

# Lightness, filling-in, and the fundamental role of context in visual perception

Michael A. Paradiso\*, Seth Blau, Xin Huang, Sean P. MacEvoy, Andrew F. Rossi and Gideon Shalev

*Department of Neuroscience, Brown University, Providence, RI 02912, USA*

**Abstract:** Visual perception is defined by the unique spatial interactions that distinguish it from the point-to-point precision of a photometer. Over several decades, Lothar Spillmann has made key observations about the nature of these interactions and the role of context in perception. Our lab has explored the perceptual properties of spatial interactions and more generally the importance of visual context for neuronal responses and perception. Our investigations into the spatiotemporal dynamics of lightness provide insight into underlying mechanisms. For example, backward masking and luminance modulation experiments suggest that the representation of a uniformly luminous object develops first at the borders and, in some manner, the center fills in. The temporal dynamics of lightness induction are also consistent with a filling-in process. There is a slow cutoff temporal frequency above which surround luminance modulation will not elicit perceptual induction of a central area. The larger the central area, the lower the cutoff frequency for induction, perhaps indicating that an edge-based process requires more time to “complete” the larger area. In recordings from primary visual cortex we find that neurons respond in a manner surprisingly consistent with lightness perception and the spatial and temporal properties of induction. For example, the activity of V1 neurons can be modulated by light outside the receptive field and as the modulation rate is increased response modulation falls off more rapidly for large uniform areas than smaller areas. The conclusion we draw from these experiments is that lightness appears to be computed slowly on the basis of edge and context information. A possible role for the spatial interactions is lightness constancy, which is thought to depend on extensive spatial integration. We find not only that V1 responses are strongly context dependent, but that this dependence makes V1 lightness constant on average. The dependence of constancy on surround interactions underscores the fundamental role that context plays in perception. In more recent studies, further support has been found for the importance of context in experiments using natural scene stimuli.

**Keywords:** lightness; filling-in; natural vision; context

Early in the 20th century, the founding fathers of Gestalt psychology powerfully demonstrated the fundamental role that context plays in visual perception. Some of the well-known laws, such as

proximity and symmetry, emphasize the importance of spatial context. Other phenomena, such as apparent motion studied by Wertheimer, underscore the interplay between spatial and temporal context. Subsequent psychophysical research has extended our knowledge of the richness of visual interactions across space and time. While

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\*Corresponding author. Tel.: +1-401-863-1159;  
Fax: +1-401-863-1074; E-mail: michael\_paradiso@brown.edu

contextual effects are often most dramatically demonstrated in illusions, the interactions are not mere curiosities; they get at the root of human visual perception. Over several decades, the importance of context has been powerfully demonstrated by Lothar Spillman and his colleagues. For example, they studied filling in of scotomas and using neon color filling they quantified the high sensitivity to contextual factors such as the continuity and orientation of inducers (Redies and Spillmann, 1981; Spillmann and Dresch, 1995). Some of the longest range influences of context ever found were reported by Pinna et al. in the watercolor effect (Pinna et al., 2001, 2003) in which border color and contrast appear to “paint” a large enclosed area.

Contextual interactions have also been explored with neurophysiological techniques. Lateral inhibition is the simplest example (Hartline et al., 1956). A considerable number of experiments have shown that the response of a neuron to a stimulus in its receptive field can be strongly modulated by other stimuli located outside the receptive field (Allman et al., 1985; MacEvoy et al., 1998; Albright and Stoner, 2002). However, aside from experiments specifically looking for larger-scale neural integration, a great many physiological studies are conducted with stimuli confined to a small receptive field.

The Gestalt psychologists argued that perception is made up first and foremost of Gestalten. The question from a neurophysiological perspective is whether an understanding of the neural basis of perception based on reduced stimuli is fundamentally flawed because of the lack of naturalistic context. Below we discuss aspects of our own research that explore the role of context and interactions in perception. From our studies, the answer to the question posed above appears to be both “no” and “yes”. No, because most of what has been learned about neural representations in simple situations is still valid in more complex ones. However, there are basic aspects of neuronal coding that appear to depend critically on context. This means that a correct and full understanding of the relationship between vision and the brain requires that context be taken into account.

## Perceptual studies of lightness, brightness, and filling-in

### *Brightness masking*

A range of visual effects illustrate that the perception of surfaces is powerfully affected by both additive and subtractive influences from throughout the visual field (Hess and Pretori, 1894; Wallach, 1948; Helson, 1963; Cornsweet, 1970; White, 1979). In particularly dramatic situations, one area of the visual field can be perceptually filled in from information derived elsewhere. This is seen at the blind spot produced by the optic nerve and also with pathological and artificially created scotomas (Poppelreuter, 1917; Fuchs, 1921; Lashley, 1941; Bender and Teuber, 1946; Gassell and Williams, 1962; Gerrits and Timmerman, 1969). Experiments with images stabilized on the retina show that a stabilized patch is filled in by the lightness and color of the surrounding area (Riggs et al., 1953; Krauskopf, 1963; Gerrits et al., 1966; Yarbus, 1967; Larimer and Piantanida, 1988).

In experiments conducted with Dr. Ken Nakayama (Paradiso and Nakayama, 1991), we used a masking paradigm to explore the spatiotemporal dynamics of filling-in. A uniformly luminous disk was briefly flashed and, after a variable stimulus onset asynchrony (SOA), a masking stimulus was presented. The mask consisted of a bright circle on a black background with the circle internal to the boundaries of the large uniform disk. Subjects viewed multiple cycles of the disk followed by the mask. Their task was to indicate which element of a palette of gray tones was most similar to the brightness perceived at the center of the disk. As we expected, with a long SOA, the disk was perceived as filled-in before the mask was presented. However, as the SOA was decreased, brightness toward the center of the disk was diminished (Fig. 1A). Outside the masking circle, the disk appeared normal except for a small area of darkening just next to the outside of the circle. Inside the circular mask, there was a much more dramatic effect — at SOAs between 50—and 100 ms, the entire area of the disk inside the circular mask was significantly darker or black (Fig. 1B).

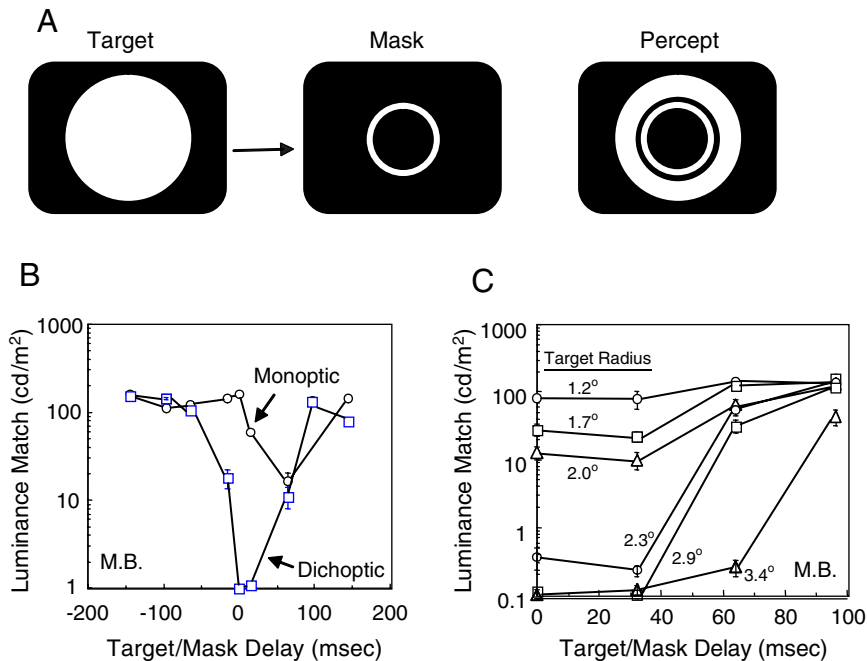


Fig. 1. Backward masking suppresses brightness. (A) When a briefly presented disk is followed by a ring-shaped mask, brightness in the interior of the disk is greatly diminished. (B) If the disk and ring are shown to the same eye (monoptic), maximal brightness suppression occurs with an SOA of 50–100 ms. With dichoptic masking, suppression is greater and maximal at zero SOA. (C) With a fixed-size mask, brightness suppression increases as the target increases in size (and the distance between the edges of target and mask increases). Masking is observed at longer delays as the target increases in size.

Under optimal conditions the brightness matches made in the center of the disk were reduced as much as 2 log units relative to the condition in which no masking was observed (i.e. at long target/mask intervals). Evidently, the circular shape of the mask was responsible for the large asymmetry in the masking strength inside and outside the circle. The normal appearance of the disk outside the area of the circular mask was consistent with the hypothesis that the outside edge of the disk played a role in determining its interior brightness and that the masking circle primarily interfered with this process inside its radius (Grossberg and Todorovic, 1988). However, if there is explicit filling-in, it appears to work at a coarse spatial scale: potent brightness masking was observed even if many small gaps were made in the masking contour; it was not the case that brightness “leaked through” the gaps. This finding is consistent with Spillmann and colleagues finding that the watercolor effect is relatively unaffected

by introducing gaps into the inducing contours (Pinna et al., 2001).

The brightness masking effect was even stronger with dichoptic than monoptic presentation (square symbols in Fig. 1B). When the target and mask were presented to different eyes, the interior of the target disk was absolutely black. The fact that the masking was effective dichoptically suggests that the stimuli interact in visual cortex where there are binocular neurons.

If there is propagation of a signal related to surface brightness, one should be able to see masking at a later time if the masking contour is farther from the edge of the target disk. To test this prediction, targets with radii ranging from 1.2° to 3.4° were used with a 2.0° radius-masking ring. Consistent with the prediction, the suppressive effect of the masks was greater as the target disk increased in size (Fig. 1C). Also, masking remained effective at longer SOAs as the distance between the edges of the two stimuli increased. On

the basis of the latest times at which masking was effective with different distances between the outer edge of the disk and circular mask, a velocity for brightness propagation was calculated. The estimated velocity was 110–150 deg/s. Using estimates of the human cortical magnification factor for primary visual cortex, this comes out to a roughly constant speed of 0.15–0.4 m/s for the propagation (if it occurred in V1).

### *Watching the filling-in process*

If filling-in is a part of normal vision, we presumably do not notice it because it is rapid. But is it possible to make filling-in visible? We explored this question by gradually increasing or decreasing the luminance of a uniform disk, in an attempt to prolong the duration of time over which the edge signal is not filled into the disk center (Paradiso and Hahn, 1996). We found that in some situations the disk's brightness is noticeably inhomogeneous as the luminance changes. Most commonly it appears that brightness changes near the center of the uniform disk lag behind changes at the disk's edge. For example, if the disk's luminance is increased, the center is darker and brightness appears to move inward. The central lag in brightness is even more pronounced when the entire computer screen is bright and a disk's luminance begins bright and gradually decreases (Fig. 2A). There is a striking percept that the center of the disk is brighter than the edge and darkness sweeps into the center.

A critical determinant of these filling percepts is the rate at which the luminance changes: the disk appears uniform if the luminance is changed rapidly or slowly but nonuniform if it is changed at intermediate rates. In qualitatively exploring the phenomenon, we tried a variety of stimulus configurations (squares, disks, etc), stimulus sizes ( $0.5^{\circ}$ – $10^{\circ}$ ), and luminance modulation paradigms (linear, exponential, etc). Generally speaking, the qualitative results did not depend critically on these parameters. For example, if the stimulus consisted of several simultaneously presented uniform patches, each patch appeared to fill in independently from its own borders. The filling-in

percepts were observed even when the modulated disk was viewed so that it encompassed the blind spot at the optic disk. This strongly suggests that the filling-in percept is based on a cortical process.

The most important variable for the perception of brightness filling-in was the dwell time at each luminance step. Spreading brightness was seen with short dwell times, but as the dwell increased above 50 ms, the darkness spreading effect decreased significantly (Fig. 2B). In other words, the perception of the modulated disk was uniform and filling-in was lost if the luminance was held longer than 50–100 ms at each luminance step.

One interpretation of the results is that the edge and center of the stimuli have different brightness when the luminance is swept up or down because the sweep speed exceeds the rate of an underlying brightness process. It is known that the brightness of an area is strongly dependent on the luminance contrast at the area's border (Hess and Pretori, 1894; Heinemann, 1972). Perhaps there is a spread of activity in visual cortex underlying perceptual filling-in. In order to account for the fact that inhomogeneities are not seen at fast luminance ramp speeds, one must postulate that the inhomogeneity exists for a period of time too short to be perceived. This would explain why we are not aware of any brightness nonuniformities in normal visual situations as we move our eyes about. Presumably, by stretching out the luminance ramp in time, an inhomogeneity can be maintained for a longer duration, making it perceptible. When the luminance ramp is very slow, each time the luminance is incremented, the filling-in process completes before the next increment and the inhomogeneity is preserved for too short a time to be perceived.

### *Dynamic lightness induction*

DeValois et al. (1986) published a surprising observation about the temporal characteristics of brightness induction that provides another piece of evidence suggesting that brightness processes are slow and involve filling-in. DeValois et al. used a stimulus in which a static gray patch was surrounded by a larger area in which the luminance was modulated sinusoidally in time. The

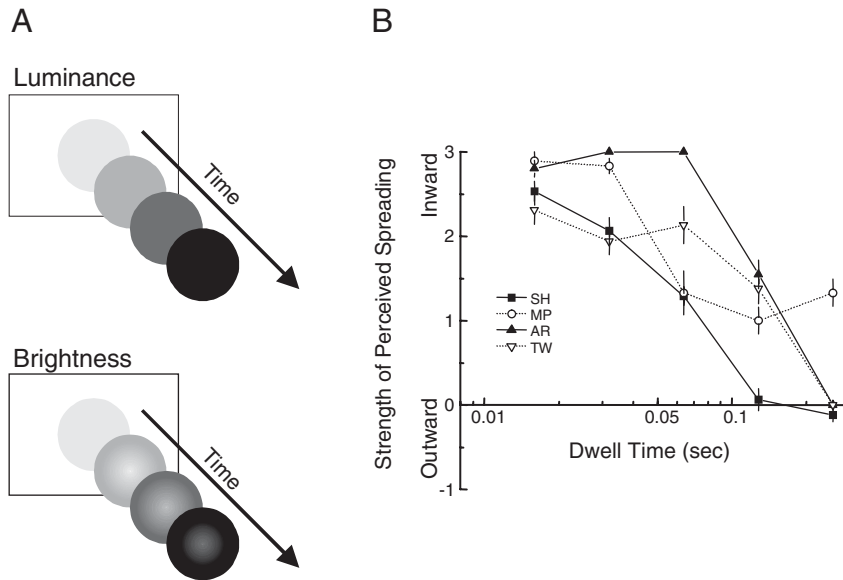


Fig. 2. Luminance sweeps produce filling-in percepts. (A) Brightness changes toward the center appear to lag behind changes at the border when the luminance of a uniform disk is progressively decreased. (B) The strength of the filling-in percept depends strongly on the dwell time spent at each luminance step. At short dwell times there are compelling filling-in percepts, but these are lost as the dwell time increases above about 50 ms.

luminance modulation of the surround produced powerful brightness induction in the gray patch, roughly in antiphase to the surround modulation. Surprisingly, brightness modulation was induced in the gray patch only when the surround was modulated at quite low temporal frequencies (i.e. below about 2.5 Hz). When the surround was modulated at higher rates the central patch appeared a static gray. This low cutoff for induced brightness modulation stands in stark contrast to the critical flicker fusion rate, which is an order of magnitude faster.

We extended the experiments of DeValois et al. to determine whether the properties of this dynamic form of brightness induction are consistent with the implications of the masking and luminance sweep experiments described above (Rossi and Paradiso, 1996). The stimulus we used was a temporally modulated squarewave grating (Fig. 3A). The grating was modulated in a manner such that the luminance of every other stripe varied sinusoidally in time and the intervening stripes had constant luminance. Perceptually, the modulation produced brightness induction in the constant

stripes, roughly in antiphase to the brightness of the luminance-modulated stripes. In light of the masking and luminance-sweep results, we were particularly interested in any dependence the temporal properties of brightness induction might have on spatial scale. Using the method of adjustment, we had observers find the highest temporal modulation rate at which induction was perceived at different spatial frequencies. We found that the lower the spatial frequency (i.e. the larger the areas of uniform brightness), the lower was the cutoff temporal modulation rate (Fig. 3B). We also quantified the amplitude of the perceived brightness modulation that was induced. This showed that the amplitude of brightness induction was greatest at low temporal modulation rates. The luminance matches to the peak and trough of the brightness modulation approach each other as the temporal frequency is increased, eventually becoming equal when there is no perceived brightness modulation. These results make it clear that below the cutoff modulation rate, the amplitude of brightness induction is graded relative to temporal frequency and induction is not

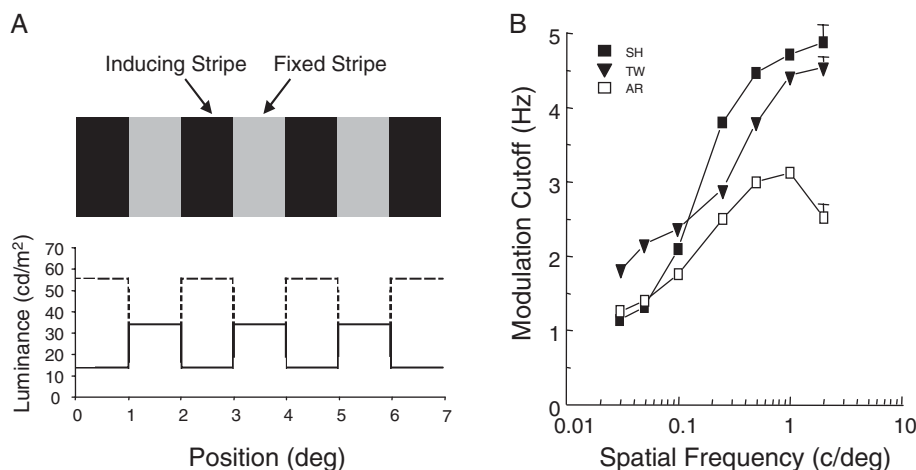


Fig. 3. Temporal properties of brightness induction. (A) Subjects viewed a fixed stripe with constant luminance while neighboring inducing stripes were luminance modulated. (B) Cutoff temporal frequencies for three observers above which induction was not observed.

simply “off” and “on” above and below the cutoff rate.

The results of the dynamic induction experiments make two important points about the mechanisms involved in brightness perception. First, the process responsible for brightness changes due to induction is considerably slower than the process responsible for brightness changes from direct luminance modulation. Second, the time course of induction is scale-dependent. The low cutoff frequency for induction and the effect of modulation rate on the amplitude of induction suggest that induction is a slow process that simply cannot “keep up” with fast modulation rates. In another way, it appears that larger spatial areas take more time to induce. Besides the fact that the cutoff rates for “real” and induced brightness changes differ by more than a factor of 10, they depend on spatial scale in opposite ways. While the critical flicker fusion rate increases with stimulus size, the cutoff frequency in our induction experiments decreases with size. The results indicate that there is a major difference between the mechanisms limiting perception of modulation with real and induced brightness. If induction were initiated at edges and propagated inward, this would explain why it takes longer to induce a larger area and why the cutoff frequency decreases with increasing size. We measured the spatial phase of induced brightness

across spatial scale and this led to an estimate of 140–180°/s for the induction process. This estimate is in rough agreement with the filling-in velocities estimated in the brightness masking and luminance sweep experiments.

To reconcile filling-in with the high CFF, we have proposed that brightness involves two mechanisms — a fast process that is relatively unaffected by the size of a uniformly luminous area, and a slow filling-in process with a duration that increases with the size of a uniformly luminous area. A fast process largely based on luminance appears to be necessary to explain the high CFF for luminance modulation and the fact that this frequency does not decrease with the size of the modulated area. A slow process driven mainly by contrast appears to be required to account for the induction results as well as results in the masking and luminance-sweep experiments. We hypothesize that when the luminance of an area is modulated, both the fast and slow processes are involved in determining the final brightness percept of that area. Previous experiments suggest that slow filling-in occurs with luminance modulation (Paradiso and Nakayama, 1991; Paradiso and Hahn, 1996), but the fast process presumably determines the CFF. The situation is different when brightness modulation occurs solely because of induction. In this case, we suggest that only the



slow filling-in process is responsible for the perceived brightness modulation of the induced area. Thus, the velocity of the filling-in process would determine the cutoff frequency for induced modulation.

### ***Implications for mechanisms***

On the basis of the psychophysical results discussed above, we can hypothesize how a surface representation and filling-in might be physiologically implemented. First, it seems that there must be some form of explicit surface representation. If surfaces were represented entirely in terms of edge signals, it is not clear why filling-in would be perceived. Second, the representation of brightness should have a scale-dependence in accord with the psychophysical results. Third, the filling-in process should be slow compared to the CFF. The psychophysical data give a measure of the expected speed. The conclusion we cannot draw from the psychophysical results is that filling-in is an isomorphic process akin to painting the interior of a surface. While this is conceivable, there is little evidence in favor of it. More likely, filling-in involves a rapid temporal process of neural interactions leading to the final surface percept; the brain representation is probably not an isomorphic representation of the stimulus. An edge-dominated process involving filling-in is a way to reconcile the psychophysical and physiological results presented here with studies showing coding of border ownership (Zhou et al., 2000).

### **Physiological studies of lightness and filling-in**

#### ***Brightness induction and the cortical representation of surfaces***

For there to be a form of neural filling-in underlying perceptual filling-in of a surface, there needs to be an explicit representation of the surface. If surfaces were represented entirely by the responses to their boundaries, nothing would need to fill-in. We investigated whether there is an explicit representation of surface brightness using the dynamic induction stimulus previously used in

psychophysical experiments. The question was whether the response of a neuron is modulated when its receptive field is positioned on the induced surface.

We recorded from single cells in the retina, lateral geniculate nucleus (LGN), and primary visual cortex of anesthetized cats (Rossi and Paradiso, 1996; Rossi et al., 1996; Rossi and Paradiso, 1999). After mapping the RF, the dynamic induction stimulus was positioned such that a large central gray patch covered the RF (middle left icon in Fig. 4A). The size of the patch was always much larger than the RF, extending 3–5° beyond the RF boundary on each side. Flanks, the same size as the central patch, were positioned to each side. The luminance of the flanking patches was modulated from light to dark sinusoidally in time. Two principal control stimuli were used (top and bottom icons to left in Fig. 4A). In one, the luminance of the area covering the RF was modulated, rather than the flanks (top row). This tested whether responses were better correlated with the luminance or brightness of the central patch. The second control had a large black patch covering the RF, instead of a gray patch, while the flanks were modulated (bottom row). If light from the flanks directly modulated the response of the neuron (e.g. scattered light), this should be revealed with this control stimulus. However, as there is no perceptual induction when the central patch is black, the neuron's response should not be affected by the flank modulation if the response represents brightness.

To study the responses of retinal ganglion cells, we recorded from their axons in the optic tract. It is important to keep in mind that the stimuli employed were sized such that the central patch encompassed both the center and surround of the RF — any effects of the flanks were from beyond the RF. As would be expected from the low-pass frequency response of retinal neurons, many cells were somewhat activated by a gray patch of light covering their RF. Furthermore, some cells responded in a phase-locked manner to luminance modulation within the RF. When the dynamic induction stimulus was used, cell responses were generally constant along with the luminance of the patch covering the RF, rather than modulated.

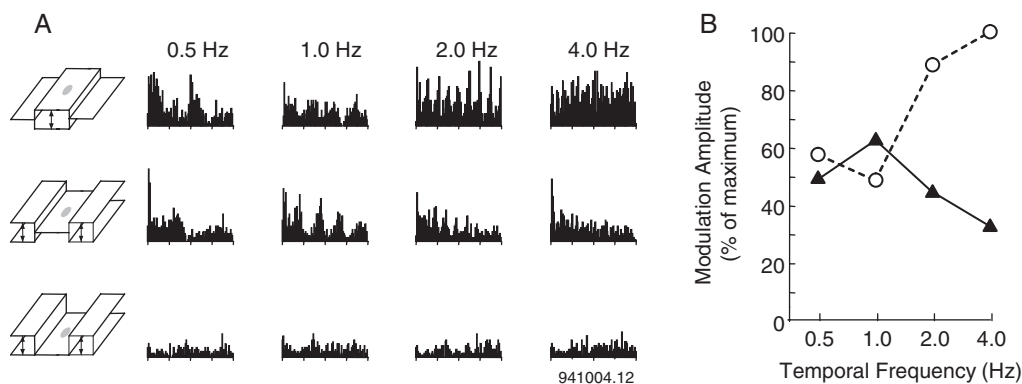


Fig. 4. Responses in cat V1 to brightness induction stimuli. (A) Responses of one cell to three stimuli (left) were recorded at four temporal modulation rates. In the stimulus icons, the small gray patch is the receptive field. The stimuli were: luminance modulation control (top), induction (center), and surround modulation control with central area black (bottom). (B) As temporal frequency increased, V1 responses on average were more modulated in the luminance modulation control (dashed line) but less modulated in the induction condition (solid line).

The optic tract recordings showed that retinal neurons are responsive to luminance in the absence of contrast, but the responses did not correlate with perceived brightness.

In many regards, the results were similar when recordings were made in lateral geniculate nucleus layers A and A1. A static gray patch in the RF often elicited a neuronal response, and the response varied as the luminance of the central patch was modulated. There were also neurons that showed modulated responses when the flank luminance was varied in time. However, the fact that the response modulation to the flanks was generally greater when the central patch covering the receptive field was black rather than gray suggests that light scattering was probably involved rather than a brightness representation. Very occasionally, cells were encountered that did appear to have responses correlated with brightness.

Many cortical neurons were found to respond only in stimulus conditions that produced perceptual changes in brightness in the area corresponding to the RF. An example of this is shown in Fig. 4A. The middle row of this figure shows the response of a neuron to the presentation of a constant gray field flanked on either side by luminance-varying fields of equal size. The RF was  $4^\circ$  wide and was centered on the central gray area that was  $14^\circ$  across. The response of the neuron was phase-locked to the frequency of the luminance modulation in the

stimulus flanks. There was no such response when the central portion of the stimulus was black (bottom row). In our sample of 160 striate neurons, 120 (75%) had responses that were modulated and phase locked to the luminance changes outside the RF.

A comparison of responses in the different conditions suggests that the firing of the neuron in Fig. 4A (and others) was more correlated with the brightness in the area covering the RF than with the luminance of any particular portion of the stimulus. This was seen in the strong response modulation when the stimulus center was gray (a condition that yields perceptual induction) compared to the weak response when the center was black (a condition that does not cause induction). A correlation with brightness is also found when comparing the responses to luminance modulation within the receptive field and luminance modulation in the flanks. When light covering the receptive field was modulated, the response was maximal when the central area was brightest (and the luminance of the modulated light was highest). When the flanks were modulated, the response was again greatest when the central area was brightest, but in this case the luminance of the modulated flanks was lowest. The response was clearly not determined by the overall amount of light present in the stimulus.

As described in the previous section, one of the hallmarks of the dynamic brightness induction



effect is that brightness changes are only perceived at low modulation rates in comparison to the rates of direct luminance modulation that elicit brightness variations. In other words, at higher modulation rates there is a significant difference in the degree of perceived brightness modulation with real and induced brightness. Physiologically, we found differences in the amplitudes of response modulation in the induction and center modulation conditions. In the induction condition (middle row), the response of the neuron in Fig. 4A was largest at low temporal frequencies and *decreased* as the rate of flank modulation was increased above 1.0 Hz. However, when the luminance of the central area was modulated (top row), the response amplitude progressively *increased* with increasing temporal frequency. A significant difference in the induction and center modulation conditions is clearly evident in the averaged data (Fig. 4B).

The responses of neurons in striate cortex correlate with perceived brightness in four ways: the neural responses were modulated at the frequency of the surrounding luminance modulation; the response modulation occurred in conditions that elicited brightness induction but not in similar conditions that did not produce induction; in the induction conditions, the response modulation greatly decreased as temporal frequency increased; there was a complete phase shift between induction and center modulation conditions. However, cells that appeared to follow brightness based on one criterion did not always do so according to other criteria. We estimate that about 30% of V1 neurons have responses correlated with brightness in all conditions.

### ***Lateral interactions in visual cortex***

The induction studies described above suggest that at least for a subgroup of neurons in striate cortex, there is an explicit representation of surface qualities such as brightness. The logical hypothesis to explain the induction physiology results is that outside cortical-receptive fields, there are areas that modulate the response to a stimulus in the RF. While there have been many studies of

interactions from outside striate-receptive fields, virtually all have used lines or gratings as stimuli (i.e. contrast within the RF). However, when a uniform surface covers the RF, interactions from areas beyond the receptive field are not reliably the same as those that would be found with line or grating stimuli (MacEvoy et al., 1998). From one cell to another, there is considerable diversity in the modulatory effects that light outside the RF has on the response to a surface covering the RF. The most common effect is surround suppression. The prevalence of surround suppression and its large spatial range, offers an explanation for the induction effect noted above. The modulatory areas outside the RF cannot drive the cortical neuron alone (i.e. no response when the area covering the RF is black), but when the cell is excited by a central stimulus, such as the gray patch, the flanks can alter the response. The “in phase” and “out of phase” responses recorded with luminance modulation of the patch covering the RF versus the flanks can be accounted for by areas beyond the RF that are either facilitatory or inhibitory.

### ***Lightness constancy in visual cortex***

Presumably, the interactions from beyond the receptive fields of V1 neurons serve some valuable purpose(s) and it appears that lightness constancy may be one such purpose. Over the course of a day and across the seasons of the year, the illumination coming from the Sun varies considerably. Humans and animals that have been tested, perceive the lightness of objects to be stable despite large variations in illumination. This perceptual constancy for lightness, and related color constancy, were presumably of great evolutionary value. For example, in the absence of perceptual constancies, there might not be reliable cues upon which to select ripe fruit to consume.

We conducted experiments in cat V1 to test responses for lightness constancy (MacEvoy and Paradiso, 2001). Stimuli consisted of monochromatic patches (i.e. a monochromatic “Mondrian” stimulus) on a computer monitor simulating surfaces with a wide range of

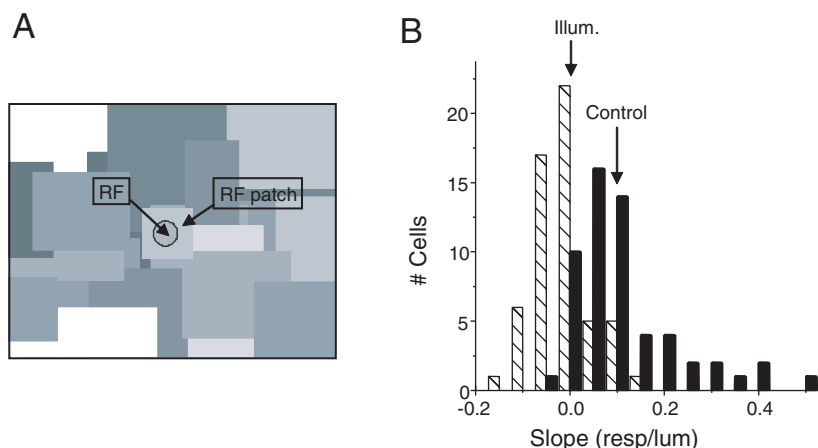


Fig. 5. Lightness constancy in cat V1. (A) On a computer display, a Mondrian of patches with different reflectances was simulated. The receptive field was centered on one of the patches (the RF patch). (B) In control conditions, only the luminance of the RF patch was varied. As shown by the solid bars and arrow, the average response was positively correlated with luminance (and lightness). In illumination conditions (hatched bars), the average response was constant as RF patch luminance changed along with the average background luminance.

reflectances (Fig. 5A). One patch of the stimulus encompassed the receptive field and the rest composed the background. Changes in the luminance values of the patches were made in a manner either consistent (illumination conditions) or inconsistent (control conditions) with overall changes in illumination. Comparisons were made between the two situations when the patches covering the receptive field in each case were identical.

In control conditions only the luminance of the patch covering the receptive field increased, a situation in which the perceived lightness of the patch increases with luminance. In contrast, in the illumination conditions the lightness percept was stable. While there was considerable cell-to-cell variability, on average the responses of V1 neurons to identical stimuli in their receptive field were significantly different in the two conditions (Fig. 5B). In the control condition the average V1 response correlated with the luminance of the RF patch. Since perceived lightness correlated with the luminance, the neural response also correlated with lightness. In marked contrast, in the illumination conditions there was essentially no change in the average V1 response as the luminance of the RF patch increased. This mirrored the perceptual

constancy of the patch. These results are reminiscent of the constancy demonstrations of Land (Land and McCann, 1971; Land, 1986). In these demonstrations, the color of patches in a Mondrian were shown to be constant when the overall illumination was varied, but viewing any single patch in isolation (for instance, through a tube) revealed that the patch luminance changed dramatically. The context provided by the changes in the larger area is essential to normalize the local percept. In our physiological studies, in both the illumination and control conditions the response correlated with lightness, but only in the illumination conditions did the response exhibit lightness constancy.

A likely basis for the response invariance in the illumination conditions is the predominant surround suppression seen with uniform patches of light (Schein and Desimone, 1990; MacEvoy et al., 1998; Wachtler et al., 2003). Evidently in the illumination conditions the increased response of the neuron that comes from more light in the RF is counterbalanced by increased suppression from the surround. What is somewhat surprising is that on average the net input to V1 neurons balances the added RF drive with increased surround suppression.

## The importance of natural visual and behavioral context

### *The effects of natural scenes and saccades on V1 activity*

The results described above suggest that in the domain of lightness, modulatory inputs from lateral or feedback connections play an important role in the V1 representation of lightness and in lightness constancy. Although Mondrian's paintings can be viewed in museums, flashing similar pictures to a fixating animal can hardly be considered a natural visual situation. Visual stimulation in the real world typically involves complex arrangements of light, color, and contrast, quite unlike the simple stimuli usually used in the laboratory. Moreover, natural stimuli fill the visual field whereas many experiments are conducted with small RF stimuli isolated on a large blank display. Another obvious difference between typical experiments and natural vision is behavioral. In a natural setting, the eyes move to bring new stimuli into view; typical fixations are about 300 ms with brief intervening saccades. In most experiments, animals are trained to hold fixation (or anesthetized) while stimuli are flashed into the receptive field.

To explore the significance of stimulus complexity and saccades on V1 responses, we

conducted an experiment in alert macaques in which the same stimulus was presented to a neuron under four different conditions, varying in how natural the visual situation was. In the first condition, the animal fixated a point on an otherwise gray visual display and a small bar was flashed into the receptive field. In the second condition the animal fixated the same point and the bar was flashed, but in this case the background was a grayscale outdoor scene (van der Schaaf and van Hateren, 1996) with the same mean luminance as the gray background. In the third and fourth conditions the background image was a uniform gray or a grayscale photo, respectively. However, in these conditions the fixation of the animal was guided such that a saccade brought the bar stimulus into the receptive field rather than it being flashed on.

We find that the response to a bar stimulus in the receptive field is influenced by both stimulus complexity and the method by which the stimulus comes into the RF (flash or saccade). Examples are shown in Fig. 6. The cell illustrated in Fig. 6A shows the difference in response associated with the gray and natural-scene backgrounds. The response to a small bar is significantly higher when the background is a uniform gray than when it is a grayscale picture. In this case the response was roughly 50% greater when the bar was presented on a gray background compared to a

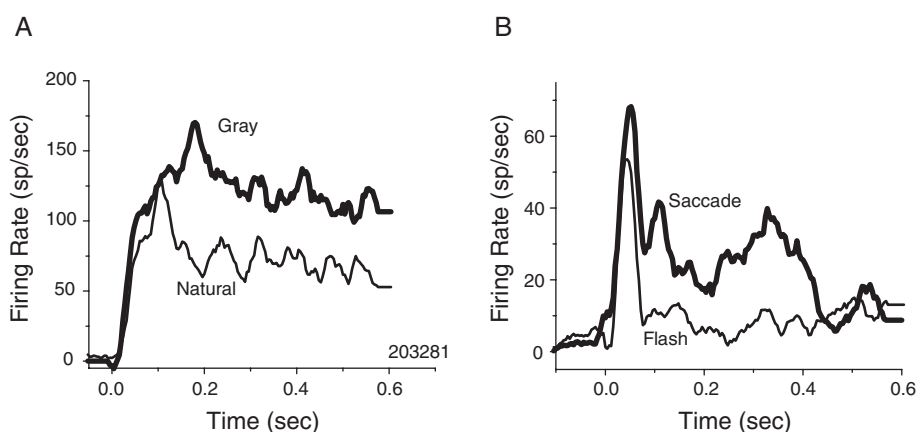


Fig. 6. Macaque V1 responses influenced by background and saccades. (A) In this neuron, the response to the same stimulus bar was significantly higher on a gray background than a natural background. (B) The response to the identical stimulus was higher when it entered the receptive field via saccade rather than being flashed.

natural scene. This response difference is found regardless of whether a saccade or flash introduced the bar into the receptive field. Also interesting is the delay in the separation of the two curves. The initial response with gray and natural backgrounds is similar but after about 50 ms there is a reduction in the natural-scene response. It is not possible to say why the response differs between the two conditions, but the natural scene obviously has contrast and structure not present with the gray background. Previous studies have reported the suppressive effect of contrast outside the receptive field (Allman et al., 1985) and our result can be interpreted in that context. The delay in the background effect suggests that different circuitry may be involved.

More surprising is the influence of presentation method shown in Fig. 6B. When a saccade brought the bar stimulus into the receptive field, the initial response was similar to a flashed stimulus, but after about 50 ms the response in the saccade condition was much larger (more than 100% greater). The neuron shown in this figure has a particularly pronounced difference, but even in the population average, the saccade response with the natural-scene background was 15% higher than the flash response on the same background. Several factors were considered to account for the response difference when a stimulus appeared in the receptive field via saccade versus flash. For example, we considered the possibility that the stimulus present in the receptive field prior to the saccade might affect response magnitude. While there was a hint of this in some cells, it could not account for most of the response difference. We also considered the possibility that stimuli swept across the receptive field during the saccade might make the saccade response greater. Again, this was not able to account for the response difference. These and other factors were considered (MacEvoy et al., 2002), and while several factors have small effects on response rate, no single factor has yet been found that can account for the bulk of the response difference.

The combined (and opposed) effects of scene complexity and saccades suggest that it is impossible to predict responses in natural situations from responses to small stimuli flashed into the receptive field.

### ***Background changes and delayed form information***

The experiments in which saccades on a natural scene brought stimuli into receptive fields represent a more natural visual situation than flashing a bar isolated to a receptive field. However, the use of complex scenes and saccades complicates interpretation of the results. For example, natural scenes had a suppressive effect on V1 activity relative to a uniform gray background, but the scene complexity made it difficult to ascertain what aspect(s) of the picture was responsible for the suppression.

In a parallel series of experiments we used a somewhat less natural visual paradigm to gain greater control over the effects of image complexity and saccades (Huang and Paradiso, 2005). When an animal makes a saccade while viewing a natural scene, the “contents” of a V1 receptive field change. Perhaps a rock was initially in the receptive field and afterwards the branch of a tree. At the same time that a new local feature is introduced, the background or context usually changes. When the branch of the tree sweeps into the receptive field, adjacent areas in the RF and outside the RF might “see” other vegetation. In our experiments we simulated this natural sort of visual stimulation in the context of a well-controlled fixation paradigm. Macaques fixated a point on the visual display and bars of light or Gabor patches were presented in the receptive field. On some trials the background was static as in most visual physiology experiments. On other trials the background luminance or pattern changed simulating what would occur with a saccade. Comparisons of neural responses were made when identical stimuli were within and beyond the RF in the static and changing background trials. The only difference between the conditions was the stimulus in the receptive field *before* the bar and background used for response measurements.

We found that when context changes with the introduction of a local feature (the changing background condition), the response pattern is qualitatively and quantitatively different than the standard static-background situation. An example of this is shown in Fig. 7. When a bar was introduced on a static background, the response

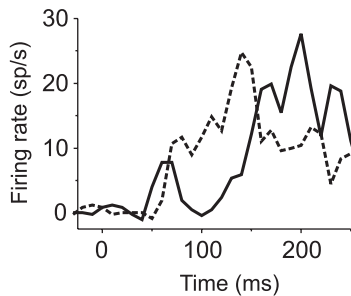


Fig. 7. Temporal context effects in Macaque V1. When a bar stimulus was flashed on a static background, the response had a single peak (dashed curve). To mimic the effect of a saccade, the same stimulus and background were shown, but preceded by a different background. In the changing background condition the response had two peaks (solid curve). With the static background, orientation was reflected in the amplitude of the initial response and contrast was anticorrelated with response latency. With the changing background the initial response carried little orientation or contrast information. Instead, these attributes were represented in the amplitude and latency of the second peak.

typically showed one peak. In this case, orientation selectivity and contrast sensitivity were represented in the amplitude and latency of the earliest response, respectively. The response is quite different in the changing background situation. The data shown in Fig. 7 were obtained when a bar stimulus appeared simultaneously with a change in background luminance, but similar results were obtained with an isoluminant background pattern change. The early response in the changing background condition appears similar to that in the static condition. However, there tended to be response suppression after the initial transient followed by rebound to a higher firing rate. In other words, the average response in the changing background condition showed two peaks rather than one. Of particular interest is the observation that form information is no longer represented in the initial transient as in the static background condition. Instead, orientation and contrast sensitivity are reflected in the amplitude and latency of the delayed second response peak. This peak occurred about 50 ms after the initial peak, suggesting that in the changing background condition, form information was delayed by this amount of time. Other neurons showed only this late response component.

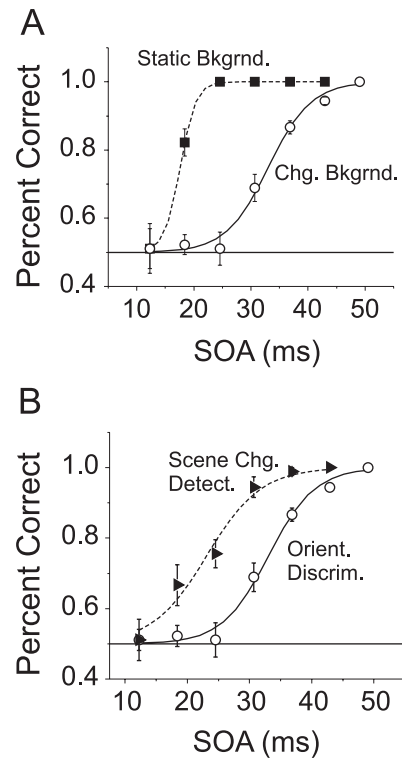


Fig. 8. Human discrimination and detection with a changing background. (A) As SOA between the stimulus and mask increased, performance in static and changing background conditions improved. Performance increased significantly faster with a static background and, at intermediate SOAs, performance was optimal when performance with a changing background was still at chance levels. (B) Subjects were able to detect a change in the scene at significantly shorter SOAs than those at which they could discriminate bar orientation.

The response differences recorded in the static and changing background conditions suggest that there might be a temporal difference in the brain's access to form information. We tested this hypothesis in a series of human psychophysics experiments (Huang et al., 2005). Bar stimuli were briefly presented and followed by a masking stimulus at various SOAs to limit the duration of visual processing (Breitmeyer, 1984). As predicted by the physiology data, it appears that perceptual access to form information (orientation and contrast) is delayed when a background change (luminance or pattern) accompanies the presentation of a bar of light. In Fig. 8A, orientation discrimination improves significantly as SOA increases with either

static or changing background. However, performance saturates at much shorter SOAs with the static background. This suggests that the orientation information is present earlier in that condition. The psychophysics experiments also showed that in the changing background situation, observers are able to detect that the scene has changed well before (about 20 ms) they are able to discriminate orientation (Fig. 8B). This suggests that in the changing background condition the early response signals that the scene has changed but does not carry the bulk of the information about the details of the stimulus.

### Abbreviations

CFF	critical flicker frequency
RF	receptive field
SOA	stimulus onset asynchrony

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