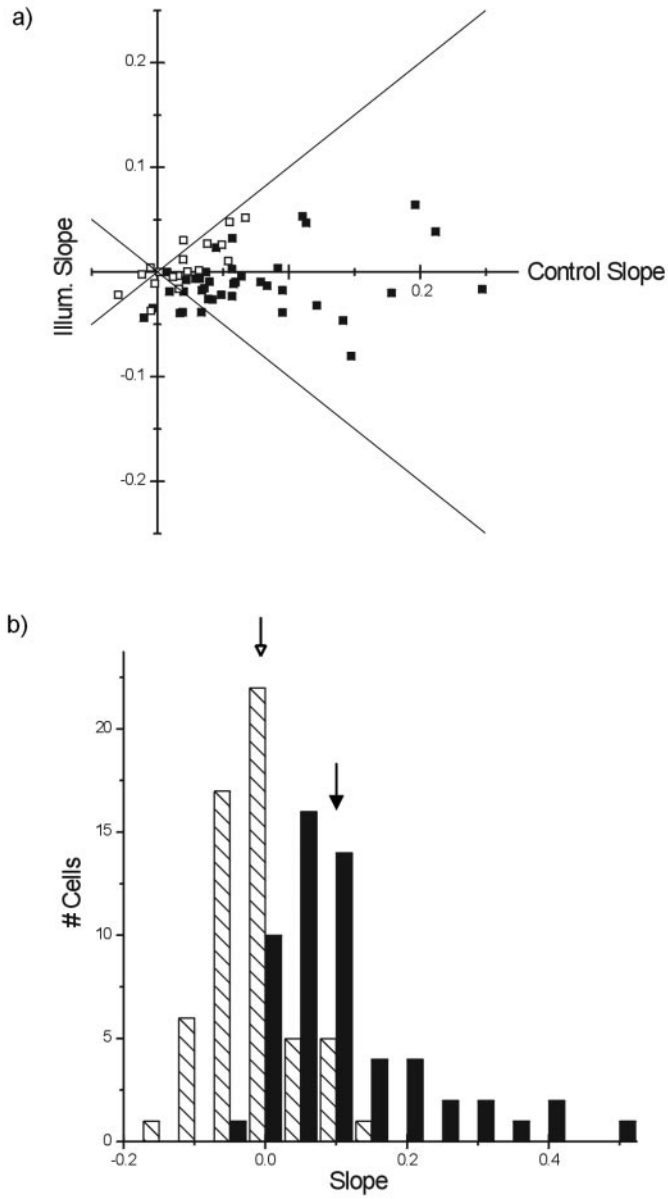

Fig. 3. Distribution of regression slopes in illumination and control conditions. (*a*) Each point represents the values of illumination and control slopes for one cell. Solid symbols indicate cells with a significant difference between control and illumination condition slopes; open symbols show cells with no significant difference. The regression slope in control conditions usually exceeded that in illumination conditions, especially among those cells with a significant difference between slopes. (*b*) The frequency of occurrence of regression slopes is compared for illumination and control conditions. A neuron exhibiting perfect lightness constancy would have a slope of 0.0 in the illumination conditions. The distribution of slopes for illumination conditions (dashed bars) had a mean significantly different from the mean of the distribution for control conditions (solid bars). The average slope in control conditions was 0.11 (filled arrow) and the average in illumination conditions was −0.01 (open arrow).

exhibiting significantly different slopes, the slope magnitude was smaller in the illumination conditions than the control conditions (solid symbols to the right of the origin between diagonal lines). In other words, for these 33 cells (58% of total) the effect of luminance changes outside the RF was to make their responses more constant. Fig. 3*b* shows the distribution of slopes in the illumination and control conditions for all 57 neurons, including those cells that exhibited no significant difference between slopes. The average slope in the control conditions was 0.11, whereas the average was −0.01 in the illumination conditions.

Thus, in the control conditions, the average response was correlated with the luminance of the patches in the RF and with

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the lightness of the patches. In the illumination conditions, the average response also was correlated with lightness but in this case, the response was lightness constant as was the stimulus perceptually. On average, in the illumination conditions, luminance changes beyond the RF counterbalanced the effect of luminance changes within it.

Discussion

When overall changes in illumination were simulated by simultaneously changing both RF-patch luminance and the luminance of surrounding Mondrian patches, the average response in V1 was approximately constant. Responses to identical stimuli within the RF were significantly less constant and were correlated with RF-patch luminance when the surrounding Mondrian had fixed-luminance values. What is surprising about these findings is not that the responses were constant in the illumination conditions or that they varied in the control conditions. Rather, it is the combined results that are surprising. The constant response in the illumination conditions conceivably could be a consequence of the fixed contrast of the bar patches on the RF patch. Neurons are sensitive to contrast so it might seem natural that they have a constant response with fixed contrast in the RF. But if this is the explanation for the data, why weren't the responses also constant in the control conditions where the identical stimuli were within the RF? Conversely, the response correlated with luminance in the control conditions might simply indicate that the neurons were sensitive to luminance, but then why didn't the response change in the same way with luminance in the illumination conditions?

The resolution of this conundrum seems to be based on the sensitivity of the neurons to luminance and luminance contrast both within the RF and outside it. Although many studies have explored the sensitivity of neurons to contrast within the RF, a smaller number of experiments have shown that the RF area of neurons in V1 is also sensitive to luminance (12–16, 18, 20). Outside the RF there are modulatory areas, sometimes extending large distances from the RF, that themselves are sensitive to luminance and luminance contrast (13, 16, 17, 21–27). Of particular importance is surround inhibition. The effects of light beyond V1 RFs are quite diverse, but most commonly light outside the RF suppresses the response to uniform illumination of the RF (13, 16). In the present experiment, we included a control condition in which the RF patch was presented against a black background instead of the usual Mondrian. The effect of removing the Mondrian surround was usually an increase in firing rate (asterisk in Fig. 2*b*). Also, we often observed that neurons deemed lightness constant with the Mondrian stimulus were progressively inhibited by uniform patches of increasing size extending well outside RF boundaries, suggesting a large area of silent suppression beyond the RF (Fig. 4; also see ref. 16). Immunity to changes in illumination may be achieved by the counteracting forces of light within and beyond the RF. However, unlike the local antagonism found in the lateral geniculate nucleus (LGN), in visual cortex the antagonism extends many degrees beyond the RF—a spatial scale more consistent with that of perceptual effects such as induction and constancy.

A role for silent suppression in lightness constancy is consistent with suggestions that a similar mechanism may underlie color constancy (17, 28–30). However, the involvement of silent suppression is more complex than it might appear at first glance. Individual cells show considerable variability in the degree to which luminance and luminance contrast outside the RF inhibit or facilitate their response and the distances from the RF at which such interactions are observed (16, 17, 22, 24). As shown in Fig. 2, some individual neurons have interactions that give them lightness-constant responses. Other neurons, even ones with surround suppression, are less constant. There is no *a priori* reason why surround inhibition should produce lightness-constant responses in individual neurons or the population average. Yet it seems that deviations from constancy average out, leaving the response of the population relatively constant (Fig. 3). It is not known whether a specialized subpopulation or the entire population of V1 neurons is responsible for the perception of lightness constancy, but the neuronal responses we observed could support either scheme.

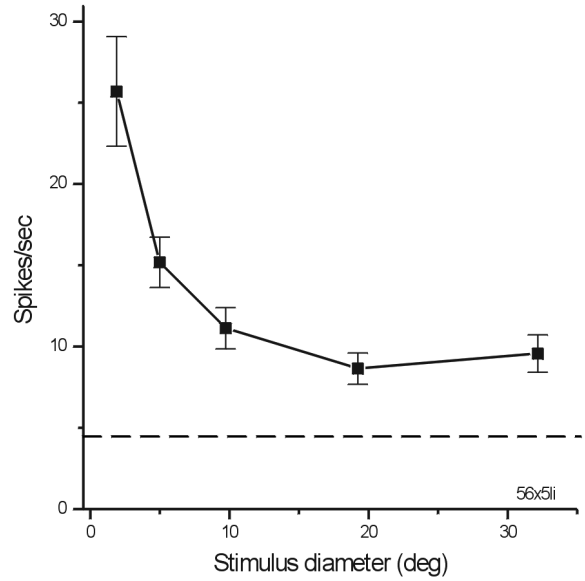

Fig. 4. Surround suppression in a lightness-constant neuron. This graph is for the same neuron illustrated in Fig. 2. The response is plotted as a function of the diameter of a uniform gray disk used to determine the modulatory effect of light outside the RF. For this neuron, and others exhibiting lightness-constant responses, there was an extensive area of silent suppression beyond the RF. The horizontal dashed line indicates the spontaneous firing rate of the neuron.

Neural Activity and Lightness Perception. Prior work has shown that neurons in V1 represent lightness in their firing rates (12–14). Consistent with the earlier findings, in the present results the average response is correlated with lightness in both the control and illumination conditions. Conceivably, higher-level mechanisms responsible for the constancy of lightness across changes in illumination might be located at a later processing stage than the initial representation of lightness. Such an argument has been made for color vision based on the consequences of cortical lesions (31). However, the present results show that lightness constancy is observed at the first visual processing stage at which a lightness representation is found.

The correlation between V1 activity and lightness exists whether one considers the RF patch, bar patches, or both to be the stimulus driving the neurons. In the control conditions, the lightness of both the bar patches and the RF patch increases as their luminance increases. Correspondingly, the firing rate is augmented as luminance rises. In the illumination conditions, lightness is perceptually constant despite increases in bar- and RF-patch luminance. In these conditions, the average neural response is unaffected by luminance increases. The response is certainly greater with the bar patches in the RF, but the fact that contrast affects firing rate is not at odds with the hypothesis that lightness is also represented in the firing rate. Thus, it seems that the neural responses represent contrast, lightness, and form information in a manner that remains to be clarified.

To reach the conclusion that the responses we observed were correlated with lightness, several complicating factors and alternative explanations were considered. For example, the bar

patches clearly play a strong role in driving the neural responses, but can the different responses in control and illumination conditions be accounted for by properties of the bar patches and the RF patch? The answer is no because the bar patches and the RF patch were identical in the control and illumination conditions. It is the Mondrian and not the stimuli within the RF that causes a different response in the illumination and control conditions. There are several possible explanations for the effect of the Mondrian. One possibility is that the responses are strongly influenced by the contrast between the RF patch and the Mondrian even though the border of the RF patch is well outside the RF. This contrast is fixed in the illumination conditions and variable in the control conditions, thus it might predict response strength. However, the strength of the response did not correlate with the contrast at the edge of the RF patch. Five different RF patch-luminance values were used, but as luminance increased the contrast at the RF-patch border reversed sign—the lowest contrast stimulus was always one of the central 3 conditions. If the responses were based on the lightness of the central patch, the firing rate should increase monotonically, but if it were based on contrast, there should be a dip at the central condition with lowest contrast. As the data show, we found the former, not the latter. Another possibility is that the Mondrian surround somehow changes the "effective contrast" of the bars in the RF, thus altering the firing rate. However, most neurons in cat and monkey V1 show responses that saturate at contrasts above about 30% (32–34). As our bar stimuli were fixed at 50% contrast, one would not expect a significant change in the firing rate even if the bar contrast were effectively altered by the Mondrian.

Our results suggest that mechanisms underlying perceptual constancy are present in the visual system as early as V1. That we observed constant neural responses in anesthetized animals suggests that constancy is mediated by "hardwired" neural interactions rather than relying on cognition. Although we have not performed the present experiment with recordings in the retina or the lateral geniculate nucleus (LGN), these earlier visual structures are unlikely to be responsible for lightness constancy. Typical retinal ganglion cell and geniculate RFs have a center surround structure that would only yield results akin to what we observed in V1 if the stimulus were sized carefully so that one Mondrian patch filled the RF center and others filled the surround. However, this specificity and small spatial scale are inconsistent with the broad range and large scale at which the constancy interactions work. The small scale of geniculate interactions underscores the significance of the finding that V1 responses are constant on average because of interactions from well outside the RF. Although it is true that broad spatial interactions can be found in the LGN in some situations (35), the responses of LGN neurons are not correlated with lightness (13, 36, 37). Indeed, it is not obvious how we would be aware of changes in illumination if such changes were filtered out before visual cortex.

Our findings add to a growing body of evidence that surprisingly high-level aspects of vision are observed at early stages of visual processing (30, 38–42). Our results also suggest an important purpose for the large areas of silent suppression that surround the small RFs of many neurons in V1.

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