



Asymmetries in the time-course of chromatic adaptation and the significance of contrast

Annette Werner ^{a,*}, Lindsay T. Sharpe ^b, Eberhart Zrenner ^b

^a Department of Optometry and Radiography, The Hong Kong Polytechnic University, Hung Hom, Kowloon, SAR Hong Kong

^b Eye Clinic, Department of Experimental Ophthalmology, University of Tuebingen, Tuebingen, Germany

Received 23 December 1998; received in revised form 8 August 1999

Abstract

The time-course of chromatic adaptation was determined as a function of the spectral content of the adaptation-light and of image-contrast. The adaptation-lights varied along the chromatic cardinal axes or one of their intermediate axes in an equiluminant plane in colour-space. We found an asymmetry in the initial time-course of adaptation (0.2–10 s) in that adaptation to middle-wavelength light was significantly faster than adaptation to short- and long-wavelength light. The asymmetry was only observed in the presence of a spatially complex pattern. It was fully supported by luminance and chromatic contrast and present under haploscopic stimulus conditions. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Human colour vision; Chromatic adaptation; Colour appearance

1. Introduction

Chromatic adaptation is a major aspect of colour vision because it ensures that colour vision can be used reliably under a wide range of different and unknown illuminations, thus providing a sensory basis for colour constancy. The proximity of the locus of daylight phases to the tritanopic confusion line has led to the speculation that the human colour vision system may have adapted during evolution in response to the natural variations of daylight (Lee, 1989; Hurlbert, 1991). This suggests that changes of the overall chromaticity along the blue–yellow (S-cone) axis might be better compensated for than those along other axes in colour space (v. Campenhausen, pers. com.). The argument is supported by findings of Worthey (1985), who projected data from a colour constancy experiment (McCann, McKee & Taylor, 1976) into an opponent system and found a general tendency for a better compensation of changes in the blue/yellow component of Munsell papers than in their red/green component. However, a number of other studies that have investigated the effect of chromatic adaptation on colour appearance

have failed to confirm this asymmetry (Jameson, Hurvich & Varner, 1979; Fairchild & Lennie, 1992; Webster & Mollon, 1994; Fairchild & Reniff, 1995).

Nevertheless, the experimental design of the study whose data were modelled by Worthey differed from those in which no asymmetry was found, in a possibly important aspect; that is, in the complexity of the adaptation-pattern. In the other studies, simple arrangements like centre-surround paradigms with mostly small adaptation-backgrounds and/or homogeneous adaptation-fields (a uniform white noise field in the case of Fairchild and Reniff's experiments) were used. In contrast, McCann et al. used a large (30 × 30 cm) and spatially complex, multicoloured Mondrian pattern, and it is therefore possible that the colour-specific effect in their data is related to the spatial parameters of their test-pattern.

It is well established that light and chromatic adaptation involve multiple mechanisms, i.e. processes of multiplicative gain-control as well as successive steps of subtractive spatio/temporal filtering (two-process model for adaptation: Jameson & Hurvich, 1972; Barlow & Lewick, 1976; Walraven, 1976; Hayhoe & Wenderoth, 1991). Furthermore, there is physiological and psychophysical evidence that not only local signals but also signals from remote areas in the visual field contribute

* Corresponding author. Tel./fax: +852-28922476.

E-mail address: amcwerner@compuserve.com (A. Werner)

to brightness and colour appearance (Valberg, Lee, Tigwell & Creutzfeldt, 1985; Creutzfeldt, Lange-Malecki & Wortmann, 1987; Wesner & Shevell, 1992, 1994). Most computational theories of colour constancy employ some kind of integration of signals over large parts of a scene in order to obtain a spectrally flat reference signal (the so called ‘grey world assumption’).

However, relatively little is known about the actual physiological processes underlying such large field computations and in particular about their role in chromatic adaptation. For example, it has been argued that during eye movements the slow time-course of chromatic adaptation would allow the computation of a space-time average over extensive parts of the visual scene, providing the reference signal for gain adjustment (D’Zmura & Lennie, 1986; Valberg & Lange-Malecki, 1990; Hayhoe & Wenderoth, 1991; Fairchild & Reniff, 1995). Earlier studies have pointed out that the same performance in colour constancy is achieved, if a complex Mondrian-like background is replaced by a uniform field, which is equivalent to the Mondrian in average chromaticity and luminance (Arend & Reeves, 1986; Valberg & Lange-Malecki, 1990; Arend, 1993). On the other hand, the majority of findings have stressed the importance of the complexity of the adaptation-background and of local contrasts for chromatic adaptation and/or colour constancy (Shapley & Enroth-Cugell, 1984; Blackwell & Buchsbaum, 1988; Walraven, Benzschavel, Rogowitz & Lucassen, 1990; Werner, 1990; Brown & MacLeod, 1991; Wesner & Shevell, 1992; Fuchs, 1992; Baeuml, 1994; Jenness & Shevell, 1995).

The present study aimed to investigate the effect of the wavelength of the adaptation-light and of image-contrast on chromatic adaptation. Because different

mechanisms of adaptation can be distinguished by their time-course (Hayhoe & Wenderoth, 1991), the effect of the test-parameters was determined for different adaptation-times between 0.2 and 120 s. The time-courses were compared for three different spatial arrangements of the test-pattern and for five different adaptation-lights, which were chosen from the cardinal axes and one of the intermediate axes in an equiluminant plane in colour space.

2. Method

2.1. Subjects

Four subjects participated in the experiments. Two were naive observers (AS, SS), one of them was the author (AW), and one observer (LR) had participated in other visual psychophysical experiments. All had normal or corrected to normal visual acuity. Normal colour vision was established for all subjects by means of Ishihara and Farnsworth–Munsell-100-Hue tests and by their individual setting of the achromatic colour locus (see below).

2.2. Apparatus

The experiments were conducted in a dark room. The stimuli were generated with a 3×12 bit colour processor (Cambridge Research Systems) and presented on a 20 in. calibrated colour monitor (Barco Reference Calibrator©). The monitor was warmed up 4 h before the beginning of the experiments and it was re-calibrated with an in-built routine before each experimental session. The outcome of this re-calibration was checked before and after the experiments with a spectral-photometer (Minolta, PR650). The screen was viewed without head fixation and from a distance of 80 cm through a box ($40 \times 40 \times 90$ cm) that enclosed the front of the monitor. The box was lined inside with black velvet, to limit specular reflectance.

2.3. Stimuli

The test-patterns were presented in the centre of the screen. Because of the residual luminance of the monitor’s background, the surrounding background was masked with black cardboard. Different types of test-patterns were used:

1. the large complex pattern ($15.4 \times 13.2^\circ$) consisted of 37 single hexagonal patches ($2.4 \times 2.2^\circ$) that were different in luminance and/or hue and chroma (Fig. 1). The different colour domains and luminance levels were distributed evenly over the pattern. The test-field was situated in the centre of the test-pattern ($F_{T/A}$ in Fig. 1).

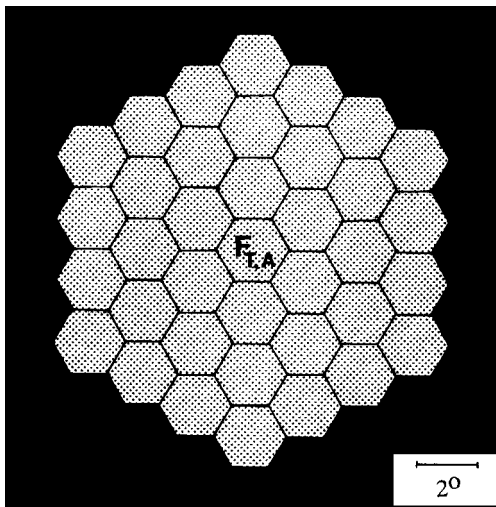


Fig. 1. Test-pattern (complex arrangement). $F_{T/A}$ marks the position of the test-patch. The underlying dot-pattern is not present in the actual test-pattern and is shown here only to indicate the presence of colour.

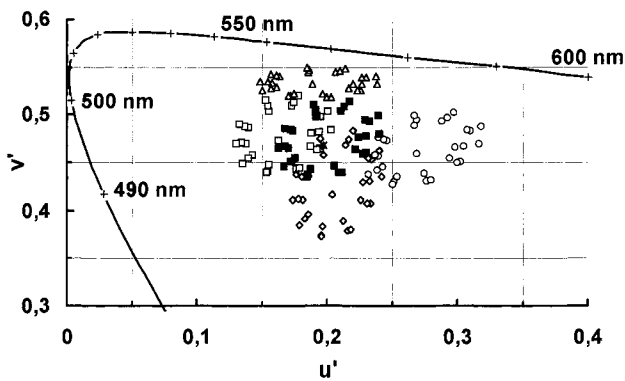


Fig. 2. Colour loci of the stimuli in the CIE (1976) UCS diagram. The filled symbols (■) represent the stimuli in the standard condition, the open symbols represent stimuli in the red (○), green (□), blue (◇) and yellow (△) test-condition. The locus of the test-patch in the standard condition, i.e. the locus of D65 is marked by an asterisk (*). Note that in order to make the direction of the colorimetric shifts more obvious, the maximal possible colorimetric shifts are depicted. For the actual experiments, the chromaticity-changes produced shifts of $22.88\Delta E_{uv}^*$ for all colour stimuli.

2. the uniform test-pattern was equivalent to the large complex pattern in size and mean luminance.
3. the dichoptic test-pattern consisted of two smaller patterns (each $11 \times 9.6^\circ$) that were presented side by side. They corresponded to the above described complex pattern (but now containing only 19 single patches) and the uniform pattern. In order to facilitate binocular fusion of the patterns, the subjects wore prism lenses during the tests.

The chromaticities of the patches were calculated from the tabled chromaticities of Munsell papers (Wyszecki & Stiles, 1982). Under the standard condition, the chromaticity of the test-patch was $u' = 0.197$, $v' = 0.468$ (chromaticity values of the illuminant D65) and its luminance was 19.3 cd/m^2 . The other stimuli differed in chromaticity and luminance (minimum luminance was 6.4 cd/m^2 , maximum luminance was 29.3 cd/m^2). The six patches directly bordering the test-patch corresponded to the Munsell designations 5R5/5, 5Y5/5, 5G5/5, 5B5/5. Two patches had the same chromaticity values as the test-patch, but differed in their luminance (29.3 and 6.4 cd/m^2).

The mean chromaticity over all patches was for the standard condition $u' = 0.199$, $v' = 0.471$ (near the chromaticity of D65), and the mean luminance was 16.75 cd/m^2 . Note that the chromaticity and the luminance of the test-patch were under all adaptation conditions near those of the mean values over the entire test-pattern.

There were six different adaptation-conditions: The standard condition (D65-adaptation) refers to the 'neutral' state of the test-pattern. The chromaticities of the patches are shown by the filled square symbols in Fig. 2. The test-conditions (blue, green, yellow, yellow-green and red adaptation) refer to the shifting of the

chromaticities of all patches along one of the cardinal axes (S- or L/M-cone-axis, as calculated after Krauskopf, Williams & Heeley, 1982) or one of their intermediate axes (see Fig. 2). These modulations were obtained by applying weighting factors to the underlying receptor values (spectral sensitivities of the receptors as derived by Vos & Walraven, 1971). The weighting factors were determined by the amount of change in the receptor responses that was necessary to shift the colour locus of the test-patch by a distance of $22.88\Delta E_{uv}^*$. The same scaling factors were then applied to calculate the new colour loci of all the other patches of the test-pattern. The effect was therefore to shift the colour loci of all patches equally along the same axis in an equiluminant colour plane.

2.4. Procedure

First, the chromaticity setting for the achromatic colour locus was recorded for each subject after a 120 s adaptation to the test-pattern in the standard condition. It was also determined at the beginning and after the actual experimental sessions. For all subjects, the settings for the achromatic colour locus were within $2\Delta E_{uv}^*$, i.e. within one just-noticeable-difference, of the colour locus of D65.

The amount of chromatic adaptation was measured for adaptation-times of 0.2, 1, 5, 10, 30 and 120 s (Fig. 3). The test pattern was viewed binocularly and without a fixation-point from a distance of 80 cm. To acquaint the subjects with the test situation and with the task, a practice session was run before the start of the actual experiments. The sessions commenced with 10 min dark adaptation and 2 min pre-adaptation to the test-pattern in the standard condition. The subjects were instructed to spend the same time looking at each of the single patches. This was followed by adaptation to the test-pattern in the respective test-condition, at the end of which the subject had to indicate whether or not the test-patch appeared achromatic ('grey'). 'Grey' was defined as 'being neither red nor green and neither yellow nor blue'. The subject was allowed to make his/her judgement only during a 0.2 s time-interval, which was delimited by two beep-tones. A void-period (black monitor screen) for 3 s followed the test-interval, in order to avoid the judgement being influenced by chromatic after-effects. The test-pattern was then presented again in the standard condition, to readapt the visual system to its previous, 'neutral' state of adaptation. The time for this re-adaptation was three times longer than the previous chromatic adaptation, but was at least 5 s (for adaptation-times of 0.2 and 1 s).

The effect of adaptation was measured by a hue-cancellation technique for the achromatic appearance of the test-patch. Although not a standard procedure, the method is similar to that presented in other research for

testing the time-course of chromatic adaptation (Fairchild & Lennie, 1992; Fairchild & Reniff, 1995). It has been shown that the achromatic colour locus shifts during adaptation along the chromaticity line between the colour loci of two adapting lights (Fairchild, 1991). The state of adaptation was therefore determined by the position of the achromatic colour locus along that axis. Complete adaptation (100%) was defined as a complete shift of the achromatic locus from the chromaticity values of the test-patch in the standard condition to those of the test-patch in the test-condition, in which case the test-patch appeared 'grey' after adaptation. When the achromatic colour locus shifted only partially towards the new locus of the test-patch, the test-patch appeared tinged.

If the test-patch no longer appeared 'grey' after the specified adaptation period, the achromatic locus was determined as follows: using a keyboard matching-device, the preceding chromaticity-change was partly cancelled. This was achieved by partly shifting the colour loci of all patches back towards their loci in the standard condition. It should be pointed out that in contrast to the procedure usually used for hue cancellation, the adjustment here affected not only the test-patch but all patches of the test-pattern. Furthermore, the test-pattern was presented with the 'reduced' chromaticity-change during the subsequent test-intervals only; during the adaptation-interval, the 'full' chromaticity-change was presented, in order to preserve the original state of adaptation. The amount of cancellation increased with each presentation until the subject reported that the test patch appeared grey. The resulting chromaticity-setting for the test-patch indicated the position of the achromatic colour locus under the prevailing adaptation and was recorded.

The effect of adaptation was quantified by calculating the CIE 1976 colour difference ΔE_{uv}^* between the

chromaticities for the achromatic colour locus after adaptation to the test-pattern in the standard condition and after adaptation in the respective test-condition. The ΔE_{uv}^* measure was used because the intention of this study was to measure changes in colour-perception, as opposed to changes in detection or discrimination thresholds. Care was taken that the colour stimuli would, in all conditions, lay within the gamut for which the CIE 1976 colour difference ΔE_{uv}^* is valid (Judd & Wyszecki, 1975). Data are presented as means and standard error of the mean (S.E.M.). Each subject repeated each setting five to ten times. The *t*-test was used for the statistical analysis of the data.

3. Results

The time-course of chromatic adaptation was measured for the blue, yellow, green and red test-conditions, respectively. To investigate the effect of image-contrast on adaptation, the time-courses of chromatic adaptation were compared for a complex and a uniform test-pattern. Complete time-courses were recorded for the observers AS and AW; for the observers LR and SS, the amount of adaptation was measured for adaptation-times of 5 and 120 s, respectively.

3.1. The time-course of chromatic adaptation with a complex background

Fig. 4a and b show the time-courses of adaptation for observers AS and AW using the complex test-pattern. The amount of adaptation varied slightly, but not significantly, between these subjects, and no differences were observed in the general form of the time-courses. The measurements in subjects LR and SS were consistent with the results of the other two subjects. There-

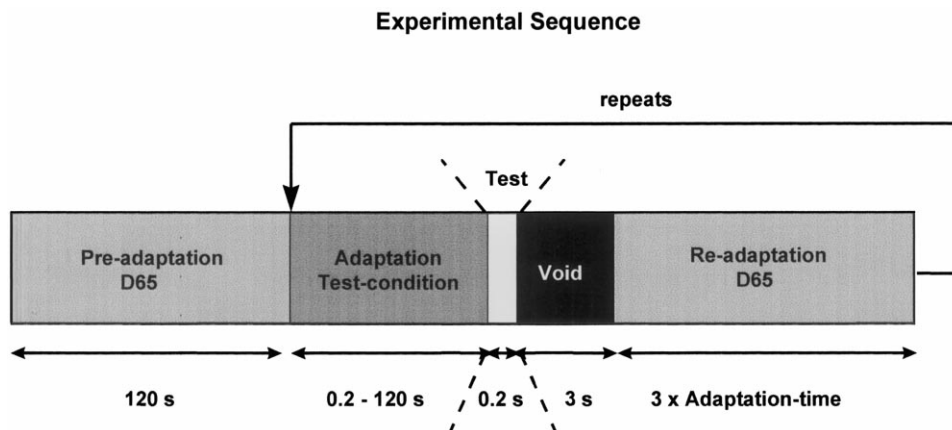


Fig. 3. Experimental sequence. Pre-adaptation D65: the pattern was presented in the standard condition for 120 s; Adaptation test-condition: the pattern was presented in the respective test-condition (blue, green, yellow-green or red adaptation); Test: time interval of 200 ms during which the observer made his/her judgement; Void: black screen presented for 3 s; Re-adaptation D65: the pattern was presented in the standard condition, for $3 \times$ the adaptation-period of the preceding test-condition.

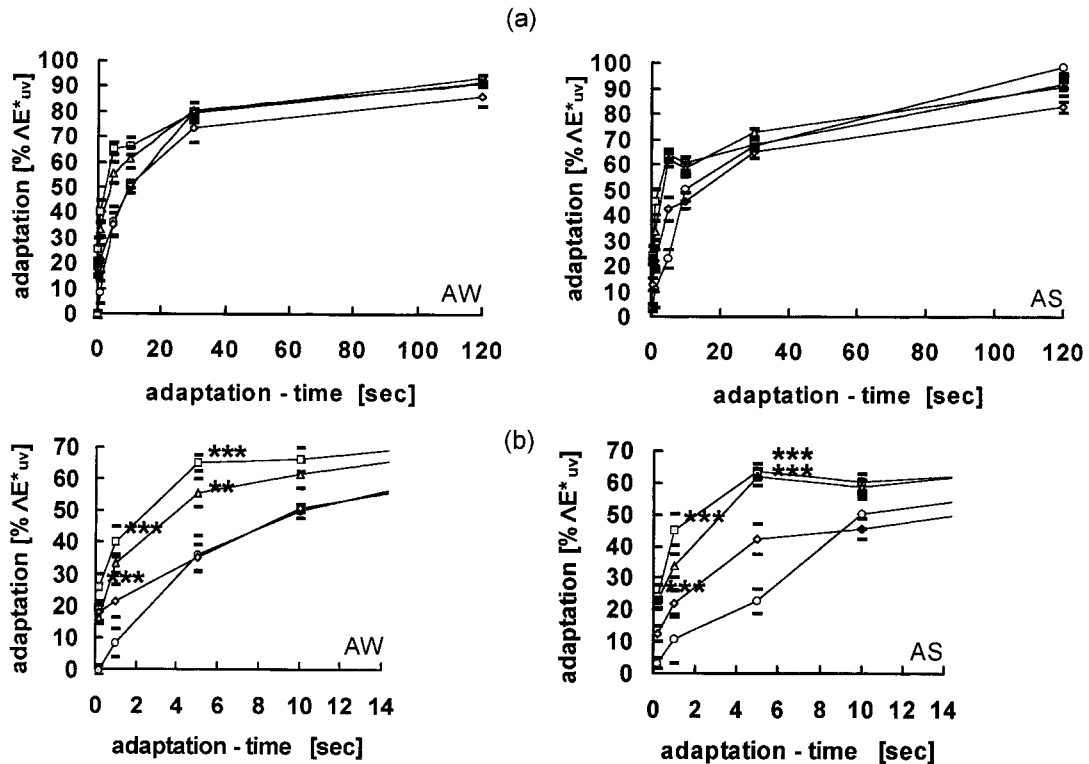


Fig. 4. Time-course of chromatic adaptation for a complex pattern. (a) Complete time-course, (b) same data, but the first 10 s in detail. Different symbols refer to the different adaptation-conditions: red (\circ), green (\square), blue (\diamond), yellow (\triangle). 100% ΔE_{uv}^* refers to the maximum possible adaptation shift, i.e. colour distance between the colour loci of the test-patch in the standard condition and in the respective test-condition. Results of subject AW are shown on the left, those of subject AS on the right. Asterisks indicate significant differences between the amount of red and green adaptation, and of blue and yellow adaptation, respectively (t -test: ***: $P < 0.001$; **: $P < 0.01$). Bars indicate the standard deviation.

fore, the results of all observers will be discussed together.

The general time-course (Fig. 4a) is biphasic and in this similar for all test-conditions. During a fast initial phase within the first 5 s, adaptation compensates for 50–60% of the chromaticity-change. This is followed by a slow asymptotic approach to a steady state over the following minutes. After 120 s, more than 80% of all changes are compensated for, irrespective of the colour of the adaptation-light. The fast initial phase, however, shows a marked difference between the different adaptations, as is shown in Fig. 4b: yellow and green adaptation occur significantly faster and reach the steady state earlier than the blue and, in particular, the red adaptation. Also, the slope of the adaptation-curve is steeper and the amount of adaptation at the earliest measured time (0.2 s) is higher for yellow and green than for red and blue adaptation. After more than 10 s, the slower red and blue adaptation ‘catch up’ with the yellow and green adaptation. No differences were observed for adaptation-times longer than 30 s.

It appears therefore that the time-courses of the different adaptations form two distinct groups, i.e. red and blue adaptation on one hand and yellow and green adaptation on the other. These two groups are distinguished by their time constants: approximately 1 s for

yellow and green and 8 s for red and blue. Furthermore, they differ by the presence of a non-monotonic section (‘overshoot’) in the yellow and green time-courses at an adaptation-time of 5 s. Although this ‘overshoot’ was not statistically significant from the value at 10 s in any of the test-series, it was observed in all experiments using the complex pattern and for yellow and green adaptation, but in none involving red and blue adaptation or when using the uniform field (see below). It appears therefore that the overshoot, though not statistically significant, is a systematic deviation from the otherwise monotonic increase of adaptation over time and is characteristic for yellow and green adaptation.

3.2. The time-course of chromatic adaptation with a uniform field

The experiment as described above was repeated, but now using the uniform test-pattern. Fig. 5 shows the results for subjects AW and AS. Again, a biphasic time-course was observed, consisting of a faster initial phase over the first 5 s and a following asymptotic phase over the next 115 s of adaptation. The steady state level obtained after 120 s, is slightly, but not significantly, lower than that in the complex pattern. In

contrast to the complex condition, no colour specific differences were found. We conclude therefore that the colour specific differences observed in the complex pattern are related to the presence of image-contrast.

In Fig. 6a–d the initial time-course of adaptation in the complex pattern and the uniform field are separately compared for each of the test-conditions. The results are similar for both observers and are therefore only shown for subject AW. It can be seen that the presence of contrast accelerates green and yellow adaptation, but has no effect on red and blue adaptation.

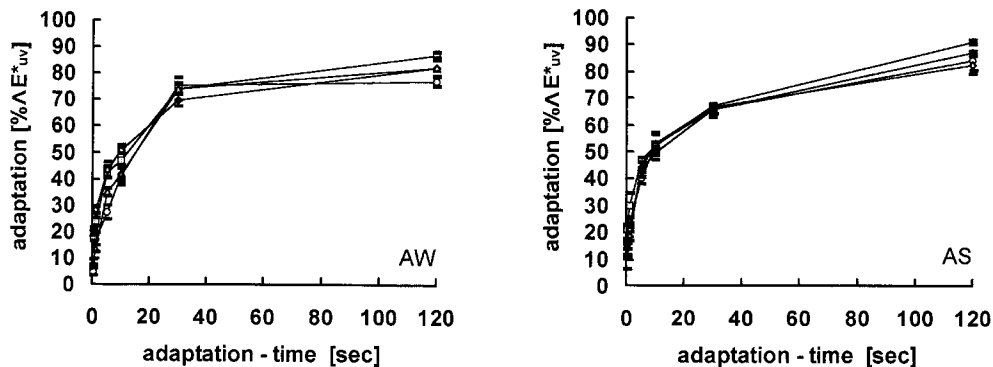


Fig. 5. Time-course of chromatic adaptation for the uniform pattern. Same symbols as in Fig. 4a–b. Results of AW are shown on the left and AS on the right.

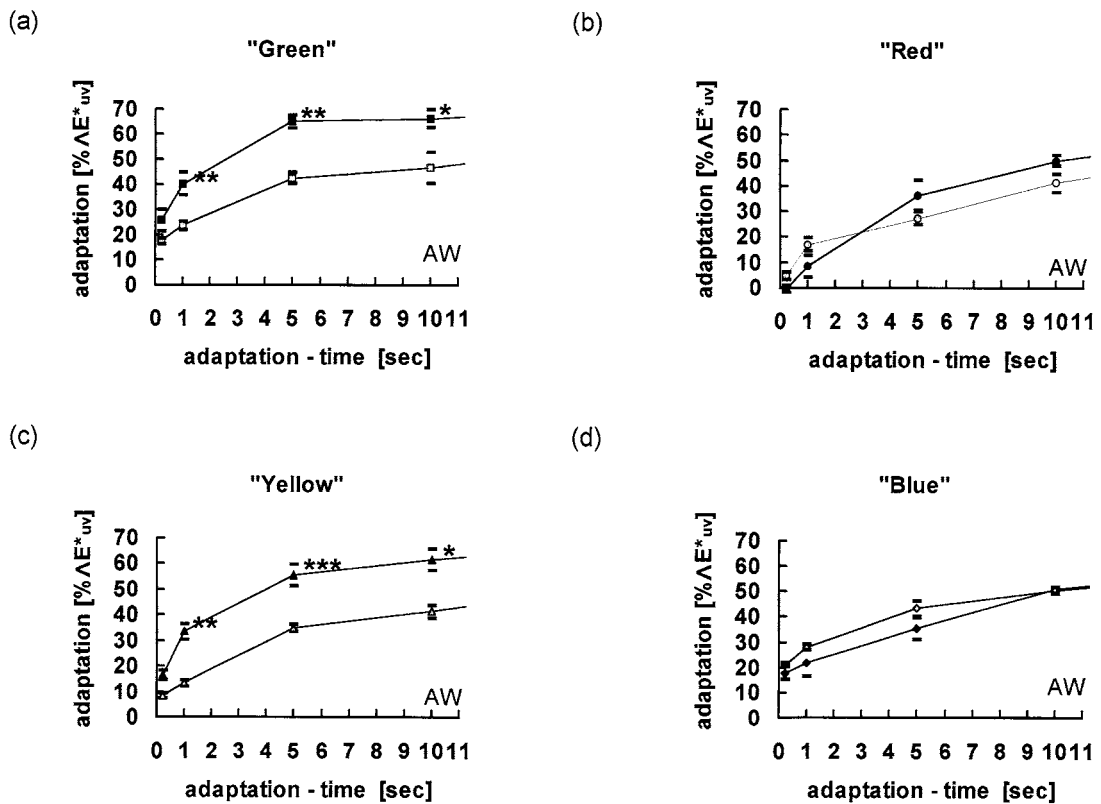


Fig. 6. The effect of contrast on the time-course of chromatic adaptation. (a) green, (b) red, (c) yellow and (d) blue adaptation. Filled symbols represent data for the contrast condition, open symbols represent data for the uniform condition. Asterisks indicate significant differences between the amount of adaptation reached after the respective adaptation-time. (*t*-test: ***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.05$). Results are shown for subject AW.

The wavelength-specific behaviour of chromatic adaptation is summarised in Fig. 7, where the effect of 5 s adaptation is presented as a function of the dominant spectral region of the adaptation-light and compared for the complex and the uniform pattern. In order to determine whether or not contrast acceleration is confined to the cardinal axes, the value for a 5 s adaptation in the complex pattern was also measured for one of the intermediate axes in colour space (yellow–green). It can be seen from this figure that the contrast related acceleration of adaptation has a single

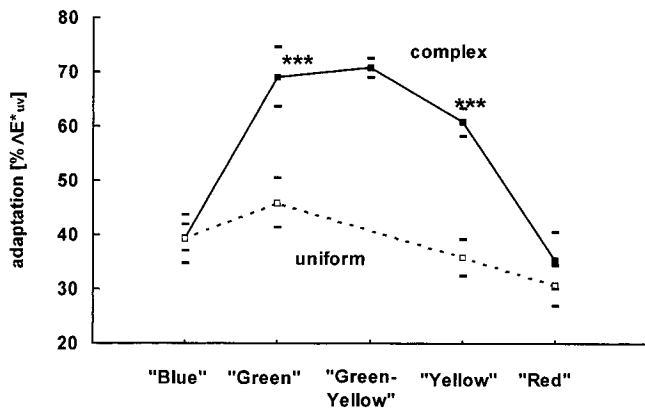


Fig. 7. The effect of the wavelength of the adaptation-light and contrast on chromatic adaptation. Same symbols as in Fig. 6. The adaptation-lights are ordered along the abscissa according to their corresponding dominant colour region. Results are shown as the average for three subjects (AW, AS and LR); SS did not take part in all experiments.

maximum for middle-wavelength-light, and that the yellow-green adaptation is as equally effective as the green adaptation. For both the short- and long-wavelength adaptation, the adaptation rate is lower and independent of the presence of contrast. There is a slight increase of green adaptation in the uniform pattern, however, this effect was not statistically significant.

3.3. Chromatic properties of the proposed contrast-mechanism

In order to find out whether luminance or chromatic contrast, both of which were present in the complex pattern, or their combination, is responsible for the observed acceleration-effect, a 5 s green as well as a 5 s yellow adaptation were measured using: (1) the uniform pattern; (2) the multicoloured pattern with chromatic plus luminance contrast; (3) an achromatic pattern with luminance contrast only; and (4) an equiluminant chro-

matic pattern with chromatic contrast only. The achromatic pattern was produced by replacing the chromaticities of each single patch by the chromaticity of the test-patch, leaving the luminance as before. The chromatic pattern was obtained by replacing the luminance value of each of the single patches by that of the test-patch.

Fig. 8a and b show the result of green adaptation for the observers AW and LR. In comparison to the uniform pattern, adaptation was enhanced similarly by using either the luminance or the chromatic pattern or the multicoloured complex pattern. The same results were obtained for the yellow adaptation.

3.4. Dichoptic presentation

The purpose of this experiment was to localise the proposed contrast-sensitive mechanism. To distinguish between retinal and cortical adaptation-sites, the interocular transfer of contrast-adaptation was tested in a dichoptic arrangement (Fig. 9) In the *contralateral* condition, the test-eye was adapted to the uniform pattern, the non-test-eye was adapted to the complex pattern. In the *ipsilateral* condition, the test-eye was adapted to the complex pattern and the non-test-eye was adapted to the uniform pattern. In the *uniform condition*, which served as a control, both eyes were adapted to the uniform field. To minimise the influence of ocular dominance, the tests were alternately performed with the left and the right eye being the test-eye. The effect of adaptation was tested by presenting the uniform field to the test-eye and a black screen to the non-test-eye.

Adaptation was measured for the yellow test-condition and for an adaptation-time of 5 s. Fig. 10 shows the results for the subjects LR and AW, respectively. In both observers, contralateral and ipsilateral adaptation yielded almost identical results and both were significantly more effective than binocular adaptation using the uniform field only. From this we conclude that the

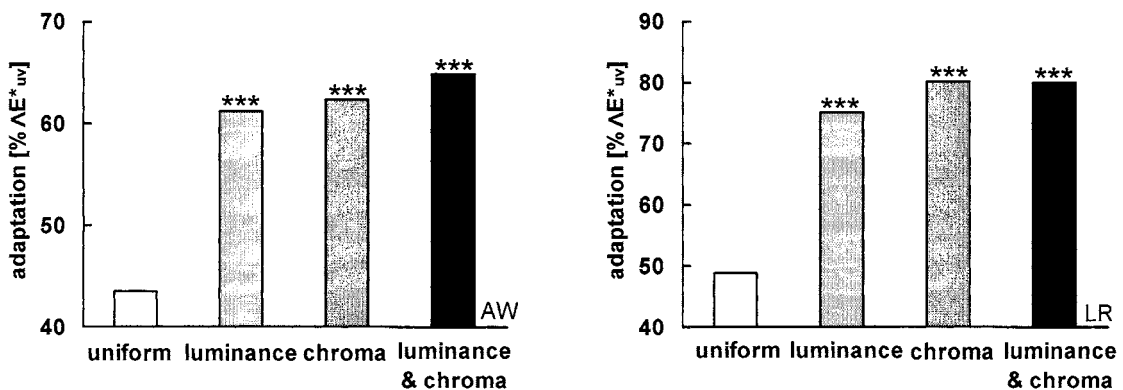


Fig. 8. Comparison of the amount of green adaptation using a uniform, luminance, chromatic, and multicoloured (luminance & chroma) test-pattern. Results of subject AW are shown on the left, those for LR on the right. Adaptation-time was 5 s. Asterisks indicate significant differences as compared with the uniform condition (t -test: ***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.05$).

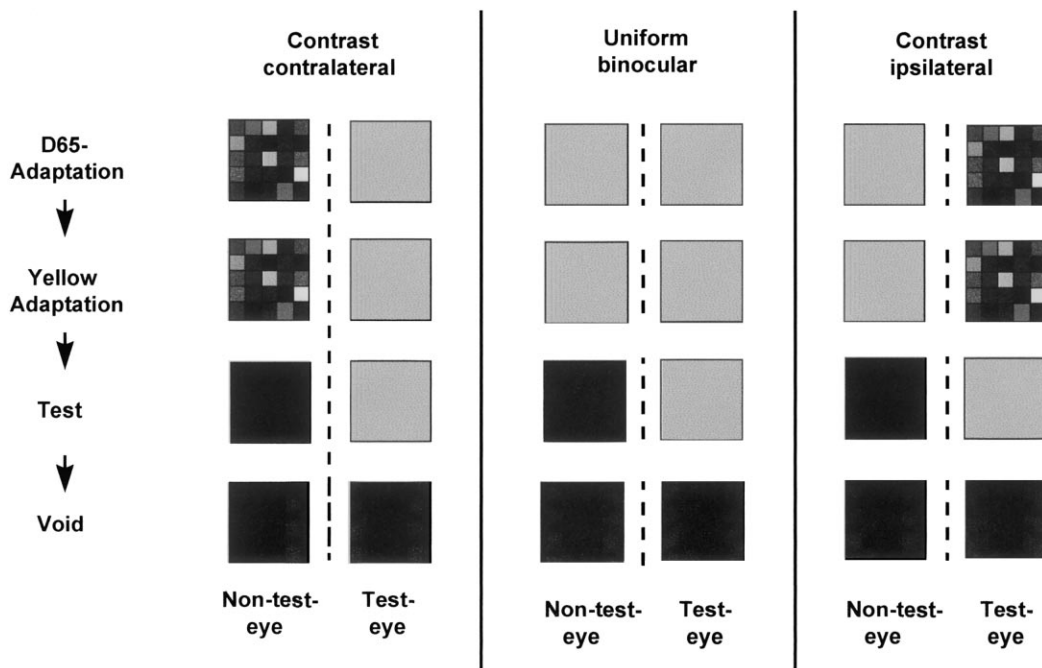


Fig. 9. Sequence of the presentation of test-stimuli in the dichoptic experiment. In the presentations shown, the right eye is the test-eye. Please note that the test-pattern shown here is only a schematic representation. Except for the smaller number of patches, the actual test-pattern resembled that used in the former experiments.

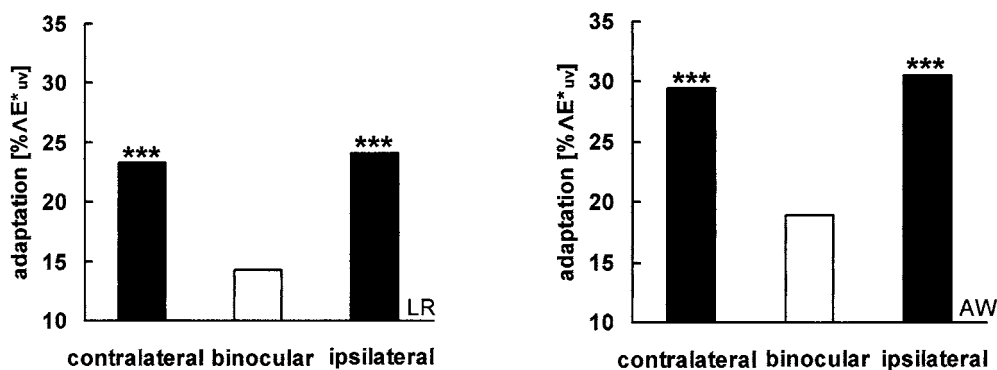


Fig. 10. Yellow adaptation in the dichoptic arrangement. Results of subject LR are shown on the left, those for AW on the right. The respective left bar represents the contralateral condition (non-test-eye adapted to the complex pattern), the respective right bar represents the ipsilateral condition (test-eye adapted to complex pattern), and the respective middle bar represents the control condition (both eyes adapted to the uniform field). Adaptation-time was 5 s. Asterisks indicate significant differences as compared with the control condition (binocular adaptation to uniform pattern; t -test: ***: $P < 0.001$).

contrast-sensitive mechanism of chromatic adaptation has a cortical site.

3.5. Modelling the time-course

We looked for a mathematical model which would be physiologically plausible and be able to incorporate the findings of the present study. We decided to model the time-courses by the sum of simultaneous exponential functions, consistent with the model of Fairchild and Reniff (1995). Our model differs however from Fairchild and Reniff's model in that their model consisted of two functions whereas in our model the spec-

tral region of the adapting light and the presence of contrast are taken into account by an additional exponential function. The general form of the model is:

$$F(t) = 100((1.0 - (a_1 e^{(b_1 t)} + a_2 e^{(b_2 t)}) + d(1.0 - (a_3 e^{(b_3 t)}); 0.2 < t > 120;$$

with

$$d = cl e^{-0.078t}; c = 0, 1; l = 0, 0.25; \text{ for } t < 5: t = 0.$$

$F(t)$ is the amount of adaptation after the adaptation-time t ($0.2 < t < 120$), $a_{1,2,3}$, $b_{1,2,3}$ and d are scaling-factors and are listed in Table 1. The first two exponential functions describe the relatively slow increase of adap-

tation over time with a combined time constant of 8 s, whereas the third exponential has a shorter time constant (0.2 s) and describes the fast initial phase of green and yellow adaptation in the presence of contrast. Its contribution is determined by the factor d , which depends on the contrast (c), the wavelengths of the adapting light (l) and the adaptation-time (t). After an adaptation-time of more than 5 s, d decays exponentially (time-constant of the decay is 9.5 s; Fig. 11a). It thus limits the observed acceleration of green and yellow adaptation in the complex condition to its initial phase and causes the non-monotonic section of the adaptation-function between 5 and 10 s. $c = 0$ for the case of the uniform pattern and $c = 1$ for the case of the

complex pattern (arbitrarily chosen for the given contrast-condition). l is 0 for the case of blue- and red adaptation and 0.25 for the case of green and yellow adaptation.

Fig. 11b shows the result of the model for chromatic adaptation in the absence of contrast (uniform pattern). The time-courses of all adaptation-functions are described by the first two (slow) exponential functions with identical parameters $a_{1,2}$ and $b_{1,2}$, whereby there is no contribution of the third exponential ($d = 0$).

Fig. 11c shows the results of the model for adaptation in the presence of contrast (complex pattern). Red and blue adaptation are again sufficiently described by the first two slow exponential functions, with identical

Table 1

	Parameters								Time-constant (s)
	a_1	b_1	a_2	b_2	a_3	b_3	L	c	
<i>Uniform condition</i>									
Red, blue	0.45	-0.013	0.45	-0.15	0.69	-2.9	0	0	8
Green, yellow	0.45	-0.013	0.45	-0.15	0.69	-2.9	0.25	0	8
<i>Contrast condition</i>									
Red, blue	0.45	-0.013	0.45	-0.15	0.69	-2.9	0	1	8
Green, yellow	0.45	-0.013	0.45	-0.15	0.69	-2.9	0.25	1	1

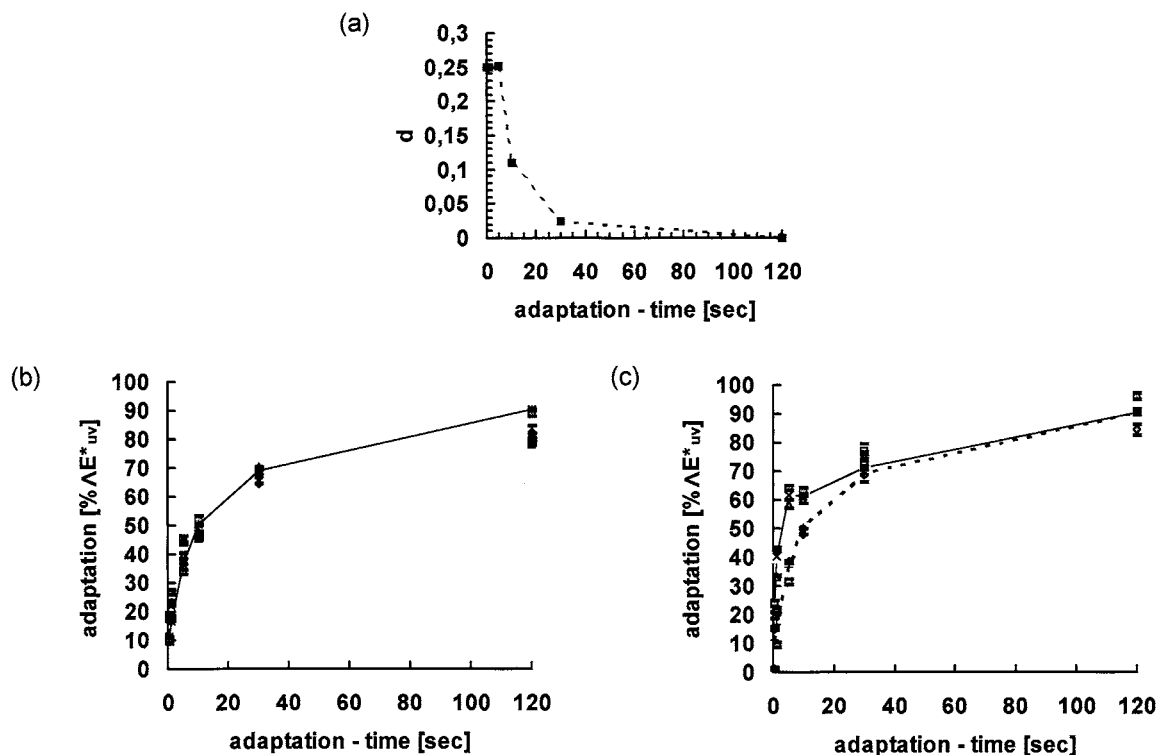


Fig. 11. a–c. Modelling of the time-course of chromatic adaptation: $F(t) = 100((1.0 - (a_1 e^{(b_1 t)} + a_2 e^{(b_2 t)}) + d(1.0 - (a_3 e^{(b_3 t)}))$; $0.2 < t < 120$. For the parameters a , b and d see Table 1. (a) Exponential decay of the factor d over time: $d(t) = 0.25e^{-0.078t}$; for $t < 5$ s: $t = 0$. (b) Model for the uniform pattern (*, continuous line). (c) Model for the complex pattern: green and yellow adaptation (\times , continuous line) and red and blue adaptation (+, broken line). The experimental data (average of observers AW and AS) are represented by the same symbols as in Fig. 4.

parameters as for the uniform condition. In order to account for the fast initial phase (0.2–5 s) and the non-monotonic behaviour of the yellow and green functions, it was necessary to introduce the contribution of a third fast exponential function. After 5 s, the contribution of the third exponential starts to decay, causing the ‘overshoot’ at 5 s and the subsequent converging of all four adaptation-functions.

4. Discussion

4.1. General time-course

The general, biphasic form of the recorded time-courses is compatible with the results from other studies, using large adapting backgrounds (Fairchild & Lennie, 1992; Fairchild & Reniff, 1995) as well as a centre-surround paradigm (Hayhoe & Wenderoth, 1991). Most of the adaptation (50–60% compensation of the chromaticity-change) takes place during a relatively fast initial phase within the first 5 s, and then, over the following minutes, approaches asymptotically a steady state (80% compensation). We did not measure adaptation times longer than 2 min and, therefore, cannot say whether or not adaptation was actually complete at that time. However, for experimental conditions comparable to ours, Fairchild and Lennie found that colour appearance after 2 min did not change with further prolonged adaptation, at least not as long as 30 min (Fairchild & Lennie, 1992). Longer times for complete adaptation (more than 10 min) have been reported for light adaptation as measured by increment thresholds (Baker, 1955). Hunt found adaptation times of 5 min (Hunt, 1950), however his data refer to a combined light and chromatic adaptation, which may take longer to complete. Also, it should be kept in mind that chromatic and light adaptation involve different processes (Hayhoe & Wenderoth, 1991) and their time-courses can therefore not be compared directly.

The general time-course could be fitted by a model consisting of the sum of simultaneous exponential components, consistent with previous models of chromatic adaptation (Hayhoe & Wenderoth, 1991; Fairchild & Reniff, 1995). Extending the sum-of-two-exponentials-model by Fairchild and colleagues, however, the present study revealed the presence of at least one additional process, described in our model by a third exponential function. This process accelerates the initial phase of adaptation, but only in the presence of contrast and only for middle-wavelength lights. In this context it is interesting to note that the test-pattern used by Fairchild showed little spatial complexity, and the time constant (8.4 s) found in their experiments is similar to that of the slower, not contrast-dependent process in our study (8 s).

The additional process is relatively fast (time constant approximately 1 s) but does not carry adaptation to its final level. Instead, a non-monotonic section (‘overshoot’) at 5 s adaptation time is observed between the fast initial rise of green and yellow adaptation and before converging to follow the adaptation pattern of the red and blue functions. It appears therefore that the fast, contrast-sensitive process either saturates at a lower level (60%) or starts to decay after 5 s adaptation-time (the latter is described by our model). The decay of the proposed fast process may either reflect the phasic behaviour of neuronal activity or be the result of an counterbalancing, inhibitory mechanism.

4.2. Asymmetries in chromatic adaptation

Adaptation with the complex pattern revealed an asymmetry in the time-course, in that adaptation to middle-wavelength light (green, yellow–green and yellow test-conditions) occurred significantly faster than that to light from the spectral extremes (red and blue). The asymmetry was only observed during the initial phase of adaptation (within the first 10 s) and was dependent on the presence of contrast. This might be the reason why, to the best of our knowledge, no such asymmetry has been reported in other studies concerning the effect of chromatic adaptation on colour appearance; in those studies, adaptation-times were either longer than 30 s (Webster & Mollon, 1994) or the adaptation-field had no or only very little spatial complexity (Fairchild & Reniff, 1995).

This asymmetry cannot be attributed to physical properties of the monitor display, e.g. different build up- or settling-times of the red, blue and green gun-phosphors, for the following reasons: (1) no asymmetry was observed in the uniform pattern, using the same experimental procedure and time-parameters as in the contrast pattern; (2) the asymmetry was found using an achromatic contrast pattern with low to medium intensities (6.3–28.8 cd/m²), i.e. without any large imbalance of the output of neighbouring pixels/guns. We conclude therefore that the observed asymmetry is indeed characteristic for chromatic adaptation.

The observed asymmetry does not support the hypothesis that chromatic adaptation is particularly related to the natural changes in daylight phases, i.e. that it is better for changes along the S-cone axis than along other axes. Rather, the results of the present study indicate that Worthey’s findings are not linked to intrinsic properties of the sensory system but might instead reflect an interference from cognitive stages. Such influences on the outcome of colour constancy experiments have been demonstrated by Arend and Reeves (1986), who showed that colour constancy was better when the subjects judged colour as a surface/object-property (paper match) rather than when they judged

the actual colour appearance of a surface (hue match). Whereas hue matches mainly reflect sensory processes, paper matches may also involve a cognitive component. Since the study of McCann et al. (on which Worthey's analysis is based) did not distinguish between paper and hue match, both types of matches have to be taken into account for the interpretation of their results.

It is important to note that the asymmetry was not established between the two opponent systems blue/yellow and red/green, although the two subsystems differ in several other aspects (Zrenner, Abramov, Akita, Cowley, Livingstone & Valberg, 1990). Instead, the time-courses differed between red- and green-wards, and between blue- and yellow-wards, thus revealing an asymmetry within each of the opponent channels, not unlike the on/off-asymmetry of the luminance channel. There are related findings of an asymmetry in the red and green receptor-channels concerning the effect of chromatic adaptation on spectral sensitivity (Strohmeier, Cole & Kronauer, 1985; Wise & MacLeod, 1996). However, the asymmetry found in our study must be of cortical origin since the effect was also present in the dichoptic arrangement.

Furthermore, it was found that the contrast related enhancement of chromatic adaptation is not confined to the cardinal axes, but that instead light from an intermediate axis (yellow–green) is equally effective for adaptation. This indicates the presence of colour mechanisms, which are not confined to the cardinal axes. Evidence for the existence of such higher order colour mechanisms comes from a number of studies, including those on chromatic habituation (Krauskopf, Williams, Mandler & Brown, 1986; Webster & Mollon, 1991, 1994), coherent motion (Krauskopf, Wu & Farell, 1996) and discrimination thresholds along cardinal and non-cardinal directions in colour space (Krauskopf & Gegenfurtner, 1992). Our finding extends these results in that they suggest not only the existence of intermediately tuned chromatic channels but also that the two polarities within an opponent axis can adapt differently. It is proposed that a contrast-dependent mechanism either acts specifically on the middle-wavelength channels or it is itself activated only by middle-wavelength light.

A significant cortical contribution to chromatic adaptation was demonstrated in the dichoptic experiment. This finding is in line with other recent reports that showed a significant effect of central mechanisms on colour perception (Land, Hubel, Livingstone, Perry & Burns, 1983; Humanski & Shevell, 1985; Shevell & Humanski, 1990). This is not necessarily a contradiction to other findings on chromatic adaptation that establish the retina as the site of origin. For example, transient tritanopia was demonstrated and extensively studied in retinal ganglion cells (Gouras & Zrenner, 1979; Zrenner & Gouras, 1979, 1981). The finding of

both, retinal and cortical sites of chromatic adaptation rather suggests a hierarchical organisation of the adaptation-processes. Early adjustment of the incoming signals is necessary in order to protect the system from saturation. Context related adaptation, which becomes available only at higher stages, may help to enhance information processing, e.g. by eliminating redundant information or by enhancing signal detection (see below).

4.3. The significance of contrast

The acceleration of chromatic adaptation by the presence of contrast in the test-pattern confirms the significance of spatial parameters for the processing of chromatic signals (Shapley & Enroth-Cugell, 1984; Blackwell & Buchsbaum, 1988; Walraven et al., 1990; Werner, 1990; Brown & MacLeod, 1991; Fuchs, 1992; Wesner & Shevell, 1992; Baeuml, 1994; Jenness & Shevell, 1995). In this respect, our findings reject the concept of an equivalent surround (Arend & Reeves, 1986; Valberg & Lange-Malecki, 1990). However, the results of the present study also show that for adaptation-times longer than 30 s, or for particular adaptation-lights, the effect of a uniform equivalent background and a complex background *can* indeed be identical. Different conclusions reached in different studies may therefore be attributed to methodological differences, such as adaptation-time or wavelength of the adaptation-light.

Furthermore, an achromatic complex background was found to be equally effective in accelerating adaptation as an isoluminant chromatic pattern or as a multicoloured (chromatic plus luminance contrast) pattern. This has important implications for the understanding of chromatic adaptation because it indicates that the contrast-dependent mechanism processes both luminance and chromatic signals. The conclusion is consistent with the numerous findings of facilitating interactions between luminance and chromatic signals (Kinney, 1962; Boynton, Hayhoe & MacLeod, 1977; Cavanagh, Tyler & Favreau, 1984; Eskew, 1989; Cole, Strohmeier & Kronauer, 1990; Logothetis, Schiller, Charles & Hurlbert, 1990; Schiller & Logothetis, 1990; Eskew, Strohmeier, Picotte & Kronauer, 1991; Gur & Akri, 1992).

It is interesting to note the parallels between the contrast related enhancement of adaptation and chromatic induction: First, similar wavelength-specific effects have been described for chromatic induction. Valberg (1974) measured the strength of chromatic induction for an achromatic test-field as a function of the wavelength of the inducing field and found it most sensitive for inducing lights with a dominant wavelength in the middle range of the spectrum. Second, chromatic induction has also been found to be enhanced by the presence of luminance contrast (Kinney,

1962; Wesner & Shevell, 1992; Jenness & Shevell, 1995). Third, a cortical component has been found to be involved in both, chromatic induction (Humanski & Shevell, 1985; Shevell & Humanski, 1990; Singer & D'Zmura, 1993) and the contrast-sensitive mechanism of adaptation (this study). Taken together, these findings imply a close relationship between the contrast-mechanisms involved in chromatic induction and chromatic adaptation.

4.4. Biological implication of the asymmetry in chromatic adaptation

In order to evaluate the implication of the colour specific asymmetry of adaptation for colour vision, natural viewing conditions should be considered: natural scenes usually contain luminance as well as chromatic contrast. The chromaticity of biologically important objects (ripe fruits, water, etc.) is either in the long- or the short-wavelength range of the spectrum whereas the chromaticity of the background is typically in the middle range of the spectrum. For the typical fixation-time of a few seconds in a visual search task the colour specific asymmetry of adaptation may improve the chromatic signal/noise-ratio and thus facilitate the detection of objects in natural scenes.

5. Conclusion

Our study revealed a wavelength-specific asymmetry during the first 5–10 s of chromatic adaptation, whereby middle-wavelength adaptation was significantly accelerated as compared with short- and long-wavelength adaptation. This effect was only observed in a spatially complex background, but not in a uniform adaptation field. The phenomenon could be evoked by either luminance or chromatic contrast and was present under haploscopic stimulus conditions. We conclude from these results the presence of two mechanisms of chromatic adaptation that differ with respect to their time-constants, wavelength-selectivity and spatial properties: a relatively slow process with a time-constant of approximately 8 s, which does not respond to image-contrast and is not colour specific; and a second, relatively fast process of cortical origin, which has a time-constant of approximately 1 s, and saturates or decays after adaptation-times of more than 5 s; the wavelength-specific activity of this mechanism gives rise to the observed asymmetry of adaptation. The results of modelling the data are consistent with this interpretation. Our findings are also evidence for a cortical stage of chromatic adaptation, and for the interaction of chromatic and luminance signals in the process of chromatic adaptation. Furthermore, our findings indicate the existence of multiple chromatic channels,

which, at a cortical stage, adapt separately from each other.

Acknowledgements

A.W. was supported by a DFG grant We 1710/1-1 and a grant from the *fortuene* program of the University of Tuebingen to L.S. The study was carried out at the Institute of Physiology, Free University Berlin, the Institute of Biophysics, University of Freiburg, and the Department of Experimental Ophthalmology, Eye Clinic of the University of Tuebingen. We wish to thank Franz Cornelissen and Karl Weiss for their help with programming, our subjects, in particular Lukas Ruettiger, for their patience, and Mirko Whitfield and Brian Brown for their help with the manuscript.

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