

Human colour perception and its adaptation

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Abstract. Information about colour is initially extracted by the visual system in terms of the activity within a small number of receptor types with different spectral sensitivities, and then recoded within channels that respond to different combinations of the receptor signals. Many insights have been gained about these post-receptoral transformations, yet their number and nature remain poorly defined. This review examines how the signals coding colour are organized within the human visual system, and how these signals are affected by the processes of adaptation. Sensitivity is controlled by two distinct classes of adaptation that adjust to different aspects of the stimulus; retinal mechanisms of light adaptation adjust for changes in the average colour across scenes, while cortical mechanisms of contrast adaptation adjust for changes in the distribution of colours. Together these exert a profound and pervasive influence on our colour perception.

1. Introduction

Our perceptual world is greatly enriched by the capacity to perceive through our colour vision the spectral quality of the physical world around us. Colour is important not only for judging the identity and state of objects (e.g. whether or not a fruit is ripe) but also for perceiving the spatial structure of scenes (e.g. where to reach for it). Colour science has provided fundamental insights into sensory processes and among the most important psychophysical paradigms. Yet the nature of the mechanisms mediating our colour vision remains in many ways obscure. The present review is focused on how information about colour is organized within the visual system, and how this organization is both revealed and altered by the processes of adaptation. We begin by considering colour coding in the cone photoreceptors and at post-receptoral levels, and then discuss two distinct classes of sensory adaptation that act at retinal and cortical levels to alter visual sensitivity to different properties of the stimulus. This will lead in the final sections to a consideration of how the two forms of adaptation combine to adjust our colour vision to the prevailing visual environment.

2. Human colour vision

Figure 1 shows an example of the spectral power distribution for two phases of daylight, and the reflectance spectrum for two objects (an orange and a leaf). The light reaching the eye from natural illuminants and objects typically has a broad but biased spectrum. Colour is the perceptual correlate of the light's spectral composition. A minimum requirement for colour vision is for the spectral characteristics of different lights to be represented in a way that is not confounded by the lights' intensities. The visual system encodes colour in two

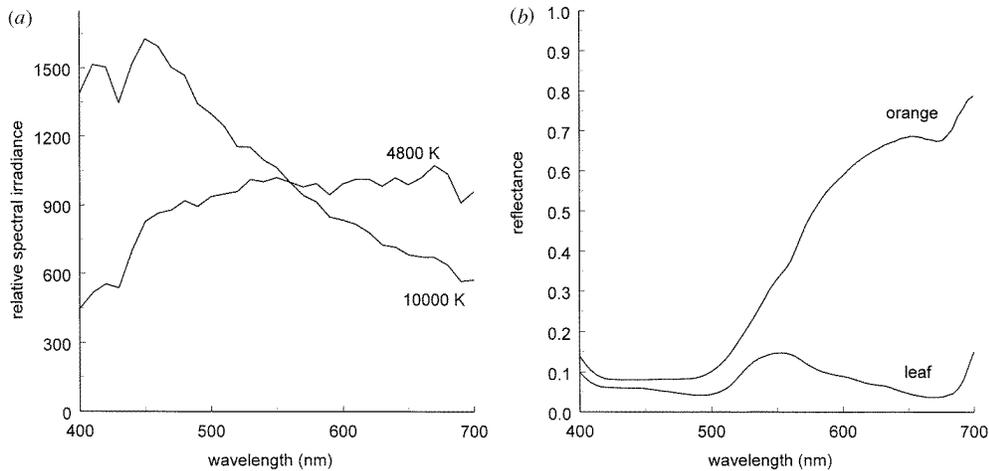


Figure 1. (a) Spectral power distribution for two phases of daylight [82]. (b) Reflectance functions for two natural objects.

general stages. Light is initially represented by the relative activity in receptors that have different but overlapping sensitivities to wavelength. Subsequently, the signals from the cone receptors are summed or differenced within post-receptor channels that respond to different combinations of the cone signals. The following sections briefly review some of the important properties of these two levels of human colour vision.

3. Receptors

Many characteristics of our colour perception are determined the moment light is absorbed by the photosensitive molecules in the receptors. The rate of photon capture by visual pigments depends on wavelength, so that the cone pigments have broad but selective absorption spectra. The spectra for different photopigments have similar bandwidths when plotted on an appropriate frequency axis, but vary widely in their peak absorbance [21, 78]. A critical feature of visual transduction is the 'principle of univariance': the wavelength of light influences the probability of absorption, but once a photon is absorbed the resulting response is independent of wavelength [15, 136]. Consequently, any single class of photoreceptor (i.e. any set of receptors that all share the same sensitivity to wavelength) is truly colour blind, as we can always equate the responses to any two lights by adjusting the relative intensities of the lights. For example, figure 2(a) shows estimates of the spectral sensitivities of human cone receptors [155]. For the receptor labelled 'L', sensitivity to a light of 600 nm (0.84) is 2.7 times its sensitivity to light of 500 nm (0.31). However, since the form of the response to either wavelength is the same, we could make the two lights indistinguishable for this receptor simply by setting the radiance of the 500 nm primary so that it is 2.7 times as great.

Colour vision therefore necessarily requires that the visual system compares the responses across different classes of photoreceptor that have different spectral sensitivities. For example, for the receptor labelled 'M' the sensitivity is 0.46 and 0.35 for the 500 and 600 nm lights, respectively. We could again equate the responses within this receptor, but then the lights would not match for the L receptor. The two wavelengths produce a different *ratio* of responses across the two receptors, and since this ratio stays constant as the light

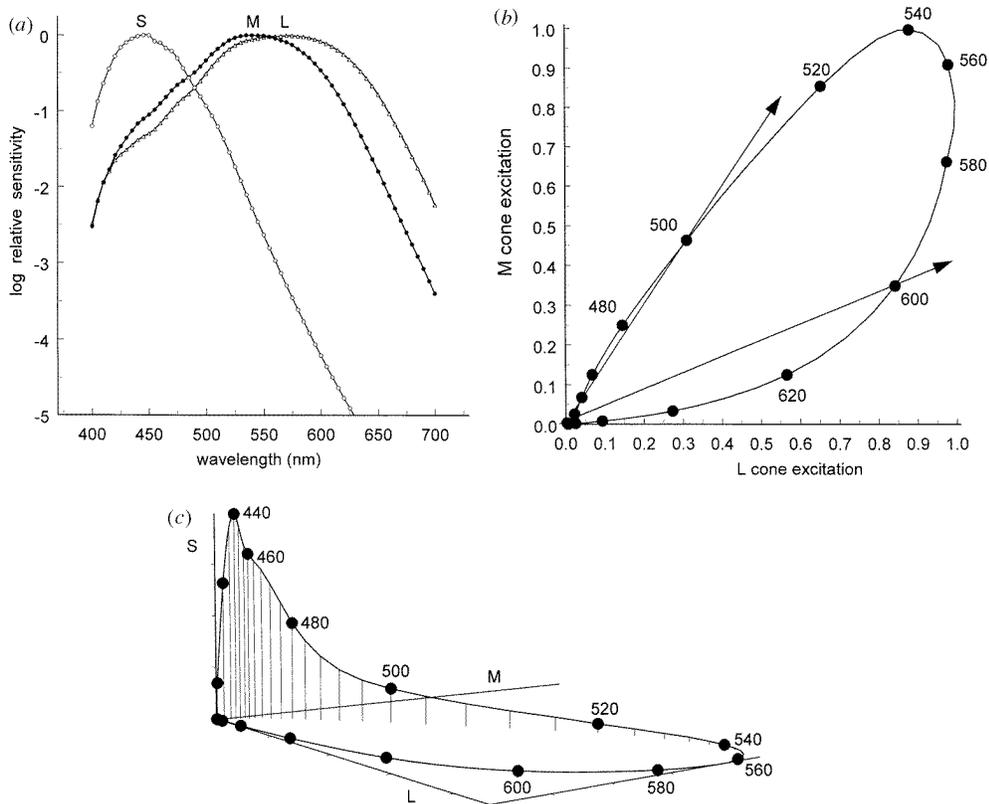


Figure 2. (a) Spectral sensitivities of the human cones [155]. (b) Cone excitation plane for L and M cones. Increasing a light's intensity moves it away from the origin along a line whose slope depends on the relative sensitivity of the two cones to the light's spectrum. The bounded contour shows the relative L and M sensitivity to different wavelengths. (c) Cone excitation space. All lights can be represented by the excitation produced in the L, M and S cones.

level is changed, it provides unambiguous information for distinguishing between the two lights (figure 2(b)).

At the dimmest light levels visible only a single receptor type (the rods) is functional, and colour perception is thus precluded. However, as figure 2 suggests, humans are generally assumed to have three kinds of cone receptor that take over from rods to operate from dim to the highest light levels. The cones are named according to their wavelength of peak sensitivity as short-, medium- or long-wavelength sensitive (S, M or L; it is also common to see them referred to as blue, green or red cones, respectively). Many techniques have been devised to estimate the spectral sensitivities of the cones and their photopigments, from measurements of the electrical response of cone outer segments [15], to microspectrophotometry of the light absorption by the outer segments [21], to absorption spectra determined for photopigment reconstituted *in vitro* [112]. The different methods have converged on similar estimates of spectral absorption and sensitivity though they differ in detail. Precise psychophysical estimates have come from analyses of colour matching data.

Because we have three cone types that each obey the principle of univariance, physically different lights that produce identical responses within all three cone classes will be

indistinguishable (metameric). To match any light requires a comparison light that has only three independently adjustable primaries. The primaries can be monochromatic or broadband. (In practice matches are generally made with three widely different primaries, such as deep red, green and blue, yet the only restriction is that one of the primaries cannot be matched by the other two.) Graphically, we can represent the colour of any stimulus as a point in a three-dimensional space whose coordinates represent the excitation produced in each class of cone (figure 2(c)). A colour match holds for any lights that have the same coordinates. Algebraically, for the three cones the colour match must satisfy the following three equations:

$$\begin{aligned} Q_t L_t &= Q_1 L_1 + Q_2 L_2 + Q_3 L_3 \\ Q_t M_t &= Q_1 M_1 + Q_2 M_2 + Q_3 M_3 \\ Q_t S_t &= Q_1 S_1 + Q_2 S_2 + Q_3 S_3 \end{aligned}$$

where the Q 's are the radiances of the test and primaries and the L , M and S terms give the sensitivities of each cone to the test and each primary. Note that when a test light falls outside the gamut of cone excitations bounded by the three primaries, the match requires adding one of the primaries to the test light in order to desaturate it. Thus we can match any light by the three phosphors on a television but we cannot produce a red on our screen that has a higher colorimetric purity than the red phosphor. Note also that the three matching equations do not provide enough information to uniquely define the spectral sensitivities of the cones. To solve for the cone sensitivities requires combining the colour matching data from normal observers with matches from colour blind observers who lack one of the cone types. The cone sensitivities derived in this way provide the best estimate of spectral sensitivities in the intact observer and are widely used for modelling human colour vision [150, 155]. (However, there are significant individual differences across normal observers [148, 173], so that in experimental work it is often important to choose the stimuli empirically.)

It is important to keep in mind that once two lights are matched to produce equivalent photon absorptions, any information about their difference is lost, and there is nothing the rest of the visual system can do to undo this. Thus the two lights will remain matched no matter what the nature of subsequent neural processing or of any changes that might occur with adaptation. Having only three cone types restricts the photon matches to only three degrees of freedom, and thus our representation of colour is necessarily only three dimensional—or trichromatic—regardless of how many ways the visual system might recombine the cone signals post-receptorally.

There are a number of striking asymmetries between the S cones and the L and M cones. First, the S cones are much rarer (< 10% of all cones), are sparsely distributed across the retina, and are absent from the central fovea where our vision is best [39]. Second, the peak sensitivity of the S cones is far removed from the L and M cone peaks, which differ by about 30 nm. The unequal spacing does not reflect biochemical constraints and thus investigators have instead looked for possible adaptive constraints (e.g. [12, 103, 118, 125, 132]). Functionally, we will see below that S cones contribute primarily (but not exclusively) chromatic information, and thus stimuli that are chosen to be visible only to the S cones show many of the spatiotemporal limitations characteristic of pure colour stimuli [101]. Genetically, the S-cone photopigment is encoded by an autosomal gene and is only 40% homologous with the L and M pigment genes or with the rod pigment gene [121]. In contrast, the L and M genes lie next to each other on the X chromosome and are 96% identical. These differences have suggested that our ancestors were dichromats, dependent for their colour perception on a single 'ancient' subsystem [114] that compared responses between

S cones and a single ancestral L/M pigment. This dichromacy characterizes the colour vision of most mammals [78]. Separate L and M pigments arose only recently (perhaps 30 million years ago) through a gene duplication on the X chromosome, giving rise to a second ‘modern’ subsystem in colour vision. This subsystem, which among mammals is specific to primates, allows discrimination between reddish and greenish colours, and may have evolved specifically for distinguishing fruit from foliage [130]. We will see below that these two subsystems are fundamental to the post-receptoral organization of the cone signals in human colour vision.

Recent studies of the genes coding the photopigments have suggested a number of further ways in which our understanding of the earliest stages of colour vision may be revised. First, there are common polymorphisms of L and M pigment genes. For example, a frequently occurring substitution of a single nucleotide is sufficient to shift the peak sensitivity of the L cones by about 5 nm [112], and is correlated with small differences in colour matches [183]. Second, most humans may have multiple copies of the M and possibly L pigment genes [121, 123]. If these copies include different alleles that are each expressed in different cones (and if these differences are preserved in post-receptoral pathways), then many observers could have the potential for representing colour with more than three degrees of freedom [122]. A second exception to trichromacy may be in female carriers of a colour deficiency known as anomalous trichromacy (who have from their two X chromosomes both the normal L and M pigment genes and a gene for a pigment with intermediate spectral sensitivity). Since both genes are likely to be expressed in different retinal areas, such females have the potential for tetrachromacy. In fact, an analogous process has been found to allow an extra dimension of colour vision in some females of new world monkey species whose males are all dichromats [78]. (This was thought to be the only example of trichromacy in new world monkeys, though there is now evidence that some new world species are like trichromatic old world primates [79].) However, it has so far proven difficult to find evidence for humans who behaviourally are more than trichromatic [81, 119].

4. Post-receptoral mechanisms

We have seen that colour vision requires comparing the responses across different cone types, and in fact early in the visual pathway the signals from the cones are recoded into post-receptoral channels that make these comparisons explicit. In some channels the inputs from different cones are of opposite sign so that the channels respond with opposite polarity to different parts of the visible spectrum. Because the response in such ‘colour-opponent’ channels is determined by the *relative* activity across cones, they encode information about the spectral composition of light. In other channels the cone inputs are of the same sign, and these ‘broadband’ channels thus pool information across the cones to carry information about luminance. (The broadband channel is also considered to be opponent insofar as it responds with opposite polarity to luminance increments or decrements.) This section first reviews the sources of evidence for a colour-opponent organization, and then considers the specific nature of the post-receptoral transformations.

Colour opponency was first suggested by the subjective appearance of lights. Any spectral light can be described as some combination of the four perceptually unique colours: red, green, blue or yellow. However, no light appears both red and green or both blue and yellow. Such observations suggested that the colour percept is mediated by two opponent channels coding red–green or blue–yellow sensations [76]. Because a single channel signalled either red or green depending on the sign of its response, no chromatic

stimulus could evoke both sensations simultaneously. Most lights would stimulate both channels to some degree and thus take on the hue qualities signalled by each (e.g. 'orange' looks both 'reddish' and 'yellowish'). However, for some lights the inputs to one of the opponent mechanisms might cancel exactly, and such lights would thus take on the 'unique' hue (e.g. a unique red, that is not tinged with yellow or blue) signalled by the remaining channel (or white if both channels were nulled).

Very different evidence for opponency comes from studies that have examined factors that influence visual sensitivity. For example, thresholds for discriminating changes along different directions in colour space suggest that sensitivity is limited by mechanisms that sum or difference the cone signals rather than by the independent cones [84, 151, 157, 164, 170]. Moreover, the luminance and chromatic thresholds change in different ways as the spatial or temporal frequency of the stimulus is varied: colour contrast sensitivity is low pass, while luminance contrast sensitivity is bandpass [83, 116] (see figure 5(c)). Colour opponency is also revealed by interactions between test lights. For example, for some pairs of wavelengths sensitivity is lower to the mixture than to either component presented alone, presumably because the two wavelengths produce opposite responses at an opponent site and thus tend to cancel [22]. Finally, opponent interactions have also been implicated by a variety of adaptation effects, which we consider in detail below.

Physiological measurements confirmed colour opponency in single neurons [43, 64, 162, 186]. The majority of ganglion cells (the output cells of the retina) and lateral geniculate cells (to which the ganglion cells project) receive antagonistic cone inputs, and thus can respond with opposite polarity (excitation or inhibition) to different parts of the visible spectrum. In some species these antagonistic interactions may arise at the first synapse in the visual pathway—between receptors and horizontal cells—and thus modulate even the responses of the receptors [30]. However, in primates and perhaps mammals in general the first site of opponency may be the bipolar cells or as late as the ganglion cells [40].

Finally, a colour-opponent organization has also been deduced from theoretical considerations. An important principle in the design of post-receptoral channels may be to represent the signals from the photoreceptors efficiently, in channels whose responses are statistically independent [6]. Because of their overlapping spectral sensitivities, the signals in the different cones for most stimulus distributions are highly redundant. Recombining the signals into three channels whose outputs are uncorrelated predicts channels that receive antagonistic cone inputs [7, 29, 96].

The observations on colour opponency led to a standard two-stage model of human colour vision, in which the outputs from the three classes of cones are combined to form three post-receptoral channels, one encoding luminance and two encoding colour (figure 3(a)). To capture the properties of colour vision at the second stage, it is useful to replace the cone excitation space of figure 2(c) with a space whose axes instead represent any light by the response it produces along different post-receptoral dimensions (figure 3(b)). A key assumption in this transformation is that at post-receptoral levels the visual system encodes relative stimulus differences, rather than absolute stimulus levels. Thus within the new space the origin is no longer zero light but usually an achromatic grey corresponding to the common neutral point for each opponent axis, and stimuli vary from the origin either as increments or decrements. Two of the dimensions are chromatic and define a plane within which only colour varies. If these dimensions refer to colour appearance, then the two axes are typically chosen to represent red–green and blue–yellow sensations, and the angle and distance from the origin represent the light's hue and saturation, respectively. The third appearance axis is achromatic and corresponds to brightness. Alternatively, the chromatic axes may be chosen to represent specific cone combinations. An increasingly popular

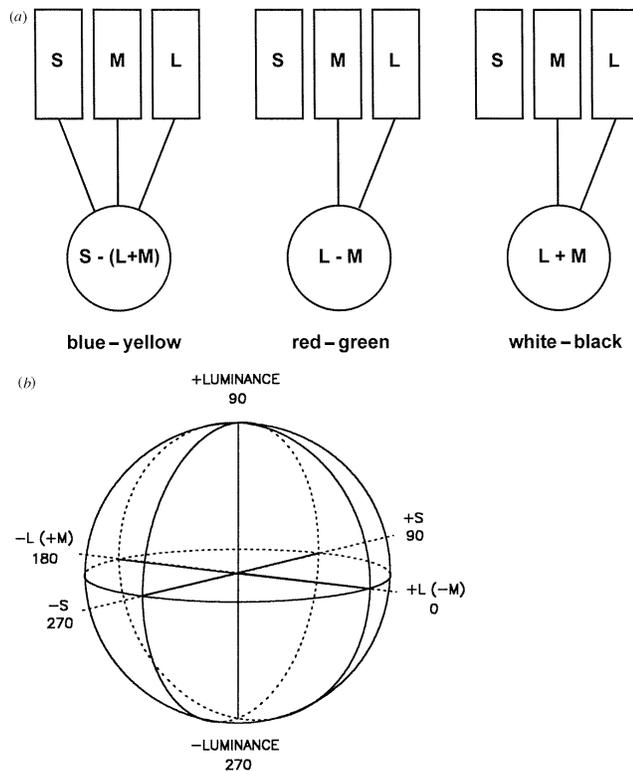


Figure 3. (a) A standard two-stage model of human colour mechanisms. Signals from the three cone types are recombined to form one luminance and two chromatic channels. (b) The cardinal axis colour space (after [47]). The origin is a medium-luminance white. Lights are represented relative to the origin as contrasts along three cone-combination axes. The $L - M$ and $S - (L + M)$ axes form a plane of constant luminance along which only colour varies (with saturation corresponding roughly to increasing distance from the origin, and hue to angle from the origin). The 'luminance' axis is an achromatic axis ($L + M + S$) along which only luminance varies, from dark (270°) to bright (90°).

representation is in terms of the three 'cardinal' axes of Krauskopf and colleagues [47, 88], which follows closely from a colour space proposed by MacLeod and Boynton [107]. In the cardinal axis space the two chromatic axes represent (i) opposing signals in the L and M cones ($L - M$), and (ii) signals in the S cones opposed by a combination of signals in the L and M cones, $S - (L + M)$. These are in fact the axes of the ancient and modern subsystems that were discussed above. The third axis is an achromatic axis ($L + M + S$) along which only luminance varies. (One drawback of such spaces is that there is no obvious metric for scaling signals along the different axes, as the luminance and chromatic axes represent qualitatively different stimulus dimensions. One approach is to scale the axes to equate the RMS cone contrasts along different dimensions. A second common approach is to scale the axes empirically so that the observer has equal sensitivity to stimulus changes along each direction, which is roughly the scaling adopted in the results presented here. Useful discussions of cardinal axis spaces are given in [26, 149]. A method for defining the $L - M$ and $S - (L + M)$ axes empirically is described in [172, 179].)

While the general framework of figure 3(a) captures some of the essential characteristics

of colour coding and continues to serve as a working model, it fails to account for many experimental results, and there is little agreement over its specific features. The following eight points look more closely at how colour information is organized within post-receptoral channels, by considering alternative models for this organization. The properties listed—some well established and others controversial—concern both the cone inputs to individual channels and the number of channels.

4.1. Spectral sensitivities of post-receptoral channels

Measurements based on colour appearance and colour sensitivity make different predictions about how the cones are combined within post-receptoral channels. Studies of threshold sensitivity and adaptation reveal chromatic channels organized along the two cardinal dimensions corresponding to $L - M$ and $S - (L + M)$ axes [23, 38, 87, 88, 94, 120, 137, 160, 176, 179]. These dimensions also appear to be orthogonal within the mechanisms underlying chromatic induction [147] and motion perception [90, 180], and characterize the average cone inputs to cells in the lateral geniculate [47]. However, the $L - M$ and $S - (L + M)$ axes differ from the red–green and blue–yellow dimensions of colour appearance. The discrepancy is largest for the red–green mechanism, as illustrated in figure 4(a). The visible spectrum appears red at both long wavelengths and short (because wavelengths shorter than unique blue appear purple, or red + blue). The triphasic spectral sensitivity for red–green is inconsistent with a mechanism that compares only the L versus M cones, and suggests instead that S cones add with L cones to contribute to redness [1]. Figure 4(b) illustrates this difference in a second way, by plotting the location of the four unique hues within the $L - M$ versus $S - (L + M)$ plane. The blue–yellow locus (which is the null for red–green sensations) falls along a negative diagonal, and thus along an axis that varies the responses in both of the cardinal mechanisms [88]. Similarly, the red–green locus (the null

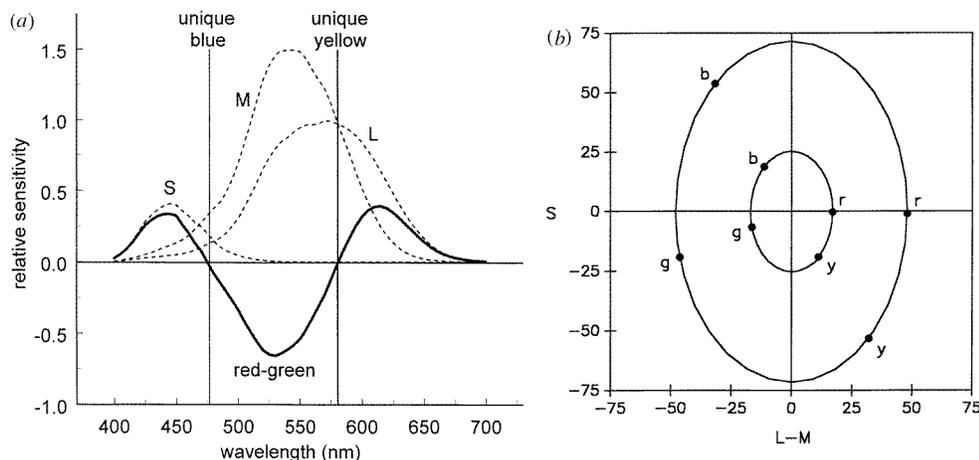


Figure 4. (a) Response of a ‘red–green mechanism’ to different wavelengths [1]. Middle wavelengths are perceived as green while both long and short wavelengths appear reddish, implying both L and S cone signals contribute to redness. Red–green sensations are nulled at two wavelengths that appear uniquely blue or yellow. (b) Unique hues measured at two contrasts, plotted as angles in the $L - M$ versus $S - (L + M)$ plane of figure 3(b) [179]. Stimuli that vary along either cardinal axis do not correspond to red–green or blue–yellow sensations (though for these measurements unique red falls close to the $+L$ axis).

for blue–yellow sensations) cannot correspond to the $L - M$ axis, because the loci for red and green are not collinear [31, 179], and, more generally, are inconsistent with any linear combination of the cones (see below).

Similar discrepancies are well known between luminance and perceived brightness. Luminance is the visual analogue of radiance, or the ‘visual effectiveness’ of light [101]. It can be measured by a variety of tasks based on nulling (e.g. of perceived flicker, motion or border distinctness) or thresholds (e.g. acuity or sensitivity). Most of these tasks reveal an additive spectral luminosity function, V_λ , that depends on a weighted sum of L and M cones (with a weak input from S cones revealed under some conditions [154, 158]). However, two stimuli with equal luminance may differ in perceived brightness, and brightness matches are not additive. Such observations have suggested that brightness reflects the outputs of both luminance and chromatic channels.

4.2. Nonlinearities

The visual system is highly nonlinear—mechanisms have thresholds and saturate, and responses can vary profoundly with adaptation. Two well known examples of nonlinearities in colour appearance are the Bezolde–Brücke effect, in which the perceived hue of most wavelengths varies with intensity [52], and the Abney effect, in which the perceived hue of most wavelengths changes when they are desaturated by the addition of achromatic light [31]. Such effects have suggested that the spectral sensitivities of post-receptoral channels depend on nonlinear combinations of the cone signals [93]. Yet for modest signals under a constant adaptation state, single-cell responses and psychophysical sensitivity are consistent with mechanisms that respond to simple sums or differences of the cone contrasts. This linearity allows a convenient characterization of the spectral sensitivity of any mechanism within a colour space defined by orthogonal cone combinations—sensitivity varies as the cosine of the mechanism’s preferred direction, and is zero for a ‘null-plane’ of points orthogonal to the preferred axis [47].

4.3. Spatial–colour coupling

In ganglion and geniculate cells colour opponency is linked to the spatial organization of the receptive field. Specifically, the antagonistic cone inputs are segregated into spatially antagonistic centre and surround subregions over which the cell pools its signals. For example, figure 5 illustrates a cell that receives opposing L and M inputs through the centre and surround. (For many cells the centre is fed by only a single receptor. It is unclear whether the surround input is from a single class of cones or is undifferentiated [99, 133].) This organization gives rise to different spatial tuning functions for luminance ($L + M$) and chromatic ($L - M$) contrast [46, 77]. For luminance the centre and surround are antagonistic and the response is bandpass. For colour the centre and surround are instead synergistic and the response is lowpass, paralleling the psychophysical contrast sensitivity functions (figure 5(c)). As a result the response in individual cells confounds information about luminance and colour.

4.4. Multiple post-receptoral stages

If early post-receptoral mechanisms are organized in terms of the $L - M$ and $S - (L + M)$ dimensions, this leaves the question of why the unique hues are such salient dimensions of our perceptual experience of colour. Two very different answers have been suggested. One is that the unique hues are not in fact tied to special states of neural activity (i.e. to the nulls of colour-opponent mechanisms) but are instead related to prominent properties of the visual environment, such as normalization to the average white [129]. An alternative suggestion

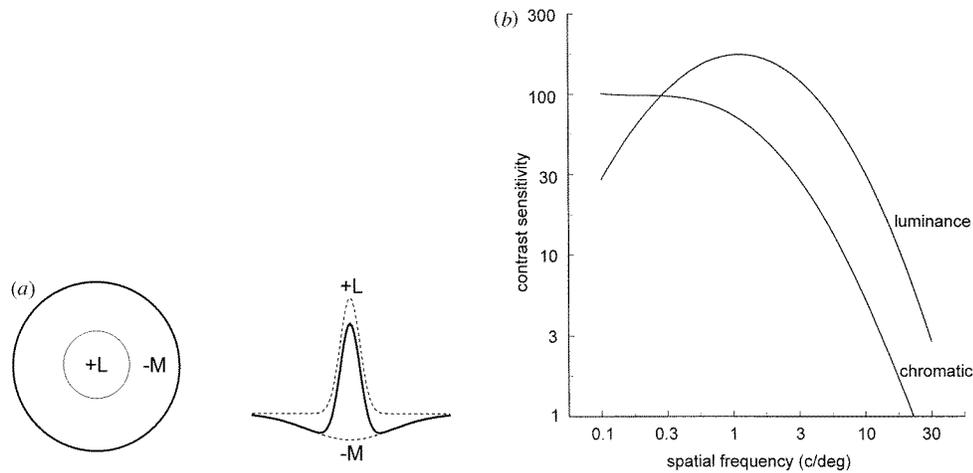


Figure 5. (a) Receptive field of a hypothetical cell in the parvocellular LGN. The opposing cone inputs are segregated into centre and surround with different spatial extents. As a result the cell exhibits spatial opponency and bandpass tuning for luminance, while spatial synergism and low-pass tuning for colour [46]. (b) Psychophysical measurements of spatial contrast sensitivity similarly reveal spatially bandpass tuning for luminance while spatially lowpass tuning for colour [116].

is that the second-stage mechanisms are recombined to form 'third-stage' mechanisms whose spectral sensitivities do agree with the unique-hue axes [45, 70]. However, beyond phenomenological observations the evidence for this specific transformation remains lacking.

A related problem concerns the separation of luminance and chromatic signals. As noted above, most geniculate cells respond to both luminance and chromatic contrast but with different spatial sensitivities, yet psychophysically luminance and chromatic contrast and colour versus spatial sensitivity appear to be separable stimulus dimensions [127]. Schemes have been proposed for recombining the geniculate cells to yield pure luminance or pure chromatic mechanisms [45, 51, 117] but such transformations have yet to be clearly confirmed in single unit studies. It is likely that colour coding in the striate cortex is, in fact, very different from the organization found in the LGN, but results from physiological studies have varied widely [98].

4.5. Multiple colour–luminance mechanisms

If trichromacy holds in the cones then this necessarily limits colour vision to be three dimensional, but does not limit the number of possible ways that post-receptoral mechanisms might recombine the cone signals. Many phenomena in colour vision, from colour naming to threshold contours for different colour–luminance directions, can be parsimoniously accounted for by assuming only three post-receptoral channels. Yet most such results could also be explained by assuming multiple colour–luminance mechanisms, each tuned to a different colour–luminance axis. There are now results from a variety of different paradigms showing that sensitivity can be selective for more than three fixed directions within colour–luminance space, suggesting either that there are multiple mechanisms or that the mechanisms can change their tuning properties depending on the specific experimental conditions [50, 59, 69, 87–90, 92, 176, 178, 179, 190, 191].

Physiologically, the true discreteness of the cone pigments stands in marked contrast to the variability in the spectral sensitivities of post-receptoral neurons [43, 47, 192]. The

preferred directions of cells in the parvocellular LGN are strongly clustered along the $L - M$ and $S - (L + M)$ axes, but there are nevertheless substantial differences in the cone inputs to individual cells, and wide variability in the elevation of preferred direction out of the equiluminant plane. Moreover, in the striate cortex any bimodality in the chromatic preferences appears to be much weaker [100]. This variability poses a problem for models that attempt to construct three discrete psychophysical channels out of mechanisms defined physiologically, and in fact offers an alternative to such models. For example, it may never be that pure luminance and chromatic mechanisms are explicitly built out of parvocellular LGN cells, since the perceptual phenomena that have suggested this transformation might be equally consistent with the pattern of responses across a population of varied cells.

The evidence for multiple colour–luminance mechanisms calls into question a fundamental assumption of three-channel models of colour vision—that stimulus variations along some axes isolate the responses of only a single post-receptoral channel. Axes can be chosen so that they are visible only to a single class of cone, but if there are more post-receptoral colour channels than cone types then there will always be more than one channel encoding the axis (with the implausible exception that preferred directions for all but one of the channels are confined to a single plane). This complicates the interpretation of studies that seek to examine the properties of ‘isolated’ channels, as in the many studies that have sought to isolate pure chromatic or luminance mechanisms [102] (though isolation might still be possible near threshold if only the most sensitive channel is responsive). Multiple channels are also inconsistent with the specific notion that unique hues reflect the nulling stimuli for individual channels, and thus add further to questions about the true substrate of colour sensations [89].

Multiple colour channels also have important implications for models of colour vision based on coding efficiency. If the number of post-receptoral cone combinations is greater than the number of cone types then there will always be some redundancy in the responses of post-receptoral channels if colour is considered in isolation. However, as noted above, colour coding is coupled to the spatial properties of receptive fields, and thus a complete account of decorrelation would also require consideration of the spatial redundancies between the channels [6, 7].

4.6. On–off pathways and rectification

Physiological recordings showed early on that a single class of cell (e.g. ‘L versus M’) must include distinct subtypes [43]. Cells that receive opposing L and M cone inputs could be either L excitatory/M inhibitory (+L/–M) or vice versa (–L/+M). In turn these two subtypes could be divided according to whether the centre or surround of the receptive field was excitatory. (In contrast, S cone inputs are more frequently excitatory and centre and surround sizes may be coextensive [65, 98]). The subclasses for colour-opponent cells follow an earlier distinction between on-centre and off-centre cells for luminance. These gave rise to the notion that increments and decrements are encoded by distinct on- and off-pathways acting in parallel. Psychophysical evidence for separate on and off channels includes the fact that sensitivity to increments and decrements may have different spatial and temporal profiles and can be affected selectively by adaptation [57]. Similarly, it is possible to selectively adapt to opposite directions along chromatic axes [88, 91], and separate red and green mechanisms have been argued for from differences in how these colours change with eccentricity [2, 161].

Ganglion and geniculate cells have high spontaneous firing rates and thus can signal both increases and decreases in activity. In comparison, cortical cells have low resting activity,

so that they can primarily respond only through excitation [44]. This half-wave rectification suggests that the cone opponency within single cells of the LGN is instead represented in the cortex in terms of different populations of cells [45, 102]; the mirror-image pairs of opponent cell types in the LGN (e.g. +L/−M and +M/−L) may be necessary precursors for these polarity-specific cells in the cortex.

4.7. Multiple contrast mechanisms

Just as there may be multiple mechanisms tuned to different axes within colour–luminance space, and to opposite poles of a single axis, there may be multiple mechanisms representing the signals *along* a single axis. Specifically, individual channels might respond to limited but overlapping contrast ranges, either because they have different contrast sensitivities and/or because their null points vary along the axis. Multiple mechanisms centred on different contrast levels have been proposed previously for the encoding of luminance [4, 61]. Below we will consider evidence from adaptation which might point to a similar basis for contrast coding along chromatic axes.

4.8. Multiple visual pathways

Beginning with the cones, the different cell types involved at each stage of colour vision are designed to extract in parallel different information about the spectral qualities of light. These channels are in turn part of parallel subsystems that encode different properties of the visual stimulus (e.g. different spatiotemporal ranges of the stimuli, or different stimulus features, such as movement or colour [102, 113, 139, 144]). Within these different subsystems the signals from the cones may be combined very differently. Two principal subsystems identified in the primate retinocortical projection are the magnocellular and parvocellular pathways (M and P, named for the different layers of the geniculate through which they project). M and P cells differ on a number of dimensions, but in the present context the most important are that M cells exhibit only weak colour opponency and are the likely substrate of conventional measures of luminance sensitivity measured with rapid flicker or motion [95]. In contrast, P cells are strongly colour-opponent, respond well to both luminance and colour, and are the likely pathway for colour and brightness appearance.

The fact that different pathways may draw on the cone signals in different ways demands caution in comparing the colour organization implied by results from different experimental paradigms. For example, Webster and Mollon [178] showed that different measures of the luminous efficiency of lights can be biased by adaptation in different ways, and this may arise in part because the alternative measures depend on different subsystems that have different sensitivities to luminance and chromatic contrast. Even a single response measure might reflect the influence of multiple pathways. For example, if luminance and chromatic thresholds are limited by separate subsystems, then the threshold contours for different directions within a luminance–chromatic plane might reveal more about the differences between the two subsystems than the organization of colour within either subsystem, and both might have little in common with the organization underlying the colour appearance of suprathreshold lights.

5. Adaptation and colour vision

We have sketched some of the possible coding schemes in the early visual analysis of colour. Yet one of the most remarkable properties of visual coding is that it changes (or adapts) its properties in response to the specific properties of the prevailing stimulus. These adjustments allow the visual system to follow and tune for the ever-varying characteristics of the visual environment. Studies of these adaptational adjustments have proven to be one of the most powerful tools for probing the nature of visual mechanisms. Yet the nature of adaptation is also of great importance in its own right, because it is central to an understanding of the kinds of information that the visual system is designed to extract, and because its properties determine the capacities and limits of our perception.

In thinking about adaptation in the context of colour vision, it is instructive to consider that the colour of any stimulus can be decomposed into two components: the overall mean colour, and the variations in colour relative to the mean. These two components are tied to two fundamentally different forms of visual adaptation. Light adaptation adjusts

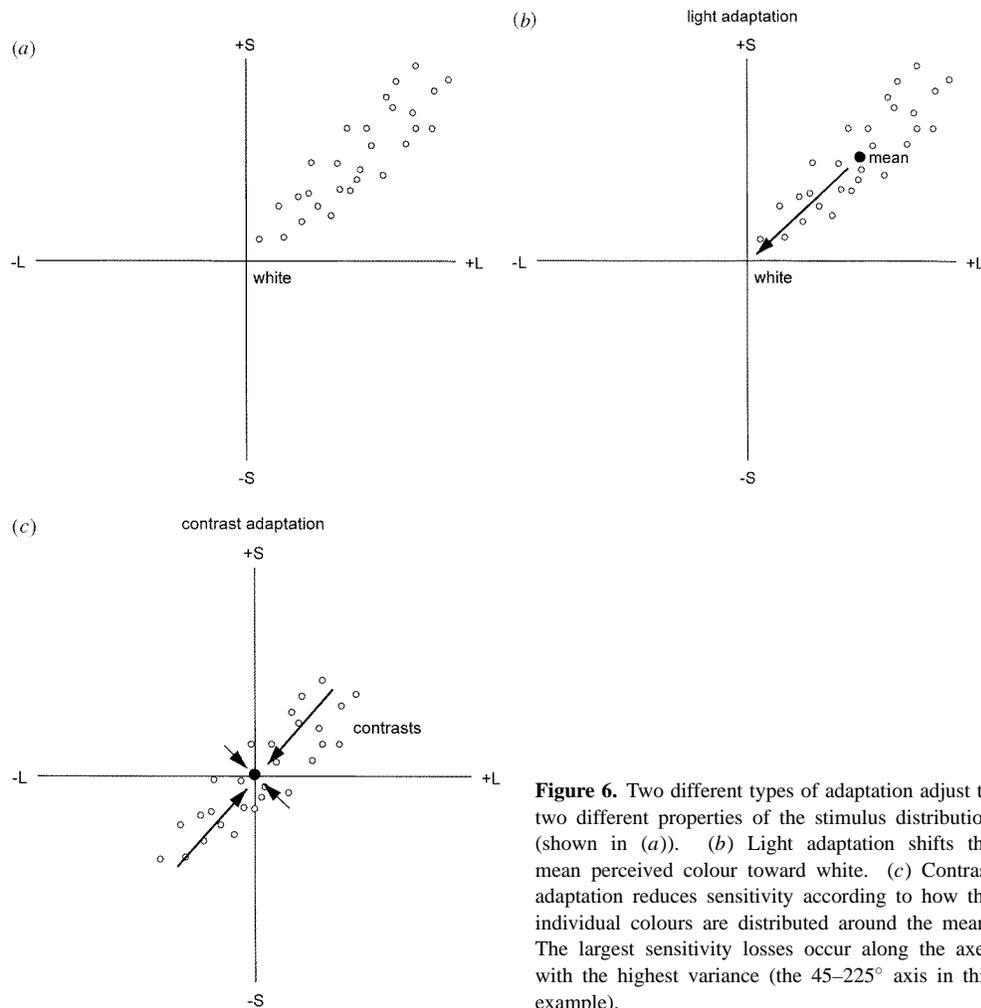


Figure 6. Two different types of adaptation adjust to two different properties of the stimulus distribution (shown in (a)). (b) Light adaptation shifts the mean perceived colour toward white. (c) Contrast adaptation reduces sensitivity according to how the individual colours are distributed around the mean. The largest sensitivity losses occur along the axes with the highest variance (the 45–225° axis in this example).

sensitivity to the mean luminance and chromaticity averaged over some time and region of the image, and produces mean shifts in colour perception. Contrast adaptation adjusts sensitivity according to how the ensemble of luminances and chromaticities are distributed around the mean, and instead alters colour appearance by changing the perceived contrast along different directions in colour space (figure 6). In the following sections we review the general characteristics of these two distinct forms of visual adjustment and then consider in detail how they combine to influence colour perception.

6. Light adaptation

That our vision adjusts to the ambient light level is common knowledge. Several minutes may be required to adapt to a dark theatre, and stars disappear against the background of daylight. The dependence of visual sensitivity on average light level can be characterized by measuring the minimum light increment visible on backgrounds of different intensities. Figure 7 shows an example of these threshold-versus-intensity (TVI) curves. Vision is limited in the dark by the absolute threshold of the system, but becomes progressively desensitized as the background intensity increases. For large fields and long flashes the slope of the curve is close to 1.0, so that the just-visible increment is a constant proportion of the background level and thus represents constant sensitivity to contrast (i.e. $\Delta I/I = \text{constant}$, known as Weber's law). However, thresholds for short, brief flashes yield shallower slopes that instead approach a limit of 0.5 [10].

In a classic series of experiments Stiles [153] measured TVI curves for tests and backgrounds that differed in wavelength. Figure 8 shows an example of these 'two-colour thresholds', for the case of a 475 nm test on a 550 nm background. The threshold follows the normal TVI curve but then there is a break followed by a new plateau from which the threshold rises again. The two branches suggest that thresholds are limited by two different mechanisms with different spectral sensitivities. While we will see below that the interpretation of these curves is more complex, we can understand the general flavour of

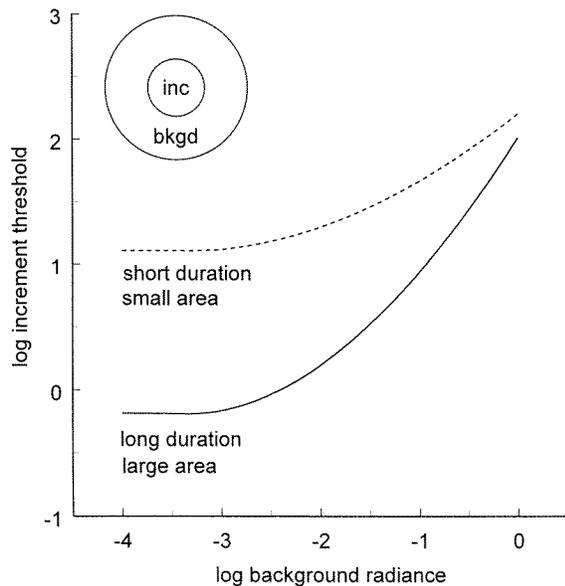


Figure 7. Threshold-versus-intensity (TVI) curves illustrate losses in sensitivity resulting from light adaptation as the background light level increases [10]. However, sensitivity to contrast ($\Delta I/I$) is maintained (large stimulus) or improved (small stimulus).

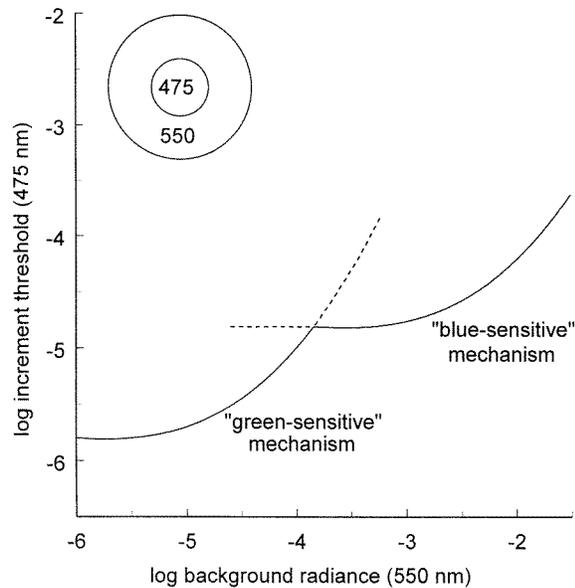


Figure 8. Two-colour thresholds. The TVI curve for a blue (475 nm) test on a yellow-green (550 nm) background reveals two branches reflecting light adaptation in different colour-selective mechanisms [152].

these results by reference to the pigment sensitivities in figure 2. Due in part to their sparsity the S cones have a much higher threshold than the L and M cones, so that in the dark the M cones are most sensitive to the 475 nm test and limit threshold. Yet the L and M cones are also much more sensitive to the 550 nm background, so that as background intensity rises they adapt more than the S cones. Eventually the greater adaptation of the M cones renders them less sensitive to the test, and the thresholds then follow the TVI curve for the S cones. By analysing a large combination of tests and backgrounds Stiles showed that to a first approximation the thresholds could be accounted for by independent adaptation in a small set of 'pi mechanisms'. The TVI curves for individual mechanisms have a constant shape, but are shifted vertically or horizontally depending on their sensitivity to the test or background wavelength, respectively.

The two-colour threshold experiments show that light adaptation is selective for the chromatic properties of the stimulus (and in this context is referred to as chromatic adaptation). Suppose this selectivity arises because light adaptation occurs independently within each class of cone. A specific formulation of this hypothesis is known as von Kries adaptation: adaptation adjusts responses in the three cone types separately and is equivalent to multiplying their fixed spectral sensitivities by a scaling constant [168]. If the scaling weights (von Kries coefficients) are inversely proportional to the absorption of light by each cone type, then von Kries scaling maintains a constant mean response within each cone class. For example, a red adapting light might stimulate the L cones more than a green light, but adaptation to the red light will be proportionately greater so that after complete von Kries adaptation the average response to the two lights is the same. We will see below that this provides a simple yet powerful mechanism for maintaining the perceived colour of objects despite changes in illumination. Under a number of conditions von Kries scaling provides a good account of the effects of light adaptation on colour sensitivity and appearance (e.g. [27, 35, 177]). Yet it does not provide a complete account.

Early measurements of chromatic adaptation and colour appearance suggested that the colour changes could be complex and could not be explained by receptor changes alone [189]. In terms of sensitivity, the pi mechanisms identified by Stiles cannot reflect

independent cone types, because more than three were required to account for all conditions, and the spectral sensitivities are broader than estimates for individual cones (though under certain conditions the curves for some pi mechanisms closely approximate receptor spectral curves). Pugh and Mollon [131] showed that the different short-wavelength pi mechanisms could be explained by assuming two sites of S-cone adaptation—one cone specific and the second resulting from polarization in opponent channels. Polarization effects also occur under conditions where detection is mediated by L and M cones [23, 157]. This second-site adaptation is consistent with a variety of chromatic adaptation phenomena (e.g. additivity failures for adapting backgrounds and ‘transient tritanopia’, an increase in short-wavelength threshold when long-wave backgrounds are turned off) [131], and is a major source of evidence for colour opponency.

A related shortcoming of von Kries adaptation is that it explains only part of the way in which the visual system adjusts to adapting backgrounds [146]. In addition to setting the gain of the visual system, backgrounds also add light physically to any increment presented on them. However, large, steady backgrounds have much less effect on colour appearance than would be predicted from the added light. For example, suppose a light that appears unique yellow is flashed as a spot on a large red background. The background may add some redness to the flash, but much less than predicted by the physical mixture. Thus the colour appearance depends much more on the light coming from the flash than from the background. To a large extent the visual system discounts or subtracts out the background so that the response is primarily to spatial and temporal transients.

The work of several authors has led to a detailed account of how multiplicative and subtractive processes combine to control visual sensitivity (see [169]). The different processes are revealed psychophysically by elaborating on the threshold-versus-intensity experiment to measure—for each single adapting background—the threshold for detecting a probe superposed on brief flashes that vary over a range of intensities. Figure 9 shows a model of the visual responses to the probe and backgrounds and how these are manifest in the measured probe–flash curve. The curves are generated by assuming that the threshold for the probe represents a fixed increment in response above the response to the flash. At any given adaptation level the dynamic range of the visual system is limited and follows a compressive nonlinearity. Thus in the dark (no background) the incremental response to the probe becomes progressively weaker as the flash intensity increases, and the response eventually saturates. If the visual system did not adapt, then adding a steady background would simply add a baseline response, compressing the dynamic range available for signalling the flashes. Backgrounds could thus greatly reduce sensitivity by themselves saturating the system. However, multiplicative adaptation restores part of the dynamic range by attenuating the response to both the background and the flashes, an effect equivalent to shifting the dynamic range by placing neutral density filters or ‘dark glasses’ [106] in front of the eyes. Subtractive processes further restore the dynamic range available for flashes by selectively attenuating the response to the background, an effect equivalent to high-pass filtering. If the background is discounted completely then the full response range is preserved for signalling the flashes, and the background serves only to set the gain of the system. This two-stage theory also provides a good account of how simple adapting backgrounds affect the perceived colour and brightness of lights [80, 182, 185].

The processes of light adaptation occur primarily within the retina [145]. At high light levels one form of multiplicative adaptation is provided by photopigment bleaching, which scales photon capture in the receptors and is in fact the mechanism that protects the cone response from saturating at bright backgrounds. (The rod system saturates below intensities

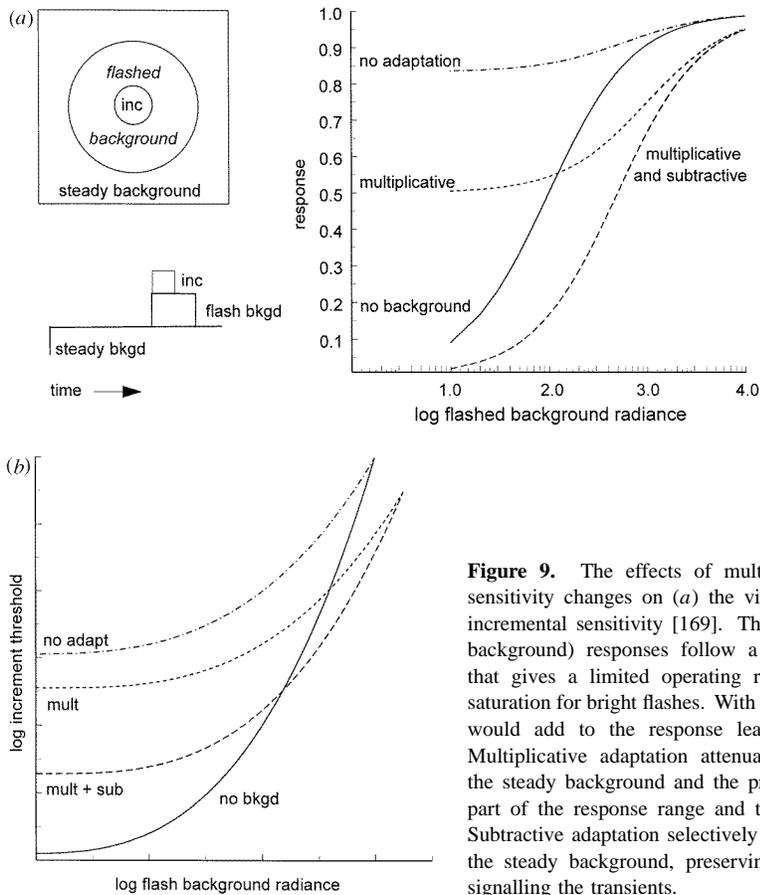


Figure 9. The effects of multiplicative and subtractive sensitivity changes on (a) the visual response and (b) the incremental sensitivity [169]. The dark-adapted (no steady background) responses follow a compressive nonlinearity that gives a limited operating range leading to response saturation for bright flashes. With no adaptation backgrounds would add to the response leading to rapid saturation. Multiplicative adaptation attenuates the response to both the steady background and the probe and flash, recovering part of the response range and thus increasing sensitivity. Subtractive adaptation selectively attenuates the response to the steady background, preserving the response range for signalling the transients.

where bleaching becomes important.) However, sensitivity changes are pronounced at light levels too low to produce significant bleaching. The site of this neural gain control is uncertain. At least some gain changes are largely cone-specific (e.g. [33, 35, 177]) and the adaptation appears to pool signals over areas no larger than the diameter of individual cones [36, 108]. Both results point to an early locus of light adaptation that may be as early as the receptors, as also suggested by electroretinogram measurements [142]. However, adaptation within individual cones is not well established physiologically, and appears to be too weak to account for psychophysical changes in sensitivity [140]. Moreover, there appears to be more than one site of multiplicative scaling. Some of the gain changes are extremely rapid while others take seconds or even minutes to asymptote [54, 72]. These may have different time constants for luminance and chromatic stimuli, thus pointing to post-receptor sites.

There also appears to be more than one process underlying subtractive adaptation. Spatial subtraction is consistent with the centre-surround antagonism of retinal cells, which filters out the response to large uniform areas and thus emphasizes spatial transients [73]. Visual acuity is better at brighter light levels, and this suggested that receptive field properties might adapt to different light levels (with surround strength increasing at higher intensities). However, these differences can also be explained by purely local light adaptation [34] or by detection within different spatially selective channels [86]. If spatial subtraction does

depend on static receptive field profiles then it is not a form of adaptation in the strict sense of this review (because it would not reflect a *change* in response properties). However, there is also a form of temporal subtraction that leads to a loss in response to the steady-state background over time. Unlike spatial subtraction, which is very rapid, this temporal subtraction requires many seconds to asymptote [74].

7. Contrast adaptation

As figure 6 illustrates, beyond light adaptation there is a second general form of perceptual adaptation that adjusts sensitivity to contrast. Individual examples may differ in their specific characteristics and thus involve different processes, but as a class contrast adaptation effects share the property that they reflect adjustments to the structure or pattern in the stimulus. This structure may refer to the spatial or temporal properties of the stimulus (e.g. the orientation of a grating or the direction of movement) or—as we focus on in this review—to the colour properties of the stimulus. Blakemore and Sutton [20] noted that exposure to the adapting pattern can cause four general classes of after-effects: (i) contrast thresholds for detecting similar patterns are elevated; (ii) above threshold the apparent contrast of similar patterns is reduced; (iii) stimuli that differ from the adapting pattern are distorted in appearance away from the adapting stimulus and (iv) a ‘neutral’ test stimulus may appear to take on the complementary property of the adapting stimulus. Examples of the perceptual distortions induced by adaptation include the tilt after-effect (in which viewing an oblique line causes a vertical line to appear tilted in the opposite direction [62]), classical figural after-effects (e.g. changes in the perceived shape of simple patterns [85]) and shifts in perceived size or spatial frequency [20]. An example of a complementary after-effect is the motion after-effect, in which adaptation to rightward motion causes a stationary object to appear to drift to the left [188]. Contrast adaptation can occur even when the adapting stimulus is itself near threshold or is viewed only briefly, and after-effects are readily induced by exposure to natural stimuli (e.g. [85, 174]). This suggests that while its effects may be more subtle, contrast adaptation—like light adaptation—exerts a ubiquitous influence on perception.

In most experiments on contrast adaptation, observers are first exposed to the adapting stimulus for a short period (usually from a few to several minutes). The stimulus is then turned off and a test stimulus presented briefly (usually less than 1 s). The long exposure and then removal of the adapting stimulus prior to testing is what distinguishes adaptation from masking paradigms [66]. Masks alter sensitivity to test stimuli by changing the response level of the visual system, whereas the contrast adaptation stimulus is thought to instead change the ‘responsiveness’ of the system, without producing its own response during the test. To maintain a constant state of adaptation, it is common to interleave repeated tests with brief re-adaptation intervals (usually several seconds). Most adaptation effects build up rapidly with only a few minutes exposure, and may decline exponentially when the adapting stimulus is removed (e.g. [67]). However, some after-effects can show very long persistence if observers are not readapted to a competing stimulus [156].

The after-effects of contrast adaptation reflect a selective loss in sensitivity to the adapting stimulus. Thus adaptation to a vertical, 2 c/deg luminance grating will reduce sensitivity to similar patterns but in general would have little influence on the thresholds for stimuli that differed by more than 45° from vertical [63], or whose spatial frequency was more than about 1 octave above or below 2 c/deg [18], or for stimuli that varied in colour rather than luminance [25]. Selective adaptation has been well established for each of the primary attributes of visual stimuli (i.e. form, motion, depth and colour). The adaptation is

also specific to retinal location, but not to the pattern of activity in individual cones. In fact, for spatial adapting patterns it is a frequent procedure to move the stimuli over the retina (or ask observers to move their eyes over the stimulus) in order to avoid afterimages due to local light adaptation. The common interpretation of contrast adaptation is that it reflects sensitivity changes in channels tuned to specific features of the visual stimulus, and that the specificity of the adaptation gives a measure of the tuning function. Indeed, in the majority of studies involving contrast adaptation, the adaptation itself is of little direct interest and instead serves only as a tool for probing the selectivities of visual channels.

While much of the adjustment in light adaptation appears to occur in the retina, three sources of evidence point to a cortical locus for contrast adaptation. First, most contrast adaptation effects show significant interocular transfer (so that adapting with one eye affects sensitivity for targets viewed with the other eye) and signals from the two eyes first converge in the striate cortex [17]. Second, the selectivity of the after-effects parallels the receptive field properties of cortical cells. For example, the striate cortex is the first level of the primate visual system to exhibit directional selectivity and strong orientation selectivity, implying that the cortex is the site of motion and tilt after-effects. Third, physiological studies have found strong response changes in cortical cells as a result of prior exposure to contrast, yet little evidence for contrast adaptation in geniculate cells [3, 109, 124, 138, 141]. While these results all point to the striate cortex as the earliest likely site for contrast adaptation, they do not preclude a role in adaptation of more central, extrastriate areas [126, 184].

In general, higher-contrast adapting stimuli lead to larger sensitivity losses, and tend to have larger effects on lower-contrast test stimuli. Yet the specific form of the response change is not well defined, and may vary considerably with the specific task. One way to examine the form of the sensitivity change is to measure the changes in apparent contrast over a range of test contrasts. Figure 10(a) shows results from Blakemore *et al* [19]. Adaptation to a high-contrast luminance grating lowered perceived contrast, but only for test gratings with physical contrasts lower than the adapting contrast. The sensitivity losses are intermediate to the contrast changes predicted by a subtractive or multiplicative change in apparent contrast, and instead closely follow a power function (i.e. on log–log axes the main effect of the adaptation is to change the slope of the line relating the match and test contrasts). Webster and Mollon [179] obtained similar results following adaptation to chromatic contrast, presented as a temporal modulation in a uniform field (figure 10(b)). However, at lower *adapting* contrasts the changes in apparent contrast may more closely approximate a subtractive change [61], and again this pattern appears similar for luminance and chromatic contrast [171].

A second method for exploring the response changes is by examining how contrast adaptation alters the ability to discriminate changes in contrast. In analogy with the probe–flash paradigm, this typically involves measuring for spatial gratings the incremental contrast (probe) as a function of pedestal contrast (flash) after adapting to contrast (background). However, unlike studies of light adaptation, the adapting stimulus is typically turned off before each presentation of the test stimulus. Before adaptation, contrast discrimination is characterized by a ‘dipper’ function with facilitation near threshold and decreasing sensitivity above threshold that follows a power function (with exponents between 0.5 and 1.0) [97]. Numerous studies have examined how this function is changed by adaptation, but results have varied widely (e.g. [14, 68, 104, 134, 187]; see also [143] for analogous measurements for temporal contrast). Figure 11(a) shows results from Webster *et al* [171] for either luminance or chromatic gratings. The contrast discrimination functions are very similar for luminance and colour [163], and prior adaptation affected both functions in similar ways—by elevating discrimination thresholds at low pedestal contrasts but not at moderate to high

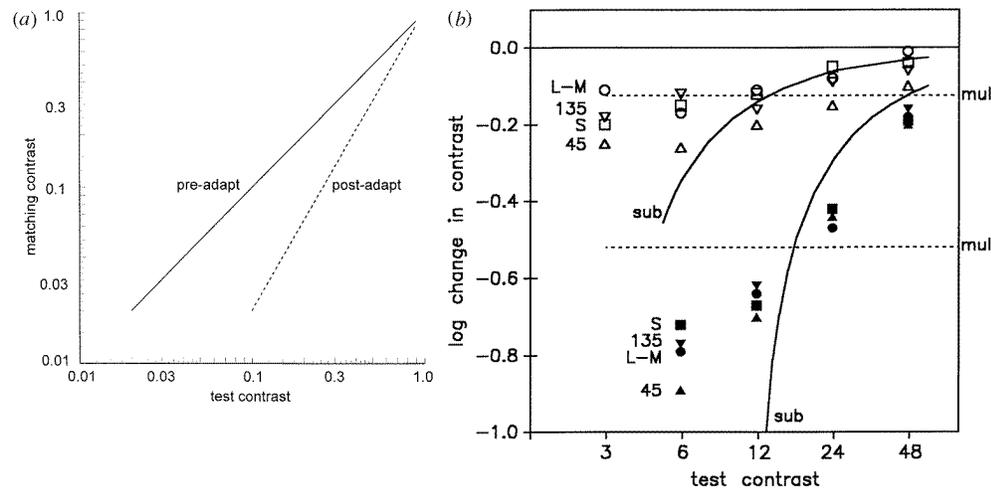


Figure 10. (a) Apparent contrast of spatial gratings as a function of physical contrast, after adapting to a high contrast grating [19]. (b) Changes in perceived contrast of chromatic stimuli, after adapting to temporal modulations along different chromatic axes [179]. Full symbols show contrast losses along the adapting axis, open symbols along the orthogonal colour direction. For both the spatial and temporal contrast, the effects of adaptation on perceived contrast are proportionately larger for lower test contrasts.

contrasts.

Webster *et al* [171] also measured how contrast adaptation influenced contrast discrimination when the test, mask and adapting grating could each be defined by either luminance contrast or chromatic contrast. Thresholds for chromatic contrast are strongly affected by the presence of a luminance pedestal, and vice versa, yet there is little cross adaptation between luminance and chromatic gratings [25, 163]. Thus stimuli could be chosen so that adaptation affected only the pedestal or only the test. (For example, for chromatic tests on luminance pedestals, luminance adaptation altered sensitivity to the pedestal contrast while chromatic adaptation altered sensitivity to the test.) The results, shown in figures 11(b) and (c), suggested that adaptation had little effect on high (pedestal) contrasts (thus resembling a subtractive sensitivity change), but approached a multiplicative change at very low (test) contrasts, and this is qualitatively consistent with the effects of adaptation on perceived contrast. The results also suggest that contrast adaptation occurs at or prior to the site of the simultaneous interactions between luminance and colour, thus supporting a cortical locus for the simultaneous interactions. (For example, if the facilitation of colour thresholds by luminance pedestals (figure 11(b)) occurred prior to the site of the adaptation, then reducing sensitivity to the luminance pedestal by luminance adaptation should not have altered the colour thresholds.)

8. Contrast adaptation and colour appearance

Contrast adaptation was first used to explore the mechanisms of colour vision by Krauskopf and colleagues [88, 89] and Guth and colleagues [16, 69, 71]. Krauskopf *et al* [88] measured the thresholds for detecting brief changes in the colour and luminance of a white field after adapting to temporal modulations of colour and luminance in the field. (For example, during adaptation observers viewed a field that might slowly flicker in luminance or colour (e.g.

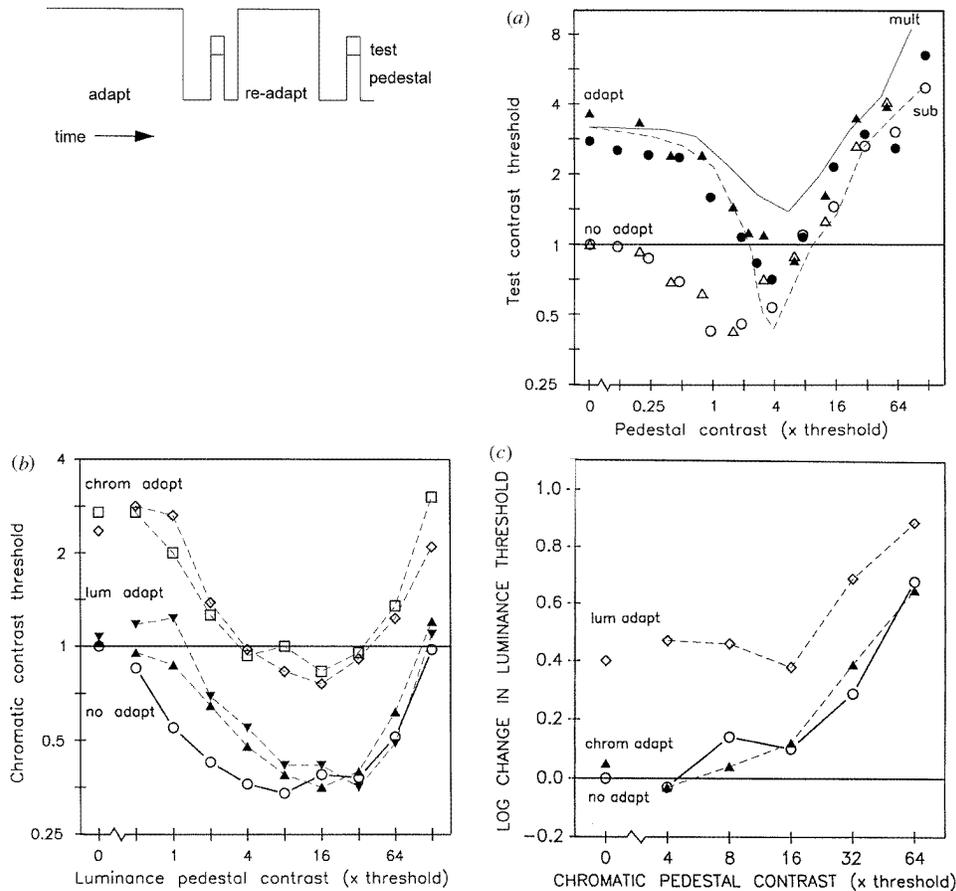


Figure 11. Contrast discrimination before or after contrast adaptation, measured with spatial gratings [171]. The three panels plot the contrast thresholds for a test grating superposed on a pedestal grating, before or after adaptation to a grating. Different panels plot the results when each component (adapt, pedestal or test) was either a luminance grating or a colour grating. (a) Adapt, pedestal and test gratings were all luminance (circles) or all chromatic (triangles). Before adaptation thresholds follow a dipper function that is similar for luminance and colour [163]. Adaptation raises the threshold at low pedestal contrasts but not at high. Lines plot the changes predicted by a subtractive (broken) or multiplicative (full) sensitivity change in the contrast response function. (b) Thresholds for detecting a colour grating superposed on a luminance pedestal grating. Moderate-contrast luminance pedestals facilitate colour detection (open circles) [163]. Adapting to a chromatic grating selectively affects chromatic sensitivity and raises thresholds on all pedestals by roughly a constant factor (open squares and diamonds, for two different contrasts of the adapting colour grating). Adapting to a luminance grating selectively affects luminance sensitivity and reduces the facilitation of colour tests by luminance pedestals, but only at low pedestal contrasts (full triangles, for two different contrasts of the adapting luminance grating). (c) Thresholds for a luminance test superposed on a chromatic pedestal show masking (open circles) [163]. Adaptation to a luminance grating raises thresholds for the luminance test (open diamonds) while adaptation to a chromatic grating does not alter the luminance thresholds (full triangles). The results for all conditions are consistent with similar but separable adaptation effects for luminance and colour that have weak effects on high contrast (pedestal) targets while strong effects that approach a multiplicative sensitivity change on very low contrast (test) targets.

along a reddish–greenish axis). The flicker was then briefly extinguished and test pulses of luminance or colour were presented in the same field. The sequence of re-adaptation and test was continued while observers set thresholds for detecting the test pulses.) The adapting modulations varied along different axes in colour–luminance space but all had the same average luminance and chromaticity, so that the state of light adaptation remained constant. Sensitivity losses were primarily selective for three adapting directions: the achromatic axis and the $L-M$ and $S-(L+M)$ chromatic axes. (For example, after adapting to modulations along the $L-M$ axis, thresholds were elevated for detecting colour changes along the $L-M$ axis, but not for changes along the $S-(L+M)$ or achromatic axes.) These directions were suggested previously to represent critical dimensions of colour vision (e.g. [23, 94, 107]), but the study of Krauskopf *et al* was central in establishing that these cardinal axes were basic

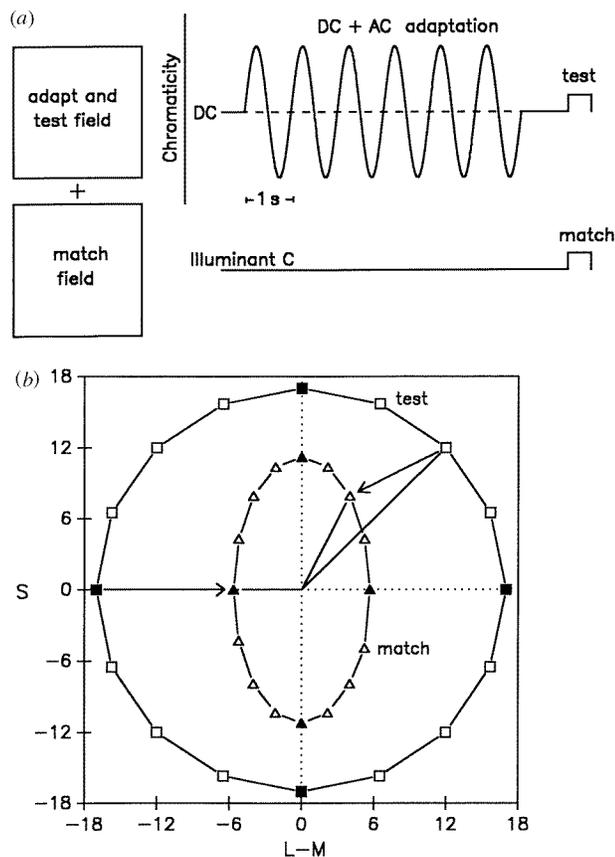


Figure 12. (a) Spatial and temporal arrangement of the asymmetric matching procedure used to examine contrast adaptation (AC) or the combined effects of light adaptation and contrast adaptation (DC + AC). (b) Colour changes in a set of test stimuli (squares) predicted by independent adaptation in two mechanisms tuned to the $L-M$ or $S-(L+M)$ axes [176]. Adaptation may desaturate tests (so that they are matched by stimuli that plot closer to the origin) but the largest and smallest changes should occur along the cardinal axes. Adapting the $L-M$ axis more should cause the perceived direction of all stimuli to rotate away from the $L-M$ axis and toward the $S-(L+M)$ axis. However, contrast adaptation to any axis should not alter the perceived direction of stimuli on either cardinal axis.

to the organization of colour in post-receptoral mechanisms. However, a second critical finding was that selectivity was not limited to these axes. Adaptation to intermediate axes tended to produce the largest threshold elevations along the adapting axis, and Guth [69] showed that perceived hue was always biased away from the adapting axis. Both results were inconsistent with sensitivity changes in only three channels tuned to fixed directions in colour space.

Webster and Mollon [176, 179] extended the adaptation paradigm of Krauskopf *et al* to examine how contrast adaptation influences suprathreshold colour appearance. In their studies observers adapted to modulations in a 2° test field placed to one side of a fixation point. Brief test stimuli were then interleaved with the adapting modulations, and were matched by adjusting the colour and luminance of a matching stimulus, presented simultaneously with the test but in a neutral matching field placed on the other side of fixation (figure 12(a)). To illustrate how contrast adaptation can be used to explore the properties of colour channels, consider the changes in colour appearance predicted by independent gain changes in only two chromatic channels tuned to the L–M and S–(L+M) axes (figure 12(b)). Adaptation could reduce perceived contrast ('saturation') by reducing sensitivity in one or both of the channels. However, the contrast losses should always be greatest or least along the L – M or S – (L + M) axes (depending on which channel is adapted more). Most stimuli produce responses in both of the channels. Adaptation could change the perceived direction ('hue') of these stimuli whenever it reduced the response in one channel more than the other; perceived hue should always rotate away from the axis of the more strongly adapted channel and toward the axis of the less strongly adapted channel. Note these hue changes are analogous to tilt after-effects, because they represent tilts in the perceived orientation of axes within colour space. However, stimuli that differ from the white background only along the L – M or S – (L + M) axes might appear desaturated but should not change in perceived direction, because these stimuli isolate a single channel and thus adaptation could not change the *relative* responses to these stimuli across the two channels.

Figure 13 shows the actual colour changes produced by adaptation to eight different directions within the equiluminant plane. Each panel plots the matches to the same set of test stimuli after adapting to modulations along two different axes, 90° apart. In each case the saturation losses are largest along the adapting axis, and weakest along an axis approximately 90° away. Thus adaptation produces changes in perceived contrast that apparently can be selective for any chromatic direction. Similar selective changes were found when the adapting and test stimuli varied in both colour and luminance, even when the chromatic variations were chosen to modulate signals only in the S cones. Thus the adaptation effects can show clear selectivity for how luminance contrast and S-cone contrast covary, even though S cones make little contribution to conventional measures of luminance sensitivity. The sensitivity changes produced by contrast adaptation are thus clearly inconsistent with models of colour vision that assume only three discrete post-receptoral channels that adapt independently.

Figure 14 illustrates how adaptation altered the perceived direction of the test stimuli. Figure 14(a) plots the angular difference between each test and its matching coordinates following adaptation to modulations along a single adapting axis (L – M), while panels (b)–(e) show the effects of different adapting directions on a single test direction along the L – M or S – (L + M) axes. In each case the appearance of test stimuli is shifted away from the adapting axis and toward a second axis approximately 90° away from the adapting axis, consistent with a selective sensitivity loss along each adapting axis. By comparing the curves it is evident that there is no test axis whose direction remains invariant across

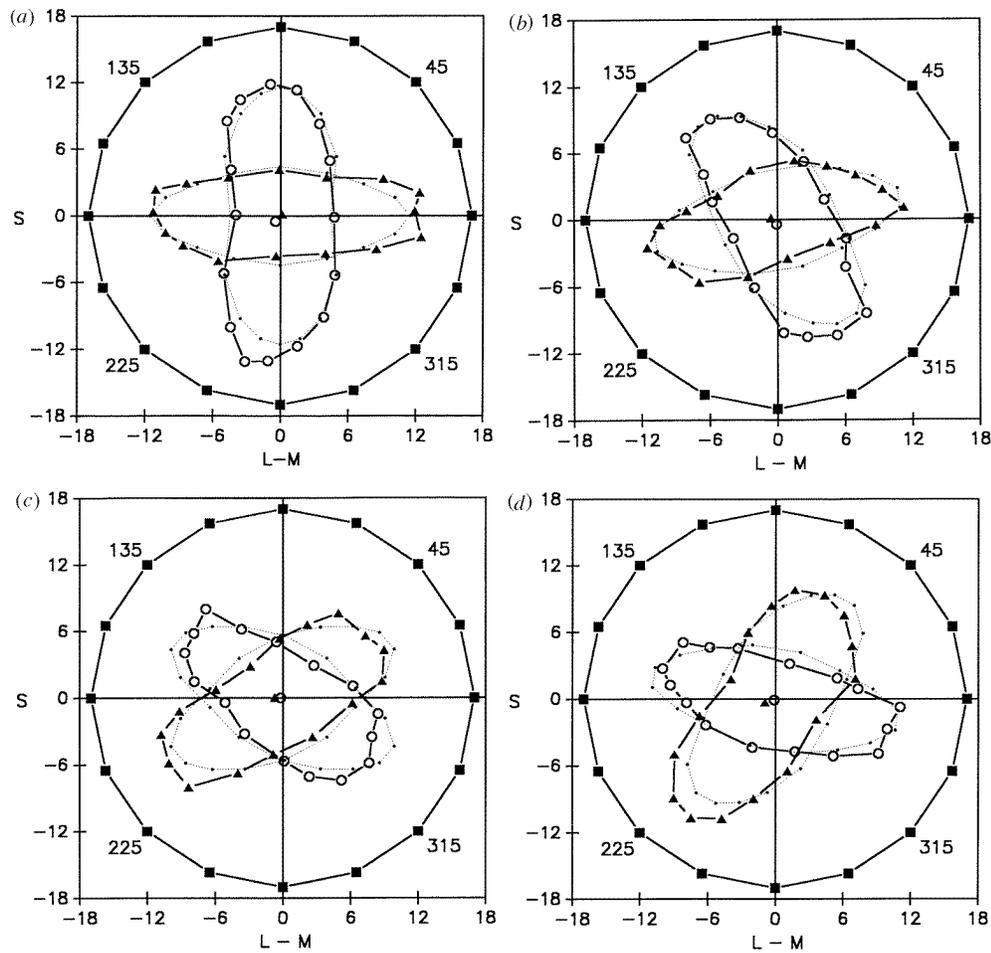


Figure 13. Matches to test stimuli (full squares) following adaptation to eight different directions within the equiluminant plane [179]. Saturation losses are always largest along the adapting axis, and weakest roughly 90° away. (a) Adaptation to the $L - M$ (open circles) or $S - (L + M)$ (triangles) axes. (b) Adapting axes of $22.5\text{--}157.5^\circ$ (open circles) or $112.5\text{--}202.5^\circ$ (triangles). (c) Adapting axes of $45\text{--}225^\circ$ (open circles) or $135\text{--}315^\circ$ (triangles). (d) Adapting axes of $67.5\text{--}247.5^\circ$ (open circles) or $157.5\text{--}337.5^\circ$ (triangles). Broken curves and small circles plot the matches predicted by a model based on multiple colour channels (see text).

different adapting directions, and thus no axis that invariably isolates a single chromatic channel. Similar changes in perceived direction are again observed when adapting and test stimuli vary in both luminance and colour. For example, adaptation to a modulation between bright red and dark green causes a luminance increment to appear greenish and a luminance decrement to appear reddish, and causes an equiluminant red to appear darker while an equiluminant green appears brighter. Again each change represents a rotation in perceived direction away from the adapting axis, and suggests that pure luminance and pure chromatic stimuli do not invariably isolate pure luminance or pure chromatic-sensitive mechanisms. Thus the adaptation effects are again inconsistent with conventional models of colour vision based on only three independently adaptable channels, and instead suggest

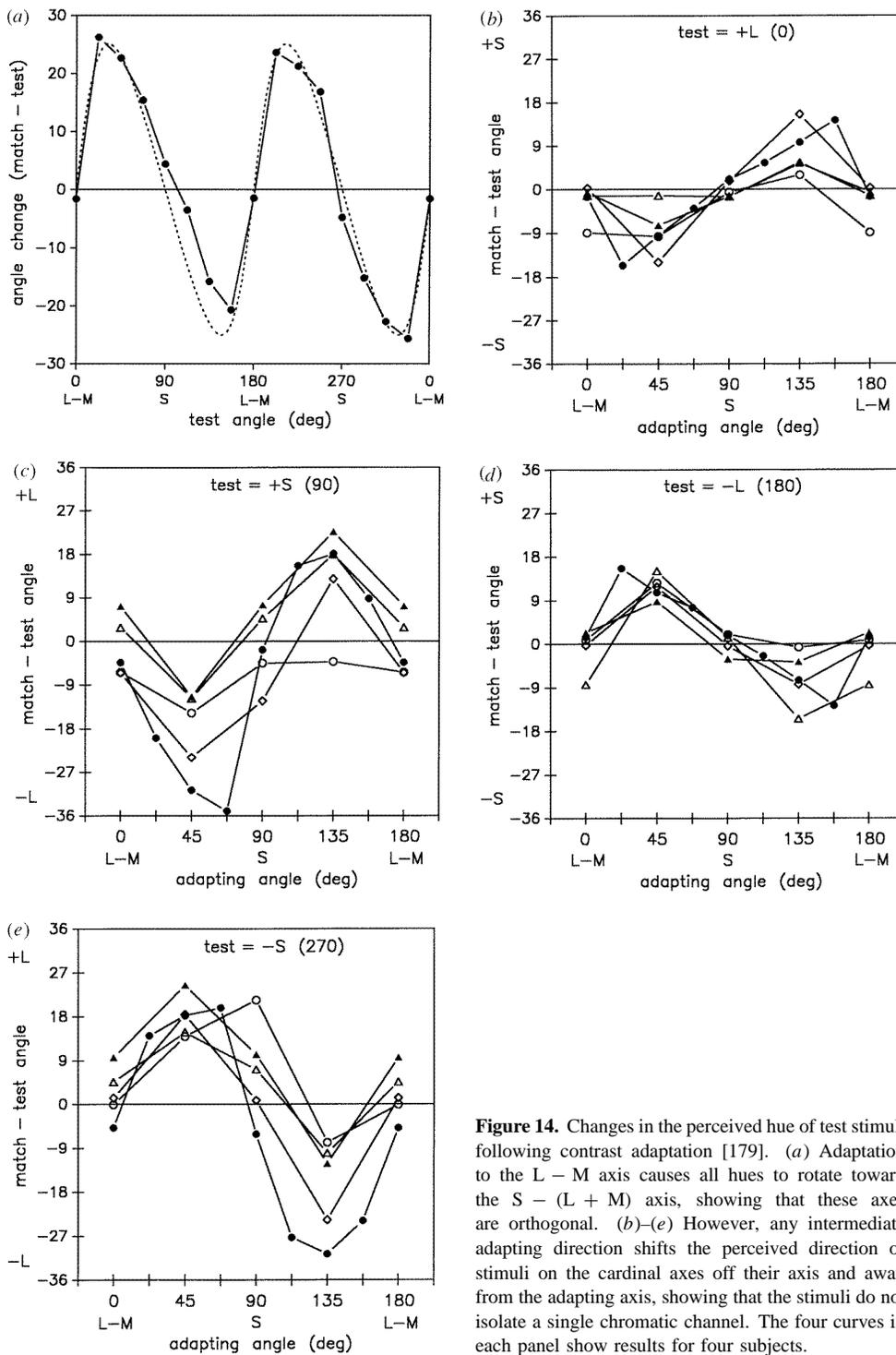


Figure 14. Changes in the perceived hue of test stimuli following contrast adaptation [179]. (a) Adaptation to the L - M axis causes all hues to rotate toward the S - (L + M) axis, showing that these axes are orthogonal. (b)-(e) However, any intermediate adapting direction shifts the perceived direction of stimuli on the cardinal axes off their axis and away from the adapting axis, showing that the stimuli do not isolate a single chromatic channel. The four curves in each panel show results for four subjects.

that the central representation of colour involves either multiple channels or channels that can alter their tuning functions through adaptation.

While changes in colour appearance were always selective for the adapting direction, greater selectivity was found for the $L-M$ and $S-(L+M)$ axes, confirming the special status of these axes. (However, for some observers the selectivity of the after-effects showed only a weak dependence on the adapting direction, and unlike the threshold changes of Krauskopf *et al*, the suprathreshold after-effects also exhibited strong selectivity for axes along which luminance and chromaticity covaried.) The greater selectivity for the cardinal axes argues against a representation of colour within the adapted channels that is organized in terms of the perceptually salient unique-hue axes [88]. This conclusion is further supported by the pattern of hue changes produced by adaptation [69, 179]. Suppose that within the adapted mechanisms red–green and blue–yellow variations were represented independently. Adaptation to a pure blue–yellow modulation should then have no effect on the perceived hue of a pure red or green stimulus. Yet blue–yellow adaptation causes a (previously) pure red to appear purplish [179]. As figure 4(b) showed, the unique red axis is not orthogonal to the blue–yellow axis within the $L-M$ and $S-(L+M)$ plane, and it is the axis 90° away that blue–yellow adaptation does not affect—a result which could not be predicted from the colour appearance of the axes. Finally, note that the axis that is ‘ 90° away’ depends on the relative scaling of stimulus contrasts along the $L-M$ and $S-(L+M)$ axes. The hue changes produced by different adapting axes provide a sensitive and consistent estimate of the relative strength of the signals along the two cardinal chromatic axes [179].

9. Spatial factors in colour contrast adaptation

In the preceding results observers adapted to temporal modulations in uniform 2° fields, yet similar after-effects occur for spatially varying adapting and test patterns, such as gratings, and demonstrate that colour contrast adaptation is also spatially selective. For example, Webster and Mollon [178] found that adaptation to gratings with correlated luminance and chromatic contrast (e.g. bright red/dark green) produced large brightness differences between the red and green components of chromatic gratings and large hue differences between the bright and dark bars of achromatic gratings. Yet these after-effects were abolished when the same luminance and chromatic adapting components were presented as temporal modulations in a uniform field, suggesting at least coarse size tuning. Flanagan *et al* [58] showed that the hue changes induced by adaptation to chromatic gratings are orientation selective, and conversely, tilt and spatial frequency after-effects are colour selective [53, 55, 59]. These suprathreshold after-effects parallel results showing that changes in threshold sensitivity following colour contrast adaptation are spatially selective [25, 159].

The classic demonstration of the spatial selectivity of colour after-effects is the McCollough effect [111]. After adapting to a vertical grating of red and black stripes alternated with a horizontal grating of green and black stripes, an achromatic vertical grating appears greenish and an achromatic horizontal grating appears reddish. Thus the adaptation induces an orientation-selective colour after-effect in the test grating. It is unclear whether such after-effects represent a special form of adaptation that is distinct from contrast adaptation. For example, compared to conventional contrast adaptation effects the McCollough effect is thought to have unusually long persistence and to exhibit less interocular transfer [156].

Many theories have been proposed to account for the contingencies between form and colour in the McCollough effect (e.g. [48, 156]), yet the selectivity of colour contrast

adaptation for any colour–luminance direction suggests an interpretation with a different emphasis. It may not only be the pairing of orientation and colour that is important, but also the correlation between luminance and chromaticity. Specifically, a bright-red grating may selectively reduce the sensitivity to bright red. A white grating subsequently appears greenish because the achromatic axis is tilted away from the adapting axis (because the response distribution of colour–luminance mechanisms encoding whiteness is biased away from bright red toward bright green). The importance of the McCollough effect is in showing that this colour–luminance selectivity is also orientation selective, consistent with the general spatial selectivity of contrast adaptation. However, an oriented or spatially structured pattern is not necessary to produce the hue shifts [176, 179], while a correlation between luminance and chromaticity is—the McCollough effect is not observed in an achromatic test grating when the adapting gratings are equiluminant (e.g. grey–red) [156], since in that case the white–black grating lies along the axis that is orthogonal in colour space to the adapting axis, and is thus the one colour–luminance direction that should not appear rotated. A further prediction of this account is that the colour after-effect induced in the dark bars of the achromatic test grating should appear to be shifted in the direction opposite to the bright bars. Indeed adaptation to a bright-red/dark-green grating does induce opposite colour shifts in the bright and dark bars of an achromatic test grating [178]. (However, one prediction that does not appear to be confirmed experimentally is that adaptation to a grating with bright-white and dark-coloured bars should induce in the bright bars of an achromatic grating colour changes that are in the same direction as the dark-adapting colour [156].)

10. Models of contrast adaptation

We have seen that colour contrast adaptation effects cannot be accounted for by standard models of colour vision based on three independent post-receptoral channels. This section considers two alternative models of post-receptoral colour vision that can predict more closely the pattern of colour changes. These differ from the standard model either by assuming many more than three channels that adapt independently, or by assuming channels whose tuning functions can be altered by adaptation-dependent interactions. The two models are thus based on different assumptions about the nature of contrast adaptation.

Webster and Mollon [179] examined whether the contrast adaptation effects they observed within the equiluminant plane were consistent with a model based on multiple chromatic channels that adapt independently. Their model is similar to conventional multiple-channel models of spatial contrast adaptation effects that have been proposed to account for phenomena such as the tilt after-effect or shifts in apparent size (spatial frequency) [24]. The logic of such models is illustrated in figure 15. The stimulus dimension (e.g. orientation) is assumed to be encoded by a large number of channels with overlapping tuning functions. A stimulus is therefore represented by the distribution of activity across a subset of channels. Adaptation desensitizes the channels that respond to the adapting stimulus, with more adaptation in channels that respond most. When a test stimulus is now presented after adaptation, the sensitivity to stimuli similar to the adapting stimulus is reduced, and stimuli near the adapting value appear shifted in appearance away from the adapting value, because the distribution representing the test has been skewed by the adaptation.

Note that the predictions in figure 12 actually represent a special case of this model, in which there are only two channels. One advantage of applying such models to colour vision is that plausible assumptions can be made about the bandwidths of individual channels.

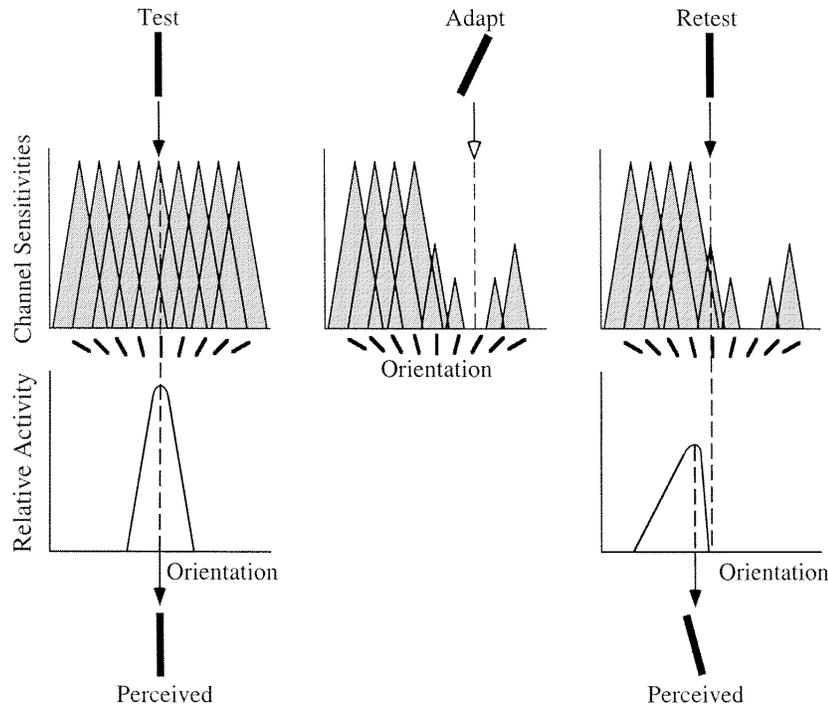


Figure 15. Multiple-channel models of contrast adaptation [24]. Adaptation to an oblique orientation reduces sensitivity to a subset of channels selective for similar orientations. This biases the distribution of responses to a vertical test line, causing it to appear tilted in the opposite direction.

Webster and Mollon assumed that the channels were formed by linear combinations of the cone signals. Because contrast adaptation effects appear most selective for the $L - M$ and $S - (L + M)$ axes, they further assumed that the preferred directions for different channels formed two Gaussian distributions centred on the cardinal axes, and then varied the standard deviation of the distributions to find the best fit to the observed colour changes. The broken curves in figure 13 show that matches predicted by this model closely approximate the observed matches and, in particular, correctly predict the saturation losses along axes orthogonal to the adapting axes. These are predicted to occur because the cosine tuning functions of individual channels suggest that any channels tuned to intermediate directions will be sensitive to (and thus adapted by) modulations along the adapting axis, and also sensitive to (and thus contribute to the response to) test stimuli along the orthogonal axis. (However, this account is not readily consistent with the independence of orthogonal adapting axes illustrated in figure 22). Figure 16 shows the channel distributions predicted from four observers' results. For the standard model the distribution would be represented by two spikes, at the $L - M$ and $S - (L + M)$ axes. In contrast, the best-fitting distributions require substantial spread in the preferred directions of the channels, though biases along the $L - M$ and $S - (L + M)$ axes are evident. Figure 16 also shows two Gaussian distributions that have the same standard deviations of preferred directions as cells in the parvocellular geniculate [47]. These are narrower than any of the distributions estimated psychophysically. The psychophysical adaptation effects could thus reflect the broader range of chromatic preferences found in the striate cortex.

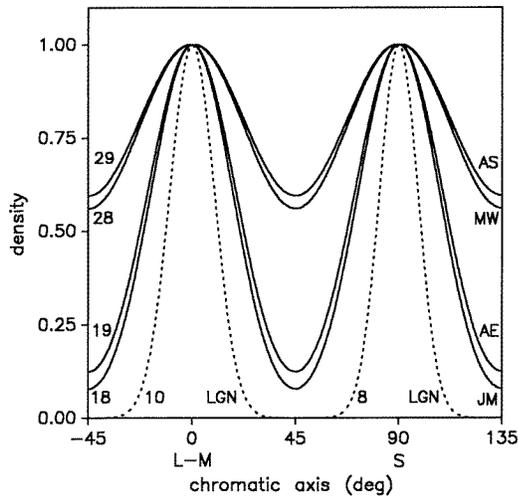


Figure 16. Distribution of colour channels estimated from colour contrast adaptation effects for four observers [179]. Broken curves plot the distribution of chromatic directions for LGN cells [47]. Note the figure does not reflect differences in absolute density along the $L - M$ and $S - (L + M)$ axes.

Several authors have suggested that adaptation does not reflect independent response changes within channels, but rather inhibitory interactions between channels (see [66]). Barlow and Földiák [11, 13] proposed a novel interpretation of contrast adaptation effects based on inhibition. They suggested that mutual inhibition builds up between two channels whenever their responses are correlated, and that this alters the tuning functions of the channels until their responses become statistically independent. For example, figure 17(a) illustrates a stimulus that produces covarying responses within a pair of mechanisms. The outputs of the two mechanisms can be decorrelated by an oblique rotation of their response axes, equivalent to mutual inhibition that subtracts from each mechanism's output some fraction of the response from the second mechanism (figure 17(b)). As a result, responses to the oblique adapting axis are selectively reduced, and all other stimuli are rotated away from the adapting axis toward the orthogonal axis. An important feature of this model is that sensitivity changes can show selectivity for stimuli to which none of the individual channels are tuned, and thus selective adaptation for a stimulus dimension does not demonstrate unequivocally the existence of a mechanism aligned to that dimension.

Webster and Mollon [176, 179] suggested that adaptation-dependent interactions of the type proposed by Barlow provided an alternative basis for the selectivity of colour contrast adaptation for multiple colour–luminance directions. Formal models of decorrelation in colour channels were subsequently developed by Atick *et al* [8] and Zaidi and Shapiro [191]. Atick *et al* showed that the results reported by Webster and Mollon could be closely predicted by a model in which decorrelation and gain control were combined with a 'locality' assumption that constrained the adaptation transform to be closest to the original representation. (This constraint is necessary because decorrelation alone does not define a unique solution.) They showed that selectivity for any adapting direction within a colour–luminance plane can be generated by a network of only two discrete mechanisms coupled by adaptable lateral feedback links. The response changes are equivalent to gain controlling the signals along the adapting and orthogonal axes so that they have equal variance. This distorts the original circle of test stimuli into an ellipse whose minor axis is aligned to the principal axis of the adapting distribution, and whose minor and major axis lengths (determined experimentally) are presumed to be inversely related to the variance in the adapting distribution along the principal and orthogonal axes. As figure 13 shows, such ellipses closely characterize the perceived colour changes in the test stimuli. To account

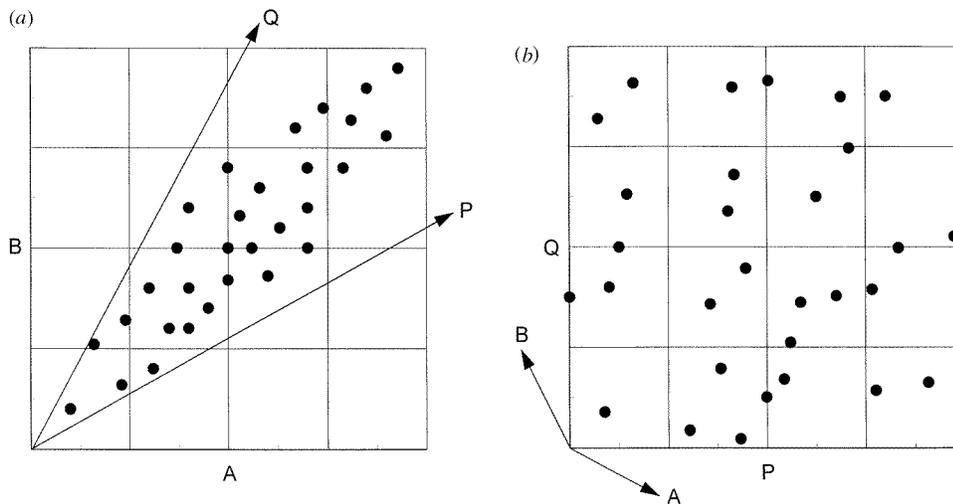


Figure 17. Decorrelation model of adaptation [11]. The stimulus distribution in the left-hand panel produces correlated responses in two mechanisms tuned to stimulus dimensions A and B. Redundancies in the responses can be removed by changing the response axes of the mechanisms through mutual inhibition, so that the mechanisms instead encode the oblique dimensions P ($= A + kB$) and Q ($= B + kA$). This results in an oblique rotation of the response axes (right-hand panel). Stimuli that originally isolated one of the mechanisms (A or B) now have an inhibitory effect on the second mechanism, so that they appear rotated in the response space away from the adapting direction.

for the observed sensitivity losses along orthogonal directions when the adapting stimulus varied along only a single axis, they suggested that the response to the adapting stimulus might be noisy, so that the effective stimulus distribution included modulations along the orthogonal axis.

The observed results for colour contrast adaptation do not clearly discriminate between these alternative models. An important insight of the decorrelation model is that it provides a functional basis for contrast adaptation, which is lacking in multiple-channel models (see below). However, results from other psychophysical paradigms suggest the presence of more than three channels even in a single state of adaptation (e.g. [89]), and again, multiple channels are consistent with the variability in cone inputs to individual cells observed physiologically. This inherent redundancy presents a challenge for models based on decorrelation. A second challenge arises from the response changes produced by adaptation, which we have seen are progressively weaker at higher contrasts. This suggests that the responses to the adapting stimulus itself are not completely decorrelated.

11. Combined effects of light adaptation and contrast adaptation

In the preceding sections we considered the effects of light adaptation and contrast adaptation in isolation, by holding one of the adjustments constant. But how do the two forms of adaptation combine to influence colour sensitivity and appearance? We can assess this by generalizing the contrast adaptation experiment of figure 13 to examine what happens when the modulations in the adapting field are now centred around different points in colour space.

Figure 18 shows results from an experiment in which observers adapted either to a static colour in a field, or to 1 Hz modulations around the mean colour along chromatic axes of $45\text{--}225^\circ$ or $135\text{--}315^\circ$ [177]. They then matched the colour of a set of test stimuli bracketing the mean. The four panels plot the results for four different mean chromaticities, centred in different quadrants of the equiluminant plane. Light adaptation (to the mean alone) reduces the apparent saturation of the mean so that it appears nearly white, and produces corresponding mean shifts in the appearance of all of the test colours. Thus the set of test stimuli in the upper-right quadrant, which all appear reddish-purple in a neutral state of light adaptation, are shifted by the light adaptation so that they are centred around white, and take on the full gamut of hues. These mean shifts occur independently along

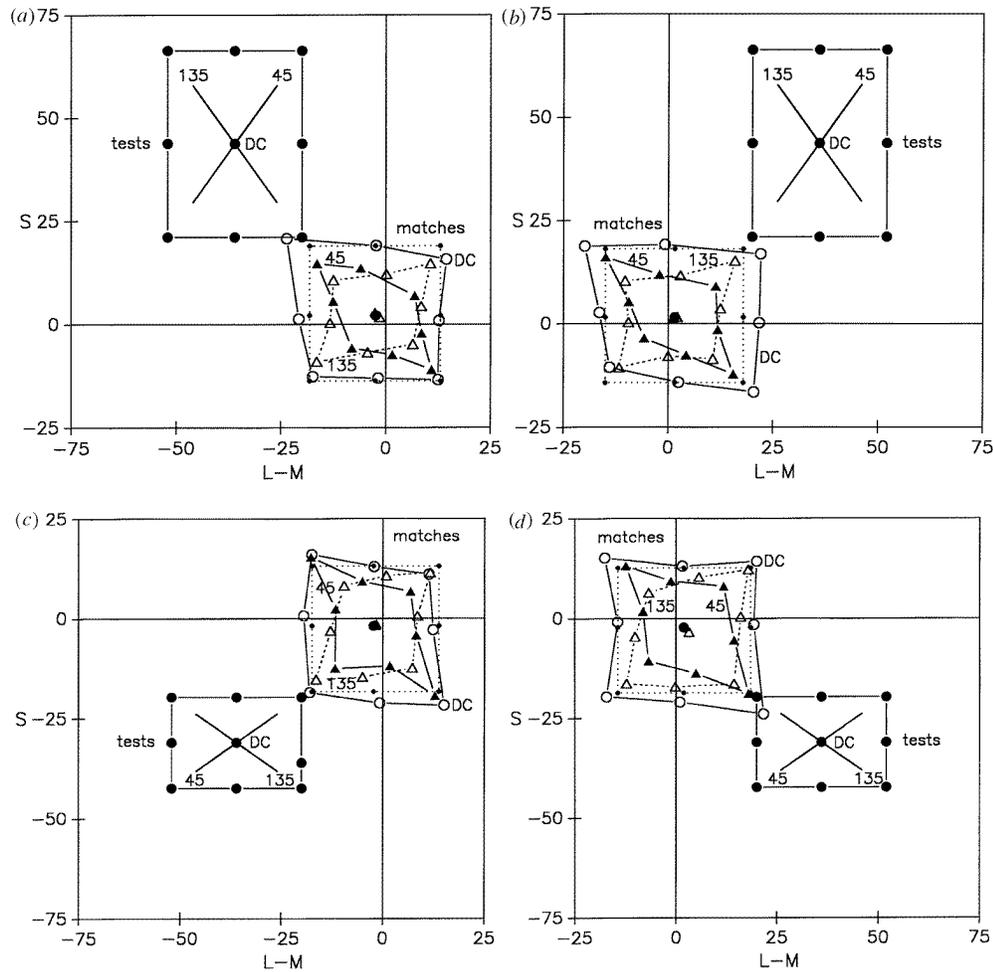


Figure 18. Combined effects of light adaptation and contrast adaptation [177]. Matches were made to test stimuli (full circles) after adapting to a static adapting colour (DC) or to modulations around the DC along the $45\text{--}225^\circ$ or $135\text{--}315^\circ$ axes. Adaptation to the DC shifts the mean colour and all test stimuli toward white, consistent with predictions for von Kries scaling (small circles-dotted lines). Contrast adaptation produces in addition a selective loss in sensitivity to the 45° (full triangles) or 135° (open triangles) adapting axis. The four panels show similar results for four different DC colours.

the $S - (L + M)$ and $L - M$ axes, and are very close to the adjustments predicted by von Kries scaling within each class of cone (broken curves). Thus for these conditions von Kries adaptation provides a largely complete account of the colour changes produced by adaptation to the background colour. (Subtractive adjustments may also be present but are not evident because the von Kries scaling has already nearly equated the background signal for the test and match fields.) Adapting to modulations centred on the mean leads to the same mean colour shifts, but in addition induces a loss in sensitivity that is selective for each adapting axis. Since these axes covary the cone signals, the selectivity for them again implies adaptation within mechanisms that combine the cone signals.

The results show that light adaptation and contrast adaptation produce independent and qualitatively different changes in colour appearance that can be readily dissociated. Light adaptation alters the cone signals available to later stages, but otherwise appears to have little influence on adaptation to contrast. Conversely, the fact that adding large modulations around the mean does not alter the state of light adaptation suggests that the visual response to contrast up to the sites of light adaptation is linear (or symmetric for opposite excursions from the mean). Thus for such conditions light adaptation and contrast adaptation can be treated as separable and successive influences on colour appearance.

12. Contrast adaptation with incomplete light adaptation

To the extent that light adaptation and contrast adaptation do represent independent and successive adjustments by the visual system, identical contrast adaptation effects should occur for the modulations within each of the quadrants of figure 18—but only if the von Kries scaling adjusts completely to the different mean colours. In fact, for the conditions of these experiments this was usually not the case. After prolonged viewing of the static coloured fields appear very desaturated, but not completely white. What does incomplete light adaptation imply for the contrast adaptation effects?

Figure 19 shows predictions based on standard assumptions. Figure 19(a) plots the sensitivity of a prototypical opponent mechanism. The zero-crossing corresponds to the 'achromatic' stimulus that elicits no response. Adapting to a DC colour alters the relative sensitivity of the cones, and this shifts the mechanism's neutral point toward the adapting chromaticity. Any residual colour in the adapting field can be accounted for by assuming that

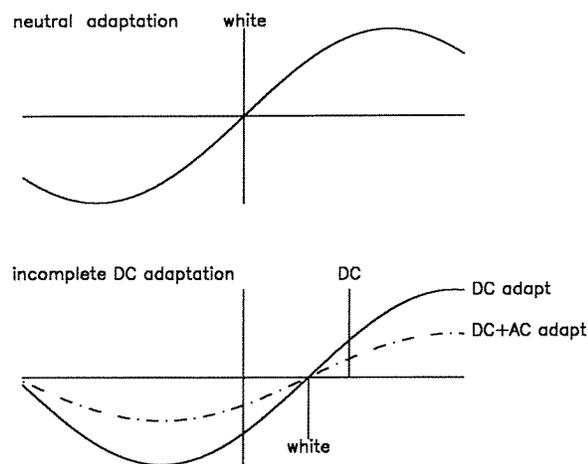


Figure 19. Predicted colour changes for contrast adaptation after incomplete light adaptation. In a neutral adaptation state, white (zero contrast) corresponds to the null point for the opponent channel. Adaptation to the DC biases the cone inputs, shifting the null toward the DC, but leaving a residual colour if the adaptation is incomplete. Contrast adaptation reduces the gain of the channel and should collapse responses relative to the mean, reducing the apparent contrast of the DC.

the von Kries scaling is incomplete, so that the zero-crossing falls short of the adaptation point. Contrast adaptation should reduce the gain of the response, without shifting the mean. Thus the response to all stimuli except at the achromatic point should be reduced. The prediction is thus that any residual perceived colour that remains in the adapting field should be greatly reduced by the contrast adaptation, shifting the response to the DC colour closer to white.

Surprisingly, this is not what happens. Contrast adaptation collapses perceived contrast relative to the mean chromaticity, and not relative to the stimulus that appears white. In figure 18 the residual mean colour is so small that this effect is difficult to see. Figure 20 shows results for a second observer who exhibited weaker light adaptation effects. In this example the subject adapted to a purple background that differed from the white reference only in S-cone excitation. Figure 20(a) shows the S-cone coordinates of matches to tests spanning the mean colour of the field, made after adapting to the static field or to modulations around the mean along the S axis. Figure 20(b) replots the matches as a function of test contrast. Light adaptation shifts the perceived colour of all of the tests toward white, but in this case the adapting field retained a perceived colour that was several times threshold. Contrast adaptation strongly reduced the perceived contrasts along the S axis, as indicated by the difference in the slopes of the regression lines fitted to the two sets of matches. The critical point is where the two fitted lines cross, since this gives an estimate of the one

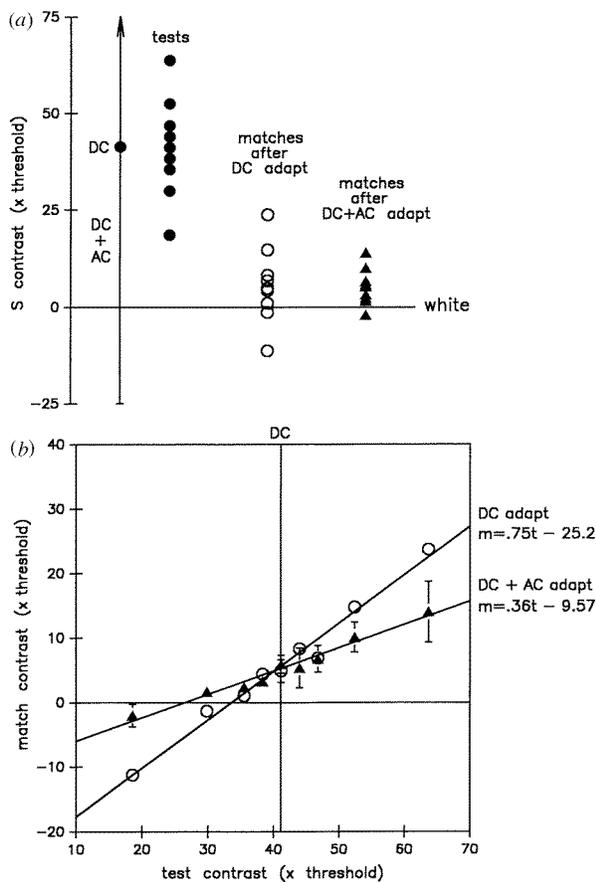


Figure 20. (a) Matches to test stimuli that lie along the S - (L + M) axis, after adapting to a mean colour change along the S axis (DC) or to modulations around the mean along the S axis (DC + AC). Light adaptation shifts the apparent colour of all tests toward white. Contrast adaptation in addition collapses perceived contrasts. (b) The DC and DC + AC matches are plotted as a function of test contrast. Contrast adaptation is indicated by the shallower slope for the DC + AC matches. The matches cross at a 'zero contrast' equal to the DC chromaticity and not at the 'zero contrast' predicted by the stimulus that appears achromatic.

stimulus that was not affected by contrast adaptation. The intersection occurs very close to the mean chromaticity, and not near the stimulus that appeared achromatic.

The adaptation effects thus reveal a dissociation between two alternative definitions of ‘zero chromatic contrast’, i.e. between the chromaticity that appears achromatic and the chromaticity that is the null point for contrast adaptation. Indeed, figure 20 suggests that there are cases when contrast adaptation might actually *increase* perceived saturation near the achromatic point by *decreasing* perceived contrast relative to the background chromaticity. It is hard to reconcile these dissociations with the notion that ‘white’ reflects an absence of activity in chromatic channels. Instead, it may be that white reflects the balance of activity across many channels, tuned not only to many different directions within colour space but also centred on different null points along any single axis.

13. The functions of adaptation

We have characterized some of the more salient properties of light adaptation and contrast adaptation, but what are the benefits of these adjustments to colour vision, and to perception in general? For light adaptation there are clear answers. The range of light levels to which we are normally exposed varies dramatically (e.g. nearly 10 log units from starlight to bright daylight), yet the dynamic range of visual cells is at best 2 to 3 log units. If cells had to devote their operating range to encoding the full range of stimulus intensities then they would have little sensitivity to small stimulus differences. This limitation is critical because the range of contrasts in any individual scene is typically small. Light adaptation thus serves to maintain high contrast sensitivity around the mean light level both by shifting the steep contrast response functions of neurons so that they are positioned near the ambient background, and by discounting responses to the background so that the dynamic range is devoted to signalling differences around the mean [169].

A second function of light adaptation is to help maintain lightness constancy. Changing the overall light level in a scene changes the amount of light reflected from any surface, but does not alter the ratio of quanta reflected from different surfaces. Thus these ratios describe stable properties of the scene (the relative reflectances of surfaces) and is the property to which our lightness perception corresponds (e.g. in our perception of dark versus light objects). The multiplicative gain controls of von Kries adaptation capture this invariance by rescaling the cone signals so that across different light levels a constant difference in outputs corresponds to a constant ratio of inputs.

Finally, light adaptation may be a major factor contributing to colour constancy. Studies of colour constancy are concerned with how and to what extent the visual system can maintain a stable representation of the colour of surfaces under changes in illumination [128]. Constancy is a problem because the colour signal reaching the eye confounds the reflectance function of the surface with the spectral power distribution of the illuminant, and is sampled by only three cone types with overlapping spectral sensitivities. (For example, the light reflected to the observer from the two objects in figure 1(b) will be very different depending on which of the two illuminants in figure 1(a) is prevailing.) Perfect colour constancy is theoretically possible only for a restricted range of lights and reflectance functions (that vary gradually across the spectrum) and then only if the visual system can estimate and discount the spectrum of the illuminant. Natural objects and illuminants do have broad and smoothly varying spectra and can be approximated by a small number of basis functions [37, 82, 110]. Because of this property the main effect of an illumination change is to rescale the absorptions within each cone class for the set of objects in the scene [42, 60]. For example, shifting from a yellow to blue illuminant will tend to increase

the S-cone response to each of the objects while decreasing the response in L cones to all objects. This is precisely the change that von Kries adaptation can compensate for—by rescaling sensitivity to maintain lightness constancy independently for each cone type [105]. However, for objects in the scene with different reflectance spectra, the relative lightnesses seen by each cone will also vary somewhat as the spectrum of the illuminant changes, so that rescaling alone cannot achieve perfect constancy.

The influence of adaptation on colour constancy is illustrated in figure 21, which simulates the visual response to a set of natural surfaces viewed under the two daylight illuminants illustrated in figure 1(a) [177]. The illuminant spectra were constructed out of the first three basis functions derived for daylight by Judd *et al* [82]. The surfaces were each constructed from the first three basis functions derived by Cohen for the reflectance spectra of Munsell chips [37]. The surfaces were chosen to form an equiluminant distribution centred on the chromaticity of the 4800 K illuminant, but with a bias along the S axis in the distribution's range. When the same surfaces are viewed under the 10 000 K illuminant, the light reflected from all of the surfaces shifts toward blue. The middle panel shows the responses to the two distributions following complete von Kries adaptation. von Kries scaling adjusts for the mean of each distribution, so that the average colour under either illuminant appears white. This factors out most of the difference introduced by the illuminant change, but residual differences remain, because the 10 000 K illuminant has also induced a systematic tilt in the distribution. Thus von Kries scaling can compensate for much of the illuminant shift but cannot discount the illuminant completely. The residual errors following von Kries adaptation have suggested that the visual system might adjust to the illuminant through a second stage of post-receptoral adaptation [41, 51]. These second-site adjustments could undo all of the illuminant change if they could estimate and correct for the weights on the basis functions defining the two illuminants. Several methods have been proposed for judging the illuminant, yet none of these are likely to provide a basis for perfect colour constancy in human observers [128]. On the other hand, there are actual 'second-site' adjustments like contrast adaptation, that could influence colour perception under the two illuminants. Before considering this additional stage of adaptation to an illuminant change, we first consider some of the functional implications of contrast adaptation.

Compared to light adaptation, the functions of contrast adaptation have proven elusive, and clear improvements in performance following contrast adaptation have been difficult to demonstrate. In fact, a common assumption is that the sensitivity losses produced by contrast adaptation are without functional benefits, and represent only temporary 'fatigue' due to prolonged stimulus exposure. However, by this account it is unclear why retinal and geniculate cells should exhibit little sign of contrast adaptation, and there are theoretical reasons for expecting the adaptation to be advantageous.

One proposed advantage of contrast adaptation is that it may adjust the visual system so that sensitivity is highest around the average *contrast* in a scene, just as light adaptation adjusts sensitivity to the prevailing mean light level. In fact this effect can be readily demonstrated in cortical neurons [3, 124, 141]. Individual neurons typically respond only over a narrow range of contrasts. Adaptation tends to centre this range on the adapting contrast level. As a result the neuron can signal differences between high-contrast stimuli that before adaptation all produced equivalent, saturating responses in the cell. Psychophysical studies have under some conditions found that contrast discrimination may be improved by prior adaptation [68, 187], yet the majority of attempts to test this have instead found no effect or decreases in sensitivity (e.g. [14, 104, 134, 171]). One reason for not expecting comparable sensitivity gains psychophysically is that the psychophysical contrast response function does not exhibit the degree of saturation observed in individual

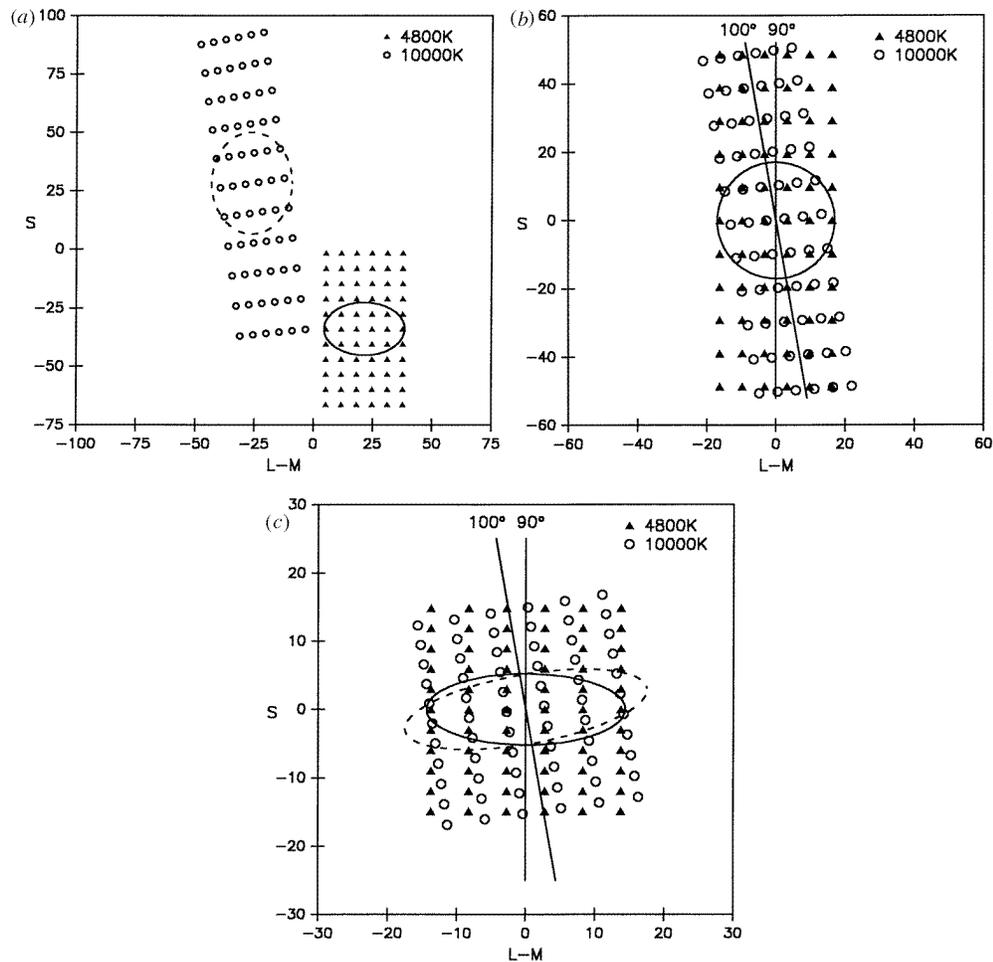


Figure 21. Light adaptation and contrast adaptation induced by an illuminant change [177]. (a) Reflectances of simulated Munsell chips were chosen to form an equiluminant distribution of chromaticities (triangles) centred on the chromaticity of the 4800 K illumination but biased along the $S - (L + M)$ axis. Circles show the distribution when the same surfaces are viewed under the 10000 K illuminant. Without adaptation the colours of the chips appear very different under the two illuminants. (b) Von Kries adaptation adjusts responses in each cone so that the mean response under the two illuminants is the same. This compensates for most of the illuminant change, giving approximate colour constancy, but the 10000 K distribution remains tilted 10° off the S axis. (c) The differences in the von Kries-scaled distributions lead to different states of contrast adaptation. Decorrelation results in sensitivity losses selective for either the 90° axis (under the 4800 K illuminant) or the 100° axis (under the 10000 K illuminant). As a result colour signals that matched at the retinal level of light adaptation (e.g. the large circle of colours in (b)) no longer match at the cortical locus of contrast adaptation (as shown by the two different ellipses in (c)).

cells (figure 11).

A related possible function of contrast adaptation is to support ‘contrast constancy’, just as light adaptation supports lightness constancy. Scenes with higher or lower contrasts will induce stronger or weaker adaptation, respectively, so that the dynamic range might tend to

be matched to the prevailing gamut of contrasts. Such adjustments might partially correct for changes in visibility owing, for example, to fog or rain [28].

Finally, we considered above the proposal that contrast adaptation reflects mutual inhibition between channels that serves to decorrelate their outputs. Combined with gain control this yields the most efficient representation of the visual stimulus because it allows each channel to devote its full dynamic range to carrying independent information about the stimulus [8, 11]. Such adjustments may be necessary because the statistical structure of images can vary markedly (see below). Barlow [9] also pointed out a further advantage. Because the mutual inhibition tends to null out the responses to prevailing stimulus contingencies, the resulting representation emphasizes 'suspicious coincidences' or novel associations in the environment, and could thus provide an important mechanism for the perception and learning of causal structure.

How is the goal of coding efficiency related to the goal in colour constancy of maintaining a stable representation of surface colour under different viewing conditions? We saw in figure 21(b) that von Kries adaptation corrects for most of the effects of an illuminant change, but leaves residual differences between the distributions. And the second-site adjustments that could in theory correct for these differences are not observed in empirical measurements of colour judgments under different illuminants [5, 27]. This suggests that differences remaining in the von Kries-scaled distributions survive to cortical sites and thus could drive the visual system to different states of contrast adaptation. The final panel in figure 21 shows the predicted colour matches under the two illuminants if contrast adaptation induces sensitivity losses that are selective for the principal axis of each distribution. The adaptation was modelled by decorrelating and normalizing the responses to the $L - M$ and $S - (L + M)$ contrasts using the algorithm of Atick *et al* [8]. The shift from the 4800 K to 10000 K illuminant tilts the initial distribution off the S (90°) axis to an axis of 100° . As a result colours that matched under the two illuminants at the level of light adaptation in the visual system, no longer match at the level of contrast adaptation, because they are embedded in different colour distributions and thus are affected by contrast adaptation in different ways (as illustrated by the ellipses within each distribution, which fall on a common circle of chromaticities after von Kries scaling but are distorted by contrast adaptation into ellipses with minor axes aligned along the different principal axes of the two distributions).

Webster and Mollon [177] showed that the colour changes produced by adaptation to random samples from the two distributions in figure 21(a) were consistent with von Kries scaling followed by selective sensitivity losses specific to each distribution. Contrast adaptation may therefore play a significant role in the visual adjustment to an illuminant change. However, while the observed contrast adaptation effects might lead to a more efficient representation of colour, they do not lead to colour constancy, as they do not undo the tilts that different illuminants induce in the colour distributions.

If contrast adaptation does serve a beneficial function in vision then it is surprising that there are so few examples of measurable improvements in performance after adapting. However, it may be that most experiments do not include the appropriate baseline for addressing this question. Adaptation effects are usually assessed relative to performance in a neutral, or zero-contrast adaptation state (or relative to an unknown state if the observer carries into the experiment the residual effects of past stimulus exposures). Neutral adaptation may be a rare anomaly in waking experience, and it may be more appropriate to look for the advantages of adaptation by comparing performance across different, natural adaptation states. Under these conditions the putative role of adaptation in increasing sensitivity to novel properties of the world might be readily confirmed.

14. Adaptation and the statistics of natural images

The preceding discussion raises the question of how the state of adaptation might depend on the colour distributions that are characteristic of the natural visual environment. In anticipating these effects it should be emphasized that adaptation induces selective changes in colour appearance even when the adapting distribution has only a modest bias in its colour direction. For example, figure 22(a) shows the effects of adapting to a fixed-contrast modulation along the $S - (L + M)$ axis, paired with varying levels of modulation along the $L - M$ axis. The two components were combined 90° out of phase in time so that the resulting stimuli varied along ellipses within the equiluminant plane. Figure 22(b) shows estimates of perceived contrast along the two axes. The sensitivity losses along the fixed-contrast $S - (L + M)$ axis remain remarkably constant, while increasing modulations along the $L - M$ axis lead to systematically larger sensitivity losses along this axis. Very similar results were obtained when the adapting components instead varied along intermediate colour directions. These results therefore suggest that even weak biases in the adapting distributions should lead to changes in colour appearance that are (at least weakly) selective for the adapting stimulus.

Few measurements have been made of the colour statistics of natural images [32, 118, 166, 181]. However, it is likely that most natural images exhibit strong biases in their colour distributions, because the characteristic colours of dominant natural surfaces (e.g. foliage, barks, and earth) are highly restricted [75, 125]. Burton and Moorhead [32] measured the colour distributions for scenes of English countryside, and found that chromaticities were biased along bluish–yellowish axes that should produce correlated responses in mechanisms tuned to the $S - (L + M)$ and $L - M$ axes. Moreover, the individual scenes varied substantially [115], so that no static set of post-receptoral mechanisms could represent different scenes efficiently. Contrast adaptation could therefore play an important role in adjusting the visual system to the properties of individual scenes.

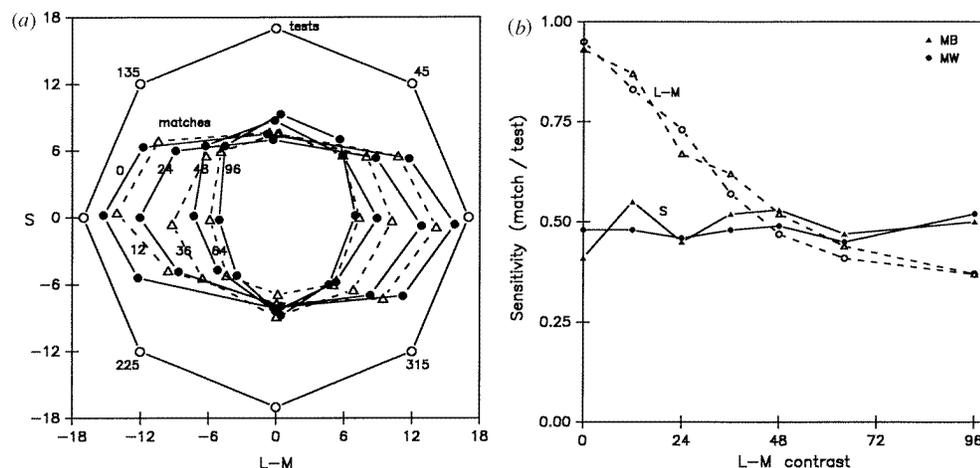


Figure 22. Contrast adaptation to biased distributions. (a) Matches to tests were made after adapting to a fixed modulation (48 times threshold) along the $S - (L + M)$ axis paired out of phase with modulations along the $L - M$ axis with varied contrast (indicated by numbers). (b) Sensitivity changes along the $S - (L + M)$ and $L - M$ axes estimated by ellipses fitted to two observers' results. Even weak biases in the relative contrasts along the two adapting axes cause changes in sensitivity that are (weakly) selective for the higher-contrast axis.

We are currently examining the changes in colour appearance that result from adaptation to natural colour distributions [181]. Physical measurements of the colour distributions in outdoor scenes are made by sampling the colour signals over a grid of spatial locations within the scene with a spectroradiometer, or by reconstructing the colour signal from successive images of the scene captured with a digital camera through 31 interference filters that span the visible spectrum. Figure 23 shows an example of the distribution obtained for a scene of a Sierra meadow backed by mountains and sky. Chromaticities are tightly clustered along a bluish–yellowish axis with very high correlations between the $L - M$ and $S - (L + M)$ axes. In contrast, for this scene there were only weak correlations between luminance and chromaticity.

Figure 24 shows measurements of asymmetric colour matches following adaptation to this colour distribution. The adaptation was achieved by presenting in a 2° field a sequence of individual colours sampled at random from the distribution every 200 ms. This simulates for a single retinal locus the temporal modulations of colour and luminance that might arise

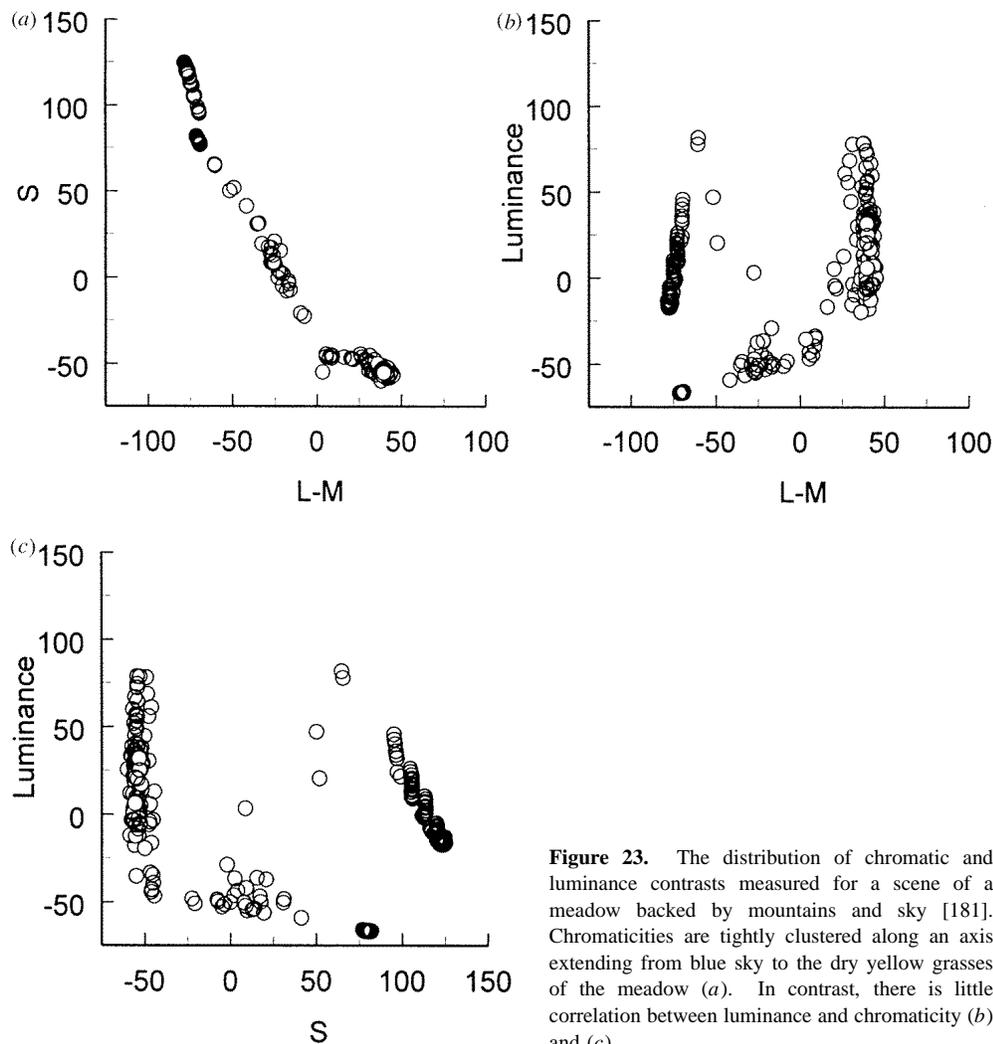


Figure 23. The distribution of chromatic and luminance contrasts measured for a scene of a meadow backed by mountains and sky [181]. Chromaticities are tightly clustered along an axis extending from blue sky to the dry yellow grasses of the meadow (a). In contrast, there is little correlation between luminance and chromaticity (b) and (c).

from random but very rapid eye movements over the scene. The resulting matches illustrate three adjustments that the visual system makes to the colour structure of the scene. Light adaptation adjusts to the mean colour, while contrast adaptation adjusts both to the range of contrasts in the scene and selectively to the bluish–yellowish axis of the distribution. (Light adaptation may also alter the effective contrasts in the scene if it is rapid enough to adjust to individual samples [167].) The changes in apparent contrast represent a partial tendency to maintain contrast constancy [28], while the selective sensitivity loss to the blue–yellow axis biases perceived colour toward the orthogonal chromatic axis, and thus toward the more novel colour directions in the image.

Such results suggest that the characteristic biases in natural colour distributions may often induce large and selective biases in our colour perception. In turn, this suggests that contrast adaptation is not a maladaptive response to aberrant stimulation, but rather—like light adaptation—is a natural and pervasive component in the visual coding of the natural environment. We are currently sampling the colour distributions for a wide range of outdoor

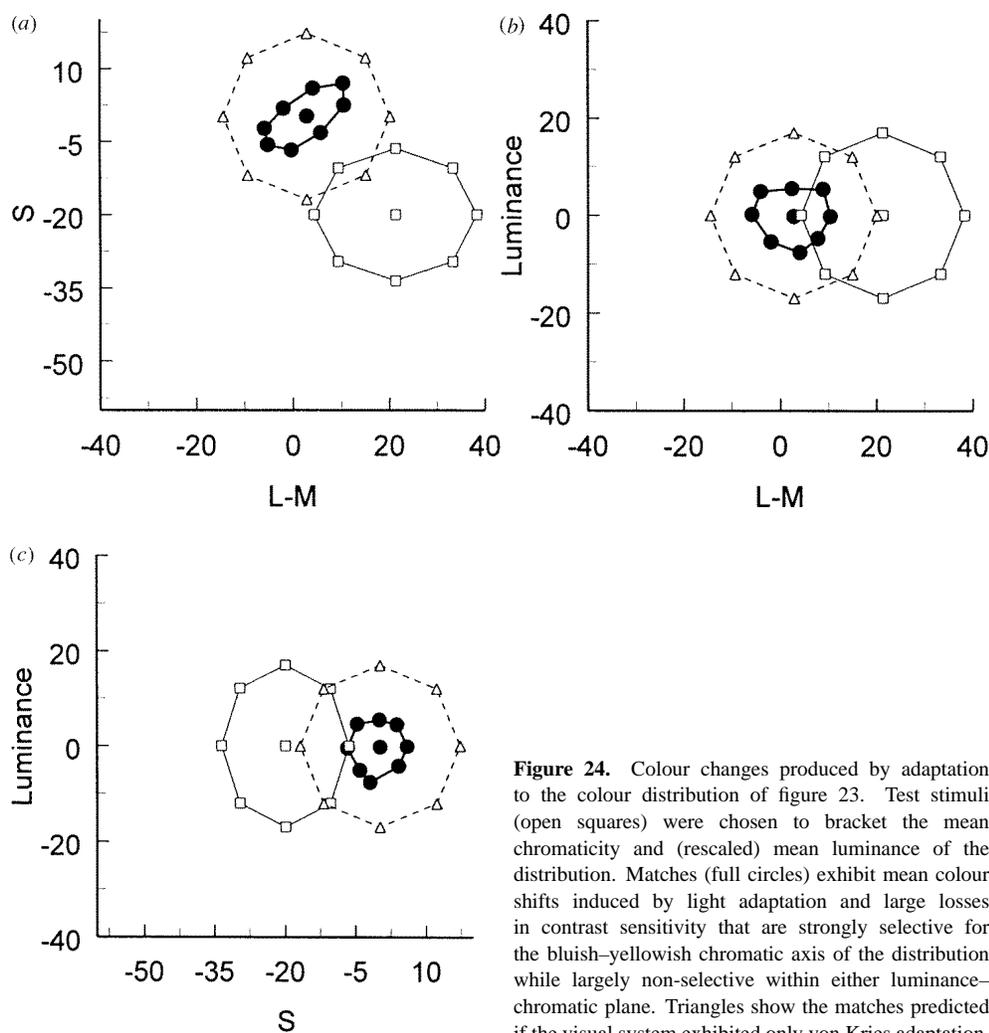


Figure 24. Colour changes produced by adaptation to the colour distribution of figure 23. Test stimuli (open squares) were chosen to bracket the mean chromaticity and (rescaled) mean luminance of the distribution. Matches (full circles) exhibit mean colour shifts induced by light adaptation and large losses in contrast sensitivity that are strongly selective for the bluish–yellowish chromatic axis of the distribution while largely non-selective within either luminance–chromatic plane. Triangles show the matches predicted if the visual system exhibited only von Kries adaptation.

scenes. There is substantial variability across scenes in the range of contrasts and in the direction and strength of biases along different colour–luminance axes. This diversity points to the possible need for adaptive adjustments, both across different scenes and within the same scene over time (e.g. because of changes in illumination, the weather or the seasons). Alternatively, the range of chromatic axes we have found thus far is limited—in most scenes colour varies principally along bluish to yellowish-green axes, with most distributions falling along axes that range from the $S - (L + M)$ axis to a unique blue–yellow axis. This limited range suggests that the natural environment may maintain the visual system in only a limited range of adapted states. Characterizing these states is important because they determine the range of natural operating states of our colour vision.

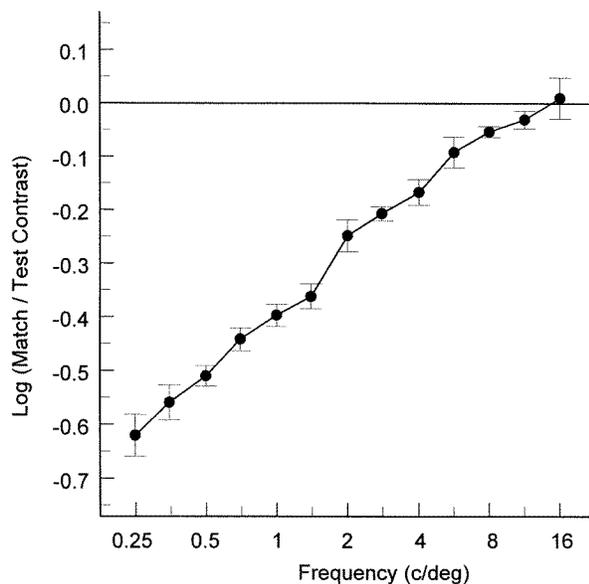


Figure 25. Changes in the apparent contrast of test gratings (of 10% contrast), following adaptation to a random sequence of grey-level images of a forest. Adaptation greatly reduced the apparent contrast of the lowest spatial frequencies but had little effect at the highest spatial frequencies, consistent with the $1/f$ amplitude spectra of the adapting images.

These results have implications beyond colour vision. For example, natural scenes have a characteristic spatial structure, with amplitude spectra that fall off with frequency roughly as $1/f$ (e.g. [32, 49, 56, 135, 165]). This structure has been found for a very diverse range of images and appears broadly similar for luminance and chromatic contrast [166, 181]. We are examining how adaptation to this spatial structure alters sensitivity to spatial contrast [174, 175]. Figure 25 shows the changes in the apparent contrast of gratings following adaptation to an ensemble of grey-level images of a forest. (The adaptation was again measured by an asymmetric matching task after observers were exposed in the adapting field to a random, rapid sequence of images.) The adaptation induces large losses in sensitivity that are selective for lower spatial frequencies, consistent with the image amplitude spectra. The characteristic spatial structure of natural images may therefore maintain the visual system in characteristic states of spatial contrast adaptation, profoundly influencing the filtering properties of our spatial vision. It is these adapted states that are most relevant for understanding how the visual system responds to natural patterns of stimulation.

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