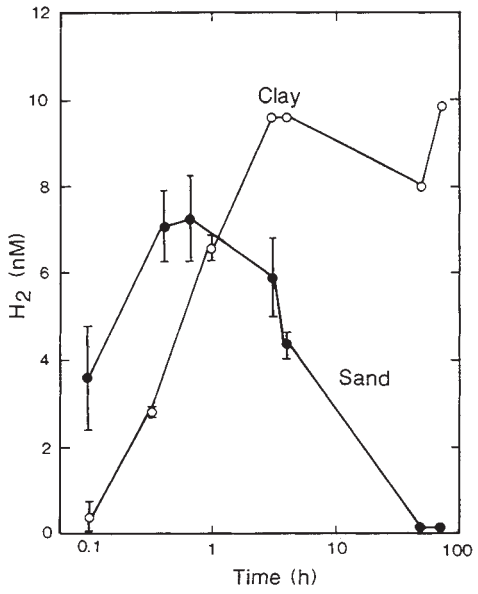

FIG. 3 Concentrations of dissolved hydrogen (H_2) in pore water of aquifer (sand) and aquitard (clay) sediments. Sediment was aseptically transferred to serum vials preflushed with N_2 immediately after core recovery, and hydrogen (H_2) concentrations were determined at specified times using a gas chromatograph equipped with a reduction gas detector[22]. Each data point represents measurements on duplicate vials.

these sediments are sulphate-reducing[16,17], we would expect the steady-state H_2 concentration in them to have stabilized at ~2 nM (ref. 22), rather than at concentrations<0.1 nM. This suggests that the fermentative capacity of these isolated aquifer sediments is not sufficient to maintain microbial respiration at sulphate-reducing levels. In the aquitard sediments, however, H_2 production was initially rapid and continued, at a slower pace, throughout the experiment, achieving concentrations well in excess of 2 nM. This indicates that there was no consumption of H_2 by sulphate-reducing microorganisms and that the fermentative capacity of the aquitard sediments is sufficient to maintain H_2 concentrations in excess of sulphate-reducing levels. Although H_2 concentrations in the aquitard sediments approach levels associated with methanogenesis[22], high dissolved sulphate concentrations in the pore water[16,17] and lack of methane production during the experiment indicate that methanogenic activity in the aquitards was not significant either.

Finally, it is unlikely that the persistence of labelled organic acids in aquitard sediments, and not in aquifer sediments, is due to depressed turnover of the label by the high *in situ* concentrations of formate and acetate. The *in situ* concentrations of formate and acetate in the aquitard sediment were only 4 times greater than in the aquifer sediment, yet the ratio of labelled formate and acetate to CO_2 in the aquitard sediment at the end of the experiment was over 1,000 times greater than that in the aquifer sediment (Fig. 2).

The diffusion of organic acids from aquitards to aquifers links the fermentation of sedimentary organic matter in aquitards to respiratory CO_2 production in aquifers and provides a driving mechanism for microbially mediated changes in the water chemistry in aquifers. In fact, the close agreement between the diffusion-derived CO_2 production rate and the rate derived from mass balance strongly suggests that respiratory activity in the aquifers is limited by the diffusion of organic substrates from aquitards. This, in turn, may explain why CO_2 production rates in different hydrological and geological environments are observed to be so similar[17]. In addition to these geochemical considerations, dissolution of aquifer sediments by microbial CO_2 and organic acids from this process may explain the widely observed phenomenon of increased secondary porosity development at sand/shale contacts[23]. □

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Changes in colour appearance following post-receptoral adaptation

Michael A. Webster & J. D. Mollon

Department of Experimental Psychology, University of Cambridge, Cambridge CB2 3EB, UK

CURRENT models of colour vision assume that colour is represented by activity in three independent post-receptoral channels: two encoding chromatic information and one encoding luminance[1]. An important feature of these models is that variations in certain directions in colour space modulate the response of only one of the channels. We have tested whether such models can predict how colour appearance is altered by adaptation-induced changes in post-receptoral sensitivity. In contrast to the changes predicted by three independent channels, colour appearance is always distorted away from the direction in colour space to which the observer has adapted. This suggests that at the level at which the adaptation effects occur, there is no colour direction that invariably isolates only a single post-receptoral channel.

We used an adaptation procedure designed to desensitize post-receptoral channels without significantly changing the sensitivity of receptors[2,3]. Subjects viewed a uniform field that was slowly modulated in chromaticity and/or luminance along a particular direction in colour space. The modulation does not change the average luminance or chromaticity of the field over time and therefore produces little of the average changes in receptor quantal absorptions that are a major factor in classical chromatic adaptation[4], yet exposure to it raises thresholds for detecting subsequently presented chromatic or luminance modulations. Krauskopf *et al.*[3] found that these sensitivity losses are highly selective if the adaptation is confined to one of three 'cardinal' directions in colour space: an achromatic axis (along which luminance varies while chromaticity is constant), and two equiluminant chromatic axes that selectively modulate either signals from short-wavelength cones (S), or opposing signals

from long- and medium-wavelength cones (L–M). The two chromatic axes stimulate two subsystems of colour vision that evolved at different times[5]: an ancient dichromatic subsystem originally based on a comparison of signals from S cones and from a single ancestral long-wave pigment, and a modern subsystem that evolved to compare the signals of L and M cones after the recent differentiation of the genes encoding their pigments[6]. In many perceptual tasks these postulated subsystems behave independently[7–10,24], yet conditions revealing interactions between them have also been found[11–14].

For our experiments, stimulus variations that corresponded to the luminance, S, and L–M axes were empirically defined on a colour monitor (as in ref. 15) and were scaled so that a unit distance along each axis equalled the threshold for detecting a change away from the white background. For each of the planes defined by these axes we then selected up to 16 test stimuli, which were spaced on a circle at 22.5° intervals and were each 17 threshold units from the background (Fig. 1). The adapting stimuli were 1 Hz sinusoidal modulations along one of the corresponding eight directions and varied over a range of ±48 times threshold. The adapting and test stimuli were alternately presented in the same 2° field, but were separated in time by blank periods (1 s before and 0.5 s after each test). The field was centred 1.2° from fixation, and was delineated by narrow black borders from the background, which had the same average colour. Observers initially adapted for 3 min to the adapting modulation. One of the test stimuli was then presented for 0.5 s in the same field, and its perceived colour was matched by adjusting the colour of a matching stimulus presented simultaneously in a second 2° field, placed symmetrically to the other side of fixation. The adjustments were made during 6 s of re-adaptation before each presentation of the test stimulus.

Figure 2 shows examples for one observer (M.W.) of the colour changes we found following adaptation to four different directions within the equiluminant plane. In Fig. 2*a* the adapting variation was along either the S or the L–M direction, whereas in Fig. 2*b* the adaptation varied along intermediate directions chosen to stimulate equally the S and L–M axes. In each case the effect of the adaptation is highly selective: the largest changes were for test stimuli lying along the adapting axis while the least change was for stimuli about 90° away. Very similar effects were found for four further adapting directions, each 22.5° from the S or L–M direction. If the channels adapt independently, then the observed colour changes require at least eight different channels tuned to eight different chromatic directions. Residual selectivity of the adaptation effect for chromatic directions intermediate to the S and L–M axes is also evident from the changes that adaptation produces in chromatic detection thresholds[11], yet it is surprisingly salient in the present measures of suprathreshold colour appearance. Ellipses fitted to the matches suggested that for two observers the selectivity for intermediate adapting directions was either comparable to (A.S.) or only slightly less than (M.W.) the selectivity for the S or L–M directions (Fig. 2*c*). For two further observers (J.M., A.E.), however, the colour changes were clearly more selective for the S and L–M directions, confirming the special status of these directions.

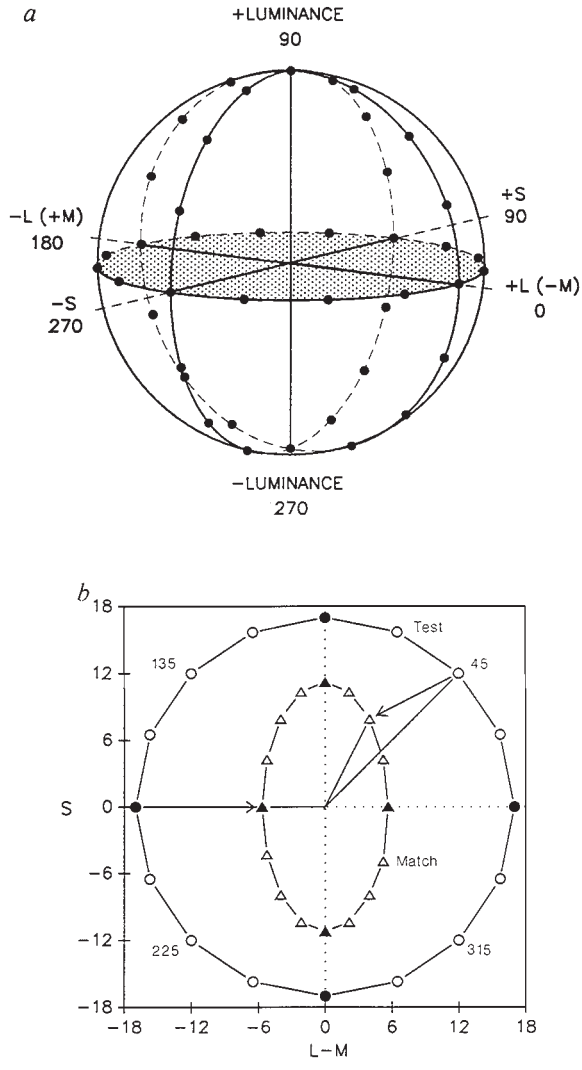

FIG. 1 *a*, Coordinates of test stimuli in a colour space defined by S, L–M, and luminance axes[21,23]. The S and L–M axes define an equiluminant plane. Within it distances from the white origin correspond very roughly to saturation while direction corresponds to hue. The achromatic axis corresponds roughly to lightness. *b*, Predicted colour changes for two independent channels tuned to the S or L–M axis. Adaptation might change colour appearance by reducing the sensitivity of one or both mechanisms. The least or greatest change should be along the S or L–M axis. Sensitivity changes could also distort perceived direction by changing the relative responses to stimuli encoded by both channels (open symbols), but should not affect the perceived direction of stimuli encoded by only one channel (closed symbols).

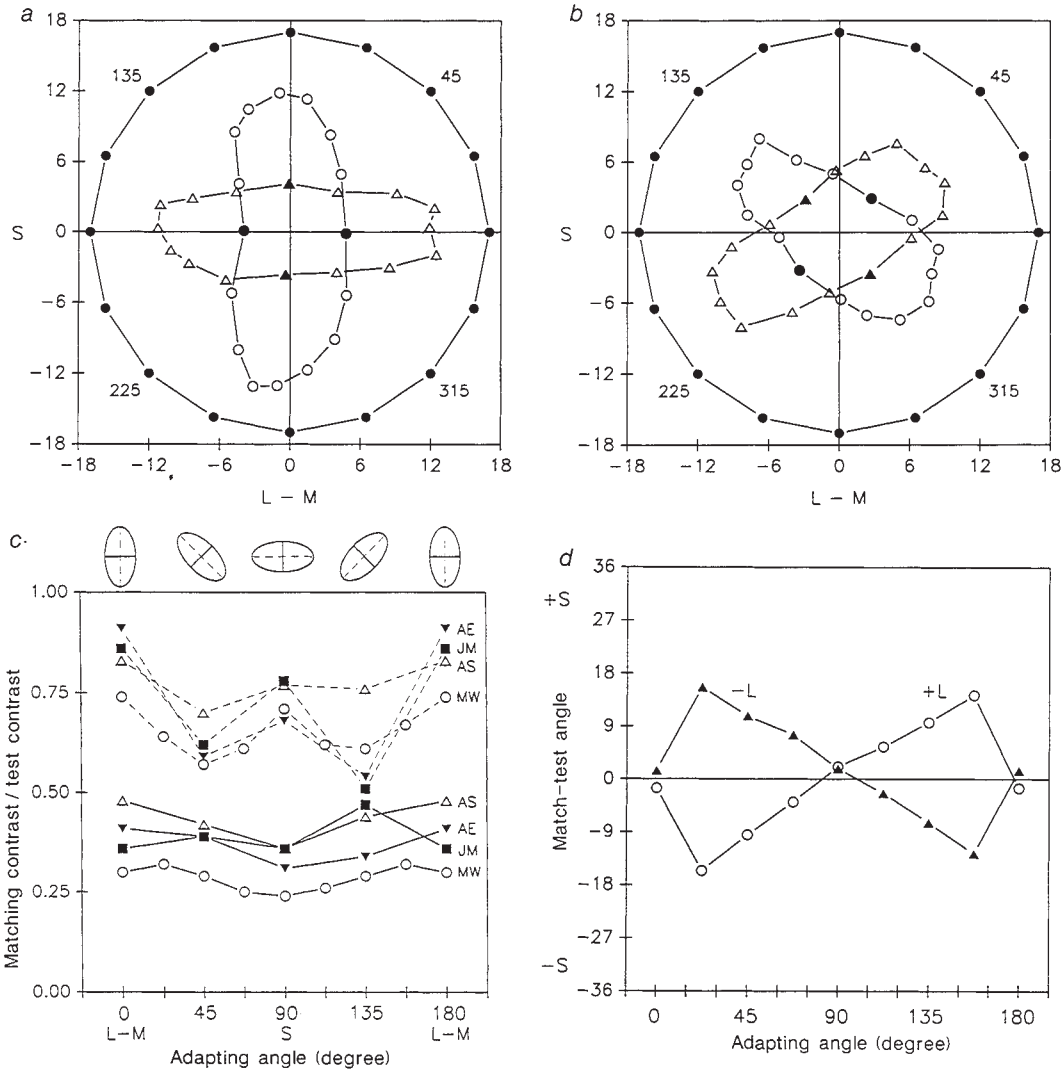

FIG. 2 Coordinates of equiluminant test stimuli (●) and of matches made to them following adaptation to different chromatic axes. In *a*, adaptation was to the L-M (○) or S (△) axis. In *b*, adaptation was to an intermediate axis at 45–225° (○) or 135–315° (△). Matches to tests that were on the adapting axes are indicated by filled symbols. *c*, The match coordinates for each adapting direction fall approximately on an ellipse, which was fitted to estimate the change in perceived contrast along the adapting axis (—) and orthogonal axis (- - -) for each of the four observers tested (the two authors and two naive subjects). *d* and *e*, Change in perceived direction of the two test stimuli lying on the L-M (*d*) or S axis (*e*), as a function of the direction of the adaptation.

Adaptation changed not only the perceived saturation of the test stimuli, but also their perceived direction (or hue). The hue changes were always rotations away from the adapting direction and towards an orthogonal direction that was ~90° away in the normalized S and L-M plane. (Tests lying on the adapting or orthogonal axes generally showed little change in perceived angle.) These changes are analogous to changes in perceived orientation[16] or spatial frequency[17] following adaptation to spatial patterns. Such after-effects are commonly explained by assuming that the appearance of the test depends on the distribution of activity in multiple channels, and that adaptation distorts appearance by reducing activity in some channels more than others[18,19]. However, suppose that some chromatic stimuli change the activity in only a single channel. Then if the only effect of adaptation is to desensitize the channels, it should still be the same channel that alone encodes the stimuli after adaptation. Consequently, such stimuli may appear desaturated, but their perceived direction should always be unaffected by the adaptation (Fig. 1*b*). Instead, we found that clear changes in perceived angle could be induced in all of the test stimuli we examined. Examples of these changes are shown in Fig. 2*d* and *e* for the two tests lying along either the L-M or the S axes. These are the tests most likely to isolate a single adaptable channel, yet adaptation to intermediate chromatic axes rotated the perceived angle of these tests off their axes. Similar distortions were found for all the test stimuli, including stimuli chosen to lie along the unique hue loci, and occurred for all four observers. This suggests that there are no chromatic directions encoded by only a single adaptable chromatic channel.

Surprisingly, adaptation also produced changes in colour appearance that were selective for stimuli varying in both luminance and chromaticity, despite previous findings that the adaptation influences detection thresholds for these dimensions independently[3]. For example, Fig. 3 shows for observer M.W. the effects of adapting to modulations along either a pure luminance or a pure chromatic (L-M) axis (Fig. 3*a*), or along two directions for which luminance and chromaticity covaried (Fig. 3*b*). Again, the adaptation produced the largest sensitivity losses

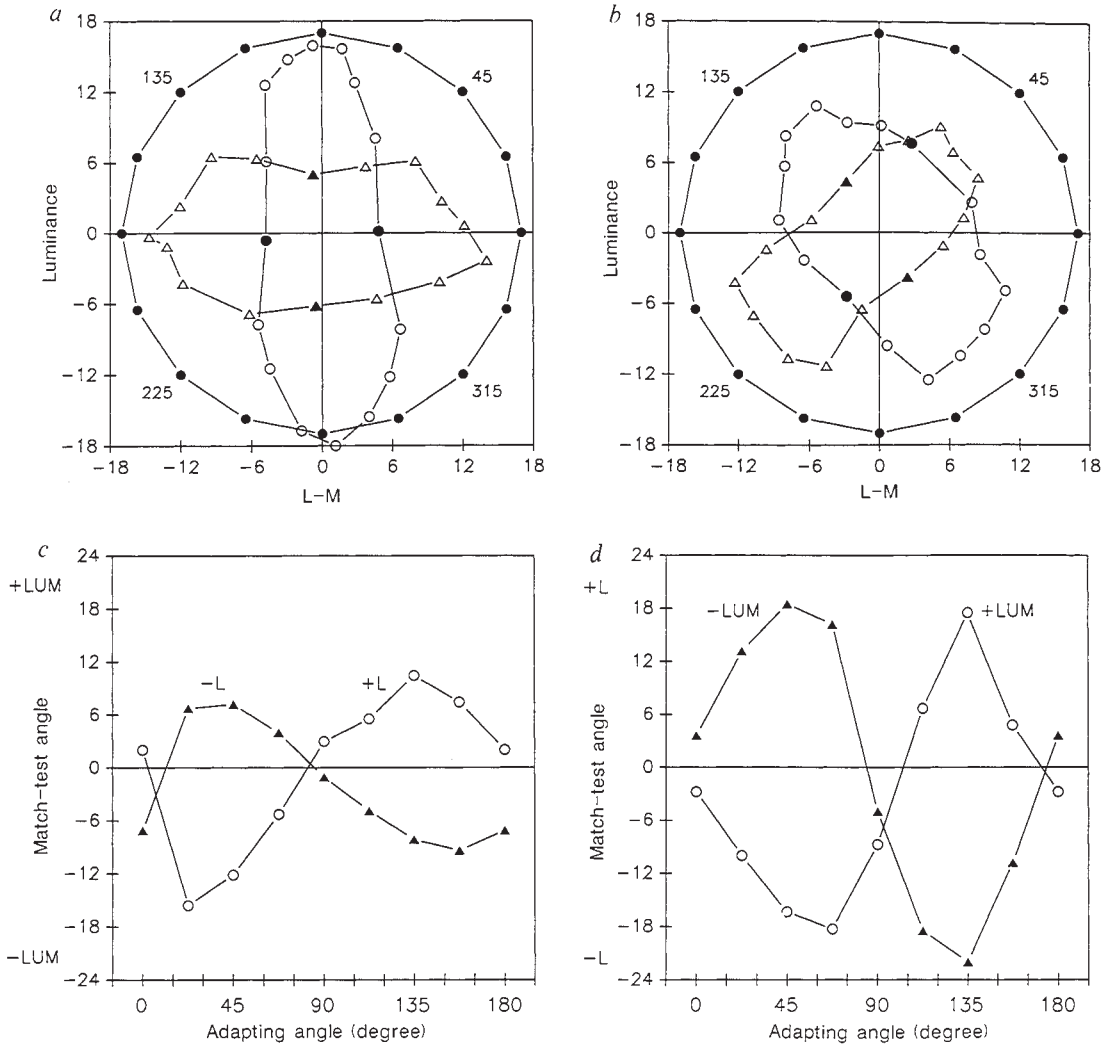

FIG. 3 *a*, Matches made to test stimuli in the L–M/luminance plane following adaptation to the L–M (○) or luminance (△) axis. *b*, Matches made to the same tests following adaptation to combined luminance and chromatic variations along axes at 45–225° (○) or 135–315° (△). *c* and *d*, Changes in the perceived direction of the two pure chromatic tests (*c*) or the two pure luminance tests (*d*) for different adapting directions.

for test stimuli that were near the adapting axis (a result confirmed for a second observer, A.S.). This selectivity was also evident when the chromatic component modulated activity only in the S cones, even though the S cones contribute very little to measures of luminance[20], and are often assumed to have access only to purely chromatic pathways. Adaptation to combined luminance and chromatic variations also produced changes in the perceived direction of luminance and/or chromatic stimuli. For example, adaptation could alter the relative lightnesses of equiluminant chromatic tests (Fig. 3*c*) and the relative hues of tests that had the same chromaticity but differing luminances (Fig. 3*d*), suggesting that these stimuli were not encoded only by purely chromatic-sensitive or luminance-sensitive channels.

These selective adaptation effects probably have a cortical locus, as physiological studies suggest that lateral geniculate neurons are little adapted by the type of stimuli we used[21]. Our results could be explained by the existence of multiple, adaptable channels, each tuned to a different direction in colour space[11]. Alternatively, however, central chromatic channels might be coupled through adaptation-dependent links that alter their tuning functions[22]. □

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