Pergamon

0042-6989(95)00206-5

Vision Res., Vol. 36, No. 10, pp. 1391–1398, 1996

Printed in Great Britain
0042-6989/96 $15.00 + .00

Temporal Limits of Brightness Induction and Mechanisms of Brightness Perception

ANDREW F. ROSSI,* MICHAEL A. PARADISO*†

Received 30 January 1995; in revised form 20 July 1995

The luminance of a squarewave grating was modulated in a manner such that every other stripe temporally varied between bright and dark and the intervening stripes had constant luminance. This produces brightness induction in the constant stripes, roughly in antiphase to the luminance modulation. We used this stimulus as a probe to explore the temporal properties of brightness induction and the mechanisms determining perceived brightness. Over a range of spatial frequencies we measured: (1) the highest temporal frequency at which brightness induction occurs; (2) the magnitude of induced brightness; and (3) the temporal phase of the induced brightness modulation. We find that brightness induction ceases with luminance modulation above a cutoff temporal frequency that depends on spatial frequency. The magnitude of induced brightness modulation is greatest at low spatial frequencies and low temporal frequencies. Induced brightness lags behind the luminance modulation and this phase lag increases as spatial frequency decreases. All of these findings can be understood as consequences of an induction process that takes longer to complete as the induction region increases in size. Copyright © 1996 Elsevier Science Ltd.

Brightness Filling-In Induction Spatial frequency Temporal frequency

INTRODUCTION

The phenomena of brightness induction, brightness assimilation, and brightness constancy demonstrate that the brightness of one area depends strongly on the luminance of surrounding areas. For example, in brightness induction, a gray patch on a bright background appears darker than the same gray patch on a dark background. The goal of the research described here is to further our understanding of the mechanisms underlying brightness perception. We have chosen to focus on brightness induction because it is both a powerful visual effect and it is easy to manipulate. A great number of previous perceptual studies have quantified the manner in which induced brightness depends on *spatial* parameters such as border contrast and the size of the inducing area (reviewed by Heinemann, 1972).

De Valois *et al.* (1986) made a surprising finding about the *temporal* characteristics of brightness induction that we think has the potential for significantly adding to our understanding of brightness mechanisms. De Valois *et al.* used a stimulus in which a static gray patch is surrounded by a larger area in which the luminance is modulated sinusoidally in time. The luminance modulation of the surround produces powerful brightness induction in the gray patch, roughly in antiphase to the surround modulation: when the surround is dark the central patch appears light, and vice versa. Surprisingly, brightness modulation is induced in the gray patch only when the surround is modulated at quite low temporal frequencies (i.e., below about 2.5 Hz). When the surround is modulated at higher rates the central patch appears a static gray. The importance of this finding is that it suggests that the mechanisms underlying brightness induction are quite slow. In the experiments described in this paper, we use an induction stimulus, similar to that used by De Valois *et al.*, as a probe to explore the relationship between the spatial aspects of visual stimuli and the temporal dynamics of brightness induction.

GENERAL METHODS

The authors and four naive observers participated in this study. Three experiments were performed using a stimulus consisting of a temporally modulated squarewave grating. 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 (Fig. 1). Perceptually, the modulation produced brightness induction in the constant stripes, roughly in antiphase to the luminance modulation of the neighboring stripes. Measurements were made over a range of spatial frequencies to quantify: (1) the maximum temporal frequency at which modulation of induced brightness is observed; (2) the amplitude of the induced brightness modulation as a function of the temporal

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

†To whom correspondence should be addressed: [*Email* michael-paradiso@brown.edu].

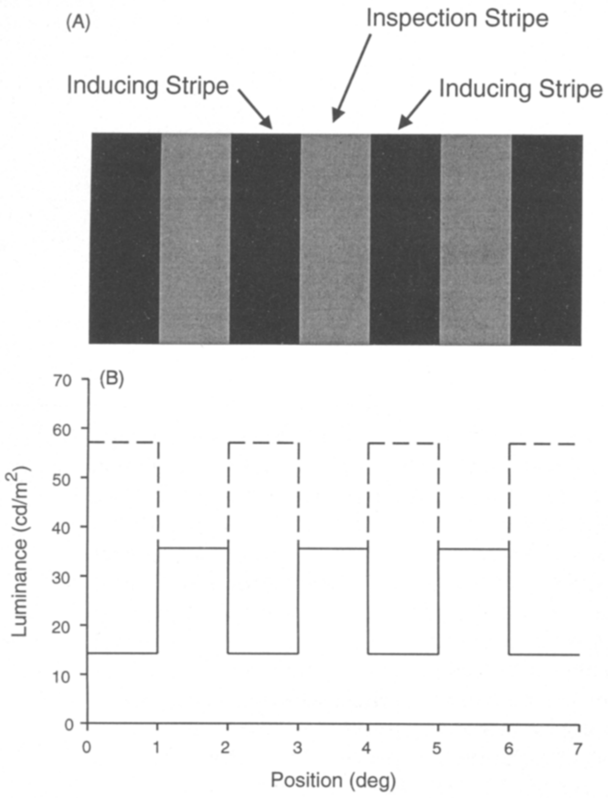

FIGURE 1. (A) Schematic view of the squarewave stimulus as it appeared to the observers. The luminance of the inducing stripes was modulated sinusoidally in time to induce brightness modulation in the static, intervening stripes. Observers made judgments based on the appearance of the inspection stripe in the center of the grating. (B) Luminance profile of the squarewave grating. The solid and dashed lines represent the extreme luminance values of the inducing stripes. The static stripes had a luminance equal to the time-average luminance of the modulated stripes.

frequency of the luminance modulation; and (3) the temporal phase of the induced changes in brightness relative to the luminance modulation. The method of adjustment was used in all three experiments.

The stimuli were generated by a Number Nine Graphics Board installed in a PC clone and displayed on a 20 in. monitor with 640 × 480 pixel resolution (18 pixels/cm) and a refresh rate of 60 Hz. At the viewing distance of 38 cm, the screen subtended 56 deg. The vertical extent of the squarewave stimulus was 16.7 deg. For each spatial frequency of the squarewave, the number of cycles presented was the maximum number that fit across the display, provided that modulated stripes were on the ends. Two vertical lines (1 × 5 pixels) were provided above and below the grating to indicate the position of the central inspection stripe. The luminance of the static stripes in the squarewave was 35 cd/m^2. Look-up table animation was used to temporally modulate the luminance of every other stripe in the squarewave stimulus, sinusoidally in time. The luminance was modulated about a mean of 35 cd/m^2 such that the squarewave had 60% Michelson contrast when the luminance was maximal and minimal. Although the observers were free to move their eyes about the display, they were instructed to make their brightness judgments based on the appearance of only the central stripe. In each experimental session observers adapted to the average screen luminance for 3 min prior to making perceptual judgments.

EXPERIMENT 1: TEMPORAL FREQUENCY CUTOFF FOR INDUCED BRIGHTNESS MODULATION

De Valois *et al.* (1986) observed that the induced brightness modulation seen in a static patch is abolished when the luminance of the inducing surround region is modulated at a rate exceeding about 2.5 Hz. Our inference from this finding is that the mechanism underlying brightness induction is rather slow. Since there is evidence that brightness changes resulting from direct luminance modulation have a timecourse that is dependent on spatial scale (Paradiso & Nakayama, 1991; Paradiso, 1991), we were interested in whether the temporal frequency cutoff for induced modulation is also scale dependent.

Methods

Observers were instructed to view the modulating squarewave pattern (Fig. 1) and adjust the temporal frequency of the luminance modulation to the lowest frequency at which the brightness of the static central stripe appeared to stop modulating between light and dark. The initial temporal frequency of the luminance modulation was 0.5 Hz and the observers adjusted the frequency in steps of 0.1 Hz by pressing buttons to increase or decrease the rate of modulation. In this way, the threshold for induced modulation was found for spatial frequencies of 0.03, 0.05, 0.1, 0.25, 0.5, 1.0, and 2.0 c/deg. Within an experimental session, the presentation order of the spatial frequencies was randomized.

Results

Figure 2 shows the frequency cutoff for induced brightness modulation as a function of the spatial frequency of the squarewave grating. The average settings of four observers are plotted. For each observer there is a clear correlation between spatial frequency and the induction cutoff frequency. In other words, the temporal frequency cutoff for induced modulation decreases as the size of the induction area increases. Across observers there are differences in the cutoff frequencies, probably attributable to differences in the subjective criterion for significant modulation of induced brightness.

EXPERIMENT 2: ESTIMATION OF THE AMPLITUDE OF INDUCED MODULATION

The results of Expt 1 show the temporal modulation rate at which the amplitude of induced modulation is zero. The intent of this second experiment was to systematically measure the amplitude of the induced brightness changes at different temporal frequencies of the luminance modulation.

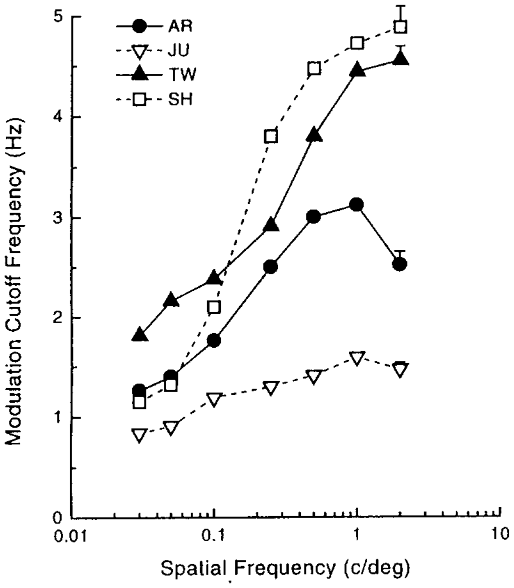

FIGURE 2. Temporal frequency cutoff for induced brightness modulation as a function of the spatial frequency of the squarewave grating. Data from four observers are shown. Error bars on the highest spatial frequency data points represent the average SEM, across frequency, for each observer.

Methods

Observers were instructed to adjust the luminance of a static comparison patch so that the patch brightness matched the maximum or minimum of the induced brightness of the central stripe in the squarewave grating (see Fig. 3). The squarewave stimulus in this experiment was the same as that used in Expt 1 except that it was 13.3 deg in height. The comparison patch had the same height as the squarewave and a width equal to one-half cycle of the squarewave. The patch was presented on a background having a luminance of 35 cd/m^2 and the same width as the squarewave pattern.

At the beginning of each session the comparison patch was given a luminance randomly chosen from the range 25–45 cd/m^2. Luminance adjustments were made in 0.5 cd/m^2 increments until a match to the maximum or minimum of the induced modulation was perceived. Observers were free to move their gaze back and forth between the inspection and comparison stimuli. Matches were made at spatial frequencies of 0.03, 0.1, 0.5, and 2.0 c/deg with temporal modulation rates of 0.5, 1.0, 2.0, and 4.0 Hz. Within an experimental session, the presentation order of the squarewave stimuli was randomized with regard to spatial frequency and the temporal frequency of the luminance modulation. For the purpose of comparison, brightness matches were also made without luminance modulation of the squarewave, with the "modulated" stripes fixed at either their lightest or darkest point (i.e., static contrast of 60% between the central stripe and flanking stripes).

Results

The results for two observers are shown in Fig. 4. These data show that, generally, induced brightness modulation has the greatest amplitude at the low temporal frequencies of the luminance modulation. The luminance matches to the maximum and minimum 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. In other words, induction is not simply "off" and "on" above and below the cutoff rate. This can be seen more clearly in Fig. 5(A) where the difference between the maximum and minimum luminance matches is plotted as a function of the temporal modulation frequency for a squarewave grating of 0.1 c/deg. For the four observers shown, the amplitude of induced brightness modulation decreases progressively as temporal frequency increases. On average, the maximum and minimum luminance matches made in this experiment converge at somewhat higher temporal frequencies than one would expect based on the cutoff frequencies measured in Expt 1. We assume this difference reflects the criterion the observers established in Expt 1 to judge perceived modulation. Also shown in Fig. 5(A) are the differences in the maximum and minimum matches for the conditions in which there was no luminance modulation. Comparing these to the data with luminance modulation indicates that the brightness induction obtained at low temporal frequencies is more powerful than static brightness induction (i.e., greater brightness variations are obtained). Conceivably, the reduced induction obtained with static surrounds could be related to a different state of light adaptation in this condition than with modulated surrounds. However, observers made the brightness matches by alternately

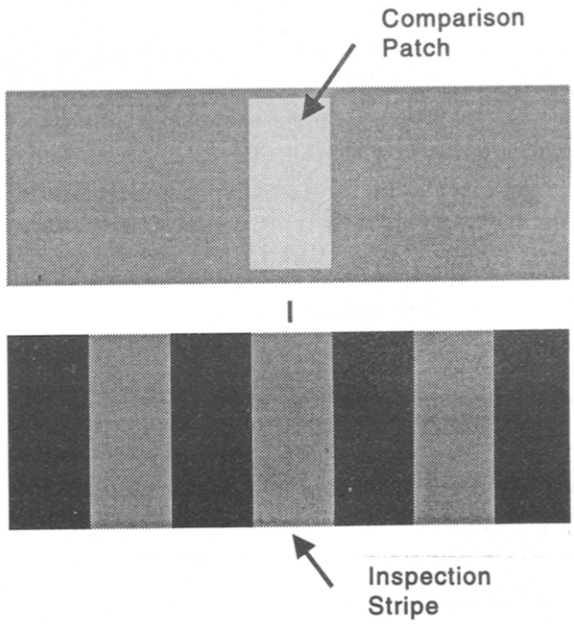

FIGURE 3. Schematic view of the display used in estimating the magnitude of induced modulation (Expt 2). The observer's task was to adjust the luminance of the static comparison patch in the upper field to match that of the maximum (or minimum) of the induced brightness changes in the inspection stripe of the grating in the lower field.

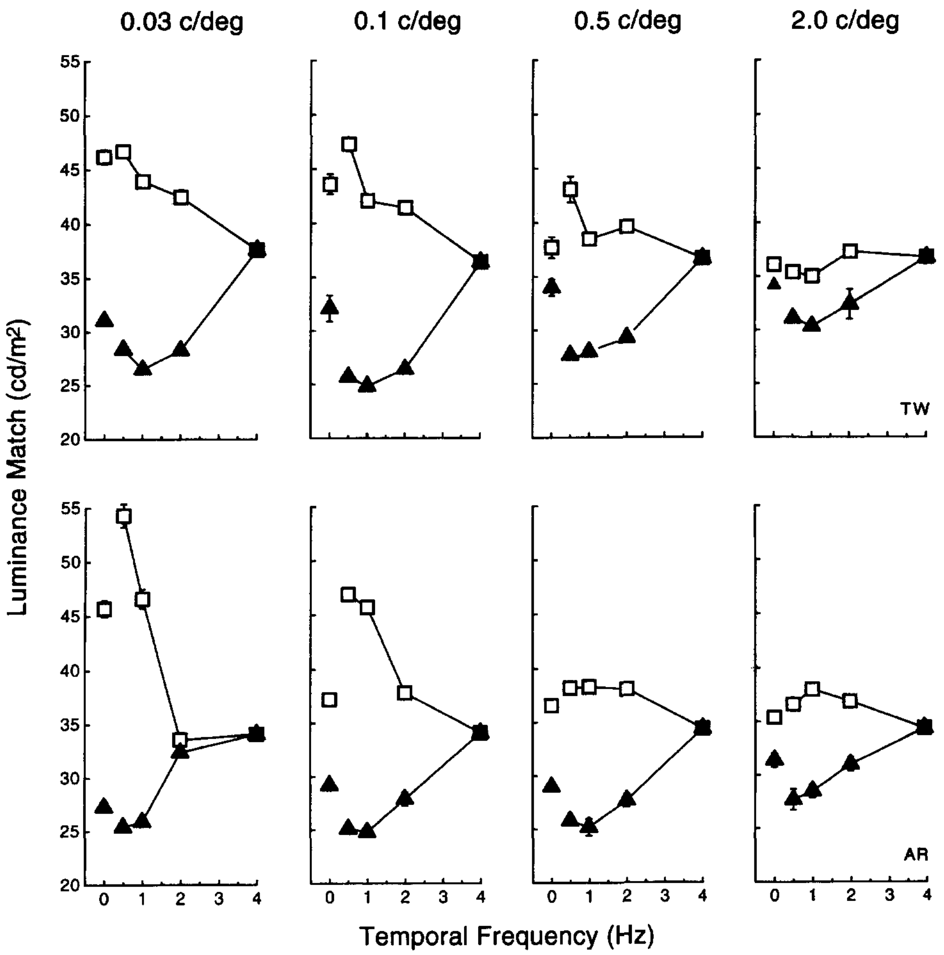

FIGURE 4. Luminance matches to the maximum (□) and minimum (▲) of the induced brightness changes for two observers. Each graph shows the matches plotted as a function of the temporal frequency of the luminance modulation for a given spatial frequency of the squarewave grating. Data points at zero temporal frequency represent matches made when the inducing stripes were static (maximum or minimum luminance). Error bars represent ±1 SEM.

foveating the test and comparison stimuli, which should have minimized any differences in adaptation.

Another feature of the data seen in Fig. 4 is that the magnitude of the induced brightness modulation is greatest at lower spatial frequencies. In Fig. 5(B), the amplitude of induced brightness modulation is plotted as a function of spatial frequency when the luminance modulation was 1.0 Hz. For three of the four observers there is a marked decrease in the magnitude of the induced modulation as the spatial frequency of the squarewave pattern increases. Observer SH shows a decrease across spatial frequency except for a comparatively low modulation amplitude at 0.03 c/deg.

EXPERIMENT 3: TEMPORAL PHASE OF INDUCED BRIGHTNESS MODULATION

In our stimulation paradigm, brightness induction of the central stripe is due to the modulation of the luminance contrast at the stripe's border and/or modulation of the surround luminance. One interpretation of the results obtained in Expts 1 and 2 is that induction only occurs at slow modulation rates because the surrounding changes in contrast and luminance take time to influence the entire central stripe. Consistent with this interpretation, we have noted that the induced brightness modulation appears to lag behind the luminance changes. In other words, the peak of the induced brightness in the center stripe lags behind the peak brightness (due to direct luminance change) of adjacent stripes by more than 180 deg of temporal phase. We reasoned that if the timecourse of induction occurs in a scale-dependent manner, as the data in Expts 1 and 2 suggest, the temporal phase of the induction may vary with the width of the center stripe.

Methods

Initially, we attempted to measure the perceived phase of the peak induced brightness by having observers match the phase of the induced patch with the phase of a comparison patch that was luminance modulated. This turned out to be more difficult than expected, giving highly variable results. De Valois *et al.* (1986) also observed the apparent lag of induced brightness and they noted the difficulty encountered in matching the phase to luminance modulation.

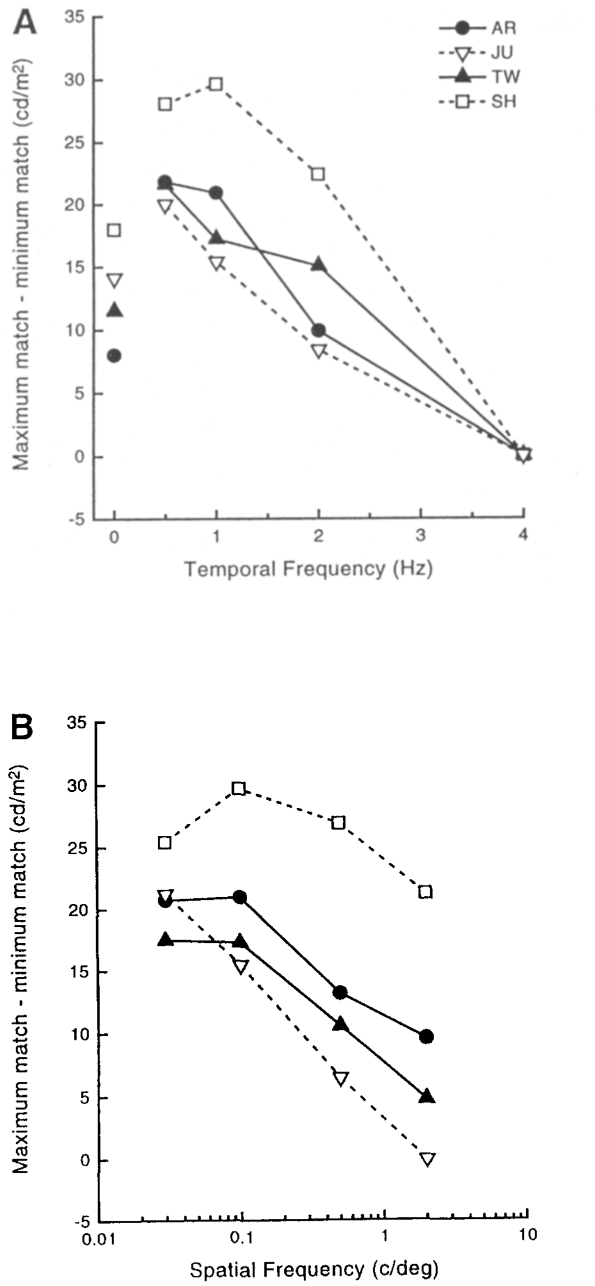

FIGURE 5. (A) Difference in the luminance matches to the maximum and the minimum of the induced brightness plotted as a function of the temporal frequency of the luminance modulation in the inducing stripes of the squarewave grating. The spatial frequency of the squarewave grating was 0.1 c/deg. Symbols at zero temporal frequency represent differences in the luminance matches for static squarewave gratings. (B) Difference in the luminance matches to the maximum and the minimum of the induced brightness plotted as a function of the spatial frequency of the squarewave grating. The temporal frequency of the luminance modulation in the inducing stripes was 1.0 Hz. Data shown for four observers.

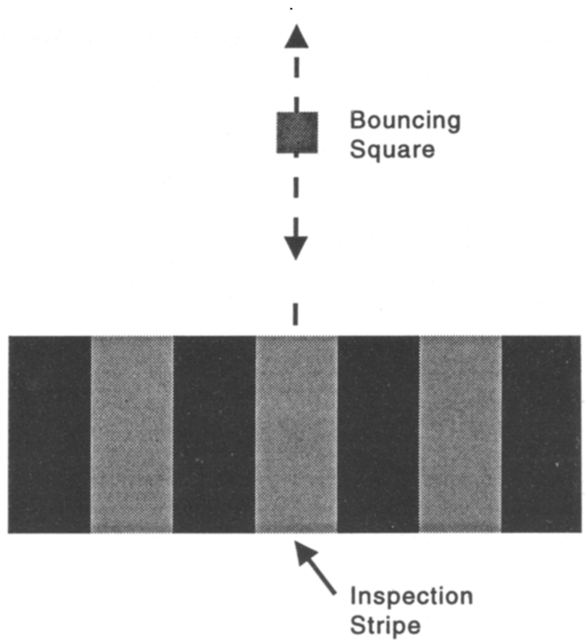

FIGURE 6. Schematic view of the display used in Expt 3. The observer's task was to adjust the phase of the vertically bouncing square to match that of the brightness changes observed in the inspection stripe in the squarewave grating.

After trying several different comparison procedures, we devised a somewhat more reliable paradigm that does not involve comparison with luminance modulation. Observers viewed a 13.3 deg high squarewave grating on the bottom half of the display (Fig. 6). The luminance of every other stripe in the squarewave pattern was modulated about the time-averaged luminance of 35 cd/m^2 (the luminance of the intervening static stripes), such that the grating had 17% contrast at the maximum and minimum luminances. Above the central static stripe in the grating was a small square that "bounced" up and down at the same temporal frequency (1.0 Hz) as the luminance modulation of every other stripe in the squarewave grating. More precisely, the square's vertical position varied sinusoidally in time. Observers were instructed to match the phase of the bouncing square to that of the induced brightness at the horizontal center of the central stripe, such that the minimum vertical position of the square coincided with the peak brightness of the central stripe. Observers could advance or retard the temporal phase of the bouncing motion in steps of 3.5 deg by pressing buttons. For comparison, we used exactly the same procedure to measure the phase of the peak brightness in the stripe just to the right of center, which was luminance modulated. Observers made temporal phase matches to the brightness modulation in the static and luminance-modulated stripes at spatial frequencies of 0.03, 0.05, 0.1, and 0.5 c/deg. Within an experimental session, the presentation order of the spatial frequencies was randomized.

Results

The phase matches made by one observer are shown in Fig. 7. Given the variability in the observer's adjustments, the phase matches to luminance modulation are effectively constant across spatial frequency. However, there is a rapidly increasing phase lag of the peak in the induced brightness at low spatial frequencies. In other words, the induced brightness at the center of the central stripe peaks at later and later times as the width of the central stripe increases.

It should be noted that the absolute magnitudes of the

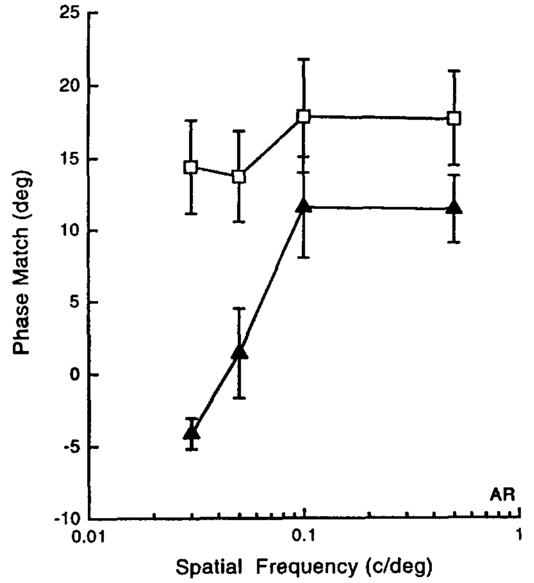

FIGURE 7. Phase matches to the induced (▲) and direct (□) brightness changes plotted as a function of the spatial frequency of the squarewave grating. The temporal frequency of the luminance modulation in the inducing stripes was 1.0 Hz. Error bars represent ±1 SEM.

phase matches in Fig. 7 may not be of any significance due to the nature of the comparison task we employed. For this reason we have focused on the differences in the phase matches made to the induced brightness changes and those due to direct luminance modulation. Figure 8 shows the average differences in these phase matches for four observers plotted as a function of the spatial frequency of the squarewave grating. The differences in the phase matches are always near zero or positive, indicating that the observers perceived the induced brightness changes at the same time or later than one would predict based on the assumption that brightness is induced in antiphase to the luminance changes. The peak of the induced brightness lags increasingly farther behind the luminance modulation for spatial frequencies below 0.1 c/deg. For some observers the phase lag was significantly larger than 180 deg only at the lowest spatial frequency, as in the averages shown in Fig. 8. For other observers, as in Fig. 7, the phase lag was significantly greater than 180 deg at both spatial frequencies below 0.1 Hz.

DISCUSSION

The results of our 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 timecourse of induction is scale dependent. We will consider these two points and their implications for the processes underlying perceived brightness.

Comparison to Flicker Fusion

The measure of real modulation sensitivity analogous to our measurement of cutoff frequency for induction, is the critical flicker fusion rate (CFF). The CFF depends on a variety of parameters including stimulus luminance, stimulus area, surround luminance, and temporal modulation waveform. Under conditions similar to those in our experiments, the CFF is in the order of tens of Hz. This is in marked contrast to the cutoff frequencies for induction which we measured in the range 1–5 Hz (Expt 1). Experiment 2 shows that above the cutoff frequency, the minimum brightness and maximum brightness of the induced area are the same and no modulation is perceived. This suggests that induction is a slow process; it is as if induction cannot "keep up" with faster luminance modulation. Consistent with induction being slow, Expt 3 shows that changes in induced brightness lag behind changes in luminance modulation. These fundamental observations about the temporal limit to brightness induction and its lag behind the driving luminance modulation are consistent with the original observations of De Valois *et al.* (1986).

Our principal new finding is that the cutoff frequency, phase lag, and degree of induction all depend on the spatial scale of the stimulus. De Valois *et al.* looked for an effect of scale but they saw none, almost surely because they used stimuli covering a smaller range of sizes than we did. We find that as spatial frequency decreases from 2 to 0.03 c/deg, there is a progressive decrease in the cutoff frequency. In other words, the brightness of a relatively large area cannot be induced at a rate as fast as a small area. At the lowest temporal frequency we used (0.5 Hz), the degree of induction was always a small amount greater than the induction seen

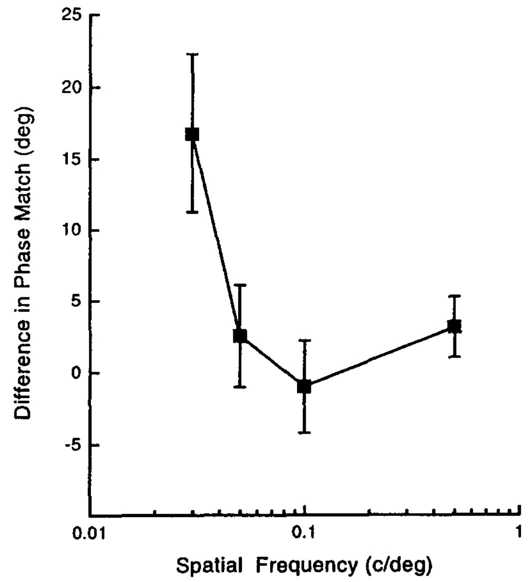

FIGURE 8. Difference in the phase matches (direct brightness changes – induced brightness changes) plotted as a function of the spatial frequency of the squarewave grating. The temporal frequency of the luminance modulation in the inducing stripes was 1.0 Hz. Data points are the averages for four observers. Error bars represent ±1 SEM.

with static stimuli. This is reminiscent of the brightness and darkness enhancement (Broca–Sulzer effect) seen with low frequency luminance modulation (Bartley, 1938; Glad & Magnussen, 1972). Magnussen and Glad (1975) observed a similar enhancement effect in brightness induction with squarewave temporal modulation, except that the enhancement is at higher temporal frequencies than in our data obtained with sinewave modulation. As the temporal frequency is increased toward the cutoff, there is progressively less induction until, at the cutoff, there is no modulation of induced brightness. This correlation between spatial scale, degree of induction, and cutoff frequency suggests that there is a limited speed at which induction proceeds, and that larger areas take more time to induce. Further support for the idea that induction depends on spatial scale is seen in the data from Expt 3: the phase at which the brightness at the center of the induced stripe appears to peak, lags increasingly more behind the luminance modulation of the surrounding stripes as spatial frequency decreases.

Comparing the induction cutoff frequencies to the CFF underscores the significant difference between "real" brightness modulation (i.e., from luminance modulation) and induced brightness modulation. According to the Granit–Harper law, the CFF for spots of light ranging from a fraction of a degree to 50 deg in diameter increases linearly with the logarithm of stimulus area (Granit & Harper, 1930; Landis, 1954; Roehrig, 1959). While the Granit–Harper law only applies to stimuli squarewave modulated in time, sinusoidal temporal modulation, as in our experiments, also yields sensitivity changes that increase with size (De Lange, 1952; Keesey, 1970). Thus, studies of flicker sensitivity show that *real and induced brightness modulation have opposite relationships between size and critical temporal frequency*. Whereas the CFF increases with size, the cutoff frequency in our induction experiments decreases with size. This indicates that there is a major difference between the mechanisms limiting perception of modulation with real and induced brightness.

What Limits the Rate of Induction?

Although numerous studies have considered the basis for the CFF, almost nothing is known about temporal limitations on brightness induction. One possibility is that induction is affected by spatial frequency because the edges of the central stripe in our stimuli moved to larger retinal eccentricities as spatial frequency decreased. However, this is clearly not the case, since the induction percepts did not change when fixation was shifted from the center to the edge of the central stripe. Since we observed cutoff frequency to decrease as spatial frequency decreased, one wonders whether contrast sensitivity might be involved. Contrast sensitivity decreases over the same range of spatial frequencies that we observe changes in the magnitude of induction, so perhaps they are related. In light of their data obtained at a single spatial scale, De Valois *et al.* (1986) proposed that there might be a "trigger" contrast for induction. In other words, as the luminance of inducing areas is modulated and the contrast increases from zero, induction does not occur until a critical contrast is reached. This would explain why induced brightness lags behind luminance modulation. It is conceivable that the phase lag increases at lower spatial frequencies, as in our data, because the trigger contrast rises when contrast sensitivity falls.

While this scheme might explain our phase results in Expt 3, there are several problems with the idea. First, De Valois *et al.* themselves found evidence inconsistent with this notion, in that induction occurred with contrast modulation below the estimated trigger contrast. Second, the changes in cutoff frequency we observed in Expt 1 are not consistent with there being a simple threshold contrast for induction. The luminance modulation we used was always far above threshold and there is no obvious reason why the cutoff temporal frequency should change in the manner we observed just because induction might be *initiated* at somewhat different contrasts. The critical point is that the timecourse of the induction changes with spatial scale, not just the phase.

A possible explanation of the data we have obtained is that a filling-in mechanism is involved in induction. By filling-in, we mean that a signal associated with luminance contrast at edges influences the perceived brightness of neighboring areas in a manner such that more distant areas are affected at later times. Many studies have pointed out that brightness induction is largely based on the contrast at the edges of a uniform region, rather than the total amount of light in neighboring areas (e.g. Heinemann, 1955; Wallach, 1948). For instance, while the brightness of a gray patch depends on the luminance of a neighboring area, the induction effect quickly saturates as the neighboring area is stretched from a thin band to a wide band (Diamond, 1955). As we have noted, our data suggest that induction has a longer timecourse as the induced area increases in size. 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. Filling-in would also account for the increasing phase lag in the brightness perceived at the center of the induced area as that area increases in size.

The velocity of filling-in can be estimated from the phase measurements obtained in Expt 3, although meaningful computations can only be carried out at spatial frequencies that produced phase lags significantly greater than 180 deg. Based on the results in Expt 3, the filling-in velocity is estimated to be in the range 140–180 deg/sec. This estimate is in approximate agreement with the filling-in velocity that Paradiso and Nakayama (1991) estimated from the results of brightness masking experiments.

Brightness from Luminance vs Brightness from Induction

On the basis of several different lines of evidence, we have previously proposed that brightness always involves a process of filling-in, aside from any induction effects

(Paradiso & Nakayama, 1991; Paradiso, 1991). The simplest way to integrate a process of filling-in with the results reported here is if the brightness of a stimulus 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 our induction results and it may also account for the large scale brightness interactions seen in brightness constancy. 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 & Nakayama, 1991; Paradiso, 1991), 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 cutoff frequency for induced modulation would be determined by the velocity of the filling-in process.

Several authors have previously proposed that brightness involves two distinct processes and there are models specifically suggesting how these mechanisms might work (Cohen & Grossberg, 1985; Gerrits & Vendrik, 1970; Grossberg & Todorovic, 1988; Heinemann & Chase, 1995; Reid & Shapley, 1988; Shevell *et al.*, 1992). There are significant differences between the models that have been proposed, but several distinguish a local process working within the luminance contrast boundary of a surface, and a more global process containing influences from beyond the nearest contrast boundary (e.g. Heinemann & Chase, 1995; Reid & Shapley, 1988; Shevell *et al.*, 1992).

The information that our data add to the understanding of brightness mechanisms concerns the spatial and temporal properties of the mechanisms. Our data suggest that one brightness process is fast, relatively unaffected by spatial scale, and significantly influenced by luminance. The other process is slow, it is scale dependent because a brightness signal must fill-in, and it is determined primarily by luminance contrast. These hypothetical processes somewhat resemble components of the brightness model developed by Grossberg and colleagues (Cohen & Grossberg, 1985; Grossberg & Todorovic, 1988). However, there does not appear to be a simple one-to-one mapping of the two mechanisms we propose onto the mechanisms in the local/global models mentioned above. The reason is that both of our mechanisms involve influences from the luminance of an area and its immediate surround. In other words, using the nomenclature of earlier studies, both mechanisms are "local" (though this doesn't mean that these mechanisms might not also include longer range interactions). One possibility is that the two mechanisms we have identified by manipulating both spatial and temporal variables are encompassed by the single "local" mechanism reported by others on the basis of experiments with static stimuli.

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

REFERENCES

Bartley, S. H. (1938). Subjective brightness in relation to flash rate and the light–dark ratio. *Journal of Experimental Psychology, 233*, 313–319.

Cohen, M. A. & Grossberg, S. (1985). Neural dynamics of brightness perception: Features, boundaries, diffusion and resonance. *Perception & Psychophysics, 36*, 428–456.

De Lange, H. (1952). Experiments on flicker and some calculations on an electrical analogue of the foveal systems. *Physica, 18*, 935–950.

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

Diamond, A. L. (1955). Foveal simultaneous contrast as a function of inducing area. *Journal of Experimental Psychology, 50*, 144–152.

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.

Glad, A. & Magnussen, S. (1972). Darkness enhancement in intermittent light: An experimental demonstration. *Vision Research, 12*, 111–115.

Granit, R. & Harper, P. (1930). Comparative studies on the peripheral and central retina II. *American Journal of Physiology, 95*, 211–228.

Grossberg, S. & Todorovic, D. (1988). Neural dynamics of 1-D and 2-D brightness perception: A unified model of classical and recent phenomena. *Perception & Psychophysics, 43*, 241–277.

Heinemann, E. (1955). Simultaneous brightness induction as a function of inducing- and test-field luminances. *Journal of Experimental Psychology, 50*, 89–96.

Heinemann, E. (1972). Simultaneous brightness induction. In Jameson, D. & Hurvich, L. M. (Eds), *Handbook of sensory physiology VII: Visual psychophysics*. New York: Springer.

Heinemann, E. & Chase, S. (1995). A quantitative model for simultaneous brightness induction. *Vision Research, 35*, 2007–2020.

Keesey, U. T. (1970). Variables determining flicker sensitivity in small fields. *Journal of the Optical Society of America, 60*, 390–398.

Landis, C. (1954). Determinants of the critical flicker-fusion threshold. *Physiological Review, 34*, 259–286.

Magnussen, S. & Glad, A. (1975). Temporal frequency characteristics of spatial interaction in human vision. *Experimental Brain Research, 23*, 519–528.

Paradiso, M. A. (1991). Temporally modulated stimuli used to explore color filling-in. *Association for Research in Vision and Ophthalmology, 32*, 2677.

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

Reid, R. C. & Shapley, R. (1988). Brightness induction by local contrast and the spatial dependence of assimilation. *Vision Research, 28*, 115–132.

Roehrig, W. C. (1959). The influence of area on the critical flicker-fusion threshold. *Journal of Psychology, 47*, 317–330.

Shevell, S. K., Holliday, I. & Whittle, P. (1992). Two separate mechanisms of brightness induction. *Vision Research, 32*, 2331–2340.

Wallach, H. (1948). Brightness constancy and the nature of achromatic colors. *Journal of Experimental Psychology, 38*, 310–324.