The spatial tuning of chromatic adaptation

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Abstract

A key question in colour research is how the colour and spatial analysis of an image interact. Traditionally, colour and form analysis have been regarded as parallel and separate processes, and documented effects of image complexity on chromatic adaptation have been attributed to a temporal integration process during eye movements. Evidence is presented here for a spatial mechanism, which tunes chromatic adaptation to the luminance structure (spatial frequency and orientation) of an image. This in turn suggests a close cooperation between colour and form analysis during chromatic adaptation. The results are discussed in relation to the "segregated pathway hypothesis" and the role of spatial aspects for the computation of colour constancy and adaptation to natural scenes.
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1. Introduction

The relation between colour and form processing is an important issue for the understanding of visual perception in three dimensional scenes, where geometrical features, texture and illumination have been shown to produce profound effects on lightness and colour perception (e.g. Adelson, 1993; Bloj, Kersten, & Hurlbert, 1999; Gilchrist, 1977; Gilchrist, Delman, & Jacobson, 1983; Knill & Kersten, 1991; Ramachandran, 1988; Zaidi, Spehar, & DeBonet, 1997). This is particularly important for understanding colour constancy in natural scenes, where the complex structure of illumination requires the consideration of the geometrical relations between objects and across the scene. How this is implemented in colour constancy remains an open question.

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 illuminations. It is therefore, in the context of the present paper, understood as the sensory basis for colour constancy. Chromatic adaptation includes multiple mechanisms, at different stages in the visual pathway. These are processes of multiplicative gain control, which can be modelled by a von Kries transformation of the receptor signals, as well as successive steps of subtractive spatio/temporal filtering (two-mechanism model for adaptation, e.g. Hayhoe & Wenderoth, 1990). In addition to retinal mechanisms, significant cortical contributions to chromatic adaptation have also been demonstrated, especially for context related adaptation (Humanski & Shevell, 1985; Land, Hubel, Livingstone, Perry, & Burns, 1983; Shevell & Humanski, 1990; Werner, Sharpe, & Zrenner, 2000). The aim of the present paper is to explore these cortical mechanisms of context related adaptation.

A number of studies have indicated significant differences between chromatic adaptation and constancy in uniform as compared to chromatically diverse patterns (e.g. Baeuml, 1994, 2001; Blackwell & Buchsbaum, 1988; Schirillo, 1999a, 1999b; Werner, 1990; Zaidi, Yoshimi, Flanigan, & Canova, 1992; Zaidi et al., 1997, 1998). Werner et al. (2000) demonstrated significantly different time-courses for middle-waveband adaptation when using a chromatically complex adaptation pattern—as compared to a uniform, but otherwise equivalent, adaptation pattern. The results indicated the presence of two mechanisms of adaptation that differ with respect to their time-constants, wavelength sensitivity and spatial properties: a relatively slow process

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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 accelerates middle-wavelength adaptation in the presence of either luminance or chromatic contrast. The wavelength specific activity of this latter mechanism gives rise to the observed asymmetry of adaptation. Furthermore, it has been shown that the latter process responds to the articulation (complexity) of the adaptation pattern, rather than to the presence of a local contrast border (Werner & Sharpe, 2001).

These findings demonstrate that the neuronal computation of signals from complex images cannot be modelled by means of large-scale filters (either temporal or spatial), as has been previously thought (D'Zmura & Lennie, 1986; Fairchild & Reniff, 1995; Hayhoe & Wenderoth, 1990; Valberg & Lange-Malecki, 1990). Rather, the results suggest that during colour processing, chromatic and spatial features of the stimuli interact in a distinct way. This is supported by studies describing cortical mechanisms that are chromatically as well as spatially sensitive (e.g. Flanagan, Cavanagh, & Favreau, 1990; Johnson, Hawken, & Shapley, 2001; McIlhagga & Mullen, 1997; Mullen, 1986; Panrey Vimal, 1997). Since borders and edges in natural scenes are mostly accompanied by a luminance contrast, the relation between luminance defined borders and colour processing also needs to be considered.

The identification and nature of such "cross-modal" interactions is important for our understanding of the visual processing in the cortex, since they challenge the idea of segregated pathways and their (as yet unspecified) combination at a higher stage. Although a number of findings in psychophysics (Bradley, Switkes, & De Valois, 1988; Flanagan et al., 1990; McCollough, 1965; Webster & Malkoc, 2000) and physiology (for reviews see Johnson et al., 2001; Kiper, Levitt, & Gegenfurtner, 1999; Lennie, 1999) strongly suggest the existence of such interactions or coprocessing of different stimulus dimensions, their properties and implementation, particularly in colour vision, are little understood.

One crucial issue is whether spatial or temporal processes are employed. Temporal modulation of chromatic signals occurs in connection with eye movements across the pattern and would, in connection with the slow time-course of chromatic adaptation, allow for the computation of contrast signals over extensive parts of the visual scene (Cornelissen & Brenner, 1990, 1995; Lennie & D'Zmura, 1988; Shevell, 1980; Webster & Mollon, 1994, 1995; Zaidi, Spehar, & DeBonet, 1998). Alternatively, contrast signals could also be based on a spatially sensitive mechanism, either within chromatic channels or by cooperation between colour and form processing. The latter would challenge the established segregated pathway hypothesis, which states that the different at-

tributes of visual stimuli are processed largely independently and only combine at a later stage in the cortex.

As a consequence of eye movements, it is experimentally difficult to dissociate temporal from spatial integration. Even in a fixation paradigm, micro eye movements do occur. If, however, the stimulus is fixed in the retinal image, fading results. The documented effects of image complexity on chromatic adaptation have, therefore, been largely attributed to temporal rather than spatial processes (Cornelissen & Brenner, 1990, 1995; Zaidi et al., 1998).

The present study will test the two hypotheses explicitly and provide evidence for the involvement of a spatial process in chromatic adaptation. Furthermore, the paper will address the nature of the spatio-chromatic interaction involved in adaptation, the role of luminance contrast, and the influence of spatial frequency and orientation of the adapting pattern.

2. General method

2.1. Rational of the experiments

The rational for the experiments is based on the findings of an earlier study (Werner et al., 2000), in which the time-course of chromatic adaptation (between 0.2 and 120 s) 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. There, a cortical process was identified which responds to the articulation (spatial complexity) of the adaptation pattern in that it accelerates the initial phase (first 10 s) of middle-wavelength adaptation. It has a time-constant of 1 s, and is most effective at an adaptation time of 5 s, after which it saturates or decays. It should be stressed that middle-wavelength adaptation is *accelerated* by this additional mechanism, not enhanced per se, since after 10 s the amount of short- and long-wavelength adaptation "catches up" with middle-wavelength adaptation and, after 120 s of adaptation, about 80–90% adaptation is reached. This is regardless of the colour of the adaptation-light or the presence of contrast (Werner et al., 2000).

In the present study, the response of the context related mechanism of adaptation is used as a tool for investigating the influence of spatial parameters on chromatic adaptation. Adaptation is measured for an adaptation time of 5 s and for the transition from D65 to middle-wavelength light ("green" or "yellow"), in order to maximize the response of the context related mechanism. The apparatus and experimental procedure in the present study were identical to those used in

earlier experiments on chromatic adaptation (Werner et al., 2000), and are described in detail below.

2.2. Subjects

Four subjects participated in the experiments. Two (AH, EL) were naive observers, one (LR) was an experienced observer in visual psychophysics but unaware of the aim of the study, whilst the fourth subject was the author (AW). All had normal colour vision as assessed by Raleigh matches and the Farnsworth 100 Hue test.

2.3. Apparatus

The experiments were conducted in a dark room. The stimuli were generated with a 3×12 bit colour processor (Cambridge Research Systems) and were presented on a 20 in. calibrated colour monitor (Barco CCID 7751). The monitor was warmed up 4 h before the start of the experiments and was recalibrated with an in-built routine before each experimental session. The outcome of the recalibration was checked with a spectral-photometer (Minolta, PR 650). 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.

2.4. Stimuli

The test-patterns ($15.4° \times 13.2°$; Fig. 1) were presented in the centre of the screen. In order to shield the residual luminance of the monitor, the surrounding background was masked with black cardboard.

Test-pattern

Fig. 1. Test-pattern (central test-field plus surround). Example shown here refers to the spatial frequency experiments.

The test-pattern was either uniform (luminance 19.3 cd/m^2) or consisted of a central test-field (hexagonal patch, square or stripe, luminance 19.3 cd/m^2) surrounded by a textured field (surround). The textured surround consisted of luminance contrast only ($L_{min} = 10.3$ cd/m^2, $L_{max} = 28.3$ cd/m^2, $L_{mean} = 19.3$ cd/m^2). Luminance contrast was selected since a previous study had demonstrated that the context-activated component of chromatic adaptation is luminance sensitive. The spatial configuration of the test-pattern was different in the different experiments and is described in detail in the corresponding sections.

In all experiments, the test-pattern was monochromatic and was presented in one of three chromatic conditions (Fig. 2a): (a) the standard condition (D65 condition) with the chromaticities of D65 (Judd x', y' chromaticities (0.316, 0.335)); this refers to the neutral state of the test-pattern and was perceived by the subjects as achromatic; (b) the green-adaptation condition (Judd x', y' chromaticities (0.278, 0.353)); (c) the yellow-adaptation condition (Judd x', y' chromaticities (0.341, $y = 0.392$)). The green- and yellow-adaptation conditions refer to a shift of the chromaticities of all patches/stripes along one of the cardinal axes (S- or L/M-cone-axis, as calculated after Krauskopf, Williams, & Heeley, 1982). 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 response that was necessary to shift the colour locus of the test-pattern by a distance of $\Delta E_{uv}^* = 22.18$.

2.5. Procedure

The chromaticity setting for the achromatic colour locus was recorded for each subject after 120 s adaptation to the test-pattern in the standard condition. 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 test-pattern was viewed binocularly and without fixation from a distance of 80 cm. The subjects were instructed to spend the same time looking at each of the single patches/stripes of the test-pattern and not to fixate the test-field, but rather to move their view freely across the entire pattern.

Each session commenced with 10 min dark adaptation and 2 min pre-adaptation to the test-pattern in the D65 condition. Chromatic adaptation was measured for the transition of the test-pattern from the D65 condition to the green-adaptation condition. In Experiment 1, the transition from D65 condition to the yellow-adaptation condition was also measured. The test-procedure is shown in Fig. 2b. After 5 s green/yellow adaptation, the subject indicated, within a 200 ms test-interval, whether or not the test-field appeared achromatic (grey). "Grey"
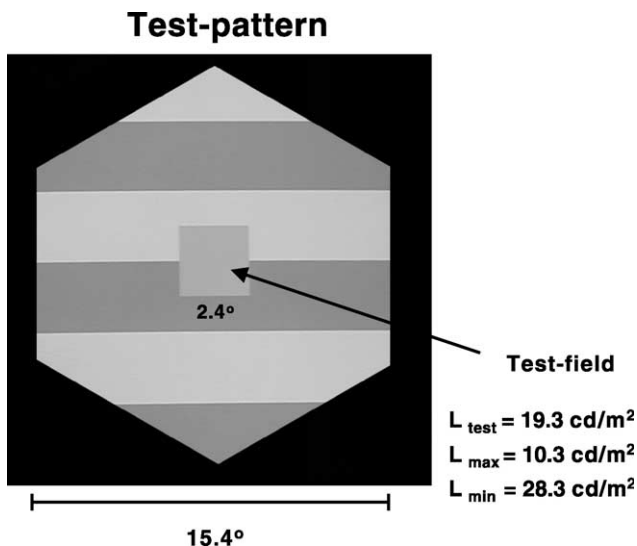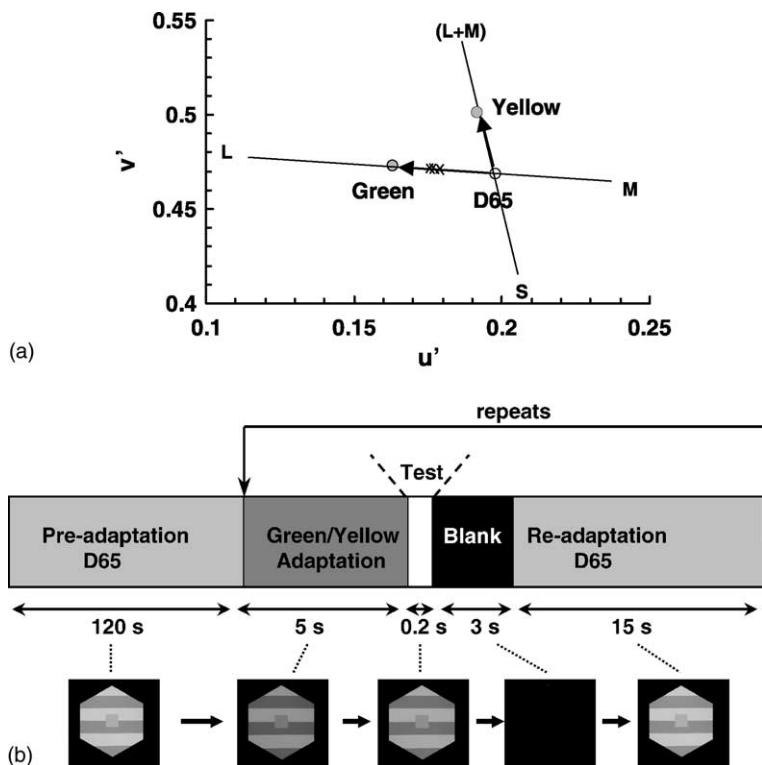
Fig. 2. (a) Stimuli in the CIE (1976) UCS diagram. The arrows indicate the equiluminant shift from D65 chromaticities ($u' = 0.197$, $v' = 0.468$) to the "green " colour locus ($u' = 0.166$, $v' = 0.472$) along the L/M-cone axis and the "yellow" colour locus ($u' = 0.194$, $v' = 0.500$) along the S-cone axis, respectively. Distance between the colour loci of standard condition and of green- and yellow-adaptation condition is $E^*_{uv} = 22.18$, respectively. "x" mark original settings of subject AW for the achromatic colour locus after 5 s green adaptation, corresponding to 64.6% adaptation (data from Experiment 2, spatial frequency 0.21 cpd). (b) Experimental sequence: Pre-adaptation D65: the pattern was presented in standard condition (D65 chromaticities) for 120 s; Green/yellow adaptation: the test-pattern was presented in the green or yellow adaptation condition, respectively. Test: time-interval of 200 ms during which the observer made his/her judgement. Blank: black screen presented for 3 s; Re-adaptation D65: the pattern was presented in the standard condition for 15 s (3 × green-adaptation time). Also shown is the test-pattern for each interval (shown for the example of Experiment 2). In the depiction, the different luminances of the test-pattern indicate the different chromaticities under which it was presented during the test-procedure.

was defined as "being neither red nor green and neither yellow nor blue". The test-interval was indicated by two beep-tones and was followed by a 3 s void-period (black monitor screen), in order to avoid the judgement being influenced by chromatic after-effects. The test-pattern was then presented again for 15 s in the D65 condition, to re-adapt the visual system to its previous "neutral" state of adaptation.

The amount of adaptation was determined by a hue-cancellation technique for the achromatic appearance of the test-field. The method is similar to that presented in other research on changes of colour appearance following chromatic adaptation (e.g. 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 the two adapting lights (Fairchild, 1991). The state of adaptation can, therefore, be 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 in the standard condition to those in the green/yellow-adaptation condition, in which case the test-field appeared "grey" after adaptation. If the achromatic colour locus shifted only partially towards the new locus of the test-field, the test-field appeared tinged. 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 chromaticity of the test-pattern back towards its locus in the standard condition. It should be emphasised that, in contrast to the procedure usually used for hue cancellation, the adjustment here affected not only the test-field but also the complete test-pattern. Furthermore, the test-pattern was presented with the "reduced" chromaticity-change during the subsequent test-intervals only. During the green/yellow 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-field appeared grey. The resulting chromaticity setting for the test-field
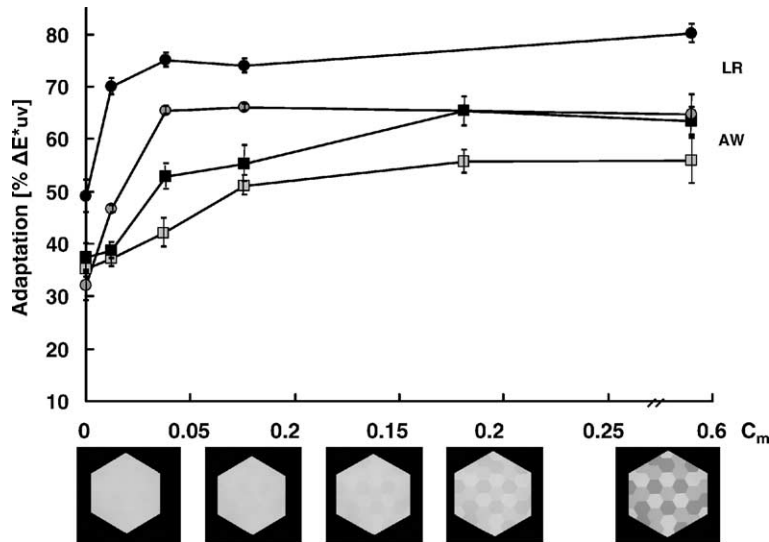
Fig. 3. Chromatic adaptation as a function of luminance contrast (Michelson contrast C_m). Figure shows the data of two subjects (AW (squares) and LR (dots)), for green adaptation (black symbols), as well as for yellow adaptation (grey symbols). Inset figures show schematics of the test-pattern at different contrast values.

indicated the position of the achromatic colour locus under the prevailing adaptation and was recorded.

Throughout the complete sequence of presentations, the luminance values of the test-field as well as that of the surround did not change. Furthermore, it should be stressed that in all experimental conditions, the change of chromaticity was always applied equally to the test-field and its surround.

For each measurement (setting), the complete cycle of presentations was repeated as described above. Each subject repeated each setting 5–10 times per test, whereby the sequence of the tests was randomised.

2.6. Quantification of adaptation

The goal of this study was to quantify adaptation related changes in colour appearance and to compare the effect of different spatial parameters on adaptation. This was done by means of quantifying the shift of the achromatic colour locus related to adaptation under the different experimental conditions. The shift of the achromatic colour locus was quantified by calculating the CIE 1976 colour difference ΔE^*_{uv} between the chromaticities of the achromatic colour locus after adaptation to the test-pattern in the standard condition and after adaptation to the green/yellow-adaptation condition, respectively. Care was taken that the colour stimuli would under 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 (SEM). Each subject repeated each setting 5–10 times. The t-test was used for the statistical analysis of the data.

3. Experiment 1: The relation between chromatic adaptation and the magnitude of luminance contrast

The first experiment was designed in order to establish the relation between the magnitude of luminance contrast and chromatic adaptation (Fig. 3). As such, the test-pattern was composed of hexagonal patches ($2.2° \times 2.4°$), with the central patch being the test-field. The magnitude of luminance contrast (test-parameter) was modified by varying the luminance of the surrounding patches whilst keeping the luminance of the test-field constant. The mean luminance was kept constant by increasing the luminance in every second patch and, at the same time, reducing luminance by the same amount in every other patch (luminance contrast was calculated as Michelson contrast, C_m).

Chromatic adaptation was measured for different magnitudes of luminance contrast ranging from $C_m = 0.012$ to 0.59 and for green adaptation condition (black symbols in Fig. 3) as well as yellow adaptation condition (grey symbols in Fig. 3). For both adaptation conditions, two observations were noted. Initially, there is an increase of adaptation with the magnitude of luminance contrast, and then, the function levels off at a relatively low contrast magnitude (0.05–0.1 C_m). For the following experiments, the maximum available contrast was used ($C_m = 0.59$).

3.1. Discussion

Although contrast-signals (signal ratios) play an important role in both adaptation and colour constancy models, this is the first time that such an intimate relation has been confirmed in a psychophysical experiment.

Similar functions have been derived for contrast adaptation in cortical neurons (Sclar, Lennie, & DePriest, 1989). Whilst adaptation increases steadily with contrast, it does so only for the lowest range of luminance contrast. At a contrast of about 0.05–0.1 C_m, it reaches a plateau, beyond which higher luminance contrast does not enhance adaptation further. This observation is—in an abstract sense—consistent with the threshold principle for the integration of contrast signals as employed in lightness algorithms (e.g. the Retinex-algorithm, after Land, 1986).

4. Experiment 2: Spatial frequency

In this experiment, the surround consisted of a square-wave grating modulated in luminance ($L_{min} = 10.3$ cd/m^2, $L_{max} = 28.3$ cd/m^2), with a central test-field (square of $2.2° \times 2.4°$; Fig. 4). Test-parameter was the spatial frequency of the surrounding grating (0.02–3 cpd). A square-wave grating, rather than a sinusoidal grating, was used in order to make the stimulus comparable to that of the previous experiments (Werner et al., 2000). The results are shown in Fig. 4. Whilst there is a difference in the overall level of adaptation of the three subjects, the curves of all subjects show marked bandpass characteristics and are tuned to the same frequency (0.2 cpd). Note how the maxima in all three subjects coincide. The shoulders of the functions are asymmetrical and broader at the higher frequencies, which may reflect the higher contrast sensitivity at spatial frequencies around 3–5 cpd. Indeed, the overall amount of chromatic adaptation in complex images has been shown to correlate with the contrast sensitivity of the subjects (Werner, pub. in prep.), which explains the inter-individual differences between the tuning curves of the three subjects.

The bandpass property of chromatic adaptation is in contrast to the typical lowpass response of chromatic mechanisms in contrast detection tasks, and indicates that chromatic adaptation is restricted to a specific spatial frequency range. Similar bandpass properties of chromatic adaptation have been described by Zaidi and colleagues (Zaidi et al., 1998), who concluded that the size of receptive fields and the amplitude of eye movements would determine the bandwidth jointly. What is intriguing here, however, is the fact that the maxima of the tuning curves of all three subjects coincide at 0.2 cpd, which in turn matches the correlated width of the test-field. This prompts the question, whether adaptation has a particular, fixed bandpass characteristic, or whether it is specifically tuned to the spatial frequency of the respective surround.

We tested the latter hypothesis by repeating the measurements as above, but now using different sizes of the test-field in order to tap into different spatial channels (Fig. 5a and b). We observed that for each size of the test-field, a different band of spatial frequencies was most effective. In other words, spatial frequencies were most effective if they matched the width of the test-field. Therefore, one can conclude that chromatic adaptation is tuned to the spatial frequency of the respective adaptation pattern.

4.1. Discussion

In this set of experiments we demonstrated that chromatic adaptation is selective for a specific band of spatial frequencies, and as such can be said to have bandpass properties. Furthermore, the bandpass characteristic of chromatic adaptation is not a fixed property of the involved channels, but rather is tuned to the spatial characteristics of the respective surround. This indicates a true interaction between chromatic and spatial analysis. We are not aware of comparable studies made with respect to chromatic adaptation, but similar observations were made for chromatic induction. Barnes, Wei, and Shevell (1999) found the magnitude of induction to be dependent on the relation between the spatial width of the central test-patch and the inducing patches of a remote surround. However, there are several differences to the present study to be noted. In the present study, the effect of luminance structure is measured, on subse-
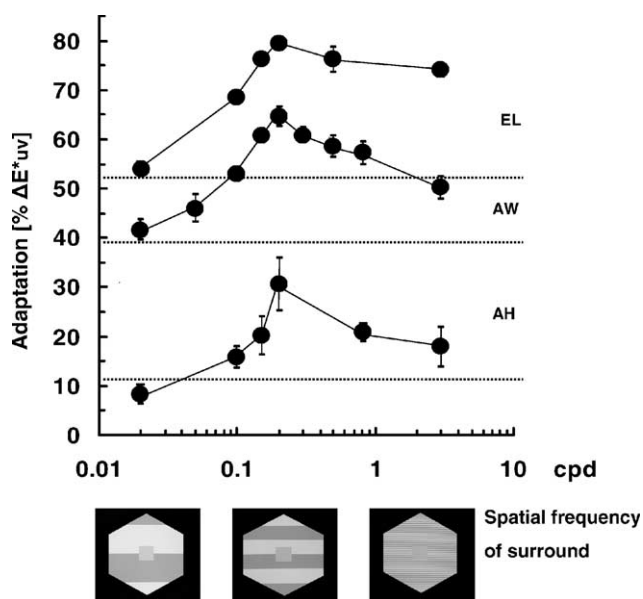

Fig. 4. Chromatic adaptation as a function of the spatial frequency of the adaptation pattern. The figure shows the data of three subjects (EL, AW, AH); note the inter-individual differences in the overall amount of adaptation, which can be correlated with corresponding differences in their contrast sensitivity functions (pub. in prep.). Note that the maxima of the curves of all three subjects coincide with the corresponding spatial frequency of the test-field (0.21 cpd). Dashed lines denote the "baseline" adaptation, i.e. the amount of adaptation when using a uniform pattern.
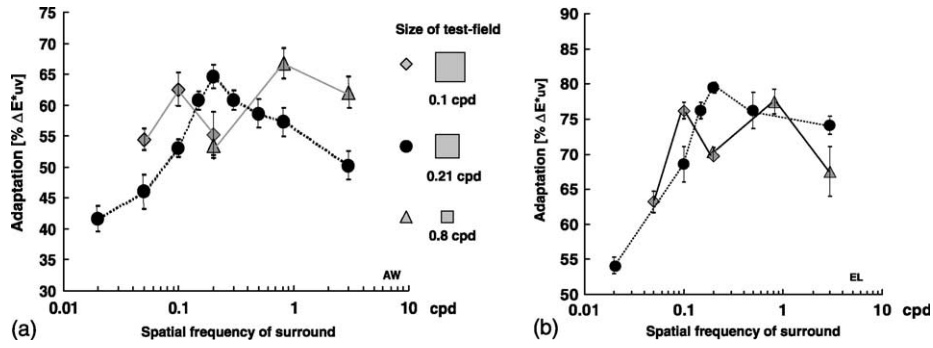
Fig. 5. (a) Spatial frequency tuning of chromatic adaptation. As in Fig. 4, adaptation is measured as a function of the spatial frequency of the adaptation pattern, whereby each curve represents the measurements for a different size of the test-field (grey diamonds: width of the test-field corresponds to 0.1 cpd; black dots: width of the test-field corresponds to 0.21cpd (data replotted from Fig. 4); grey triangle: width of the test-field corresponds to 0.8 cpd). Data are shown for subject AW. (b) Spatial frequency tuning of chromatic adaptation; same symbols as in Fig. 5a, data of subject EL.

quently presented stimuli. The stimuli used by Barnes et al. consisted of chromatic contrast, and investigated their effect on simultaneously presented stimuli. In another related study, Wolf and Hurlbert (2002) found that the effectiveness of chromatic induction depends on the relation between the textural structure of the surround and of the centre-patch.

5. Experiment 3: Orientation selectivity

In the next set of experiments we investigated the orientation selectivity of adaptation. Again, a square-wave grating was used as the surround pattern, but in these experiments the test-field was a stripe of the same width as the surround-stripes. The orientation of the test-stripe was varied relative to that of the surround-stripes (orthogonal, oblique or parallel) as shown in Fig. 6. Results are shown for two subjects (EL, AW). It was found that adaptation is most pronounced if the test-stripe possesses the same orientation as the surround-

stripes. In other words, adaptation is tuned selectively to the orientation of the test-pattern. Further tests with different orientations of the surround-stripes (Fig. 7) revealed that this is irrespective of the actual orientation of the stripes, the only relevant parameter being the relation between the orientations of test-stripe versus surround-stripes.

5.1. Discussion

The observation of orientation selectivity of chromatic adaptation may suggest a relation with contingent after-effects (adaptation to colour associated with form)—such as the McCollough after-effect (MAE). The MAE describes the phenomenon that after alternating fixation of e.g. a horizontal green and a vertical red grating, a white horizontal/vertical grating appears to be tinged in the respective complimentary colour. However, the observed orientation specificity of chromatic adaptation cannot be identical to the MAE, since they differ with respect to several characteristics: (1) the MAE
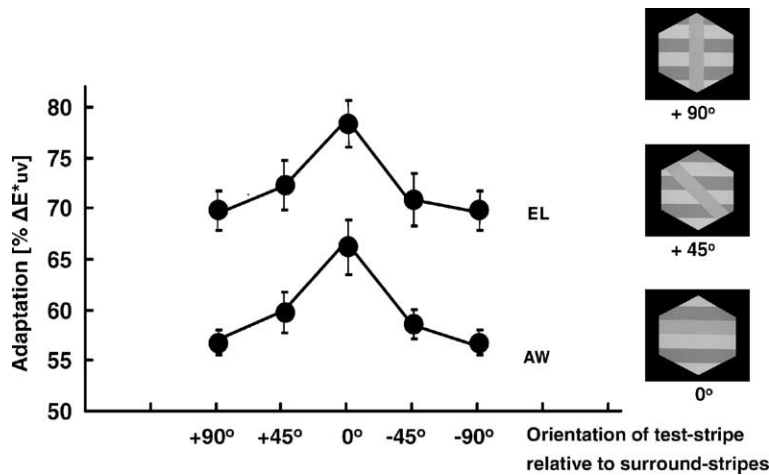

Fig. 6. Orientation selectivity of chromatic adaptation. Adaptation is measured as a function of the orientation of the test-stripe relative to the orientation of the adaptation pattern (horizontal). Most adaptation is measured for the horizontal orientation of the test-stripe. Subjects EL (upper curve) and AW (lower curve).
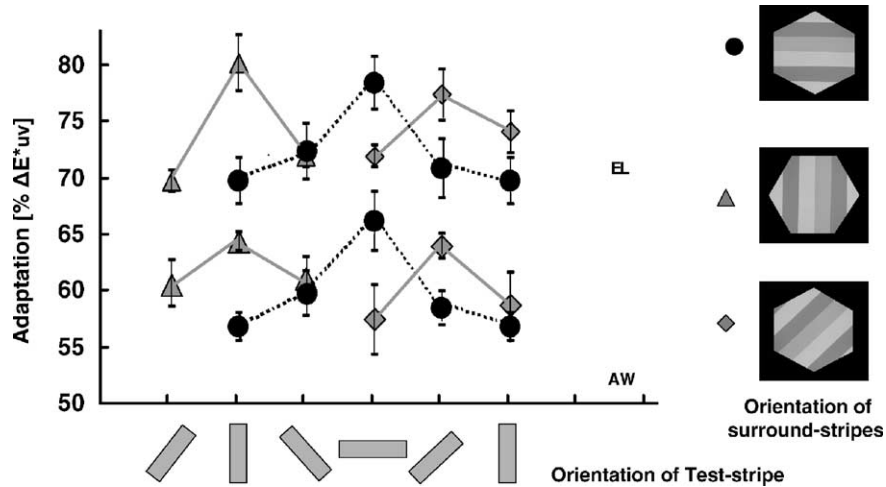
Fig. 7. Orientation tuning of chromatic adaptation. As in Fig. 6, adaptation is measured as a function of the relative orientation of the test-stripe, whereby each curve represents a different orientation of the adaptation pattern (background): vertical (grey triangles), horizontal (black dots; data replotted from Fig. 6) and oblique (grey diamonds). Subjects EL (upper curves) and AW (lower curves).

responds to green as well as red adaptation, whereas the orientation selectivity of chromatic adaptation is restricted to the middle-wavelength range; (2) the MAE shows a preference for a horizontal–vertical combination of orientations, whereas the orientation tuning of chromatic adaptation shows no such asymmetry; (3) different from the orientation tuning of chromatic adaptation, the MAE persists for hours or even days.

6. Experiment 4: Spatial or temporal mechanism

The orientation selectivity of chromatic adaptation offers an opportunity to test whether the underlying

contrast mechanism is a temporal or a spatial process. In that case, the experiments were carried out with a modified stimulus pattern (inserts in Fig. 8), whereby test-stripe and surround-stripes had the same orientation. In Experiment A, the orientation of the stripes was identical during adaptation condition and test-interval. As expected, the resulting green adaptation in Experiment A is relatively high in both subjects (Fig. 8). In Experiment B, however, the stripe-orientation differed by 90° between the adaptation condition and test-interval. As such, the patterns presented during adaptation condition and test-interval differed in their spatial orientation, but produced the same temporal modulation in the visual system if the eyes of the test subject are
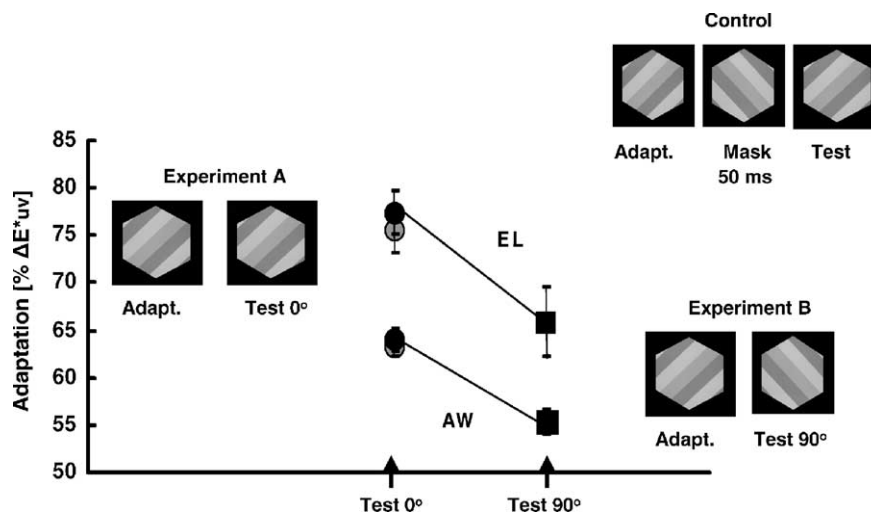

Fig. 8. Test for spatial versus temporal mechanism. The amount of green adaptation is compared for two conditions: in Experiment A (black dots), the stripe orientation is identical for adaptation and test; in Experiment B (square dots), their orientation differs by 90° (see inserted pictures of the stimuli). Data are shown for subject EL and AW. The grey symbols in each set marks the result of the control-condition: pattern-orientation during adaptation and test was identical, but a rotated pattern was presented during a 50 ms interval before the test-interval. Note that adaptation is not affected by the presentation of the rotated pattern. Instead, adaptation drops significantly in Experiment B, indicating a spatial rather than a temporal mechanism as underlying process.

moved across the pattern. Therefore, one would expect a spatial mechanism to detect the orientation difference, whereas a temporal mechanism would not show orientation selectivity.

As can be seen from Fig. 8, adaptation drops significantly when tested with the paradigm of Experiment B (rotated orientation) as compared to when tested with the paradigm of Experiment A (adaptation and test have the same orientation).

A control experiment was designed in order to test whether the lower adaptation rate in the last experiment was due to the difference in experimental design, i.e. the sudden change of the test-pattern, which could partially abolish the effect of adaptation (due to de-sensitisation of the system). For the control experiment, the orientation during adaptation condition and test-interval was kept identical (as in Experiment A), but in between presentations the orientation was changed for a 50 ms time-interval by 90° ("control condition" in Fig. 8). If adaptation were disrupted by this inter-presentation, we would expect the adaptation result to drop. Instead, adaptation was found to be as high as in the comparable experiment without interruption (grey symbols in Fig. 8). It is concluded, therefore, that the drop in the amount of adaptation in Experiment B as compared to Experiment A is due to the detection of a difference in orientation.

An additional experiment was performed in order to approximate the effect of a temporal contrast integration by a temporal square-wave modulation of the luminance of the test-pattern. In this experiment, the test-pattern consisted of a uniform field whose luminance alternated between $L = 10.3$, 28.3 and 19.3 cd/m^2. The different luminance values were presented with a temporal frequency of 1, 5 or 10 Hz, whereby the mean luminance over the adaptation time was constant (19.3 cd/m^2). This corresponded to presenting 5, 25 or 50 different luminance steps within the period of the 5 s green adaptation. The temporal modulation was presented throughout the standard condition and the green-adaptation condition. Two subjects (AW and AH) participated in this experiment, with consistent results. Fig. 9 shows the results of subject AW. In contrast to the increase in adaptation that was observed in the presence of spatial luminance contrast, the temporal luminance modulation did not result in an increase in adaptation, compared to the static presentation of a 19.3 cd/m^2 uniform test-pattern (Fig. 9).

6.1. Discussion

From the findings of this section it is concluded that the orientation selectivity of chromatic adaptation is due to a spatial and not a temporal process. Consistent with this conclusion is the observation that the effect of spatial contrast could not be mimicked by a temporal
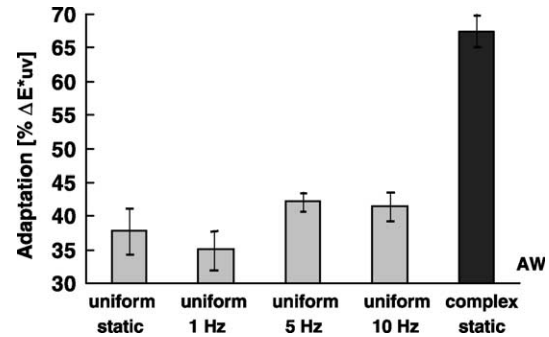

Fig. 9. Mimicking the effect of temporal contrast integration. During the standard and green-adaptation condition, the luminance of a uniform test-pattern was alternating presented at a luminance of 10.3, 28.3 and 19.3 cd/m^2. The effect of adaptation was measured for 1, 5 or 10 Hz temporal frequency of the presentation of the different luminance steps ("uniform 1 Hz/5 Hz/10 Hz"). The results are compared with the amount of adaptation using a static uniform test-pattern ("uniform static", luminance 19.3 cd/m^2), and a spatially complex test-pattern (hexagonal patches as in Experiment 1, "complex static"). Results are shown for subject AW.

contrast modulation (at least not within the range of the tested temporal frequencies).

However, it should be stressed that the results of this study do not exclude the involvement of temporal processes in chromatic adaptation and colour constancy in general. Rather, it suggests that spatial and temporal processes coexist, possibly at different stages in the visual pathway (e.g. retinal and cortical).

It has been suggested that local edge adaptation might explain orientation sensitivity of chromatic adaptation, especially if the subjects (against experimental instructions) did not move their eyes continuously across the pattern but rather fixated the test-stripe (Zaidi, pers. commun.). Therefore, the test-pattern with its changed orientation would not excite the adapted neurons but rather non-adapted neurons, and consequently the measured rate of adaptation would drop. However, as the experiments in the previous Section 5 (Figs. 6 and 7) demonstrated, chromatic adaptation is sensitive to the relation between the orientation of test-stripe and surround stripes, and not to the edge position per se, since here the position of the edges was identical in the adaptation- and test-condition. Therefore, local edge adaptation cannot explain the orientation selectivity of chromatic adaptation.

7. General discussion

The results of this study emphasize the importance of form parameters for the processing of chromatic information in complex scenes. They also provide a possible explanation for the observed effect of segmentation of the adaptation pattern in previous experiments (e.g. Werner et al., 2000; Werner & Sharpe, 2001). Furthermore, these

experiments also help to explain why no such spatial effect was found in the Fairchild and Lennie study where the spatial features (spatial frequency and orientation) of the test-field and spatial components in the surrounding background did not match. Consequently, no pattern-specific effect is to be expected.

Recent work has indicated that the effect of an uniform or spatially complex (articulated) surround on chromatic and achromatic adaptation is larger for incremental than for decremental test-fields (Baeuml, 2001; Schirillo, 1999a, 1999b). This prompts the question of whether the spatial tuning of chromatic adaptation also shows such an asymmetry. However, no increment–decrement asymmetry was found for the acceleration of chromatic adaptation by articulated surrounds (findings were presented at ARVO, Werner & Sharpe, 2001). Moreover, there are a number of other differences between the two phenomena that should be noted: (a) whereas the increment/decrement asymmetry appears to be a border-contrast phenomenon, the context-related acceleration is not enacted in a center-surround arrangement, but rather requires an articulated surround (Werner & Sharpe, 2001); (b) the context related acceleration of adaptation has a cortical site (Werner et al., 2000), whereas for the increment/decrement asymmetry a retinal locus is assumed (Baeuml, 2001). Therefore, it can be concluded that the mechanism of spatial tuning of chromatic adaptation is not related to the mechanisms underlying the increment/decrement asymmetry of adaptation.

The modulation of adaptation by the spatial features of the surround is reminiscent of the phenomenon of contrast gain control, and may accordingly be called "spatial adaptation gain control". Contrast gain control refers to the phenomenon that apparent contrast in a central area is regulated by the magnitude of contrast in its surround, whereby this also is selective for orientation and spatial frequency (Bradley et al., 1988; Cannon & Fullenkamp, 1991; Chubb, Sperling, & Solomon, 1989; D'Zmura & Singer, 1999; Singer & D'Zmura, 1994; Solomon, Sperling, & Chubb, 1993). This would suggest that the underlying mechanisms of spatial adaptation gain control and contrast gain control are closely related. The observations of the present study cannot, however, directly be explained by a mechanism of contrast gain control, as has been argued for the attenuation of chromatic induction by complex surrounds (Barnes et al., 1999). Indeed, the reduction of contrast sensitivity by contrast gain control would reduce adaptation in a complex pattern rather than enhance it. Furthermore, contrast gain control has been shown to be chromatically selective, whereas the contrast mechanism described here is not (luminance contrast affects adaptation for equiluminant shifts in colour space).

The significance of the present study can be summarised in three major points. Firstly, it demonstrates that chromatic adaptation is selective for specific spatial channels. In other words, adaptation is linked to the basic form features of the test-pattern (spatial frequency and orientation), classifying it as a new type of contingent after-effect.

In addition, an influence of purely luminance-defined edges on chromatic adaptation is demonstrated, thus indicating an interaction between the colour and the luminance structure of the image during its analysis. This result supports and extends the findings of several previous studies, which demonstrated fasciliatory interactions between luminance and chromatic signals (e.g. Eskew, Strohmeyer, Picotte, & Kronauer, 1991; Gur & Akri, 1992; Logothetis, Schiller, Charles, & Hurlbert, 1990; Werner et al., 2000).

Also, the spatial mechanism of chromatic adaptation does not show fixed spatial properties, such as those reflecting receptive field properties of neurons in a chromatic channel. Instead, the results illustrate the effect of a dynamic (in the sense of not-fixed) tuning to the spatial frequency and orientation of the respective test-pattern. The phenomenon of selective channel adaptation is of course well known in the spatial domain (e.g. Blakemore & Campbell, 1969; Blakemore & Nachmias, 1971), and has also been shown to occur for the spatial structure of natural scenes (Webster & Miyahara, 1997). This study, however, demonstrates that selective channel adaptation not only affects luminance contrast but also chromatic sensitivity.

Finally, the effect of spatio-chromatic interactions in chromatic adaptation is not—as has previously been postulated—based on a temporal modulation of chromatic signals while viewing a variegated scene, but rather involves a direct interaction between colour and spatial parameters. This would strongly suggest that colour, form and luminance closely cooperate during adaptation. The implications of this conclusion are important with respect to under-standing the relationship between form and colour during the processing of visual information, and the role of spatial aspects in the computation of colour constancy and the adaptation to natural scenes.

7.1. Co-processing of form and colour in the visual pathway

The results are in opposition to the segregated pathway hypothesis, i.e. the independent and parallel processing of the different stimulus attributes. Rather, they support the concept of a multidimensional or close coupled analysis of visual scenes (Lennie, 1999) either via interactions between chromatic and spatial channels or by spatio-chromatic processing within the same population of neurons. Related observations that support this conclusion include studies on contingent after-effects (Bloj et al., 1999; Flanagan et al., 1990;

McCollough, 1965), physiological experiments that have demonstrated the connection between colour and form processing in different cortical areas (Gegenfurtner, Kiper, & Fenstermaker, 1996; Zeki & Shipp, 1989) and multidimensional response characteristics of V1 neurons (Johnson et al., 2001). Also of particular interest are recent observations on the suppressive surround interactions in V4 neurons, which occur "for multiple dimensions of the stimulus, including spatial frequency and, notably, orientation" (after Lennie, 1999: Müller, Krauskopf and Lennie, unpubl. results).

Furthermore, previous studies have shown that the contrast effect can be transferred interocularly (Shevell & Wei, 2000; Werner et al., 2000), which suggests that chromatic adaptation is not restricted to a low level retinal process. It appears to be a multi-stage process, which involves the co-processing of colour and form at cortical stages. It also implies that colour is not processed per se, but in connection with form analysis and gives weight to the idea of an integration of colour in a multidimensional analysis of image-features.

7.2. Significance of the results for colour constancy

In a co-planar, two-dimensional scene with matt surfaces and a single illuminant, the effect of the illumination can be relatively easily compensated by computing the signals as ratios (Wallach, 1948). This, in effect, is a normalisation of the responses by a factor common to all surfaces as it is commonly applied in lightness algorithms. In a three-dimensional natural scene, however, this problem is complicated by virtue of the fact that the illumination is not uniform: there are differences in illumination caused by the casting of shadows, mutual illumination from other objects, and by the different orientations and distances of surfaces relative to the illumination source. In such situations, therefore, it is essential for any mechanism of colour constancy not only to recognize and take into account the classification of edges (illumination edges and reflectance edges) but also to account for the geometrical relations across a scene and objects.

We know that the visual system does indeed take spatial relations into consideration, mainly from their effects on lightness (Adelson, 1993; Gilchrist, 1977; Gilchrist et al., 1983; Knill & Kersten, 1991; Ramachandran, 1988; Schirillo & Shevell, 1993; Zaidi, Spehar, & Shy, 1997). This has been explained by mid-level processes, such as the classification of the form of edges in terms of their geometry (Guzman, 1968; Zaidi et al., 1997) as well as grouping factors related to the Gestalt concept (e.g. coplanarity; Gilchrist et al., 1999). In comparison, little is understood about the influence of spatial relations on colour perception, although recently, a significant influence has been demonstrated by three-dimensional shape perception (Bloj et al., 1999).

Also, Schirillo and Shevell (2000) reported colour induction to be influenced by the perceptual grouping of regions that share a common illuminant. They suggested that this phenomenon might be an important mechanism for colour constancy (see also Katz, 1935; Koffka, 1935). How the spatial parameters do in fact interact with the mechanisms for colour constancy remains so far unanswered. However, the spatial tuning of chromatic adaptation may serve to implement perspective and geometric cues in colour constancy by linking together adaptation in those areas that share similar geometrical features (not unlike a physiological pendant to a Gestalt grouping factor).

7.3. Significance of the results for adaptation in natural scenes

The visual system adapts to the spatial structure of natural images (Webster & Miyahara, 1997) as well as to the distribution of their chromatic contrast (Webster & Mollon, 1997). It has been suggested that this enhances coding efficiency by means of a decorrelation of the responses between channels (Atick, Li, & Redlich, 1993; Barlow & Földiák, 1989). In view of the fact that these adaptation effects are very selective, they have the potential to improve the signal/noise ratio for the detection of unusual or novel features of an image (Barlow, 1990; Webster & Mollon, 1997). In this context, contingent after-effects, such as the spatial tuning of chromatic adaptation, are of particular interest since they confer even stronger selectivity.

The spatial tuning of chromatic adaptation may therefore play an important role in object recognition and signal detection in general. The fact that this mechanism operates in the middle wavelength range makes it particularly suited for natural scenes, since its spectral characteristics match those of mean reflectance and illumination in natural scenes (e.g. Burton & Moorhead, 1987; Endler, 1993; Hendly & Hecht, 1949; Krinov, 1947; Osorio & Bossomaier, 1992; Webster & Mollon, 1997). Experiments are underway to test this hypothesis.

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