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Temporal properties of the chromatic and achromatic Craik–O'Brien–Cornsweet effect

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Abstract

The Craik–O'Brien–Cornsweet effect (COCE) is a visual illusion in which a difference in brightness is observed between two regions of equal luminance separated by a contrast edge with opposite luminance gradients on each side. The COCE also occurs with chromatic contrasts. It has been hypothesized that the COCE is mediated by a cortical filling-in process. According to the filling-in hypothesis, the filling-in or spreading of neural activity proceeds at finite speed, and therefore exhibits some temporal tuning as a function of the width of the area to be filled in. In the present study, observers varied the temporal frequency of a COC grating to determine the maximum temporal frequency at which a temporal modulation of brightness or color was perceived. In the achromatic COCE, contours were modulated along the luminance axis of the DKL color space; in the chromatic COCE, contours were modulated either along the L − M or the S − (L + M) axis. For the achromatic condition, the critical temporal frequency at which the COCE was still perceived had the shape of an inverted U, inconsistent with the filling-in hypothesis: the critical temporal frequency increased with increasing spatial frequency only up to 0.2 cycles/deg, but then decreased for higher spatial frequencies. For the chromatic COCE, the critical temporal frequency decreased with increasing spatial frequency, which is also inconsistent with filling-in. Thus, the results of the present study are inconsistent with the idea that the temporal dynamics of the COCE, both achromatic and chromatic, are due to filling-in. Instead, our results are consistent with the spatial filtering properties of the luminance and chromatic systems.

Keywords: Filling-in; Craik–O'Brien–Cornsweet effect; Temporal frequency; Spatial frequency

1. Introduction

The Craik–O'Brien–Cornsweet effect (COCE) is a visual illusion in which two surfaces with the same luminance appear to differ in brightness because of an intervening luminance gradient at the borders (Cornsweet, 1970; Craik, 1966; O'Brien, 1958). The surface adjacent to the decrement part of the contour appears darker, while the surface adjacent to the increment part of the luminance gradient is seen as lighter. Thus, the visual impression of a COC grating is similar to a square-wave grating (Fig. 1). It has been shown that the COCE also occurs with chromatic borders (van den Brink and Keemink, 1976). However, the COCE is more pronounced for achromatic than for chromatic stimuli (Cole, Hine, & Scott, 1993; Wachtler & Wehrhahn, 1997; Ware & Cowan, 1983). Similarly, a weaker effect at isoluminance has been also shown for the missing-fundamental illusion in which a square wave with its fundamental Fourier component removed still appears like a square wave (Kingdom & Simmons, 1998).

It has been hypothesized that the COCE is mediated by a cortical filling-in processes (Grossberg and Todorović 1988; Neumann, Pessoa, and Hansen, 2001; Ratliff and Sirovitch, 1978; Todorović, 1987). Filling-in is a process where neural activity at the boundaries of a region spread into the interior region. Filling-in assumes that brightness information is represented in a cortical map and is thus an isomorphic theory. In the COCE, contrast information from the luminance

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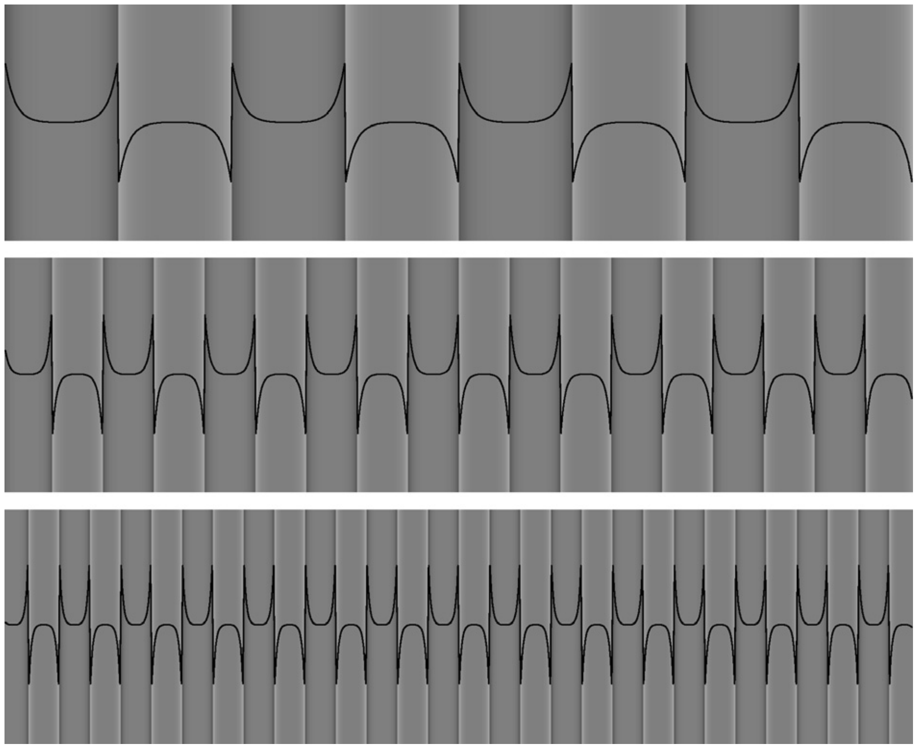

Fig. 1. Example of a Craik–O'Brien–Cornsweet effect (COCE) used in the first experiment. In this phenomenon, the central regions differ in perceived brightness, although the intensity of each of these regions is similar. The intensity profile (solid scalloped lines) has been added for illustration only and was not visible during the experiment.

gradients is thought to fill-in the homogeneous interior regions, such that observers perceive something different from the physical background depending of the surrounding area. Most neurons in the early visual system are sensitive to luminance discontinuities and respond less to homogeneous achromatic surfaces. Only a subset of cortical neurons responds well to uniform fields (Rossi, Rittenhouse, & Paradiso, 1996). According to the filling-in theory, brightness information signaled by contrast-sensitive neurons spreads from the luminance contrast at the edges towards the homogeneous inner region of the bars in the COC grating. Filling-in assumes an active spreading of neural activity, which proceeds at a finite speed, and should consequently exhibit a temporal tuning as a function of the size of the region to be filled-in: the larger the region, the more time is needed for filling-in. Davey, Maddess, and Srinivasan (1998) have investigated this hypothesis by manipulating the temporal modulation frequency of an achromatic COCE for various spatial frequencies. For each spatial frequency, there is a temporal frequency at which the brightness changes will not occur because the filling-in process does not have enough time to complete. The critical temporal frequency should vary with the width of the induced area and with the temporal frequency of the flickering contours. The principle finding of Davey et al. (1998) was that induced modulations were stronger and persisted to higher temporal frequencies for higher spatial frequencies, consistent with the isomorphic filling-in hypothesis. Along similar lines, Rossi and Paradiso (1996) investigated brightness induction in temporally modulated square-wave gratings and found that the highest temporal frequency at which brightness induction occurs decreased as the area of the stripes in the square-wave grating increased. Their findings are also consistent with an induction process such as filling-in that takes longer for larger areas.

Davey et al. (1998) (see also Maddess, Srinivasan, & Davey, 1998) suggested that their results could also support an interpretative hypothesis (called also the symbolic theory; for a review, see von der Heydt, Friedman, & Zhou, 2003). The early visual system is relatively insensitive to *achromatic* low-spatial frequency stimulation and shows only small responses to homogenous *achromatic* regions (Campbell & Robson, 1968). Thus, the retinal response pattern elicited by an achromatic square-wave is quite similar to the retinal response for an achromatic COCE. These similar patterns could be interpreted at a later stage by a symbolic "default-to-square-wave" rule (Campbell, Howell, & Johnstone, 1978; Ratliff & Sirovitch, 1978). For Maddess et al. (1998), this hypothesis is consistent with their results because the time required for the recognition process might be influenced by spatial frequency. Information about lower spatial frequencies is processed over greater cortical distance, thus the limiting process might be the speed at which the brain recognizes the low- or high-spatial frequencies in the image. This line of thinking indicates that the experiments by Davey et al. (1998) did not necessarily demonstrate that an isomorphic filling-in occurs in the COCE, and that the interpretative theory cannot be rejected.

If an isomorphic filling-in underlies the COCE, the critical temporal frequency should increase with increasing spatial frequency both for achromatic and chromatic patterns. However, if the interpretative theory supports COCE perception then the result should take into account the chromatic and achromatic contrast sensitivity function. It is well known that chromatic contrast sensitivity is low pass (Mullen, 1985; van der Horst & Bouman, 1969). Thus, due to the interpretative theory, we should not expect a missing-fundamental illusion or a COCE at isoluminance, because the retinal pattern of a chromatic square-wave is fundamentally different from the pattern generated by a chromatic COCE (Kingdom & Simmons, 1998). Another idea is that the critical modulation frequency at which the COCE persists depends on the spatio-temporal characteristics of the visual system and will be limited by the recognition of low-spatial frequencies for an achromatic COCE and by the recognition of high spatial frequencies for a chromatic COCE. To test these ideas, we extended the experiment done by Davey et al. (1998) with an achromatic COCE to higher spatial frequencies, and into the chromatic domain using isoluminant COC gratings modulated along the $L-M$- and $S-(L+M)$ axes.

We found that the critical temporal frequency had an inverted U-shape function for the achromatic COCE, and decreased with increasing spatial frequency for the chromatic COCE, both inconsistent with filling-in. Results are also inconsistent with an interpretative theory, which would predict no illusion with chromatic stimuli. However, the overall profile of the temporal frequency curve had a characteristic similar to the spatial filtering properties of the luminance and chromatic systems.

2. General methods

2.1. Observers

Four observers ranging in age from 26 to 32 years participated in each experiment. All had normal color vision (assessed by the Farnsworth plate), and had normal or corrected-to-normal visual acuity. Three observers were naïve regarding the purpose of the experiment, and the fourth observer was one of the authors (F.D.). Experiments were performed in accordance with the principles of the Declaration of Helsinki for the Protection of Human Subjects.

2.2. Apparatus

Stimuli were presented on a SONY Multiscan 20SE II color CRT monitor driven by a Cambridge Research ViSaGe graphic board (14 bits per gun) (Cambridge Research Systems, Rochester, United Kingdom). The experimental software was written in Matlab 7 using the CRS Toolbox extensions. The monitor was calibrated using an OptiCal photometer with the calibration routines of Cambridge Research Systems.

2.3. Stimuli

Stimulus patterns consisted of a COC grating with different spatial frequencies. In the main experiment we used three spatial frequencies (0.05, 1.25 and 0.2 cycles/deg). In a control experiment for achromatic stimuli we also employed higher spatial frequencies (0.4, 0.8 and 1.2 cycles/deg). The COC grating could have any color direction and contrast in DKL color space (Derrington, Krauskopf, & Lennie, 1984; Krauskopf, Williams, & Heeley, 1982; MacLeod & Boynton, 1979); three different directions were used. The first direction contained only variation of contrast along the $L-M$ cone contrast axis. In the second direction, stimuli had variation of contrast along the $S-(L+M)$ cone contrast axis. These two chromatic axes intersect at the gray point and span an isoluminant plane through the gray point. All lights in this direction have the same luminance as defined by the $V(\lambda)$ photopic luminosity function (Judd, 1951; see Wyszecki & Stiles, 1982).

The COC stimulus was designed to have a central region in the middle of each bar with no intensity modulation. Any observed brightness modulation in this area was therefore illusory. To achieve this, we defined a single COC flank by an exponential function that was confined to 3/4 of a quarter cycle (half the width of a single bar in the grating). Two COC flanks thus define modulations in 3/4 of a half-cycle and leave an area of one quarter of the width of a bar without any modulation. The profile of a single COC flank with x_i confined to 3/4 of a quarter cycle was defined with the following equation:

$$F(x_i) = c\left(\frac{e^{\frac{\alpha x_i}{n}} - 1}{e^{\alpha} - 1}\right)$$

where $x_i \in \{0, 1, \ldots n-1\}$ is the spatial index of the pixels and n is the number of pixels in 3/4 of a quarter cycle. The value c defines the contrast (0.1 or 0.9) in the DKL color space. The parameter $\alpha = 5$ controls the steepness of the COC flank. Note that all chromaticity coordinates for both contour sides producing the COCE are in opposite directions in DKL color space. Since the COCE was also displayed in an isoluminance condition, we determined for each observer the luminance match for the two contours with the luminance background to be tested using a variation of the minimally distinct border technique of Boynton and Kaiser (1968).

2.4. Procedure

Observers first adapted for 3 min to the mean luminance of the CRT (30 cd/m^2) in an otherwise dark room. Observers were then asked to vary the temporal frequency of a COC grating to determine the maximum temporal frequency at which a temporal modulation in brightness or color was perceived in the central regions of all bars of the grating. Observers were instructed to freely move their eyes, but to ignore the transition areas of the COC gratings, and just take the central regions of the bars into account. The initial value of the adjustable temporal frequency was chosen such that the COCE was clearly visible. To prevent hysteresis effects, observers had to adjust the cutoff temporal frequency from two directions (ascending and descending). Temporal frequency thresholds were determined for the three different spatial frequencies. Observers used a CB6 button box (Cambridge Research System, Rochester, United Kingdom) to increase or decrease the temporal frequency. Two steps were provided (0.25 and 1 Hz) to optimize the adjustment. The minimal step size of 0.25 Hz was fine enough for the observers to accomplish the task. This sequence was repeated continuously until the observer made a satisfactory setting and pressed a separate button on the response box to end the trial and start the next one. A training session preceded the experiments; thereafter each observer made ten settings in each condition tested. Possible effects of contrast sensitivity were evaluated in two separate experiments. First, we extended the main experiment by adding three high spatial frequencies (0.4, 0.8 and 1.2 cycles/deg) for an achromatic pattern presented at low contrast. Two observers, who had participated in the previous task, performed this experiment. Finally, one observer was asked to adjust the temporal frequency at which no brightness or color modulation was perceived in the COCE. The presentation order of the stimuli was randomized in all conditions. All experiments were performed in a dark room. Observer position was stabilized by a chin rest so that the screen was viewed binocularly at a distance of 52 cm.

3. Results

The means of the temporal frequency thresholds for the achromatic COCE for four observers and for both contrast conditions are shown in Fig. 2 (top panels). The regression lines indicate the cutoff temporal frequency required to perceive the COCE for three spatial frequencies. A regression analysis revealed that the temporal frequency significantly increased for the achromatic COCE and decreased for the isoluminant COCEs with increasing spatial frequency both for high and low contrast. In particular, the temporal frequency for an achromatic induction effect increased significantly with increasing spatial frequency at low contrast ($F(2,6) = 66.56,\ P < 0.0001$) and at high contrast ($F(2,6) = 27.80,\ P < 0.0001$). For a COC grating modulated along the $S - (L + M)$ axis, the main results showed that the temporal frequencies decreased for increasing spatial frequencies. This result is displayed in Fig. 2 in the middle panels. The regression indicated that there was a significant effect at a low chromatic contrast ($F(2,6) = 126.76,\ P < 0.0001$), and also for high chromatic contrast ($F(2,6) = 22.55,\ P < 0.0001$). Finally, a similar result was found for a COC grating modulated along the $L - M$ axis, where, the temporal frequency decreased significantly with increasing spatial frequency both for at low contrast ($F(2,6) = 107.15\ P < 0.0001$) and at high contrast ($F(2,6) = 37.00,\ P < 0.0001$). For all conditions, there are some differences across observers in the cutoff temporal frequencies; this is probably the consequence to differences in the subjective criterion of induced brightness or color. Fig. 3 summarizes the results for the achromatic and the chromatic modulated COC gratings for the low contrast condition.

In the achromatic conditions we found an increase of the temporal cutoff frequency with increasing spatial frequency. This increase is suggestive of a filling-in process, and one can estimate the speed of propagation with the following equation:

$$v = \frac{1}{\text{sf}} \times \frac{1}{4} \times \text{tf} \times 2 = \frac{1}{2}\frac{\text{tf}}{\text{sf}},$$

where ‘sf’ is the spatial frequency used in the experiment and ‘tf’ is the temporal frequency adjusted by the observer. The factor ¼ corrects the spatial frequency because the filling-in process needs to proceed only across a quarter of a cycle, i.e., across half of a bar from either the left and right edge to the center. The factor 2 corrects the temporal frequency, because two inductions occur during each temporal modulation. This velocity determines a lower limit of an assumed filling-in process, because the inducing contrast at the edges is not constant but decreases to zero during twice the temporal frequency. For the achromatic conditions with three spatial frequencies (0.05, 1.25 and 0.2 cycles/deg) and measured average cutoff temporal frequencies of 5.13, 6.32 and 7.41 1/s the velocities were 51.30, 25.28 and 18.50 deg/s. The velocities decrease considerably and consistently with increasing spatial frequencies. This is inconsistent with filling-in, which would predict that the velocities should be approximately the same and independent of spatial frequency.

In the second experiment, the task was extended to higher spatial frequencies for an achromatic COC grating at low contrast. The mean results presented in Fig. 4 show that the cutoff temporal frequencies decreased for spatial frequencies higher than 0.2 cycles/deg, deviating from the pattern predicted by a isomorphic filling-in theory.

Fig. 5 shows the results where the observer adjusted the temporal limit at which no modulation at all is seen for a COC grating modulated along the luminance, the $S - (L + M)$ axis and the $L - M$ axis (in dashed lines). Data from previous experiments are displayed for the same observer and conditions (solid lines). The cutoff temporal frequency at which a modulation can be detected, is above and similar to the results from the perceived COCE.

4. Discussion

The filling-in hypothesis assumes a temporal spreading of neural activity, a process that takes time. Consequently, larger areas are assumed to take longer to be filling-in, and therefore the cutoff temporal frequency at which the COCE is perceived is predicted to increase with increasing spatial frequency. We investigated achromatic and chromatic COC gratings and measured for different spatial frequencies the maximum temporal frequency at which a brightness or color modulation was perceived. For both achromatic and chromatic COC gratings we found a pattern of results that was inconsistent with filling-in: For the achromatic COCE with spatial frequencies between 0.05 and 1.2 cycles/deg the cutoff temporal frequency had the shape of an inverted U, peaking at 0.2 cycles/deg. For the chromatic COC gratings modulated along either the $L - M$ or $S - (L + M)$ axis of DKL colour space the cutoff temporal frequency monotonically decreased with increasing spatial frequency. In a control experiment we asked observers to adjust the temporal frequency until no modulation at all was seen. The resulting curves for chromatic and achromatic COC gratings followed the same pattern as before but where shifted to higher temporal frequencies.

All observers reported that the COCE was stronger in the low contrast than the high contrast condition. This observation is consistent with previous experiments showing a reduction in the COCE with increasing achromatic (Burr, 1987) or chromatic contrast (Cole et al., 1993).

4.1. Comparison to other studies

The experiment with the achromatic COC grating was motivated by a similar study by Davey et al. (1998), who found that the critical temporal frequency increased with increasing spatial frequencies, i.e., that the dynamics of the achromatic COCE are consistent with filling-in. Davey et al. (1998) studied achromatic COC gratings of only rel-

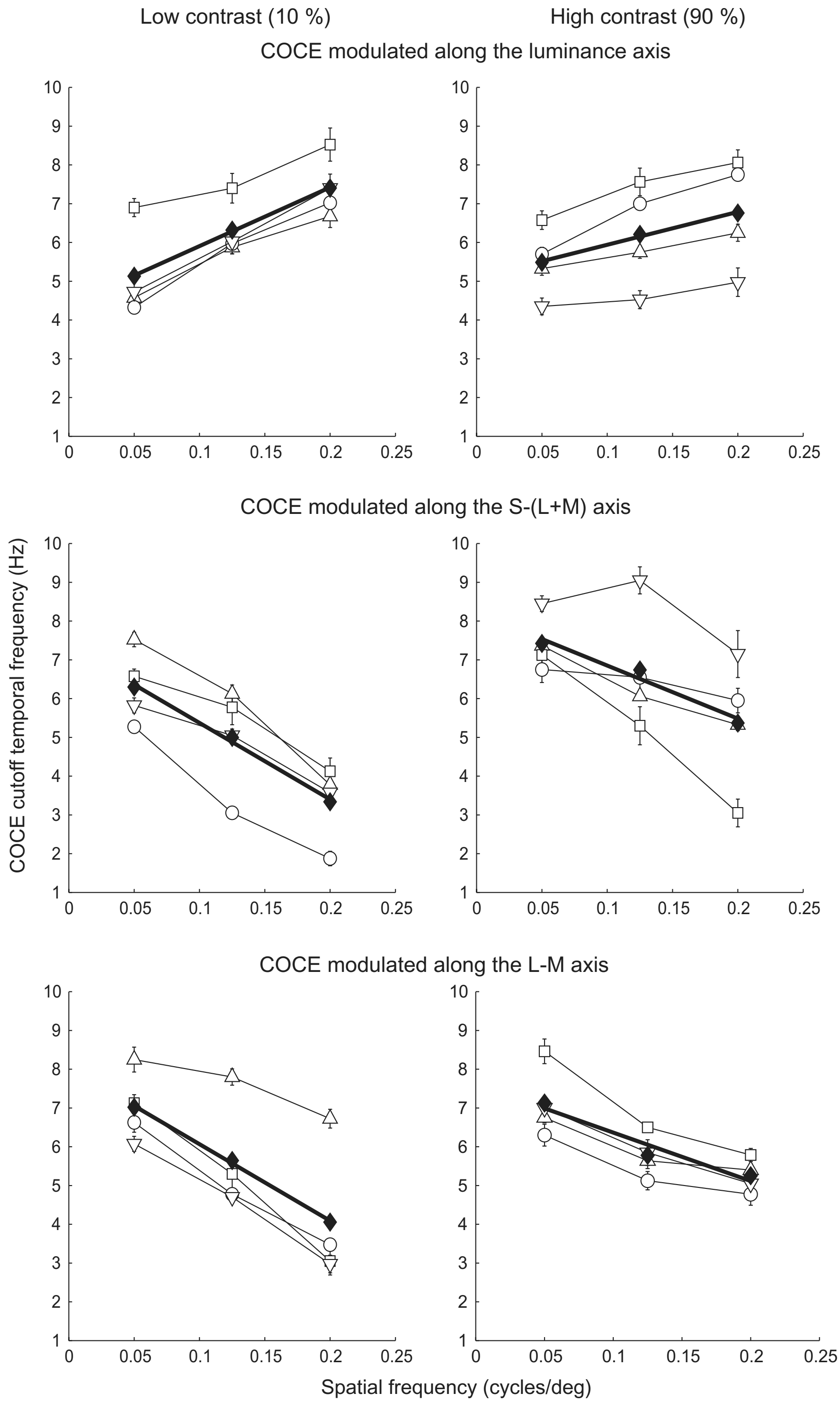

Fig. 2. Cutoff temporal frequency for a COC grating as a function of spatial frequency. Results are displayed for COC gratings modulated along the luminance (top panels), L − M (middle panels) and S-(L + M) axis, and for low (left panels) and high (right panels) contrast conditions. Symbols denote the mean for four different observers: subject 1 (□), subject 2 (○), subject 3 (▽) and subject 4 (△). Mean is shown by (⧫). Error bars show S.E. The bold line represents the fitted regression line.

atively low spatial frequencies below 0.212 cycles/deg. Here we employed also higher spatial frequencies up to 1.2 cycles/deg. For low spatial frequencies (below 0.2 cycles/deg) we found the same monotonic relationship between temporal and spatial frequencies as Davey et al. (1998). However, when the spatial frequencies increased above 0.2 cycles/deg, the cutoff temporal frequencies decreased, such that the overall pattern obtained for the achromatic COCE was inconsistent with filling-in. For the chromatic COCE, our data does also not support the

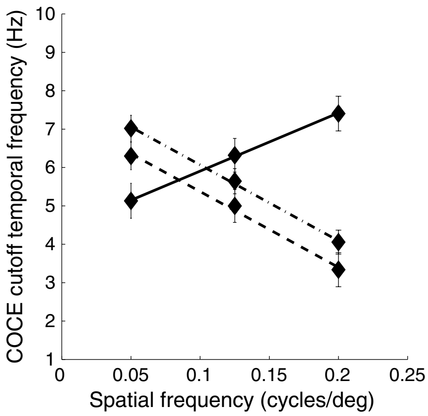

Fig. 3. Mean results at low contrast are displayed for the COCE modulated along the luminance axis (solid line), the S-(L + M) axis (dashed line) and the L − M axis (dash-dotted line). Error bars show S.E.

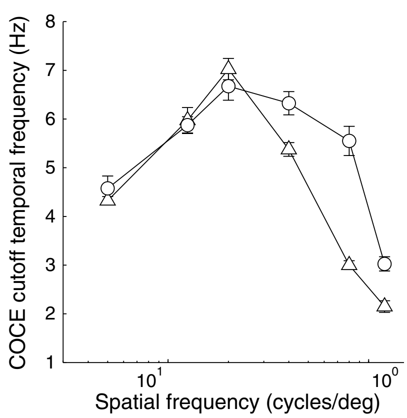

Fig. 4. Cutoff temporal frequency for an achromatic COCE at low contrast for six spatial frequencies ranging from 0.05 to 1.2 cycles/deg. Symbols indicate the mean results for two observers. Error bars show S.E.

filling-in hypothesis. For chromatic COC gratings modulated either along the S − (L + M) or L − M cone contrast axis, the critical temporal frequency decreased monotonically with increasing spatial frequency.

In a related study Rossi and Paradiso (1996) investigated the temporal limits of brightness induction in temporally modulated square-wave gratings. They found that the cutoff temporal frequency at which brightness induction occurs increased with increasing spatial frequency, consistent with the filling-in hypothesis. Rossi and Paradiso (1996) studied relatively high spatial frequencies up to 2 cycles/deg. The differences to the present study may be due the different stimuli used (square wave vs. COC gratings). Interestingly, for one observer (AR, their Fig. 2) Rossi and Paradiso (1996) also found a decrease in the cutoff temporal frequency for the highest spatial frequency.

The present data support the idea that features are detected early by the visual system, and that higher cortical areas compute surface brightness and color. This result is consistent with a previous fMRI study by Perna, Tosetti, Montanaro, and Morrone (2005). In their experiment, authors showed that the caudal region of the intraparietal sulcus and the lateral occipital sulcus responded specifically to the COCE, but V1 responded mainly to the retinotopic location of the edge but not to brightness illusion. This is also in agreement with electrophysiological studies showing that in cats a strong response to the COCE is recorded in V2, but a limited signal is recorded in V1 (Roe, Lu, & Hung, 2005). It has been shown for other patterns that V1 is neither the locus of conscious visual experience nor for filling-in. Krauskopf (1963) showed that stabilizing the contour of a red disk surrounded by a green annulus lead to the percept of a all-green disk, as if the green annulus filled-in the interior disk. Using a similar stimulus, von der Heydt et al. (2003) found that the neuronal response did not change while recording from neurons in V1 of the trained monkey, although the behavioral response indicated a perceptual change from red to green.

4.2. Implications for models of brightness perception

The present empirical study investigated the temporal aspects of the COCE and showed that the time course of the effect is inconsistent with models that assume a longer computation time for larges areas, such as filling-in on a single scale. This particular kind of model can be ruled out, while other models are still possible, such as a reweighting of spatial frequencies (Dakin & Bex, 2003), filtering approaches (Blakeslee & McCourt, 1999, 2001) or filling-in at multiple scales (Grossberg & Hong, 2006; Sepp & Neumann, 1999).

Filling-in models involve at least an implicit temporal component. The filling-in theory explains the COCE by a diffusion of activity from neurons responding to the edge to neighboring neurons corresponding to the illusory surface. Long-range interactions via horizontal cortical axons in area V1 have been assumed to provide the neural substrate of the large-scale convergence necessary for the filling-in process (Gilbert, 1996; Gilbert, Das, Ito, Kapadia, & Westheimer, 1996; Spillmann & Werner, 1996). Filling-in is based on an "isomorphic" representation, which assumes that brightness or color signals spread from the borders into uniform regions. The isomorphic filling-in hypothesis predicts a temporal cutoff for the perception of an induced brightness in the COCE, and this temporal frequency should increase with increasing spatial frequency. The results for the achromatic COCE (Fig. 4) and for the chromatic COCE are both inconsistent with this hypothesis.

To salvage filling-in for the present data, one would need to assume that it operates on multiple spatial scales, being largely independent of the size of the region to be filled in. Multi-scale filling-in approaches have been proposed for the processing of synthetic aperture radar images (Grossberg, Mingolla, & Williamson, 1995), to infer 3D shape from texture (Grossberg, Kuhlmann, & Mingolla, 2007) and to model brightness perception (Grossberg & Hong, 2006; Sepp & Neumann, 1999). The features that are filled in need to be detected, and thus filling-in breaks

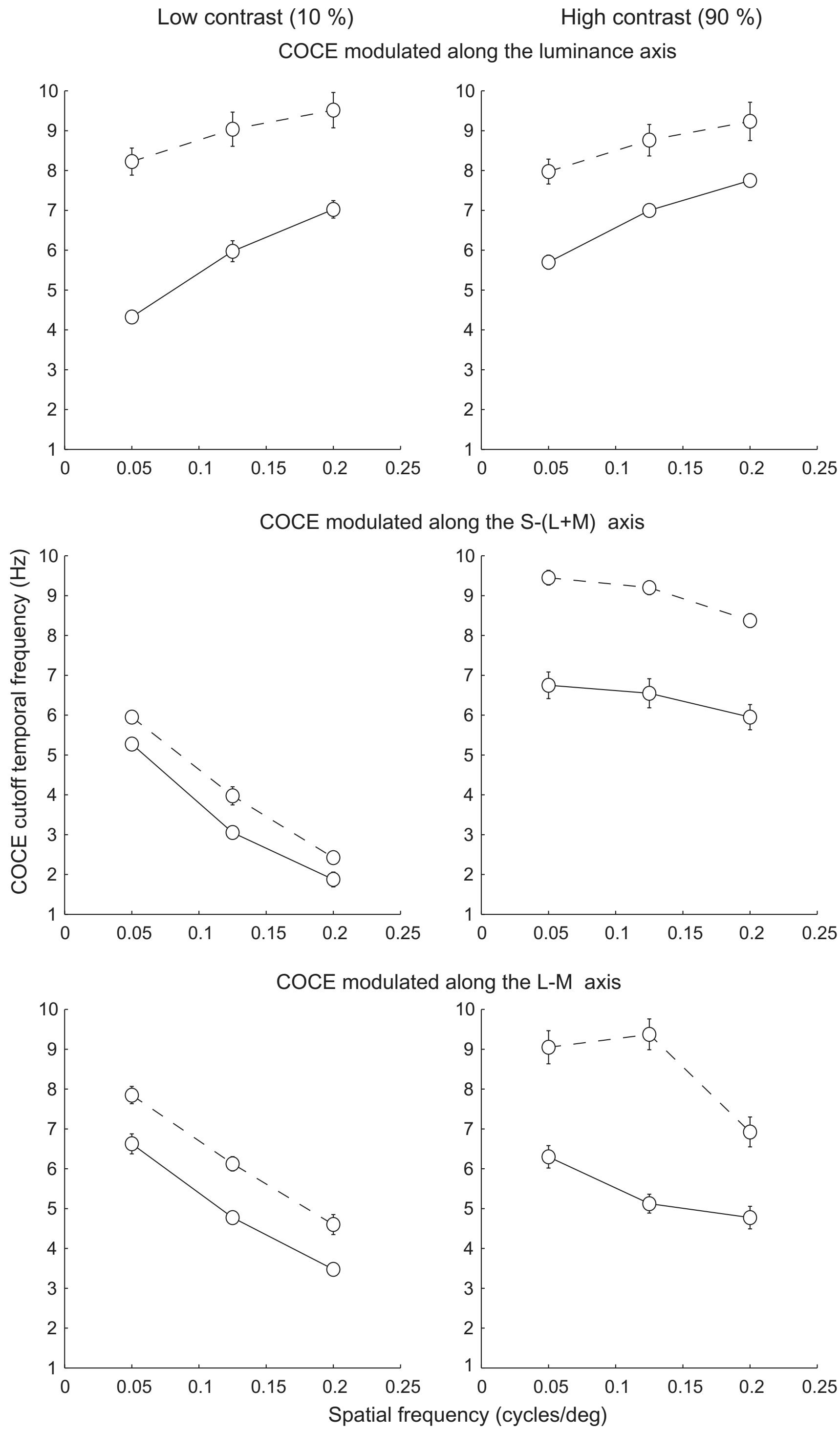

Fig. 5. Cutoff temporal frequency for the achromatic and the chromatic COCE at low and high contrast as a function of the spatial frequency. The solid lines represent the results for the main task where the observer adjusted the temporal COCE until it still perceived and the dashed lines indicate the results for the second task while observer adjusted the temporal frequency until no modulation at all was perceived. Error bars show S.E.

down with a characteristic similar to the spatio-temporal detection curves for achromatic and chromatic features.

The COCE has also been explained by a reweighting of the amplitude of spatial frequencies channels to match the average statistics of natural images (Dakin & Bex, 2003). The amplitude spectrum of natural images has on average a 1/f fall-off with spatial frequency (Field, 1987). The model of Dakin and Bex (2003) works iteratively by adjusting the measured amplitude of spatial frequency channels to match the average spatial frequency spectrum of natural images. Since the achromatic COCE deviates from the average statistics by having too little energy at low-spatial frequencies, these responses are amplified, causing the illusory brightness in the interior regions. In principle, the model by Dakin and Bex (2003) has a temporal component because it works iteratively and could thus make predictions about the temporal cutoff frequency of COCE modulations. However, Dakin and Bex (2003) regard this iterative reconstruction only as a vehicle to evaluate the way in which images are represented, and not as a model of an active reconstruction process occurring in human visual processing.

The natural scene statistics for achromatic and chromatic images are to a large degree similar (Párraga, Brelstaff, Troscianko, & Moorehead, 1998; Wachtler, Lee, & Sejnowski, 2001). We found that chromatic COCE exists, as has been shown previously (Van den Brink and Keemink, 1976; Wachtler and Wehrhahn, 1997; Ware and Cowan, 1983). This is accordance with the core idea of Dakin and Bex (2003) that an adjustment procedure reflects the statistics of natural scenes. However, we found that the temporal cutoff differed between chromatic and achromatic COC gratings, which cannot be explained by natural scenes statistics. An extended model of brightness and color processing to the temporal domain has to take information other than natural scene statistics into account.

The COCE has also been explained by a symbolic or interpretative theory. The symbolic theory assumes that the signals from the edge-detectors are integrated at a higher level to produce a response that represents the color or brightness of the surface. Symbolic models are largely unspecified and do not make any predictions about the time course of the COCE. To reconcile the symbolic theory with our data one has to assume recognition processes that are spatial frequency dependent, requiring communication between distant cortical cells. Then such an interpretative mechanism would have a propagation speed. Thus, recognition processes should be faster at lower spatial frequencies for an achromatic COCE and at higher spatial frequencies for a chromatic COCE.

The present results might also be explained by the difference between the shapes of the achromatic and chromatic contrast sensitivity function (CSF). The human achromatic CSF has a band-pass shape; the visual system is most sensitive to a band of spatial frequencies in the middle of the range. The chromatic CSF is low-pass; sensitivity is highest at low frequencies and decrease at middle and high frequencies (Mullen, 1985; Van der Horst & Bouman, 1969). Consequently, the chromatic COCE could be stronger than an achromatic COCE at low-spatial frequencies. This distinction might explain the fact that the chromatic COCE is persistent at higher temporal frequencies for low-spatial frequencies, while the achromatic COCE is persistent at higher temporal frequencies for medium spatial frequencies. The results of the two last experiments are in agreement with this explanation. Indeed, the second experiment showed that the cutoff temporal frequency of the achromatic COCE decreased with spatial frequencies increasing above 0.2 cycles/deg (Fig. 4). This decrease occurs at high spatial frequencies, inconsistent with filling-in but consistent with the band-pass shape of the achromatic CSF. Finally, the data from the third experiment indicated that the maximum temporal frequency at which a modulation can be detected at all is higher than the critical temporal frequency for the perception of the COCE.

To summarize, our results are inconsistent with the idea that the temporal dynamics of the COCE, both achromatic and chromatic, are due to a process that takes longer for larger areas, such as a basic filling-in model operating on a single scale. We found that the chromatic and achromatic COCEs break down with a characteristic similar to the spatio-temporal detection curves for achromatic and chromatic features.

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