Time course of chromatic adaptation for color appearance and discrimination

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Abstract

Adaptation to a steady background has a profound effect on both color appearance and discrimination. We determined the temporal characteristics of chromatic adaptation for appearance and discrimination along different color directions. Subjects were adapted to a large uniform background made up of a CRT screen and a $45 \times 64°$ wall, illuminated by computer controlled lamps. After an instant change in background color along a red–green or blue–yellow color axis, we measured thresholds for the detection of increments along the same axes at fixed times between 25 ms and 121 s. Analogously, color appearance was determined using achromatic matching. Three components of adaptation could be identified by their temporal characteristics. A slow exponential time course of adaptation with a half-life of about 20 s was common to appearance and discrimination. A faster component with a half-life of 40–70 ms — probably due to photoreceptor adaptation — was also common to both. Exclusive for color appearance, there was a third, extremely rapid mechanism with a half-life faster than 10 ms. This instantaneous process explained more than 50% of total adaptation for color appearance and could be shown to act in a multiplicative manner. We conclude that this instantaneous adaptation mechanism for color appearance is situated at a later processing stage, after mechanisms common to appearance and discrimination, and is based on multiplicative spatial interactions rather than on local, temporal adaptational processes. Color appearance, and thus color constancy, seems to be determined in large part by cortical computations. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Chromatic adaptation; Chromatic induction; Color appearance; Color discrimination; Color constancy; Cones

1. Introduction

Chromatic adaptation and contrast are central concepts in color vision. Spatially or temporally related surrounds can have profound effects on the color appearance of illuminated objects (Kirschmann, 1891; Jameson & Hurvich, 1972; Zaidi, 1999). Therefore, adaptation and contrast are tightly related to color constancy, the stability of object color appearance under different illuminations. The relationship between color appearance and chromatic adaptation has been investigated in the past with a variety of color induction paradigms (Walraven, 1976; Shevell, 1978; Krauskopf & Zaidi, 1986; Zaidi, Spehar & DeBonet, 1997) and in a large variety of color constancy experiments (Brainard & Wandell, 1992; Bäuml, 1994; Arend, 1993; for reviews, see Hurlbert, 1998; Maloney, 1999). Photoreceptor sensitivity changes (Chichilnisky & Wandell, 1995), multistage adaptation and gain control mechanisms (Shevell, 1978; D'Zmura, 1999) and higher order color mechanisms (Krauskopf, Zaidi & Mandler, 1986) all contribute to the complex effects of adapting backgrounds on color appearance.

But not only the appearance of objects changes under different adapting conditions; the discriminability of colors also depends strongly on an observer's adaptational state (Loomis & Berger, 1979; Wandell, 1985). Chromatic discrimination as a function of adaptation can be described in a straightforward way: Thresholds for detecting chromatic differences are lowest for the color the observer is adapted to, and higher if the adapting background is farther away in color space from the discriminated colors (Krauskopf & Gegenfurtner, 1992; Shapiro & Zaidi, 1992; Yeh, Pokorny &

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Smith, 1993). In these experiments, the state of adaptation was fixed by a large uniform background, on which small and brief pulses were presented. Of course, when the observer is adapted to different background colors, the appearance of the pulsed stimuli and the background also changes. Krauskopf and Zaidi (1986) found that thresholds for test colors surrounded by an annular region that was modulated in color over time depended on the induced appearance rather than on the physical color of the central disk. Loomis and Berger (1979) interpret the coincident behavior of appearance and discrimination following adaptation in terms of a sliding into the working-range of color opponent cells.

Although it has been shown that appearance and discrimination are influenced by chromatic adaptation, it is still unclear if both phenomena are based on the same adaptation mechanisms. This is partly the case because different paradigms are typically used to explore the effect adaptation has on appearance and on discrimination. Appearance is usually measured by matching techniques, whereas discriminability is determined by threshold measurements. We circumvented this problem by looking at the time courses of the effect adaptation has on appearance and on discrimination. Time courses do not suffer from the restrictions of different measurement techniques and are independent of absolute effect sizes, given that there is a proportional relationship between the measured entity and internal adaptation state.

So far, most studies concerned with the time course of adaptation have looked at light adaptation. For light adaptation, a wealth of psychophysical data for periodic and aperiodic stimuli is available (e.g. Crawford, 1947; Hood & Finkelstein, 1986; Hood, Graham, von Wiegand & Chase, 1997). Adaptation of thresholds for detecting luminance increments or decrements was mostly explored with adaptation times shorter than 1 s (Geisler, 1978; Hayhoe, Benimoff & Hood, 1987). Several fast components, multiplicative and subtractive, as well as contrast gain control are used to model the time course of adaptation within the 1st s (for an overview, see Kaiser & Boynton, 1996). But there is also evidence for slower components (Jameson, Hurvich & Varner, 1979; Hayhoe et al., 1987) that are usually assigned to a second site of adaptation following opponent subtraction (Pugh & Mollon, 1979).

Very few studies have looked at the temporal characteristics of color appearance. Fairchild and Reniff (1995) explored the dynamics of appearance changes under different adapting daylights. They found two components, a fast initial component with a time constant of approximately 1 s and a slow component with a half-life of about 30 s. About 50% of total adaptation was complete after 1 s. But because the first measurement was made at an adaptation time of 1 s, the exact initial time course remains unclear. In a study of Arend

(1993), the effect of adaptation to different daylights on color appearance was also measured for adaptation times of 1 s or longer. As in Fairchild's study, a large part of total adaptation was reported to occur within the 1st s, but again the exact initial time course remained unexplored. Furthermore, using different daylights as adapting colors restricts any conclusions to small changes in adaptational state, and to changes along the blue–yellow color axis (Hurlbert, 1991).

We therefore explored the full time course of color appearance and discrimination by measuring thresholds and adjustments with adaptation time as the independent variable. In these experiments, we used psychophysical paradigms that are well established for use in the steady state. Both phenomena were characterized over the whole time scale from several milliseconds up to 2 min. We explored chromatic adaptation isolated from changes in luminance by using purely isoluminant changes of the adapting background, both along the red–green and the yellow–blue cardinal color axes.

We found three highly distinct temporal phases in chromatic adaptation. A fast process, with a half-life of less than 100 ms, and a slow component, with a half-life between 15 and 20 s, were common to appearance and discrimination. But, exclusively for color appearance, we found an instantaneous change in appearance after changing backgrounds that explained more than 60% of total adaptation.

Preliminary reports of some of these data have been presented in Rinner and Gegenfurtner (1999).

2. General methods

Observers were sitting in front of a gray wall illuminated by computer controlled fluorescent lamps. Through a hole in the wall they could see the monitor on which the stimuli and the adapting background were displayed (see Fig. 1a). Subjects initially adapted to a reference color, then the monitor background and the lamps simultaneously switched to the adapting color and, at different times after onset of the adapting color, subjects performed a discrimination task or a color appearance task. The color appearance task was to adjust a central patch to obtain an achromatic appearance (achromatic matching); in the discrimination task a four alternative forced choice paradigm was employed.

2.1. Stimulus display

Stimuli were displayed on a BARCO CCID 121 color CRT monitor that was driven by a Cambridge Research VSG 2/3 graphics board at a refresh rate of 120 Hz non-interlaced. The images were generated on the monitor by reading through the picture memory in a

raster scan and then interpreting the numbers in each location as a color defined in a 256-element color lookup table. Two 8-bit-digital-to-analog converters, which were combined to produce an intensity resolution of 12 bits, were used to control the intensity of each of the three monitor primaries. The luminances of
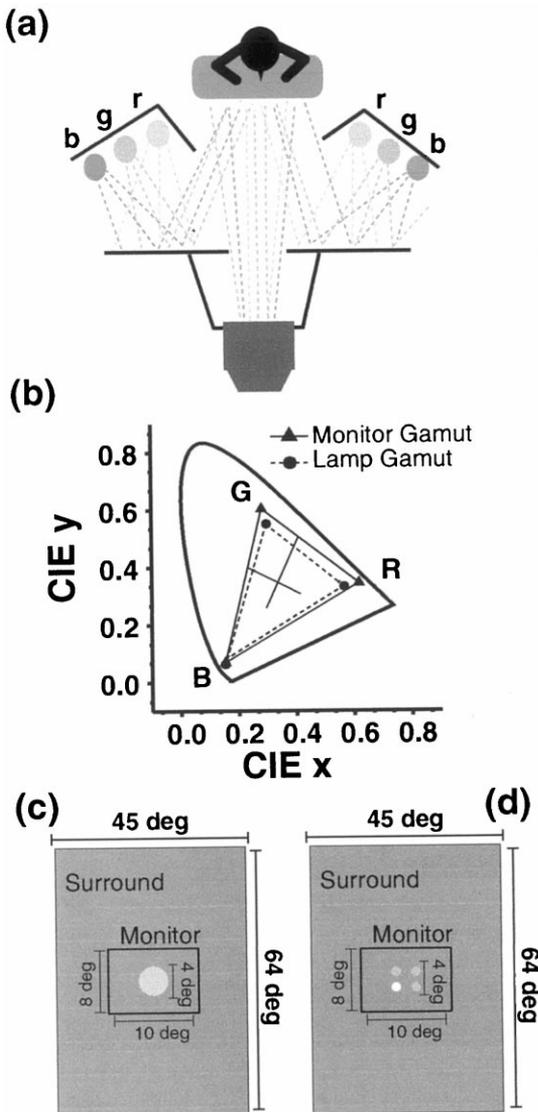

Fig. 1. Experimental setting. Observers were sitting in front of a gray wall looking binocularly at a monitor screen. The wall was illuminated by computer controlled fluorescent lamps. The light from the lamps could not reach the monitor (a). The gamut of the monitor and fluorescent lamps is shown in (b), with the primaries of the monitor and the lamps indicated on the corners of the triangles. The lamps could deliver virtually every monitor chromaticity. The two lines show the position of the cardinal red–green and the blue–yellow color axes. The spatial arrangement of the stimuli for the color appearance and chromatic discrimination task are shown in (c) and (d). The monitor screen and the surround were uniformly illuminated with the adapting light. In the color appearance task (c) subjects adjusted the central patch to an achromatic appearance. For discrimination (d), the task for the observer was to report which patch differed from the others.

each of the phosphors were measured at various output voltage levels using a Graseby Optronics Model 370 radiometer with a model 265 photometric filter. A smooth function was used to interpolate between the measured points and lookup tables were generated to linearize the relationship between voltage output and luminance. We also made sure that additivity of the three phosphors held over the range of intensities used in these experiments (Brainard, 1989). All the displays in the present experiments had a space-time averaged luminance of 26.0 cd/m^2. A Photo Research PR 650 spectroradiometer was used to measure the spectra of the red, green and blue phosphors at their maximum intensity setting. The spectra were multiplied with the CIE 1931 color matching functions, as revised by Judd (1951; see Wyszecki & Stiles, 1982, Table 1 (Section 5.5.3)), to derive CIE x, y chromaticity coordinates and the luminance Y of the phosphors (Irtel, 1992). All further references to luminance and photometric luminance refer to the $V(\lambda)$ curve as modified by Judd (1951), and values are given in cd/m^2. All CIE coordinates also use the Judd correction. The primaries of our monitor had x, y, Y coordinates of 0.617, 0.346, 15.52 (red), 0.281, 0.604, 34.90 (green) and 0.153, 0.069, 4.223 (blue). The monitor spectra were multiplied with the Smith and Pokorny (1975) cone fundamentals to calculate absorptions and contrasts in the L-, M- and S-cones.

The front wall of the dark room was painted with a neutral gray. Two sets of three Osram L36W/ 66 fluorescent lamps (red, green, and blue) illuminated this wall from two sides. The lamps where controlled by six Osram Quicktronic HF $1 \times 36/230$–240 DIM dimmbars, which were in turn controlled by six digital-to-analog converters with a resolution of 12 bits per DA channel. Even though the relationship between voltage and intensity was almost linear for the lamps, small residual nonlinearities were corrected by using lookup tables. The chromaticities of the three lamp-pairs were measured on the painted wall with the Photo Research PR650 spectroradiometer. The paint of the wall was chosen to make the reflected lamp primaries similar to the monitor primaries, resulting in nearly the same gamut for the background illumination and monitor (see Fig. 1b).

The rgb triplets used to control the lamps were transformed into the color space of the monitor, in order to obtain identical colors on the monitor and the adjacent parts of the wall. For each given vector of monitor phosphor values ($\mathbf{rgb}_M$), the corresponding vector for the lamps ($\mathbf{rgb}_L$) could be calculated by performing a matrix transformation. It consisted of a linear transformation and an additive correction for the offset $\mathbf{xyz}_0$ (0.33, 0.30, 0.63 in CIE coordinates) delivered by the lamps with no voltage input. This offset was treated as constant additional source of

Table 1
CIE coordinates and cone contrasts of adapting and reference backgrounds[a]

Hue	CIE coordinates		Cone contrasts (%)		
	x	y	L	M	S
Red	0.379	0.307	6.2	−11.7	0.24
Green	0.261	0.366	−6.2	11.7	−0.24
Yellow	0.373	0.436	−0.8	−1.1	−57.3
Blue	0.297	0.271	0.8	1.1	57.3

[a] The luminance of all colors was 26.0 cd/m^2.

illumination. With $[\mathbf{XYZ_M}]$ being the 3×3 matrix containing the primaries of the monitor and $[\mathbf{XYZ_L}]$ being the matrix of the lamp primaries, the uncorrected vector $\mathbf{rgb_L^*}$ was calculated as $\mathbf{rgb_L^*} = [\mathbf{XYZ_M}][\mathbf{XYZ_L}]^{-1} \cdot \mathbf{rgb_M}$. To correct for the offset of the lamps, the rgb values that would produce the given offset were subtracted: $\mathbf{rgb_L} = \mathbf{rgb_L^*} - [\mathbf{XYZ_L}]^{-1} \mathbf{xyz_0}$.

2.2. Color space

Adaptation occurred along the two isoluminant color axes of the DKL color space (Krauskopf, Williams & Heeley, 1982; Derrington, Krauskopf & Lennie, 1984), which is based on the MacLeod and Boynton (1979) chromaticity diagram. In this color space coordinates are defined relative to a neutral gray point. The chromaticity of the gray point was (0.33, 0.35) in CIE x, y coordinates as revised by Judd (1951), and its luminance was 26.0 cd/m^2.

Two chromatic axes intersect at the gray point, which span an equiluminant plane. All lights in this plane have the same luminance as defined by the $V(\lambda)$ photopic luminosity function (Judd, 1951; see Wyszecki & Stiles, 1982). Modulation along the $L-M$-cone axis is invisible to the short- (S) wavelength-sensitive cones and changes the excitations of the long- (L) and medium- (M) wavelength-sensitive cones so that their sum (luminance) is kept constant. Lights along this axis typically appear reddish and bluish-green. Modulation along the $S-(L+M)$ cone axis changes the excitation of S cones only and is invisible to L and M cones. Lights along this axis typically appear yellow-greenish or purplish. The length of a vector that lies along a particular half axis can be described in terms of contrast delivered to the cone mechanisms (Smith & Pokorny, 1975). The maximum value of contrast that could be provided to S-cones by modulating lights along the $S-(L+M)$ axis was 80.9%. By modulating lights along the $L-M$ axis 9.1% contrast to the L-cones 17.5% to the M-cones could be provided.

2.3. Display setting

Subjects were sitting 114 cm away from the front wall, which was illuminated by the fluorescent lamps. These illuminated about $64 \times 46°$ of the viewing field in a fairly homogeneous fashion. In the center of the wall there was a 25.5×20 cm ($10 \times 8°$) rectangular hole through which the monitor, placed 65 cm behind the wall in a felt tunnel, was visible. The monitor surface was unreachable for the light from the fluorescent lamps (see Fig. 1a). Observers saw only the light emitted from the monitor phosphors and the light reflected from the wall. In all experiments the adapting monitor background had the same chromaticity as the surround consisting of the illuminated wall. When the adaptation conditions changed, the lamps changed their chromaticity synchronously with the monitor, synchronized to the vertical refresh signal of the monitor.

2.4. Paradigm

In all experiments there was a reference color to which subjects initially adapted, and an adapting color to which subjects adapted to over time. Four different chromaticities (red, green, yellow, blue) for adapting and reference colors were used. They were chosen from each side of the two color axes. Chromaticities and cone contrasts of the adapting colors are given in Table 1.

Note that we did not equate cone contrasts across the different color axes. This means that S-cone contrasts were much higher for changes on the blue–yellow axis (57.3%) than the contrasts for L- and M-cones for changes along the red–green axis (6.2 and 11.7%, respectively). We explored the consequences of this potential confound in detail in Experiment 3 (below).

In the color appearance task, subjects had to adjust a central 3° patch until it appeared achromatic (see Fig. 1c). Most of the time, the CRT screen was uniformly illuminated with the adapting color or the reference color. The stimuli were briefly presented for 83 ms (ten frames) on the adapting background. After this brief presentation subjects could adjust the appearance for the next presentation along the color axes for which adaptation took place. For example, if the adaptation was from red to green, subjects could add more red or green along the $L-M$ cardinal axis to the central patch; when adapting from yellow to blue subjects adjusted the patch along the $S-(L+M)$ cardinal axis. The chromaticity changed only along the same cardinal axis, thus considerably reducing the complexity of the task. It has been shown that isoluminant adaptation along a single cardinal axis results in matches that differ mainly along the same cardinal axis (Würger, 1996). Our own preliminary experiments, where observers were allowed unconstrained three-dimensional ad-

justments in color space, confirmed this result for the experimental settings used here.

The Ganzfeld setting we used gave a strong impression of illumination. To get an achromatic appearance, in steady state, subjects added as much or slightly more chromaticity to the central patch as was present in the surround. With increasing adaptation over time, the central patch vanished at some point when it had the same chromaticity as the background. Therefore, the central patch was always presented with a slight increment in luminance of 2 cd/m^2. The induction effect is not or only slightly decreased under these conditions (Valberg, 1974), but this procedure ensured that the patch was always visible over the whole range of adjustments.

Chromatic discrimination was measured by a four alternative choice method with similar stimuli as used by Krauskopf and Gegenfurtner (1992). On each experimental trial, four discs of 1° diameter were presented for 83 ms (ten frames). The centers of the discs were located on the corners of a 1.7° imaginary square centered on the display (see Fig. 1d). Three of the discs (test patches) were of the same color, a randomly chosen fourth disc (comparison patch) differed slightly in increments of chromaticity along one cardinal axis. The observers task was to indicate the position of the comparison patch by pressing one of four buttons on a keypad.

2.5. Observers

One author (OR) and two naive female subjects (AS, MB) with normal color vision, one of them with corrected acuity, participated in this study. Two subjects (OR, AS) participated in discrimination and appearance experiments, one (MB) performed appearance experiments only.

3. Experiment 1: slow phase of adaptation

We initially investigated the slow phase of adaptation, similar to Fairchild and Reniff (1995), but using adapting colors both along the red–green and blue–yellow cardinal axes. Our goal was to compare the time courses of adaptation for appearance changes and changes in discriminability, and also to compare adaptation along different color directions.

3.1. Methods

The basic methods were described above in Section 2. Here, we describe the temporal paradigm that was used to measure the time course of adaptation for adaptation times between 1 s and 2 min. To avoid long periods of adaptation and re-adaptation, we used the 'method of a thousand staircases' (Cornsweet & Teller, 1965; Mollon, Stockman & Polden, 1987) to simultaneously make measurements at all adaptation times during the same experimental session. Here, subjects initially adapted to the reference color, which was one of four colors described in Table 1. After an initial 120 s of adaptation to the reference color, the monitor background and the lamps switched synchronously to the adapting color, which was always opponent to the reference color on the same cardinal axis. For green as reference color, the adapting color was red and vice versa. For yellow as reference color, the adapting color was blue and vice versa.

At fixed times after switching to the adapting background (adaptation time), test patches were presented for 83 ms and observers had to make a decision. In the discrimination experiments, subjects indicated the position of the comparison patch; in the appearance task subjects signaled the color direction into which the chromaticity of the central patch should be pushed to obtain an achromatic appearance.

The first measurement was made at an adaptation time of 1 s. Five seconds later the next stimulus appeared, and so on, until 121 s adaptation time (see Fig. 2a). Subjects did not have any problems responding within the 5 s time interval up to the next measurement. At the end of one run observers were fully adapted to the adapting color. Instead of re-adapting to the reference color to make the next run, this adaptational state was used to measure adaptation in the other direction along the same color axis. This way, no time consuming re-adaptation procedures were necessary.

In the discrimination experiments the chromatic contrast of the comparison patch was adjusted with a staircase procedure (Levitt, 1971). The discriminated colors were also one of the four chromaticities described in Table 1. They were chosen to have maximal thresholds when adapted to the reference colors and minimal when adapted to the adapting color. For example, when measuring the time course of adaptation from red to green, observers had to discriminate between green patches. Initially, after switching from red to green, the thresholds were high. At the end, when fully adapted to green, the thresholds were low. The discriminated colors for the other adaptation conditions were chosen analogously. The experiments started with the same increment values for all adaptation times. Thirty trials for each color direction were performed by the observers, divided in 5 × 6 trials per session. The thresholds and the slope of the psychometric functions were then calculated using probit analysis (Finney, 1971).

In the appearance experiments, the chromaticity of the central patch was adjusted by a staircase procedure with decreasing step size after each reversal. The patch initially had the same chromaticity at all adaptation

times. Chromaticity was changed into one of two directions on the color axis of adaptation, according to the answers of the observers. The achromatic loci were calculated applying a probit analysis to the choices.

The resulting time courses of discrimination and color appearance were fitted with exponential decay functions of the form $y = y_0 + A \cdot e^{-kt}$. To judge the significance of differences of time constants for adaptation along different color axes, we estimated the confi-

dence intervals for the exponential half-lives, which can be calculated from the time constant as $t_{0.5} = (\ln 2)/k$. Because there is no analytical method that gives the confidence interval for an exponential decay fit as a function of the confidence intervals of the individual thresholds, we applied a parametric bootstrap method (Efron & Tibshirani, 1998).

For each time course, 1000 samples were created by varying each measured threshold or adjustment according to the confidence interval given by the probit analysis. To each of these samples, an exponential decay function was fitted. The distribution of the resulting half-lives can be used to deduce a confidence interval. Because the distributions were not always normally distributed, we took the median and the quartiles as robust estimators for the true half-lives and the confidence regions. Note that the estimates of the half-lives or of their confidence intervals do not depend on the chosen units.

3.2. Results

Time courses were measured for three observers (OR, AS, MB) in the color appearance task, and for two observers (OR, AS) in the discrimination task. Four different color directions were measured for each observer. Fig. 2 shows the exponential half-lives for all observers and color directions, both for appearance changes (Fig. 2b) and discrimination changes (Fig. 2c). For adapting from yellow to blue the thresholds of observer AS were out of range for the chromaticities chosen as the adapting background. For this observer, the time course of discrimination could not be determined for this condition, whereas the time course of color appearance could be measured. Inspection of the 75% confidence intervals shows that there are no marked differences between the four different color directions. Half-lives are typically on the order of 15–25 s, with some variation between observers and very little variation between color directions. There might be a tendency for adaptation along the blue–yellow axis to occur slightly quicker, but it is questionable whether the small difference we observed (5 s on average) is of any practical significance when looking at such a slow overall timescale

Therefore we decided to average the curves to get more statistical power for the comparison between appearance and discrimination. Fig. 3 shows the result, percentage of adaptation between 1 and 121 s as a function of time, for appearance (circles) and discrimination (squares). The average curves were calculated by normalizing the individual curves with $y_0 = 0$ and $A = 100$ before averaging, giving equal weight to each data set. The simple first order exponential decay model describes the data quite well in the time interval from 1 to 121 s. The data show no systematic deviation from
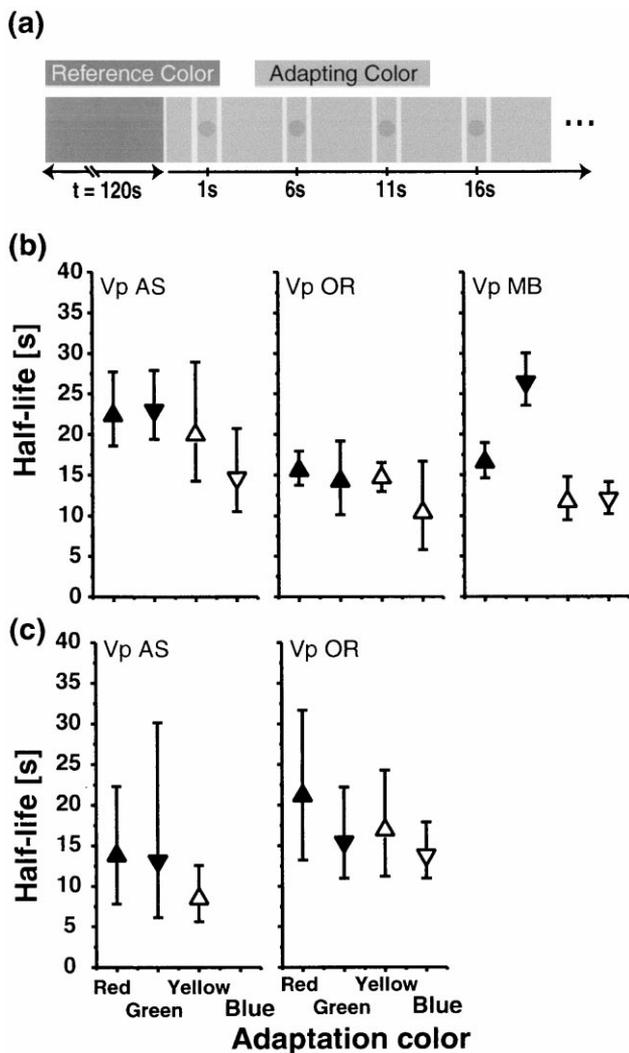

Fig. 2. (a) Temporal paradigm used to measure the time courses of adaptation from 1 to 121 s adaptation time. The stimulus configuration for the appearance task is shown, the same paradigm was used for chromatic discrimination. Observers initially adapted to a reference color (symbolized by dark gray). After switching to the adapting color (light gray), stimuli were displayed at fixed adaptation times. Observers made their decision in between the stimulus presentations. Stimuli were presented for 83 ms (ten frames). (b and c) Slow phase of adaptation. Comparison of half-lives across subjects and color axes. Fits were performed for 1–120 s adaptation time. On the *x*–axis the adapting colors are indicated; reference colors were always the opponent colors. The half-lives and confidence intervals were computed from median and quartiles of the bootstrap distribution of time constants. (b) Color appearance. (c) Discrimination.
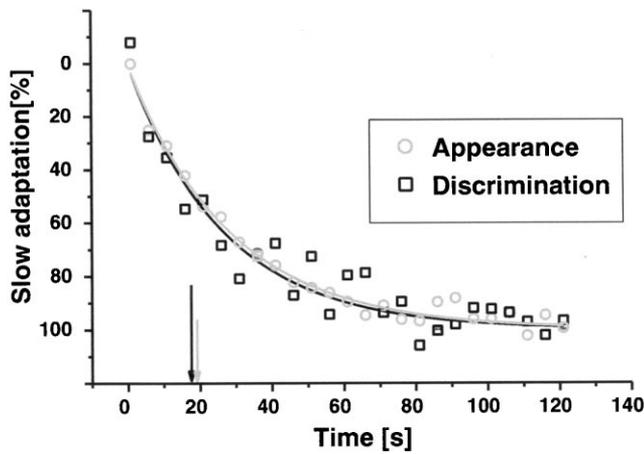
Fig. 3. Slow phase of adaptation. Averaged thresholds and adjustments for two subjects (OR, AS) and three adaptation conditions (red–green, green–red, blue–yellow) for which data for both discrimination and appearance was available. Individual fits were normalized to an offset of 0% and an amplitude of 100% before averaging. The fits of the averaged data were also normalized to 100% amplitude (details in text). The half-lives of the averaged curves were 18.4 s for discrimination and 19.6 s for appearance.

the exponential function. For the color appearance data, which are less noisy than the threshold data, the first order exponential function is an almost perfect model. The estimated half-lives for appearance and discrimination were 19.6 ± 0.8 and 18.4 ± 1.8 s, respectively, which is insignificant for statistical as well as practical purposes.

3.3. Discussion

These results show convincingly that there are changes in both appearance and discrimination occurring up to 2 min after changes in adaptation. The same, or similar, adaptational mechanisms seem to be involved for discrimination and appearance, since the time courses are practically identical for both dependent measures during that interval. Furthermore, adaptation seems to work in the same manner in all four different color directions we investigated here. This is interesting, because natural daylight changes, which occur on such a slow time scale, are almost exclusively along the blue–yellow color axis (Worthey, 1985; Hurlbert, 1991). Therefore, one could have imagined that such a slow mechanism might have evolved only along that axis. However, this was not the case.

Interestingly, no obvious physiological basis for this slow phase of adaptation has been described yet. Since it is functional in both appearance and discrimination, we speculate that it should occur at the retino-geniculate or an early cortical level. Yeh, Lee and Kremers (1996) have described chromatic adaptation effects in the lateral geniculate nucleus of macaque monkeys on a

similar time scale. And recent data by Müller, Metha, Krauskopf and Lennie (1999) indicate adaptational changes of single neurons in primary visual cortex of macaques that occur on a time scale of 8 s or even slower.

4. Experiment 2: fast phase of adaptation

The first order exponential model describes the data well in the time interval from 1 to 121 s, but only a small percentage of the total adaptation — defined as the difference in steady states between reference and adapting color — occurs during that interval. Most of adaptation occurs within the 1st s. To explore this initial component, we had to resort to a different paradigm. In the following, we will describe the time course of adaptation during the 1st s.

4.1. Methods

Methods were as above, with the exception of a different temporal paradigm. As in the experiments for the long time scale, observers initially adapted to a reference background for 2 min. Again, stimuli were presented for 83 ms at several fixed times after switching to the adapting background. However, 250 ms after the stimulus was displayed, the background switched back to the reference color and 15 s of re-adaptation occurred (see Fig. 4a). This re-adaptation ensured that adaptation always started from a defined state. Again, different adaptation times were interleaved within each experimental session. For discrimination experiments, 12 staircase reversals for each threshold were measured; for appearance ten reversals were used. Thresholds and achromatic loci were determined as above for the slow phase. The chromaticities of adapting background and reference background also were the same as in the previous experiments, described in Table 1. For brevity, we constrained our measurements to one color direction on each axis, from green to red, and from blue to yellow.

For the time course of discrimination, thresholds for five different adaptation times, ranging from 25 to 500 ms, were measured. For color appearance, achromatic adjustments at six different adaptation times were made. Steady state thresholds or adjustments when adapted to the reference color were determined in the same experimental sessions. The procedure for these steady state values was the same except for the background, which did not change its chromaticity on these trials, but remained constant. A comparison of these steady state measurements to measurements without any changes to adaptation showed that the 15 s re-adaptation period completely erased any effect the adapting color might have had on the state of adapta-

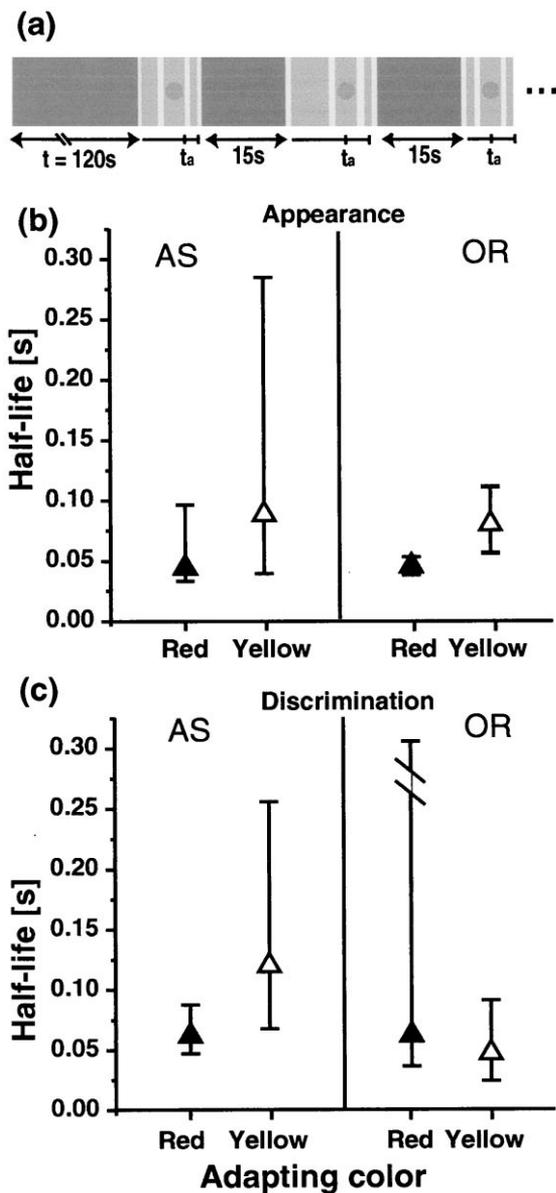tion. This was not the case for shorter periods of re-adaptation, as determined by preliminary experiments.
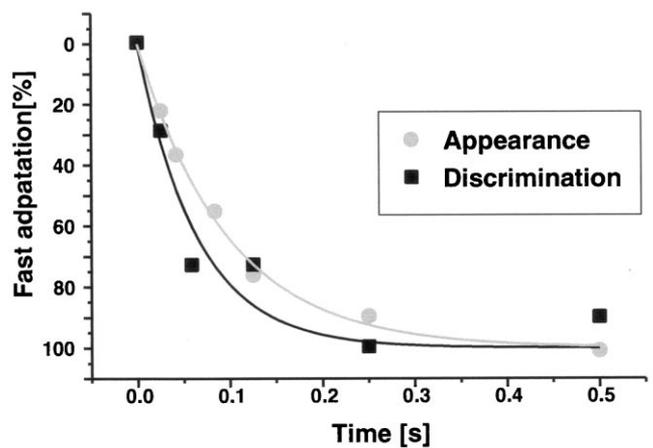

Fig. 5. Fast phase of adaptation. Averaged data of two subjects (OR, AS) and two adaptation conditions (green–red, blue–yellow) were fitted with a first order exponential decay function. Averaging was done as in Fig. 3. The half-lives of adaptation for the averaged curves are 44 ms for discrimination and 67 ms for color appearance.

4.2. Results

Fig. 4 shows the bootstrapped half-lives for color appearance and discrimination. As before, the data were fitted with first order exponential decay functions. Although the fits were not as good as for the slow phase, the deviations from this type of kinetic function were not systematic, making it reasonable to calculate the half-lives by using the time-constants. These were derived by bootstrapped fits from 25 to 500 ms for color appearance and from 0 to 500 ms for chromatic discrimination. Due to the high sensitivity of this method, and the small number of data points, the confidence intervals are relatively large. Half-lives varied between 34 and 92 ms. Again, as for the slow phase of adaptation, there is no significant difference across different color directions. Differences between the two observers were negligible.

We therefore averaged the individual curves to compare the time course of appearance and discrimination for that initial time period. Fig. 5 shows the percentage of fast adaptation as a function of adaptation time. Averaging was done as described above for the slow phase. On average, across color directions, the half-life of this fast adaptation process is 67 ms for appearance and 44 ms for discrimination.

4.3. Discussion

For both, color appearance and discrimination, there is a fast phase with half-lives between 40 and 70 ms. This is roughly similar to time constants found for receptoral processes in light adaptation (Hayhoe, Benimoff & Hood, 1987), and the cones themselves are indeed the most likely candidates for a neuronal sub-

Fig. 4. (a) Temporal paradigm for the short time interval with 0 s–500 ms adaptation time. Observers initially adapted to a reference color (symbolized by dark gray). After switching to the adapting color (light gray), stimuli were displayed at fixed adaptation times. After the stimulus presentations observers made their decision. A 15 s re-adaptation to the reference background occurred after each stimulus presentation. Adaptation times are symbolized as t_a. Stimuli were presented for 83 ms (ten frames). (b and c) Fast phase of adaptation. Comparison of half-lives between the two subjects and two color axes. Fits were performed from 0 s–500 ms for discrimination and 25–500 ms for color appearance. On the *x*-axis the adapting color is indicated. Reference colors were the opponent colors. The half-life and confidence intervals were computed from median and quartiles of the bootstrap distribution of time constants. (b) Appearance. (c) Discrimination.

strate of this fast adaptational process although it is probably not a reduced sensitivity of single cones (Nunn, Schnapf & Baylor, 1984). Note that because this phase of adaptation occurs both in appearance and discrimination, it has to be situated at a rather early processing stage.

The properties of the time course of adaptation and the differences between discrimination and appearance are best demonstrated by looking at the total time course. Fig. 6 shows typical data for one adaptation condition (green to red) for one subject (AS) for color
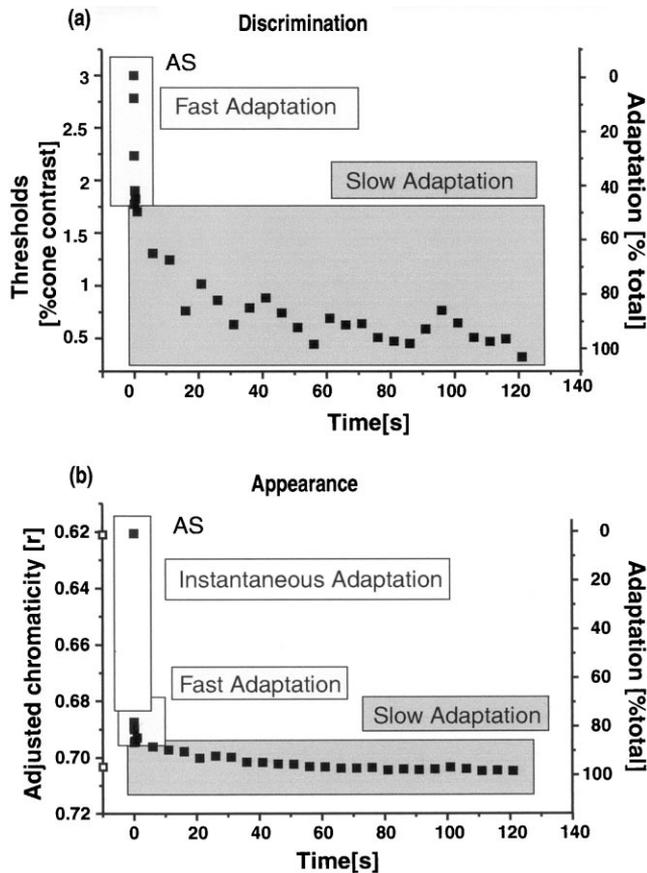

Fig. 6. (a) Full time course of adaptation of chromatic discrimination for a single observer (AS) for adaptation from green to red, as described in Table 1. On the x-axis the time after switching from reference background to adapting background (adaptation time) is plotted. The two boxes indicate the time intervals explored by the two separate experiments. The y-axis on the left shows the decrease of thresholds expressed as rms cone contrast. On the right y-axis adaptational state is expressed as percent adaptation scaled to the steady state thresholds, when adapted to the reference color or the adapting color. (b) Time course of color appearance for a single observer (AS) for adaptation from green to red. The y-axis shows the adjusted chromaticity of the central patch expressed as MacLeod–Boynton r color coordinate. The three boxes mark the time intervals that were explored in different experiments. On the right y-axis adaptational state is expressed as percent adaptation scaled to the steady state adjustments, when adapted to the reference color or the adapting color. The open symbols on the left y-axis indicate the chromaticity of the reference and the adapting background.

discrimination (Fig. 6a) and appearance (Fig. 6b) over the whole range of adaptation times. The first data points at 0 s adaptation time are the steady state thresholds or adjustments when adapted to the reference color. As adaptation time increases, thresholds decrease by about a factor of 7. For color appearance, with increasing adaptation time the chromaticity of the patch is pushed towards the background chromaticity. Dependent on observer and background, the stimuli are adjusted to 86–110% of the background chromaticity on steady state.

The time course of color discrimination thresholds as function of adaptation time in Fig. 6a was explored in two separate experiments. The light gray and the dark gray boxes mark the range of adaptation times measured using the two paradigms described for Experiment 2 and 1. For color discrimination there is an initial fast phase within the first 500 ms, and the rest of adaptation is carried out within about 2 min. Although measured in different experiments, the time courses of the two intervals overlap reasonably well to assume a smooth decrease in thresholds with our settings.

The time course of color appearance is shown in Fig. 6b. As in Fig. 6a, the boxes mark the time intervals where adaptation was measured with different experiments. As before, the effects of adaptation were measured in two intervals. The left y-axis shows the adjusted chromaticity of the central patch. The open symbols on the axis mark the chromaticity of the reference background and the adapting background. The right y-axis is scaled in percentage of total adaptation with the steady state adjustments, adapted to the (green) reference color and the (red) adapting color, as 0 and 100%. Again, we observe the same two phases, fast and slow, as in the discrimination experiments.

Although the slow and the fast phase together make up a single transition function of the adapting system, it is correct to fit the two phases separately because of the huge differences in their time constants. These differences between slow and fast phase were not caused by the different paradigms used to make the measurement, since there is good agreement for the adaptation times between 500 ms and 1 s. The offsets between the two time windows are always smaller than 8% of the total range of thresholds between the two steady state conditions. In both appearance and discrimination, the fast phase contributes about as much to adaptation within the first 500 ms, as does the slow phase between 1 s and 2 min.

Are these two phases all the processes that contribute to adaptation? While this is the case for color discrimination, as can be seen in Fig. 6a, it is clearly not the case for color appearance (Fig. 6b). Rather, the largest part (about 60%) of color appearance changes occur before we made our first measurement for the fast phase, thereby suggesting half-lives significantly shorter

Table 2
CIE coordinates and cone contrasts of adapting and reference colors used in color appearance experiments for the instantaneous phase of adaptation[a]

Hue	Adapting colors		Reference colors					
	Red	Yellow	Green 1	Green 2	Green 3	Blue 1	Blue 2	Blue 3
CIE x	0.379	0.373	0.309	0.290	0.261	0.361	0.307	0.297
CIE y	0.307	0.436	0.343	0.351	0.366	0.314	0.295	0.271
L	6.2%	−0.8%	−1.8%	−3.5%	−6.2%	0.2%	0.4%	0.8%
M	−11.7%	−1.1%	3.3%	6.7%	11.7%	0.3%	0.6%	1.1%
S	0.24%	−57.3%	−0.05%	−0.09%	−0.24%	16.4%	32.7%	57.3%

[a] Adapting colors remained the same along a color axis. The reference colors varied from only slightly saturated to highly saturated. The luminance of all colors was 26.0 cd/m^2.

than 25 ms, more on the order of 10 ms. We performed another experiment to characterize this instantaneous step more rigorously.

5. Experiment 3: instantaneous adaptation step for color appearance

Since this instantaneous step in adaptation occurred only for appearance, we only measured appearance adjustments in this experiment. We initially tried to characterize the exact temporal characteristics by increasing the temporal resolution of our measurements, but these attempts failed. The measurements at even shorter adaptation times (8 or 17 ms) turned out to be very noisy. Instead, we used reference colors of different saturation to investigate whether this process acts in a multiplicative or in a subtractive manner.

5.1. Methods

Again, we measured chromatic adjustments in steady state, after 25 and 250 ms. Three subjects (OR, AS, MB) participated in these experiments. The experimental paradigm was the same as in the experiments for the fast phase of adaptation. To figure out if this instantaneous component acted in a subtractive or rather in a multiplicative way, we used different reference backgrounds with a single adapting background. Adaptation occurred from different saturated greens to red as described in Table 2. Along the $S - (L + M)$ axis adaptation occurred from different saturated blues to yellow as described in Table 2. To measure the ratio of this initial process with reference to total adaptation, we also measured the adjustments in the steady state, fully adapted to the adapting color. If the adaptational process involved here are multiplicative, then the curves for the different reference backgrounds should completely overlap when plotted as a function of the total

adaptation. If a subtractive process is contributing, then the different curves will not overlap, but will be shifted relative to each other.
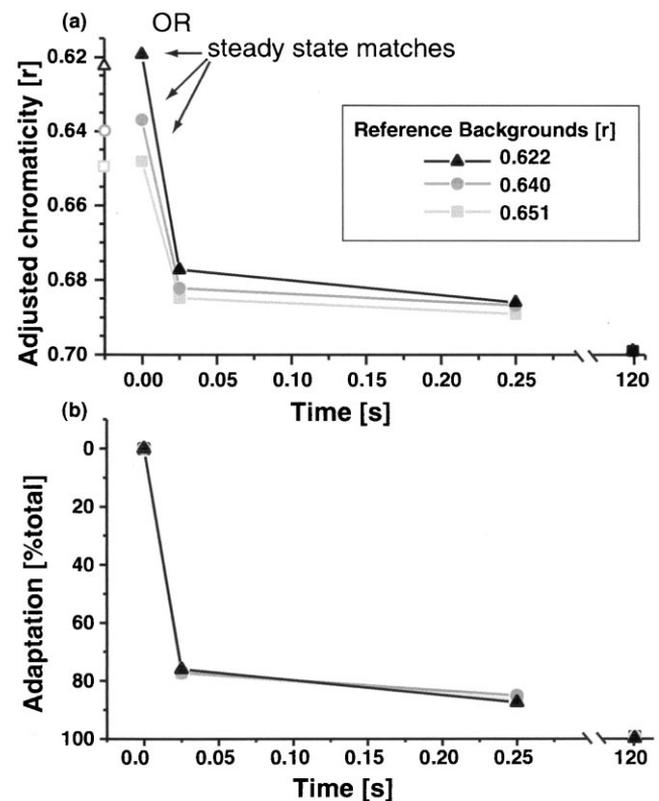

Fig. 7. Instantaneous phase of adaptation. Data of one subject (OR) for adaptation from three different green reference backgrounds to the same red adapting background is shown. In (a) chromaticity is indicated as MacLeod–Boynton color coordinate r. The chromaticities of the reference and adapting backgrounds are indicated by open symbols on the y-axis. The first points at 0 s mark adjustments in steady state, when adapted to the reference background. The last point at 120 s shows the adjustment in steady state when adapted to the red reference background. In (b) the same data, plotted as percentage of total adaptation, are shown. The first values in (a) at 0 s are 0%, 100% is the steady state adjustment, adapted to the red background.

5.2. Results

Fig. 7 shows the results for one subject (OR) for adaptation from green to red. The adjusted chromaticity (as the MacLeod–Boynton *r* coordinate) is shown as a function of adaptation time. For the least saturated background, adjustments at 25 ms after switching to the red background are already far on the red side. For the higher saturated green backgrounds, adjustments are grayish, and the absolute size of the initial steps becomes bigger.

Scaled as total adaptation, with 0% as steady state setting, adapted to reference background, and 100% as steady state setting, adapted to adapting background, the initial step explains 68% of adaptation, independently of the reference background. The same result, with step sizes varying between 60 and 75% were found for the other subjects and for the $S - (L + M)$ axis. These data are not shown here. These findings indicate a very fast, multiplicative mechanism which explains the major part of color appearance changes under changing illumination conditions.

5.3. Discussion

Because this instantaneous mechanism does not act in adaptation of discrimination thresholds, it can not be located at the retinal level. Otherwise discrimination thresholds should also be influenced by this component with its huge effect size. Therefore the fastest mechanism is of the highest order, located after the two others which were common to color appearance and discrimination. These results are in line with models that ascribe color induction to higher order, cortical sites. Since this initial step occurs more or less instantaneously, we think that it reflects higher order spatial interactions that have been described in steady state experiments (Krauskopf & Zaidi, 1986; Vimal & Shevell, 1987; Zaidi, Spehar & DeBonet, 1998; Shevell & Wei, 1998). It is probably based on interactions of the test stimuli with the spatial surround, and not on local, temporal changes of adaptation. In other words, this is a color contrast phenomenon, rather than a strict adaptational effect.

Since this instantaneous step made the biggest contribution to color appearance, this implies that higher order processes are more important for appearance than low level, retinal processes, such as von Kries receptor scaling. Less than 40% of the appearance changes can be explained by classical adaptation of cones or opponent channels. While the data argue against a strict interpretation of the von Kries law as a scaling occurring in the photoreceptors themselves, they agree quite well with a more generalized version of the von Kries law, which assumes the scaling to occur along three arbitrary axes of color space (see, for example, Bäuml, 1999).

6. General discussion

In summary, three phases of adaptation could be identified by their temporal characteristics. A slow phase with a half-life of 15–20 s and an exponential decay characteristic is common to appearance and discrimination. After about 2 min, chromatic adaptation has reached its steady state. A fast phase with a half-life between 40 and 70 ms is also common to color appearance and discrimination. The time course of adaptation for color discrimination consists of these two components only. Exclusive for color appearance, there is a third phase which is complete after no more than 25 ms, and makes the biggest contribution of all adaptation processes, about 60% of the total adaptation for color appearance. No differences between different color directions were found for any of these phases.

6.1. Contrast versus adaptation

We think that the differences between these three temporal components reflect the properties of two classes of steady state color appearance phenomena: successive contrast and simultaneous contrast, as defined for example by Kirschmann (1891). Classical adaptation processes located on retinal or opponent channel sites contribute to relatively slow appearance changes and to slowly decreasing aftereffects, in what is usually called successive contrast. A higher order, non adaptive, process changes the appearance of stimuli that are simultaneously presented with the background. We have shown here that these are indeed effects occurring at completely different time scales. All the processes described here contribute together to the induction effect in steady state.

6.2. Slow adaptation

Slow chromatic adaptation processes have been reported by Fairchild and Reniff (1995) for adaptation to different daylights. They used a sum of two exponential decay functions to describe the full time course. The slower part had a half-life of about 30 s. Our results for the slow phase of chromatic adaptation agree with Fairchild's results, although they indicate a slightly faster half-life of about 20 s. By using more highly saturated adapting colors that deliver contrast also to the *L*- and *M*-cones we were able to extend these findings to the red–green channel. The half-lives we found are also quite similar to those found in other experiments on color appearance (Shevell, 2000) and color detection (Krauskopf et al., 1982).

6.3. Fast adaptation

A second adaptive component is also common to

color appearance and discrimination for both cardinal color axes. This mechanism is faster; it has a half-life of 40–70 ms. This fast component, is responsible for about 50% of total adaptational effects on discrimination in our setting. Because of its timescale, this mechanism might correspond to local receptor adaptation, as described in light adaptation psychophysics (Hayhoe et al., 1987). For chromatic adaptation this fast part has not been described yet.

Data from the psychophysics of light adaptation (Hayhoe et al., 1987; Graham & Hood, 1992) indicate more than one component in the early adaptation process for light adaptation, making a first order exponential decay fit a bad description. Graham and Hood (1992) use a multiplicative and a subtractive module before a compressing nonlinearity. To account for adaptive behavior with periodic stimuli, additional modules have to be included (Hood et al., 1997). The reason why in our experiments this adaptation process can be roughly described by a low pass filter function could be the enormous differences in cone contrasts between light adaptation and purely chromatic adaptation. Whereas for chromatic adaptation the change in cone excitations is only about 10–15%, in light experiments cone excitations differ by log units.

On a physiological basis, the nonlinear relationship between quantum catch and receptor excitation can be modeled by four factors: pupil responses; cone photopigment bleaching (Rushton, 1972); cone response nonlinearity; and cellular adaptation as described by Boynton and Whitten (1970). All these processes contribute to a adjustment of cones working range, but not all processes will become visible with small cone contrast changes. Pigment depletion for example, which clearly plays a role in light adaptation, is not significantly involved here. Thus, a first order exponential decay function for the fast adaptation phase may occlude more complex mechanism in early adaptation processes, but under low contrast conditions it seems to be a satisfying approach.

6.4. Instantaneous adaptation

Whereas the above two adaptation mechanisms affect discrimination and appearance, probably by acting on the input to the visual cortex at some stage, the instantaneous component is a higher order mechanism, affecting only color appearance. It acts in a multiplicative manner. Independent of reference background, more than 60% of the total induction effect is complete within 25 ms. In studies with adaptation times of 1 s or more (Arend, 1993; Fairchild & Reniff, 1995; Werner, Sharpe & Zrenner, 1999) this extremely fast component could not be distinguished from the slower

processes described above. Since the instantaneous process does not contribute to chromatic discrimination, it must be acting on the color signal at a rather late stage, certainly after primary visual cortex, V1. Since this process also makes the largest contribution to color appearance changes, it follows that appearance, and with it color constancy, is mainly determined by higher-order, cortical processes, and only to a small extent by retinal adaptation or gain-control mechanisms, such as suggested by von Kries (1902).

At first sight, it seems odd that the fastest mechanism should be the one acting last. However, it has to be kept in mind here that our adaptation times cannot be equated with absolute processing times. Rather, they correspond to the temporal difference between reference background and adapting background. Simultaneous contrast is most likely mediated by areas in extrastriate visual cortex, which typically have latencies of 60–120 ms (Nowak, Munk, Girard & Bullier, 1995). Our results simply show that *after* such a latency, the reference background is taken into account almost immediately. Most likely, this is done by long-range spatial interactions, such as have been described in macaque area V4 (Schein & Desimone, 1990).

7. Conclusions

The effects of adaptation on color appearance and chromatic discrimination are mediated by at least two common mechanisms: A fast desensitization with a half-life of 40–70 ms and a slower component with a half-life of about 20 s. Chromatic adaptation is essentially complete after 2 min. Color appearance but not discrimination is strongly influenced by a third, extremely fast mechanism. This rapid component is therefore due to cortical computations, and situated after the other adaptive stages. This agrees with a recent neuropsychological study by Rüttiger, Braun, Gegenfurtner, Petersen, Schönle and Sharpe (1999) who found selective deficits for color constancy, but not for color discrimination, after circumscribed unilateral lesions of cortex.

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