Pergamon

PII: S0042-6989(96)00033-8

Vision Res., Vol. 36, No. 17, pp. 2657–2663, 1996

Printed in Great Britain
0042-6989/96 $15.00 + 0.00

Filling-in Percepts Produced by Luminance Modulation

MICHAEL A. PARADISO,*† SIGRID HAHN*

Received 28 August 1995; in revised form 17 January 1996

We report that when the luminance of a homogeneous spot of light is gradually increased or decreased, there are conditions in which the brightness of the spot is spatially nonuniform. When the spot luminance is increased, brightness changes in the spot's center lag behind changes at the edge and brightness appears to sweep inward. Conversely, if the luminance of the spot is decreased, there is a relative lag in the darkening toward the center of the spot and darkness seems to spread inward. In Experiment 1 we found that with both increasing and decreasing luminance sweeps, the strength of the brightness filling effects was strongest with luminance sweep durations of 0.25–0.5 sec. In Experiment 2, the sweep duration was held constant at 0.5 sec; the filling effect was seen when the dwell time spent at each luminance step was less than about 100 msec, but nonuniformities were not observed at longer dwell times. In Experiment 3, a spot of light was positioned to surround the optic disk in one eye. Surprisingly, when the spot was luminance modulated from bright to dark, darkness appeared to sweep from the edge to the center of the modulated disk, even though most of the disk's interior was imaged on a portion of the retina devoid of photoreceptors. These findings are consistent with the hypothesis that a neural filling-in mechanism in visual cortex plays a key role in brightness perception. Copyright © 1996 Elsevier Science Ltd.

Brightness Darkness Filling-in Induction Illusion

INTRODUCTION

While the brightness of an area in the visual field is related to the luminance of the area, demonstrations such as simultaneous contrast (Heinemann, 1972; Hess & Pretori, 1894) illustrate that, depending on context, an object which reflects a constant amount of light to the retina can appear anywhere between black and white. Perceived brightness appears to be based on a complex set of spatial interactions such that the brightness perceived in one area depends on the luminance of that area, the luminance in neighboring areas, and the luminance at more distant locations. The interactions between luminance and/or luminance contrast at different locations in the visual field are the essence of brightness perception and are thought to account for simultaneous contrast (Heinemann, 1972; Hess & Pretori, 1894), lightness constancy (Cornsweet, 1970; Helson, 1943; Jameson & Hurvich, 1964), and brightness illusions produced by Craik–O'Brien–Cornsweet (COC) edges (Cornsweet, 1970; O'Brien, 1958).

While many studies have quantified the spatial properties of brightness perception, the mechanisms that determine brightness are not well understood. Two brief examples will highlight the mechanistic issues we have investigated. First, consider the standard demonstration of simultaneous brightness contrast in which a gray disk appears to be lighter or darker depending on whether it is placed on a black or white background. Even when the gray disk is 10 deg or larger in diameter, the influence of the luminance contrast at the disk's edge extends all the way to the center of the disk. Second, consider a large uniform gray field that has a COC edge running vertically up its center. The presence of such an edge can make a large area to the left of the edge look uniformly darker than the area to the right. In both of these examples, information at an edge strongly influences the brightness of a large area. But, through what mechanism does this occur? Is the brightness 1 deg, 3 deg, and 5 deg from an edge in a simultaneous contrast or COC stimulus simultaneously "set" by a cognitive process to the same value? If the surround luminance in a simultaneous contrast stimulus is changed, does the brightness at all locations within the central disk simultaneously change or is there a spatial progression? If brightness is based on lateral connections in a neural network, there might be a relationship between the configuration of a stimulus, the distance of brightness interactions, and the time that interactions take to influence perception. Issues such as

*Department of Neuroscience, Box 1953, Brown University, Providence, RI 02912, U.S.A.

†To whom all correspondence should be addressed [*Email*: Michael_Paradiso@brown.edu].

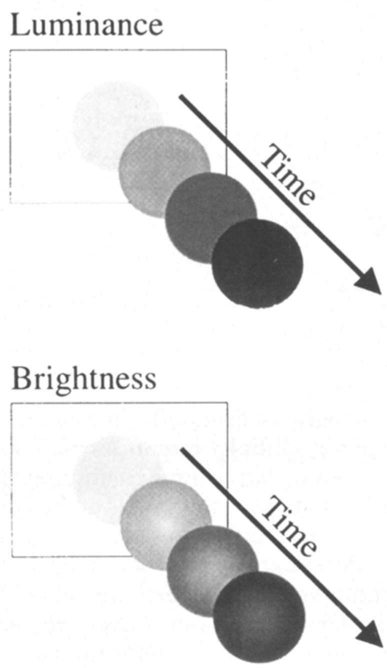

FIGURE 1. When the luminance of a spot of light is swept downward at certain rates, the perceived brightness of the spot is inhomogeneous and darkness appears to fill inward.

these led us into the present study in which we examined perceived brightness changes resulting from changes in luminance.

PRELIMINARY OBSERVATIONS

The three experiments described below were motivated by a preliminary investigation in which we noticed that interesting inhomogeneities are seen when stimuli of various shapes have their luminance temporally modulated. Suppose that on a dark computer screen the luminance of a spot one to several degrees in diameter is gradually increased from dark to bright. Does the brightness increase simultaneously and equivalently everywhere throughout the spot? The answer is that under some conditions the brightness does appear to change uniformly. However, in other situations the spot's brightness is noticeably inhomogeneous as the luminance changes. Most commonly it appears that brightness changes toward the center of the uniform spot lag behind changes at the spot's edge. In other words, the center is a bit darker and it looks as if brightness is moving inward from the spot's edge. The lag in brightness changes is even more pronounced when the entire computer screen is bright and a spot's luminance begins bright and gradually decreases. There is a striking percept that the center of the spot is brighter than the edge and darkness sweeps into the center (Fig. 1).

A critical determinant of these brightness lag or filling percepts is the rate at which the luminance is changed: the spot appears uniform if the luminance is changed rapidly or slowly but nonuniform if it is changed at intermediate rates. In qualitatively exploring the phenomenon, a variety of stimulus configurations (squares, spots, etc), stimulus sizes (0.5–10 deg), and luminance modulation paradigms (linear, exponential, etc) were employed. Generally speaking, the qualitative results do not critically depend on these parameters. The perceptual lag of brightness and darkness is seen with stimuli of different shapes and sizes. For example, if the stimulus consists of several arms of a windmill radiating from the point of fixation, each arm appears to fill in separately from its borders. The particulars of the temporal modulation are more important, but even here the basic effect is seen with schemes as different as linear changes in luminance vs exponential changes. In the three experiments described below we explored the manner in which brightness inhomogeneities resulting from luminance modulation depend on various aspects of the luminance modulation.

GENERAL METHODS

Subjects in the experiments consisted of the authors and three naive observers. Visual stimuli were generated by a Number Nine Graphics Board installed in a PC clone and displayed on a NEC GS2A grayscale monitor with 640×480 pixel resolution (28 pixels/cm) and a refresh rate of 60 Hz. At the viewing distance of 57 cm, the screen subtended 25 deg. Fine control of stimulus luminance was achieved by driving the monitor with the output of a video attenuator connected to the computer's RGB outputs (Pelli & Zhang, 1991).

The visual stimuli were disks of uniform luminance. The size of the disk used in each experiment was a compromise between larger sizes, which gave clearer effects, and smaller sizes, which had more homogeneous luminance. The luminance of the disk was temporally modulated in equally detectable steps, rather than equal steps in luminance, because this seemed appropriate.

Dealing with CRT inhomogeneities

Because the subject of this study was the inhomogeneous appearance of temporally modulated stimuli, we were particularly concerned that our experimental apparatus itself might introduce inhomogeneities. Virtually all computer monitors have significant spatial variations in luminance, typically having the highest luminance near the center and a fall-off of about 20% toward the sides. Two tactics were used to minimize the effects of this inhomogeneity. First, a number of different monitors were tested to find the most uniform, and the stimuli were centered on the screen where there is an area of fairly uniform luminance. Second, despite the fact that the brightness lag effects work well with large stimuli (e.g. 5–10 deg spots), relatively small spots (1 deg in diameter) were used in the experiments described below. We verified that the small stimuli had uniform luminance across their diameter, while they were temporally modulated, by measuring luminances with an array of photodiodes placed across the stimuli. The inhomogeneities we studied were perceptual and not due to monitor deviations from uniform luminance.

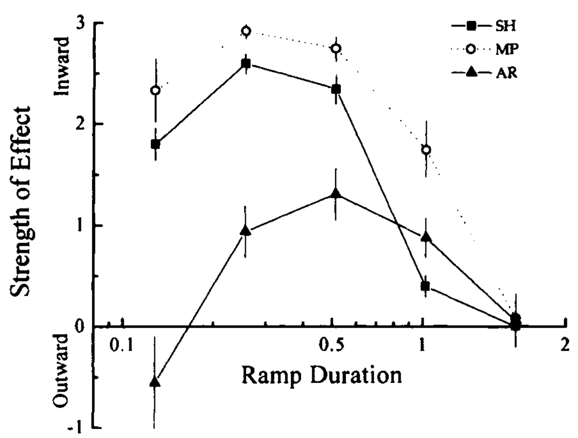

FIGURE 2. The effect of ramp duration on the strength of the percept involving inward filling of *brightness* obtained with *upward* luminance ramps. The dwell time at each luminance step was 16 msec and the overall luminance range swept was 60 cd/m^2. Data are shown for three observers.

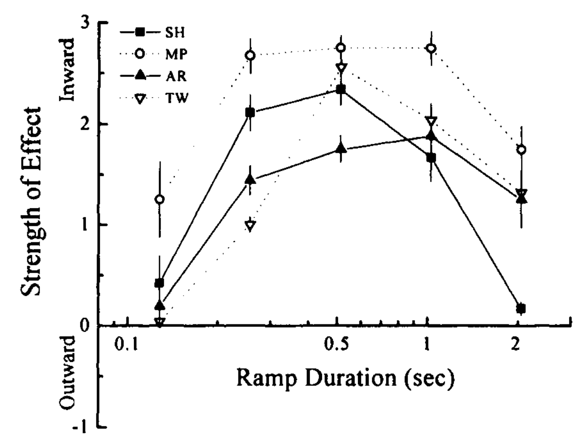

FIGURE 3. The effect of ramp duration on the strength of the percept involving inward filling of *darkness* obtained with *downward* luminance ramps. The dwell time at each luminance step was 16 msec and the overall luminance range swept was 60 cd/m^2. Data are shown for four observers.

EXPERIMENT 1: FILLING-IN PERCEPTS PRODUCED BY LUMINANCE RAMPS

In this experiment, observers rated the strength of brightness inhomogeneity as a function of the temporal modulation rate. Experiments were conducted with both upward and downward luminance ramps.

Methods

The visual stimulus was a spot of light 1 deg in diameter centered on the computer screen. For the upward luminance ramps the background luminance was 0.1 cd/m^2 and the luminance of the spot was modulated from 0.1 to 60 cd/m^2. Luminance was incremented every 16 msec in exponential steps to give approximately equal changes in brightness. The downward ramps used the same luminance levels as the upward ramps, in reverse order, and the background luminance was 60 cd/m^2. In pilot experiments with these forms of modulation, we found that naive observers consistently reported the same percepts. They stated that the brightness toward the center of the spot appeared different than the brightness at the edge or that brightness or darkness spread inwards. These percepts were quantified by asking subjects to rate the strength of the sensation that brightness or darkness spread inward. In the upward (downward) ramp experiments, a rating of 1, 2, or 3 meant that there was a weak, moderate or strong sensation that brightness (darkness) spread inward. Zero meant that no spreading was perceived and negative values meant that brightness (darkness) appeared to spread outwards.

In this experiment the strength of brightness inhomogeneity was rated as a function of the duration of the luminance ramp. To accomplish this the overall luminance range was held constant at 60 cd/m^2 and the number of luminance steps was varied. In a typical run of the experiment, eight different sweep durations were randomly interleaved. The observer could view unlimited repetitions of the luminance sweep before making a response. Between each sweep there was a pause of 5–10 sec in which the screen was filled uniformly to minimize aftereffects and masking between successive sweeps. Additionally, observers were instructed that they should take breaks if they felt that they were seeing an aftereffect interfering with their ability to perform the brightness task. To register a decision about the percept, the observer hit a key on the computer keyboard and then there was a 5–10 sec delay before the next randomly selected sweep was initiated. We are confident that aftereffects and masking did not confound our results because the same perceptual observations were made with individual luminance sweeps.

Results

Before presenting the data obtained in Experiment 1, a few qualitative observations are in order. The first point is that the appearance of the brightness spreading did not always look identical for different observers or on every trial for the same observer. Sometimes the effect was a symmetric inward spread of brightness or darkness but in other cases there appeared to be a somewhat asymmetrical "winking" of brightness. A second observation is that the sensation of darkness spreading obtained with downward luminance sweeps was almost always stronger than the sensation of brightness spreading in the upward sweeps. This is partially reflected in the subjective ratings because some subjects had a difficult time rating the inward brightness spread as "strong" if they had previously seen an inward spread of darkness that was more compelling. In any event, we asked the observers to try and establish independent scales for rating the strength of percepts for upward and downward sweeps.

When a 60 cd/m^2 luminance range was swept upward, the greatest sense of brightness flowing inward was obtained when the sweep had a duration of 0.25–0.5 sec (Fig. 2). When the luminance ramp was more gradual, with a duration longer than 1 sec, there was little sense of inhomogeneity or inward flow of brightness. Conversely,

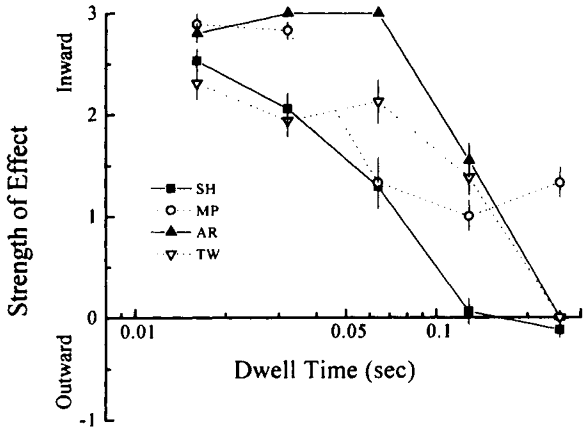

FIGURE 4. Dependence of the strength of inward filling of darkness on the dwell time spent at each luminance step. The overall luminance range swept was 60 cd/m^2 and the duration of the ramp was 0.5 sec. Data are shown for four observers.

when the luminance was changed over a time duration shorter than about 0.25 sec, the filling percept was weakened.

Figure 3 shows that similar duration downward luminance ramps also gave the strongest sensation of darkness moving inward in the stimulus spot. However, there were some differences between upward and downward luminance ramps. As noted above, all observers reported that the inhomogeneity of the disk and the sensation of moving brightness were noticeably greater with downward ramps. The strongest inhomogeneous percepts were obtained with ramp durations of about 0.5 sec and the effect was much reduced with durations of 2 sec. There was a clearer weakening of the percept at short ramp durations compared to the data in Fig. 2 for upward ramps.

EXPERIMENT 2: DEPENDENCE OF FILLING-IN PERCEPTS ON STIMULUS DWELL TIME

Experiment 1 quantified the ramp durations that maximized the perception of brightness or darkness sweeping inward as spot luminance was modulated. With the fixed luminance range and exponential luminance ramp we used, the ramp duration was determined by two factors—the number of luminance steps and the dwell time spent at each luminance setting. In this experiment we further characterize the conditions under which the brightness inhomogeneity is observed by systematically varying the dwell time.

Methods

Since observers found the percepts resulting from downward ramps somewhat easier to rate than those from upward ramps, we used downward ramps to study the effect of dwell time. As in Experiment 1, the luminance sweep range was held constant at 60 cd/m^2. A ramp duration of 0.5 sec (32 frames on the monitor at 16 msec/frame) was used because this produced a maximal effect in Experiment 1. In Experiment 1 the dwell was always one frame (16 msec), but in this experiment we randomly interleaved ramps using dwell times of 1, 2, 4, 8, and 16 frames. The number of luminance steps in the ramp decreased accordingly as the dwell increased. The strength of the perceived inward spread of darkness was recorded by computer using the same rating scheme used in Experiment 1.

Results

Consistent with Experiment 1, strong effects were obtained with short dwell times (Fig. 4). The strength of the darkness spreading effect decreased significantly as the dwell time increased above 50 msec (i.e. 4, 8, and 16 frame dwells). In other words, the perception that the modulated disk is nonuniform and filling-in, is lost if the luminance is held longer than 50–100 msec at each luminance step.

EXPERIMENT 3: FILLING-IN PERCEPTS WITHIN THE BLIND SPOT

To determine whether the filling-in percept might be based on mechanisms within the retina, we presented the luminance modulated disk so that it surrounded the blind spot resulting from the lack of photoreceptors at the optic disk. In preliminary experiments we were surprised that the perception of brightness or darkness filling-in was unaffected. For instance in downward ramps, darkness appeared to sweep from the edge to the center of the modulated disk even though most of the disk's interior was imaged on a portion of the retina devoid of photoreceptors.

Methods

To more carefully study the filling-in percept across the blind spot, we first performed a simple monocular perimetry experiment on each observer. A head holder and voluntary fixation were used during perimetry, but eye movements were not monitored. While the observer fixated, a spot 0.35 deg in diameter was flashed randomly in and around the blind spot. The spot was presented at locations spaced by 0.5 deg horizontally and vertically, filling a rectangular area. Each time a spot was presented, a tone sounded. The observer indicated by pressing a button on the computer's mouse whether the spot was detected. The perimetry spot was presented five times at each location in the rectangular area.

Having established the approximate boundaries of the blind spot in one eye, a disk with a diameter of 8–10 deg was placed so that it surrounded the blind spot. The blind spots for all observers were about 5 deg across, so the disk extended about 1.5–2.5 deg to each side. The luminance of the disk was modulated in downward ramps exactly as in Experiment 1. Separate monocular and binocular trials were conducted. In monocular trials, observers eccentrically fixated so that the disk covered one eye's blind spot and the other eye was covered by a patch. Fixation was identical in binocular trials with both eyes open.

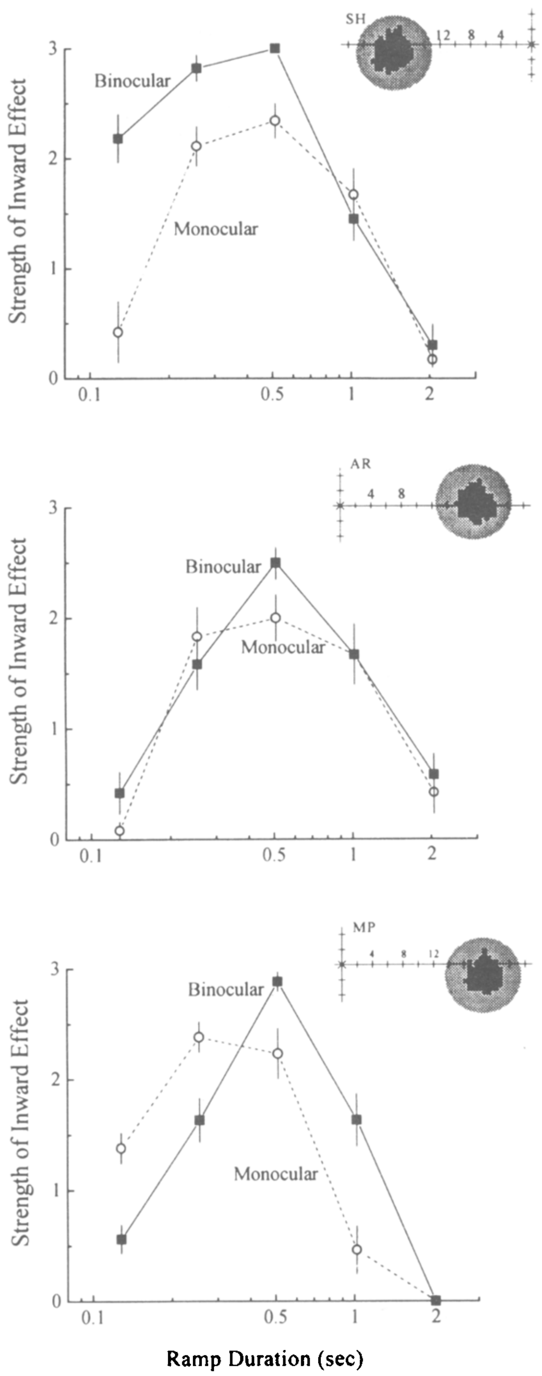

FIGURE 5. Comparison of the strength of binocular filling percepts with monocular percepts obtained with stimuli spanning the blind spot. In the upper right of the graph for each observer a plot of the blind spot obtained by perimetry is shown in black. The gray disk shows the approximate size of the luminance modulated stimulus. Downward luminance ramps were used and the inward filling of darkness was rated.

Results

The binocular results presented in Fig. 5 are qualitatively similar to those in Fig. 3, even though the eccentricity was about 15 deg rather than 0 deg. The only noticeable difference between the curves in these two figures is that the strength of the darkness inward effect fell off more rapidly with increasing ramp duration when the fixation was peripheral. The largest effects were still obtained with durations of about 0.5 sec.

When the stimulus disk was presented to only one eye with its image surrounding the blind spot, the strength ratings were similar. The observers found the percept of darkness sweeping inward to the center of the disk to be just as compelling monocularly, even though the only part of the stimulus that was imaged on photoreceptors was an annulus about 1.5–2.5 deg wide.

DISCUSSION

When the luminance of a spot of light is increased at certain rates, it appears that brightness spreads inward from the edge of the spot toward the center. Conversely, when the luminance is swept downward the center of the spot is brighter and darkness appears to spread inward. These percepts are seen with variously shaped stimuli as small as 0.5 deg across to over 10 deg across. The filling-in percepts are nearly identical even when the stimulus spans the blind spot. Despite the fact that the only part of the stimulus activating photoreceptors is an annulus, it appears that brightness or darkness sweeps all the way to the center of the disk. This finding suggests that the filling percepts are based on the activation of neurons in visual cortex rather than in the retina.

The inhomogeneous percepts we observed conceivably could be due to CRT nonuniformities or aftereffects. However, measurements with a photometer and an array of photodiodes confirmed that the appearance of inhomogeneity was strictly perceptual. Perceptual aftereffects and adaptation are unlikely explanations of the percepts because of the long intertrial intervals in which the computer screen was blank. Also, the inhomogeneous percepts were seen even when single luminance ramps were made.

We considered three mechanisms as possible explanations for the filling percepts we observed: irradiation, spatial frequency effects, and neural filling-in.

Irradiation

It has been known at least since the last century that brighter objects appear to be larger than darker objects of the same size. von Helmholtz refers to this phenomenon as irradiation (von Helmholtz, 1896/1924, Vol. 2, p. 186). When a spot of light has its luminance suddenly increased, the spot appears to swell in size. In other words, the outer edge appears to move outward. In some conditions, we observe irradiation in our stimuli, but it is distinct from the filling percepts. The direction of the brightness movement is opposite in irradiation (outward) and in our stimuli (inward). Moreover, in our stimuli the movement of brightness is in the interior of the luminance modulated disks, not at the edge as in irradiation.

Spatial frequency effects

Another possibility is that brightness filling results from the temporal response characteristics of perceptual mechanisms sensitive to luminance contrast at different spatial scales. If the response to lower spatial frequencies

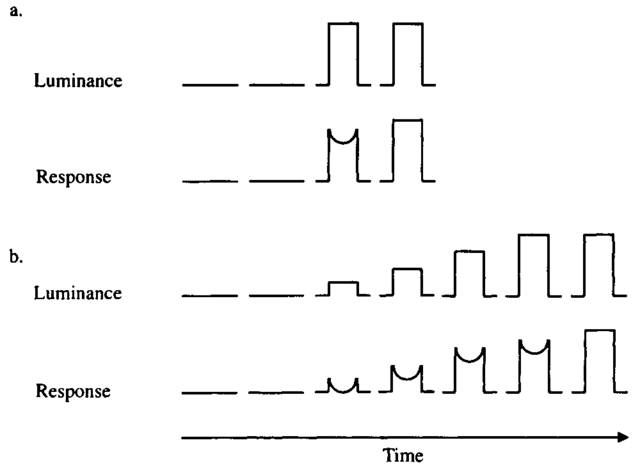

FIGURE 6. Hypothetical explanation of brightness inhomogeneity seen during luminance ramps. (a) When luminance is rapidly increased from low to high, the response may be spatially nonuniform for a period too brief to be perceived. (b) With more gradual luminance ramps, it may be possible to lengthen the duration of the brightness inhomogeneity.

is slower than that to higher frequencies, one might expect the center of a uniform region to perceptually lag. A compelling, but misleading, case can be made for this explanation with reference to the spatial and temporal contrast-sensitivity functions. For instance, at a modulation rate of 1 Hz, contrast sensitivity is highest at about 3 c/deg and progressively declines at lower spatial frequencies (Robson, 1966). Perhaps this insensitivity to contrast changes at low spatial frequencies underlies the observation that the center of a uniform stimulus perceptually lags behind changes in stimulus luminance. A problem with this argument is that it is based on measurements made at threshold and there is no reason to expect it to apply to suprathreshold luminance increments that produce the filling percepts. Perhaps more important is the fact that the filling percepts are obtained with luminance steps rather than requiring gradual luminance changes. This is important because there is evidence demonstrating that rapid luminance increments actually produce faster responses at lower spatial frequencies rather than higher frequencies. This is found in studies which measure reaction time vs spatial frequency (Harwerth & Levi, 1978; Lupp *et al.*, 1976) and also in recordings of evoked potentials (Vassilev *et al.*, 1983). Thus, in conditions similar to those used in our psychophysical experiments, the temporal responses to different spatial frequencies do not provide an explanation of the filling percepts.

Neural filling-in

One way to view our experimental 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 (Heinemann, 1972; Hess & Pretori, 1894). The perceptual lag of brightness at the center of a uniform area could be accounted for by a lateral interaction process in which a signal derived from luminance contrast progressively influences areas farther from the border. In other words, a *neural* filling-in process might account for *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 (Fig. 6). When the ramp is very slow, each time the luminance is incremented, the filling-in process may complete before the next increment, meaning that the inhomogeneity is preserved for too short a time to be perceived.

Several lines of evidence suggest that a filling-in mechanism plays a key role in the determination of brightness. For example, images (Krauskopf, 1963; Larimer & Piantanida, 1988; Yarbus, 1967) and scotomata (Bender & Teuber, 1946; Fuchs, 1921; Gerrits *et al.*, 1966) that are stabilized on the retina fill in with the brightness and color of the surrounding area. Also, masking stimuli consisting of one or more contours have been found to interfere with the perception of uniform brightness in a previously presented homogeneous target (Paradiso & Nakayama, 1991). This backward masking appeared to interfere with a filling-in process that was estimated to have a duration of 50–100 msec. In Experiment 2 of the present study we found that there were inhomogeneous brightness percepts with dwell times up to 50–100 msec but the inhomogeneities were lost with longer dwell times. Thus, the present results are consistent with the earlier masking experiments in suggesting that a process with a duration of 50–100 msec is at least partially responsible for the homogeneous brightness percept of stimuli with uniform luminance. This duration is also consistent with recent estimates obtained from dynamic induction experiments (Rossi & Paradiso, 1996). Indeed, dynamic induction experiments provide a third line of evidence suggesting that a filling-in mechanism is used in brightness computations. The luminance of a surround is sinusoidally modulated in time inducing brightness modulation in a static center roughly in antiphase to the surround modulation. The modulation of the central patch stops at a surprisingly low temporal frequency (DeValois *et al.*, 1986; Rossi & Paradiso, 1996) and this cutoff frequency is inversely correlated with the size of the central patch in the stimulus (Rossi & Paradiso, 1996). In other words, the larger an area is, the longer the brightness process takes to complete. The speed of this process is comparable to that estimated in the present study.

There are no relevant physiological data, but several different filling-in mechanisms have been proposed (Gerrits & Vendrik, 1970; Grossberg, 1983; Hamada, 1985; Paradiso & Nakayama, 1989). It is an important point that the final form of the neural response need not be isomorphic with the physical stimulus. While our data suggest that brightness involves a cortical filling-in process, this is probably not the only determinant of brightness. Presumably there is also a direct neural response to the onset of light and this is modified by filling-in. We speculate that the filling-in component of brightness is responsible for the spatial interactions characteristic of brightness perception.

REFERENCES

Bender, M. B. & Teuber, H. L. (1946). Phenomena of fluctuation, extinction and completion in visual perception. *Archives of Neurology and Psychiatry, 55*, 627–658.

Cornsweet, T. N. (1970). *Visual perception*. New York: Academic Press.

DeValois, R. L., Webster, M. A., DeValois, K. K. & Lingelbach, B. (1986). Temporal properties of brightness and color induction. *Vision Research, 26*, 887–897.

Fuchs, W. (1921). Completion phenomena in hemianopic vision. *A source book of gestalt psychology*. London: Kegan Paul.

Gerrits, H. J. M., de Haan, B. & Vendrik, A. J. H. (1966). Experiments with retinal stabilized images. Relations between the observations and neural data. *Vision Research, 6*, 427–440.

Gerrits, H. J. M. & Vendrik, A. J. H. (1970). Simultaneous contrast, filling-in process and information processing in man's visual system. *Experimental Brain Research, 11*, 411–430.

Grossberg, S. (1983). The quantized geometry of visual space: The coherent computation of depth, form and lightness. *Behavioral and Brain Sciences, 6*, 625–692.

Hamada, J. (1985). Asymmetric lightness cancellation in Craik–O-Brien patterns of negative and positive contrast. *Experimental Brain Research, 35*, 37–46.

Harwerth, R. S. & Levi, D. M. (1978). Reaction time as a measure of suprathreshold grating detection. *Vision Research, 18*, 1579–1586.

Heinemann, E. G. (1972). Simultaneous brightness induction. In: Jameson, D. and Hurvich, L. M. (Eds), *Handbook of sensory physiology* (Vol. 7/4, pp. 146–169). New York: Springer.

von Helmholtz, H. (1896/1924). In Southall, J. P. C. (Trans.), *Helmholtz's treatise on physiological optics*. Rochester: Optical Society of America.

Helson, H. (1943). Some factors and implications of color constancy. *Journal of the Optical Society of America, 33*, 555–567.

Hess, C. & Pretori, H. (1894). Messende Untersuchungen über die Gesetzmässigkeit des simultanen Helligkeitscontrastes. *Albert von Graefe's Archiv fuer Ophthalmologie, 40*, 1–24.

Jameson, D. & Hurvich, L. M. (1964). Theory of brightness and color contrast in human vision. *Vision Research, 4*, 135–154.

Krauskopf, J. (1963). Effect of retinal image stabilization on the appearance of heterochromatic targets. *Journal of the Optical Society of America, 53*, 741–744.

Larimer, J. & Piantanida, T. (1988). The impact of boundaries on color: Stabilized image studies. *Society of Photo-Optical Instrumentation Engineers, 901*, 241–247.

Lupp, U., Hauske, G. & Wolf, W. (1976). Perceptual latencies to sinusoidal gratings. *Vision Research, 16*, 969–972.

O'Brien, V. (1958). Contour perception, illusion, and reality. *Journal of the Optical Society of America, 48*, 112–119.

Paradiso, M. A. & Nakayama, K. (1989). Color filling: Psychophysical evidence and a neural network model. *Society for Neuroscience Abstract* 497.1.

Paradiso, M. A. & Nakayama, K. (1991). Brightness perception and filling-in. *Vision Research, 31*, 1221–1236.

Pelli, D. G. & Zhang, L. (1991). Accurate control of contrast on microcomputer displays. *Vision Research, 31*, 1337–1350.

Robson, J. G. (1966). Spatial and temporal contrast sensitivity functions of the human visual system. *Journal of the Optical Society of America, 56*, 1141–1142.

Rossi, A. F. & Paradiso, M. A. (1996). Temporal limits of brightness induction and mechanisms of brightness perception. *Vision Research, 36*, 1391–1398.

Vassilev, A., Manahilov, V. & Mitov, D. (1983). Spatial frequency and the pattern onset-offset response. *Vision Research, 23*, 1417–1422.

Yarbus, A. L. (1967). *Eye movements and vision*. New York: Plenum Press.

Acknowledgement—This research was supported by a grant from the National Eye Institute (EY09050).