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People perceive roughly constant surface colors despite large changes in illumination. The familiarity of colors of some natural objects might help achieve this feat through direct modulation of the objects' color appearance. Research on memory colors and color appearance has yielded controversial results and due to the employed methods has often confounded perceptual with semantic effects. We studied the effect of memory colors on color appearance by presenting photographs of fruit on a monitor under various simulated illuminations and by asking observers to make either achromatic or typical color settings without placing demands on short-term memory or semantic processing. In a control condition, we presented photographs of 3D fruit shapes without texture and 2D outline shapes. We found that (1) achromatic settings for fruit were systematically biased away from the gray point toward the opposite direction of a fruit's memory color; (2) the strength of the effect depended on the degree of naturalness of the stimuli; and (3) the effect was evident under all tested illuminations, being strongest for illuminations whose chromaticity was closest to the stimulus chromaticity. We conclude that the visual identity of an object has a measurable effect on color perception, and that this effect is robust under illuminant changes, indicating its potential significance as an additional mechanism for color constancy.

Keywords: color appearance, color constancy, natural objects, memory colors

Citation: Olkkonen, M., Hansen, T., & Gegenfurtner, K. R. (2008). Color appearance of familiar objects: Effects of object shape, texture, and illumination changes. *Journal of Vision, 8*(5):13, 1–16, http://journalofvision.org/8/5/13/, doi:10.1167/8.5.13.

Introduction

Color signals from object surfaces change substantially with varying illumination. Despite this, color appearance of objects remains roughly constant. Color constancy is not a trivial challenge because an infinite amount of illuminantreflectance combinations could cause the same activity in the three retinal cone photoreceptors (Maloney, 1999; Smithson, 2005). It has been the goal of a large body of research to determine (1) the conditions under which it is computationally possible to extract the surface reflectance from the light coming to the eye (e.g., Brainard & Freeman, 1997; D'Zmura & Lennie, 1986; Hurlbert & Poggio, 1988; Land & McCann, 1971; Maloney, 1986; Maloney & Wandell, 1986) and (2) the conditions under which humans indeed are, and to what degree, color constant (e.g., Arend & Reeves, 1986; Brainard & Wandell, 1992; Hansen, Walter, & Gegenfurtner, 2007; Kraft & Brainard, 1999; Yang & Maloney, 2001). One important regularity in the real world constraining the amount of necessary computations is the approximate invariance of relative cone excitation ratios of surfaces under an illuminant change (Foster & Nascimento 1994; Ives, 1912), which seems to be used by the visual system in certain color constancy tasks (e.g., Craven & Foster, 1992).

Color constancy models have commonly assumed that the average reflectance over the whole scene is neutral or at least known (Maloney, 1999); in these models, color constancy is achieved by using the average light over an extended image region as a reference for illuminant estimation (e.g., Buchsbaum, 1980; Land, 1983; Land & McCann, 1971). However, these models work only if the surfaces and illuminants are not biased to any chromaticity (Brainard & Wandell, 1986). This does not hold for natural surfaces (Webster & Mollon, 1997), and human performance is also not much affected by biases in the mean reflectance of a scene (Smithson & Zaidi, 2004). Moreover, the effect of a homogeneous surround on the appearance of a stimulus can be different from the effect of a textured surround with the same average chromaticity (Bäuml, 1994; Brown & MacLeod, 1997; Jenness & Shevell, 1995; Linnell & Foster, 2002; Shevell & Wei, 1998; Singer & D'zmura, 1994; Zaidi, Spehar, & DeBonet, 1997). Kraft and Brainard (1999) have also shown that none of the commonly postulated mechanisms, namely adaptation to spatial average, to the most intense image region, or to the local surround are sufficient to explain color constancy performance with natural scenes because removal of these cues does not cause color constancy to completely break down.

Color constancy improves as the amount of valid cues to the illuminant is increased (Jin & Shevell, 1996; Kraft & Brainard, 1999; Kraft, Maloney, & Brainard, 2002; Yang & Maloney, 2001). However, color constancy is incomplete even in realistic experimental settings, which poses the question of whether there might be additional mechanisms at play that cannot be revealed with simplified stimulus arrangements. von Helmholtz (1867) was one of the first to emphasize the role of previous experience together with sensory input in the formation of a perceptual image (Anschauungsbild). Along the same lines, Hering (1920) suggested that the knowledge of an object's typical color might be a clue in estimating an unknown illuminant. Studies on memory colors indicate that the knowledge of an object's typical color can indeed affect an object's perceived color (Adams, 1924; Bruner, Postman, & Rodrigues, 1951; Delk & Fillenbaum, 1965; Duncker, 1939; Hansen & Gegenfurtner, 2006; Hansen, Olkkonen, Walter, & Gegenfurtner, 2006; Hurlbert & Ling, 2005; but see Bolles, Hulicka, & Hanly, 1959). Duncker (1939) showed that when subjects were presented with a donkey and a leaf cut from the same material, the leaf was matched to a significantly greener color in a color wheel than the donkey. However, the effect only showed reliably in 55-75% of the subjects. Later reports on the memory color effect are somewhat contradictory, some showing a strong effect in various settings (Delk & Fillenbaum, 1965), others finding the effect only in settings where stimulus information was much reduced or the matching task otherwise made difficult (Bolles et al., 1959; Bruner et al., 1951). Observers could not adjust the stimulus color themselves in any of these studies. Moreover, in most cases, the matching was done over a spatial or a temporal interval, which necessarily required keeping the color in memory during matching (Adams, 1924; Bolles et al., 1959; Bruner et al., 1951; Duncker, 1939; Hurlbert & Ling, 2005). Even in cases where simultaneous matching was possible, subjects had to give a verbal response (Bruner et al., 1951; Delk & Fillenbaum, 1965). These limitations might have led to measuring other than purely perceptual effects-for instance, an observer might have asked the experimenter to set the color wheel to a greener hue in the case of the leaf merely because leaves tend to be greener than donkeys.

Finally, it has become clear that color is not processed in isolation from other types of visual information such as form even at the earliest processing stages (for a review, see Gegenfurtner, 2003). Color is processed along with spatial frequency and orientation in early visual cortical areas (Johnson, Hawken, & Shapley, 2001, 2004) and together with complex features in the inferotemporal cortex (Edwards, Xiao, Keysers, Földiák, & Perrett, 2003). Color information also enhances performance in many tasks, such as perception of shape from shading (Kingdom, 2003), scene recognition (Gegenfurtner & Rieger, 2000; Wichman, Sharpe, & Gegenfurtner, 2002), and object recognition (Tanaka & Presnell, 1999). Moreover, surface color perception is strongly influenced by scene geometry and three-dimensional shape (Bloj, Kersten, & Hurlbert, 1999).

Here we study the effect of memory colors on color appearance of natural objects presented under various simulated illuminations. We made sure that our task would only be measuring observers' color perception by letting them adjust stimulus colors themselves and by not requiring any verbal report during the experiments. Firstly, we asked observers to set the color of various fruit images to their respective typical colors and, secondly, to gray. The rationale behind the second task was to tease out any "illusory" color percept induced by the typical color of the object, showing as a shift in the achromatic settings as a function of the typical color. In Experiment 1 with a neutral illumination, we found that observers consistently set the fruit to a color off the white point toward the opposite direction from the typical color. This was contrary to what we found in a control experiment with discs and outline shapes, where no shift was evident. An additional control experiment with fruit images varying in naturalness showed that the strength of the effect was tied to the amount of relevant visual cues to object identity. We observed in Experiment 2 with chromatic illuminants that the memory color bias shifted almost fully with the illuminant. The robustness of the memory color effect suggests that it might be an important additional determinant in color constancy by making the color appearance of familiar objects more stable over illuminant changes, and also possibly by helping to identify other, unknown surfaces in the scene.

Parts of Experiment 1 have been reported elsewhere (Hansen et al., 2006).

Experiment 1

Methods

Observers

Fifteen naive observers participated in the first part of Experiment 1 where the color appearance of fruit stimuli was studied. Seven additional subjects participated in the second part of Experiment 1, where the effect of visual stimulus features on color appearance was investigated. All observers had normal or corrected-to-normal visual acuity and normal color vision as tested with the Ishihara color plates.

Apparatus

The stimuli were displayed on a Sony Multiscan GDM-F520 monitor with a spatial resolution of 1280×1024

pixels and a refresh rate of 100 Hz. The monitor was driven by an NVIDIA graphics card with a color resolution of 8 bits per channel. The monitor was placed in the far end of a viewing chamber and was viewed through a 10×8 deg aperture in the wall. The chamber was illuminated with two sets of three fluorescent lamps (red, green, and blue) placed behind a diffusing sheet on both sides of the chamber. The output of the monitor across the whole voltage range was measured with a UDT Instruments model 370 optometer with a model 265 photometric filter, and the phosphor spectra were measured with spectroradiometer (Photo Research PR650). The Judd-revised CIE xyY values of the phosphors were $R = (0.62 \ 0.34 \ 18.71)$, $G = (0.28 \ 0.60 \ 56.82), \text{ and } B = (0.15 \ 0.08 \ 6.70).$ The output of the lamps at different voltages and the chromaticities of the lamp primaries were measured with the PR650 spectroradiometer. The lamps and the monitor phosphors were corrected for nonlinearities in the input/ output relationship with look-up tables, and a transformation matrix was calculated to convert between the lamp and the monitor primaries. The perceptual match of the monitor and the lamp chromaticities was ensured by collecting matches from three observers for the test illuminant chromaticities between the monitor background and the abutting wall. The calibration of the set-up is described in detail in Rinner and Gegenfurtner (2000).

The experiments were written in Matlab (The Mathworks, Inc.) with the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997).

separate control over chromaticity and luminance, and secondly because it is directly based on the physiological properties of the visual system (Derrington, Krauskopf, & Lennie, 1984; Krauskopf, Williams, & Heeley, 1982; MacLeod & Boynton, 1979). The DKL color space is a three-dimensional opponent modulation space based on the Smith and Pokorny (1975) cone fundamentals. The sum of the L and M cone excitations varies on one axis (luminance), the L cone excitation opposed to the M cone excitation varies on the second axis (L - M), and the S cone excitation opposed to the sum of the L and M cone excitations varies on the third axis (S - (L + M)). Saturated lights on the L - M axis appear reddish or bluegreen, and on the S - (L + M) axis, purple or yellowgreen. We scaled the DKL axes between -1 and 1, where ± 1 corresponds to the maximum contrast achievable for each axis on our monitor. The DKL color space is not perceptually uniform, but taken that we are interested in comparing data across conditions in which the chromatic information remains the same while other stimulus features vary, this should not pose a serious problem. We also plotted achromatic and typical settings from a previous experiment in the DKL as well as in the CIE L*u*v* and L*a*b* color spaces, which strive for perceptual uniformity, and verified that the pattern of the data did not depend on the choice of color space. In addition, no known color spaces are completely uniform (Wyszecki & Stiles, 1982).

Stimuli

Color space

Stimuli were represented in the DKL color space. We chose the DKL space firstly because it allows for the

The basic set of stimuli used in Experiment 1 included photographs of eight different fruit and vegetables (Figures 1A and 1B). In addition, uniform discs, discs



Figure 1. (A) The fruit stimuli, a uniform disc and a disc with 1/f noise texture. (B) Chromaticities of the digitized photographs projected on the (L + M) - S, L - M plane of the DKL color space. (C) An example of the control stimuli used in Experiment 1. In order to create fruit with reduced surface texture, real fruits were painted with matte white paint and photographed (top). The photographs were colored according to the scrambled chromaticity distribution of the original fruit (middle). Outline shapes were uniformly colored (bottom).

with 1/f noise texture, and fruit outline shapes were used as control stimuli. An additional control experiment was run to further investigate the influence of stimulus features for color appearance, for which a subset of five fruit from the original set were chosen. Three versions of each of these stimuli were used: original photographs, photographs of painted fruit, and outline shapes (Figure 1C).

All photographs were taken under an illuminant metameric to D65 with a camera whose white balance was manually set to correspond to the illuminant. In order to create fruit stimuli with no surface texture, real fruit were painted with matte white spray paint and photographed under a neutral illuminant. To color the photographs afterward, the chromaticity distribution of the original fruit photographs was combined with the luminance distribution of the photographs of the painted fruit. This was achieved by converting the RGB images to the DKL color space, which resulted in images with one plane for the luminance variation and two planes for chromatic variation on each of the two cardinal axes. A new DKL image for each fruit was created by combining the luminance plane from the painted fruit photograph with the two chromatic planes from the original photograph. The spatial positions on each chromatic plane were scrambled to get rid of the spatial variation (texture) of the chromaticities while preserving the chromatic variation. Outline shapes were created by replacing the stimulus surfaces with a uniform color.

The mean luminance of the stimuli and the luminance of the monitor background was 41 cd/m². The luminance of the uniform disc stimulus and the fruit outline shapes was slightly higher than the background (42.5 cd/m²) in order to avoid their blending in the background during achromatic settings. The fruit stimuli subtended on average 2×2 deg and the discs 2×2 deg of visual angle. The monitor background and the light reflecting off the surrounding wall were metameric to D65 throughout the experiment.

Manipulation of stimulus chromaticity

It is evident from Figure 1B that the chromaticities of fruit and vegetables vary between the white point and the most saturated point in the chromatic distribution when projected on the isoluminant L - M, S - (L + M) plane. This allows us to change the chromaticity of a textured stimulus by rotating and scaling the whole distribution by a given amount, which has the advantage that the stimulus can be rendered completely achromatic by scaling the amplitude to zero. In order to manipulate lookup tables in the adjustment procedure, the digital photographs were quantized into 256 colors with 8 bit for each RGB color channel. Only the values in the nominally isoluminant L - M, S - (L + M) plane were changed while keeping luminance constant. For the rotation, the angle and the amplitude of each point in the chromatic distribution in

the isoluminant plane were determined. The most saturated point was chosen as the reference for the subsequent rotation and scaling of the distribution (Figure 2). Let $\mathbf{c} = (r, \theta)$ be the reference point of the initial distribution in the isoluminant plane, given in polar coordinates, and let $\mathbf{c}' = (r', \theta')$ be the position of the new adjustment of the reference point. The chromaticities of all pixels $\mathbf{c}_i = (r_i, \theta_i)$ were adjusted to a new position on the isoluminant plane according to

$$\mathbf{c}_{i}^{\prime} = \left(r_{i}\frac{r^{\prime}}{r}, \theta_{i} + \theta - \theta^{\prime}\right),\tag{1}$$

where \mathbf{c}_i' is the *i*th rotated point in the chromatic distribution, r_i is the amplitude of the *i*th point in the initial distribution, r' is the amplitude of the new adjustment, r is the amplitude of the reference point, θ_i is the azimuth of the *i*th point in the distribution, θ is the reference azimuth, and θ' is the azimuth of the new adjustment. The luminance distribution of the stimuli was held fixed throughout the adjustment procedure.

Procedure

Subjects viewed the display at a distance of 187 cm with head stabilized on a chin rest. Stimuli were presented one at a time on a uniform background. The initial color



Figure 2. The method of adjusting stimulus color. The distribution of stimulus chromaticities projected on the isoluminant plane of the DKL color space was rotated and scaled according to a reference value (black cross) that observers were changing with four keys. Images corresponding to the two chromatic distributions are shown in the inset.

of the stimulus was picked randomly from the L - M, S - (L + M) plane around the adaptation point within a radius of 0.5 (half the maximum saturation). Observers were asked to set the color of the stimulus either to gray (so that it did not include any red, green, blue, or yellow) or to the fruit's typical color depending on the block. The chromaticity of the stimulus in the L - M, S - (L + M) plane could be changed with four keys corresponding to these directions, while luminance was held fixed. When pressing a key, the experimental program recorded the new color value and calculated the required rotation and scaling of the whole chromatic distribution according to Equation 1. The stimulus was continuously shown during the setting procedure, which was not time limited. Pressing return recorded the final setting and initiated the next trial.

The achromatic and typical settings for the fruit stimuli and the achromatic settings for the discs were collected in three separate blocks, whose order was counterbalanced across observers. One block of fruit stimuli consisted of five repetitions of each of the eight stimuli in a randomized order. One block of disc stimuli consisted of five repetitions of each of the two stimuli (uniform disc and 1/f noise disc) in a randomized order. The three blocks took the observers about 45–60 minutes to finish with short breaks between blocks. Data for different stimulus types in the second part of Experiment 1 were collected in separate blocks.



Figure 3. (A) Mean achromatic settings for fruit photographs. Achromatic settings for the uniform disc and the noise disc are denoted with the black circle and square, respectively. Lines are drawn from the disc settings to the typical settings for each fruit; the data points for the typical settings fall outside the scale of the plot. Achromatic settings for fruit outline shapes are plotted similarly in B. The color angles of the mirrored achromatic settings are plotted as a function of the color angles of the typical settings for photographs (C) and outline shapes (D). Small dots are data from individual subjects, and large symbols are the means for each fruit. Black lines indicate the unity line.

Data analysis

A memory color index was defined in order to quantify the magnitude and the direction of the offset of the achromatic settings from the subjective white point of each observer (defined as the mean of the individual achromatic settings for the uniform disc and noise disc). First, the data for each observer were re-centered such that the origin of color space coincided with the observer's subjective white point. Then, the typical setting for a given fruit was mirrored relative to the origin and the achromatic setting for this fruit projected to the mirrored typical setting. The memory color index (MCI) was defined as the ratio of the projection length to the length of the respective typical setting:

$$MCI = \frac{\mathbf{s}_1 \cdot (-\mathbf{s}_2)}{\|\mathbf{s}_2\|^2},\tag{2}$$

where s_1 denotes the achromatic setting vector and s_2 the typical setting vector. If the achromatic settings aligned fully with the mirrored typical settings, the projection would correspond to the length of the achromatic vector, in which case the memory color index would increase with the amplitude of the offset. However, if the achromatic setting was in a direction orthogonal to the typical setting, the projection would be near zero independent of the amplitude of the achromatic setting, resulting in a small memory color index.

Differences between fruit stimuli and stimulus manipulations were tested with repeated measures ANOVA and the significance of the memory color indices with *t*-tests.

Results

The mean achromatic settings for fruit photographs and outline shapes are shown in Figures 3A and 3B. The black circle and square denote the achromatic settings for the uniform and noise discs, respectively. Typical settings are outside the scale of the plot, but the direction of the typical settings is indicated with the vectors drawn from the disc settings. The achromatic settings for the photographs were not centered on the origin but deviated from the gray point toward the opposite direction from the typical settings. The effect was largely diminished for the outline shapes. The relationship between the color angles of the typical and achromatic settings for photographs is depicted in Figure 3C. Most of the data points fall close to the unity line depicted in black, which indicates that the achromatic settings were more or less opponent to the typical settings for all stimuli except the strawberry. In contrast, no such relationship was evident for the outline shapes (Figure 3D).

Figure 4A shows the memory color indices for the fruit photographs and the outline shapes. Indices were on



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Figure 4. (A) Memory color indices for fruit photographs (black) and outline shapes (white) measured in the first part of Experiment 1. (B) Memory color indices from the second part of Experiment 1 for fruit photographs (black), painted fruit (gray), and outline shapes (white). Error bars denote one standard error of the mean.

average 7.6% for the photographs and 2.3% for the outline shapes, this difference being statistically significant (F(1, 14) = 6.3, p = 0.025). There were also significant differences between fruit stimuli, the effect being largest for the lemon and the banana and weakest for the strawberry (range -1.9% to 16.8%; F(7, 98) = 4.41, p < 0.001). The memory color indices along with significance levels for the fruit photographs are listed in the first column of Table 2. None of the indices for the outline shapes differed significantly from zero (-0.2% to 1.6%, p-values > 0.13).

In the second part of Experiment 1, achromatic and typical settings were collected for fruit photographs, outline shapes, and painted fruit with seven new subjects. The memory color indices for this experiment are plotted in Figure 4B. The memory color indices were on average

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	X	У	Y
Neutral	0.301	0.340	41.3
Purple	0.288	0.288	41.2
Yellow-green	0.338	0.414	41.3
Blue-green	0.269	0.359	41.1
Reddish	0.344	0.323	41.4

Table 1. CIE31 chromaticity coordinates of the wall surrounding the monitor under the five experimental illuminants.

9.5% for photographs (range 0.3-22.2%), 5.6% for painted fruit (1.0–11.4%), and 1.2% for outline shapes (-0.4 to 2.5%). The overall difference between stimulus types was significant (F(2, 12) = 12.18, p = 0.001). The differences between stimuli were also significant, the effect being again strongest for the banana (F(4, 24) = 3.31, p = 0.027).

To summarize, the magnitude of the compensation for the perceived memory color was greatest with the most natural stimuli and decreased monotonically with decreasing stimulus realism, being absent for the fruit outline shapes.

Experiment 2

Experiment 1 showed that the color appearance of natural objects can be affected by their typical colors, and that this effect is modulated by the visual features of the stimuli. In Experiment 2, we investigated the dependence of the memory color effect on illumination by replicating the first part of Experiment 1 with fruit photographs under four chromatic illuminants, in both optimal and reduced viewing conditions.

Methods

Observers

Ten observers from Experiment 1 took part in Experiment 2. All subjects ran the experiment under four fullfield illuminants, and four of the subjects participated in an additional viewing condition where the cues to the illuminant were reduced.

Apparatus

The apparatus was the same as used in Experiment 1.

Stimuli

The eight fruit and vegetable photographs from Experiment 1 served as stimuli. In addition, uniform discs and discs with 1/*f* noise texture were used as control stimuli. Four chromatic illuminants were chosen from the cardinal axes of the DKL color space at half of the maximum achievable saturation: a purple and a yellow-green illuminant from the S - (L + M) axis and a blue-green and a reddish illuminant from the L - M axis. The CIE 1931 chromaticity coordinates of the four illuminants are listed in Table 1. In order to simulate the effect of an illuminant change on the light reflecting off the stimulus surfaces, the chromatic distributions of the stimuli were shifted by the amount of the illuminant change. In general, the effect of illuminant changes on the light reflecting off a surface cannot be described by such a rigid shift. However, the departures from rigidity are most significant for surfaces with narrow-band reflectance spectra and small for natural objects such as fruit whose reflectance spectra are broadband (MacLeod & Golz, 2003; Maloney, 1986) and for moderate illuminant changes such as employed in this experiment. We investigated the rigid shift assumption by photographing fruit under our experimental illuminants. The chromaticities of two lemons photographed under the neutral and the blue-green illuminant are shown in Figure 5; the physical illuminant change is denoted with a black arrow. The overall shift of the chromaticities closely follows the illuminant change even though the transformation is not fully rigid. This



Figure 5. Lemon chromaticities under an illuminant change. The lemon in the rightward inset is photographed under a neutral illuminant, and the chromaticities of the lemon pixels are plotted above. The lemon in the leftward inset is photographed under a blue-green illuminant, with the corresponding chromaticities shown above. The black arrow indicates the magnitude and direction of the illuminant change from neutral.

pattern was verified by measuring the spectra of fruit under the same illuminants. It was important for the rationale of this study to ensure that subjects were able to render the stimuli physically achromatic under all illuminants. Shifting the chromatic distribution by the amount of the illuminant change, although only approximating the effects of real illuminant change, was important for meeting this requirement as it allowed the rotation and scaling of the chromatic distribution around any given adaptation point.

We manipulated the amount of information about the illuminant in two viewing conditions: In the full-field viewing condition, the whole field of view was illuminated by the illuminant, and in the low-cue viewing condition, illuminant cues were present only in the stimulus area. In the low-cue condition, the visual field was limited to the monitor with a viewing tunnel lined with black cloth, and the stimuli were displayed on a black background. Sparse cues to the illuminant were given by substituting the stimulus every 5 s for a second with a homogeneous area of the same shape that had the chromaticity of the illuminant. In addition, the chromatic distribution of the stimuli was always biased to the illuminant due to the illuminant simulation described above. All four illuminants were used in the full-field condition; in the low-cue condition, the purple and yellow-green illuminants were used.

Procedure

The procedure was identical to that employed in **Experiment 1**. Data for the different illuminants were collected in separate sessions.

Data analysis

Memory color indices were calculated for each subject, stimulus, and viewing condition separately as defined in Equation 2. In addition, a color constancy index was calculated to quantify the magnitude of the shift in the achromatic settings as a function of the illuminant change. Achromatic settings for the same subjects from Experiment 1 with the neutral illuminant were used as the baseline in the calculation. Since the subjects were free to make their settings in a two-dimensional plane, the shifts in the settings might not be parallel to the illuminant change. Hence, we first calculated the projection of the change in the data to the change in the illuminant and related the length of the projection to the amount of illuminant change:

$$CI = \frac{(\mathbf{b}_2 - \mathbf{b}_1) \cdot (\mathbf{a}_2 - \mathbf{a}_1)}{\|\mathbf{b}_2 - \mathbf{b}_1\|^2},$$
(3)

where \mathbf{a}_1 is the achromatic setting under the reference illuminant, \mathbf{a}_2 is the same setting under the test illuminant,

 \mathbf{b}_1 is the chromaticity of the reference illuminant, and \mathbf{b}_2 is the chromaticity of test illuminant. Indices close to one indicate a high degree of color constancy, and indices close to zero indicate poor constancy.

This type of color constancy index is sensible for achromatic settings because the color signal from a uniformly reflecting surface takes on the chromaticity of the illuminant, and the degree of color constancy can be determined by relating the amount of shift in the settings to the amount of illumination change. This does not apply directly to chromatic surfaces, in which case the changes in the color signal can be much larger for some illuminants as compared with others due to nonuniform surface reflectance. When subjects are asked to make typical settings, that is, to set the stimulus color to a certain *chromatic* point in color space, it is not obvious to which magnitude to relate the change in observers' settings. We calculated color constancy indices for the typical settings using either the change in the illuminant or the change in the reflected light from fruit surfaces under real illumination changes (the proximal stimulus) as the denominator in Equation 3. Again, typical settings for the same subjects from Experiment 1 were used as the baseline in the calculation.

Differences between stimuli and viewing conditions were tested with repeated measures ANOVA and significance of the memory color indices with *t*-tests.

Results

Full-field viewing condition

Typical and achromatic settings for fruit photographs were collected in Experiment 2 under a reddish, bluegreen, purple, and yellow-green illuminant. Achromatic settings were also collected for uniform and 1/f noise discs. The mean change in the fruit achromatic settings from the baseline is plotted in Figure 6A separately for each illuminant. The achromatic settings for fruit and discs shifted generally close to the chromaticity of the test illuminant. The shifts in the achromatic settings were more or less parallel to the illuminant change under all illuminants, whereas the pattern of the shifts in the typical settings was dependent on the particular illuminant change (Figure 6B). Under the reddish and the blue-green illuminant, the shifts in the typical settings were mostly parallel to the illuminant change and also of comparable magnitude for those fruit whose typical colors were not too close to the illuminant chromaticity. Under the purple and the yellow-green illuminant, however, the typical settings compressed toward the axis of the illuminant change in addition to a shift parallel to the change. The magnitude of the shifts was also overall slightly less than the magnitude of the illuminant change.

Mean color constancy indices for all stimulus types are plotted in Figure 7A. Constancy for uniform discs was between 88% and 100% for all illumination changes.



Figure 6. (A) The mean shifts in the fruit achromatic settings from neutral under the reddish (upper left), blue-green (upper right), yellowgreen (lower left), and purple (lower right) illumination. Symbols denote settings under the neutral illuminant, and arrowheads denote settings under chromatic illuminants. Black lines indicate illuminant changes from the white point. (B) The mean shifts in the fruit typical settings under the four chromatic illuminants. Details are as in A. Note the overall scale difference between A and B.

Constancy was somewhat lower for the noise discs (74–96%) and for the fruit achromatic settings (73–95%). Differences between the illuminants (F(3, 27) = 5.53, p = 0.004) as well as between stimulus types were statistically significant (F(3, 27) = 36.14, p < 0.001). The lower overall color constancy for the yellow-green illuminant was mostly due to the low indices for the noise discs and fruit stimuli.

Because the color signals from chromatic surfaces, as opposed to achromatic surfaces, do not necessarily change in proportion to illumination changes, we calculated color constancy indices for fruit typical settings both in relation to the amount of illuminant change and to the amount of change in the proximal stimulus. For the L - M axis, constancy indices were very similar for both types of reference (on average 75%). For the S - (L + M) axis,



Figure 7. (A) Color constancy indices in the full-field viewing condition are depicted for uniform discs (circles), noise discs (squares), fruit achromatic settings (open diamonds), and fruit typical settings (closed diamonds). Error bars denote one standard error of the mean. (B) Color constancy in the low-cue viewing condition. Details as in A.



Figure 8. Achromatic (open symbols) and typical (filled symbols) settings for the banana (A) and the zucchini (B) are plotted for each fullfield illuminant. Symbol color indicates illuminant chromaticity. Error bars denote one standard error of the mean. Achromatic settings for the uniform disc are plotted with filled circles. Dotted lines connect the typical and achromatic settings through the disc settings for each illuminant condition.

however, the indices were much higher when based on the change in the proximal stimulus (average indices of 130% vs. 70%). An index of 130% means that the subjects' settings shifted much more than the shift in the proximal stimulus under a similar illuminant change. In contrast, when the constancy index was based on the illuminant change directly, color constancy was on average 70% and similar to the fruit achromatic settings. It thus seems that observers did not differentiate between making settings with achromatic and chromatic surfaces, at least on the S – (L + M) axis.

The achromatic settings for fruit stimuli shifted almost fully under all illuminant changes, which indicates that any memory color effect present under the neutral illuminant was also present under the chromatic illuminants. The average achromatic and typical settings for the banana under all illuminants are shown in Figure 8A. The

	Neutral	Red	Blue- green	Yellow- green	Purple
Lemon	12.3**	11.3**	8.4*	19.5**	7.5**
Grapes	5.0**	10.7*	7.8	13.0*	9.7**
Orange	4.9**	8.3*	2.3	11.0*	3.1
Banana	16.8**	15.3*	12.7*	16.8*	14.2**
Carrot	5.2*	7.2*	3.8	12.5**	5.0
Zucchini	10.5	11.2	38.6	59.6**	7.3
Lettuce	7.2**	8.0*	12.8**	19.2*	4.1
Strawberry	-1.9	20.1**	0.9	13.7**	0.1

Table 2. Average memory color indices in percent for each stimulus under each full-field illuminant. *Note*: **Indicates that the index is greater than zero with a 0.01 error probability. *0.05 error probability (uncorrected).

achromatic settings for discs are plotted for reference with filled circles. The shift of the achromatic settings for the banana (open diamonds) in the direction opposite to the typical settings (filled diamonds) was on average 13% and very similar under all illuminants. This was to some degree true for all fruit stimuli, although the effect tended to be strongest for the illuminations closest to the stimulus chromaticity. This was especially evident for the zucchini: The achromatic settings were most offset from the disc settings under the yellow-green and blue-green illuminants (Figure 8B). Figure 9A and Table 2 summarize the memory color indices for all stimuli under all illuminants. For all stimuli but the strawberry, there was a bias under all illuminations, even though the magnitude varied as a function of the illuminant. The memory color effect was on average 12% under the reddish, 7.7% under the bluegreen, 20% under the yellow-green, and 6% under the purple illuminant. The average memory color index for the zucchini under the yellow-green illuminant was extremely large (60%), and zucchini was therefore excluded from statistical analyses. Memory color indices for all but the blue-green illuminant were significantly greater than zero (Bonferroni corrected *p*-values <0.0183). The indices were highest for the green and yellow fruit (between 4.1% and 59.6%) and lowest for orange and red fruit (between -1.9% and 20.1%). The differences between fruit stimuli (F(7, 63) = 4.79, p < 0.001) as well as between illuminants (F(4, 36) = 6.8, p < 0.001) were statistically significant.

Low-cue viewing condition

In order to investigate whether the pattern of results obtained with full-field illuminants would hold when the



Figure 9. (A) Memory color indices in the full-field viewing condition. Diamond: neutral; square: yellow-green; circle: purple; triangle: reddish; leftward triangle: blue-green illuminant. Error bars denote one standard error of the mean. (B) Memory color indices in the lowcue viewing condition. Square: yellow-green; circle: purple illuminant. The indices for the zucchini under the yellow-green illuminant were extremely large in both viewing conditions (60/130%) and are plotted as outliers on top of the graphs.

task was made more difficult, typical and achromatic settings for fruit photographs and achromatic settings for uniform and noise discs were collected additionally for four observers with only temporal cues to the illuminant chromaticity (cf. Hansen et al., 2007). Color constancy indices for fruit, uniform discs, and noise discs are plotted in Figure 7B. Color constancy under the purple illuminant was on average 73%, and 43% under the yellow-green illuminant. In contrast to the full-field conditions, constancy was higher for the fruit stimuli as compared with the discs for both illuminants (52% vs. 22% for the yellow-green illuminant and 75% vs. 65% for the purple illuminant), even though this difference did not reach statistical significance due to variability between subjects. Memory color indices for the low-cue illuminants are plotted in Figure 9B. The average index for zucchini under the yellow-green illuminant was again much larger than the rest of the indices, 130%, and was excluded from statistical analyses. The average memory color indices without the zucchini for the purple and yellow-green illuminants were 11% and 13%, respectively. The indices for the yellow-green illuminant were significantly greater than zero (Bonferroni corrected *p*-values <0.02).

Discussion

We measured color appearance of natural stimuli with varying degrees of visual cues to stimulus identity and under various viewing conditions. Observers perceived fruit stimuli slightly tinted in their typical color even when every pixel of the stimulus was achromatic. They compensated for this percept by setting the fruit color slightly in the direction opposite to the respective typical color. The effect was largest with the original photographs, smaller with stimuli that had the 3D shape of the fruit but no texture, and absent with outline shapes. The effect was also robust to illuminant changes.

Color constancy

Observers showed nearly complete color constancy under full-field illumination, which is in agreement with other recent studies (Hansen et al., 2007; Murray, Daugirdiene, Vaitkevicius, Kulikowski, & Stanikunas, 2006; Rinner & Gegenfurtner, 2002). Constancy for 1/*f* noise discs and for the fruit was slightly lower as compared with the uniform discs. This is in line with Hurlbert and Wolf (2004), who found that differences in texture between the surround and the stimulus weaken chromatic induction, which again is important for color constancy under full-field viewing.

Color constancy was expectedly poor when illuminant cues were constrained to the stimulus area, especially so for the yellow-green illuminant. Interestingly, observers were most color constant when making typical and achromatic settings with the fruit under these impoverished conditions, contrary to the full-field conditions where constancy was best for uniform discs. Without a common border between the illuminant and the test field, simultaneous chromatic contrast is not the determining factor in color constancy. In this case, the information about the illuminant contained in a variegated surface, such as the surfaces of our fruit and noise stimuli, could facilitate making color constant settings (cf. Hurlbert & Ling, 2006). However, the fact that color constancy was even better for the fruit stimuli as compared with the noise discs suggests an additional advantage for stimuli with a typical color in this kind of color constancy task.

Because the changes in color signals from chromatic surfaces depend on both the surface reflectance and the illumination change, one might expect typical settings to shift in varying amounts depending on the particular fruit stimulus and illuminant change. We found instead that observers' typical settings shifted to the same degree under all illumination changes, similarly to the achromatic settings. This is in agreement with Speigle and Brainard (1999), who showed that the amount of color constancy for chromatic stimuli could be predicted quite well from achromatic settings.

Constancy of the memory color effect

Color constancy indices for the fruit achromatic settings were fairly high, showing that the memory color effects occurring under the neutral illuminant shifted together with the change in the illuminant. In addition to showing how robust the effect of memory colors on color appearance is, this result is important evidence for the way our observers made the achromatic and typical settings. Observers could, in principle, assume that the display background was neutral regardless of the illuminant chromaticity and merely match a phenomenal relation between the test field and the background rather than adjusting the appearance of the test field itself. However, we saw offsets from the white point for the achromatic settings only for fruit and not for control stimuli, which suggests that the observers were indeed adjusting the color appearance of the stimulus. Strictly speaking, a matching strategy could still give rise to a memory effect, if the influence of previous knowledge was an additive determinant of color appearance. If observers were matching the perceived color of the stimulus to the perceived color of the background, the match would not need to be veridical if the color appearance of the stimulus was biased. Although this possibility cannot be ruled out, the argument does not directly bear upon the main finding of this study: that the color appearance of familiar objects is affected by memory colors in a stimulus-dependent and an illumination-independent way.

The invariance of the memory color effect under illumination changes was especially clear for the banana, for which the effect was practically identical under all illuminations. For the other fruit, the effect magnitude was generally strongest under the illuminant closest to the stimulus chromaticity. For instance, subjects were largely unbiased when making achromatic settings with the strawberry under the neutral and the purple illuminants but had a large bias under the reddish and the yellowgreen illuminants. This suggests that even though color constancy was good under the reddish illuminant, the strawberry was perceived redder than under other illuminants and redder than other fruit under the reddish illuminant. Overall, the memory color effect was strongest and most consistent for the yellow-green and reddish illuminants. It is noteworthy that the chromaticities of all our stimuli and indeed chromaticities of most edible fruit and vegetables generally fall between these color axes when projected on the isoluminant plane of the DKL color space (cf. Figure 1).

Also the chromaticities of green vegetables such as lettuce and zucchini align with the S - (L + M) axis, even though we found observers' typical settings for green fruit and vegetables to be offset toward the L - M axis. It seems as if subjects had an idea of the typical color for green vegetables and fruit, which was clearly bluer than the actual chromaticity. This is similar to the phenomenon documented by Bartleson (1960), who found that memory colors usually tend toward the "most impressive chromatic attribute" of the object, which is often more saturated than the actual color but can also differ in hue.

Special significance has been attached to illuminants varying in chromaticity between yellowish-orange and blue since the chromaticities of natural daylight illuminants fall along this locus (Taylor & Kerr, 1941), and it has been proposed that a daylight prior might be used to make illuminant estimates (Brainard et al., 2006; Rutherford & Brainard, 2002). Our data agree with recent findings showing that the visual system does not appear to be more color constant for illumination changes in a particular color direction (Brainard, 1998; Delahunt & Brainard, 2004; Hansen et al., 2007). We found comparable amounts of color constancy under all illuminations and a comparable bias in the color appearance of fruit stimuli, which strengthens Hering's idea about the importance of familiar colors for color perception in the natural world.

Relation to previous research

The task employed in this study differed in many respects from the tasks used previously to measure memory effects on color appearance. In most studies the stimuli had been cut out of paper (e.g., Bruner et al., 1951; Duncker, 1939), and color matches were only possible along one axis (yellow-red; brown-green). Furthermore, observers were not able to change the color of the stimuli themselves but had to ask the experimenter to either match the perceived color on a color wheel or to change the color of the object. We have avoided the confusion between semantic and perceptual effects by using a method where the observer was able to adjust the color of the stimulus with two degrees of freedom without having to recruit either short-term memory or language. These differences in the methods are also a probable cause for the fact that we found only minor effects with outline shapes, stimuli with which most previous memory color effects have been shown.

Possible cognitive and neural mechanisms

Object identity affected perceived color most with realistic photographs having the correct chromatic and luminance texture, less with fruit stimuli without appropriate surface texture, and not at all with outline shapes. Therefore, the effect must be specifically tied to the visual aspects of the stimulus. Observers surely recognized the fruit outline shapes, which would also activate a semantic representation of the stimulus, but this did not have any effect on perception. This is in line with Naor-Raz, Tarr, and Kersten (2003), who used a variation of the Stroop paradigm to show that color and other visual features of familiar objects are linked together in an inherently visual representation. In addition to showing a color naming advantage for fruit stimuli with congruent color-shape combinations, Naor-Raz et al. showed that pictures do not prime words, i.e., that the visual and semantic representations of objects are separable. Considered together with our results, this suggests that to activate the visual representation strongly enough to induce an illusory color percept, the object has to have all relevant visual features-shape, shading, and texturepresent.

How could these effects come about in the visual system? The lateral occipital complex (LOC) in the ventral path of visual information processing plays an important role in object recognition (for a review, see Grill-Spector, Kourtzi, & Kanwisher, 2001), similarly to the inferotemporal (IT) cortex in nonhuman primates (for a review, see Tanaka, 1996), which is considered homologous to the LOC (e.g., Denvs et al., 2004). Some tentative differences have been found in how the visual system processes shapes defined by contours and shapes defined by richer cues such as shadowing (Denys et al., 2004; Kourtzi, Erb, Grodd, & Bülthoff, 2003). Gray scale images cause more activation in the primary visual cortex than outline shapes, even though this difference in activation decreases toward higher visual areas (Denys et al., 2004). Furthermore, partly non-overlapping regions in the LOC process shape defined by contours and shape defined by shading (Kourtzi et al., 2003). In addition to shape, color seems to be an important stimulus property in the IT cortex: A significant proportion of the neurons respond vigorously to color, and congruent color information facilitates the processing of familiar objects (Edwards et al., 2003). All this taken together suggests that the effects of familiar colors on color appearance could take place in the neuronal populations in the LOC that respond preferentially to realistic stimuli. Alternatively, the responses of these neurons could modulate the activity of color selective cells in earlier visual areas. Modulatory feedback is a candidate neural mechanism underlying the integration of bottom-up incoming data and top-down expectations (Grossberg, 1980; Hupé et al., 1998; Mumford, 1992).

Conclusions

We found the color appearance of natural objects to be not only determined by their reflectance but also by their typical colors. This effect is dependent on the visual features of the stimuli: It is strongest for photographs and decreases when stimuli are rendered less realistic. The robustness of the effect under varying illumination attests to its significance in color perception and object recognition in the natural world.

Acknowledgments

We thank Lukas Kaim and Walter Kirchner for technical assistance and Toni Saarela for helpful discussions. This research was supported by the German Science Foundation grant Ge 879/5.

Commercial relationships: none.

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