

# “Tilt” in color space: Hue changes induced by chromatic surrounds

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**The perceived color of a chromatic stimulus is influenced by the chromaticity of its surround. To investigate these influences along the dimension of hue, we measured hue changes induced in stimuli of different hues by isoluminant chromatic surrounds. Generally, induced hue changes were directed in color space away from the hue of the inducing surround and depended on the magnitude on the hue difference between stimulus and surround. With increasing difference in hue between stimulus and surround, induced hue changes increased up to a maximum and then decreased for larger differences. This qualitative pattern was similar for different inducers, but quantitatively, induction was weaker along some directions in cone-opponent color space than along other directions. The strongest induction effects were found along an oblique, blue-yellow axis that corresponds to the daylight axis. The overall pattern of the induction effect shows similarities to the well-known tilt effect, where shifts in perceived angle of oriented stimuli are induced by oriented surrounds. This suggests analogous neural representations and similar mechanisms of contextual processing for different visual features such as orientation and color.**

## Introduction

The perceived color of a chromatic stimulus is influenced by the chromaticity of its surround. For example, a gray stimulus patch looks reddish on a green background and greenish on a red background. Generally, a chromatic context changes the appearance of a test stimulus in a direction in color space away from the inducing chromaticity when surround and test field are presented simultaneously (Jameson & Hurvich, 1961;

Krauskopf, Zaidi, & Mandler, 1986; Shevell & Wei, 1998; Valberg, 1974; Valberg & Seim, 1983; Wachtler, Albright, & Sejnowski, 2001; Ware & Cowan, 1982; Webster, Malkoc, Bilson, & Webster, 2002) or when presented in succession (Rinner & Gegenfurtner, 2000; Takahashi & Ejima, 1983; Werner & Walraven, 1982). While for other visual features such contextual influences on stimulus appearance are typically viewed under the aspect of “illusions” (Gilbert & Wiesel, 1990; O’Toole & Wenderoth, 1977), in the realm of color the focus is often on their evident interpretation in terms of computations for color constancy (Gilbert, Hirsch, & Wiesel 1990; Hurlbert, 2003).

Studies on the influence of chromatic surrounds on color appearance often investigated induction on nearly achromatic stimuli or along specific axes in color space (Brainard, Brunt, & Speigle, 1997; Ekroll, Faul, & Niederée, 2004; Kinney, 1962; Krauskopf et al., 1986; Teufel & Wehrhahn, 2004). Much less is known about induction along the dimension of hue (i.e., how the perceived hue of a colored stimulus is influenced by a colored surround). In hue-scaling experiments, Webster et al. (2002) found systematic hue changes induced by chromatic surrounds, indicating color channels that can be tuned to directions intermediate to the cardinal color directions. In these experiments, surround stimuli were composed of two opponent chromaticities each. Their effect thus was a combination of color induction and color contrast induction. Because color contrast induction can have pronounced effects on color appearance (Brown & MacLeod, 1997; Harrar & Viénot, 2005; Hurlbert & Wolf, 2004; Monnier & Shevell, 2004), the effect of a single surround chromaticity on stimulus hue remains unresolved. We therefore systematically measured hue changes induced in stimuli of different chromaticities by uniform chromatic surrounds.

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## Methods

### Subjects

Five subjects, three male and two female, ranging in age from 22 to 44 years, took part in the experiments. Three of the subjects were naive with respect to the purpose of the study, and two subjects were the authors. All observers had normal or corrected-to-normal visual acuity and normal color vision as determined by Landolt C optotypes and Ishihara's Tests for Color Deficiency, respectively. Subjects gave informed consent to participate in the study.

### Stimuli

Stimuli were presented on a 21-inch Sony GDM F520 CRT screen controlled by a Matrox Millennium G450 graphics card. The screen resolution was 1280 × 1024 pixels at a refresh rate of 85 Hz. The display was calibrated using a PhotoResearch (Chatsworth, CA) PR-650 spectroradiometer. Chromaticities of stimuli were defined in an opponent cone-contrast color space (cf. Derrington, Krauskopf, & Lennie 1984; MacLeod & Boynton, 1979), with the two coordinate axes defined by L-M and S-cone contrast, respectively (Wachtler, Sejnowski, & Albright, 2003). In this color space, distance from center corresponds to chroma, and azimuth angle corresponds to hue, with +L-M at 0° azimuth and +S at 90° azimuth. The orthogonal third axis corresponds to luminance contrast. Cone contrasts were defined with respect to a neutral gray (40 cd/m<sup>2</sup>, CIE [x, y] = [0.310, 0.316]). S-cone contrasts were scaled by a factor of 2.6, yielding approximately equally salient stimuli for all hues (Teufel & Wehrhahn, 2000). Individual perceptual isoluminance with respect to the reference gray was determined for 16 stimuli of different hues using heterochromatic flicker photometry (Kaiser & Boynton, 1996). From these data, an isoluminant plane in cone opponent color space was calculated for each subject (Teufel & Wehrhahn, 2000). Stimuli were uniform isoluminant 2° square patches presented in uniform surrounds. Test stimulus chromaticities were regularly spaced along the azimuth of color space and moderately saturated with a cone contrast  $c = 0.2$ , with respect to the gray surround. The neutral gray and eight additional chromaticities, regularly spaced along the azimuth, were used as surrounds. The saturation of chromatic surrounds was slightly lower than for the stimuli ( $c = 0.16$ ) to ensure that stimuli were discernible even in trials in which surround and stimulus had the same hue. The display was divided to form two surrounds, each subtending 11° by 17° of visual angle. One surround was neutral

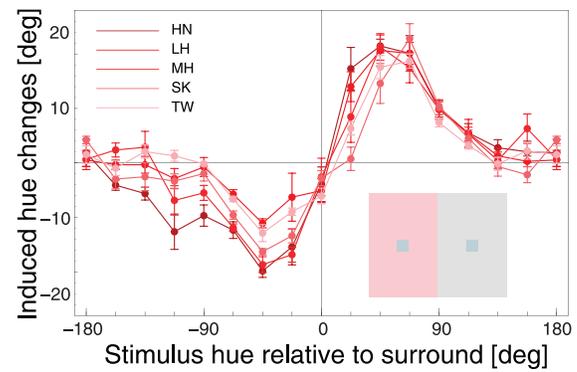


Figure 1. Hue changes induced by a chromatic surround. Data of five subjects for the 0° (+L-M) surround. Data points are averages of six presentations each. Induced hue changes are plotted as a function of the angular distance between the hue (azimuth angle) of the test stimulus and the hue of the chromatic surround. Bars denote standard error. Inset in the lower right corner depicts the display configuration.

gray, and the other was isoluminant with a chromaticity corresponding to one of the surround chromaticities (see Figure 1). Stimuli were presented in the center of each surround.

### Procedure

During an experiment, the subject sat in a dimly lit room and viewed the display binocularly from a distance of 1.14 m. Subjects were instructed to maintain their gaze on the screen but were otherwise not restricted in viewing. Each experiment began with at least 5 min of adaptation to the lighting conditions, during which the subject received instructions and performed test trials that were not included in the analysis. Experimental sessions were organized in blocks of 128 trials, with one presentation of each stimulus condition (16 stimuli presented in each of eight surrounds) in randomized order. In each trial, the subject performed asymmetric matching by adjusting the hue of the stimulus in the neutral surround to match it to the test stimulus in the chromatic surround. Hue adjustment was done by moving a computer mouse, which changed the chromaticity along the azimuth of cone opponent color space. There were no time constraints on adjusting the hue, but on average, a match was performed within about 20 s. The chromatic surround was presented on the right or left half of the screen at random, and the initial hue of the match stimulus was selected randomly. After a subject had indicated that a satisfactory match was achieved by pressing a button, a 20-Hz flickering checkerboard pattern of chromatic squares filling the whole screen was presented for 2 s to prevent afterimages of the stimulus patches. Chromaticity of each 2° × 2°

checkerboard square was selected randomly out of the 16 test stimulus chromaticities. Each observer performed six experimental sessions, resulting in 768 trials.

## Data analysis

Hue changes were determined as the difference in hue angle between the test stimulus displayed in the chromatic surround and the match set by the subject in the gray surround and were plotted as a function of angular distance between the chromaticity of the test stimulus and the chromaticity of the respective surround. To determine peak positions and values of the resulting curves, gamma distribution functions were fitted to the data for interpolation.

## Results

Matches of stimuli in gray surrounds to test stimuli in chromatic surrounds set by the subjects showed systematic differences in chromaticity. Chromatic induction led to a shift in color space of the perceived hue away from the surround hue. Thus, perceptually, the difference between stimulus and surround was enhanced. Figure 1 shows induced hue changes for one of the surround chromaticities ( $0^\circ$ , +L-M). When the hue difference between test stimulus and surround was zero, matches set by subjects were close to the test stimulus chromaticity. With increasing difference between test and surround, subjects' matches showed an increasing induction effect, up to a maximum of about  $18^\circ$  on average for this surround at a distance between stimulus and surround near  $45^\circ$ . Beyond the maximum, the amount of induced hue change decreased to about zero. This indicates that induced hue changes depend on the difference in chromaticity between test and surround. The results for the five subjects were very similar, and the settings of each individual subject were highly reproducible.

For other surround chromaticities, similar results were obtained. Figure 2 shows average induced hue shifts as a function of the angular distance between the chromaticity of the test stimulus and the chromaticity of the surround for all surrounds tested. In all cases, the perceived hue was shifted away from the inducing surround. For all chromatic surrounds, induced shifts depended on the difference in chromaticity between test and surround.

To determine whether the scaling of the S-cone contrast had an influence on the results, we repeated the experiments with two subjects using different S-contrast scaling factors ranging between 2 and 3. Results are shown in Figure 3 for surround hue angles

of  $0^\circ$  (+L-M) and  $90^\circ$  (+S). The curves concur in shape for the different S-contrast scalings. Likewise, data for the other six surround chromaticities were highly consistent (data not shown).

Qualitatively, the curves for different surround hues were similar in shape, but the magnitude of induced hue change varied with surround hue, with maximal induced hue changes between  $7^\circ \pm 2^\circ$  and  $23^\circ \pm 2^\circ$  (Figure 2). Although the positions of the maxima also varied with surround hue, peak values and peak positions of the curves were not significantly correlated ( $r = -0.12 \pm 0.23$ ). The variation of mean induction strength around the hue circle was paralleled by a variation in its interindividual spread, which was larger for stimulus chromaticities for which the inducing effect was large and vice versa.

To analyze the relationship between the magnitude of induction and surround chromaticity, we quantified the induction effect of each surround by averaging the absolute peak values in both directions and plotted the resulting values as a function of azimuth angle of the inducing surround (Figure 4). The eccentricities of the ellipses indicate that, on average, induced shifts in hue angle varied by a factor of about two across surrounds. For all subjects, the data show largest effects for surrounds at an oblique axis in color space and smallest effects for surrounds orthogonal to this axis. We fitted ellipses to the data to determine the surround hue angles that induced the largest shifts. On average, the fits indicated the largest shifts for surround chromaticities at  $23.1^\circ \pm 3.0^\circ$  and  $203.1^\circ \pm 3.0^\circ$  with respect to the horizontal L-M axis. Because induction was tested along the azimuth and therefore orthogonal to the direction of the surround chromaticity, the direction of the largest hue shifts was along an axis with an angle of  $113.1^\circ$ . This axis coincides closely with the axis of variation of natural daylights and the perceptual blue-yellow axis. For example, the unique-blue/unique-yellow direction as determined by the line connecting the chromaticities corresponding to monochromatic lights of 476 nm and 576 nm (Mollon, 2006) has an inclination of  $112^\circ$  in our color space and thus aligns well with the direction of largest induction. This suggests that color induction is not so much related to the cardinal mechanisms of opponency as to the spectral properties of the natural environment and perceptually relevant color space directions.

In our experiments, surrounds were composed of only one chromaticity; therefore, the mean chromaticity of the stimulus display was different for different surrounds. Presentation time was short, with subjects requiring on average 20 s for a match while alternating their gaze between the half of the display with the neutral surround and the half of the display with the chromatic surround. Nevertheless, some degree of chromatic adaptation to the chromatic surround, or

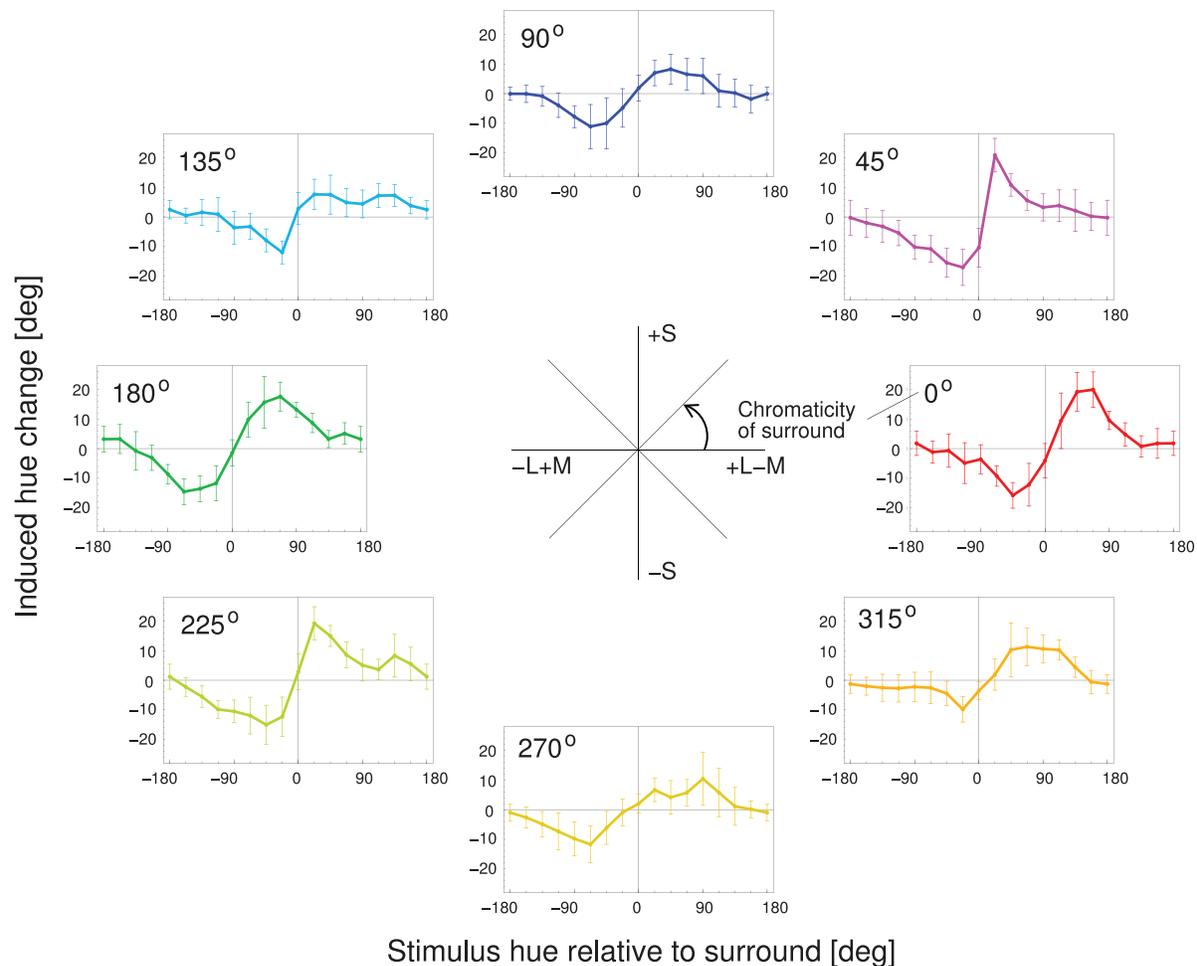


Figure 2. Induced hue changes for eight surround chromaticities. Each panel shows hue shifts induced in the test stimulus as a function of the angular distance between the chromaticity of the test stimulus and the chromaticity of the chromatic surround. Data points are averages across five subjects; bars denote standard deviation. Different panels show results for different surrounds and are plotted in the direction corresponding to surround chromaticity.

contrast adaptation to the contrast between the neutral and the chromatic surround, may have occurred. Under these conditions, a mean shift or compression in the direction of the surround chromaticity (Webster, 1996) would be expected, which in our experiments would appear as hue shifts. We therefore tested to what extent the results could be explained by a translation and compression in color space by fitting corresponding models to the data (Clifford, Wenderoth, & Spehar, 2000). The fits for data obtained with different surrounds indicated contributions of a translation corresponding to between 7% and 25% of the cone contrast of the surround. However, with few exceptions, fits were very poor. Based on the chi-square statistics, only some of the curves for 90° or 270° surrounds yielded acceptable fits. For the other surrounds, the data showed systematic deviations from the models. Overall, the average amplitudes of the residuals for the mean shift model were between 3° and 18° of hue angle and for the combined model of shift

and compression between 2° and 14° of hue angle. These strong deviations indicate that the hue shifts measured in our experiments could not be explained based solely on a translation or compression.

In a previous study, color stimuli in chromatic surrounds similar to those used here have been applied to investigate the tuning properties of single neurons in the primary visual cortex (V1) of awake macaque monkeys (Wachtler et al., 2003). The results showed changes in the chromatic tuning of V1 neurons when test stimuli were presented in chromatic surrounds as compared with achromatic surrounds. To compare those results with the perceptual shifts measured here, we represented the color shifts estimated from the V1 tuning changes and the psychophysically measured color shifts in the same way. Figure 5 shows the average induction effects for six of the test stimuli relative to the inducing surround. Likewise, neural response data, which were measured with various surround chromaticities, were averaged relative to the inducing sur-

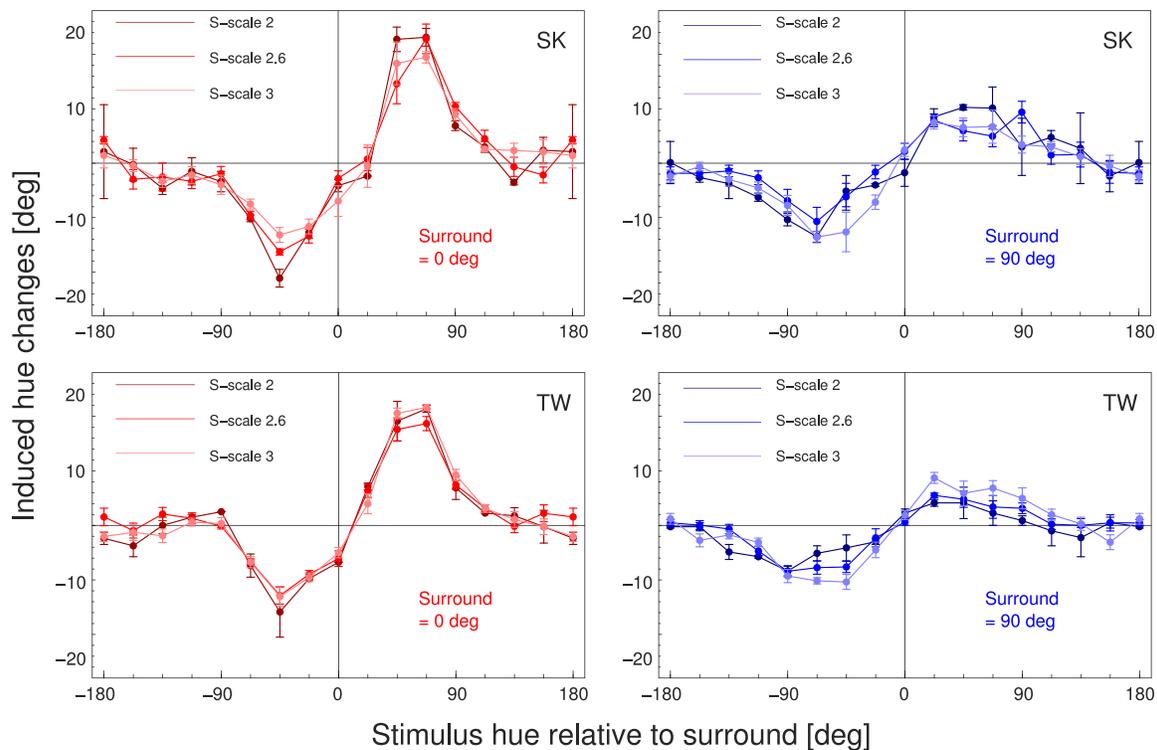


Figure 3. Comparison between different S-contrast scalings. Induced hue changes are plotted as a function of hue difference between test stimulus and surround. Data of two subjects for surround hues of  $0^\circ$  (+L-M, left) and  $90^\circ$  (+S, right) are shown. Different curves show data measured using S-contrast scaling factors of 2, 2.6, and 3, respectively. Error bars denote standard error. The curves for different S-contrast scalings are very similar.

round. Qualitatively, average neural response changes match the effects of color induction measured in human perception under corresponding stimulus conditions, indicating a similar qualitative dependence of induced hue shifts on the difference in chromaticity between stimulus and surround in humans and in monkeys. Data derived from physiology and psychophysics show corresponding shift directions away from the inducing surround. Likewise, for both data sets, induced hue shifts vary systematically with increasing chromatic distance between test stimulus and surround. Quantitatively, hue shifts derived from the neural responses tended to be larger than shifts obtained psychophysically in human observers, which may be due to a slight sampling bias in the neurophysiological experiments (see the Discussion section).

## Discussion

In agreement with previous studies, our results show that induction by a homogeneous, simultaneously presented surround shifts the perceived hue away from the chromaticity of the surround (Eichengreen, 1976; Ekroll et al., 2004; Hansen, Walter, & Gegenfurtner, 2007; Smith & Pokorny, 1996; Ware & Cowan, 1982).

Such shifts are consistent with a compensation of illumination color to achieve color constancy. Our experiments were designed to specifically investigate induction of hue (i.e., induction along the azimuth of cone-opponent color space). Stimulus variation was restricted to isoluminant changes in hue with fixed saturation. Chromatic contrast along the S-axis was scaled relative to the LM axis to achieve approximately equally salient stimuli (Teufel & Wehrhahn, 2004; see also Webster et al., 2002). Scaling of the S-axis has a strong effect on appearance but, as our results confirm, is uncritical in our experiments. Chromaticities of inducers, test, and match stimuli were represented in the same color space. Thus, with changing S-cone contrast, the relative S contribution to chromaticities of test stimuli, match stimuli, and surrounds changed in the same way, yielding matches at the same hue angles.

In our experiments, saturation was slightly lower for surrounds than for the stimuli, to enable identifying the stimulus patches under all conditions. When stimulus and surround had the same hue, a small induction in chroma might be expected, which, however, was not tested in our experiments. For some test stimuli, an offset in hue setting was observed in this condition (Figure 2). In these cases, subjects may have attempted to compensate for the induced difference in chroma by a change in hue setting. Nevertheless, subjects were

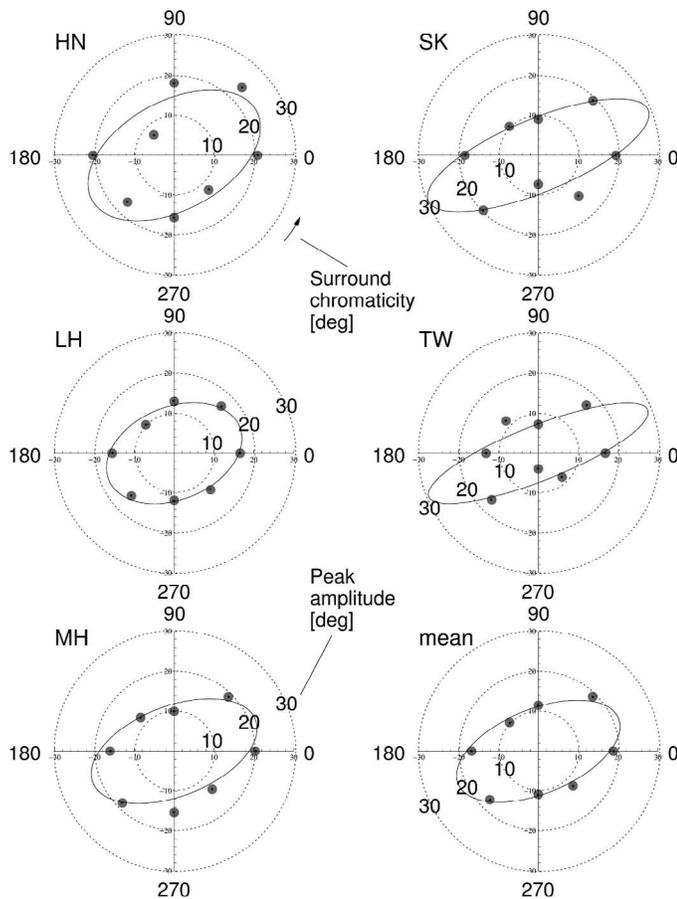


Figure 4. Induction strengths of different backgrounds. Polar diagrams show averaged amplitudes of induction curves as a function of surround hue angle for each subject, illustrating the dependence of induction strength on surround hue. Polar angle corresponds to surround chromaticity. Distance from center corresponds to average amplitude. Best-fitting ellipses indicate the surround chromaticities inducing the largest and smallest shifts. Note that in the experiments, the direction of induction was perpendicular to the direction of the hue of the respective surround. The directions of largest induction effects were therefore along the minor axes of the ellipses.

typically able to achieve satisfactory matches, although for some combinations of test and surround, this was harder than for others. Similarly, given that the observed hue changes correspond to a change of sensitivity along the inducing axis, one could expect changes in perceived contrast. For the largest hue shifts in our experiments, these would correspond to about 6% of the stimulus contrast, or a change of cone contrast of about 0.012 in a stimulus of cone contrast 0.2. However, in the case of adaptation, such estimates seem to overestimate the perceived changes (Mizokami, Paras, & Webster, 2004). We had confirmed this in a pilot experiment in which subjects had the option to adjust not only hue but also chroma. Subjects very rarely made use of this possibility, indicating that

generally induction of chroma was negligible in our experiments.

Our results are consistent with the findings by Webster et al. (2002), who had used surrounds composed of multiple chromaticities in their experiments. Their data thus reflect the inducing effect of more than one surround chromaticity as well as chromatic contrast induction or adaptation, whereas our experiments revealed the hue induction for single background colors separately. Our data are also in line with the rotation in color space of color category borders away from the illumination color observed by Hansen et al. (2007) in color-naming experiments.

In the primary visual cortex (V1) of macaque monkeys, the tuning of color-selective neurons is influenced by colors outside the receptive field in a way that implies a repulsive shift of the encoded hue (Wachtler et al., 2003). A comparison of our psychophysical results to data derived from tuning curves of color-selective V1 neurons showed that effects are similar in both cases. Quantitatively, the hue shifts predicted from the neural responses were slightly larger than the psychophysically measured shifts. A reason for this quantitative difference could be that surround color in the physiological experiments had been chosen preferentially from the range of colors to which the respective neuron was responsive (Wachtler et al., 2003). This introduced a slight sampling bias in favor of surrounds with stronger effects on the neurons' responses and could have led to an enhancement of the average magnitude of color shifts.

The close correspondence between the effects of surround color at the perceptual and the physiological levels suggest that contextual modulation of responses at early stages of the visual system contributes to the perceptual phenomena associated with color induction and color constancy. Contextual influences are also well known to occur in responses of orientation-selective neurons to oriented stimuli (Blakemore & Tobin, 1972; Gilbert & Wiesel, 1990; Knierim & van Essen, 1992). Those have been hypothesized to underlie contextual effects in orientation perception as in the tilt illusion (Gibson & Radner, 1937; O'Toole & Wenderoth, 1977; Smith, Clifford, & Wenderoth, 2001). Analogies between color and orientation have been drawn in the context of adaptation effects (Clifford et al., 2000). Likewise, the hue shifts induced by colored surrounds found in our experiments, when plotted as a function of hue angle difference between test and surround (e.g., Figure 1), show a striking similarity to the induced orientation shifts in the tilt effect (e.g., O'Toole & Wenderoth, 1977): When stimulus and surround are similar, their difference is perceptually enhanced, and this enhancement increases first with increasing difference between stimulus and surround but then becomes weaker again for larger differences.

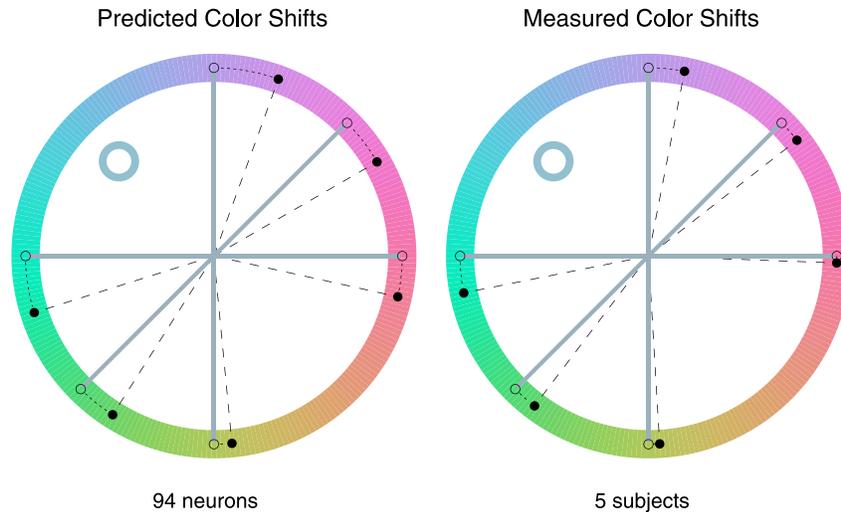


Figure 5. Comparison of induction effects in visual cortex responses and perception. (Left) Predicted hue shifts derived from tuning curves of neurons in macaque primary visual cortex. Data from Wachtler et al. (2003). (Right) Psychophysically measured shifts in perceived hue averaged across all subjects and surround conditions. In both cases, data for test stimuli at  $45^\circ$ ,  $90^\circ$ , and  $135^\circ$  distance from the respective surround were chosen (open dots) and averaged across all surrounds tested. Filled dots indicate average matches as predicted from neural responses or measured by asymmetric matching, respectively. For illustration purposes, data are plotted relative to an arbitrarily chosen bluish surround, indicated by the blue circle. Physiological and psychophysical data indicate similar qualitative dependence of induced hue shifts on chromatic distance from the surround.

These similarities suggest viewing the color appearance shifts measured in our experiment as “chromatic tilt”—an induced shift in hue angle, analogous to the shift in orientation that is observed in the tilt illusion.

Explanations for the tilt illusion in terms of neural mechanisms have focused on primary visual cortex (V1) and proposed gain control and/or tuning curve shifts in neurons that represent orientation in a population code (Clifford et al., 2000; Gilbert & Wiesel, 1990; Schwartz, Sejnowski, & Dayan, 2009). Similar to the neural encoding of orientation in the visual cortex, tuning curves of color-selective neurons in V1 overlap to a considerable degree, indicating a population code for hue in this cortical area (Wachtler et al., 2003). Simple mechanisms of contextual interactions in population codes similar to models proposed to explain the tilt effect or tilt aftereffect (Clifford et al., 2000; Gilbert & Wiesel, 1990; Schwartz, Hsu, & Dayan, 2007) would also predict hue induction or adaptation effects as measured in our experiments (Figure 6). Note that in these models, adaptation is described by the same effects on the neural population code as induction but at different time scales.

This supports the notion that orientation and color are represented in the visual cortex by similar neural mechanisms based on population coding (Webster & Wilson, 2000) and that similar neural circuitry underlies the processing of orientation and color (Clifford et al., 2000). Moreover, in the domain of color, the characteristic signature of contextual influences, notably the dependence on the difference between stimulus

and inducer, is also observed for the dimensions of brightness and saturation, where it has been termed the *crispening effect* (Takasaki, 1967; Whittle, 1992). Color shifts obtained in induction experiments not restricted to isolated dimensions of color (e.g., Ware & Cowan, 1982) suggest that these effects likely reflect a common mechanism of contextual influences in three-dimensional color space (Ekroll & Faul, 2009). Here we considered solely the dimension of hue, but with multivariate tuning functions covering all dimensions of color space (see also Lehky & Sejnowski, 1999) the population coding model with contextual modulation (Figure 6) would account for induction effects along any direction in color space, including induction of hue in an achromatic test stimulus. Neurophysiologically, neurons in the visual cortex show tuning along all three dimensions of color (e.g., Hanazawa, Komatsu, & Murakami, 2000; Wachtler et al., 2003); thus, it is conceivable that at the neural level, neither the encoding of these stimulus aspects nor its modulation by contextual interactions are separated. It seems reasonable to hypothesize that underlying this is an even more general principle of neural processing that applies not only to color and orientation but also to other domains of vision (Schwartz et al., 2007) and even to other sensory modalities.

Perceptual shifts similar to those described here, which were obtained with simultaneously presented stimulus and surround, have been found as a result of adaptation (Webster, 1996; Webster & Mollon, 1991). In the orientation domain, there are likewise similarities

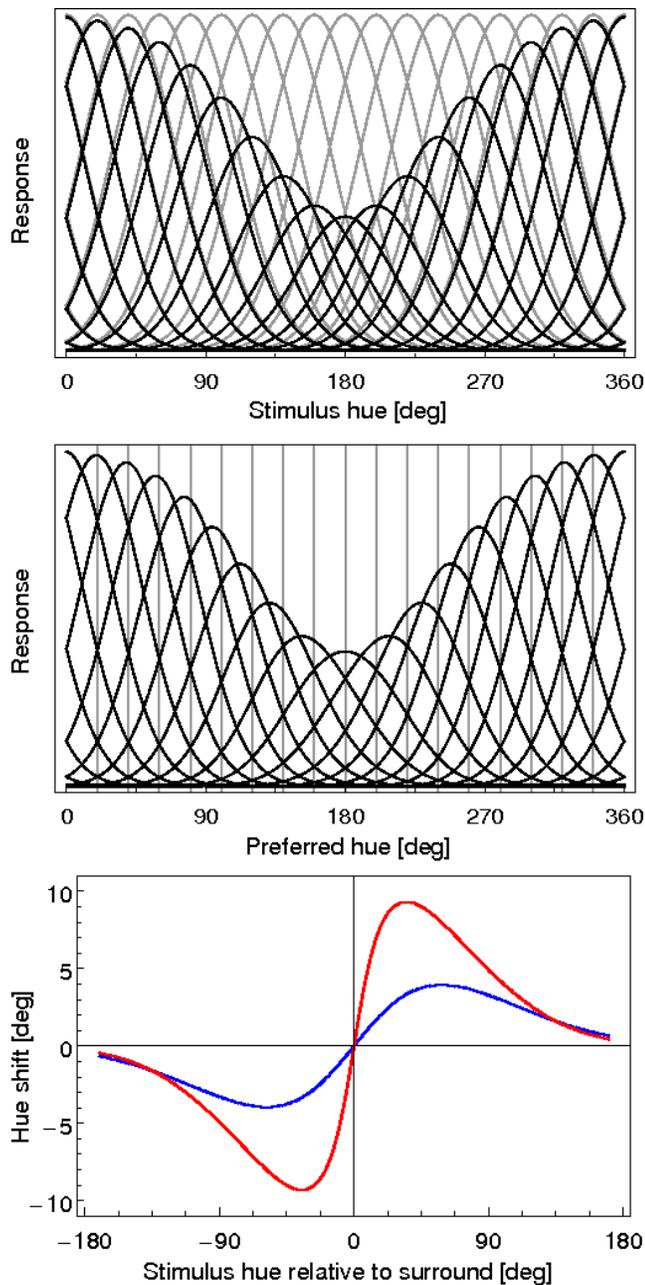


Figure 6. Population coding model of hue induction. (Top) Contextual modulation of model neuron responses. Gray curves show Gaussian tuning functions of  $60^\circ$  width for hue preferences at multiples of  $20^\circ$  around the hue circle. Black curves illustrate the assumed contextual response modulation, represented by a reduction of tuning curve amplitude, caused by an inducing surround with hue corresponding to  $180^\circ$ . (Middle) Population responses under contextual modulation. Black curves represent the activity profiles of a population of neurons with different hue preferences to stimuli with different hues at multiples of  $20^\circ$  (gray vertical lines). Note that, because of the modulation as illustrated in the top panel, the maxima of response profiles for stimuli near the inducing hue at  $180^\circ$  are shifted away from this hue. (Bottom) Population code readout →

between perceptual shifts induced by spatial and by temporal context (Gibson, 1937; Gibson & Radner, 1937), which led Schwartz et al. (2007) to hypothesize that common properties shape induction and adaptation. The underlying commonality may be that visual inputs tend to be smooth in both space and time (Schwartz et al., 2007). However, in natural viewing, there is even an actual coupling between spatial and temporal contexts, imposed by eye movements. Because of the statistics of saccades in natural viewing, successive gaze positions tend to fall at different but nearby points in the visual field. These regularities imply a degree of predictability of the visual input after the next saccades. Induction may provide an adjustment that prepares the visual system for the stimulus conditions that most likely will be encountered due to upcoming eye movements, thus approximating the expected effect of adaptation almost instantaneously, in an anticipating fashion. Consequently, it could be expected that the spatial range of lateral interactions would be matched to the distribution of eye movements.

In contrast to the tilt effect in orientation, we found that for color defined in a color space derived from cone-opponent pathways, the overall magnitude of induction varies systematically for different directions in color space. Quantitative differences between different surround chromaticities in adaptation and induction have been reported in previous studies, but these studies focused on comparison of the cardinal axes (Brenner & Cornelissen, 1991; Wachtler et al., 2001; Wuerger, 1996; Zaidi, Yoshimi, Flanigan, & Canova, 1992). In our experiments, the strongest effects were found for induction along an oblique color space axis (Figure 4) that is of perceptual and ecological relevance (Mollon, 2006). This axis connects perceptual unique blue and yellow and largely coincides with the line of natural daylights (Mollon, 2006), including sunlight as well as light from the blue sky. It thus covers the most common differences in illumination within natural scenes, where some parts of the scene are illuminated by sunlight and some parts are in the shade, illuminated just by skylight. In

← bias. Curves represent biases of stimulus hue estimated from the maxima of the population activity as a function of the hue difference between stimulus and inducer. The only effect of the inducer assumed was the response modulation depicted in the top panel. No changes in tuning curve shapes have been assumed (cf. Clifford et al., 2000; Gilbert & Wiesel, 1990). The two curves were obtained assuming tuning widths of  $60^\circ$  as in the above panels (red) and  $70^\circ$  (blue) and modulatory interactions of twice the respective tuning widths. Thus, variations in tuning parameters might explain observed variations in induction effects.

such a situation, rapid adjustment as provided by induction (Wachtler et al., 2001) is particularly important to achieve color constancy for finding or identifying objects by shifting the gaze between differently illuminated areas.

Along this oblique blue-yellow color space axis, there is a high variation in natural spectra (Webster & Mollon, 1997) and correspondingly high variation in human cone signals (Wachtler, Lee, & Sejnowski, 2001). It also has a pronounced representation in the primary visual cortex by a strong cluster of color preferences of color-selective neurons (Wachtler et al., 2003). Likewise, sensitivity is lower and variability in perceptual performance is higher along this direction (Beer, Dinca, & MacLeod, 2006; Boynton, Nagy, & Eskew, 1986; Danilova & Mollon, 2010; Goddard, Mannion, McDonald, Solomon, & Clifford, 2010; Krauskopf & Gegenfurtner, 1992; Witzel & Gegenfurtner 2013; see also Figure 2). This indicates a perceptual nonuniformity of cone-opponent color space corresponding to an expansion along the blue-yellow axis: To achieve a certain perceptual difference, a larger distance is needed along the blue-yellow axis than orthogonal to it. We speculate that the induction effects observed in our experiments reflect this nonuniformity for stimuli at the suprathreshold level and that measurements of induction across locations and directions in color space might provide a basis for defining a perceptual color metric. In line with the various reports that indicate a special role of noncardinal directions in color space, our results support the notion that color vision is adapted to the chromatic properties of the natural environment.

*Keywords:* color vision, contextual processing, color induction

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