Induction effects for heterochromatic brightness matching, heterochromatic flicker photometry, and minimally distinct border: implications for the neural mechanisms underlying induction

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Brightness induction refers to the finding that the apparent brightness of a stimulus changes when surrounded by a black versus a white stimulus. In the current study, we investigated the effects of black/white surrounding stimuli on settings made between red and green stimuli on three different tasks: heterochromatic brightness matching (HBM), heterochromatic flicker photometry (HFP), and minimally distinct border (MDB). For HBM, subjects varied the relative luminance between the red and green stimuli so that the brightness of the two colors appeared equal. For the two other tasks, matches were made based on minimizing red/green flicker (HFP) or the saliency of a red/green border (MDB). For all three tasks, the presence of black/white surrounding stimuli significantly altered red/green settings, demonstrating the existence of induction effects. These results are discussed in terms of which underlying color pathways (L+M versus L−M) may contribute to induction effects for the different tasks. © 2005 Optical Society of America

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1. INTRODUCTION

Brightness induction, first described in 1839,[1] refers to the finding that the apparent brightness of an object is influenced by the context in which it is presented. In the simplest example of brightness induction, a gray disk surrounded by a black annulus appears brighter than the same gray disk surrounded by a white annulus. This result is interpreted as the annulus inducing the brightness of the central disk. A simple way to quantify the magnitude of induction is to employ an "achromatic brightness matching" (ABM) task, in which subjects are asked to adjust the luminance of a gray test disk (presented by itself) to match the apparent brightness of a gray disk surrounded by a black or white annulus. In various forms of this task, subjects have been found to need more luminance in the gray test disk if the comparison disk is surrounded by a black annulus than if the comparison disk is surrounded by a white annulus.[2–5]

In the current study, we investigated induction effects by employing chromatic (red versus green), rather than gray, test stimuli. Our stimuli consisted of red and green stimuli presented alone or surrounded by inducing white and black stimuli (see Fig. 1). Akin to the ABM task described above, our subjects conducted a heterochromatic brightness matching (HBM) task, adjusting the relative luminance of the red versus green stimuli so that the two colors appeared equally bright,[6] both in the absence and in the presence of surrounding inducing stimuli. Induction is shown if the red/green luminance ratio at equibrightness is altered by the presence of the inducers. The induction effects obtained on the HBM task were compared with those obtained on two other tasks: heterochromatic flicker photometry (HFP) and minimally distinct border (MDB). In the HFP task, subjects viewed a stimulus flickering between red and green (both in the absence and in the presence of surrounding black/white stimuli) and adjusted the relative luminance of the two colors until the percept of flicker was least salient.[7–9] In the MDB task, subjects viewed red and green stimuli placed in spatial juxtaposition (both in the absence and in the presence of surrounding black/white stimuli) and adjusted the relative luminance of the two colors until the border between them was least salient.[10] Note that unlike for HBM, for HFP and MDB the subject's task does not involve comparing any property of the red versus green stimulus *per se*. However, common to all three tasks, the obtained settings provide a measure of *equality* between the red and the green. To reflect this commonality, we use a single term, equality settings, to describe the settings made for all three tasks. What is thought to actually be equated between the red and the green is the amount of neural response elicited by the two stimuli within the relevant color pathway(s) of the visual system.

Three postreceptoral pathways have been described in color vision. The L+M pathway (referred to as the luminance pathway) signals a weighted sum of long-wavelength-sensitive (L) and medium-wavelength-sensitive (M) cones [with some debate regarding the

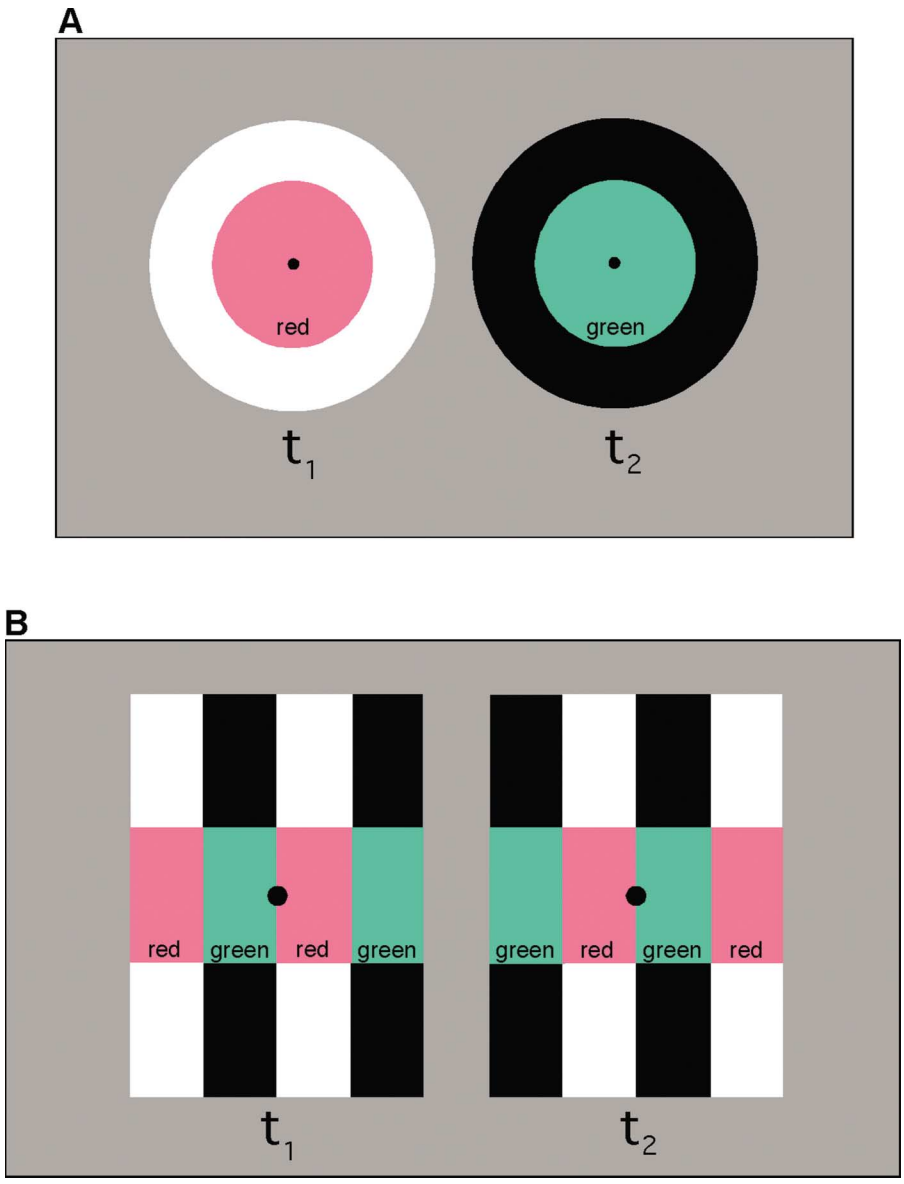

Fig. 1. Stimuli used in these experiments. A. Alternating disk and annulus stimulus used in Experiments 1 and 2. Shown is the induction condition in which a red disk surrounded by a white annulus (time t_1) was alternated with a green disk surrounded by a black annulus (time t_2; referred to as the green–black condition). The red–black induction condition (not shown) consisted of the disk and annulus in the opposite phase relationship. The noninduction condition (not shown) consisted only of the central disk alternating between red and green. "Red" and "green" and "t_1," "t_2," are shown here to aid the reader and were not present in the actual stimulus. B. Red/green grating with black/white flankers stimulus used in Experiment 3. Shown is the induction condition in which the black stripes were spatially in phase with the green stripes (referred to as the green–black condition). The red–black induction condition (not shown) consisted of the black stripes spatially in phase with the red stripes. The noninduction condition (not shown) consisted only of the red/green grating. Some conditions used temporally reversing gratings. Some conditions used static stimuli (as shown here). Note that there were slight differences in the stimulus depending on whether the task was HFP (which used sinusoidal gratings), HBM (which used square wave gratings and a thin black line at the red/green borders), and MDB (which used square wave gratings, shown here). See text for further details.

contribution of short-wavelength-sensitive (S) cones[11–13]. The L−M pathway (referred to as the red/green chromatic pathway) signals a difference between L and M cones. The S−(L+M) pathway (referred to as the tritan chromatic pathway) signals a difference between S cones and the sum of L and M cones. The HFP and MDB tasks described above are thought to rely exclusively on signals in the L+M pathway, and thus HFP and MDB settings are typically referred to as equiluminance settings. At the point of minimal flicker (or minimal border), the two colors employed (for example, red and green) are thought to elicit equal neural responses within the L+M pathway. The equating of neural responses elicited by red and green on a task that relies on the L+M pathway (such as HFP or MDB) can be described mathematically as

$$P_L L_r + P_M M_r = P_L L_g + P_M M_g, \quad (1)$$

where L_r and M_r refer to the L- and M-cone responses, respectively, elicited by the red stimulus; L_g and M_g refer to

the cone responses elicited by the green stimulus; and P_L and P_M are weighting factors that refer to the relative proportion of L and M cones, respectively.[14] In contrast to HFP and MDB, HBM is thought to rely on a combination of signals in all three color pathways, L+M, L−M, and S−(L+M). Together, these pathways are thought to constitute the brightness mechanism, and, accordingly, HBM settings are typically referred to as equibrightness settings. In the case of HBM, two colors will be perceived as equally bright when some combination of the responses within the three color pathways elicited by the two colors is equated.

Under conditions of *induction*, i.e., when the red and green stimuli are surrounded by white and black stimuli, respectively (or vice versa), the neural responses to red and green (and the equating thereof) are expected to be modulated. Note that we assume that this modulation occurs within the color pathway(s) that underlies the task itself. Staying with the example from Eq. (1), in which the task is one that relies on the L+M pathway, this modulation can be described mathematically as

$$(P_L L_r + P_M M_r)^* X = (P_L L_g + P_M M_g)^* Y, \quad (2)$$

where X and Y are proportional to the summed L- plus M-cone excitation produced by the white and the black annulus, respectively. Consider the case where red is surrounded by white and green by black. Conceptually, the white surround stimulus should inhibit (i.e., decrease) the neural response to the red test stimulus compared with the case where the red stimulus is presented alone. To implement this in Eq. (2), the X on the left side of the equation would take a value less than 1.0. Conversely, the black surround stimulus might facilitate (i.e., increase) the neural response to the green test stimulus compared with the case where the green stimulus is presented alone. To implement this in Eq. (2), the Y on the right side of the equation would take a value greater than 1.0. [Note that the modulatory surround effects in Eq. (2) map loosely onto center/surround receptive field organization known to exist for ganglion cells in the retina and cells of the LGN. Although the size of receptive fields in the retina and the LGN are clearly smaller than the stimuli used in our experiment, it is reasonable to assume that some cells with receptive fields falling at the borders of the center and surround are affected in this manner and could contribute to the induction phenomenon.] Thus, a pair of red and green stimuli that produce equally weighted sums of L- and M-cone activity in the absence of black/white inducing stimuli [Eq. (1)] cannot produce equally weighted sums in the presence of the inducing stimuli [Eq. (2)]. In the presence of inducing stimuli (white surrounding red, black surrounding green), to create an equal response to red and green, L_r and M_r would need to be increased (which the subject achieves by increasing the luminance of the red stimulus), or L_g and M_g would need to be decreased (which the subject achieves by decreasing the luminance of the green stimulus), or both. The difference in the red/green luminance ratio in the presence versus the absence of the inducing stimuli is termed the induction effect.

We set out to investigate the contribution of the different color pathways to induction. To simplify our study, we restricted our investigation to the L+M and L−M pathways (by using stimuli that do not modulate the S cones). In Experiment 1, we measured induction effects on the HFP task. Although HFP is thought to rely only on the L+M pathway, this is likely to be restricted to high temporal frequencies; at low temporal frequencies, both L+M and L−M are likely to contribute[9,15] (see below and Section 4). For this reason, we employed a range of temporal frequencies (4–28 Hz), including those high enough to eliminate contribution from the L−M pathway (i.e., greater than 10–15 Hz). The results of this experiment revealed significant induction effects on red/green equality settings, indicating that induction effects can occur explicitly within the L+M pathway. In Experiments 2 and 3, we compared the magnitude of induction effects produced across the three different tasks (HFP, HBM, and MDB) as a means to investigate the relative degree of induction occurring within the L+M versus L−M pathways. For these experiments, we used lower temporal frequencies (0–4 Hz) because it is very difficult to conduct HBM and MDB above ~4 Hz. Here we found comparable magnitudes of induction effects for the HFP and HBM tasks but significantly smaller induction effects for the MDB task. This result can be explained by proposing that at low temporal frequencies, induction effects on HFP and HBM equality settings invoke both the L+M and L−M pathways (whose signals add together), while induction effects on MDB settings rely only on signals within the L+M pathway. This hypothesis is further supported by the results from correlational analyses performed in Experiment 3, which showed that the magnitude of induction effects for HFP and HBM correlated positively with each other but not with the magnitude of induction effects for MDB.

2. METHODS

These experiments measured red/green settings for three different tasks: HFP, HBM, and MDB. Although HFP and MDB settings are typically called "equiluminant" and HBM settings are typically called "equibright" (see Section 1), in the current study we refer to the settings obtained from all three tasks as "equality settings" to stay agnostic regarding the mechanisms (i.e., luminance versus brightness) contributing to these settings. Also note that our use of the term equality settings is meant to reflect the fact that the red/green setting for a given task is presumably that which produces an equal neural response to the red and green stimulus within the color pathways that are involved in that task (see Section 1). Data were obtained in three separate experiments. Experiment 1 addressed whether red/green equality settings obtained using HFP are susceptible to the induction effects of a black/white surround and whether these induction effects vary across temporal frequencies. The stimulus consisted of a disk alternating between red and green, surrounded by an annulus alternating between black and white (in phase with the red/green alternation). Experiment 2, which used the same stimuli as in Experiment 1, addressed whether the magnitude of induction effects on equality settings obtained using HFP differ from those obtained using HBM. In Experiment 3, we compared the

magnitude of induction effects on equality settings for all three tasks (HFP, HBM, and MDB). Here we used red/green gratings (rather than disk stimuli) because the MDB task requires the presence of a red/green border.

A. Subjects

A total of 29 subjects participated as either volunteers or paid research subjects in the three separate experiments. All had normal or corrected-to-normal vision and normal red/green color vision as assessed by the Ishihara Tests for Colour Deficiency. Both Experiments 1 and 2 included five subjects (Experiment 1 age range, 19 to 34 years; mean, 23.8±6.0 years. Experiment 2 age range, 17 to 34 years; mean, 23.8±6.3 years). Twenty-two subjects participated in Experiment 3 (age range, 21 to 40 years; mean, 27.9±4.6 years). Note that the reason for the large number of subjects in Experiment 3 was to allow us to conduct correlation analyses on the data. First author KLG participated in all three experiments, and research assistant BDA participated in Experiments 1 and 2. With the exception of these two subjects, all other subjects were naïve to the purpose of the study.

B. Apparatus

For all experiments, visual stimuli were generated in Matlab (The MathWorks, Inc.), interfaced with stimulus software (version 6.111) from Cambridge Research Systems (CRS). In Experiments 1 and 2 these were presented on a ViewSonic P95f monitor (19-in. display, 1024 $\times$768 pixels, 100 Hz refresh) driven by a CRS VSG 2/4 video board. The 15-bit video board allowed for 32,768 discrete luminance levels. In Experiment 3, visual stimuli were presented on an NEC MultiSync FE750+ monitor (17-in. display, 1024$\times$768 pixels, 100 Hz refresh) driven by a CRS VSG 2/3 video board. This 12-bit video board allowed for 4096 discrete luminance levels. For all experiments, the maximum output for the monitor was calibrated to equal-energy white (CIE chromaticity coordinates = 0.333, 0.333), and the voltage/luminance relationship was linearized independently for each of the three guns in the display, using a Gamma Correction System and an OptiCAL 256M (CRS).

C. Stimuli

In Experiment 1, we obtained HFP equality settings. Stimuli (see Fig. 1A) consisted of a disk (3.5° diameter) that counterphase-reversed (temporal sinusoidal) between red [CIE coordinates = 0.354, 0.325; MacLeod–Boynton (M–B) coordinates: M/L=0.320, S=0.016] and green (CIE coordinates = 0.311, 0.345; M–B: M/L =0.350; S=0.016), through equal-energy white (CIE coordinates =0.333, 0.333; M–B coordinates: M/L=0.335, S =0.016) at a mean luminance of 28 cd/m^2. This alternation modulated the L cones and M cones by 2.28% and 4.15%, respectively, resulting in a rms cone contrast of 3.35%. Note that the red/green colors were chosen to selectively modulate the L and M cones, while keeping the S-cone excitation constant. The purpose of silencing S-cone modulation was to eliminate the contribution of the S−(L+M) (tritan) color pathway, allowing us to selectively study the contribution of the L+M (luminance) and L−M (red/green) color pathways. The background was of the same mean chromaticity and luminance as the red/green disk.

The disk was presented in three different configurations. In the first, the noninduction condition, it was presented by itself. In the two other conditions, the induction conditions, the disk was surrounded by an annulus (6° diameter) that counterphase-reversed (temporal sinusoidal), in phase with the red/green disk reversal, between black (0 cd/m^2) and white (56 cd/m^2). The mean luminance (28 cd/m^2) and chromaticity (equal-energy white) of the annulus matched that of the alternating red/green disk and of the background. The Michelson contrast $[(\mathrm{Lum}_{\mathrm{white}}-\mathrm{Lum}_{\mathrm{black}})/(\mathrm{Lum}_{\mathrm{white}}+\mathrm{Lum}_{\mathrm{black}})]$ produced by alternating the annulus was 100%, which translates into a cone contrast in L and M cones of 100%. In one induction condition, the black phase of the annulus was temporally in phase with the green phase of the disk [which we refer to as the green–black condition; see Fig. 1A]. In the other induction condition, the black phase of the annulus was temporally in phase with the red phase of the disk (which we refer to as the red–black condition). The disk/annulus stimulus was presented at seven different temporal frequencies: 4, 8, 12, 16, 20, 24, and 28 Hz. Note that because the vertical refresh of our monitor was 100 Hz, the temporal sinusoids for the higher temporal frequencies in this experiment were necessarily sparsely sampled, and therefore the temporal modulation in these cases would have been closer to a square wave than to a sine wave. This should have the effect of producing higher temporal frequency harmonics in the stimulus (although these harmonics will be of lower amplitude). In addition, in the case where the temporal frequency both was high and did not divide evenly into 100 Hz (e.g., 28 Hz), the sampling would have been somewhat irregular. We believe that these temporal sampling artifacts (sparse or irregular sampling) had negligible effects on the results from Experiment 1 since we observed systematic effects of increasing temporal frequency on the magnitude (and direction) of induction (see Section 3). Although we do not feel that these temporal sampling artifacts affected the data in Experiment 1, we did see substantial individual differences across subjects in the magnitude of induction effects at temporal frequencies higher than 4 Hz. For this reason, in Experiment 2, we tested subjects only at and below 4 Hz.

In Experiment 2, we obtained both HFP and HBM equality settings using disk/annulus stimuli with the same spatial configurations as those employed in Experiment 1 (see Fig. 1A). In this experiment, HFP settings were obtained at 4 Hz, and HBM settings were obtained at 4 Hz and 0.5 Hz. Our reason for using a 0.5 Hz condition for HBM was to try to match as nearly as possible the 0 Hz temporal frequency used in previous HBM studies, i.e., where settings are made using two simultaneously presented static fields (e.g., one red, one green). The use of temporally alternating stimuli in the current HBM task was required in order to use the same stimulus configuration as was used for HFP, where a single disk stimulus was presented and red/green comparisons were made over time.

In Experiment 3, we obtained HFP, HBM, and MDB equality settings using vertically oriented (0.5 c/deg) gratings (see Fig. 1B) that were either counterphase-reversed (temporal sinusoid) or static. In the noninduction condition, the stimulus consisted of red/green gratings presented in a rectangular (5° horizontal by 1.5° vertical) aperture, which was similar in area (7.5 deg^2) to the red/green disk employed in Experiments 1 and 2 (9.6 deg^2). The gratings were presented with the zero crossing positioned in the center of the stimulus to ensure equal number of red and green stripes in the stimulus. In the two induction conditions, black/white gratings (size: 5° horizontal × 1.5° vertical) appeared juxtaposed above and below, and were spatially in phase with, the red/green grating. In the green–black induction condition, the black phase of the flanking luminance grating was aligned with the green phase of the red/green grating (see Fig. 1B), analogous to the green–black disk/annulus arrangement of Experiments 1 and 2. In the red–black induction condition, the black phase was aligned with the red phase of the red/green grating. As with the disk stimulus in Experiments 1 and 2, the red/green gratings in Experiment 3 were modulated through equal-energy white (CIE coordinates = 0.333, 0.333; M–B coordinates: $M/L=0.335, S=0.016$), at a mean luminance of 28 cd/m^2, and produced 3.35% rms cone modulation in L and M cones, while the S-cone excitation was kept constant. Like the black/white annulus in Experiments 1 and 2, the flanking black/white gratings in Experiment 3 were modulated 100% and were the same mean luminance and chromaticity as the red/green gratings.

In Experiment 3, we obtained settings for HFP (at 4 Hz), HBM (at 4 and 0 Hz), and MDB (at 4 and 0 Hz). Note that unlike in Experiment 2, 0 Hz, rather than 0.5 Hz, was employed for the HBM task in Experiment 3, as the use of red/green gratings allowed the red-versus-green brightness comparison to be made spatially, without the need for temporal alternation. Also note that the stimuli in Experiment 3 varied slightly with task, as follows. In the HFP task, the gratings were spatially sinusoidal, whereas in the HBM and MDB tasks, the gratings were spatially square wave. Square waves were needed in the MDB to provide a border for subjects to minimize. Square waves are also commonly used for the HBM task. While subjects were performing the HBM task, we added a single-pixel-width vertical black line separating each phase of the grating to prevent subjects from attempting to minimize the border.[10]

D. Paradigm

For all experiments, subjects were tested in a dark room, viewed the video display binocularly from a chin rest situated 57 cm away, and were instructed to maintain fixation on a central black dot. For all tasks (HFP, HBM, and MDB) subjects adjusted the red/green luminance contrast to meet a specific criterion (defined differently for each task; see below). As explained above, for all tasks we refer to the red/green setting at this criterion as the equality point. Subjects made these adjustments in either coarse steps (2.5% Michelson contrast) or fine steps (0.5% Michelson contrast), depending on how near they were to the equality point, using specified toggle switches on a response box. Note that we are restricted to describing the properties of our red/green stimuli in terms of luminance contrast ($[Lum_{red}-Lum_{green}]/[Lum_{red}+Lum_{green}]$), since monitor calibration is necessarily in units of luminance. This is not to be confused with the concept of luminance as one of the three color pathways.

In Experiment 1, subjects made HFP equality settings. On each trial, the disk stimulus appeared centered on the fixation dot, and the subject adjusted the luminance contrast between the red and the green phases until the percept of flicker was least salient. HFP settings were obtained at seven different temporal frequencies (4–28 Hz). It is perhaps important to point out that HFP settings, although thought to be difficult at low temporal frequencies,[16] are nonetheless possible (i.e., flicker can still be minimized). At times the stimulus looks almost iridescent—simultaneously red and green without flickering between the two, an effect that Boynton and Kaiser[17] referred to as a "flickerless exchange" or a "temporal analog of the melting borders reported in minimally distinct border." Data were obtained for each of three stimulus configurations: one noninduction condition (no annulus) and two induction conditions (red–black and green–black). Subjects were tested in blocks of ten trials, with a single condition presented per block. The order of presentation of the 21 blocks of trials (seven temporal frequencies × three stimulus configurations) was randomized across subjects. The equality point for each subject and each condition was determined from the mean setting across ten trials. For each subject, six to eight hours were required to complete the entire experiment, with testing divided into 1.5- to 4-hour blocks.

In Experiment 2, subjects made HFP settings at 4 Hz and HBM settings at 4 Hz and 0.5 Hz. On an HFP trial, settings were made as described for Experiment 1. On an HBM trial, the disk stimulus appeared centered on the fixation dot, and the subject adjusted the luminance contrast between the red and the green phases until the two colors were perceived to be equally bright. HFP and HBM settings were performed for each of the three stimulus configurations: one noninduction condition (no annulus) and two induction conditions (red–black and green–black). Subjects were tested in blocks of ten trials, with a single condition presented per block. For the duration of each block, the appropriate task instructions appeared at the top of the screen (i.e., "minimize flicker" or "match brightness"). The order of presentation of the 18 blocks (one HFP frequency × three stimulus configurations + two HBM frequencies × three stimulus configurations, two ten-trial blocks/condition) was randomized across subjects. Equality points for each subject and each condition were determined from the mean setting across 20 trials. For each subject, 6 to 15 h were required to complete the entire experiment, with testing divided into 1.5- to 2.5-hour blocks.

In Experiment 3, subjects made HFP settings at 4 Hz, HBM settings at 4 Hz and 0 Hz, and MDB settings at 4 Hz and 0 Hz. On an HFP or an HBM trial, settings were made as described for Experiments 1 and 2. On an MDB trial, the subject adjusted the luminance contrast between the red and the green phases of the grating until the borders between the two were least salient. HFP,

HBM, and MDB settings were performed for each of three stimulus configurations: one noninduction condition (no flanking luminance grating) and two induction conditions (red–black and green–black). Subjects were tested in blocks of 16 trials, with a single condition presented per block. For the duration of each block, the appropriate task instructions appeared at the top of the screen (i.e., "minimize flicker," "match brightness," or "minimize border"). The order of presentation of the 15 blocks (one HFP frequency × three stimulus configurations + two HBM frequencies × three stimulus configurations + two MDB frequencies × three stimulus configurations) was randomized across subjects. Equality points for HFP, HBM, and MDB for each subject and each condition were determined from the mean setting across 16 trials. For each subject, 3.5 to 9.5 h were required to complete the entire experiment, with testing divided into 1.5- to 2-h blocks.

E. Data Analysis

There were two main measures in this study. (1) Red/green equality settings (HFP, HBM, and MDB) for the different temporal frequencies and induction conditions. These values are expressed in terms of Michelson luminance contrast. (2) Induction effects. For each task/temporal frequency, an induction effect was calculated as the difference in luminance contrast between a subject's red/green setting in the induction condition (red–black or green–black) and the noninduction condition. In Experiment 1, there were substantial individual differences in the magnitude and direction of the induction effect as a function of temporal frequency, and thus data were not combined across subjects. This was not an issue in Experiments 2 and 3, so here data were averaged across subjects. In addition, because the magnitude of the induction effect in Experiments 2 and 3 was found to be statistically indistinguishable for the red–black versus green–black induction conditions, the absolute values of the magnitudes of induction were averaged for each subject before averaging across subjects.

3. RESULTS

A. Experiment 1: Investigating Induction Effects on HFP Settings

HFP settings for the disk stimulus (Fig. 1A) are plotted as a function of temporal frequency (4–28 Hz) in Fig. 2. Data are presented separately for the noninduction condition (diamonds) and the two induction conditions: red–black (squares), green–black (circles). Equality settings are presented in terms of luminance contrast between the red and green ($[Lum_{red}-Lum_{green}]/[Lum_{red}+Lum_{green}]$), with zero denoting photometric equiluminance (V_λ), positive values denoting red-more-luminous-than-green, and negative values denoting green-more-luminous-than-red. Note that data are presented separately for the five subjects (rather than obtaining a group mean), since the effects of temporal frequency on induction effects were found to differ across individuals.

In the noninduction condition, equality settings were essentially constant, and were close to photometric equiluminance (V_λ), across temporal frequencies. This lack of a temporal frequency effect runs contrary to previous studies that have shown temporal frequency effects on HFP settings obtained by using gratings.[9,15] The discrepancy suggests that some interaction of temporal frequency and spatial structure (gratings versus disks) could influence HFP settings.

Induction effects can be observed by comparing data in the noninduction condition with those in the two induction conditions. Here we found that at the lowest temporal frequency tested (4 Hz), all subjects exhibited induction effects in the predicted direction. For example, in the green–black induction condition (i.e., when the green and red phases of the disk were in phase with the black and white annuli, respectively, circles), luminance contrasts of the red/green equality settings were more positive than those observed in the noninduction condition (diamonds). These settings indicate that subjects had to increase the relative luminance of the red disk to make a match to the green disk. Presumably this occurred, as displayed in Section 1 in Eq. (2), because the black annulus surrounding the green disk increases the neural response to the green disk while the white annulus surrounding the red disk decreases the neural response to the red disk, and thus to equate the neural response elicited by the red and green, the luminance of the red disk must be increased to compensate. Likewise, an induction effect at 4 Hz in the red–black induction condition (squares) is evidenced by the fact that equality settings were less positive in this condition compared with those observed in the noninduction condition (although the effects in the red–black condition do not appear as strong as those in the green–black condition).

Most interesting in these data is the fact that the effect of the black/white annulus varied systematically with temporal frequency; results were consistent with an induction effect, no effect, or a *reversal* of the induction effect, depending on temporal frequency. And, the temporal frequencies at which these different effects occurred varied across subjects. A reversal in the induction effect, which occurred at the higher temporal frequencies (specifically for subjects KLG, FA, and TO), is evidenced by the fact that the luminance contrasts of the equality settings in the green–black condition were less positive than those observed in the noninduction condition (and vice versa for the red–black condition). At first glance, this reversal could be interpreted as the black/white annulus producing *assimilation* effects (e.g., that a black annulus surrounding a green disk *decreases* the neural response to the green disk), which is conceptually the opposite of an induction effect. We believe, however, that a more likely reason for this reversal is that it reflects true induction but that at (or before) the stage in visual processing where induction occurs, there exists a response lag between the processing of the alternating red/green disk stimulus and the alternating black/white annulus. At low temporal frequencies (i.e., 4 Hz), this response lag will be inconsequential, producing induction effects in the predicted direction. At some higher temporal frequency, the response lag between the processing of the disk and annulus will produce a 1/4 cycle phase shift between them,

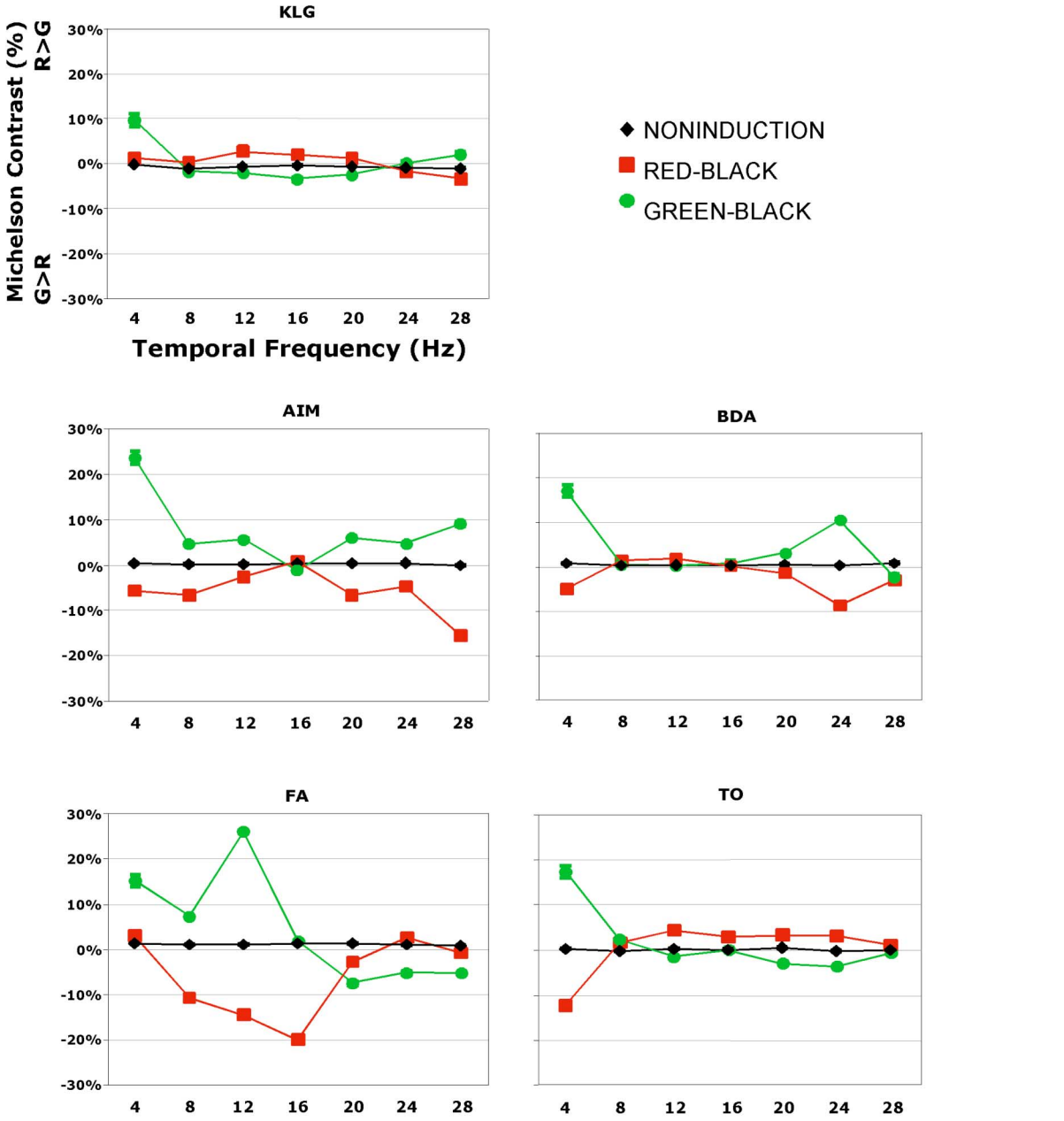

Fig. 2. (Color online) HFP data from Experiment 1. Plotted for each of the five subjects are HFP equality settings as a function of temporal frequency, for one noninduction condition (diamonds) and two induction conditions: red–black (squares) and green–black (circles). Equality settings are presented in terms of luminance contrast between the red and the green ($[Lum_{red} - Lum_{green}]/[Lum_{red} + Lum_{green}]$), with zero denoting photometric equiluminance (V_λ), positive values denoting red-more-luminous-than-green and negative values denoting green-more-luminous-than-red. Error bars, often smaller than the symbols, represent ±1 SEM (standard error of the mean).

which will result in no effect of the annulus (since the time-average luminance of the annulus during the processing of both the red and green disks will be gray). At some even higher temporal frequency, the response lag between the processing of the disk and annulus will produce a 1/2 cycle phase shift between them. This will produce a reversal in the psychophysically measured induction effect, which will masquerade as an assimilation effect. This account can explain the systematic variation in effects of the black/white annulus as temporal frequency is increased. Note that in two of three subjects who showed a reversal effect, as the temporal frequency was increased even further the reversal effect either went away (subject TO), which suggests a 3/4 cycle phase shift, or reversed again to produce results in the predicted direction for induction (subject KLG), which suggests a full cycle phase shift. Even in subjects who did not show a clear reversal effect (subjects AIM and BDA), there was a loss of the induction effect, followed by a re-emergence, as temporal frequency was increased. And, for subject BDA, at even higher temporal frequencies (around 28 Hz), the induction effect disappeared again, which suggests a one and one fourth cycle phase shift between the processing of the alternating red/green disk and the alternating black/

white disk.

In sum, the results from Experiment 1 demonstrate induction effects of a black/white annulus on HFP equality settings. However, the effects of the black/white annulus varied with temporal frequency and inconsistently from one subject to another (presumably because the degree of response lag varies across subjects). We return to possible neural substrates for this result in Section 4. The exception to this were data obtained at 4 Hz, where all subjects showed the same pattern of results, i.e., induction effects in the predicted direction. For this reason, Experiments 2 and 3 were conducted at frequencies of 4 Hz or lower.

B. Experiment 2: Comparing the Magnitude of Induction Effects on HFP versus HBM Settings

In this experiment, we used the same stimuli as in Experiment 1 but compared the magnitude of induction effects on HFP versus HBM equality settings. Group mean equality settings (obtained at 4 Hz for both HFP and HBM and at 0.5 Hz for HBM) are plotted in Fig. 3A in terms of luminance contrast between the red and green (error bars denote ±1 SEM). Data are presented separately for the noninduction condition (diamonds) and the two induction conditions that contained the black/white annulus: red–black (squares) and green–black (circles).

These data reveal that in the noninduction condition, equality settings (at both temporal frequencies) were statistically indistinguishable [$F(2,8)=1.229, p=0.3424$], and all values were close to photometric equiluminance (V_λ). With regard to induction effects, these data show that for all three task/temporal frequency conditions (HFP at 4 Hz, HBM at 4 and 0.5 Hz), the effects of the black/white annulus were in the predicted direction. That is, the green–black condition (circles) yielded red/green equality settings that were more positive than those observed for the noninduction condition (diamonds), while the red–black condition (squares) yielded settings that were less positive. To evaluate more directly the effects of the black/white annulus on red/green equality settings, we plot collapsed induction effects in Fig. 3B. The induction effect was calculated as the absolute difference in luminance contrast between the red/green setting in the induction condition (red–black or green–black) and the non–induction condition. Because the magnitude of the

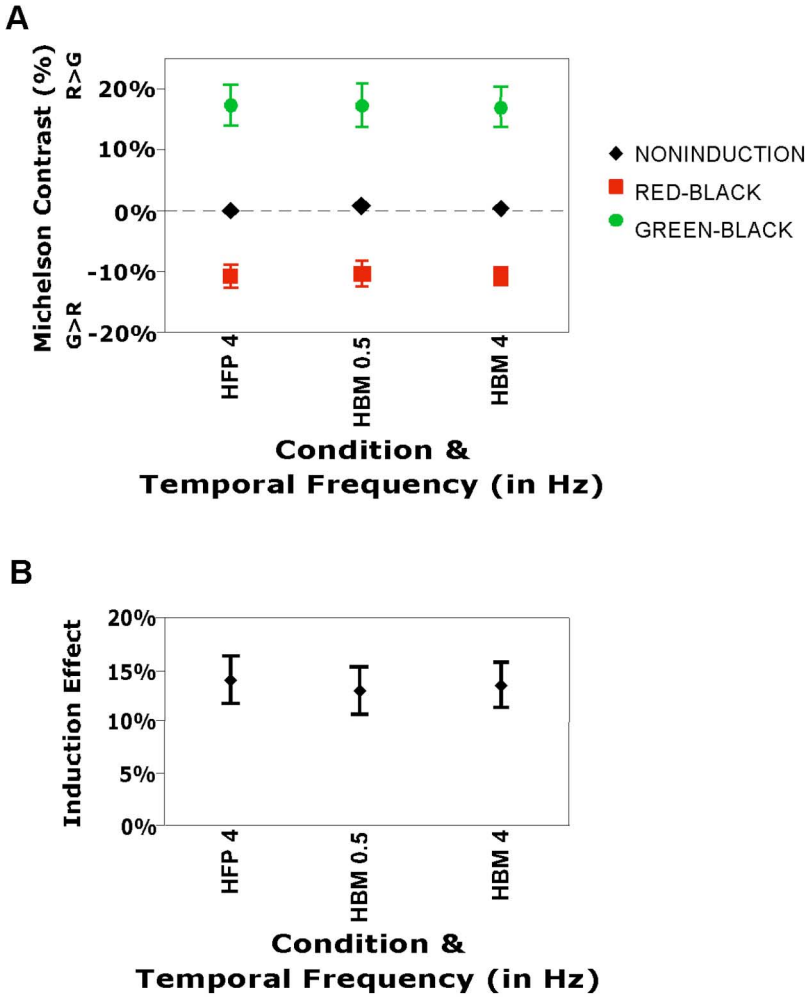

Fig. 3. (Color online) HFP and HBM Data from Experiment 2. A. Group mean HFP (at 4 Hz) and HBM equality settings (at 0.5 and 4 Hz) are plotted in terms of red/green luminance contrast for one noninduction condition (diamonds) and two induction conditions: red–black (squares) and green–black (circles). B. Group mean induction effects are plotted for the different conditions (see text for details). Error bars represent ±1 SEM.

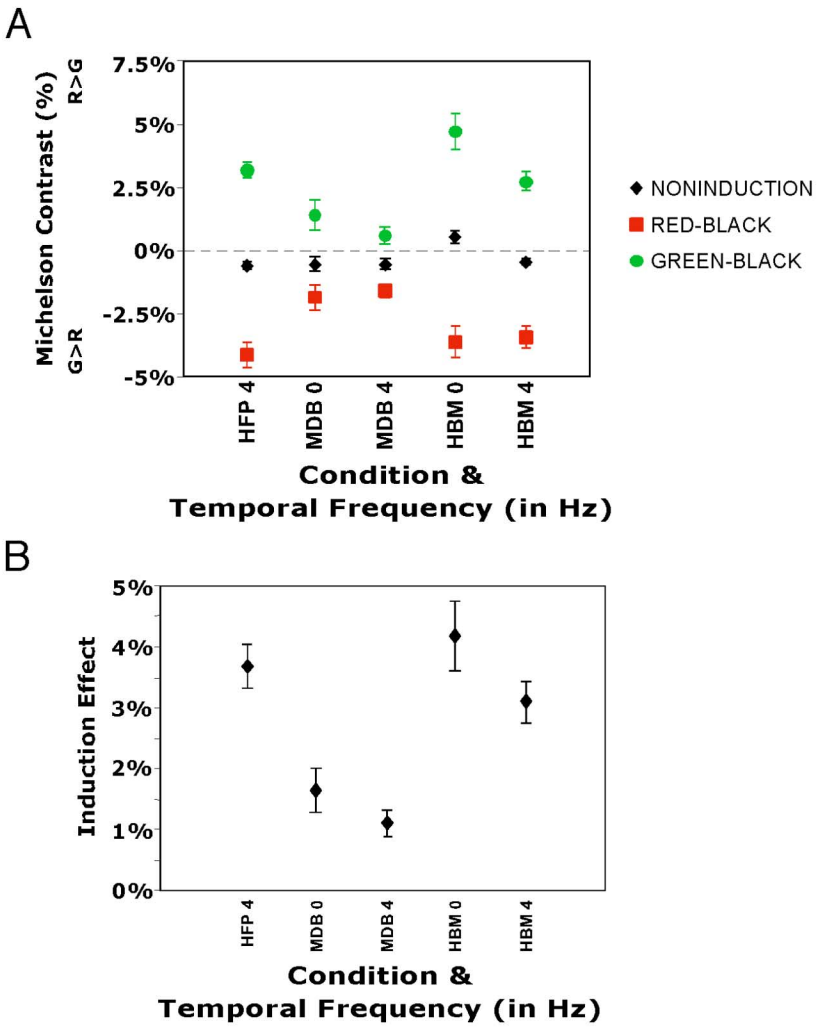

Fig. 4. (Color online) HFP, HBM, and MDB data from Experiment 3. A. Group mean HFP (at 4 Hz), HBM (at 0 and 4 Hz), and MDB (at 0 and 4 Hz) equality settings are plotted in terms of red/green luminance contrast for one noninduction condition (diamonds) and two induction conditions: red–black (squares) and green–black (circles). B. Group mean induction effects are plotted for the different conditions (see text for details). Error bars represent ±1 SEM.

induction effects were found to be statistically indistinguishable for the red–black versus green–black induction conditions (t-test p-values were all >0.12), data for the two were averaged for each subject before averaging across subjects. For all three task/temporal frequency conditions (HFP at 4 Hz, HBM at 4 and 0.5 Hz), induction effects were significant, as evidenced by values significantly greater than zero ($p \leq 0.0027$ for all conditions, 1-tailed t-test, which passed the Bonferroni corrected α of 0.0167, i.e., 0.05/3 conditions). In addition, there was no significant difference in the magnitude of induction effect across the one HFP and two HBM conditions [$F(2,8) = 0.297, p = 0.7508$].

These results from Experiment 2 replicate the results from Experiment 1, demonstrating induction effects of a black/white annulus on HFP equality settings. In addition, these results show that the magnitude of induction effects are statistically indistinguishable on the HBM versus HFP tasks. We return to possible explanations for these results in Section 4.

C. Experiment 3: Comparing the Magnitude of Induction Effects on HFP, MDB, and HBM Settings

In this experiment, we added another measure for equality, MDB. Owing to the nature of the MDB task, we needed to use stimuli containing red/green borders, and therefore this experiment employed red/green gratings (see Section 2 and Fig. 1B). Group mean HFP settings (obtained at 4 Hz), MDB settings (obtained at 4 and 0 Hz), and HBM settings (obtained at 4 and 0 Hz) are plotted in Fig. 4A (error bars denote ±1 SEM). Data are presented separately for the noninduction condition (diamonds) and the two induction conditions: red–black (squares), green–black (circles). In the noninduction condition, a significant effect of condition was found [$F(4,84) = 10.745, p = 0.0001$]. Post-hoc analyses revealed that this was driven by a difference between HBM settings at 0 Hz and all other settings. With regard to induction effects, the effects of the black/white annulus were in the predicted direction, i.e., the green–black condition (circles) yielded red/green equality settings that were more positive than

those observed for the noninduction condition (diamonds), while the red-black condition (squares) yielded settings that were less positive.

To evaluate more directly the effects of the black/white annulus on red/green equality settings, we plot induction effects in Fig. 4B. Because induction effects were found to be statistically indistinguishable for the red–black versus green–black induction conditions (t-test p-values were all >0.27), data for the two were averaged for each subject before averaging across subjects. For all five task/temporal frequency conditions (HFP at 4 Hz, HBM at 4 and 0 Hz, MDB at 4 and 0 Hz), induction effects were significant, as evidenced by values significantly greater than zero ($p<0.00002$ for all conditions, 1-tailed t-tests, which passed the Bonferroni corrected α of 0.01, i.e., 0.05/5 conditions). These significant induction effects for HFP and HBM settings replicate those observed in Experiments 1 and 2. Interestingly, however, the overall magnitude of the induction effects was much smaller in Experiment 3 than in Experiments 1 and 2, by a factor of about 3. This difference is likely due to differences in spatial structure (or dominant spatial frequency) between the experiments, since previous studies have shown that spatial parameters can affect the magnitude of induction.[4,18] That is, Experiment 3 used gratings of 0.5 c/deg (i.e., each stripe was 1° in width), while Experiments 1 and 2 used a disk/annulus of 3.5° and 6° diameter, respectively. In addition, in Experiments 1 and 2, the red and green disks were fully surrounded by the annulus (black or white), while in Experiment 3, each red and green stripe of the grating was flanked by a black or white stripe only at the top and bottom.

The results from Experiment 3 revealed no significant difference between the magnitude of induction effects in the one HFP and two HBM conditions [$F(2,42)=3.185, p=0.0515$], a finding that is in line with those from Experiment 2. However, the magnitudes of the induction effects for the MDB task were significantly smaller than those obtained on both the HFP and HBM tasks. This was confirmed by collapsing induction effects across the one HFP and two HBM conditions and comparing the result with induction effects collapsed across the two MDB conditions [paired, 1-tailed $t(21)=2.20$, $p=0.00004$]. We return to possible explanations for these results in Section 4.

D. Experiment 3: Correlating the Magnitude of Induction Effects on HFP, MDB, and HBM across Subjects

As a way of addressing whether common or separate mechanisms underlie the induction effects on the different tasks/temporal frequencies, we performed correlation analyses on the magnitude of the induction effect obtained across our 22 subjects in Experiment 3. The logic behind these analyses is that tasks/temporal frequencies for which induction effects are correlated across subjects are likely to be mediated by the same underlying mechanisms, whereas tasks/temporal frequencies for which induction effects are not correlated across subjects are likely to be mediated by separate underlying mechanisms.[19] The results from these analyses are shown in Fig. 5 in a table format. These analyses reveal two main findings. First, there were significant positive correlations (speckled boxes) between the one HFP condition (4 Hz) and the two HBM conditions (4 Hz and 0 Hz), suggesting that the induction effects for these two tasks (and two different frequencies for HBM) are subserved by common underlying mechanisms. Second, the magnitudes of induction effects for HFP and HBM did not correlate positively with those for MDB (at either 0 or 4 Hz), suggesting that induction effects for HFP and HBM are subserved by separate mechanisms than are induction effects for MDB. In fact, MDB induction effects at 0 Hz correlated negatively with HBM induction effects at both 0 and 4 Hz (gray boxes). This negative correlation indicates that there is an inverse relationship between the extent of induction occurring in mechanisms subserving induction on the HBM versus MDB task and perhaps, by transitivity, also between HFP and MDB. We return to possible explanations for this relationship in Section 4.

4. DISCUSSION

Several previous studies have demonstrated brightness induction; i.e., the apparent brightness of a stimulus changes when surrounded by black versus white stimuli. In the current study, we replicated this basic finding by employing HBM, demonstrating significant effects of black/white inducing stimuli on the apparent brightness of red versus green test stimuli. In addition, the current study demonstrated significant induction effects on red/green settings obtained from two other tasks, HFP, and MDB. For these tasks, subjects adjusted the luminance contrast between the red and green stimuli in order to either minimize flicker (HFP) or minimize the salience of a border (MDB). These induction effects observed for HFP and MDB suggest that brightness induction can occur even when subjects are not comparing the apparent brightness of two colors *per se*.

For the remainder of this discussion, we address potential mechanisms underlying our results. Specifically, we address the relative contributions of two of the three color pathways in vision: the L+M (luminance) pathway and the L−M (red/green chromatic) pathway. Note that the contribution from the third color pathway [S−(L+M), or tritan] is discussed only briefly in this section, as the stimuli in the current study were designed to isolate the contribution of the L+M and L−M pathways. We begin by discussing evidence from previous studies suggesting that HFP and MDB settings rely exclusively on the L+M pathway, while HBM settings rely on both L+M and L−M pathways. Note that this discussion will be

	HFP 4 Hz	HBM 0 Hz	HBM 4 Hz	MDB 0 Hz
HBM 0 Hz	0.452*			
HBM 4 Hz	0.621**	0.630**		
MDB 0 Hz	-0.291	-0.451*	-0.447*	
MDB 4 Hz	0.281	0.077	0.168	0.378

Fig. 5. Pearson r values for the magnitude of induction effects across different tasks/temporal frequencies: HFP 4 Hz, HBM 0 Hz, HBM 4 Hz, MDB 0 Hz, and MDB 4 Hz. Significant positive and negative correlations are depicted by speckled and gray boxes, respectively. Single asterisks denote $p<0.05$; double asterisks denote $p<0.01$.

based on data obtained at the *prototypical* temporal frequency for each task (i.e., HFP at 15 Hz, MDB at 0 Hz, and HBM at 0 Hz). We then discuss results from the current study, addressing the degree to which the observed induction effects, some of which were obtained at nontypical temporal frequencies for a given task, rely on the different color pathways.

A. Potential for Rod Contribution

Before proceeding with the discussion, we address the possibility that signals in the rod photoreceptors contributed to our results. The mean luminance employed in the current study (28 cd/m^2) may not have been high enough to saturate the rods completely,[20] and thus our red/green stimuli may have modulated activity in the rods by as much as 15% for red/green stimuli at photometric equiluminance. (This value was obtained by convolving the spectral radiance of the red phase of our stimuli with the scotopic spectral sensitivity. This value was subtracted from the value calculated from the green phase of the stimulus, the difference of which was then divided by the sum of the two.) However, at least for red/green settings obtained in the *noninduction* conditions of the current study, our results suggest that the rod contribution was minimal, if not absent, for two reasons. First, if rods contributed, red/green settings should have been biased away from photometric equiluminance (specifically, toward needing more red to match the green). This was not the case for any Experiment, 1, 2, or 3 (see diamonds in Fig. 2–4). Second, if rods contributed to red/green settings, their influence should have fallen off substantially with increasing temporal frequency, with the result that red/green settings would vary with temporal frequency.[21] Contrary to this prediction, red/green settings obtained from the HFP task in Experiment 1 were clearly constant across a large range of temporal frequencies (4 to 28 Hz).

Although it is more difficult to determine whether the rods were involved in the induction effects of the current study, we would deem it unlikely given their negligible effects on red/green settings in the absence of inducing stimuli. More importantly, we would argue that rod contribution (had it existed) does not bear on the issue of which postreceptoral pathways, L+M, L−M, or both, mediate our results, since neurophysiological studies have shown that rods provide input to both pathways.[22,23] Given the intermingling of rod and cone signals at the postreceptoral level, it is likely that both rod and cone signals can contribute to induction effects revealed psychophysically. This possibility is supported by recent findings that a surround stimulus that isolates the rods can alter the apparent brightness of a center stimulus that isolates the cones (and vice versa).[24]

B. Color Pathways Underlying HFP, MDB, and HBM Settings: Evidence from Previous Literature

In this subsection, we discuss which color pathways (L+M versus L−M) are thought to underlie red/green settings obtained with HFP, MDB, and HBM under the typical testing conditions employed for each task. For all three, we refer to the red/green settings as "equality settings" since the assumption is that a setting reflects an equal neural response elicited by the red and by the green phases of the stimulus within the color pathway(s) that are involved in that task.

There are three main lines of evidence suggesting that HFP at relatively high temporal frequencies (~15 Hz) relies exclusively on signals in the L+M pathway. First, the spectral sensitivity function (also referred to as the luminous efficiency function, or V_λ) produced by using HFP to match monochromatic lights across the visible spectrum to a reference light (often white) is well modeled by a weighted sum of the L- and M-cone spectra.[25,26] Second, when HFP is conducted at 15 Hz, the conscious perception of "color" is obliterated, i.e., the stimulus appears as gray flicker. Because it is the L−M, and not the L+M, pathway that is thought to signal color *per se* ("red" or "green"), this result suggests that the L−M pathway is not involved in HFP settings at 15 Hz. Third, neurophysiological studies in macaques (whose visual systems are very similar to that of humans) have concluded that phasic retinal ganglion cells (which receive L+M input and are thus considered the neural substrate for the L+M color pathway), and not tonic retinal ganglion cells (which receive L−M input and are thus considered the neural substrate for the L−M color pathway), underlie human HFP settings.[16] Analogous to minimizing flicker in HFP, Lee *et al.*[16] measured the luminance of a monochromatic light necessary to minimize neural response when this light was alternated (at 10 Hz) with a reference light. Taken across wavelengths, this yields the spectral sensitivity curve of the neuron. Phasic cells yielded clear minima and yielded spectral sensitivity curves that mirrored those obtained psychophysically by using HFP in humans. By contrast, tonic cells did not yield clear response minima at any relative radiance of the test and reference light. Thus their responses did not correlate with, and were deemed unlikely to account for, HFP settings revealed psychophysically.

In addition to the fact that tonic (L−M) cell responses at 10 Hz do not correlate with HFP settings, there is another reason why tonic cell responses are thought unlikely to contribute to HFP settings, at least for HFP conducted at relatively high temporal frequencies. It is believed that high-temporal-frequency tonic cell signals are lost downstream because they pass through a stringent temporal filter at the cortical level (corner frequency ~5 Hz, whereas the signals from phasic cells pass through a cortical temporal filter with a much higher corner frequency, ~20 Hz[27,28]). Where in visual cortex this filtering occurs is not clearly known. One study has shown that some chromatically opponent (L−M) cells in V1 can still follow high temporal frequencies.[29] Thus the filtering might occur past V1, yet at an early enough stage of processing that does not reach conscious perception. Also note that this temporal filtering of tonic cell signals presumably explains why the colors of a flickering stimulus are not perceivable at high temporal frequencies (see above).

Like HFP at 15 Hz, MDB (which is typically performed on static, 0 Hz, stimuli) is thought to rely exclusively on signals in the L+M pathway. This is because, like HFP, the V_λ spectral sensitivity curve yielded by MDB at 0 Hz can be modeled by a weighted sum of the L- and M-cone

spectra. That is, HFP settings at 15 Hz and MDB settings at 0 Hz yield identical V_λ spectral sensitivity curves.[30] Also, like the neural data described above for HFP settings, neurophysiological studies in macaques have demonstrated that phasic (L+M) retinal ganglion cells yield clear response minima to chromatic borders at relative intensities that mirror MDB settings obtained psychophysically in humans.[31] By contrast, tonic (L−M) retinal ganglion cells do not yield clear response minima at any relative intensity of the colors making up the chromatic border, and thus their responses are unlikely to contribute to MDB settings. Together, these data suggest that MDB settings rely on signals in the L+M, and not the L−M, pathway.

In contrast to HFP and MDB, HBM settings (which are typically performed on static, 0 Hz, stimuli) are thought to rely on signals in both the L+M and L−M pathways [as well as the S−(L+M) pathway]. The best known evidence for this notion comes from comparing the spectral sensitivity curve obtained from HFP (i.e., the V_λ curve) with that obtained by using HBM (referred to as the brightness function). The brightness function, although very similar to V_λ, is wider and has a characteristic dip at about 570 nm, known as the Sloan notch. The brightness function can be thought of as the V_λ function (produced by the L+M pathway) over which is added the sensitivity from the L−M and S−(L+M) pathways. The trough of the Sloan notch occurs at a wavelength where L- and M-cones are equally excited, and thus the notch is explained by the fact that the L−M component is zero at this point.[32] That signals in the L−M pathway contribute to HBM settings is also supported by results showing that HBM settings are influenced by chromatic annuli[33,34] and the state of chromatic adaptation.[35] Further, results from several studies that have modeled HBM data by computing the weights of the color pathway inputs support contribution from all three[36–40] (but see Refs. 41–43 for discrepancies regarding whether all pathways contribute). In sum, the HBM brightness function is thought of as a composite of activity in all three color pathways.

C. Which Color Pathways Underlie Induction: L+M, L−M, or Both?

Because brightness settings (such as those obtained in HBM) are thought to rely on signals in both the L+M and the L−M color pathways, it is reasonable to assume that *induction effects* on brightness settings likewise occur within both the L+M and the L−M pathways. However, it is also logically possible that brightness induction relies exclusively on signals within one of these two pathways. To date, two neurophysiological studies have investigated the neural substrate for brightness induction, one in cats[44,45] and one in macaque monkeys.[46] Using achromatic stimuli, these investigators found that the response of some V1 and LGN neurons to stimuli placed in their receptive field is enhanced when flanking stimuli of lower luminance are placed just outside the receptive field (and vice versa, i.e., that responses are diminished when the flanking stimuli are of higher luminance), in a manner that mirrors brightness induction revealed psychophysically. Unfortunately, because the Rossi *et al.*[44,45] studies were performed in cats, who do not possess a chromatically opponent L−M pathway, these neurophysiological data do not allow us to address whether L+M, L−M, or both underlie induction effects. The Kinoshita and Komatsu[46] study, although utilizing monkeys who do possess the L−M pathway, did not address this issue.

Below, we discuss how the psychophysical data of the current study, which employed tasks thought to rely selectively on responses in the L+M pathway or on both the L+M and the L−M pathways, might be used to answer the question of which color pathways are involved in induction effects.

D. Evidence for Induction in the L+M Pathway

In Experiment 1 of the current study, we observed induction effects for HFP settings over a range of temporal frequencies (4–28 Hz), which included those typically employed in HFP experiments (~15 Hz). Because responses in the L−M pathway should be obliterated (as a result of temporal filtering in cortex) above at least 15 Hz, our results provide evidence that induction effects can occur exclusively within the L+M pathway. In addition, Experiment 1 showed that induction effects waned and waxed as temporal frequency was increased. As discussed in Section 3, we believe that this temporal frequency effect reflects the existence of a response lag between the processing of the alternating red/green disk stimulus and the alternating black/white annulus. It is likely that the response lag results from the fact that the red/green disk in our study was of much lower contrast (3.35% cone contrast) than that of the black/white annulus (100% cone contrast), since previous neurophysiological studies have shown that response latencies in visual areas (such as V1) decrease with increasing stimulus contrast.[47,48] This effect of contrast on response latency has also been reported for magnocellular cells (which receive input from phasic retinal ganglion cells) in primate LGN.[49] This result is particularly relevant given that magnocellular cells, like phasic retinal ganglion cells (see above), are considered part of the neural substrate for the L+M color pathway. That is, the known existence of responses lags in the L+M pathway is consistent with the notion that the effect of temporal frequency on the induction effect is occurring in the L+M pathway.

Like the current study, previous studies have reported that the magnitude of brightness induction decreases with increasing temporal frequency.[45,50–54] However, unlike Experiment 1 of the current study, in which red/green settings were made using the HFP (minimal flicker) task, these previous studies used *achromatic* stimuli in brightness matching tasks. In addition, these previous studies tested only up to the point at which induction "disappears" (4–10 Hz, depending on the study). None of these studies went to higher frequencies, where they, too, might have revealed the reversal and/or re-emergence of the induction effect observed in the current study. Also unlike the current study, the previous studies did not interpret the observed effects of temporal frequency on induction in terms of response lags between the processing of the inducer and the inducee. For example, Rossi and Paradiso[52] accounted for decreasing induction effects with increasing temporal frequency by proposing that induction effects are based on a filling-in process that takes time. They

suggested that the induction effect of the annulus begins at the border between the disk and annulus, spreading over time to affect the entire disk. At higher temporal frequencies, they suggested, there is not enough time for the filling-in process to be completed, and thus the induction effect is diminished. This explanation, however, cannot account for the results of Experiment 1 of the current study, where induction effects re-emerged as temporal frequency was increased further.

E. Evidence for Induction in the L−M Pathway

Although none of the tasks in the current study were designed to isolate the L−M pathway, we might be able to estimate the degree of induction occurring in the L−M pathway by comparing the magnitude of induction produced in a task that relies only on the L+M pathway with the magnitude of induction produced in a task that relies on both the L+M and the L−M pathways. Here the assumption is that induction effects within the L+M and, the L−M pathways are summed, so that the magnitude of induction effect for a task that relies on both pathways is predicted to be larger than the magnitude of induction effect for a task that relies on just the L+M pathway. On the basis of data from previous studies (see Subsection 4.B, above), the HFP/MDB and HBM tasks performed in Experiments 2 and 3 of the current study would seem to fulfill these roles. However, the assumption that HFP relies exclusively on the L+M pathway may require that the HFP stimulus alternate at a high enough temporal frequency to obliterate responses generated in the L−M pathway (by temporal filtering at the cortical level; see above). At lower temporal frequencies, such as those employed in Experiments 2 and 3 (i.e., 4 Hz), L−M signals could contribute to HFP settings. Despite the lack of neurophysioloigcal data bearing on this question (i.e., neural correlates for HFP settings have been investigated using only relatively high, 10 Hz, stimuli; see above), results from several previous psychophysical studies (including from our own laboratory) do seem to suggest that HFP settings at 4 Hz rely on responses in *both* the L+M and the L−M pathways.[9,15,35] Presumably, these psychophysical HFP settings are based on minimizing the difference between the combined responses within the two pathways to the red versus the green phase of the stimulus. On the basis of these previous studies, we continue with our discussion of the HFP data obtained in Experiments 2 and 3 of the current study with the assumption that HFP at 4 Hz invokes both L+M and L−M pathways.

Given that HFP (at 4 Hz) relies on both the L+M and the L−M pathways, and that the same is true for HBM (at 0 and 4 Hz), and if we assume that induction effects for a given task occur within the pathway(s) that mediates the tasks themselves, it might come as no surprise that the magnitude of the induction effect for HFP and HBM settings were the same in Experiments 2 and 3. In addition, given that induction effects sum between the L+M and L−M pathways, and given that induction effects for MDB occur only in the L+M pathway (which is thought to be the case; see above), this could explain why, in Experiment 3, the magnitude of induction effects for the MDB task were significantly smaller than those for the HFP and HBM tasks. In sum, the pattern of results observed in Experiments 2 and 3 suggests that induction effects occur within the L−M pathway and that these effects sum with the induction effects occurring in the L+M pathway.

	strength of induction		overall induction	
Subject	L+M	L-M	HBM	MDB
1	3	6	9	3
2	2	10	12	2
3	7	1	8	7
4	7	2	9	7
5	5	5	10	5
6	3	8	11	3
7	6	2	8	6
8	3	7	10	3
9	6	3	9	6
10	1	7	8	1

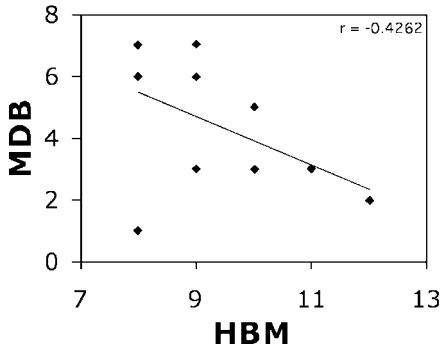

Fig. 6. Hypothetical data producing negative correlation in the magnitude of induction between HBM and MDB. Shown are hypothetical induction values (in arbitrary units) within the L+M and the L−M pathways for ten hypothetical subjects. This model assumes that the overall induction for each subject is the sum of induction within the pathways involved in the task. Accordingly, for HBM the overall induction is the sum of induction in both L+M and L−M. For MDB the overall induction is the induction in the L+M pathway only. To account for our results (larger magnitude of induction for HBM than for MDB settings, and an inverse relationship between the magnitude of induction on the two tasks), we intentionally created an inverse relationship between the magnitude of induction occurring within the L+M and L−M pathways. Plotted below is the resulting negative correlation between the magnitude of induction on the HBM and MDB tasks.

A link between HFP and HBM tasks and a dissociation of both tasks with MDB is also supported by the results from our correlational analyses. Here we found that the magnitude of induction effects on HBM and HFP settings correlated positively with each other, but neither correlated positively with those observed on MDB settings (see Fig. 5). In fact, we found a significant negative correlation between the magnitude of induction effects on MDB (at 0 Hz) and HBM (at 0 and 4 Hz) settings. A model of how this could occur is presented in Fig. 6. Shown are hypothetical induction values (in arbitrary units) within the L+M and the L−M pathways for ten hypothetical subjects. As described above, we assume that the magnitude of induction effects observed for each subject is the sum of the induction effects within the pathways involved in the task. Accordingly, for HBM, the predicted magnitude of induction is the sum of induction in both the L+M and the L−M pathways. For MDB, the predicted magnitude of induction is the induction in the L+M pathway only. Note that in order to account for our results, we intentionally

created an inverse relationship between the amount of induction occurring within the L+M versus the L−M pathway. In line with the results from Experiment 3, this model produces (1) larger induction effects on the HBM task than on the MDB task and (2) a negative correlation between the magnitude of induction on the HBM and MDB tasks. Interestingly, our data therefore suggest that subjects with a greater-than-average amount of induction within the L+M pathway tend to have a lower-than-average amount of induction in the L−M pathway (and vice versa). Further studies will be required for testing this hypothesis.

In sum, the results of these psychophysical experiments demonstrate significant effects of induction on HBM settings and on two other tasks that do not rely on making brightness matches, HFP and MDB. The fact that induction effects were observed for conditions that should eliminate contribution from the L−M pathway (i.e., HFP at high temporal frequencies in Experiment 1 and MDB in Experiment 3) suggest that induction can occur solely within the L+M pathway. In addition, given that HFP and HBM at low temporal frequencies rely on both L+M and L−M pathways, the fact that the magnitudes of induction effects for HFP and HBM (at low temporal frequencies) were comparable to each other yet significantly larger than those observed for MDB (Experiments 2 and 3) suggests additional induction occurring within the L−M pathway.

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REFERENCES

1. M. E. Chevreul, *The Principles of Harmony and Contrast of Colors and Their Applications to the Arts*, Original English Translation 1854; republished in 1967 (Reinhold, 1839).
2. E. G. Heinemann, "Simultaneous brightness induction as a function of inducing- and test-field luminances," J. Exp. Psychol. **50**, 89–96 (1955).
3. E. G. Heinemann, "The relation of apparent brightness to the threshold for differences in luminance," J. Exp. Psychol. **61**, 389–399 (1961).
4. E. W. Yund and J. C. Armington, "Color and brightness contrast effects as a function of spatial variables," Vision Res. **15**, 917–929 (1975).
5. S. K. Shevell, I. Holliday, and P. Whittle, "Two separate neural mechanisms of brightness induction," Vision Res. **32**, 2331–2340 (1992).
6. H. G. Sperling and W. G. Lewis, "Some comparisons between foveal spectral sensitivity data obtained at high brightness and absolute threshold," J. Opt. Soc. Am. **49**, 983–989 (1959).
7. V. C. Smith and J. Pokorny, "Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm," Vision Res. **15**, 161–171 (1975).
8. M. Ikeda and H. Shimozono, "Luminous efficiency functions determined by successive brightness matching," J. Opt. Soc. Am. **68**, 1767–1771 (1978).
9. J. Kremers, H. P. N. Scholl, H. Knau, T. T. J. M. Berendschot, T. Usui, and L. T. Sharpe, "L/M cone ratios in human trichromats assessed by psychophysics, electroretinography, and retinal densitometry," J. Opt. Soc. Am. A **17**, 517–526 (2000).
10. R. M. Boynton and P. K. Kaiser, "Vision: the additivity law made to work for heterochromatic photometry with bipartite fields," Science **161**, 366–368 (1968).
11. A. Eisner and D. I. A. MacLeod, "Blue sensitive cones do not contribute to luminance," J. Opt. Soc. Am. **70**, 121–123 (1980).
12. R. M. Boynton, R. T. Eskew, and C. X. Olson, "Blue cones contribute to border distinctness," Vision Res. **25**, 1349–1352 (1985).
13. A. Stockman, D. I. A. MacLeod, and D. D. DePriest, "The temporal properties of the human short-wave photoreceptors and their associated pathways," Vision Res. **31**, 189–208 (1991).
14. K. L. Gunther and K. R. Dobkins, "Individual differences in chromatic (red/green) contrast sensitivity are constrained by the relative number of L- versus M-cones in the eye," Vision Res. **42**, 1367–1378 (2002).
15. K. R. Dobkins, K. L. Gunther, and D. H. Peterzell, "What covariance mechanisms underlie green/red equiluminance, luminance contrast sensitive and chromatic (green/red) contrast sensitivity?" Vision Res. **40**, 613–628 (2000).
16. B. B. Lee, P. R. Martin, and A. Valberg, "The physiological basis of heterochromatic flicker photometry demonstrated in the ganglion cells of the macaque retina," J. Physiol. (London) **404**, 323–347 (1988).
17. R. M. Boynton and P. K. Kaiser, "Temporal analog of the minimally distinct border," Vision Res. **18**, 111–113 (1978).
18. B. Blakeslee and M. E. McCourt, "Similar mechanisms underlie simultaneous brightness contrast and grating induction," Vision Res. **37**, 2849–2869 (1997).
19. D. H. Peterzell, J. S. Werner, and P. S. Kaplan, "Individual differences in contrast sensitivity functions: longitudinal study of 4-, 6- and 8-month-old human infants," Vision Res. **35**, 961–979 (1995).
20. M. Aguilar and W. S. Stiles, "Saturation of the rod mechanism of the retina at high levels of stimulation," Opt. Acta **1**, 59–65 (1954).
21. J. D. Conner and D. I. A. MacLeod, "Rod photoreceptors detect rapid flicker," Science **195**, 698–699 (1977).
22. T. N. Wiesel and D. H. Hubel, "Spatial and chromatic interactions in the lateral geniculate body of the rhesus monkey," J. Neurophysiol. **29**, 1115–1156 (1966).
23. V. Virsu and B. B. Lee, "Light adaptation in cells of macaque lateral geniculate nucleus and its relation to human light adaptation," J. Neurophysiol. **50**, 864–878 (1983).
24. H. Sun, J. Pokorny, and V. C. Smith, "Rod-cone interactions assessed in inferred magnocellular and parvocellular postreceptoral pathways," J. Vision **1**, 42–54 (2001).
25. H. deVries, "The heredity of the relative numbers of red and green receptors in the human eye," Genetica (The Hague, Neth.) **24**, 199–212 (1948).
26. M. L. Bieber, J. M. Kraft, and J. S. Werner, "Effects of known variations in photopigments on L/M cone ratios estimated from luminous efficiency functions," Vision Res. **38**, 1961–1966 (1998).
27. B. B. Lee, P. R. Martin, and A. Valberg, "Sensitivity of

macaque retinal ganglion cells to chromatic and luminance flicker," J. Physiol. (London) **414**, 223–243 (1989).
28. B. B. Lee, J. Pokorny, V. C. Smith, P. R. Martin, and A. Valberg, "Luminance and chromatic modulation sensitivity of macaque ganglion cells and human observers," J. Opt. Soc. Am. A **7**, 2223–2236 (1990).
29. M. Gur and D. M. Snodderly, "A dissociation between brain activity and perception: chromatically opponent cortical neurons signal chromatic flicker that is not perceived," Vision Res. **37**, 377–382 (1997).
30. G. Wagner and R. M. Boynton, "Comparison of four methods of heterochromatic photometry," J. Opt. Soc. Am. **62**, 1508–1515 (1972).
31. P. K. Kaiser, B. B. Lee, P. R. Martin, and A. Valberg, "The physiological basis of the minimally distinct border demonstrated in the ganglion cells of the macaque retina," J. Physiol. (London) **422**, 153–183 (1990).
32. J. Thornton and E. N. Pugh, Jr., "Red/green color opponency at detection threshold," Science **219**, 191–193 (1983).
33. L. Kerr, "Effect of chromatic contrast on stimulus brightness," Vision Res. **16**, 463–468 (1976).
34. C. Ware, "Evidence for an independent luminance channel," J. Opt. Soc. Am. **73**, 1379–1382 (1983).
35. M. A. Webster and J. D. Mollon, "Contrast adaptation dissociated different measures of luminance efficiency," J. Opt. Soc. Am. A **10**, 1332–1340 (1993).
36. S. L. Guth, N. J. Donley, and R. T. Marrocco, "On luminance additivity and related topics," Vision Res. **9**, 537–575 (1969).
37. S. L. Guth and H. R. Lodge, "Heterochromatic additivity, foveal spectral sensitivity and a new color model," J. Opt. Soc. Am. **63**, 450–462 (1973).
38. H. Yaguchi and M. Ikeda, "Subadditivity and superadditivity in heterochromatic brightness matching," Vision Res. **23**, 1711–1718 (1983).
39. H. Yaguchi and M. Ikeda, "Contribution of opponent-colour channels to brightness," in *Colour Vision*, J. D. Mollon and L. T. Sharpe, eds. (Academic, 1983), pp. 353–360.
40. E. Miyahara, J. Pokorny, and V. C. Smith, "Increment threshold and purity discrimination spectral sensitivities of X-chromosome-linked color defective observers," Vision Res. **36**, 1597–1613 (1996).
41. P. Whittle, "The brightness of coloured flashes on backgrounds of various colours and luminances," Vision Res. **13**, 621–638 (1973).
42. L. E. Marks, "Blue-sensitive cones can mediate brightness," Vision Res. **14**, 1493–1494 (1974).
43. M. Kalloniatis and M. J. Pianta, "L and M cone input into spectral sensitivity functions: a reanalysis," Vision Res. **37**, 799–811 (1997).
44. A. F. Rossi, C. D. Rittenhouse, and M. A. Paradiso, "The representation of brightness in primary visual cortex," Science **273**, 1104–1107 (1996).
45. A. F. Rossi and M. A. Paradiso, "Neural correlates of perceived brightness in the retina, lateral geniculate nucleus, and striate cortex," J. Neurosci. **19**, 6145–6156 (1999).
46. M. Kinoshita and H. Komatsu, "Neural representation of the luminance and brightness of a uniform surface in the Macaque primary visual cortex," J. Neurophysiol. **86**, 2559–2570 (2001).
47. D. G. Albrecht, "Visual cortex neurons in monkey and cat: effect of contrast on the spatial and temporal phase transfer functions," Visual Neurosci. **12**, 1191–1210 (1995).
48. T. J. Gawne, T. W. Kjaer, and B. J. Richmond, "Latency: another potential code for feature binding in striate cortex," J. Neurophysiol. **76**, 1356–1360 (1996).
49. J. B. Levitt, R. A. Schumer, S. M. Sherman, P. D. Spear, and J. A. Movshon, "Visual response properties of neurons in the LGN of normally reared and visually deprived macaque monkeys," J. Neurophysiol. **85**, 2111–2129 (2001).
50. S. Magnussen and A. Glad, "Temporal frequency characteristics of spatial interaction in human vision," Exp. Brain Res. **23**, 519–528 (1975).
51. M. A. Paradiso and S. Hahn, "Filling-in percepts produced by luminance modulation," Vision Res. **36**, 2657–2663 (1996).
52. A. F. Rossi and M. A. Paradiso, "Temporal limits of brightness induction and mechanisms of brightness perception," Vision Res. **36**, 1391–1398 (1996).
53. R. L. DeValois, M. A. Webster, K. K. DeValois, and B. Lingelbach, "Temporal properties of brightness and color induction," Vision Res. **26**, 887–897 (1986).
54. A. G. Shapiro, A. D. D'Antona, J. P. Charles, L. A. Belano, J. B. Smith, and M. Shear-Heyman, "Induced contrast asynchronies," J. Vision **4**, 459–468 (2004).