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Nonlocal interactions in color perception: nonlinear processing of chromatic signals from remote inducers

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Abstract

The perceived color of an object depends on the chromaticity of its immediate background. But color appearance is also influenced by remote chromaticities. To quantify these influences, the effects of remote color fields on the appearance of a fixated 2° test field were measured using a forced-choice method. Changes in the appearance of the test field were induced by chromaticity changes of the background and of 2° color fields not adjacent to the test field. The appearance changes induced by the color of the background corresponded to a fraction of between 0.5 and 0.95 of the cone contrast of the background change, depending on the observer. The magnitude of induction by the background color was modulated on average by 7.6% by chromaticity changes in the remote color fields. Chromaticity changes in the remote fields had virtually no inducing effect when they occured without a change in background color. The spatial range of these chromatic interactions extended over at least 10° from the fovea. They were established within the first few hundred milliseconds after the change of background color and depended only weakly on the number of inducing fields. These results may be interpreted as reflecting rapid chromatic interactions that support robustness of color vision under changing viewing conditions.

Keywords: Color induction; Lateral interactions; Color constancy; Spatial integration; Forced choice

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1. Introduction

Although color vision is intensively studied, the mechanisms underlying color appearance remain elusive. It is well known that the color of an object depends on the chromatic context in which it is seen. However, there is no simple relationship between the chromaticities surrounding an object and its perceived color. The contrast with the immediate background has a strong influence on color appearance (Whittle, 1994). But results from many studies indicate that local contrast only approximately explains the perceived color of an object. An influence of remote chromaticities on color appearance has been reported by Jameson and Hurvich (1961). Walraven (1973) measured how a remote annulus affected the perceived color of a flashed test field and found a distance-independent induction effect even after correcting for possible influences of stray light. In a color matching task, Tiplitz Blackwell and Buchsbaum (1988) found induction effects when a colored surround was not adjacent to the test field. Induction by remote inducers is qualitatively different from induction by adjacent inducers (Wesner & Shevell, 1992). Brenner, Cornelissen, and Nuboer (1989) used remote inducers of different geometries and reported that the magnitude of induction was essentially unrelated to distance, surface area or total edge length of the inducers. Jenness and Shevell (1995) showed that even very sparse chromatic information could alter the appearance of a test field. Nonlocal interactions and nonlinear spatial summation have also been reported for the induction of color contrast (Zaidi, Yoshimi, Flanigan, & Canova, 1992; Singer & D'Zmura, 1994). Recently, Kraft and Brainard (1999) investigated achromatic settings under different illuminants and scene

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compositions and found that both local contrast and nonlocal stimulus features influence color appearance. In this paper, we describe experiments to separate nonlocal from local chromatic interactions and to quantify their spatial and temporal properties. Our goal is to better understand the role of these long-range interactions in color perception and color constancy.

Spatial integration of color signals by long-range neural mechanisms is considered important for the achievement of color constancy (Land & McCann, 1971; Land, 1986a; Hurlbert & Poggio, 1988; Courtney, Finkel, & Buchsbaum, 1995). In order to measure and specify the properties of this integration in human vision, the spatial parameters of the stimuli must be varied systematically. Therefore, we chose to use stimuli in which a test field appears on a homogeneous background and a few additional color fields appear nonadjacent to the test field. Varying the positions of these remote color fields allows the spatial properties of their inducing effect to be probed. Our stimuli had spatial patterns that were more complex than simple center-surround stimuli. They were, however, simpler and more controllable than Mondrian stimuli, in the sense that there was a clear distinction between color fields and background and, in particular, that only the background was adjacent to the test field. Stimulus patterns with such properties have been used in earlier studies to measure color appearance (e.g. Jameson & Hurvich, 1961; Tiplitz Blackwell & Buchsbaum, 1988; Brenner et al., 1989; Brainard & Wandell, 1992; Lucassen & Walraven, 1993; Bäuml, 1994; Jin & Shevell, 1996). In those studies, observers were allowed to scan the stimuli freely. To control the spatial and temporal properties of stimulation, we restricted eye movements by having subjects fixate a target during stimulus presentation. Stimulus durations were chosen in the range of fixation times during natural viewing (Yarbus, 1967). In this way, we obtained the same temporal integration that is effective under free viewing conditions, but avoided spatial integration by eye movements (Cornelissen & Brenner, 1995). In order to test color appearance under these conditions, we chose a forced-choice technique in combination with the method of constant stimuli. Forced-choice methods are well established for psychophysical studies, but so far have only rarely been used to investigate color appearance (Bramwell, 1997). In a comparison between different methods, Bramwell and Hurlbert (1996) observed that, when measured with a forced-choice task, color constancy values are less variable and slightly higher than when determined in an adjustment task. Apart from that, the forced-choice method allows for experimental designs in which viewing conditions can be easily controlled. Making use of these features, we were able to measure the spatial properties of the neural mechanisms involved in color perception.

Our results show that nonlocal induction effects range over at least 10° from the fovea. These effects were measurable in our experiments only when a change in background color was introduced. The magnitude of induction depended only weakly on the total area or number of inducers. These nonlinear properties of nonlocal induction may be a mechanism to solve the contradictory goals of color constancy (Whittle & Challands, 1969). On one hand, they may provide robustness with respect to scene composition under constant illumination. On the other hand, they lead to spatial integration of chromaticities under illumination changes, which may serve to discount the illuminant.

2. Methods

2.1. Subjects

Four naïve subjects and one of the authors participated in the main experiments. Three additional naïve subjects were tested on a subset of the experiments to assess interindividual variability. All subjects had normal or corrected-to-normal visual acuity and were color normal, as assessed with the Farnsworth–Munsell 100-Hue test.

2.2. Apparatus

Stimuli were presented on a calibrated CRT screen (EIZO Nanao T650i or SONY GDM-2000TC). The display was controlled by an 8-bit graphics board (Number Nine Pepper SGT). An additional bit of chromatic resolution was obtained by spatial dithering using minimally different DAC values (see Brenner & Cornelissen (1991) and Webster & Mollon (1994)). A spectrophotometer (PhotoResearch PR-650) was used to periodically calibrate the display and verify the chromaticities in the stimulus patterns. Stability of chromaticities over the time of the experiments was within measurement accuracy.

2.3. Stimuli

2.3.1. Spatial pattern

The stimuli were composed of homogeneous 2° square color fields on a homogeneous 32 × 24° background. One of the color fields, the ‘test field’, was presented in the center of the display. Other square color fields (‘remote fields’) were placed in a symmetrical fashion at certain distances around the test field (see Fig. 1 for an example). Four black dots (size 3 min of arc) marked the central 1° of the test field, to indicate the fixation target. These dots were continuously visible throughout the trial.

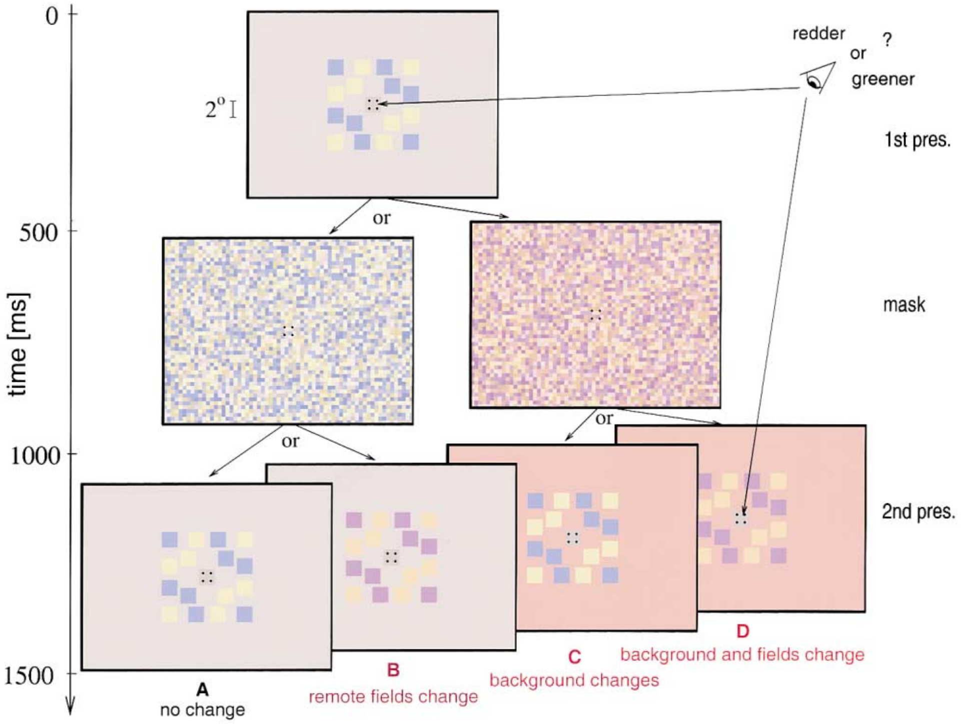

Fig. 1. Schematic of stimulus sequence, with time running from top to bottom in 500 ms intervals. The possible stimulus patterns on the screen are shown for each interval. Patterns varied spatially in luminance and along a blue–yellow axis, temporal color variations were along a red–green axis. The colors shown in the figure are only approximations for illustration. See text for details of the actual stimulus colors. Color changes in the test field are not shown in the figure.

2.3.2. *Colors*

Colors were specified by cone contrast on the basis of the cone fundamentals proposed by Stockman, MacLeod and Johnson (1993) relative to the neutral background. Cone contrast was defined as the square root of the sum of squared contrasts in the long (L), medium (M) and short-wavelength (S) selective cones:

$$c_c = \sqrt{\left(\frac{\Delta L}{L}\right)^2 + \left(\frac{\Delta M}{M}\right)^2 + \left(\frac{\Delta S}{S}\right)^2} \qquad (1)$$

The colors used for each of the stimulus patterns varied in luminance and also in color along a blue–yellow axis with respect to the neutral background. The luminance of the homogeneous neutral gray background (CIE $(x, y) = (0.321, 0.337)$) was 44.8 cd^{-1} m^{-2}. The test field was of slightly lower luminance (Michelson luminance contrast -7.5% relative to the background), the remote fields' luminances were slightly higher ($+3.4\%$ relative to the background). The small luminance differences were chosen to provide for the same contrast sign relations between the stimulus elements for all subjects, regardless of interindividual variability. Bergström and Derefeldt (1975) had reported slightly larger induction effects for brighter than darker inducers. However, during pilot experiments, we had observed no clear differences when reversing the contrast signs for our stimulus conditions.

At the beginning of each trial, the chromaticity of the test field was the same as that of the background, while the colors of the remote fields differed from this color along a blue–yellow axis. Half of the remote fields were blue (S-cone contrast $+0.2$, with respect to the background chromaticity) half were yellow (S-cone contrast -0.2) In each trial, this stimulus pattern was presented twice. Between the first and the second presentation, the colors of background, remote fields and test field could change. These temporal color changes were along a red–green axis, with constant luminance and constant S-cone excitation, in the direction of increasing L-cone and decreasing M-cone excitation ('red'). Thus, temporal color changes were along chromatic directions orthogonal to the spatial variations in the stimulus patterns, in order to minimize adaptation effects (Gegenfurtner & Kiper, 1992). Background or remote fields changed by either 0 or by a cone contrast of 0.1. Thus, there were four conditions with respect to temporal color changes: (A) No change in either background or remote fields; (B) change in remote fields alone; (C) change in background alone; and (D) change in both background and remote fields. The color change in the test field between first and second presentation was variable in steps of cone contrast 0.005. In an additional experiment (see Section 3), the chromatic directions of spatial and temporal changes were interchanged.

The two stimulus presentations in each trial had to be temporally separated, in order to avoid successive color contrast in the test field. This temporal separation was achieved by displaying a full-screen random-dot pattern between stimulus pattern presentations. In the following, we will use the term 'mask' for this random dot pattern, partly because its purpose was to mask the color change between first and second presentation. The mask consisted of 0.25° color squares. The color of each square was randomly assigned from a set of nine colors, obtained by combining three chromaticities (the chromaticities of background and remote fields of the stimulus pattern) with three luminances (the luminance of the background of the stimulus pattern and 12% higher and lower luminances). The mean chromaticity of the mask matched that of the background of the stimulus in the second presentation. Thus, in the trials where the background color did not change, the mean chromaticity of the mask was a neutral gray, whereas in the trials in which the background color changed to red, its mean chromaticity was red. This allowed, by changing the duration of the mask, testing of color appearance after a variable time of adaptation. These mask durations were between 117 and 2000 ms, a temporal range where memory effects are unlikely to play a role (see Section 4).

2.4. Procedure

The observer sat in a dark room, viewing the display from a distance of 57 cm. Head position was stabilized with a chin rest. Preceding the experiment, the mask pattern whose mean chromaticity was gray, was displayed on the screen and viewed by the observer for 2 min to allow adaptation. In addition, the data from the first 4 min of each experiment were excluded from further analysis.

The observer initiated each trial by pressing a button while fixating the center of the test field. After a delay of 150 ms, the first stimulus pattern, the mask, and the second stimulus pattern were presented in succession, each for 500 ms, as shown in Fig. 1. (Presentation times differed in experiment 3, see below.) After the second stimulus presentation, the gray mask pattern was displayed again and the observer pressed one of two buttons to indicate whether the test field in the second presentation appeared redder (or less green) or greener (or less red) than in the first presentation. Observers were instructed to maintain fixation at the center of the test field throughout the trial and to judge the color in the center of the test field, ignoring everything else in the display. Observers were encouraged to make a small eye movement after each trial, in order to reduce afterimages from the remote fields and the border of the display.

The experiments were performed in daily sessions of 1–1.5 h duration. Each session consisted of nine blocks of 120 trials. Within each block, stimuli representing each of the four color change conditions (A–D) and five different test field color changes were presented in randomized order. The five values for the test field color changes were adjusted between sessions to the new estimate of the subject's individual psychometric function. Each data point in Figs. 3–8 was typically derived from 480 trials. Other stimulus parameters, such as distance and number of remote fields or presentation times, were fixed within each block, but varied from block to block.

2.5. Quantifying appearance changes

For every condition (A–D), the observer's responses for different changes in the test field chromaticities were recorded. The fraction of responses indicating a 'redder' appearance in the second presentation, plotted as a function of actual chromaticity change, shows a transition between 0 and 1 with a sigmoid shape (see Fig. 2). A cumulative Gaussian function was fitted to these data to determine the chromaticity change c_p for which both responses had equal probability. c_p is the cone contrast of the chromaticity change necessary to cancel the perceptual effect of the chromaticity changes in the other stimulus elements. It serves as a measure of the induced change in perceived color. 95% confidence intervals for this parameter are shown as error bars in Figs. 3–8. Estimates of significance of differences based on the χ^2 statistic are given in the text.

3. Results

3.1. Equal changes in background and remote fields

As explained in Section 2, there were four different stimulus conditions: (A) None of the stimulus elements was changed between first and second presentation; (B) only the remote fields were changed; (C) only the background was changed; and (D) background and remote fields were changed. Examples of psychometric functions obtained for the four conditions are shown in Fig. 2. We first compare the results for conditions (A) and (D) below.

Condition A serves as a control, to determine variability and bias of the observer. For all observers, the bias was usually small, independent of stimulus parameters and constant over time over a few weeks. Slight bias differences were found between experiments separated in time by several months. In condition D, relative color changes are equal for all elements of the scene (except the test field). Approximately equal relative color changes would be expected under natural

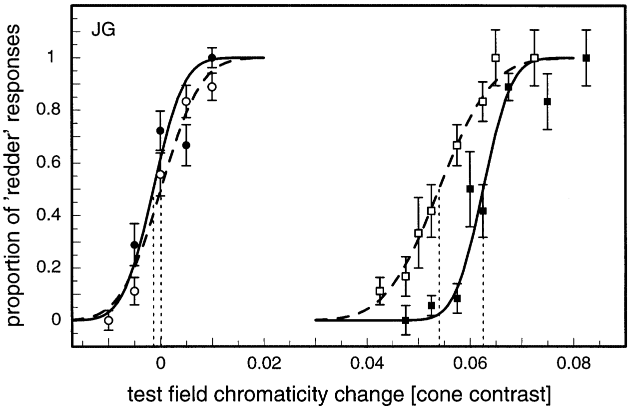

Fig. 2. Example psychometric functions for the four conditions. Subject: JG. Data points indicate the proportions of responses for which the subject reported that the test field looked redder in the second presentation than in the first presentation, as a function of the actual chromaticity change in the test field. Cone contrast of the background change in conditions C and D was 0.1. Filled circles, solid line: Condition A; Open circles, dashed line: Condition B; Open squares, dashed line: Condition C; Filled squares, solid line: Condition D. Error bars denote the expected binomial S.E. given the numbers of trials for each data point, with a slight modification to account for finite variability for probabilities 0 and 1. Lines represent cumulative normal distributions fitted to the data points. Dashed vertical lines indicate the cone contrast values corresponding to a probability of 0.5.

illumination changes (Foster & Nascimento, 1994) and human observers tend to judge illumination changes on the basis of cone ratios (Nascimento & Foster, 1997). Therefore, for this condition, we can compare the results with those of other studies investigating color constancy. If color appearance were determined exclusively by the spectral composition of the test field, then there would be no induced color change. If an observer would disregard the spectral composition of the test field completely and judge the color solely by the color contrast with respect to the other chromaticities in the scene, the induced color change would be as large as the actual change in the display. For our subjects, the induced color changes when background and remote fields changed by a cone contrast of 0.1, were between 0.05 and 0.095, i.e. the induced color changes were between 50 and 95% of the actual color changes. These values are slightly higher than those reported by other studies (Arend & Reeves, 1986; Tiplitz Blackwell & Buchsbaum, 1988; Valberg & Lange-Malecki, 1990; Arend, Reeves, Schirillo, & Goldstein, 1991; Fairchild & Lennie, 1992; Lucassen & Walraven, 1996).

3.2. Influence of the remote fields

3.2.1. General findings

By pairwise comparison of the conditions with and without background changes, we can extract the contribution of the remote color fields on the appearance of the test field.

The results for conditions A and B, which differed only in the color change of the remote fields, were almost identical (see Fig. 2). For some observers, there seemed to be a consistent but small difference between those two conditions. However, in general the differences were not significant at the 95% level for single pairs of data points.

As with condition pair A and B, conditions C and D differed only in the color change of the remote fields. However, the results for these two conditions were significantly different ($P < 0.02$). The appearance change for condition C, where the remote fields did not change, was smaller than for condition D, where the color change of the remote fields were equal to that of the background. Fig. 3 shows the perceived color shifts for condition C (vertical axis) versus condition D (horizontal axis), for eight subjects. The data lie below the diagonal, since perceived color shifts in condition C were always smaller than color shifts in condition D. Quantitatively, there was a considerable degree of variability between observers. The results for condition C were between 1.7 and 21% (median: 7.6%) lower than for condition D. For all subjects, the difference was larger than the difference between conditions A and B. Note that the relative stimulus differences between the conditions are equal for the two pairs. But in conditions A and B, the background was unchanged, whereas in conditions C and D, the background chromaticity changed between the first and second presentation. Changes in the remote fields alone did not affect the appearance of the test field, but modulated appearance changes induced by changes in the background.

3.2.2. Distance of remote fields

In order to investigate the spatial characteristics of induction, we varied the distance between the central test field and the peripheral remote fields. For this experiment, four remote fields were used with the center-to-center distance between test and remote fields varying from 2.6 to 10°. Note that for a distance of 2.8°, the corners of the remote fields coincided with the corners of the test field. For smaller distances, the remote fields were moved off the diagonals, to avoid intersections with the test field.

Fig. 4 shows the results for three observers. The inducing effect of the remote fields with background changes (difference between results for conditions C and D) was still significant ($P < 0.02$) at 10° and only slightly smaller than at 3°. Thus, color fields at a distance of 10° have almost the same inducing effect as color fields in the near vicinity of the test field. For the smallest distances, however, the effect of the remote fields became slightly larger.

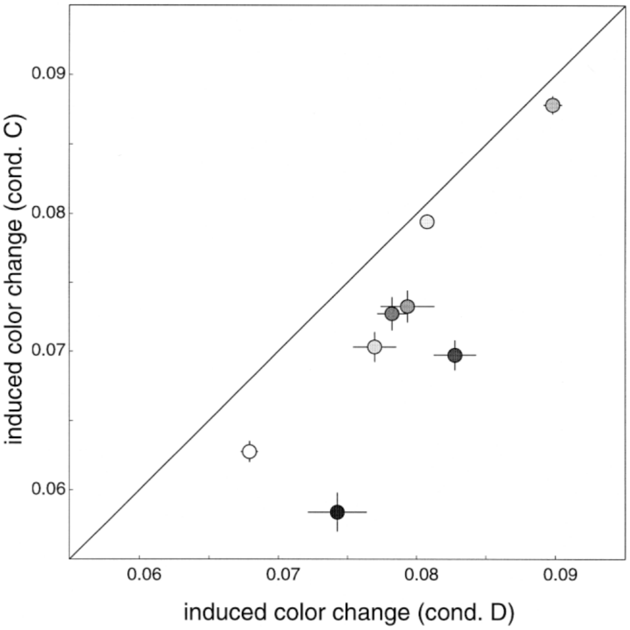

Fig. 3. Comparison of the magnitude of induction for eight subjects. Induced change in test field color for condition C (vertical axis) versus condition D (horizontal axis) Cone contrast of the change in background color was 0.1. Gray values of symbols encode subject, from dark to light: AG, AK, CD, EN, GN, JA, JG, TW. Horizontal and vertical lines for each data point denote 95% confidence intervals. Data were obtained with four remote fields at a distance of 4.5° from the test field.

3.2.3. Number of remote fields

A simple mechanism that could underlie the dependence of remote field induction strength on background color changes is linear spatial summation of chromatic contrast followed by an accelerating nonlinearity (Albrecht & Hamilton, 1982; Sclar, Maunsell, & Lennie, 1990). This would cause the effective gain to be small when there are no large color changes (condition A and B) and to be higher for the cases where the background is changed (conditions C and D). Thus, the same small chromaticity differences (change of remote fields) would lead to a small perceptual difference in one case and to a larger difference in the other case. We tested this hypothesis by varying the number of remote fields. If spatial chromaticities were linearly summed, increasing the number of remote fields should increase the result of this integration, which would lead to a small perceptual difference in the low-gain case (conditions A and B) and to a larger perceptual difference in the high-gain case (conditions C and D). For this experiment, we used stimulus displays with 4, 8, 16 and 148 remote fields. The four remote fields closest to the test field were placed at a distance of 3.5° at the diagonal positions. The next four fields had roughly the same distance from the test field, but were located horizontally and vertically from the test field. In the display with 16 remote fields, the remote fields were arranged in a way shown in the stimulus example of Fig. 1. For the condition with 148 remote fields, the rest of the screen was filled with a regular pattern of remote fields, alternating in color. In all cases, there was a gap of at least 0.5° between neighboring remote fields.

Fig. 5 shows the results for varying the number of remote fields. For conditions A and B, there was no detectable difference for any number of remote fields. The results for condition C indicate some influence of the number of remote fields for two of the three subjects tested, whereas the color shifts in condition D were almost independent of the number of remote fields. Therefore, the difference between color shifts in condition C and D increased slightly with the number of remote fields. To quantify this increase, we fitted a line to the difference of condition C and D as a function of the logarithm of the number of remote fields. This procedure yielded slopes of 0.0012 ± 0.004 (CD), -0.025 ± 0.006 (JG) and -0.020 ± 0.005 (TW). For subjects JG and TW, the perceived color shift depended on the number of remote fields approximately according to a power law with an exponent between 0.2 and 0.25. This is much less than exponents of 2 or 1, which would be expected from a summation of total remote field area or border length, respectively.

3.2.4. Contrast of remote fields

To test the role of the remote fields' contrast, we performed a set of experiments where an extended range of contrasts was used. So far, the contrast of the change in the remote fields was either 0 or 0.1, i.e. as large as the change in background color. We additionally tested contrasts of 0.15, i.e. the change in the remote fields was larger than in the background, and of -0.05, i.e. the remote fields changed in the chromatic direction opposite to the background change. The results are shown in Fig. 6. In the case of increased contrast, the induced color shift was larger, in the case of decreased contrast, the shift was smaller than for the intermediate contrasts. For two of the three subjects, these differences were significant ($P < 0.05$) in all cases. For subject CD, only the decrease in color shift was significant. The finding that the remote fields' influence depends on their contrast is in accordance with the results of Barnes, Wei and Shevell (1999). Furthermore, our results suggest that remote chromatic signals cannot only attenuate, but also enhance the induction from the immediate surround.

3.2.5. Chromatic direction of color changes

To investigate whether the results were specific to color changes in the $+\mathrm{L}-\mathrm{M}$ direction, we performed a set of experiments where the color changes were in the direction of decreasing L-cone contrast ($-L+M$ direction), or in the directions of increasing or decreasing S-cone contrast ($+S$ and $-S$ direction). In the

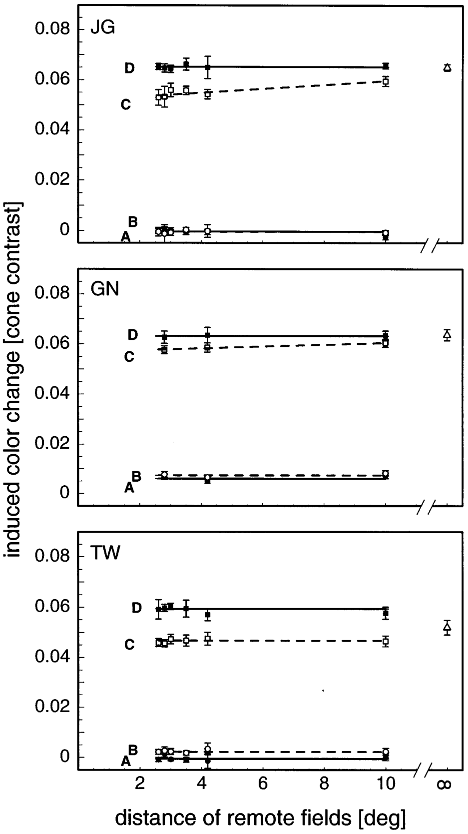

Fig. 4. Effect of spatial separation between test field and remote fields on induction. Four remote fields were used, positioned symmetrically along diagonals through the test field. Plots show data for three subjects. Each plot shows the induced color change for the four conditions. (A) Filled circles, solid line; (B) Open circles, dashed line; (C) Open squares, dashed line; and (D) Filled squares, solid line. Error bars denote 95% confidence intervals for the fits as described in Fig. 2. Lines indicate the mean of values for conditions A, B and D and a linear regression for condition C. The isolated data points (triangles) represent perceived color shifts for background changes without remote color fields present.

latter cases, the spatial pattern varied in luminance and $L-M$ contrast, again to minimally interfere with the temporal color changes. Results for the different chromatic directions are shown in Fig. 7 (conditions C and D only). Note that S-cone contrast in the stimuli was twice as high as $L-M$ contrast, to yield approximately equal saliency of the stimuli. The data in Fig. 7 have been scaled by the contrast of the background color changes. While there were quantitative differences in the induced color shifts for different chromatic directions, qualitatively the effects were similar for two of the three subjects tested. Subject EN, who showed very small effects along the red–green directions, showed clear effects along the blue–yellow directions. A difference between red–green and blue–yellow in remote induction is apparent in the data of Brenner and Cornelissen (1991), where S-cone inducers on average seem to have an effect over a much longer spatial range than $L-M$ inducers. In this case, a possible reason for this difference could be some degree of variability between observers, which would be supported by our findings. A qualitative difference between S- and $L-M$-cone induction was also reported by Barnes et al. (1999), who found that the inducing effect of $L-M$-cone stimulation depends on contrast, whereas for S-cone induction the overall stimulation is the relevant parameter.

3.2.6. Temporal properties

The larger effect of the remote fields for the conditions when the background changed could be due to imperfect chromatic adaptation. The chromatic contrast of the remote fields might influence the time course of adaptation, thus giving rise to different results if the adaptation is not complete. Therefore, we investigated how adaptation duration affects the induction from the remote fields. We varied the duration of the mask between the two stimulus presentations from 117 to 2000 ms. The stimulus patterns were presented for 117 ms in these experiments. Since the mean chromaticity of the mask equalled that of the background in the second presentation, color appearance was measured after a variable time of adaptation to the new background color. The results are shown in Fig. 8. For

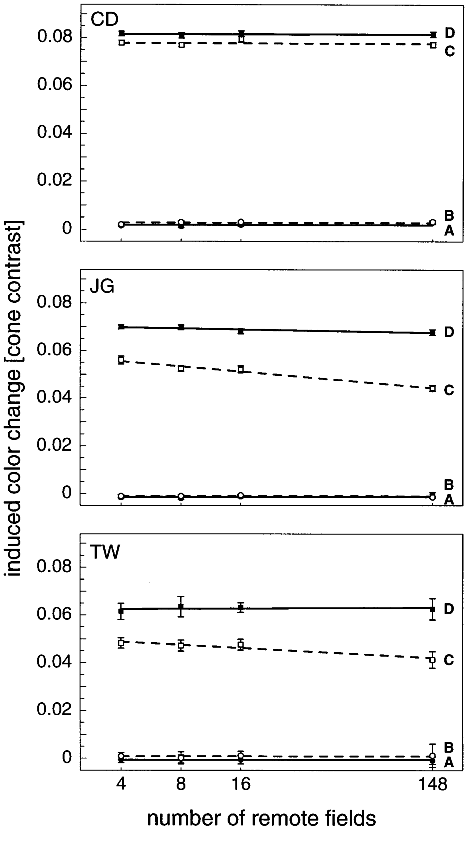

Fig. 5. Dependence of induction on the number of remote fields. Data for three subjects are shown. Symbols as in previous figures. Note that the horizontal axis is log scaled.

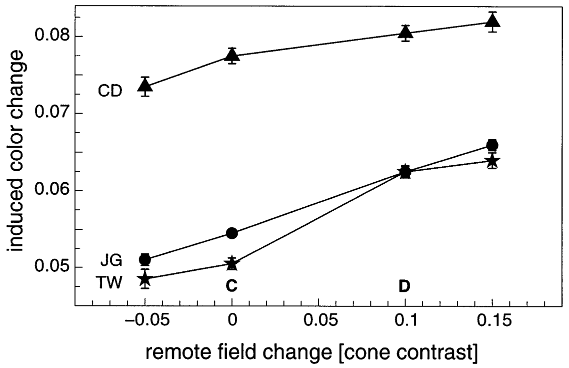

Fig. 6. Dependence of induction on the contrast of remote fields. Induced color changes as a function of the color change in the remote fields. Color change in the background was 0.1, as in conditions C and D in previous figures. Thus, remote field changes of 0 and 0.1 correspond to conditions C and D, respectively. Data for three subjects (CD, JG, TW).

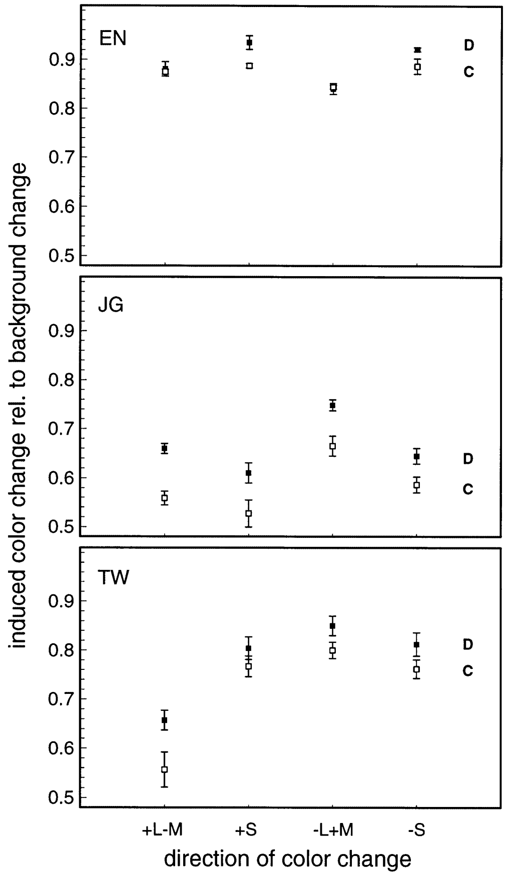

Fig. 7. Induction along different axes in color space. Results of three subject for conditions C and D for color changes in different chromatic directions. $+L-M$: increasing L-, decreasing M-cone stimulation. $+S$: increasing S-cone stimulation. $-L+M$: decreasing L-, increasing M-cone stimulation. $-S$: decreasing S-cone stimulation. For changes along the S axis, cone contrast of background change was 0.2, for changes along the $L-M$ axis, it was 0.1. The data points show induced color changes as fractions of the respective changes in background.

condition D, with color changes in all stimulus elements, the appearance change was almost as strong for mask durations as short as 117 ms, as for durations of 2 s. There was only a slight increase over that temporal range. This finding is consistent with results from studies on the time course of chromatic adaptation (Hayhoe, Benimoff, & Hood, 1987; Fairchild & Reniff, 1995). Chromatic adaptation has a rapid onset with a time constant of the order of hundreds of milliseconds, which leads to 50–60% complete adaptation within the first few seconds. The remaining adaptation has a much longer time constant of several seconds to minutes (see also Valberg, 1974). The induction from the remote fields (difference between conditions C and D) is as strong for the shortest mask durations as for the longest ones. This means that nonlocal induction effects are established within a few hundreds of milliseconds.

3.2.7. Relevance of color changes

In order to investigate the relevance of the color changes in the background for the effect of the remote fields, we did a control experiment in which the adapting background was the red background of the previous experiments. The color of the remote fields could be neutral or red. In this experiment, the task was slightly different. We did not ask subjects to compare two presentations, but rather asked them to indicate after only one presentation whether the test field looked red or green. Under constant adaptation to the red background, we found the ratio between the induced and the actual color change to be higher than 0.9 for all of three subjects tested (JG, GN and TW, data not shown). The effect of the color of the remote fields was largely reduced and almost as small as in the conditions with neutral backgrounds (A and B) in the first experiments. The fact that the remote fields had almost no effect in this case indicates that it is not the color of the background as such that determines the induction effects of the remote fields. This suggests that the temporal changes of colors trigger the induction from the remote fields.

4. Discussion

The experiments were designed to investigate nonlocal lateral interactions between colors in a visual scene. Our methods allowed us to measure the spatial and temporal properties of chromatic induction by remote inducers. We found that remote inducers showed a significant inducing effect only when the color of the background changed. This effect was measurable over distances of at least 10°, was established within a few hundred milliseconds, and was relatively insensitive to variation in the number of inducers.

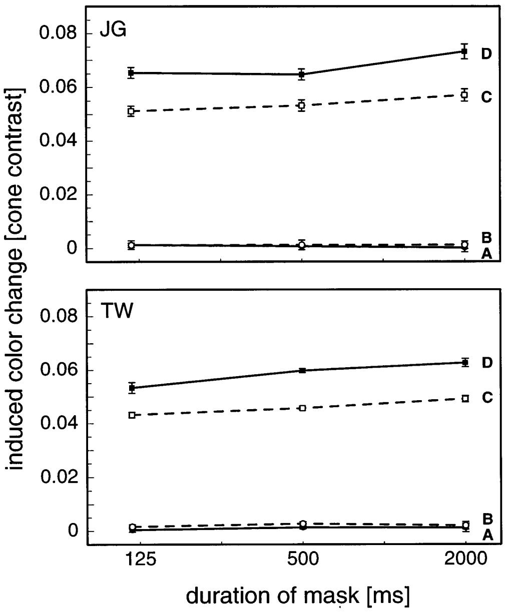

Fig. 8. Dependence of induction on duration of adaptation. Results for conditions A–D for different durations of the mask between stimulus presentations. Data for subjects JG and TW. Symbols as in previous figures. Figs. 3–5. Note that the horizontal axis is log scaled.

Our results are consistent with known properties of induction from remote inducers. The main effect of remote chromatic contrast is not directly on the test field, but rather on the magnitude of induction from the immediate surround of the test (Wesner & Shevell, 1992; Shevell & Wei, 1998). Quantitatively, the effect of remote inducers seems to be smaller than in other experiments. While we find modulation of the effect of the background by up to 21%, the data of other studies often show much stronger attenuation of the induction from the immediate surround (e.g. Shevell & Wei, 1998). There are several possible reasons for this difference. Probably the most important factors are that we used very brief adaptation, relatively large test fields (see Barnes et al., 1999) and low contrasts. As the results by Barnes et al. (1999) and our results show, the effect of remote inducers depends on their contrast. In addition, there is little effect when there is no chromatic contrast between test and immediate surround (Shevell & Wei, 1998). This could explain why we find no effect of remote fields when the background remains neutral. However, our experiment with constant red background suggests that the color change, not only the color itself, is relevant.

We systematically investigated the spatial and temporal properties of remote chromatic induction. We found that increasing the total area occupied by remote fields by increasing their number does not result in a proportional increase in the magnitude of induction. There is very little difference even for a > 30-fold increase in inducer area. A similar result was reported by Jameson & Hurvich (1961). Their explanation was that induction between inducers tends to attenuate their induction strength, such that the resulting induction is the same for increasing numbers of inducers. Walraven (1973) concluded that ‘this enigmatic effect is generated only by the contour(s) of the surround’. However, the effect is similarly independent of contour length. Independence of these spatial parameters was also reported by Brenner et al. (1989). Using a nulling method, Zaidi et al. (1992) found that spatial integration of brightness is linear, whereas spatial integration of chromatic stimuli is nonlinear. Brown and MacLeod (1997) reported results demonstrating that the variance of colors in a scene influences color appearance. The experiments presented here do not allow us to distinguish between effects of overall chromaticity, chromatic contrast and chromatic variance, since these variables were confounded in our stimuli. We can exclude, however, the possibility that induction is determined by the total variance across the visual field, because this would lead to an increase in induction strength when the number of remote color fields is increased, which is contrary to our findings (Fig. 5). The general rule seems to be that the *presence* of a color determines the magnitude of induction, not so much the spatial extent of the color or the frequency of its occurrence in the visual field (Walraven, 1973). This notion is supported by our finding that the distance of the remote fields from the test field plays only a small role and that remote induction effects can be measured over long distances. Previous studies had reported induction for remote inducers with distances up to 6°. Our experiments extend this range to 10°.

Our findings are in accordance with an interpretation of chromatic contrast affecting a gain control for the response to the chromatic contrast at the test field border (Shevell & Wei, 1998). The experiments where the contrast of the remote fields was varied (Fig. 6) demonstrate that this effect can lead not only to an attenuation of induction, but also to an enhancement. Barnes et al. (1999) varied the contrast of a remote checkerboard pattern and found increasing attenuation with increasing contrast of the pattern. In these experiments, the red of the immediate surround corresponded to the red that gave maximal contrast in the checkerboard. From our results, we would expect that if a 'weaker' (i.e. yellowish) red would be used for the surround, the induction could be enhanced, not attenuated, with a high-contrast red in the remote pattern.

With respect to the temporal properties of induction by remote fields, almost the full magnitude was present with presentation times of 117 ms. Thus, induction effects over spatial distances are established relatively fast, consistent with similar findings for color discrimination (Cropper, 1998) and color constancy (Foster, Craven, & Sale, 1992). Our results are consistent with estimates of lateral propagation speed during filling-in (Paradiso & Nakayama, 1991). Studies investigating the time course of chromatic adaptation (Hayhoe et al., 1987; Fairchild & Lennie, 1992; Fairchild & Reniff, 1995) have found a fast onset, leading to $>50\%$ complete adaptation after a few hundreds of milliseconds. It is feasible that the effect studied here has a similar time course and that the slight increase in induction with adaptation time shown in Fig. 8 corresponds to the slow late part of the chromatic adaptation. The rapid onset, together with the fact that relatively high magnitudes of induction were found under restricted fixation, suggests that scanning a scene with eye movements is not a necessary condition for color constancy (Cornelissen & Brenner, 1991, 1995).

Our method, using sequentially presented stimuli, requires comparison with a color that is not visible at the time of comparison. Color memory has usually been investigated for comparatively long delays of around 1 min or longer (Newhall, Burnham, & Clark, 1957; Brainard & Wandell, 1992; Arend, 1993) and it has been shown that strong memory effects occur between a few seconds and a few minutes (Jin & Shevell, 1996; Pèrez-Carpinell, Baldovi, de Fez, & Castro, 1998). However, the time between presentations in our experiments was usually below 1 s, which is in the range of delays that occur even in simultaneous matching. It was possible to compare the test fields without any effort to memorize colors. Furthermore, the control condition had identical stimuli in both presentations and the main interest was in the differences between the results for the four conditions rather than in the absolute effects. Thus, memory effects are unlikely to play a role in our experiments.

The mask pattern that was displayed between stimulus presentations could potentially interfere with the judgments. The pattern was designed such that it had no contrast in the chromatic direction of the color changes, in order to minimize its effect on the judgments (Gegenfurtner & Kiper, 1992). However, if cross-talk between contrast adaptation along the S- and $L-M$ axes existed, the effect of the remote fields might be reduced. In experiments using homogeneous masks (data not shown), subjects had reported seeing afterimages of the test and remote fields during mask presentation. But the results of these experiments did not differ from those reported here.

Color judgments are known to depend on the instructions given to the observer (Arend & Reeves, 1986; Arend et al., 1991). The task of our observers was to compare the colors of the central part of the test field in the two presentations and to make a judgment about their relative positions on a chromatic axis. It was never suggested that the test field could represent a real object. The naïve subjects reported to informal questions after the experiments that they did not view the stimuli as objects. The naïve subjects' results are similar to the results of subject TW, who made hue-saturation judgments. Furthermore, observers had only limited time to view the stimuli and usually responded very quickly. Therefore, we are confident that our subjects made comparisons on the basis of hue and saturation of the test field, not on the basis of its appearance when imagined as a piece of paper. However, the induction effects we found were higher than in other hue-saturation match experiments with similar stimuli (Arend et al., 1991; Arend, 1993; Cornelissen & Brenner, 1995). One reason for this may be the fact that we used relatively small color contrasts. Methodological differences may also play a role. Forced-choice tasks tend to give higher color constancy values (Bramwell & Hurlbert, 1996). Further factors may be the limited presentation time, which tends to enhance induction effects (Wachtler & Wehrhahn, 1996) and absence of large eye movements in our experiments. The latter, however would be expected to decrease magnitude of induction (Cornelissen & Brenner, 1991).

4.1. Relation to cortical color processing

Several interpretations of the results are possible. The magnitude of induction from the remote fields may have to do with whether the test field and remote fields can be perceived as a single figure. For example, if only the background changes (condition C), the non-changing fields (test and remote fields) might be seen as one figure on a changing background, in which case the inducing effect of the background may be weaker. Minor changes in stimuli can lead to measurable differences in perceived lightness if they lead to a different figural interpretation of the stimulus (Adelson, 1993). In the results presented here, the test field and remote fields had the same size, which may be a cue for grouping. Remote induction effects are strongest when the spatial frequency range of the test field and the remote inducers agree (Barnes et al., 1999). The hypothesis of figural grouping can neither be proved nor rejected on the basis of the experiments presented here. What may speak against it, however, is the fact that our stimulus patterns did not present cues for interpretation of the patterns as real objects and that the distance between the test and remote fields had only a weak influence on the results.

Other explanations for the observed effects may be possible that do not require the assumption of figure-ground assignments. Modulatory long-range induction effects have been reported for neurons in the visual cortex. Schein and Desimone (1990) found color selective cells in area V4 of the macaque visual cortex that showed a response modulation by color stimuli outside their classical receptive fields. When stimulated by a color bar in its receptive field center, the response of such a cell was attenuated by a remote bar of the same color several degrees away from the receptive field. The cell did not respond to the remote bar alone. These interactions could be demonstrated even across hemispheres (Desimone, Moran, Schein, & Mishkin, 1993). Analogously, we found that the remote color fields influence the induction from the background (the immediate surround of the test field) and that these interactions span relatively long distances. There is evidence for similar effects on a smaller spatial scale in V1 (Wachtler, Sejnowski, & Albright, 1999). As Shevell and Wei (1998) pointed out, there may be multiple interaction stages at various levels of the visual system. Results of several studies indicate that induction by the immediate surround can be mediated by long-range retinal mechanisms, while induction by non-adjacent inducers is based on cortical mechanisms (Land, Hubel, Livingstone, Perry, & Burns, 1983; Pöppel, 1986; Wehrhahn, Heide, & Oetersen, 1990; Shevell, Holliday, & Whittle, 1992; Hurlbert, Bramwell, Heywood, & Cowey, 1998; Rüttiger, Braun, Gegenfurtner, Petersen, Schönle, & Sharpe, 1999). This suggests a hierarchy of chromatic processing, where each subsequent stage in the visual system contributes to chromatic interactions with increasing complexity.

We favor an interpretation of the results reported here in terms of chromatic interactions that may be advantageous under natural viewing conditions. As Whittle and Challands (1969) have pointed out, color constancy implies two opposing goals. On one hand, the appearance of an object should be invariant under changes in illumination. A proposed solution to this problem involves spatial integration over a wide area (e.g. Land, 1986b; Hurlbert & Poggio, 1988). But on the other hand, color appearance should not be influenced by changes in the chromatic composition of the scene. The interactions demonstrated by our experiments may be a way to achieve both kinds of constancy to some degree. We found that remote chromatic fields have no effect under constant background color. This means that color perception is robust against localized changes in the distribution of chromaticities in the visual field, as long as the illumination conditions do not change. However, when the illumination changes, our visual system has to infer the chromatic properties of the new illuminant from the distribution of chromaticities in the scene. This integration may underlie our results for the spatial properties of non-local induction (Fig. 4). This recalibration of color processing has to be rapid (Fig. 8) because a change in illumination conditions can occur during a saccade, when our gaze shifts, for example between a part of our visual surrounding that is lit by sunlight to a part that lies in the shade.

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