

arrow 1). A few drops of milk were added to the saline so that the path of the beam became visible. The results confirmed our calculations: the chicken lens focused the laser beam at a distance of 39 mm (Fig. 2c, arrow 2), but there was no focal point behind the chameleon lens and there was even some divergence of the beam. To our knowledge, a lens with negative power has not been described before in vertebrates.

Two possible evolutionary pressures may have produced the unusual optical design: (1) a lens with negative power at relaxed accommodation may further extend the range of accommodation and/or (2) a negative lens in combination with a high powered cornea may maximize the relative retinal image size. Although we cannot prove the validity of the first assumption, we have tested the second. Comparing transcleral images in excised chameleon and chicken eyes (both had an axial length of about 10 mm), we found that the retinal image is 15% larger in the centre of the visual field of the chameleon eye than in the chicken, but drops off to a similar size 40 degrees off-axis (Fig. 2d). To evaluate the significance of this observation, we compared retinal image sizes in a variety of vertebrate eyes after scaling them down to similar size (10 mm axial length; Fig. 2e). It can be seen that, for the given eye size, the chameleon indeed has the largest retinal image. The large image size is only achieved because the ratio of the power of the lens to the power of the cornea is lower than in all other vertebrates and even has

a negative value. This phenomenon is not restricted to a single species of chameleons; we have also tested two *Chamaeleo calyptratus* and found a similar optical design with a negatively powered lens. □

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Colour constancy influenced by contrast adaptation

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VISUAL sensitivity is controlled by at least two distinct types of adaptation: light adaptation adjusts sensitivity to the mean luminance and colour in the stimulus¹, and contrast adaptation adjusts sensitivity to the variations in luminance and colour^{2–5}. Light adaptation is thought to be important in maintaining the perceived colour of objects despite changes in illumination ('colour constancy'), compensating for the mean changes in the light reflected from scenes under different illuminants⁶. But for naturalistic colour signals, we show here that changes in an illuminant can also alter colour contrasts in images (how colours are distributed around the mean) enough to alter the state of contrast adaptation. Thus perceived colour under different illuminants may also be noticeably influenced by contrast adaptation.

We used a matching task to examine how light adaptation and contrast adaptation combine to influence colour appearance (Fig. 1). Observers fixated between two fields; in one field they adapted either to a static chromaticity or to 1 Hz modulations around a particular chromaticity. (Using an electrical analogy, we refer to the former as a DC stimulus and the latter as DC+AC.) The perceived colour of test chromaticities in the adapting field was then matched by adjusting chromaticity in the second, neutral-adaptation field. Figure 2 shows the effects of adapting to four different DC chromaticities or to modulations around each DC value along two different chromatic directions (at nominal angles of 45–225° or 135–315° within an L-M cone versus S cone colour plane⁷). Before adaptation the four DC chromaticities appear a moderately saturated blue (Fig. 2a), purple (Fig. 2b), yellow-green (Fig. 2c) or orange (Fig. 2d). However, adaptation to each static chromaticity causes it to appear nearly (but not completely) achromatic, and produces concomitant shifts in the appearance of test stimuli. Thus test stimuli that all appeared blue (Fig. 2a) before adaptation, are matched after

adaptation by a wide range of hues bracketing white. These shifts occur independently along the S and L-M axes, consistent with independent sensitivity changes within each cone class that rescale the cone signals so that the mean response is (nearly) the same before and after adaptation (von Kries adaptation⁸). Adaptation to the DC+AC stimuli produces the same mean colour shifts, but in addition reduces the perceived contrast of test stimuli relative to the DC match. The saturation losses are always largest along the colour direction defining the adapting contrast. (For example, after adaptation to each DC chromaticity, the 135–315° modulations all appear to vary between blue and yellow, and produce the largest saturation losses on that axis.) Saturation losses selective for these directions imply an interaction between different cone classes at sites central to the sites of light adaptation^{5,9}. Our results suggest that the DC and AC adapting components produce independent and qualitatively different changes in colour appearance. Light adaptation rescales the cone signals available to subsequent levels, but otherwise appears to have little influence on the properties of contrast adaptation, and there is no evidence of contrast adaptation to the static adapting stimulus. Conversely, the addition of large AC components does not significantly alter the mean perceived colour relative to the DC match, suggesting that the response to chromatic contrast up to the sites of light adaptation is roughly linear (or symmetrical for opposite excursions from the mean).

We examined the influence of illuminant shifts on contrast adaptation, first by modelling the visual response to an illuminant change and then by testing the model empirically. The model was based on two stages of adaptation: an initial von Kries scaling of the cone signals to the mean luminance and chromaticity in the image, followed by losses in contrast sensitivity that are selective for the directions in colour space along which colour signals in the image vary. The observed selectivity of contrast adaptation for any arbitrary colour direction can be modelled either as response changes in multiple post-receptoral channels that each receive a different combination of cone inputs^{5,9}, or as adaptation-dependent interactions between a small set of channels that alter their colour selectivity^{5,10,11}. The latter model, which we assume below for convenience, derives from the hypothesis that contrast adaptation decorrelates the responses across visual channels in order to encode image contrasts more efficiently².

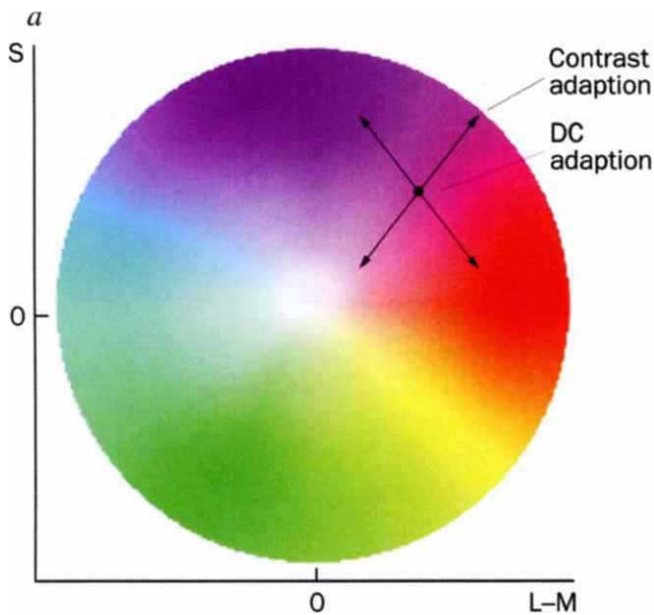
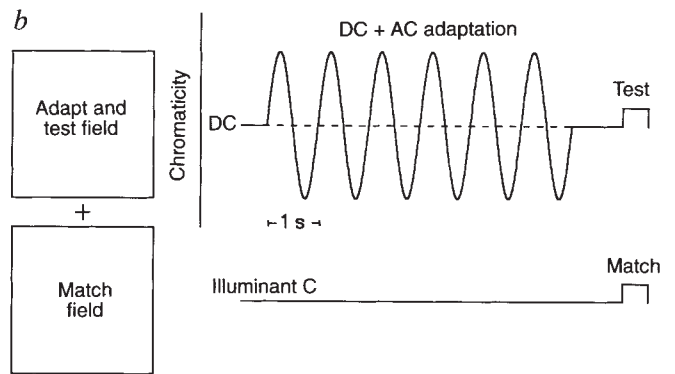


FIG. 1 a, A schematic illustration of the equiluminant colour plane used in this study. Stimuli varying along a vertical axis differ only in the excitation of the short-wave cones, whereas stimuli varying along a horizontal axis differ only in the difference of long-wave and middle-wave cone excitations. We refer to DC adaptation when the subject adapts to a static coloured field (solid point in the figure) and to contrast adaptation when the adapting field varies in chromaticity around the DC colour (two examples are indicated by the double-headed arrows).

It is evident that very large changes in contrast could be realized by an arbitrary choice of illuminants and reflectance spectra, but less obvious whether significant contrast changes can also occur when illuminants and surfaces are constrained to have the gently varying spectra of natural stimuli (though see ref. 12). To examine this, we followed several previous studies (such as refs 13, 14) by restricting illuminants to simulated phases of daylight¹⁵, and surfaces to simulated Munsell chips¹⁶. Figure 3a, b shows a pair of examples in which we model the effects on a set of surfaces of shifting the daylight illuminant from 4,800 K to 10,000 K or *vice versa*. In each case the surfaces were chosen to form a distribution of equiluminant colours under the first illuminant with a mean chromaticity equal to the illuminant chromaticity, but with a strong bias along the S axis in the distribution's range. Figure 3c, d shows plots of the predicted matches following von Kries adaptation to the distribution means. von Kries scaling compensates for most of the difference between the two distributions, but cannot discount the illuminant completely^{17,18}. The shift from 4,800 K to 10,000 K tilts the initial distribution off the S axis (90°) to an axis of 100° . The converse shift tilts the distribution from 90° to 77° . In either case the illuminant change has biased the colour direction of the distributions, and should thus alter the state of contrast adaptation. In Fig. 3e, f we model contrast adaptation as a sensitivity loss selective to each axis, by decorrelating and normalizing the responses to the L-M and S contrasts using the algorithm of ref. 10. Colour signals that matched across the two illuminants at the level of light adaptation no longer match, because they are embedded within different contrast distributions and are thus biased by contrast adaptation in different ways. For example, the chromaticities defined by the pair of ellipses in Fig. 3a should give rise to the same set of matches if the visual system adjusts to the illuminant change only through von Kries adaptation. (Thus both ellipses map on to the same circle in Fig. 3c.) Yet because of contrast adaptation, matches to these chromaticities instead plot as ellipses whose minor axes are oriented along the primary axes of the distributions, reflecting the selective sensitivity loss to the different adapting colour directions.



b, Adaptation effects were assessed with an asymmetrical matching procedure. Observers viewed a colour monitor with both eyes and fixated between two 2° fields (0.4° apart). Narrow black borders delimited each field from a white (equivalent to Illuminant C) surround of the same luminance (27.5 cd m^{-2}). Adapting stimuli were presented in the upper field, and consisted of a static colour (the DC chromaticity, chosen to induce a change in light adaptation), or 1 Hz sinusoidal modulations of chromaticity around the DC value (DC + AC, chosen to induce changes in both light adaptation and contrast adaptation). After 3-min initial adaptation, a test chromaticity was presented for 500 ms in the adapting field, and then continued interleaved with 7.5-s re-adaptation intervals (with only the DC adapting component present 1 s before and 0.5 s after each test). Observers matched the perceived colour of the test by adjusting the chromaticity of a matching stimulus presented simultaneously with the test, but in the lower, neutral-adaptation (Illuminant C) field.

We measured the empirical colour changes produced by adaptation to the four distributions illustrated in Fig. 3a, b, again using the matching procedure. Test stimuli included the mean chromaticity plus 16 chromaticities spanning the ellipses illustrated for each distribution. The observer adapted either to the static mean chromaticity of each distribution (DC), or to successive random samples from each distribution drawn every 200 ms (DC + AC). The latter simulates for a single retinal locus the temporal modulations of chromaticity that might arise from very rapid and spatially random eye movements over the image. Models of colour constancy have suggested that eye movements could allow spatially local mechanisms to light adapt to the mean colour signal in the image, if light adaptation is slow enough to integrate over many fixations (for example, ref. 19). However, such eye movements should also provide a potent stimulus for contrast adaptation, for we have observed strong contrast adaptation over a wide range of modulation rates, from higher than fixation changes could generate²⁰, to many times lower than are required to maintain light adaptation to the mean chromaticity of our stimuli. (Although we consider here only temporal contrasts, contrast adaptation to spatially distributed patterns (such as gratings) is well established², and appears to induce similar changes in colour appearance (for example, refs 21, 22)).

Figure 4 shows the colour changes produced by adaptation to each distribution. Colour matches following adaptation to the distribution mean are again closely approximated by incomplete von Kries scaling, that is, the matches fall roughly on a circle centred slightly off the origin. Adaptation to the actual samples from the distributions produces a pronounced contrast adaptation effect (in addition to the DC colour change), distorting into ellipses the matches to the nominal circle of test chromaticities. The orientation of each ellipse is close to the orientation predicted in Fig. 3e, f. Thus the illuminant change induces significantly different contrast adaptation effects that are in qualitative agreement with the model.

Our results suggest that the state of contrast adaptation will often change when the illumination changes, and this may both limit and promote the constancy of colour appearance. On the

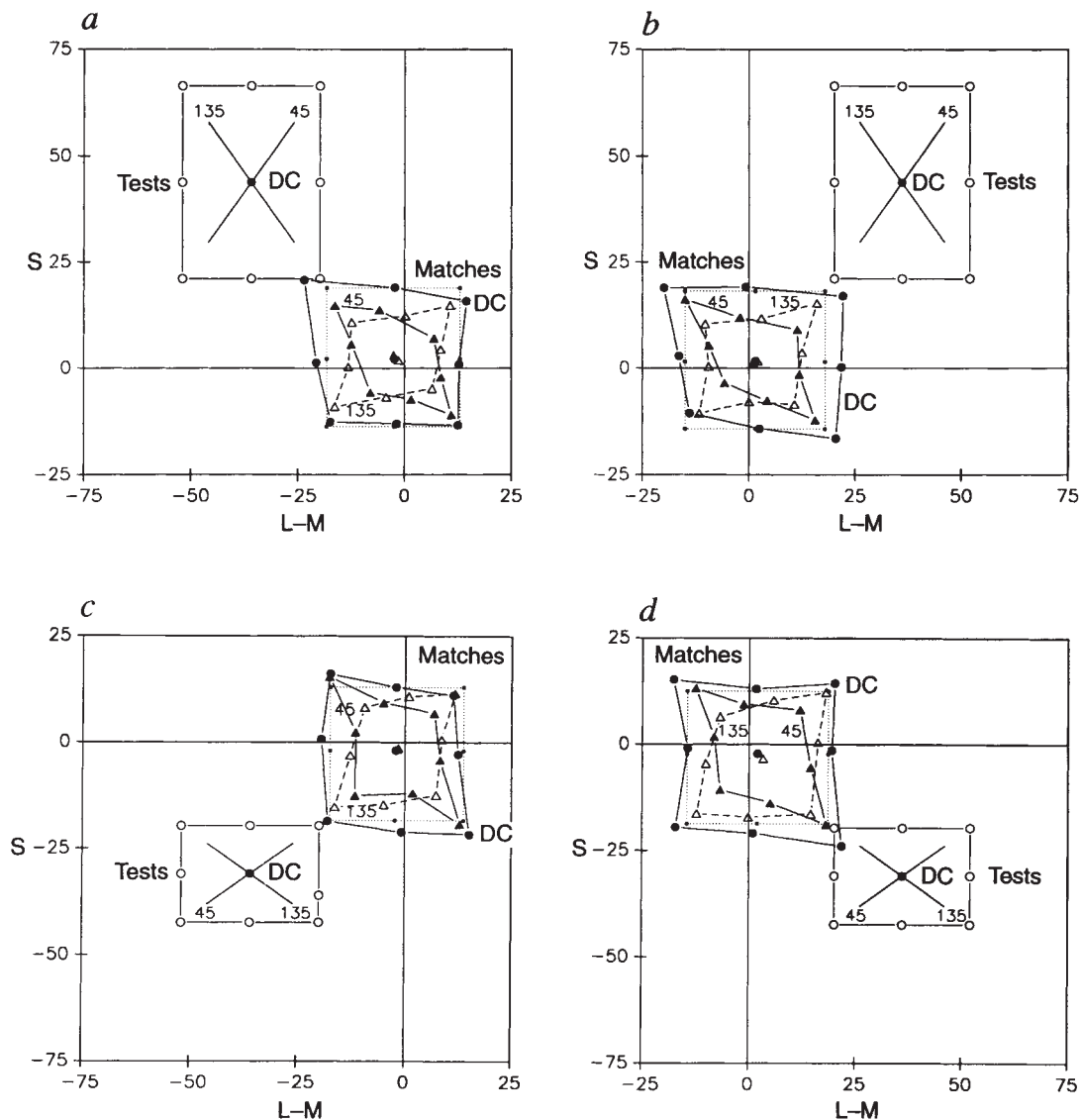
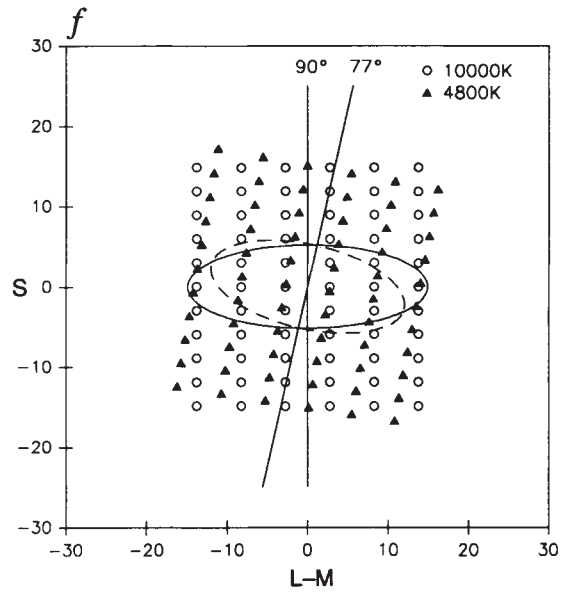
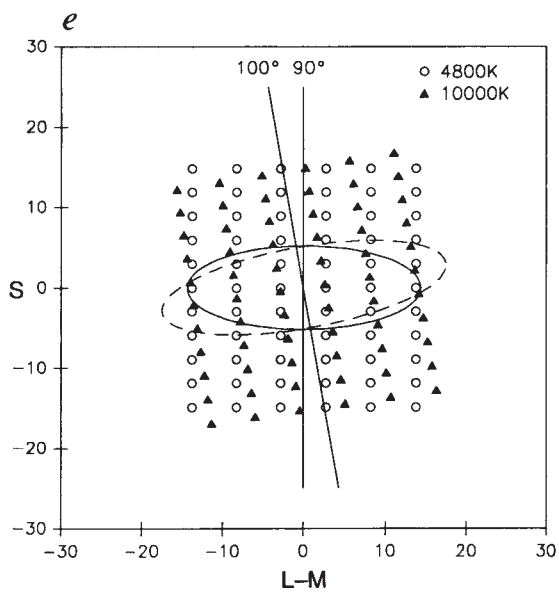
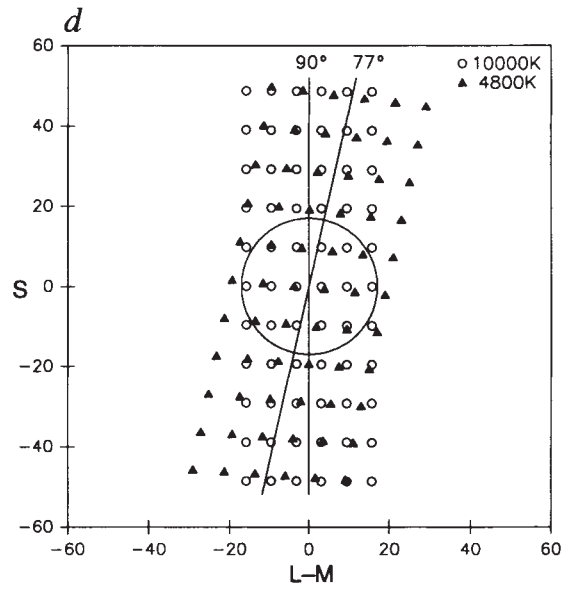
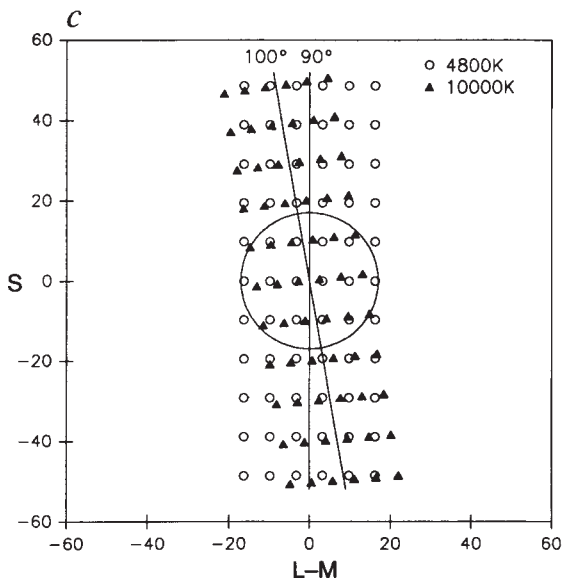
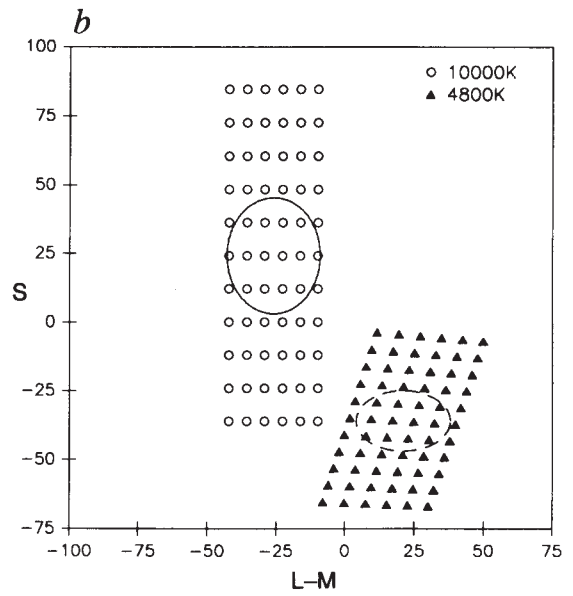
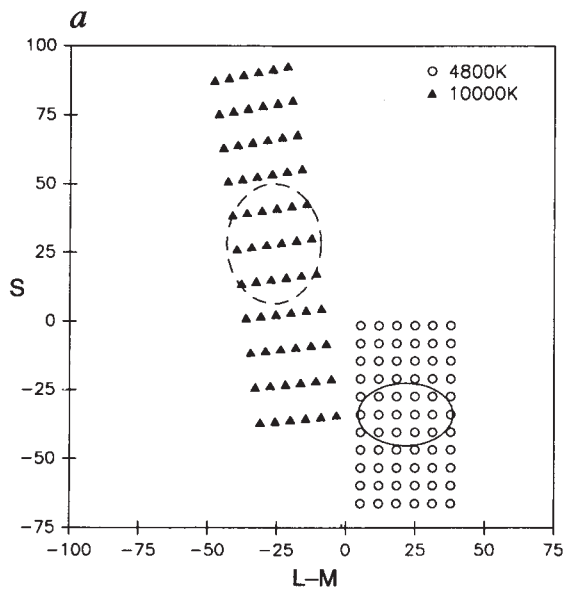


FIG. 2 Matches to test stimuli (open circles) following adaptation to a static colour (DC, filled circles), or to modulations around the DC colour (DC + AC, triangles). All stimuli were equiluminant (27.5 cd m^{-2}) and are plotted within a colour plane⁷ defined by an L-M axis, representing the relative excitation of L versus M cones to each chromaticity, and an S axis, representing S cone excitation. The two axes intersect at an origin corresponding to the chromaticity of Illuminant C, and were scaled for equal contrast sensitivity at the origin (based on measured thresholds). Unit distances along the S and L-M axes correspond to cone contrasts of 0.010 (S), 0.00151 (M) or 0.00079 (L). Each panel plots the matches for DC or DC + AC adapting colours centred in a different quadrant of the S versus L-M plane. AC modulations around each DC varied over a range of $\pm 48 \times$ threshold and varied along nominal angles of $45\text{--}225^\circ$

(yielding matches shown by filled triangles) or $135\text{--}315^\circ$ (matches shown by open triangles). (Test and adapting stimuli in different quadrants were scaled *a priori* to compensate for differences in von Kries adaptation.) Dotted lines/small symbols plot the matches predicted by von Kries adaptation, (based on rescaling each cone's signals according to the match to the DC adapting colour). The cone-specific scaling predicts that changes in perceived colour along the S axis do not depend on the level of L versus M cone excitation (or *vice versa*). This is consistent with the observed DC adaptation effects, but not with the matches following DC + AC adaptation, which reveal pronounced interactions between colour changes along the two axes. Results reported are the average of 3 or more matches to each test for author M.W. All measurements were confirmed on a second, naive observer.

FIG. 3 Simulations of adaptation to an illuminant change. Illuminants were approximated using the first three basis functions derived from daylight spectra by ref. 15. Surface reflectance spectra were simulated with the first three basis functions derived by ref. 16 for Munsell chips. a, Chromaticities of lights reflected from a set of chips viewed under 4,800 K daylight (circles), or the same set under 10,000 K daylight (triangles). The surfaces were chosen so that under the 4,800 K illuminant, the reflected colour signals form an equiluminant distribution centred on the illuminant chromaticity and biased along the S axis (so that the ratio of S to L-M contrasts = 3, following von Kries scaling). (The small effect that the illuminant shift has on luminance is not shown). b, The converse example in which the S-biased distribution is defined for the 10,000 K illuminant (circles) and then viewed under the 4,800 K illuminant (triangles). c, d, Matches to each chip predicted by von Kries

adaptation. Each cone's responses are rescaled by the ratio of the mean excitation (to each distribution) to the reference excitation (to Illuminant C, whose chromaticity plots at the origin). Solid lines show the dominant axis of each distribution. e, f, Matches predicted by contrast adaptation to the von Kries-scaled cone signals. The adaptation was simulated with the algorithm of ref. 10, which rescales sensitivity along the dominant and orthogonal axes of the distributions until (we assume here) responses along the S and L-M axes are decorrelated and normalized to an arbitrarily chosen variance ($\sigma = 9.5$). The matches predicted are consistent with the colour changes that contrast adaptation induces in moderate test contrasts^{4,10}, but probably overestimate changes at the extremes of the distributions, for contrast adaptation has much less effect on high contrast stimuli than predicted by the model's divisive gain control^{5,24}.



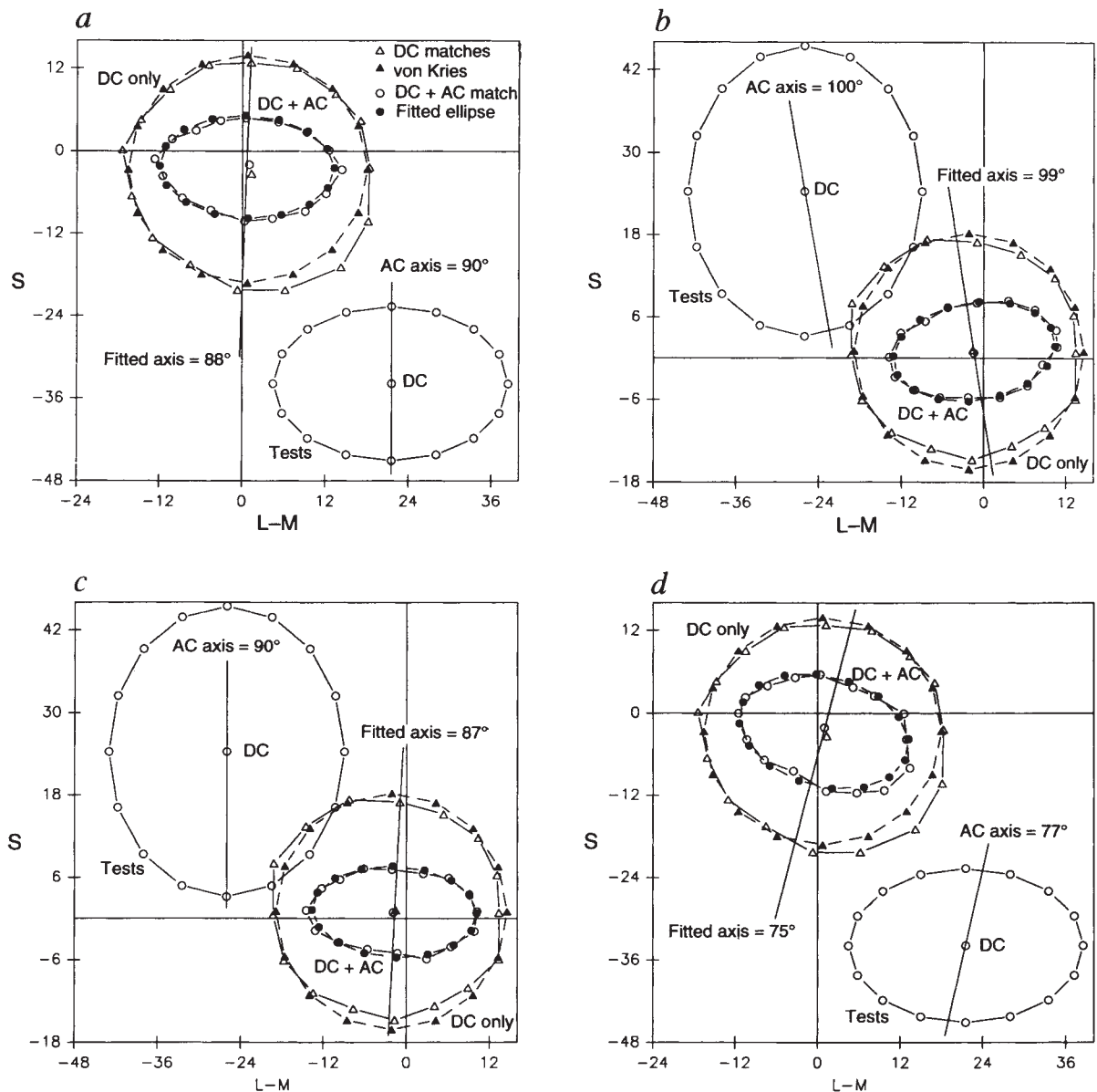


FIG. 4 Empirical matches following adaptation to the four colour distributions shown in Fig. 3a, b. Matches were made after adapting to the distribution mean (DC, open triangles), or successive random samples from each distribution (DC + AC, open circles). Filled triangles plot the matches predicted by von Kries adaptation. Filled circles are predicted matches derived by divisively scaling the von Kries coordinates along

two orthogonal axes to find the least-squares fit to the observed matches. The angles of the two axes were covaried to estimate the best-fitting adapting axis (solid lines). a, b, Matches for the initial S distribution under 4,800 K or the same surfaces under 10,000 K. c, d, Matches for the initial S distribution under 10,000 K or the same surfaces under 4,800 K.

one hand, contrast adaptation biases colour appearance relative to the axes of the adapting distributions, and thus it cannot undo tilts that different illuminants produce in these axes. On the other hand, contrast adaptation rescales apparent contrast according to the range of signals in the stimulus array, and this partially compensates for changes in the colour range introduced by changes in the illuminant or in viewing conditions (for example fog or rain²³). □

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