Journal of Vision (2007) 7(14):19, 1–14 http://journalofvision.org/7/14/19/

Color constancy improves, when an object moves: High-level motion influences color perception

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Color constancy refers to our remarkable ability to perceive the color of objects nearly constant despite considerable changes in the spectral content of the illumination. As such it is most important for object recognition. Visual motion can make object recognition harder because it limits the viewing time and increases the likelihood that an object encounters illumination changes. However, color constancy, as human color perception in general, has long been thought to be "motion blind." Here I show that, on the contrary, human color constancy is influenced by motion and improves when a color surface moves. Psychophysical experiments revealed that color constancy is influenced specifically by slow object motion and depends on the saliency of the moving figure. These surprising findings cannot be explained by low-level co-processing of color and motion signals. Instead they demonstrate a previously unknown influence of attention-driven, high-level motion processes on cortical color computation. Since motion is a frequent aspect of natural visual scenes, the synergistic integration of color and motion signals is an important mechanism for improving color identification. The new findings speak against a strict segregation of color and motion processing in the human visual cortex and suggest a network for encoding object color, which includes specialized ventral as well as dorsal visual areas.

Keywords: color constancy, color, object motion, perception, visual pathways, cortex

Citation: Werner, A. (2007). Color constancy improves, when an object moves: High-level motion influences color perception. *Journal of Vision, 7*(14):19, 1–14, http://journalofvision.org/7/14/19/, doi:10.1167/7.14.19.

Introduction

The functional segregation of color and motion processing has been a cornerstone in our understanding of the organization of primate visual cortex (segregated pathway hypothesis: Livingstone & Hubel, 1988; Zeki, 1990). Color—together with other object-related features such as form and texture—is analyzed primarily in the ventral pathway, which extends from V1 through V2 to V4 and to the inferotemporal cortex, where object recognition is mediated (Gegenfurtner, 2003; Werner, Smith, Pokorny, Kremers, & Greenlee, 2005). On the other hand, motion patterns such as global motion, motion parallax, biological motion, and object motion are analyzed within networks in higher tier areas of the dorsal pathway (Blake, Sekuler, & Grossman, 2004; Werner et al., 2005).

However, recently the strict segregation of color and motion processing has been questioned. A wealth of physiological, psychophysical, and functional magnetic resonance imaging (fMRI) studies have demonstrated chromatic sensitivity of motion processes in several areas of the dorsal pathway (as reviewed in Cropper & Wuerger, 2005; Hawken & Gegenfurtner, 1999). In particular, a high-level, color-sensitive motion system has been identified in the human inferior parietal lobe (Claeys, Lindsey, De Schutter, & Orban, 2003; Lu, Lesmes, & Sperling, 1999; Seiffert & Cavanagh, 1999). Likewise, motion sensitivity has been demonstrated in monkey area V4 (Tolias, Keliris, Smirnakis, & Logothetis, 2005) and anatomical studies show neural connections between motion processing areas in the dorsal pathway and color processing areas in the ventral pathways (Felleman & van Essen, 1991). The functional consequences, however, of these findings for color perception are not known.

Here, I investigate the influence of motion on the perceptual phenomenon of color constancy. Color constancy is a central aspect of our color vision since it aims at the representation of color as an intrinsic property of objects, independent of their illumination or background. In humans, color constancy is mediated by a series of sensory, perceptual, and cognitive processes, which start in the retina and culminate in the ventral pathway of the visual cortex. Computational steps to achieve color constancy include local and global sensory mechanisms of sensitivity adjustment by temporal adaptation to the ambient light conditions and the encoding of visual signals as spatial contrasts (Hurlbert & Wolf, 2004; Kraft & Brainard, 1999; Land, 1986; Smithson, 2005). Spatial contrast contributes to color constancy because the resulting signals represent ratios, which tend to be invariant under changes of daylight illumination (Foster & Nascimento, 1994). In addition, perceptual factors play an important role, for example scene segmentation (Brill, 1990; Hurlbert, 1998; Werner, 2006). High-level cognitive influences, such as the knowledge about the effect of mutual illumination in three-dimensional scenes (Bloj, Kersten, & Hurlbert, 1999), have also been demonstrated. Activity of the human V4 complex in the ventral occipitotemporal cortex has been associated with color constancy (Bartels & Zeki, 2000; Zeki, Aglioti, McKeefry,

doi: 10.1167/7.14.19 Received March 13, 2007; published December 28, 2007

& Berlucchi, 1999) although the processes leading to this phenomenon do not seem to be restricted to one cortical area alone (Barbur, de Cunha, Williams, & Plant, 2004; Hurlbert, Bramwell, Heywood, & Cowey, 1998; Walsh, 1999).

Color constancy has been investigated extensively since its first description in 1789 (Monge's study as cited in Mollen (2006); von Helmholtz, 1867; Land, 1964; see also review in Smithson, 2005). However, to my knowledge, all studies considered exclusively static stimuli. This is surprising, since under realistic viewing conditions, the retinal image nearly always moves: the motion of the observer produces global motion patterns (translation, rotation, expansion, and contraction); frequently, visual objects themselves move actively or passively (object motion); finally, fixating an object while the observer moves will produce relative motion of objects in other depth planes (motion parallax). So, what happens to color constancy when the image moves?

To understand whether and how motion influences color constancy, the phenomenon was quantified in psychophysical experiments using multicolored displays with moving stimuli. Five observers (four naïve observes as well as the author) participated in the experiments. The results revealed a strong and specific influence of object motion on color constancy and suggest input from high-level motion systems into cortical color computations.

Methods

Experimental set up

The stimuli were presented in a dark room on a calibrated 21-in. CRT monitor (BARCO) at a refresh rate of 100 Hz. The monitor was driven by a VSG2/4f graphic board (Cambridge Research Systems) with 15 bits resolution per gun.

In order to shield any stray light in the room from the monitor display, a box lined inside with black velvet was attached to the front of the monitor screen (Figure 1). The observers used a headrest and viewed the stimuli from a distance of 80 cm binocularly through this "black box."

Subjects

Five subjects aged between 19 and 47 years were individually tested. All but one (AW) were naïve to the purpose of the experiments and all had normal color vision (Cambridge Color Test) and normal or corrected-to-normal visual acuity. The Ethics Commission of the University of Tuebingen Medical Faculty approved the experiments and informed consent was obtained from each observer.

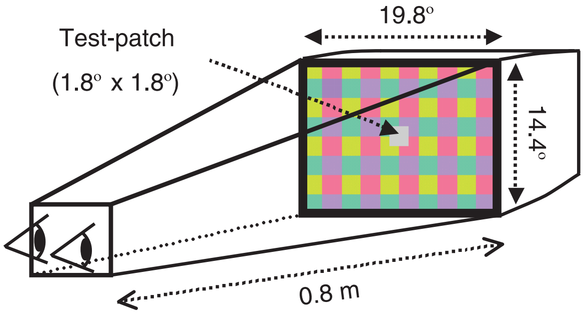

Figure 1. The experimental set up.

Stimuli

The test pattern (14.4° × 19.8°) covered the entire display (Figure 1). It consisted of 1.8° × 1.8° patches, which were arranged in the form of a checkerboard.

The rectangular test patch (1.8° × 1.8°) was presented in front of the checkerboard. Two types of background-patterns were used, a heterochromatic and a gray-level version. For the heterochromatic pattern, the chromaticities of the patches were chosen from the $L - M$ and $S - (L + M)$ axes in color space (Figure 2). Their CIE 1976 $L^*u^*v^*$ coordinates were in the standard condition: 50.60, 0.20, 0.47 (test patch), 40.40, 0.23, 0.46 (red patch), 40.40, 0.17, 0.47 (green patch), 50.60, 0.20, 0.44 (blue patch), 50.60, 0.19, 0.50 (yellow patch), the mean over the background was 45.49, 0.20, 0.47. The chromaticity of the gray-level pattern was equivalent to the mean of the heterochromatic pattern [under standard condition: 40.40, 0.20, 0.47 (dark patches) and 50.60, 0.20, 0.47 (light patches)].

Color constancy was measured for the transition from a neutral illumination (D65, standard condition) to one of two colored test illuminants ("Red" or "Green" test conditions, Figure 2; for the experimental sequence, see Figure 3). For the illumination changes, the color loci of all patches were shifted equally by a specific distance (CIE 1976 ($L^*u^*v^*$) color difference: 66.7 ΔE^*_{uv}; Equation 2) along the $L - M$ axis in an equiluminant plane in color space (see arrows in Figure 2). This was achieved by applying weighting factors to the underlying receptor values (Vos & Walraven, 1971). The weighting factors were determined by the amount of change in the receptor values that was necessary to obtain the specified shift for the color locus of the test patch. Identical scaling factors were then applied to calculate the new color loci of the other patches of the test pattern.

Color constancy was examined for one static and four different motion conditions. In the case of the static condition, the test patch remained fixed in the center of the static background, as shown in Figure 1. In the motion conditions, either the test patch alone, the background alone or both together moved. The actual combinations of background and test patch motions depended on the respective test condition and are described in connection with the actual experiments.

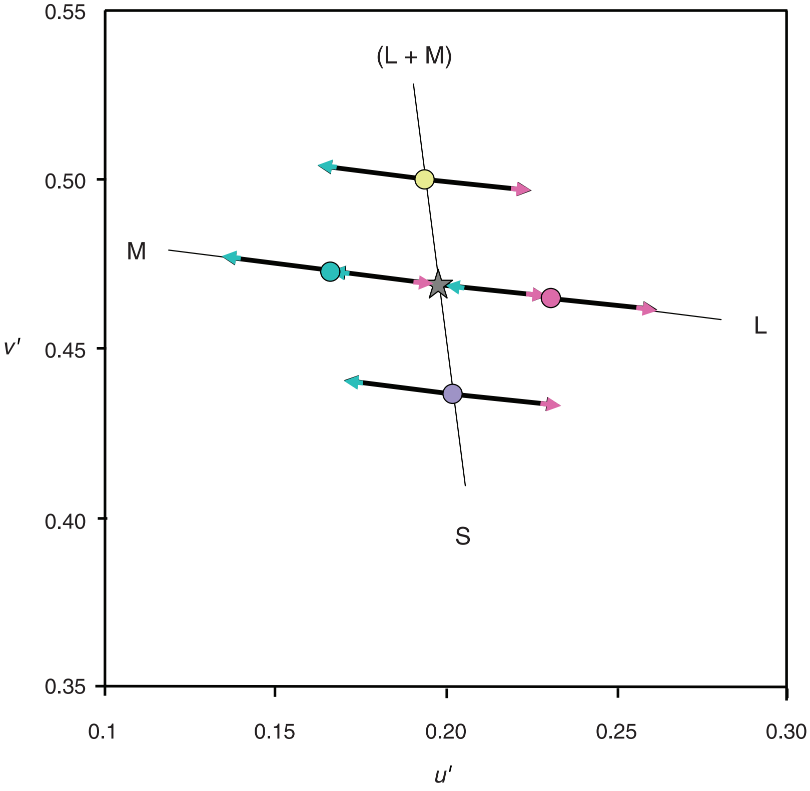

Figure 2. CIE 1976 UCS diagram illustrating the *u*′, *v*′ coordinates of the heterochromatic test pattern in the different illumination conditions: star refers to the color locus of D65 and of the test patch in standard condition; filled circles refer to the color loci of the background patches in standard condition; arrowheads indicate the shift of the color loci of test and background patches following the illumination changes toward "Green" and toward "Red," respectively. Thin black lines indicate the L − M and the S − (L + M) axes.

In the motion conditions, the test patch moved horizontally with a constant velocity (2.4° s^{-1} in Experiments 1–3, 1.2° s^{-1} to 14.4° s^{-1} in Experiment 4) and continuously along the mid-line of the background pattern, from the right edge of the display to its left. The test patch then disappeared and at the same moment re-appeared on the right side of the screen to continue its motion in the same direction as before across the display.

The background motion was a continuous, horizontal displacement from right to left, with a speed of 2.4° s^{-1}.

Procedure

In order to achieve an equilibrium state of adaptation, each session commenced with a 600-s dark adaptation period, which was followed by a 120-s adaptation period to the test pattern under standard condition. At the beginning of a test series, the individual achromatic color locus ("Gray") was determined for each subject and was in all cases less than 1 ΔE^*_{uv} from the color locus of D65. "Gray" was defined as neither reddish nor greenish and neither bluish nor yellowish.

The actual experimental sequence (Figure 3) started with a 15-s adaptation to the test pattern under standard illumination (D65). Thereafter, the illuminant setting was changed to one of the test illuminants ("Red" or "Green") and this test adaptation was presented for 5 s. During the adaptation to the new test illuminant, the initially perceived greenish or reddish tint of the test pattern gradually diminished. This was followed by a 600-ms test interval, within which the observer was required to judge whether or not the test patch appeared achromatic (i.e., "Gray"). Color constancy was then quantified by an achromatic setting (see below). The test sequence was completed by a 3-s presentation of a blank (black) screen, in order to avoid the subsequent perception of colored aftereffects, which may influence the color judgments of the observers.

The sequence was then repeated, starting with re-adaptation to the test pattern under standard illumination. This procedure was used in order to ensure that color constancy was measured for a constant state of adaptation, i.e., 5 s adaptation to the new test condition. Both, the test patch and the background were visible during the entire duration of a test sequence, except during the last 3 s, where a blank screen was presented. Also, please note that the test patch (and/or the background) continued moving throughout the entire sequence (except of course, in the static condition).

The achromatic setting was achieved by a hue-cancellation method: If the test patch did not appear achromatic

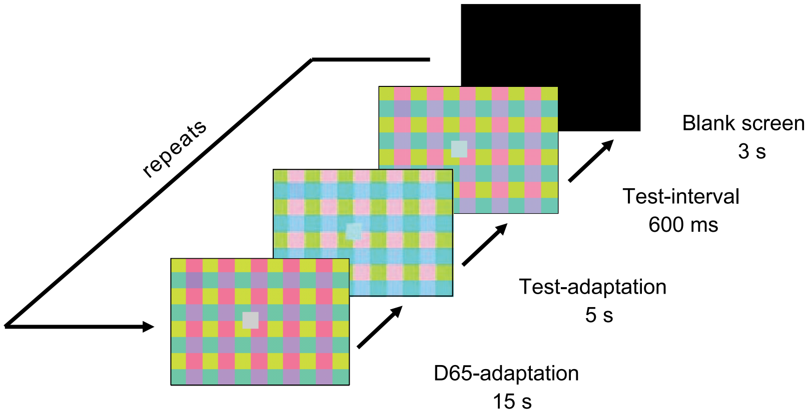

Figure 3. Experimental sequence. The experimental sequence commenced with 15 s adaptation to the pattern in standard condition (D65 adaptation), followed by 5 s adaptation to the pattern in “Red” or “Green” condition (test adaptation, here: green) and the 600-ms test interval. After the presentation of a 3-s black screen, the sequence was repeated.

during the test interval, the remaining tint was nulled using a keyboard device. The nulling was achieved by changing the illuminant setting of the entire test pattern so that the chromaticities of all patches (test and background) were changed equally. In other words, the effect of the nulling was to “reduce” the previous illumination change. Thus, rather than changing the chromaticities of the test patch alone, this procedure ensured that the chromatic ratios between the test patch and the background remained constant throughout the experiment.

The new setting was presented during (and only during) the following test interval in order to ensure that the observer would not adapt to the new setting.

The nulling procedure was repeated until the subject was satisfied with the setting of the achromatic color locus, which was then recorded.

Altogether, each achromatic setting took approximately 10 min and was repeated ten times, during two sessions on consecutive days.

Data analysis

Data are presented as CIE1976 $L^*u^*v^*$ coordinates of the averaged achromatic settings of each observer and the corresponding constancy indices (CI). The CI were used to quantify color constancy and refer to the shift of the subjective achromatic color locus relative to the shift of the color locus of the illuminant. A constancy index of 1 indicates perfect color constancy, a constancy index of 0 indicates no color constancy. The statistical analysis was carried out using single factor ANOVA.

Calculation of the constancy index (CI)

The CI is calculated as the relative color difference between the adjusted achromatic color locus in the standard condition ($\mathrm{Ach}_{\mathrm{D65}}$) and the test condition ($\mathrm{Ach}_{\mathrm{Test}}$) compared to the color difference between the color locus of the standard illuminant ($\mathrm{Cl}_{\mathrm{D65}}$) and the test illuminant ($\mathrm{Cl}_{\mathrm{Test}}$):

$$\mathrm{CI} = |\mathrm{Ach}_{\mathrm{D65}} - \mathrm{Ach}_{\mathrm{Test}}| / |\mathrm{Cl}_{\mathrm{D65}} - \mathrm{Cl}_{\mathrm{Test}}|. \tag{1}$$

The color differences between the color loci, each given in terms of L^*, u^*, v^*, is calculated from the CIE 1976 ($L^*u^*v^*$) color difference formula as

$$\begin{aligned} \Delta E^*_{\mathrm{uv}} &= \sqrt{(\Delta L^*)^2 + (\Delta u^*)^2 + (\Delta v^*)^2} \\ L^* &= 116(Y/Y_n)^{1/3} - 16 \\ u^* &= 13L^*(u' - u'_n) \\ v^* &= 13L^*(v' - v'_n), \end{aligned} \tag{2}$$

where Y_n, u'_n, and v'_n are the luminance and chromaticity values of a white reference (50.60, 0.20, 0.47), which also happens to be the test patch under standard illumination.

Results

Experiment 1

In the first series of experiments, color constancy was compared for the static and the motion condition. In the

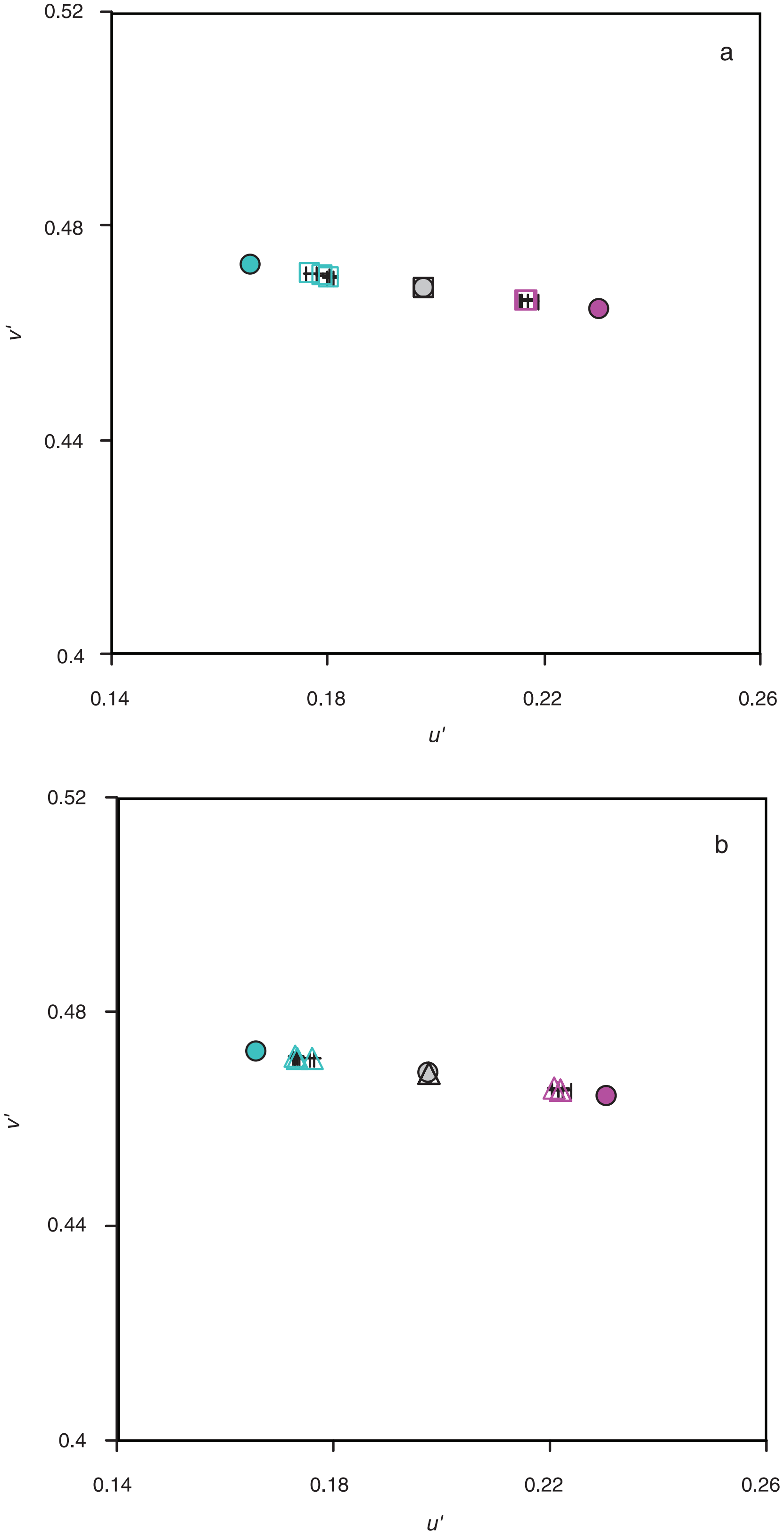

Figure 4. CIE 1976 UCS diagram showing the *u*′, *v*′ coordinates of the achromatic settings from Experiment 1. (a) Individual achromatic chromaticities of four observers (EM, AW, II, BR) in the static condition (open squares). (b) Achromatic chromaticities of the same observers in the motion condition (open triangles). Green and red open symbols refer to the settings after illumination changes toward "Green" and "Red," respectively. Black open symbols indicate the achromatic settings in the standard condition. Filled circles (gray, red, and green) refer to the chromaticities of the test patch under the respective illuminations (D65, "Red," and "Green"). Error bars show ±1 *SEM*.

static condition, the test patch remained fixed in the centre of the background. In the motion condition, the test patch moved horizontally with a constant speed of 2.4° s^{-1} across the background, which remained static. The background pattern was heterochromatic and color constancy was measured for illumination changes toward red and green.

Figure 4 shows the individual achromatic settings in the static and the motion condition, obtained from four observers, and for two illumination changes (from D65 to either “Red” or “Green”). Note that the inter-individual differences between the settings were very small. Following an illumination change, the subjective achromatic color locus of each observer shifted from its location in the standard condition (near D65) toward the locus of the test patch under the new illumination. These shifts were larger in the motion condition than in the static condition, as quantified by calculating the corresponding constancy indices (Equation 1).

Figure 5 shows the individual constancy indices of each observer and both illumination changes, in the static and the motion condition: Color constancy performance of all observers increased significantly in the motion condition as compared to the static condition (ANOVA: AW (Red): $F(1, 18) = 29.48$, $P = 3.7 \times 10^{-5}$; AW (Green): $F(1, 18) = 18.76$, $P = 0.0004$; EM (Red): $F(1, 18) = 11.09$, $P = 0.0037$; II (Red): $F(1, 18 = 9.87$, $P = 0.0056$; II (Green): $F(1, 18) = 188.02$, $P = 5.73 \times 10^{-11}$; BR (Green) = 16.13, $P = 0.0008$).

Experiment 2

The following experiments were conducted in order to identify the functional stage of motion analysis, which is involved in color constancy. If low-level motion signals from an early stage in the visual pathways were involved, then an enhancement of color constancy would be expected for all types of motion patterns. If, however, higher stages of motion processing were involved in color constancy, then a more specific influence of particular motion patterns, such as object motion, global motion, or motion parallax on color perception would be expected. In the following experiments, color constancy was measured using test patterns that corresponded to these different motion paradigms.

The object motion condition was identical to the motion condition as described in the previous experiment. For the global motion condition (translation), the background and the test patch moved with identical speed and direction. For the motion parallax condition, only the background moved, while the test patch remained statically in the centre of the screen. Motion speed and direction were identical in all experiments (horizontally with a constant speed of 2.4° s^{-1}). In order to ensure that

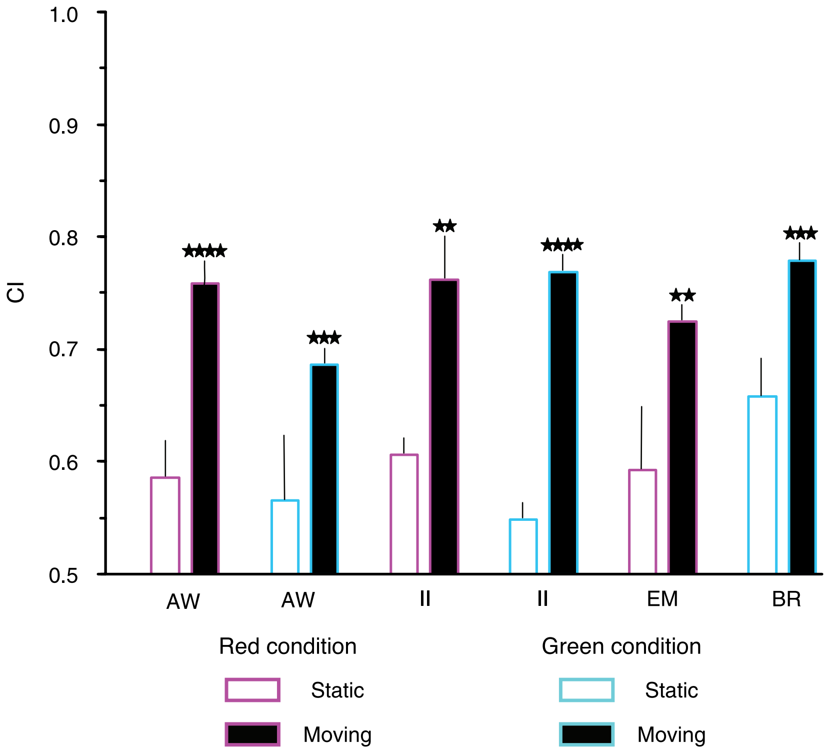

Figure 5. The influence of motion on color constancy. The figure shows the constancy indices of the same observers and test conditions as in Figure 4, whereby the color of the bars refers to the color of the illumination change (toward “Red” or “Green”). The open bar of each double block refers to the static condition, and the filled bar to the motion condition. Error bars show ±1 *SEM*.

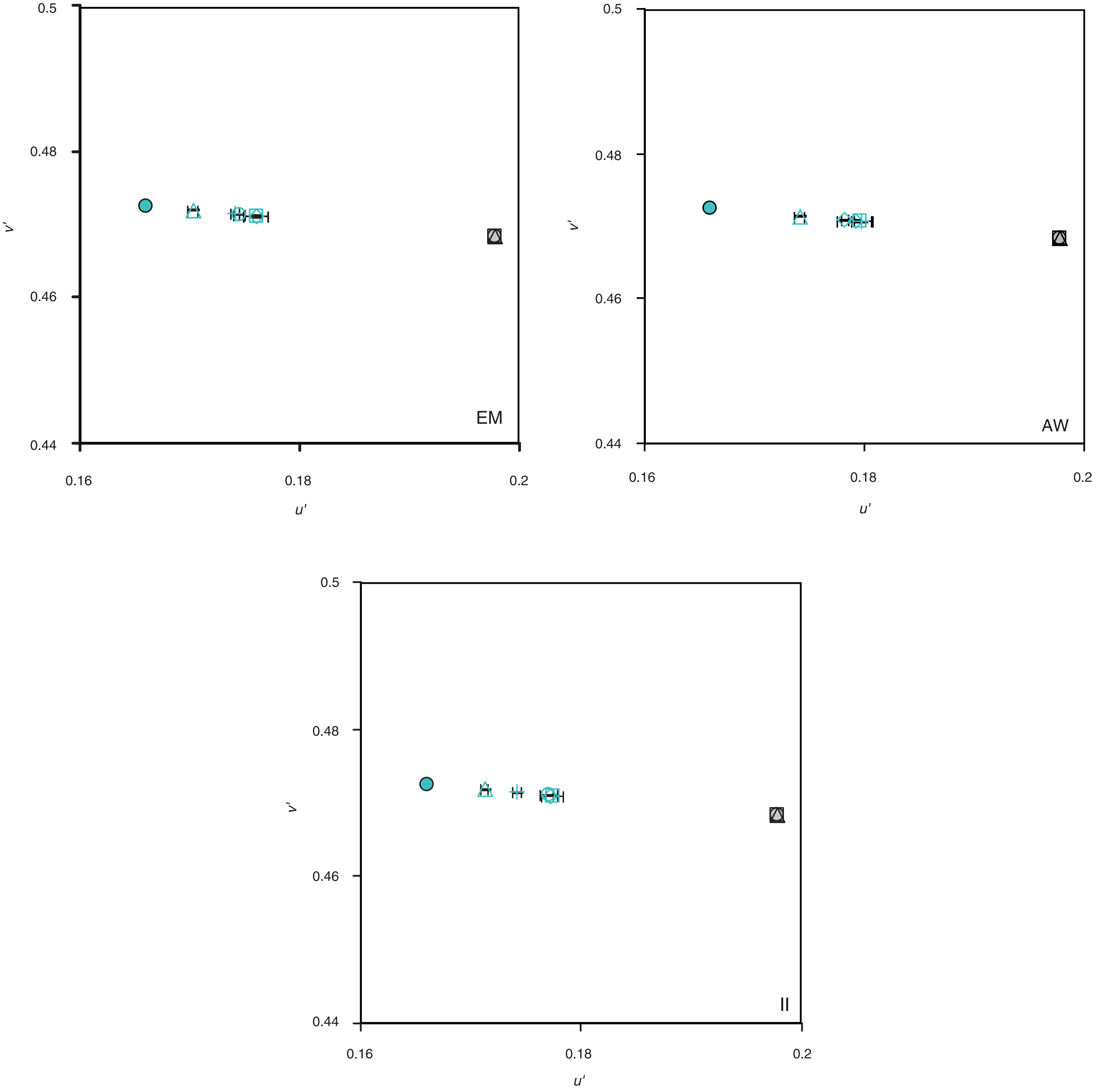

Figure 6. CIE 1976 UCS diagram showing the *u*′, *v*′ coordinates of the achromatic settings from Experiments 2 and 3. Individual data of each of the three observers (EM, AW, and II) are shown. Open green symbols refer to the settings after illumination change toward “Green” in the following test conditions: square: static condition; circle: global motion; diamond: motion parallax; triangle: object motion; cross: ambiguous motion. Open black symbols indicate the achromatic settings in the standard condition. Filled circles (gray and green) refer to the chromaticities of the test patch under the respective illumination (D65 and “Green”). Error bars show ±1 *SEM*.

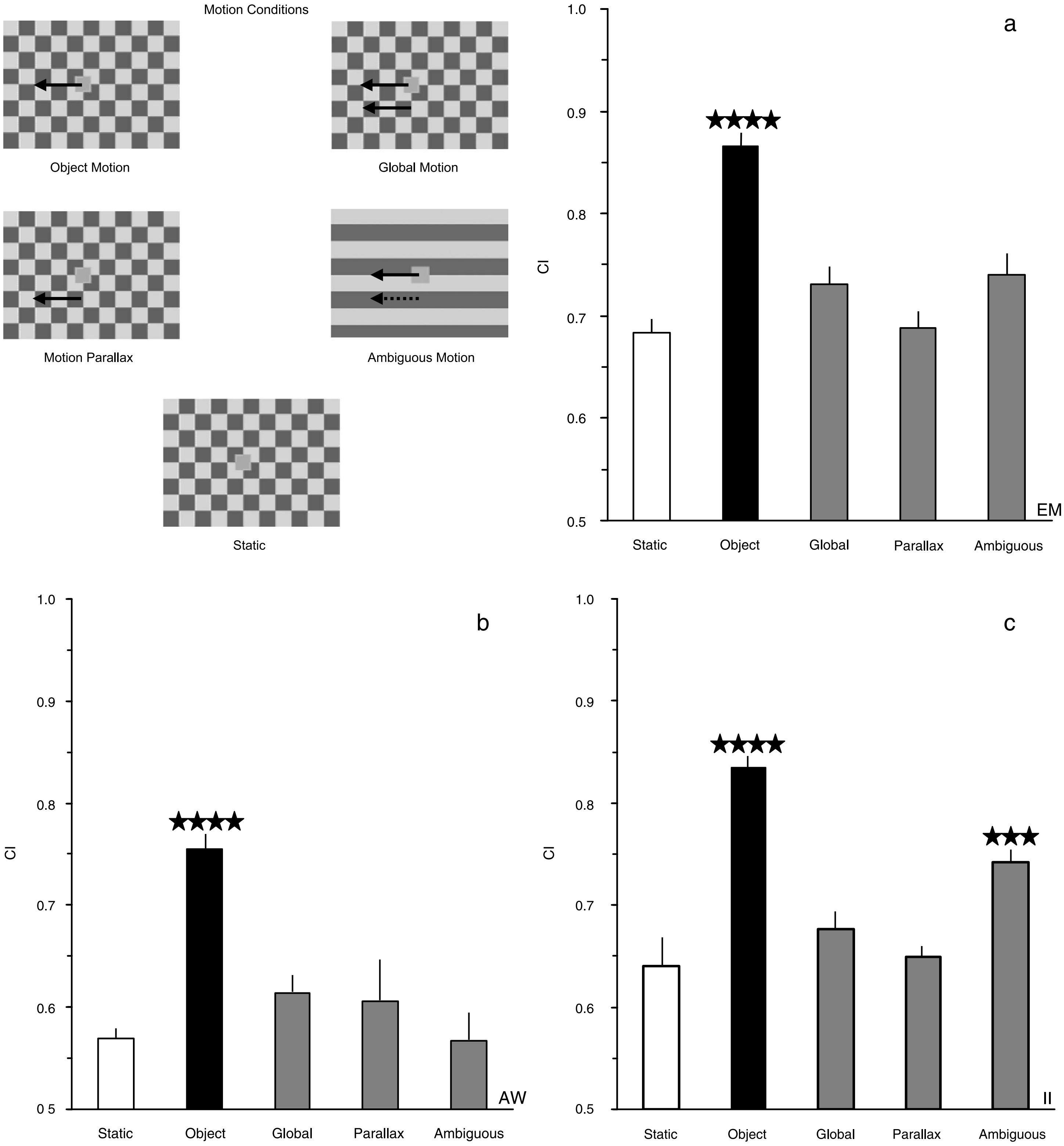

Figure 7. Color constancy measured for different motion paradigms. Panels a–c show the constancy indices of three different observers (EM, AW, and II), the inset on the left illustrates the different motion conditions. Static: color constancy with static test patch; object motion: motion of the test patch relative to the static background; global motion: test patch and background move with identical speed and direction; motion parallax: background moves relative to the static test patch; ambiguous motion: test patch moves along a static horizontal grating. Error bars show ±1 *SEM*.

the saliency of the test patch was determined by the motion patterns, and not by color contrast, the heterochromatic test pattern was replaced by an equivalent gray-level pattern, which was perceived under standard condition as achromatic. All other experimental parameters remained unchanged. Data were obtained from three of the four subjects (EM, AW, II) who took part also in Experiment 1, the fourth subject (BR) was no longer available for the tests.

Figure 6 shows the achromatic settings of each of the observers, measured for the different motion paradigms as well as for the static condition. Figure 7 presents the corresponding CI values.

The results demonstrate that object motion significantly enhances color constancy relative to the static condition (ANOVA: EM: $F(1, 18) = 32.45$, $P = 2.11 \times 10^{-5}$; AW: $F(1, 18) = 88.81$, $P = 2.21 \times 10^{-8}$; II: $F(1, 18) = 48.43$, $P = 1.68 \times 10^{-6}$) but that global motion and motion parallax do not (ANOVA: AW: $F(2, 27) = 0.91$, $P = 0.42$; EM: $F(2, 27) = 1.16$, $P = 0.33$; II: $F(2, 27) = 1.11$, $P = 0.35$). In other words, color constancy is *specific* for the object motion.

Experiment 3

Another set of experiments was carried out in order to discriminate between the role of lower and higher order motion systems in color constancy. Low-level, energy-driven motion systems analyze luminance modulations and texture differences, respectively. On the other hand, high-level motion analysis is engaged when tracking a moving object and depends on the saliency of the target (Cavanagh, 1992; Lu & Sperling, 1995). Moreover, it shows a much lower temporal cut-off frequency (3–6 Hz) than that of low-level motion systems (around 12 Hz; Lu & Sperling, 2001).

First, the significance for color constancy of the saliency of object motion was tested. The background of the test pattern consisted of a horizontal grating of the same spatial frequency as the test patch; its chromaticities, luminance values, and image contrast were identical to the previous gray-level test patterns. The test patch moved with constant speed (2.4° s^{-1}) horizontally along the middle stripes of the background grating (see inset "ambiguous motion" in Figure 7). After prolonged (more than 30 s) viewing of this pattern, the observers reported that either the test patch appeared to move across a static background or the target and the background both appeared to move together—like an object on a conveyer belt, whereby the strength of this impression varied across observers.

As can be seen from Figure 7, color constancy in the ambiguous condition did not reach the amount measured for the object motion condition (ANOVA: EM: $F(1, 18) = 58.66$, $P = 4.53 \times 10^{-07}$; II: $F(1, 18) = 44.33$, $P = 3.02 \times$

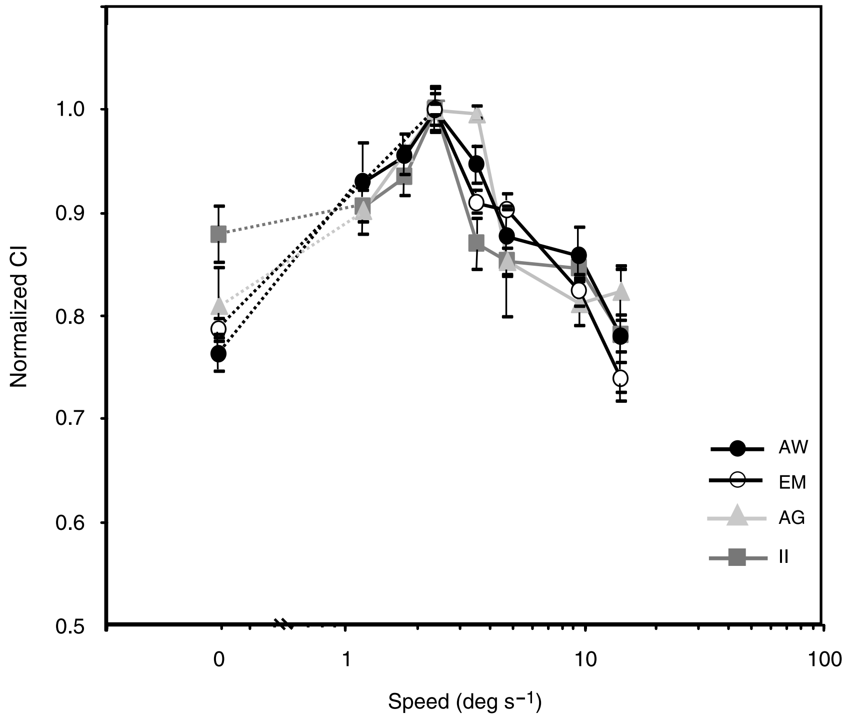

Figure 8. Color constancy as a function of object speed. The different solid symbols refer to the color constancy performance of four different observers. The data were normalized with respect to the maximum of each individual curve. Error bars show ±1 *SEM*.

10^{-06}; AW: $F(1, 18) = 42.8$, $P = 3.79 \times 10^{-6}$), although in one observer, it was raised relative to the static condition (ANOVA: II: $F(1, 18) = 13.18$, $P = 0.002$). For the other two other observers, color constancy in the ambiguous condition was not different from that in the static condition (ANOVA: EM: $F(1, 18) = 3.16$, $P = 0.09$; AW: $F(1, 18) = 0.006$, $P = 0.94$). It is therefore concluded that the reliable identification of object motion against the background motion is an important factor for inducing the enhancement of color constancy.

Experiment 4

Next, color constancy was determined as a function of the speed of the test patch. In these experiments, the test patch moved across the gray-level checkerboard pattern as before in the object motion condition, but its speed was varied between the experiments from 1.2° s^{-1} to 14.4° s^{-1} (corresponding to 0.33 Hz to 4 Hz temporal frequency). By varying, at motion onset, the starting position of the moving test patch along its horizontal track, it was ensured that the test patch was during the test interval always in the center of the screen.

The results of four observers revealed that color constancy is a band pass function of the speed of the moving target (Figure 8): Color constancy first increased with increasing speed of the test patch and showed a maximum at speeds between 2.4° s^{-1} and 3.6° s^{-1}, which was strikingly consistent amongst the 4 observers. With a further increase in speed, the performance dropped sharply (half value of the decrease was in the range of 2.9° s^{-1} to 5.7° s^{-1}). At a speed of 14.4° s^{-1}, the color constancy performance of all observers was level with static color constancy.

Discussion

The experiments clearly demonstrated that color constancy is improved when we judge the color of a moving object as compared to a static object. This phenomenon cannot simply be explained by a decrease in color discrimination as a result of the motion of the test patch, since motion facilitates rather than inhibits the detection of a chromatic change (Kreegipuu, Murd, & Allik, 2006). So, how can one explain the influence of image motion on color constancy?

The findings here are consistent with the reported facilitation of a number of other color tasks by motion: image segmentation by color (Moller & Hurlbert, 1997), the spreading of illusory colors (Chen & Cicerone, 2002), the detection of chromatic changes (Kreegipuu et al., 2006), and the perception of color transparency (Gerardin, Roud, Süsstrunk, & Knoblauch, 2006). It has been proposed that these effects may be explained by interactions between color and motion at an early stage in the visual pathway, for example by co-processing in double-duty neurons in V1 (Leventhal, Thompson, Liu, Zhou, & Ault, 1995; Vidyasagar, Kulikowski, Lipnicki, & Dreher, 2002). However, the exact origin of these enhancements and their implications for color perception remained unclear.

The fact that the enhancement of color constancy is specific for object motion (Figure 7) argues against an explanation based on a low-level co-processing of color and motion. If this were the case, we would have expected an unspecific enhancement of color constancy by all types of motion patterns. Instead, the phenomenon clearly is object specific. So, what distinguishes object motion from the other motion paradigms and how may this influence color constancy?

One possibility is that it may increase the amount of information available for the computation of color constancy, i.e., the number of contrast signals available. Furthermore, the motion of the test patch relative to the stationary background produces a temporal modulation of chromatic signals at its edges, which in turn may result in stronger contrast signals in the visual system. Both could be significant for the observed enhancement of color constancy, since an increase in the articulation of a visual scene has previously been shown to enhance color constancy (Werner, Sharpe, & Zrenner, 2000). However, in that case we would have to expect a similar increase for all conditions involving relative motion, that is object motion and motion parallax alike. Furthermore, it was shown in previous, independent experiments that color constancy is not enhanced by the temporal modulation of the test pattern (Werner, 2003). Thus, increased contrast processing does not explain the results.

Recently, the importance of image segmentation for color constancy has been stressed on theoretical as well as empirical grounds (Brill, 1990; Hurlbert, 1998; Werner, 2006). Since image segmentation by color is improved if motion is added (Moller & Hurlbert, 1997), this may explain the findings. But again, enhanced segmentation would then have been expected also for the motion parallax condition.

Another possible explanation is the influence of tracking eye movements, which have been reported to affect chromatic adaptation (Bompas & O'Regan, 2006), another key sensory process for color constancy. However, eye tracking was also present in the global motion condition, where *no* enhancement of color constancy was observed. Thus, this alone also cannot explain the results.

Alternatively, attention may play a role, since it is known to improve visual performances, such as contrast sensitivity, spatial resolution or apparent stimulus contrast (Carrasco, Ling, & Read, 2004; Carrasco, Penpeci-Talgar, & Eckstein, 2000; Yeshurun & Carrasco, 1998). But attention was directed to the color of the test patch in all experiments, and it is therefore difficult to understand why attention should have been more effective in the object motion condition.

However, attention could be involved in a different way: The motion of the test patch is likely to capture attention because of its high saliency and this could in turn activate a high-level motion system (Cavanagh, 1992; Lu & Sperling, 1995). The results of the "conveyer belt experiment" demonstrated that the saliency of the moving object is indeed crucial for the enhancement of color constancy. For such an involvement of a high-level motion system also speaks the observed drop of color constancy performance at speeds higher than 3.6° s^{-1}, which is consistent with the low pass characteristics of third order motion (Lu & Sperling, 2001; Seiffert & Cavanagh, 1999). In comparison, the first and second order motion systems continue to respond with high sensitivity to far higher speeds (cut-off frequency is around 12 Hz; Lu & Sperling, 2001). Taken together, I therefore conclude that the specific enhancement of color constancy in the object motion condition is mediated by the influence of a high-level motion system on color processes, which is activated by the heightened saliency of the moving test patch.

The enhancing effect of the motion input to color constancy may be explained by the heightened neuronal activity due to an additive effect when integrating color and motion signals. It is well known that the integration of features of the same object can increase neuronal activity and that this correlates with an enhancement of perceptual performances (Bach, Schmitt, Quenzer, Meigen, & Fahle, 2000; Nothdurft, 2000; Rivest & Cavanagh, 1996; Self & Zeki, 2005). For color and motion integration in particular, increased neuronal activity and a related increase in perceptual performance has been demonstrated in the lateral occipital cortex (Self & Zeki, 2005), an area known for object processing (Kourtzi & Kanwisher, 2001). Additive effects from feature integration may also explain the facilitation of other color tasks by motion, such as the faster detection of chromatic changes (Kreegipuu et al., 2006), the spreading of illusory colors (Chen & Cicerone, 2002), and the perception of color transparency (Gerardin et al., 2006).

The binding of color and motion has been suggested at stages in the visual pathway as early as V1 (Blaser, Papathomas, & Vidnyánsky, 2005). The motion-related facilitation of the detection of color changes (Kreegipuu et al., 2006) would indeed be consistent with a low order motion input, since it was observed at relatively high speeds (up to 35° s^{-1}). The fact that the enhancement of color constancy is specific for *slow* object motion indicates that here the underlying integration takes place at a higher, object-related level. Taken together, this suggests that color and motion interact at several stages during information processing.

Attention-based high-level motion processes have been identified by recent fMRI studies in human inferior parietal lobe (Claeys et al., 2003). Anatomical evidence from monkeys indicate connections between sub-regions of the inferior parietal lobule and high order visual areas in the temporal cortex, including V4 (Andersen, Asanuma, Essick, & Siegel, 1990; Rozzi et al., 2006). It would be interesting so see how color responses in the human V4 complex are influenced by motion, since this area is implicated a central role in cortical color processing and for color constancy (Bartels & Zeki, 2000).

How color is constructed in the brain and, in particular, how it is integrated with other object features is still not fully understood. The "coloring book model," as proposed by Livingstone and Hubel (1988), has been proven insufficient. Based on the segregated pathway hypothesis, this model assumed the independent processing of the different visual attributes of an object (color, texture, form, motion, and depth) and the subsequent filling-in of color. However, recent psychophysical and physiological evidence suggest significant interactions between color and other "ventral features," such as form and texture (Barnes, Wei, & Shevell, 1999; Edwards, Xiao, Keysers, Földiak, & Perret, 2003; Werner, 2003). Now the new findings demonstrate that there is also cooperation between color and high order motion. This suggests that the cortical construction of color involves not only ventral but also specialized dorsal visual areas, which are activated in the context of a moving object.

It is interesting to consider the biological significance of a facilitation of color by motion. Motion is a frequent aspect in real visual scenes and may reduce the time during which an object is exposed for viewing. The enhancement of color processes by motion is therefore important for the reliable identification of objects. This is particularly true for color constancy because in a natural environment it is likely that surfaces encounter illumination changes while they move.

In conclusion, the study shows that human color constancy improves when an object moves, demonstrating that color perception is not motion blind. Thus, the new findings have a strong impact on the modeling of human color perception in natural scenes and our understanding of the integration of color and other visual features.

Acknowledgments

The study was supported by a DFG research grant (We 1710/2-1). I thank Mirko Whitfield for his help with preparing the manuscript and Andreas Bartels for his valuable comments on an earlier version of the manuscript. I also like to thank John Mollon and Daniel Osorio for their interest and discussions.

Commercial relationships: none.
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