The effect of luminance differences on color assimilation

Xim Cerda-Company Computer Vision Center, Computer Science Department, Universitat Autonoma de Barcelona, Barcelona, Spain

Xavier Otazu Computer Vision Center, Computer Science Department, Universitat Autonoma de Barcelona, Barcelona, Spain

Nilai Sallent Computer Vision Center, Computer Science Department, Universitat Autonoma de Barcelona, Barcelona, Spain

C. Alejandro Parraga Computer Vision Center, Computer Science Department, Universitat Autonoma de Barcelona, Barcelona, Spain

The color appearance of a surface depends on the color of its surroundings (inducers). When the perceived color shifts towards that of the surroundings, the effect is called "color assimilation" and when it shifts away from the surroundings it is called "color contrast." There is also evidence that the phenomenon depends on the spatial configuration of the inducer, e.g., uniform surrounds tend to induce color contrast and striped surrounds tend to induce color assimilation. However, previous work found that striped surrounds under certain conditions do not induce color assimilation but induce color contrast (or do not induce anything at all), suggesting that luminance differences and high spatial frequencies could be key factors in color assimilation. Here we present a new psychophysical study of color assimilation where we assessed the contribution of luminance differences (between the target and its surround) present in striped stimuli. Our results show that luminance differences are key factors in color assimilation for stimuli varying along the *s* axis of MacLeod-Boynton color space, but not for stimuli varying along the *l* axis. This asymmetry suggests that koniocellular neural mechanisms responsible for color assimilation only contribute when there is a luminance difference, supporting the idea that mutual-inhibition has a major role in color induction.

Introduction

The phenomenon of color induction (which occurs when the perceived color of an object changes according to the colors of the objects around it) has been known and exploited by artists for centuries (Chevreul, 1839; Von Bezold, 1876). There are two types of color induction: color contrast and color assimilation. Color contrast occurs when the perceived color (the target) shifts *away* from the surrounding color (the inducer), and color assimilation occurs when the perceived color shifts *towards* the inducer. For instance, given a gray object surrounded by green objects, if the first is perceived as reddish (the color complementary to green), we say that color contrast is occurring. On the other hand, if the gray object is perceived as greenish, we say that color assimilation is happening. The type of induction (contrast or assimilation) depends on the spatiochromatic characteristics of the surround. Psychophysical research has shown that uniform surrounds tend to induce color contrast, whereas striped surrounds tend to induce color assimilation (Monnier & Shevell, 2003, 2004; Otazu, Parraga, & Vanrell, 2010). The effects of achromatic contrast (either luminance or brightness contrast) on color induction have received relatively less attention from the scientific community. Luminance is the photometric measure of luminous intensity per unit area of light travelling in a given direction and is usually measured by photometric devices. Brightness is the perception elicited by the luminance of a visual target, which is not necessarily proportional to luminance. Below we review the color induction literature, discriminating between both concepts.

Color contrast

Color contrast has been reported under a wide range of spatiochromatic conditions: *unconstrained*, when there are luminance and color differences between the target and the inducer (Monnier & Shevell, 2003, 2004;

Citation: Cerda-Company, X., Otazu, X., Sallent, N., & Parraga, C. A. (2018). The effect of luminance differences on color assimilation. *Journal of Vision*, *18*(11):10, 1–23, https://doi.org/10.1167/18.11.10.

https://doi.org/10.1167/18.11.10 Received April 19, 2018; published October 16, 2018 ISSN 1534-7362

Gordon & Shapley, 2006; Otazu et al., 2010); *equiluminant*, when there are no luminance differences between the target and the inducer (Gordon & Shapley, 2006; Kaneko & Murakami, 2012); and *equibrightness*, when there are no brightness differences between the target and the inducer (Gordon & Shapley, 2006; Faul, Ekroll, & Wendt, 2008; Bimler, Paramei, & Izmailov, 2009). In general, researchers have found that color contrast does occur under all these conditions with various degrees of strength, which depends mostly on luminance or brightness differences (Gordon & Shapley, 2006). Several psychophysical studies (Gordon & Shapley, 2006; Faul et al., 2008; Bimler et al., 2009) indicate that color induction follows Kirschmann's Third Law (Kirschmann, 1891), which says that color contrast is highest when the stimulus is equibrightness (but not equiluminant) and, as brightness contrast is either increased or decreased, color contrast is reduced.

Color assimilation

Although color assimilation is more common than color contrast in daily life (De Valois & De Valois, 1988), it has been less studied. As color contrast, assimilation has been studied under several spatiochromatic conditions such as unconstrained (Van Tuijl & De Weert, 1979; Ejima, Redies, Takahashi, & Akita, 1984; Watanabe & Sato, 1989; De Weert & Spillmann, 1995; Pinna, Brelstaff, & Spillmann, 2001; Monnier & Shevell, 2003, 2004; Cao & Shevell, 2005; Devinck, Delahunt, Hardy, Spillmann, & Werner, 2005; Otazu et al., 2010), and equiluminant (Fach & Sharpe, 1986; Watanabe & Sato, 1989; De Weert & Spillmann, 1995; Pinna et al., 2001; Devinck et al., 2005; Cerda-Company & Otazu, 2017). It has also been studied using several patterns such as the pincushion (Schachar, 1976) and watercolor (Pinna, 1987) illusions and those of Van Tuijl (1975) and Ehrenstein (1941). Using the pincushion illusion, De Weert and Spillmann (1995) used red and green stripes on different chromatic backgrounds and measured the color induction on the background when it was either higher, lower, or the same as the luminance of the inducers. Although they did not report the details of their results, they concluded that color assimilation is induced when the luminance of the target's surface is higher than that of the inducers, but not when it is lower. Moreover, they reported that no color change is induced by equiluminant stimuli. In line with this work, Pinna et al. (2001) and Devinck et al. (2005) studied, among other features, the effect of luminance contrast between the two inducers on the strength of the watercolor effect. They concluded that when the two inducers are nearly equiluminant, color spreading is still present but weak, suggesting that the watercolor effect is the result of a luminance-dependent mechanism (Devinck et al., 2005; Devinck, Spillmann, & Werner, 2006). Using concentric rings, Cao and Shevell (2005) found that assimilation occurred along the *l* axis of the MacLeod-Boynton color space (Boynton, 1986) when the inducer's luminance was lower than that of the target, but not when it was higher. In the *s* axis, they found that color assimilation occurs when the inducer's luminance is either lower or higher than that of the target, but its strength depends on the spatial configuration of the inducers (i.e., on both spatial frequency and spatial separation). In the same line, several researchers (Fach & Sharpe, 1986; Smith, Jin, & Pokorny, 2001) studied the role of the spatial frequency in color assimilation using equiluminant stimuli. They observed that by making stripes increasingly thicker, it is possible to make the transition from assimilation to contrast (Smith et al., 2001). Other researchers (Monnier & Shevell, 2003, 2004; Otazu et al., 2010) found similar effects using unconstrained stimuli and observed that thinner stripes induce stronger color assimilation (Otazu et al., 2010). In summary, there seems to be two major stimuli characteristics that induce color assimilation: spatial frequency content and luminance differences.

Brightness induction

Achromatic inducers change the perceived brightness of the target region (brightness induction), an effect that has been widely studied for different stimuli (White, 1979; Blakeslee & McCourt, 1977, 2004; McCourt, 1982; Kingdom, 2011). Using a similar paradigm to ours (see below), Hong and Shevell (2004) concluded that the luminance of both the first and the second inducers contribute to brightness induction, suggesting that luminance differences between the target region and its surrounds (i.e., the context) are important. Moreover, other studies reported an asymmetry between "brightness" and "darkness," pointing out that the strength of the effect depends on whether the target region is surrounded by bright or dark inducers (Beck, 1966; Festinger, Coren, & Rivers, 1970; Hamada, 1984; De Weert & Spillmann, 1995).

Optics considerations

There are optical effects that influence visual perception and may account for some of the properties of assimilation. The most often cited are wavelength-independent spread light and wavelength-dependent chromatic aberration. Spread light is a consequence of optical imperfections in the lens which change the light of the test stimulus that reaches the retina (Devinck,

Pinna, & Werner, 2014). To calculate the influence of spread light, Smith et al. (2001) used the function derived by Williams, Brainard, McMahon, and Navarro (1994) and a method similar to Shevell and Burroughs (1988). They calculated the amount of light that spread into their test stimulus region considering an equiluminant square-wave grating and observed that, as spatial frequency increases, the spread light contribution (to the center of the test stimulus region) increases. In their case they obtained that for stimuli of 4 cycles/° and below the spread light contribution was negligible.

Chromatic aberration is also a source of spread light which depends on spectral wavelength and increases with higher spatial frequencies. Smith et al. (2001) found that even for square-gratings of 9 cycles/°, the effects of chromatic aberration were small, concluding that it does not appear to be a key factor for color assimilation. Similarly, Bradley, Zhang, and Thibos (1992) concluded that chromatic aberration is more relevant at higher spatial frequencies than at lower ones (Devinck et al., 2014).

Although these optical effects could account for part of the color assimilation results, most authors agree that even for high spatial frequencies there are clear neural contributions (Helson, 1963; De Weert & Kruysbergen, 1997; Monnier & Shevell, 2003; Cao & Shevell, 2005; Devinck et al., 2014).

Color processing by the human visual system

The initial stages of visual information processing by the human visual system (HVS) are by far the most understood. Light is absorbed by rods and cones in the retina. Cones operate in well-lit (photopic) conditions and belong to three classes: L, M, and S which are sensitive to long, middle, and short electromagnetic wavelengths (LWS, MWS, and SWS) of the visible spectra respectively. Visual information is segregated by ganglion cells into three nearly independent (Livingstone & Hubel, 1988; Sincich & Horton, 2005) pathways called magno-, parvo-, and koniocellular and sent to a structure in the thalamus called lateral geniculate nucleus (LGN). The magnocellular pathway carries mainly low-resolution, spatially opponent luminance (LWS + MWS) information, while the other two carry spatio-chromatically opponent information—the parvocellular pathway carries high-resolution luminance alongside LWS vs. MWS opponent signals, and the koniocellular pathway carries SWS versus LWS+MWS opponent signals (Derrington, Krauskopf, & Lennie, 1984; Nassi & Callaway, 2009). There are several chromatic spaces consistent with retinal and LGN physiology, the most popular being the ones by MacLeod and Boynton (1979) and Derrington et al. (1984). The LGN receives feedback from higher areas but projects mainly to cortical area V1, which has three different types of neurons: single-, double-, and non-opponent neurons (Johnson, Hawken, & Shapley, 2001; Shapley & Hawken, 2002; Johnson, Hawken, & Shapley, 2008; Shapley & Hawken, 2011). Single-opponent neurons (or Color neurons) respond best to large chromatic areas; double-opponent neurons (or Color-Lum neurons) respond to both chromatic and luminance variations; and nonopponent neurons (or Lum neurons) respond best to luminance variations. Considering spatial frequency selectivity, Lum and Color-Lum neurons are band-pass (i.e., they respond best at medium spatial frequency stimuli of 2 cycles/°) and Color neurons are low-pass—they respond optimally to spatial frequencies < 0.5 cycles/° and do not respond at all to spatial frequencies > 2 cycles/° (Johnson et al., 2001, 2008; Shapley & Hawken, 2011; Xing et al., 2015; Nunez, Shapley, & Gordon, 2018). Although to fully silence Lum neurons is difficult, equiluminant stimuli of medium to high spatial frequency only produce weak responses in them. In fact, equiluminant stimuli of high spatial frequency (>3 cycles/°) also suppresses parvocellular responses (Granger & Heurtley, 1973; Derrington et al., 1984; Skottun, 2013).

The neural mechanisms behind color induction are not completely understood. Some explanations rely on retinal mechanisms (Kamermans, Kraaij, & Spekreijse, 1998; VanLeeuwen, Joselevitch, Fahrenfort, & Kamermans, 2007; Sabbah, Zhu, Hornsby, Kamermans, & Hawryshyn, 2013) whereas others rely on low-level (Xing et al., 2015; Nunez et al., 2018) or higher cortical mechanisms or combinations of both (Gegenfurtner, 2003; Horiuchi, Kuriki, Tokunaga, Matsumiya, & Shioiri, 2014). There are also important interactions between brightness and color that might produce changes in color appearance. For example, increases in the variance of surround colors cause color objects to appear desaturated—they appear more vivid and richly colored against low-contrast gray surrounds than against high contrast multicolored surrounds (Brown & MacLeod, 1997). The same occurs for increases in surround brightness contrast (Faul et al., 2008; Bimler et al., 2009). These effects have been explained by inhibition in cortical V1 circuits generated by local brightness contrast at the boundary between the target and the surround (Xing et al., 2015). In consequence, an important contribution to color induction (both color contrast and color assimilation) is likely to come from these neural mechanisms in V1 (Zaidi, Yoshimi, Flanigan, & Casanova, 1992; Rossi, Rittenhouse, & Paradiso, 1996; De Weert & Kruysbergen, 1997; Zaidi, 1999; Shapley & Hawken, 2002; Cao & Shevell, 2005), with double-opponent neurons playing a major role in color appearance (Nunez et al., 2018).

In addition to not having a comprehensive explanation for the phenomenon, there are few observations on how achromatic information interacts with the chromatic channels to produce color induction. In previous work, Monnier and Shevell (2003, 2004) reported color assimilation with a luminance difference of +5 cd/m^2 between the target and inducers. Given that in a previous study we used similar but equiluminant stimuli and we did not observe color assimilation (Cerda-Company & Otazu, 2017), we wanted to test whether a transition from color contrast (or no induction) to color assimilation occurs just by increasing or decreasing the luminance of the target with respect to its inducers (De Weert & Spillmann, 1995; Monnier & Shevell, 2003, 2004; Cao & Shevell, 2005; Otazu et al., 2010; Cerda-Company & Otazu, 2017). To this end, we present a new psychophysical study where we systematically measured the contribution of luminance differences in color induction. We measured the colors induced in five different luminance conditions: (a) when the target's luminance was much lower than the inducers' luminance ($\Delta Y = -10$ cd/m^2); (b) when the target's luminance was noticeably lower than the inducer's ($\Delta Y = -5$ cd/m^2); (c) when the stimuli were equiluminant ($\Delta Y = 0$ cd/m^2); (d) when the target's luminance was noticeably higher ($\Delta Y = +5$ cd/m^2), and (e) when it was much higher ($\Delta Y = +10$ cd/m^2). As the luminance differences were increased or decreased, we expected to observe significant differences in the strength of color induction because in the equiluminant condition, responses come mostly from Color and Color-Lum neurons, whereas in the unconstrained conditions all neurons respond (Xing et al., 2015; Nunez et al., 2018).

Methods

Apparatus

All experiments were conducted inside a dark room with stimuli presented on a calibrated CRT monitor (21-in. SONY GDM-F500R, at 100 Hz, screen subtending 17.3° × 13.0°). The stimuli was viewed binocularly (subject's head was not constrained) from a distance of approx. 132 cm. We used the Cambridge Research Systems ViSaGe MKII Stimulus Generator, capable of displaying 14-bit color depth. The monitor was calibrated via the customary software (Cambridge Research Systems, Ltd., Rochester, UK) and a ColorCal (Minolta sensor) suction-cup colorimeter. All the light in the room was from the monitor's screen, and the walls were black to avoid interreflections. The subject's responses were collected using a Logitec© gamepad.

Stimuli

Two different circularly symmetric patterns (test and comparison stimuli) were simultaneously presented to the observers side by side on the CRT monitor (see Figure 1). The test stimulus (presented on the left side) was composed by 11 concentric rings of the same width (equivalent to 15.5 arcmin of visual angle), which included the *test ring*. The test ring was always achromatic ($l = 0.66$ and $s = 0.98$) and its luminance depended on the luminance condition evaluated. The other concentric rings had a fixed luminance of $Y = 20$ cd/m^2. We defined five different luminance conditions depending on the luminance of the test ring relatively to the other rings (see Figure 2): $\Delta Y = (-10, -5, 0, +5, +10)$ cd/m^2. The inducer surround consisted of two types of rings, called the first and the second inducer according to their physical distance to the test ring. These inducer rings always had opponent chromaticities (e.g., when the first inducer was red, the second one was green and vice versa) forming an equiluminant surround (see further equiluminance details in the Section entitled "Equiluminance point measure"). Thus, in two luminance conditions the test ring was brighter than its surround, in two it was darker, and in one had the same luminance. We also defined four chromatic conditions according to the first and second inducer's chromaticities: red-green, green-red, purple-lime, and lime-purple. These were: red ($l = 0.69$, $s = 0.98$); green ($l = 0.63$, $s = 0.98$); purple ($l = 0.66$, $s = 1.38$); and lime ($l = 0.66$, $s = 0.58$). The colorimetric properties of the inducer's rings were selected to represent orthogonal axes in the MacLeod-Boynton color space (Boynton, 1986) with the achromatic locus at the centre. To facilitate the correct identification of the test ring by the subjects, in all conditions, we placed small pairs of dots in four different positions (see Figure 1).

The comparison stimulus (presented on the right side) was the same across all conditions (see Figure 1). It consisted of a uniform achromatic disk ($l = 0.66$, $s = 0.98$, $Y = 20$ cd/m^2) containing the *comparison ring*. Both the test and comparison rings had the same physical dimensions and their respective surrounds (the inducer and the comparison surrounds) had exactly the same size. The rest of the screen was set to its minimum possible value (dark background). Subjects were asked to modify the chromaticity and luminance of the comparison ring to match that of the test ring using the gamepad to navigate on the MacLeod-Boynton color space. We chose to define all chromaticities in the MacLeod and Boynton color space (Boynton, 1986), which is a commonly used opponent color space (red-green, purple-lime, and bright-dark), based on the Smith and Pokorny (1975) cone fundamentals.

All stimuli were implemented in MATLAB (MathWorks, Natick, MA), and the video processor was

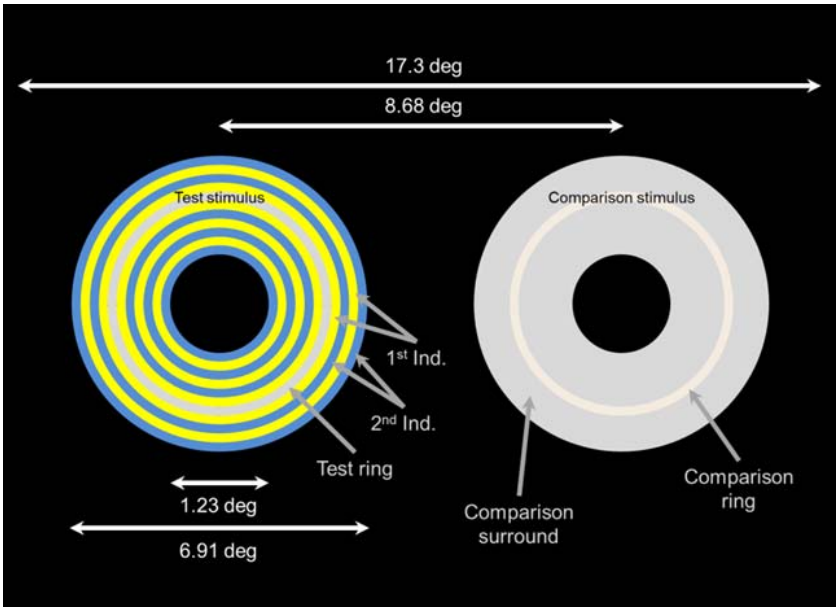

Figure 1. Stimuli design. The first and second inducers consisted of equiluminant ($Y = 20$ cd/m^2) pairs of rings of opposing chromaticities such as red-green or purple-lime. The test ring was always achromatic ($l = 0.66$ and $s = 0.98$) and could have five different luminance values (luminance conditions): $Y = (10, 15, 20[\textit{equiluminant}], 25, 30)$ cd/m^2. Although it is difficult to see in this figure because of their size, eight black dots of 1 pixel size were drawn around test ring for easier detection: four dots in the inner radius of the ring and four points in the outer radius (at 0°, 90°, 180°, and 270°). Subjects had to match the color of the comparison ring to that of the test ring. Colors in this figure might not be the same as those in the experiment because they were created for illustrative purposes.

controlled via a Cambridge Research System custom-made toolbox.

Equiluminance point measure.

Equiluminant (or isoluminant) color stimuli are defined as containing variations only in chromaticity. It is commonly used to separate magno- and parvocellular responses in psychophysical experiments, because they are processed by physiologically distinct channels from the retina to the visual cortex. Equiluminant stimuli have been reported as having special perceptual properties. For example, artists use these properties to make a painting to appear unstable (or "jittery") and to cause motion illusions (isoluminant chromatic motion). An equiluminant display consists of an array of stimuli of different colors whose luminances have been selected to maximize these effects. Because the effects are a consequence of the physiology, the *equiluminant point* varies slightly from one observer to the next. In this work, we generated equiluminant stimuli by finding the colorimetric input that generates equiluminance in each of the subjects. Before starting the experiment described above, subjects participated in an equiluminant-point measure procedure, which lasted 3 hr and was performed in three different days. We measured individual equiluminant points using the Minimally Distinct Border method (MDB; Boynton, 1973; Boynton & Kaiser, 1968; Brill, 2014; Kaiser, 1971; Kaiser, Lee, Martin, & Valberg, 1990; Wagner & Boynton, 1972). The stimuli consisted on two juxtaposed semicircular disks presented in the same apparatus as the experiment. One of the disks was achromatic ($l = 0.66$ and $s = 0.98$) and the other had one of the colors defined in the experiment's chromatic conditions (i.e., red, green, purple, or lime) plus an achromatic condition, for control. We set the luminance of the achromatic disk at $Y = 20$ cd/m^2 and asked subjects to adjust the luminance of the colored disk until "the border between the colored and the achromatic disks was minimal," i.e., when only chromatic but not luminance differences are perceived. Ideally, there would be no border between the two disks (in fact, it happened in the control condition), but in our case, at least a chromatic border was always perceived. At the end of the whole procedure, we obtained an average (from eight measures) of the luminance necessary to match each of the four colors to the achromatic disk for each subject. These luminance values were used to construct the inducer rings of the test stimulus (see left panel of Figure 1).

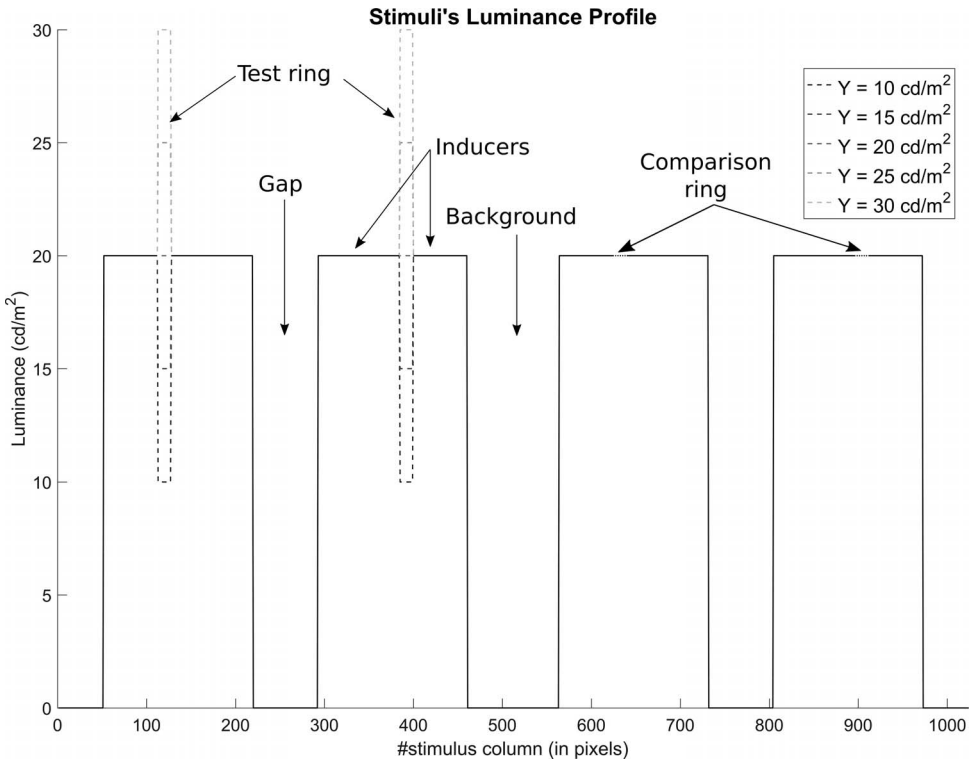

Figure 2. Luminance profile of stimuli. This profile was calculated using the central row of Figure 1. We used a dark background, inducers formed an equiluminant surround, and the luminance of the comparison ring was adjustable (dotted line). We defined five different luminance conditions for the test ring (dashed lines); in two of them the test ring's luminance was below that of the inducers' luminance ($Y = 10$ and 15 cd/m^2), in two it was above ($Y = 25$ and 30 cd/m^2), and in one it was equiluminant ($Y = 20$ cd/m^2). For simplicity's sake, the small black dots that marked the test ring were removed from this figure (they would be placed in both sides of the test ring).

Subjects

Seven subjects recruited from our academic community participated in the experiment. Five of them were familiar with color spaces (DB, MM, NS, XC, and XO), and two of them were not (AC and CG). All of them signed the consent form to participate in the experiment, where the aim of the study was described. Four of them were completely naïve (AC, CG, DB, and MM) while the others were some of the authors (NS, XC, and XO). The age range was between 18 and 46 years old. Six of them were male (AC, CG, DB, MM, XC, and XO) and one of them female (NS). All subjects had normal or corrected-to-normal vision, and they scored as normals in the Ishiara's test (Ishihara, 1972) and the D-15 Farnsworth Dichotomous Test (Farnsworth, 1947). The experiment was approved by our university's ethics committee (Comissio d'Etica en l'Experimentacio Animal i Humana -CEEAH- de l'Universitat Autonoma de Barcelona) in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

Experimental procedure

Subjects adjusted the color of the comparison ring until "it was perceived the same as the test ring" (asymmetric matching task). To do this, subjects could adjust the chromaticity and the luminance of the comparison ring navigating the MacLeod-Boynton color space using the gamepad buttons. We spent the first (training) session making sure that all subjects were familiar with the apparatus.

The whole experiment consisted of a training session (discarded) and five experimental sessions lasting about 40 min each. Each of the sessions consisted of three parts: a 3 min dark adaptation and two trials containing 20 matching *runs* each. Individual trials included all possible random combinations of the chromatic and luminance *conditions* of the first and second inducer rings (red – green, green – red, lime – purple, purple – lime) $\times$ (10, 15, 20, 25, 30) cd/m^2, totaling 20 runs each. In a single day, a subject would come to the laboratory and spend about 80 min (80 runs) in two sessions (between sessions, subjects took 10 min break). After five sessions, the subject would

have ideally finished 10 trials, totaling 200 runs (matches).

Results

To estimate the strength of color induction, we used a one-dimensional metric (see Equation 1) which is sensitive to both color contrast and color assimilation (Cerda-Company & Otazu, 2017). In Equation 1, ΔC_i is the strength of the induction phenomenon along any of the two axes of the McLeod-Boynton color space (i = [l, s]), and C_i^c is the chromaticity of the comparison ring along the axis considered. Similarly, C_i^t and C_i^s are the chromaticities of the test ring and first inducer ring along the same axis respectively.

$$\Delta C_i = \frac{C_i^c - C_i^t}{C_i^s - C_i^t}, \quad (1)$$

According to Equation 1, when ΔC_i is negative, color contrast is induced because the chromaticity difference between the comparison ring and the test ring ($C_i^c - C_i^t$) shifts *away* from that of the first inducer ($C_i^c - C_i^t$ has different sign from $C_i^s - C_i^t$). Similarly, when ΔC_i is positive, color assimilation is induced because the chromaticity difference between the comparison ring and the test ring shifts *towards* that of the first inducer ($C_i^c - C_i^t$ has the same sign as $C_i^s - C_i^t$).

It is important to note that there is a region below the just noticeable difference (JND) where no color changes are perceived and, therefore, no color induction (neither contrast nor assimilation) is induced. We estimated this region ($\Delta E = 1$) from the CIELab color space, which is an approximately perceptually uniform. Because both inducers were defined on the same color axis, we defined induction in each of the orthogonal axes i separately.

Figure 3 shows the contribution of luminance to color induction. The x axis represents the luminance difference ($\Delta Y = Y^t - Y^s$) between the test ring and its surround (five luminance conditions). Negative values indicate that the test ring was darker than its surround; positive values indicate the opposite and zero difference indicates the equiluminant condition. The y axis represents color induction as defined by Equation 1 for each luminance and chromatic condition, averaged across subjects with their corresponding standard errors of means (*SEM*, $N = 7$). Outlier points were detected using the interquartile range measure (Disraeli, 1996) and were removed from the analysis. Each panel in Figure 3 details a chromatic condition (20 runs in total). The gray region shows the JND region, where no chromatic difference is perceived.

Notice that the results depend on both luminance and chromatic conditions. For instance, along the l axis (top panels: red-green and green-red chromatic conditions), results are not symmetric. When the first inducer was red (top-left panel), weak color assimilation (positive ΔC_l) was often induced including at the equiluminant point. Conversely, in the top right panel, color contrast (negative ΔC_l) was always induced when the first inducer ring was green and the test stimulus was darker than its surround, even for the equiluminant condition.

Regarding the s axis, the results of the two chromatic conditions (bottom panels) are quite similar, as if a "mirroring" of the two chromatic conditions (purple-lime and lime-purple) occurs. Here, color assimilation (positive ΔC_s) was induced in all cases when the stimuli were unconstrained (not equiluminant). When the first inducer was purple (bottom left panel), the assimilation was stronger when the test ring was darker than its surround. Similarly, when the first inducer was lime, assimilation was stronger when the test ring was lighter than its surround. It is also noticeable that the red-green chromatic condition (top-left panel) is the only one that induced color assimilation at equiluminance. Individual observer results for all conditions are detailed in the Appendix.

Because subjects were allowed to manipulate both chromaticity and luminance, we can also analyze whether there was any luminance effect in the matches. Table 1 shows the averaged luminance differences and their *SEM*s as defined in the Macleod-Boynton space between the match (i.e., the comparison ring after each trial) and the comparison surround (ΔY_{comp}). The first column shows the luminance differences between the test ring and its surround (luminance conditions). We observe that the values produced by the subjects are quite close to those of the first column (save some weak brightness induction effects), and they do not vary for the different chromatic conditions. Given that from a luminance point of view, inducer rings in the test stimulus on the left of Figure 1 are matched to the 20 cd/m^2 of the comparison surround on the right (see Section entitled "Equiluminance point measure"), these results show that brightness induction does not depend on the chromaticity of the inducers and, thus, it does not depend on the chromatic induction. In general, rings that induce color contrast induce similar brightness as rings that induce color assimilation. For instance, red-green inducers at $\Delta Y = -10$ induce color assimilation and a brightness induction of $\Delta Y_{\text{comp}} = -11.4$ cd/m^2, while green-red inducers at the same luminance condition induce color contrast and a similar brightness induction of $\Delta Y_{\text{comp}} = -11.3$ cd/m^2.

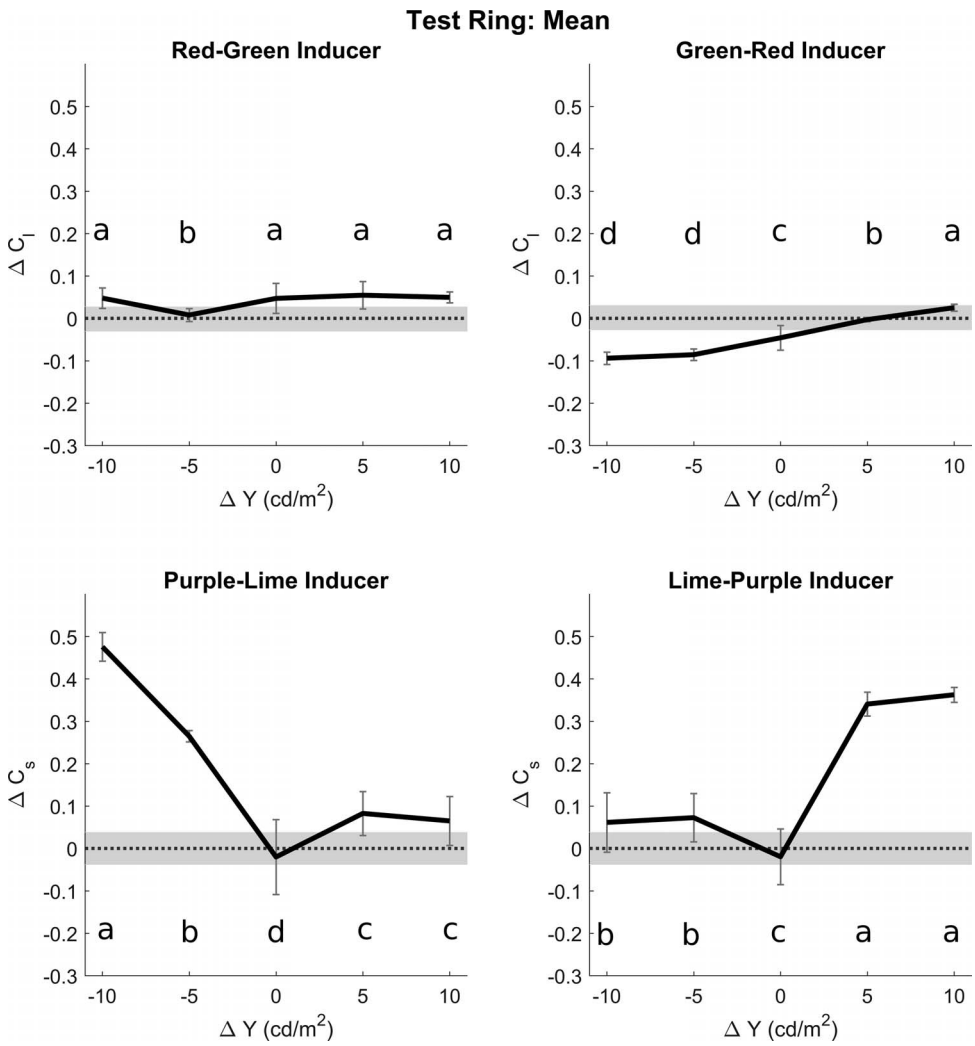

Figure 3. Color induction for the 20 combinations (runs) of luminance and chromatic conditions. Abscissas show different luminance conditions, and panels show different chromatic conditions. The gray region shows the Just Noticeable Difference (JND) region, where no chromatic difference is perceived. The ordinates show color induction as defined by Equation 1: when $\Delta C > JND$ color assimilation is induced, and when $\Delta C < -JND$ color contrast is induced; and the error bars indicate ± 1 *SEM*. We observe that the results are very different for the *l* and *s* color opponent axes. In particular, assimilation is stronger along the *s* axis. Moreover, color assimilation is only induced by an equiluminant stimulus when the first and second inducers are red and green, respectively. The letters above or below the error bars show the results of Fisher's LSD posthoc analysis, i.e., they indicate whether the differences in our color induction's measures are significant or not: Measures that have the same letter cannot be considered different, and measures with different letters can.

Statistical analysis

To test whether luminance conditions induce different chromaticities, we performed a statistical analysis of the results obtained in our experiment. Our independent variables (IVs) consisted of chromatic condition, luminance condition, subject identification, and trial. Our dependent variables (DVs) were the chromaticities induced in the *l* and *s* color space directions (in the metric units defined by Equation 1). Our null hypothesis was that all luminance conditions induced the same strength of chromatic induction. We did a nested ANOVA analysis (subject identification nested in luminance condition) for each chromatic condition to analyze the induction differences at different luminance conditions. The results showed that, in all chromatic conditions, the null hypothesis should be rejected. Therefore, significant differences in color induction exist at different luminance conditions (see Table 2 for the ANOVA details). We did a Fisher's Least Significant Difference (LSD) posthoc analysis to study which luminance conditions induce different chromaticities. The letters in Figure 3 relate which luminance conditions produce statistically similar results (same letter implies no statistical difference).

	ΔY_{comp}			
ΔY	Red-green	Green-red	Purple-lime	Lime-purple
−10	−11.4 ± 0.08	−11.3 ± 0.10	−10.5 ± 0.11	−11.1 ± 0.07
−5	−6.3 ± 0.08	−6.6 ± 0.10	−5.7 ± 0.10	−6.0 ± 0.08
0	−1.3 ± 0.15	−1.1 ± 0.19	0.0 ± 0.06	−0.2 ± 0.04
5	4.9 ± 0.16	4.9 ± 0.21	6.3 ± 0.15	5.5 ± 0.08
10	10.2 ± 0.07	10.7 ± 0.25	11.9 ± 0.11	11.3 ± 0.15

Table 1. Luminance differences obtained for the comparison ring in different luminance conditions. *Notes*: From a luminance point of view, the inducer rings on the left of Figure 1 and the uniform comparison surround of 20 cd/m^2 on the right are the same. The values in the table are the mean and the standard error of means (*SEM*) of the luminance difference between the comparison ring and the comparison surround, calculated for all subjects ($N = 7$). The values of ΔY_{comp} are similar to those of ΔY, confirming that a small brightness contrast is induced by the inducer rings. Because these brightness contrasts are very similar for different chromatic conditions, the results suggest that luminance is independent of the chromaticity of the inducer (inducers of the same luminance but different chromaticity induce similar brightness).

Discussion

Some of the results described above are consistent with previous work and some are novel. In this section we will try to interpret them in terms of previous psychophysical results and the neural correlate of color perception.

Psychophysics

Chromatic and brightness induction have been studied using many psychophysical paradigms (e.g., matching, cancellation tasks, etc.) that generally rely in sharp-edge patterns presented on a computer screen (White, 1979; Pinna et al., 2001; Devinck et al., 2006; Monnier & Shevell, 2003; Otazu et al., 2010). In our case, the stimuli are composed by concentric rings with sharp edges that contain energy within a broad range of spatial frequencies (see Figure 1). The general case of the Fourier decomposition for a square-wave is

$$f(x) = \frac{4}{\pi} \sum_{n=1,3,5\ldots}^{\infty} \frac{1}{n} \sin \frac{n\pi x}{L} \quad (2)$$

Chromatic Condition	$F(4, 306)$	p
Red-green	5.5	< 0.001
Green-red	44.3	< 0.001
Purple-lime	181.6	< 0.001
Lime-purple	162.9	< 0.001

Table 2. Details of nested ANOVA analysis of our results. *Notes*: We used ANOVA to determine whether luminance conditions influence color induction. The null hypothesis (no difference in chromatic induction among all luminance conditions) was rejected in all chromatic conditions. Thus, color induction depends on the luminance condition.

where L is the period of the square-wave, and n are odd integers (Weisstein, 2018). The dominant term of the decomposition ($n = 1$) has the same spatial frequency as the original square-wave and its closest term in the series has a frequency three times higher than that (all Fourier components have greater spatial frequencies than that of the square-wave). The relative contributions of the extra terms are 1/3, 1/5, 1/7, etc. To produce the square-wave, all sinusoidal terms become zero at the edges. Although we did not assess the contribution of the $n > 1$ terms, we assumed it to be small because most cortical neurons respond weakly to spatial frequencies outside a one-octave range (De Valois, Albrecht, & Thorell, 1982). Following this, and in order to compare our results to those of the literature, we used concentric rings of fixed spatial frequency (1.94 cycles/°) whose dominant sinusoidal Fourier component also had this spatial frequency. From this point forward we will refer to the square-wave spatial frequency and the dominant Fourier component indistinctly.

Equiluminant stimuli are widely used to study color induction (Fach & Sharpe, 1986; De Weert & Spillmann, 1995; Smith et al., 2001; Gordon & Shapley, 2006; Kaneko & Murakami, 2012; Xing et al., 2015) but, as mentioned in the Introduction, color assimilation is not as comprehensively studied as color contrast. Some studies used striped equiluminant stimuli, but they mainly focused on the effects of spatial frequencies (Fach & Sharpe, 1986; Smith et al., 2001) or the spatial configuration of the inducers (Cao & Shevell, 2005), concluding that, for equiluminant stimuli, the spatial frequency distribution is a key factor in color assimilation. In particular, they observed that very thin stripes (9 cycles/°) induce color assimilation and thick stripes induce color contrast (0.7 cycles/°), with a transition point from assimilation to contrast near 4 cycles/° (Smith et al., 2001). Regardless of this, at equiluminance, our stimuli, which are composed by stripes of 1.94 cycles/°,

can induce color contrast (green-red chromatic condition), color assimilation (red-green chromatic condition), or generate no induction at all (purple-lime and lime-purple chromatic conditions). These effects of luminance distribution on color induction have been only sparsely studied. De Weert and Spillmann (1995) did a preliminary psychophysical experiment pointing out that the luminance of a spatial distribution could affect color assimilation, but they did not provide any quantitative support to their results. They measured color induction on a colored background, which had a lower spatial frequency (0.59 cycles/°) than our test ring, and their inducers had red and green chromaticities. As in our case, the luminance of the inducers did not vary, but the luminance of the background (the target) was varied. The authors concluded that no color induction (neither contrast nor assimilation) is induced at equiluminance and that the backgrounds should have higher luminance than its inducers to induce color assimilation. For similar chromatic conditions (see red-green and green-red chromatic conditions in Figure 3 at equiluminance) we observed color assimilation when the first inducer is red and the second is green, and color contrast when the first is green and the second is red. Apart from equiluminance, they measured color induction at two different luminance conditions ($\Delta Y = [-2.7, +4.7]$ cd/m^2) finding color assimilation in both chromatic conditions when the background's luminance was higher ($\Delta Y = +4.7$) than the inducers' luminance. We did not measure color induction in exactly the same luminance conditions, but at similar ones. We agree that color assimilation is not induced in either of the red-green or green-red chromatic conditions at low luminance ($\Delta Y = -5$ cd/m^2 in our case) and it is induced in red-green at high luminance ($\Delta Y = +5$ cd/m^2), but we have never found color assimilation when the chromatic condition was green-red. Moreover, we found color assimilation in red-green making the test ring even darker than their low luminance condition. In a subsequent study, Cao and Shevell (2005) also measured color assimilation in two different luminance conditions ($\Delta Y = [-1.33, +2]$ cd/m^2) and eight chromatic conditions, covering a range. As De Weert and Spillmann, they concluded that in the *l* direction, the luminance of the inducer has to be lower than the targets' luminance to induce color assimilation; and they observed that in the *s* direction color assimilation does not depend on the luminance difference, but on the spatial configuration of the inducers (spatial frequency and spatial separation). In their work, they did not use equiluminant stimuli (they did not compare against equiluminance) but compared against different luminance conditions. Conversely, we observed that in the presence of a luminance difference, color assimilation is induced in the *s* direction with a strength that depends on this difference. This could be explained by the spatial frequency content of the stimulus given that both, De Weert and Spillmann (1995) and Cao and Shevell (2005), used stimuli of higher spatial frequency than we did. Regarding the stimulus configuration, we measured color induction in similar conditions as Monnier and Shevell (2003, 2004) did (see purple-lime and lime-purple chromatic conditions at $\Delta L = +5$ cd/m^2), and we reproduced their results. They observed stronger induction than us we, but with higher spatial frequency stimuli (3.3 cycles/°) and more saturated colors (purple chromaticity *l, s* = [0.66, 2.0] and lime chromaticity *l, s* = [0.66, 0.16]; Monnier & Shevell, 2003, 2004). As Otazu et al. (2010) reported in a similar study, the higher the spatial frequency of the striped stimuli, the stronger the color induction.

The effect of luminance on color assimilation has been studied using a variety of patterns (Van Tuijl & De Weert, 1979; Ejima et al., 1984; Watanabe & Sato, 1989; Bressan, 1995; Pinna et al., 2001; Devinck et al., 2005; Devinck et al., 2006). For example, the Watercolor effect (Pinna, 1987) is usually studied on a white background because its color assimilation is stronger on that background than on either gray or black (Pinna et al., 2001). As we observed in our results, the strength of color assimilation is not the same when the target region is either brighter or darker than the inducers. In their case, not only the luminance of the target region, but also the luminance contrast of both inducers is important: When both inducers are equiluminant, color assimilation is only weakly induced (Pinna et al., 2001; Devinck et al., 2005). Interestingly, some authors found that the strength of the effect also depends on the chromaticity of the inducers (Schober & Munker, 1967), pointing out that when the inducer was yellow, color assimilation was weaker (Fach & Sharpe, 1986; Devinck et al., 2005). We also found that color assimilation depends on the chromaticity of the inducers, but our weakest effect occurred when the inducer was green, not yellow (for that chromaticity, color assimilation never occurred). Fach and Sharpe (1986) explored the effects of spatial frequency on color induction using equiluminant square-wave gratings whose bars varied from 2 to 20 arcmin. They measured color induction for 10 and 20 arcmin bars, but unfortunately they did not explore spatial frequencies similar to ours (15.5 arcmin). For red-green and blue-yellow equiluminant gratings, they reported color contrast (or no color induction), but never color assimilation. Similarly to them, at equiluminance we only observed color assimilation when the first inducer was red and the second one was green.

Neurophysiology

It is well established in the literature that the type of neuron responding in V1 largely depends on stimulus properties such as spatial frequency or chromatic and luminance spatial distribution (Johnson et al., 2001, 2008; Shapley & Hawken, 2011; Xing et al., 2015; Nunez et al., 2018). In terms of their responses, single-opponent cells are nonorientation selective, being activated mostly by uniform color stimuli while double-opponent cells are orientation selective and responsive to both color and luminance patterns. Nonopponent cells are mostly responsive to luminance patterns (Johnson et al., 2008). Because our test stimuli were composed of colored concentric rings of medium spatial frequency (1.94 cycles/°), it is safe to assume that both types of color-responsive neurons (single- and double-opponent) were always activated. In fact, double-opponent neurons might have been close to their maximum sensitivity, which is at 2 cycles/° (Johnson et al., 2001, 2008). At equiluminance ($\Delta Y = 0$), nonopponent neurons are weakly responsive (Skottun, 2013), but by our increasing the luminance contrast, these neurons become responsive (Johnson et al., 2001, 2008). Thus, by our presenting several luminance conditions, our stimuli is likely to activate different numbers of nonopponent neurons in V1, varying the strength of the inhibition (mutual-inhibition) on both single- and double-opponent neurons. According to the mutual-inhibition hypothesis (Xing et al., 2015; Nunez et al., 2018), as luminance contrast is increased, color response is inhibited. In terms of color induction, this means that (a) color contrast is greatest at equiluminance when color response is maximal (mutual-inhibition is minimal; Xing et al., 2015; Nunez et al., 2018), and (b) color assimilation increases with luminance contrast, i.e., when mutual-inhibition is greatest, color response is reduced.

Although we have used equiluminant stimuli with striped instead of uniform surrounds (Xing et al., 2015), we observed (see purple-lime and lime-purple chromatic conditions in Figure 3) that color assimilation is stronger as luminance contrast is increased. This seems to support the mutual-inhibition hypothesis, which might be related to the "probably inhibitory" (Zaidi, 1999) lateral connections between neurons that are the principal ingredient for color induction. Considering that our results could only be explained by an interaction between the chromatic and the luminance channels, they do not support models where color induction occurs earlier than V1 (Kamermans et al., 1998; VanLeeuwen et al., 2007; Sabbah et al., 2013). In the same way, we cannot rule out models where color induction occurs at higher levels (Gegenfurtner, 2003; Horiuchi et al., 2014).

Our color induction results are completely different depending on whether the stimuli are defined in the *l* or the *s* directions of MacLeod-Boynton color space, suggesting that mutual-inhibition mechanisms are different at different pathways or at different layers of V1. When the stimuli are defined in the *l* direction (red-green and green-red chromatic conditions), the parvocellular pathway is activated, and when they are in the *s* direction (purple-lime and lime-purple chromatic conditions), the koniocellular pathway is activated (Nassi & Callaway, 2009). From a feedforward point of view, the parvocellular pathway is first processed in layer $4C\beta$ and then in layer 2/3 (Sincich & Horton, 2005); the koniocellular pathway projects its S-ON channel to layer 2/3 and its S-OFF channel to layer $4A$ (Chatterjee & Callaway, 2003; Callaway, 2014; Kaplan, 2014); and the magnocellular pathway first projects to layer $4C\alpha$ and then to layer 2/3 (Sincich & Horton, 2005; Kaplan, 2014). Although this is highly speculative and there is no neurophysiological evidence, the dissimilarity of color induction regarding the *l* and *s* directions could be due to the different circuitry and composition of the V1 layers—there are different amounts of single-, double- and nonopponent neurons in the different layers (Johnson et al., 2001, 2008). Another possibility is that color induction in the *l* direction is different from that in the *s* direction because of some "pre-" processing at layer $4C\beta$.

In any case, it is surprising to find dissimilarities between the red-green and green-red chromatic conditions because both of them are processed by the same layers (assumingly) in a similar fashion (Solomon & Lennie, 2007). A plausible reason for this asymmetry might be ecological, because it has been suggested that tropical fruits have coevolved with the trichromatic color vision of Old World monkeys to facilitate their detection over a background of green leaves (Mollon, 1989; Reagan et al., 1998). In this framework, it makes sense for the HVS to want to enhance their visual targets (via chromatic contrast) when placed against such chromatic backgrounds. This could also explain why we did not observe any instance of chromatic assimilation when the first inducer was green.

The "mirroring" effect observed in the purple-lime and lime-purple chromatic conditions (bottom panels in Figure 3) could be produced by mutual-inhibition, or inhibition itself. Looking at the results in more detail, we find that for the purple-lime chromatic condition (bottom-left panel), assimilation is stronger when the test ring is darker than when it is brighter (negative values of ΔL), and the opposite is true for the lime-purple chromatic condition (assimilation is stronger when the test ring is brighter than when it is darker, positive values of ΔL). For a given dark purple-lime

stimulus ($\Delta L < 0$ in bottom-left panel in Figure 3), the test ring activates the S-OFF and the Lum-OFF postreceptoral channels (konio- and magnocellular pathways, respectively) because the gray test ring excites less the S-cones than the surrounding purple and also has a lower luminance than the first inducer. Conversely, for a bright purple-lime stimulus ($\Delta L > 0$ in bottom-left panel in Figure 3), the test ring activates the S-OFF and the Lum-ON postreceptoral channels (the chromatic information does not change, but luminance does). A possible explanation of this stronger assimilation when the S- and the Lum-OFF channels are activated is that channels of the same polarity inhibit more each other than channels of opposite polarity do. The same might occur in the lime-purple chromatic condition: It activates the S-ON channel while the low luminance condition ($\Delta L < 0$ in bottom-right panel in Figure 3) activates the Lum-OFF channel. The later leads to a weaker inhibition and, thus, to a weaker chromatic assimilation than the higher luminance condition ($\Delta L > 0$, which activates the Lum-ON channel).

We also considered the influence of nonneural (optical) effects in our results. Because our stimuli had relatively low spatial frequency (1.94 cycles/°), we could consider that the effects of spread light in our results (see Section "The effects of optics" in the Introduction) are much lower than the variability of our observers and therefore negligible.

Conclusions

We performed a psychophysical experiment based on the well-known color induction paradigm of Monnier and Shevell (2003, 2004) in particular, their color assimilation results. Our paradigm was similar to theirs, except that we varied the luminance difference between the target ring (where the induction was measured) and its surround. We obtained similar results for the same luminance condition they tested ($\Delta Y = +5$), and observed that for other conditions, color assimilation depends on the luminance contrast of the inducer. This outcome suggests that the magno-, parvo- and koniocellular pathways cannot be considered as having independent processing mechanisms, or at least they have a significant interaction in V1. In particular, our results show that luminance influences color induction, but not the opposite (different chromatic conditions result in similar brightness induction). Moreover, at equiluminance, color assimilation is only induced when the first and second inducers are red and green, respectively.

We were not able to find a simple and global explanation for our results based on linear combinations of chromatic and luminance signals from the visual pathways. Indeed color assimilation depends on both luminance contrast and chromatic condition (see a visual summary of our results in Figure 4). Remarkably, in the red-green and green-red chromatic conditions, subjects always see the test ring as "reddish" or "gray" regardless of the spatiochromatic configuration of the inducers or luminance conditions. Also, color assimilation for the red-green and purple-lime color pairs is completely different, and luminance contrast seems to play a more important role in the koniocellular than in the parvocellular pathway.

Although our results are significant, they need to be taken with caution because we did not explore other

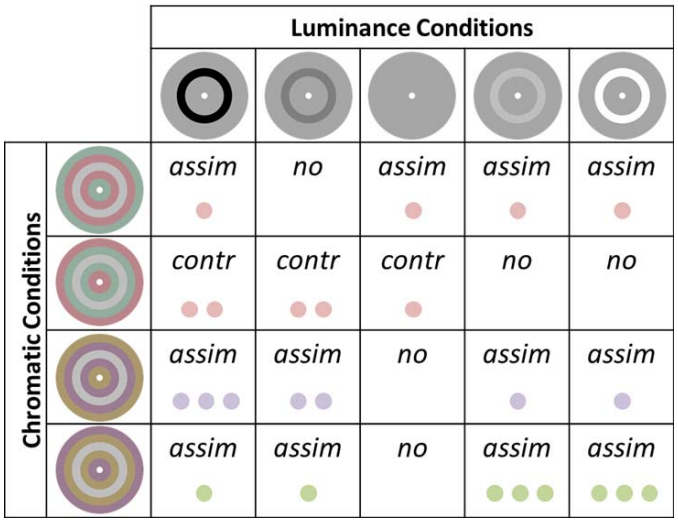

Figure 4. Visual summary of the results. The columns correspond to the five different luminance conditions. We fixed the luminance of the inducers at 20 cd/m^2 (gray disks), and we evaluated five different luminance conditions of the test ring $\Delta Y = (-10, -5, 0, +5, +10)$ cd/m^2 (black, dark gray, gray, light gray, and white rings, respectively). The rows correspond to the four different chromatic conditions (red-green, green-red, purple-lime, and lime-purple). The colors of the concentric rings and their spatial configuration only have an illustrative purpose (we used 11 rings in our experiment instead of five). The colored dots in the figure indicate the match performed by the subjects, the number of dots indicates the strength of the color induction, and the abbreviations above them indicate the type of color induction effect, e.g., assimilation, contrast, or no effect. We observed that (a) color assimilation at equiluminance occurs only on the first row, (b) color assimilation is never induced in the second row—in other words, subjects only see the test ring as "reddish" or "gray" regardless of the spatiochromatic configuration of the red/green inducers or luminance conditions-, (c) a "mirroring" effect occurs between the third and the fourth rows, (d) color assimilation depends on both luminance contrast and chromatic condition. These results support the hypothesis that mutual-inhibition between color and luminance neurons plays a major role in color induction.

stimuli configurations such as different spatial frequencies or patterns, other color pairs, etc. We did not intent to explore all possible combinations but to concentrate on luminance differences which allowed us to test a single unexplored aspect of color assimilation.

In summary, our results support the hypothesis that mutual-inhibition between V1 neurons plays a major role in color appearance (Xing et al., 2015; Nunez et al., 2018), or at least in color induction. Furthermore, because our results strongly depend on the studied chromatic condition, they suggest that this mutual-inhibition mechanism is different for the parvo- and koniocellular pathways, with a "mirroring" effect occurring between the two koniocellular (S-ON and S-OFF) channels.

Future work

We observed that the luminance difference between the target ring and its surround plays a major role in color assimilation. In future work it will be interesting to perform a similar experiment varying the relative luminances of the first, second, and both inducers. By doing so, the contribution of the inducers' luminance to color assimilation could be measured.

A new computational model of color induction capable of reproducing these results should be implemented. Color induction models such as CIWaM (Otazu et al., 2010), ODOG (Blakeslee & McCourt, 1999), etc. (Spitzer & Barkan, 2005) are likely to fail to reproduce these results because they assume independent chromatic and luminance channels (i.e., parvo- and konio-, and magnocellular pathways). Thus, a further biologically plausible computational model should include some mutual-inhibition mechanism or at least, some kind of brightness-chromatic interaction.

Keywords: psychophysics, color induction, color assimilation, luminance differences, striped stimuli

Acknowledgments

The authors would like to thank all the subjects for their valuable time. This work is partially supported by the Spanish Ministry of Economy, Industry and Competitiveness through research project DPI2017-89867-C2-1-R, by the Agencia de Gestio d'Ajuts Universitaris i de Recerca (AGAUR) through 2017-SGR-649, and CERCA Programme/Generalitat de Catalunya.

Commercial relationships: none.
Corresponding author: Xim Cerda-Company.
Email: ximcer@cvc.uab.es.
Address: Computer Vision Center, Computer Science Dept., Universitat Autonoma de Barcelona, Barcelona, Spain.

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Appendix

Individual results

In this section we show the individual results for each of the seven subjects (Figures A1 through A7) in the different runs. Thin light gray lines show all the 10 different trials of each run. The thick dark gray lines show the mean values of these trials and the error bars show ± 1 *SE*. The x axis represents the evaluated luminance conditions, and the y axis represents the chromatic induction defined by Equation 1. The gray region indicates the just noticeable difference (JND) region where no color differences can be perceived.

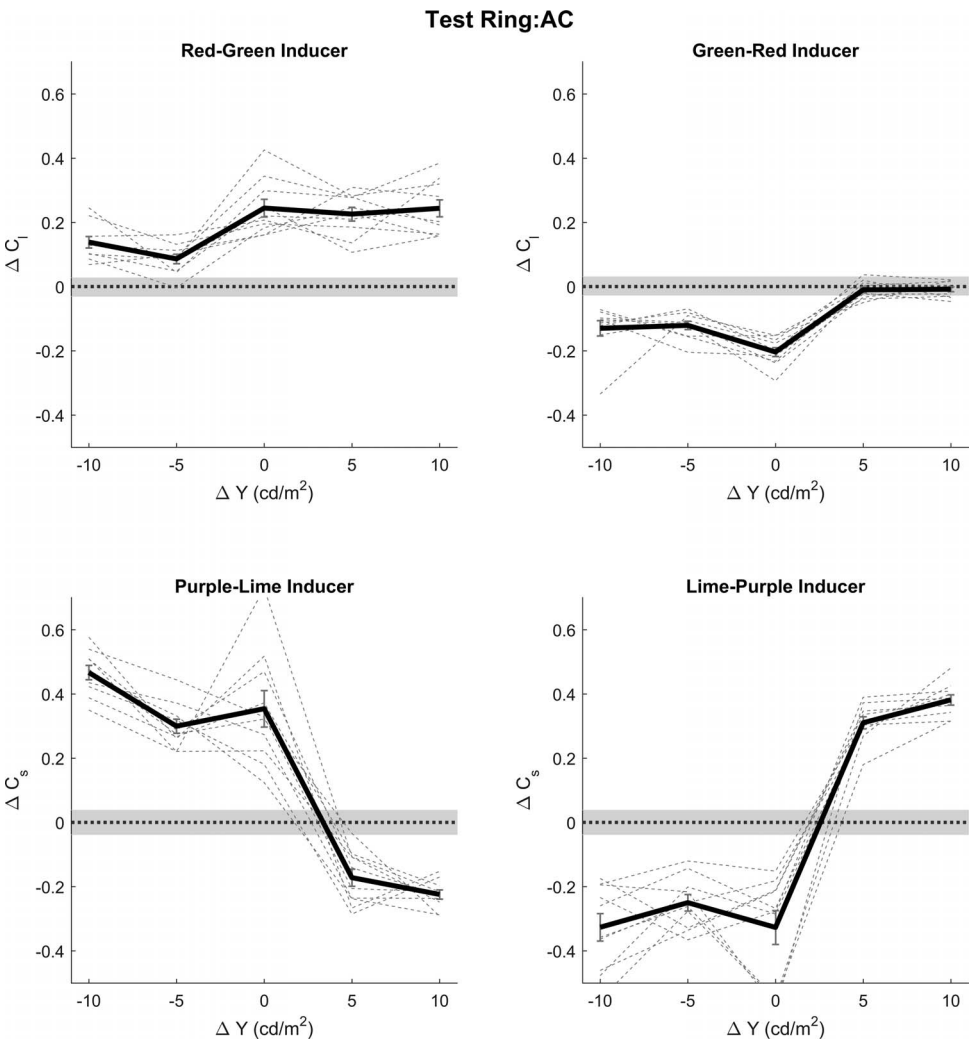

Figure A1

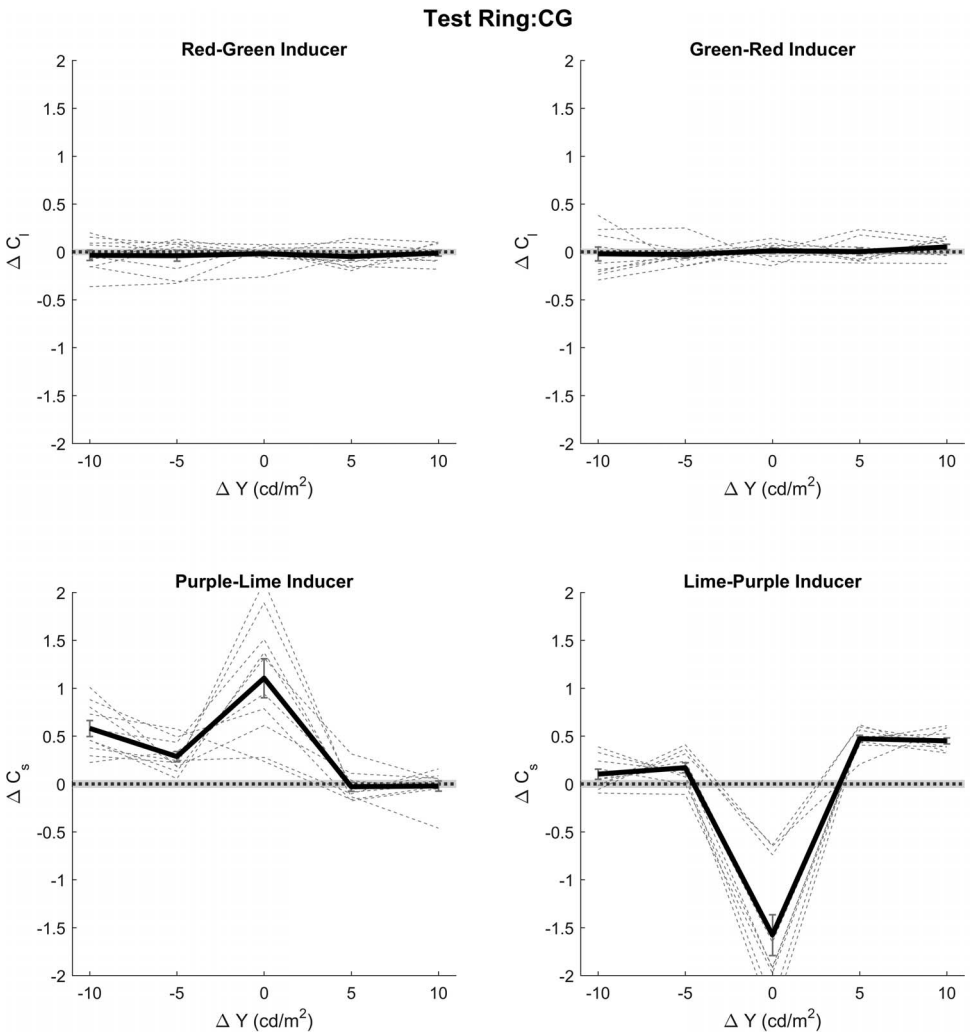

Figure A2

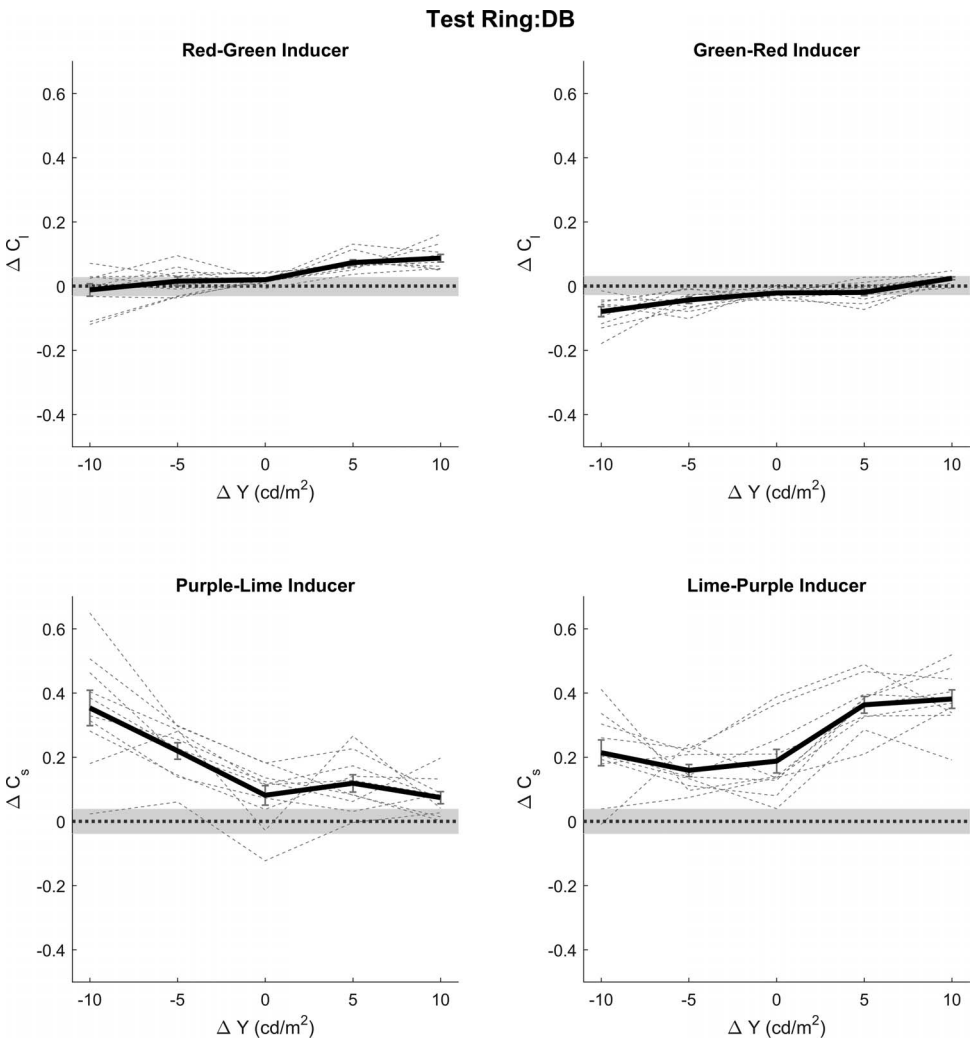

Figure A3

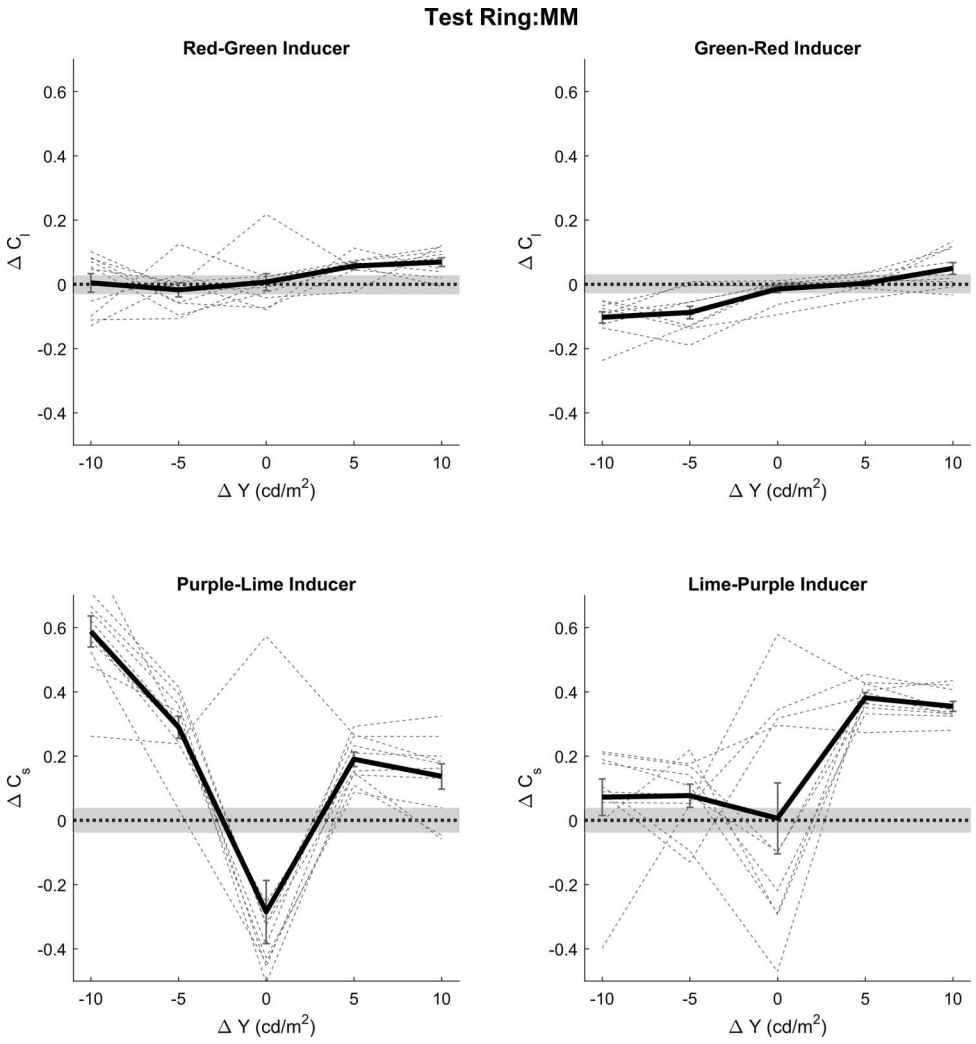

Figure A4

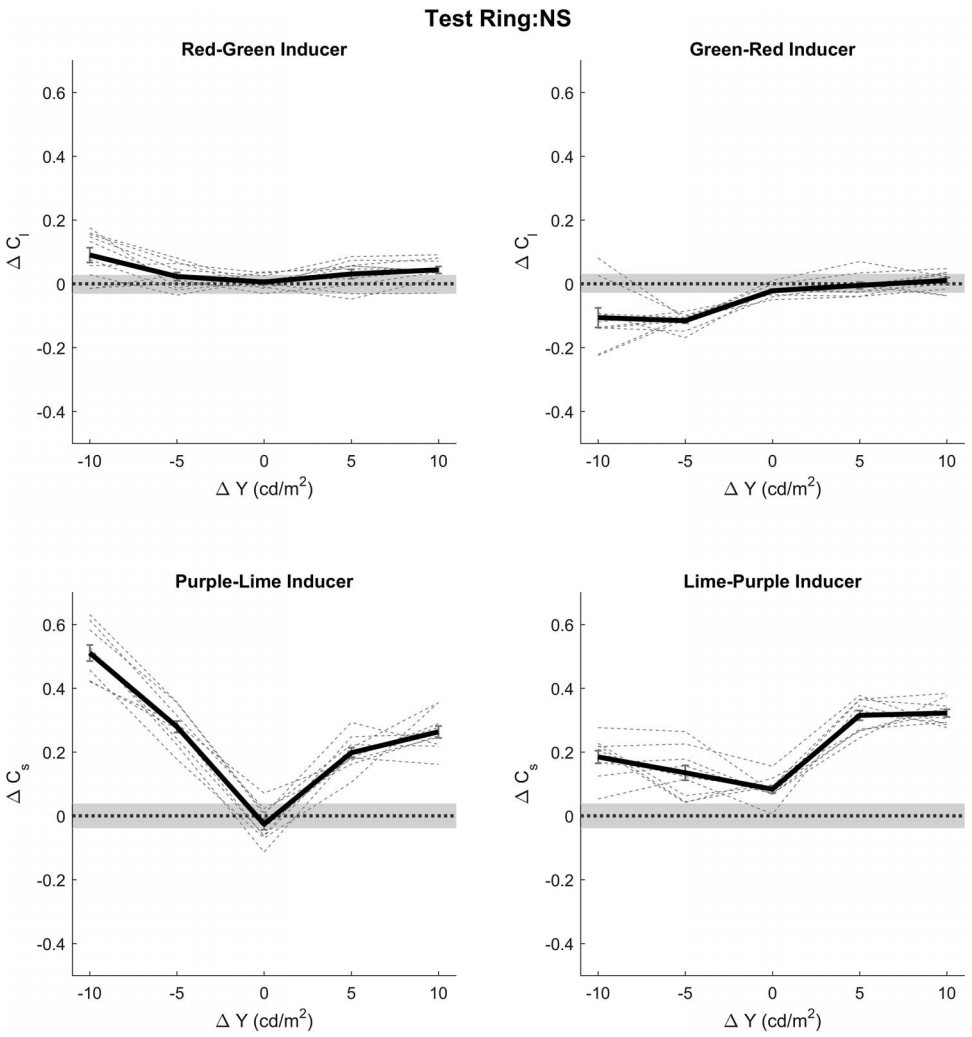

Figure A5

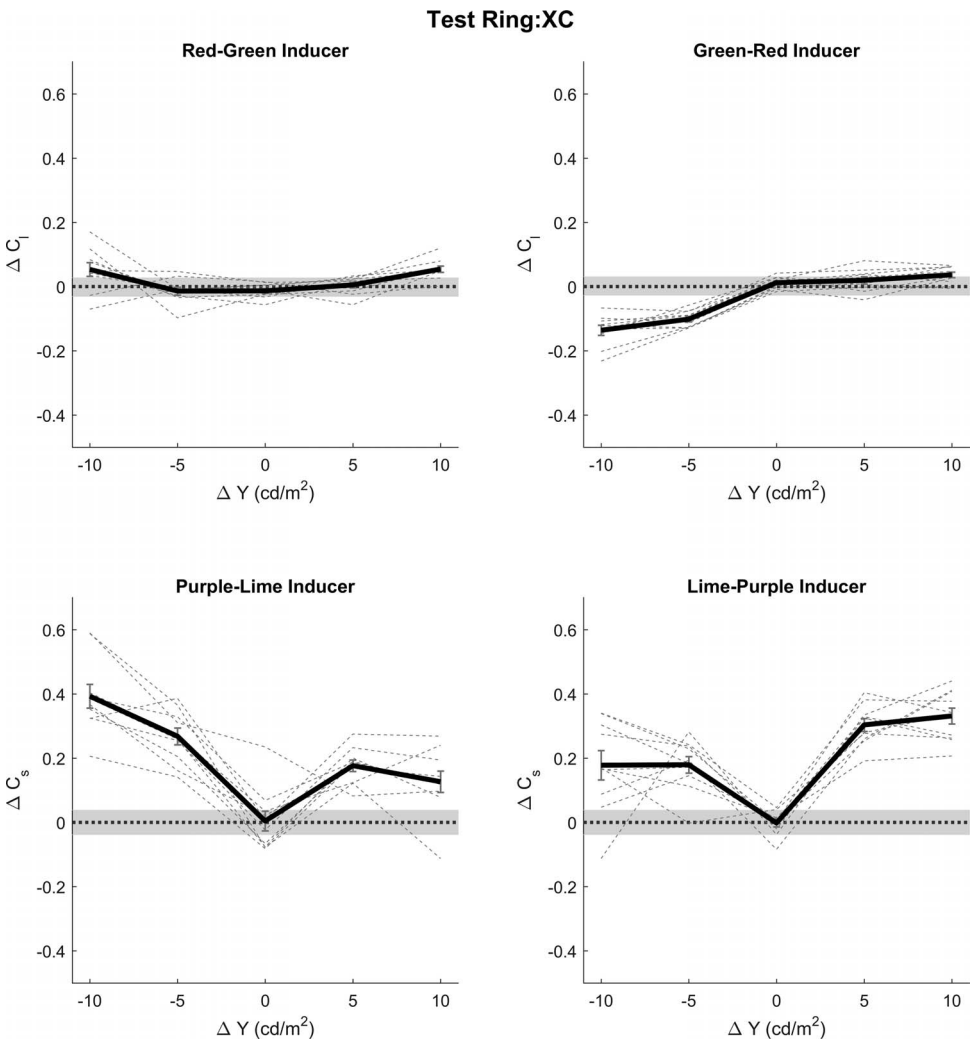

Figure A6

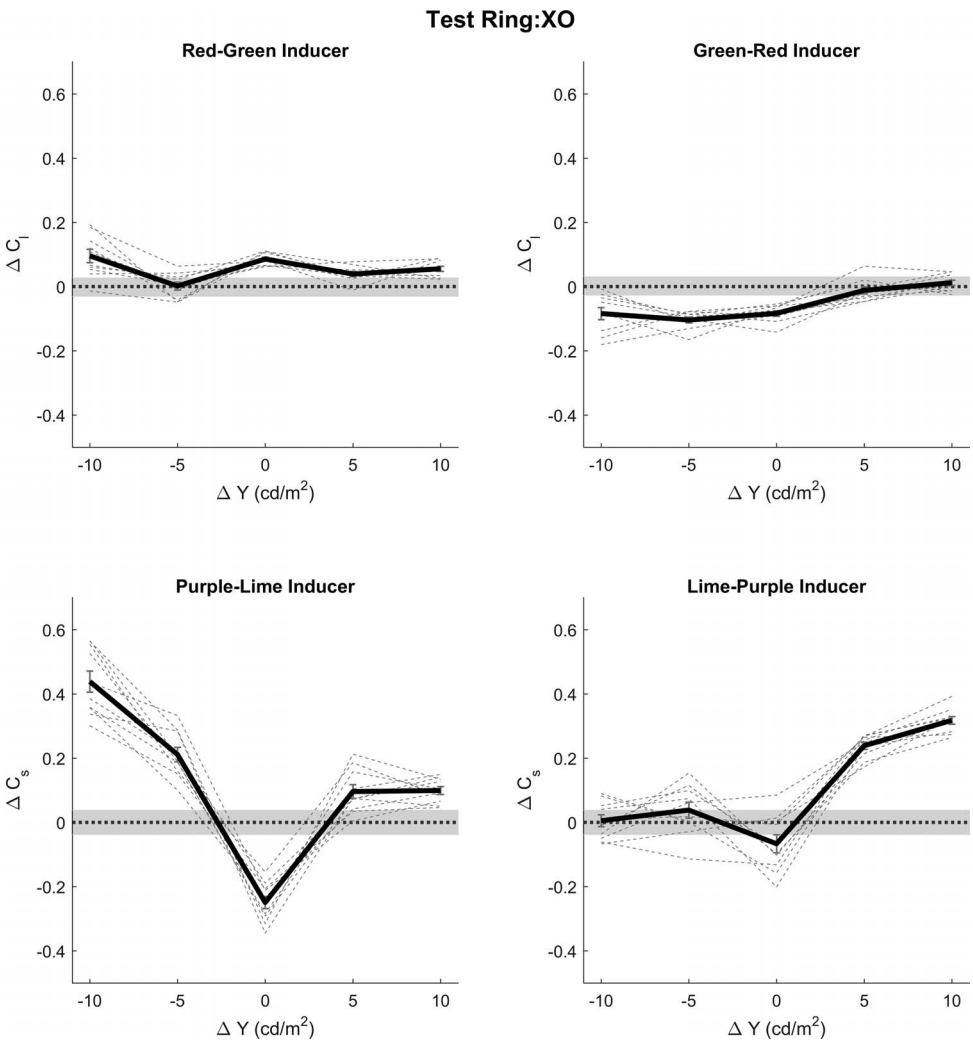

Figure A7