Spatial nonuniformities and velocity of filling-in in dynamic brightness induction

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There is converging evidence that brightness induction is neither spatially uniform nor instantaneous. In the temporal domain, multiple studies have shown a relatively low (2–3 Hz) temporal frequency cutoff in brightness induction from temporally modulated surrounds (De Valois, Webster, De Valois, & Lingelbach, 1986; Paradiso & Nakayama, 1991; Rossi & Paradiso, 1996). It was also demonstrated that the temporal frequency cutoff depends on the spatial frequency of the stimulus (Rossi & Paradiso, 1996; see also Robinson & de Sa, 2008). These findings are consistent with the idea that brightness induction is mediated by a filling-in process that begins at the borders and travels at a relatively low velocity. However, in contradiction to observed low temporal cutoff in brightness induction, all earlier attempts to directly estimate the induction velocity resulted in very high estimates (e.g., 100–200°/s). In the present study, using a novel paradigm, we obtained velocity estimates that are in line with predictions based on temporal frequency cutoff. In addition, the use of the same stimulus set to measure spatial nonuniformities, temporal frequency cutoff, and velocity allowed direct comparison of different velocity estimates.

Introduction

Simultaneous brightness induction is defined as a change in the brightness (perceived luminance) of a test stimulus with a change of surround luminance. A gray disk, for example, appears brighter if it is embedded in a dark surround than if it is embedded in a light surround. If the surround luminance is temporally modulated from dark to light and back to dark again, the disk appears to flicker roughly out of phase with the surround modulation—from light to dark and back to light. There is substantial evidence that brightness induction is nonuniform both spatially and temporally (McCourt, 1982; Foley and McCourt, 1985; De Valois, Webster, De Valois, & Lingelbach, 1986; Kingdom & Moulden, 1988; Paradiso & Nakayama, 1991; Rossi & Paradiso, 1996; Blakeslee & McCourt, 1997, 1999, 2004; Pereverzeva & Murray, 2008; see also Paradiso & Hahn, 1996 for temporal nonuniformity in luminance change perception). The specific characteristics of the spatial and temporal nonuniformities can potentially provide important constraints on the types of mechanisms underlying brightness induction.

In the spatial domain, in the case of induction from static surrounds, there is a decrease in induction strength with an increase of distance from the inducing field, consistent with the predictions of most spatial filtering models (Blakeslee & McCourt, 2004; Blakeslee, Pasieka, & McCourt, 2005; Robinson & de Sa, 2008; Blakeslee & McCourt, 2013). For induction from surrounds modulated in luminance at the fixed temporal frequency, there is less induction at the center of the test disk than at the disk–surround border (Pereverzeva & Murray, 2008; see also Cornelissen, Wade, Vladusich, Dougherty, & Wandell, 2006). These findings were recently confirmed by Blakeslee and McCourt (2013), who used quadrature-phase motion cancellation paradigm to find a decrease in induction with an increase of the distance from the inducing edge. However, it is possible that the spatial nonuniformities that have been observed in these experiments, particularly in case of disk–surround induction, are the result of the stimulus occupying different retinal positions. It is known that flicker sensitivity varies across the retina (Tyler & Torres, 1972; McKee & Taylor, 1984). It is therefore possible that any perceptual spatial nonuniformities observed using a flickering stimulus were due to retinal position rather than actual distance from the border with the inducing surround. This issue is addressed in the current study by having subjects monitor different


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spatial positions of the test disk either by direct fixation or through covert spatial attention.

In the temporal domain, there is a temporal delay in brightness induction modulation (De Valois et al., 1986; Paradiso & Nakayama, 1991; Rossi & Paradiso, 1996; Davey, Maddess, & Srinivasan, 1998; see also Zaidi, Yoshimi, Flanigan, & Canova, 1992). For example, Rossi and Paradiso (1996) demonstrated a small phase offset between the inducer (surround) and the induced brightness variation in the test. A temporal delay in brightness induction would be indicative of filling-in, the process in which a neural “brightness” signal takes a certain amount of time to spread from the edges to the center of the cortical area being filled-in. In other words, filling-in would have a certain propagation velocity (for simplicity, we assume that the velocity is constant), defined as the distance being covered divided by the time it takes to cover it.

Brightness induction has also been shown to decrease with increasing temporal frequency of the surround modulation (De Valois et al., 1986; Rossi & Paradiso, 1996; Davey et al., 1998; see also Zaidi, Yoshimi, Flanigan, & Canova, 1992). The cutoff induction frequency, which usually occurs at about 2–3 Hz, is presumably the frequency at which a filling-in process is slower than the luminance change at the border. This is because the decrease in brightness induction will occur when the filling-in process is slower than the luminance change (frequency) at the border. Brightness induction would then depend on both the velocity of filling-in and the distance the brightness signal has to travel from the border, so a general decrease in cutoff temporal frequency is expected, and observed, with an increase in stimulus size (Rossi & Paradiso, 1996; Davey et al., 1998; but see also Robinson & de Sa, 2008).

Based on this reasoning and temporal cutoff induction frequency estimates from previous studies (De Valois et al., 1986; Rossi & Paradiso, 1996), such a filling-in mechanism should be relatively slow. For instance, reanalyzing Rossi and Paradiso’s (1996) spatio-temporal data, Davey et al. (1998) determined a 95% confidence interval for filling-in velocity at 4°/s–19°/s. Paradoxically, however, all attempts to identify brightness filling-in mechanisms have resulted in much higher velocity estimates, which cannot possibly account for the empirical loss of brightness induction at relatively low temporal frequencies of approximately 2–3 Hz. For example, using masking and briefly presented stimuli, Paradiso and Nakayama (1991) showed that brightness induction has a temporal delay of 110°/s–150°/s. Later, Rossi and Paradiso (1996) used perceived phase shifts in induction from temporally modulated in luminance square wave gratings to arrive at a filling-in velocity estimate of 140°/s–180°/s. Several recent studies showed that a filling-in process can be even faster (Robinson & de Sa, 2008) or nearly instantaneous (Blakeslee & McCourt, 2008).

We had several goals in the present study. First, it became clear from our earlier experiments that brightness induction from temporally modulated surroundings is spatially nonuniform, generally tapering down as the distance from the border increases, and so, especially in larger test fields, the results would be dependent on both spatial setup and subject instructions. We wanted to obtain spatio-temporal brightness induction estimates free of these possible artifacts. As we were intrigued by large discrepancies in filling-in velocity estimates from different studies (Paradiso & Nakayama, 1991; Rossi & Paradiso, 1996; Robinson & De Sa, 2008) and even bigger inconsistencies in temporal frequency cutoff and velocities measured directly by other methods (Rossi & Paradiso, 1996; Blakeslee & McCourt, 2008), we felt that a new design may be a key to the problem (Experiment 2). On that note, we also wanted to confirm that the spatial nonuniformities we observed in our earlier studies (Pereverzeva & Murray, 2008) are related to the distance from the edge rather than just the retinal position (Experiment 1). Finally and most importantly, we used a novel paradigm to directly assess the velocity of filling-in (Experiment 3) and compare this assessment to the spatio-temporal sensitivity estimates of Experiment 2. This method was based on our observation that at certain temporal frequencies of surround luminance modulation an illusory “dartboard” pattern appears in the static disk (Figure 1). This pattern consists of regular light and dark concentric rings within the disk. We hypothesized that this percept was caused by the spread of induction “waves” propagating from the border of the disk towards the center. In this case, propagation velocity can be directly estimated from the distance between the rings in the pattern, providing a spatio-temporal measure of the filling-in process.

## Methods

### Subjects

Ten subjects participated in the experiments: Five subjects participated in Experiments 1 and 2 and five subjects in Experiment 3. An additional six subjects were tested with a subset of stimuli of Experiment 3a but were not invited to further studies because they did not get a clear illusory dartboard percept (as in Figure 1), required for Experiment 3b. The subjects were graduate students and faculty of the University of Washington, aged 24 to 40 years. All had normal or
of the disk. In Experiment 2, disks of different sizes (1°, 2°, 4°, 8°, 16°, and 24°) were embedded in a 51° by 41° surround. Four black dots, designating the corners of an imaginary 1° square test patch were always present in the central location of the disk. In Experiment 3, disks of different sizes (1°, 2°, 4°, and 8°) were presented centrally in a 34° by 26.6° surround.

For simplicity, all stimulus luminances will be specified in Instrument Luminance (IL), defined as 100% \times (L − Lmin)/(Lmax − Lmin), where L is the stimulus luminance, Lmin is the black level of the monitor, and Lmax is the maximal available luminance of the display.

The stimuli had the following characteristics: The time-average luminances of both disks and surrounds were constant throughout all experiments at 50% IL. The surrounds varied in luminance sinusoidally, from 38% IL to 62% IL, with the amplitude of 24% of allowable luminance range. In Experiments 1 and 2, the test disk varied in luminance sinusoidally, in phase with surround modulation, with amplitude that could be adjusted from 0% (static test field) to 140% of the amplitude of the surround. In Experiment 3, the luminance of the test disk was constant. The rate of surround modulation was either 1 Hz (Experiment 1); intermixed conditions of 0.5, 1, 2, and 4 Hz (Experiment 2); or adjustable from 0.4 to 10 Hz (Experiment 3).

Procedure: Experiments 1 and 2

The observer’s task was to adjust the amplitude of the test modulation in such a way as to make the perceived brightness of a 1° square test patch designated by black dots in the corners constant or as constant as possible. The observer was asked to ignore the perceived brightness flicker in all other areas of the test disk. He was instructed either to look directly (foveate) at the test patch while making an adjustment (Experiment 1 Condition 2 and Experiment 2) or fixate on the fixation point in the middle of the disk (Experiment 1 Condition 1) in which case the patch was presented peripherally. The dots designating the patch and the fixation point stayed on during the trial.

The adjustments were done in increments or decrements of luminance amplitude of 0.8% IL steps by pressing the “up” or “down” keys. Once a match was achieved, the observer would press the space bar, recording the setting and initiating a new trial. The new trial would always begin with the physically unchanging test stimulus at 0% luminance modulation amplitude. An auditory signal indicated the maximum and minimum of the available luminance modulation amplitude range.
All conditions (i.e., distance from the border in Experiment 1, and test disk size and temporal frequency of surround modulation in Experiment 2) were randomly intermixed within the respective experiment, with each condition presented on average four times. Prior to the experiment, subjects performed several training sessions, to familiarize them with the task and to ensure that fixation would be maintained as instructed.

Procedure: Experiments 3a and 3b

Experiment 3 was motivated by the observation that at some frequencies of surround modulation, a faint illusory concentric ring pattern appeared in the disk (Figure 1). To explore this phenomenon systematically, we first identified the spatio-temporal conditions at which the pattern was most salient (Experiment 3a) and then explored spatial characteristics of the pattern under these conditions (Experiment 3b).

The observer’s task in Experiment 3a was to adjust the frequency of surround luminance modulation in such a way as to make the perceived concentric circle pattern in the disk as salient as possible. The adjustments were done in increments or decrements of temporal frequency in 0.05 Hz steps by pressing the “8” or “2” keyboard keys. Once the match was achieved, the observer would press the “5” key, recording the setting and initiating a new trial. The new trial would always begin with a 500-ms presentation of a uniform gray screen (50% IL), followed by surround modulation at 0.75 Hz, at the floor of the available temporal frequency range of 0.4–10 Hz. An auditory signal indicated when the maximum or minimum frequency of the available luminance modulation amplitude range was reached. The disks of four different sizes (1°, 2°, 4°, and 8°) were presented pseudo-randomly in a session, until the total of six trials per disk size was reached. To ensure stability of the percept over time, subjects completed either two or three such adjustment sessions, each on a different day. The fixation on the fixation point in the center of the disk was maintained throughout Experiment 3.

The observer’s task in Experiment 3b was to measure the width of perceived concentric rings. This was done by moving two small markers across the disk until they were aligned with the outer and inner rim of a particular ring. The markers were black spots 0.1° in diameter, which could be moved across the disk horizontally in 0.033° steps by pressing the designated keyboard keys. A “space” key press recorded the outer and inner marker positions and initiated a new trial. In addition to adjusting the marker position, subjects were asked to report the number of rings perceived. A total of 40 trials (10 trials per disk size) per subject were collected in each session. As in Experiment 3a, disks of four different sizes (1°, 2°, 4°, and 8° in diameter) were presented. The temporal frequency of surround modulation was individually chosen for subject or disk size as a median frequency of the settings obtained in Experiment 3a. The subjects were asked to fixate on the fixation point in the center of the disk during each trial. To avoid possible border artifacts, the subjects were also asked to choose the innermost distinctive ring for width measurement.
Results

Experiment 1

The purpose of this experiment was to measure the size of brightness induction in different spatial locations. Condition 1 is essentially a replication of one of the conditions of the behavioral experiment from our earlier work (Pereverzeva & Murray, 2008), in which we found that brightness induction is strongest at or near the border and gets weaker towards the center. Condition 2 addresses the possibility of the retinal position influencing the induction effect. Flicker sensitivity is known to vary across the retina (Tyler & Torres, 1972; McKee & Taylor, 1984); therefore, it is possible that any perceptual nonuniformities were due to the retinal position rather than distance from the border.

In Condition 1, subjects were instructed to fixate on the fixation point in the center of the test disk at all times. The test patches were thus presented at different retinal eccentricities. In Condition 2, all the stimulus parameters were identical to those in Condition 1, but the subjects were instructed to foveate the test patch while making amplitude adjustments. Thus, the test patch was always presented at the same retinal location, and any observed location effect could only be due to the distance from the border.

The results of Condition 1 for five subjects are shown in Figure 3A. The nulling amplitude of the test patch, required to achieve the perception of constant or minimally varying brightness, is plotted along the ordinate as the percentage of surround modulation amplitude. The eccentricity of the test patch is plotted along the ordinate in degrees of visual angle. Each data point is the mean of 16 trials. The error bars represent the standard error of the mean. All five subjects demonstrated a robust increase in perceived flicker near the border. For three of the subjects (RS, JL, and NF) this increase was only apparent near the border but not in the central locations; for others (SM and MP), induced flicker steadily decreased towards the center.

To quantify dissipation of brightness induction as a function of distance from the border, the nulling amplitude was regressed against eccentricity for individual subjects, resulting in the following 95% confidence intervals for the slope estimates: 5.59–7.78, 3.72–6.00, 1.37–2.71, 0.84–2.44, and 0.71–2.19 for subjects SM, MP, JL, NF, and RS, respectively.

The results of Condition 2 for five subjects are shown in Figure 3B. As in Condition 1, there was a clear dissipation of brightness induction with distance from the border. All five subjects showed a considerable increase in perceived flicker near the border. For some of the subjects (RS and NF), this increase only appeared near the border but not in the central locations. For others (SM and MP), induced flicker steadily decreased towards the center. To quantify dissipation of brightness induction as a function of distance from the border, the nulling amplitude was regressed against eccentricity for individual subjects, resulting in positive slopes with the following 95% confidence intervals for the slope estimates: 4.14–5.96, 4.2–6.42, 1.25–3.43, 0.23 to 1.56, and 0.38–1.49 for subjects SM, MP, JL, NF, and RS, respectively.

To test for the possibility that viewing condition affects brightness induction, we analyzed the data by means of a two-way repeated-measures ANOVA with factors viewing condition (fixation or foveation) and eccentricity (six eccentricities). As expected, it revealed significant main effect of eccentricity ($F = 2.97$, $df = 5$, $p = 0.02$). However, there was no effect of viewing condition.
condition \((F = 0.08, df = 1, p > 0.77)\), indicating that the observed eccentricity effect is determined by the physical distance from the border rather than the retinal position.

**Experiment 2**

The purpose of this experiment was to further explore the spatial characteristics of brightness induction under a variety of temporal conditions. In order to better estimate the size of brightness induction as a distance from the border, we chose to use circularly symmetrical stimuli with central patch locations equally distant from all borders. These imaginary test patches were designated by four corner dots in the centers of test disks of different sizes. In addition, we varied the rate of surround modulation. While conceptually similar studies were done before (Rossi & Paradiso, 1996; Robinson & de Sa, 2008), they did not take into account spatial nonuniformities, in either the stimulus design or subject instructions, which may have affected their results. In particular, two critical stimulus manipulations were introduced to the current work: central symmetry and the measurement of the effect in the specified small central location.

We reasoned that if the observed spatial nonuniformity of the brightness induction is purely spatial, and brightness induction is instantaneous, the effect should be the same for all temporal frequencies at which brightness induction occurs. If brightness induction is a relatively slow process, however, the brightness induction effect would be attenuated for higher temporal frequencies.

The results of Experiment 2 for five subjects are shown in Figure 4. The nulling amplitude of the test patch, required to achieve the perception of constant or minimally varying lightness, is plotted along the ordinate as the percentage of the surround amplitude modulation. The panels on the left show the changes in nulling amplitude of the central 1° patch as a function of the test disk size for different frequencies. The diameter of the test disk is plotted along the ordinate in degrees of visual angle. The same data are replotted on the right to show changes in nulling amplitude as a function of temporal frequency for different eccentricities. The temporal frequency of modulation is plotted along the ordinate in hertz. Each data point is the mean of four trials. The error bars represent the standard error of the mean.

As seen in the left column of panels, all subjects exhibited a notable decrease in nulling amplitude with an increase of test disk size for all but the lowest temporal frequencies. For the frequency of 0.5 Hz the functions of nulling amplitude from the test disk size were essentially flat for two subjects: NF and RS. For subject MP, the function of nulling amplitude from the test disk size was notably shallower for the frequency of 0.5 Hz than for other frequencies.

For all subjects, on average, the nulling amplitudes for higher temporal frequencies tended to have greater fall-off (faster decrease with the increase of test disk size) than the nulling amplitudes for lower frequencies. Interestingly, for smaller disk sizes (right column of panels), there was little to no effect of temporal frequency for all five subjects. However, with the exception of subject JL, for larger disc sizes, nulling
Experiment 3

The experiment was motivated by the observation that at certain temporal frequencies of surround luminance modulation, an illusory dartboard pattern appeared in the static disk (Figure 1, in Introduction). We wanted to further explore this phenomenon to see whether it could be explained by a mechanism causing spatio-temporal induction nonuniformities in Experiments 1 and 2. In particular, we were interested in the possibility of a standing-wave–like process caused by the interference of induction waves spreading from the border of the disk towards the center.

The experiment consisted of two conditions. In the first condition, the optimal temporal frequency for observing the concentric ring pattern was determined. In the second condition, subjects were asked to measure the width of the illusory concentric rings produced by surrounds modulated at such optimal frequency. In addition, we asked the subjects to report the number of clearly visible rings. This was done to ascertain that the subjects observed the ring pattern rather than just a sharp fall-off in induction near the border of the disk, documented in Experiment 1 (which potentially could look like one ring at the border).

The results of Experiments 3a and 3b are summarized in Figure 5. Temporal frequency best estimates for each disk size for every individual subject are represented along the abscissa. The best estimates were calculated as a median of six adjustments for each disk size in Experiment 3a. The symbol sizes represent consecutive disk sizes, from the smallest, 0.5° radius, to the largest, 4° radius disk. Average ring width, in degrees, is plotted along the ordinate. If the observed ring pattern is caused by a wave-like filling-in process from sinusoidal luminance change at the border, then the velocity of the brightness induction spread can be calculated by multiplying temporal frequency by wavelength, for which the wavelength measure is obtained by doubling the ring width, or nodal distance. Figure 6 shows velocity estimate as a function of disk size for each subject (solid lines). The mean velocity estimate, averaged across five subjects, is shown by the black dashed line.

There are two striking features in the velocity estimate data. First of all, it represents a very slow process. For example, an average velocity of brightness induction spread for 0.5° radius disks is estimated at 0.24°/s ± 0.03°/s. Second, the process appears to speed up with an increase of travel distance. For instance,
when the disk radius increased to 4°, the velocity estimate increased to 0.58°/s ± 0.07°/s.

### Discussion

#### Spatio-temporal nonuniformities in dynamic brightness induction (Experiments 1 and 2)

The results of Experiment 1 verified that spatial nonuniformities in dynamic brightness induction are due to the border distance and not to retinal location. An increase in induction near the border was evident and very similar both when subjects were keeping central fixation and the stimulus patch (imaginary 1° square, defined by four small dots in the corners) was presented peripherally, and when subjects were focusing the stimulus patch.

In order to avoid the possibility that asymmetrically placed borders contribute unequally to brightness induction (Zaidi et al., 1992), we used only central (and centrally symmetric) stimulus locations in Experiment 2. Also, rather than estimate overall perceived flicker in the disks, the subjects were explicitly instructed to attend only to a small central patch (defined similarly to Experiment 1), while ignoring any other locations. The results of Experiment 2 were consistent with low temporal frequency drop-off, observed in other studies (De Valois et al., 1986; Rossi & Paradiso, 1996; but see Blakeslee & McCourt, 2008). This decrease in induction effects was clearly a function of both temporal frequency and distance from the border. At temporal frequencies 1 Hz and above, all subjects exhibited a notable decrease in brightness induction with an increase of test disk size. For all subjects, the induction effect at higher temporal frequencies tended to have greater fall-off with increase in the distance from the border than at lower frequencies.

Interestingly, for smaller disk sizes, there was little to no effect of temporal frequency for all five subjects. This could partly be because of the relatively large size of the patch over which the brightness judgments were made—perceived flicker at the disk border, near the patch, could have affected brightness judgment within the patch. Potentially, such an effect from nearby borders could lead to an overinflated induction report, and to a consequent overestimate of induction propagation velocity. However, for larger disk sizes, nulling amplitudes decreased rapidly with an increase in temporal frequency (for four out of five subjects).

To estimate velocity of brightness induction propagation from this data set, we can look at the individual data sets in the right column of panels of Figure 4. For example, for disks of 2° radius, a decrease in induction is starting around 2 Hz, or even 1 Hz for some subjects. To reach the center of the disk in time for a half-cycle, at 1 Hz, it should take the induced signal less than 500 ms to travel the distance of 2°, which results in a velocity estimate of 4°/s (8°/s for 2 Hz fall-off).

#### Velocity of brightness induction propagation (Experiment 3)

Our estimates of propagation velocity, based on the assumption that the spatial nonuniformities observed in Experiment 3 were a manifestation of a standing-wave–like process, were even smaller. For example, for the smallest disk sizes we tested (0.5° radius), an average estimated velocity of brightness induction spread was about 0.25°/s.

To the best of our knowledge, the only study reporting directly measured slow velocities explored the timing of phantom propagation across a variable width gap (Meng, Ferneyhough, & Tong, 2007). Visual phantom phenomenon, defined as a perceptual filling-in, occurs in the empty gap separating two sets of low-contrast collinear gratings (Tynan & Seculer, 1975). The “phantom” appearing in the gap looks like a faint continuation of the inducing gratings. Meng et al. (2007) used binocular rivalry to explore the likelihood of observing phantoms in the time period following the inducer’s dominance onset. They found (not surprisingly) that the likelihood of observing phantoms in the time period following the inducer’s dominance onset increases over time, but also—surprisingly—that larger gaps required disproportionally longer time to fill in than smaller gaps. The gaps 2° in width took around 1200 ms on average to fill in, while the 5° gaps took 1600 ms. Taking into account 200-ms reaction time (reviewed by Kosinski, 2012), the velocity of filling-in was about 1°/s for 2° gaps and about 1.8°/s for 5° gaps (i.e., progressively higher velocity for larger gaps). While slightly higher than velocity estimates from the present study, the results from Meng et al. (2007) are similar to ours both in effect size and in the finding that filling-in velocity increases as a function of stimulus size.

In addition, the studies of the Craik–O’Brien–Cornsweet effect (Davey et al., 1998; Devinek, Hansen, & Gegenfurtner, 2007) provide further evidence that the propagation speed of the induction effect is related to the distance the induced signal has to travel. Similar to our findings, the results of these studies were consistent with higher propagation speeds if the propagating signal had to travel larger distances, and lower speeds if the distances were smaller.

Using the direct measurement of propagation velocity, we have isolated a very slow, slower than 1°/s, brightness induction mechanism. The propagation velocity of this mechanism is in the ballpark of the
velocity estimated from spatio-temporal brightness induction fall-off. The correspondence was the best for larger stimuli. For example, for a 4° radius stimulus, the average velocity calculated from the nodal distances in Experiment 3 was about 0.5°/s. For stimuli of this size in Experiment 2, the temporal frequency fall-off was noticeable for all frequencies tested, placing an upper limit well under 4°/s on the velocity estimate. One possible explanation of better correspondence between two velocity estimates in large stimuli is that in the case of smaller stimuli in Experiment 2, the flicker judgment may be influenced by border proximity, leading to overestimation of propagation velocity.

To the best of our knowledge, this is the first time that the directly measured velocity of brightness spread was roughly in agreement with temporal frequency fall-off predictions. We believe that the patterns observed in Experiment 3 present the signature of a very slow brightness induction mechanism. Ironically, the existence of such a mechanism raises more questions than it answers. The first question is, what is an underlying physiological mechanism?

Physiological mechanisms: Cortical propagation velocity estimates

The jury is still out on the mechanisms governing brightness induction (Adelson, 1993; Gilchrist, 2005), but there is considerable evidence indicating significant involvement of cortical mechanisms. This evidence is based on the findings of animal single-cell physiology (Rossi, Rittenhouse, & Paradiso, 1996; Rossi & Paradiso, 1999; Kinoshita & Komatsu, 2001; MacEvoy & Paradiso, 2001; Sasaki & Watanabe, 2004; Roe, Lu, & Hung, 2005; Hung, Ramsden, & Roe, 2007), human electrophysiology (McCourt & Foxe, 2004), and human functional magnetic resonance imaging research (Boucard, van Es, Maguire, & Cornelissen, 2005; Boyaci, Fang, Murray, & Kersten, 2007; Pereverzeva & Murray, 2008; but see also Perna, Tosetti, Montanaro, & Morrone, 2005; Cornelissen et al., 2006).

Lateral propagation of neural signals in V1 was studied extensively (reviewed by Angelucci & Bressloff, 2006). If we work through a sample velocity calculation provided by Angelucci and Bressloff (2006) and assume conduction velocity of 0.1 m/s (Girard, Hupe, & Bullier, 2001), parafoveal cortical distance of 10° with 2.3 mm/deg magnification factor at 5° eccentricity (Van Essen, Newsome, & Maunsell, 1984) would correspond to 23 mm of cortical surface. Uninterrupted propagation at 0.1 m/s would take 230 ms—but we also need to take into account the synaptic connection time. Assuming about 4-mm radius for lateral connections (Angelucci et al., 2002) and integration time of about 15 ms at each synaptic relay (Nowak & Bullier, 1997; Azou & Gray, 1999), we need to add 45 ms to travel time, for a total time of 275 ms. This calculation would give us an estimated velocity of 1°/27.5 ms, or about 35°/s—which is relatively slow—but still at least an order of magnitude faster than what we need to account for our results.

Individual differences in brightness induction

A notable feature of our results is a large size of individual differences. For example, in Experiment 1 the size of induction in the center of the disk varied from approximately 25% to approximately 60% of surround modulation. Similarly, in Experiment 2, the induction at high temporal frequencies in the larger disks varied from 0% to approximately 70% for different subjects. During the subject recruitment for Experiment 3, only 5 out of 11 subjects reported seeing clear dartboard percepts (the low inclusion number could be partly due to the selection process because we were careful to ask for the subjects’ percepts rather than describe a dartboard pattern to them so not to influence their reports). While beyond the scope of this paper, the questions of size, consistency, stability, and underlying causes of individual differences in brightness perception have been addressed in the past (for example, Bowen, 1984, 1986; Pereverzeva & Teller, 2005; Logvinenko & Tokunaga, 2011) and large individual differences in brightness perception were noted. The individual differences we have observed are in line with these findings.

Attenuation of contrast towards the center—Argument against simple filling-in models?

Another interesting question is what causes attenuation of brightness induction effect as a function of distance from the border. Attenuation was observed in all three experiments. In Experiment 1 null amplitudes in central locations were smaller than those near the border for both fixation and foveation conditions (Figure 3). A similar effect was observed in Experiment 2 (Figure 4), with progressive attenuation as a function of disk size (i.e., distance from the border). We were not measuring the size of induction in Experiment 3, but the pronounced attenuation in ring contrast was observed toward the disk center.

While attenuation, or dissipation of edge-generated signals, with distance from the edge is predicted by most (fast-acting) spatial filtering models (e.g., Blake-slee & McCourt, 2004; Blakeslee et al., 2005; Robinson, Hammon, & de Sa, 2007; reviewed in Blakeslee & McCourt, 2013), it is not consistent with a simple filling-in interpretation, which assumes spatial unifor-
mity. Our findings call for a model integrating slow- and fast-acting mechanisms of brightness induction.

Keywords: brightness induction, dynamic brightness induction, filling-in

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