

in good than in bad moods. Likewise, in good moods, performance increases for assimilative memory tasks like free recall and decreases for accommodative memory tasks like recognition. Note that, in line with these considerations, Maratos *et al.* [5] (cited by Lewis and Critchley), found no behavioural effect of valence on subsequent memory. This can be nicely explained by their use of an accommodative retrieval task, that is, recognition. We, in contrast, intentionally chose a free-recall paradigm, which affords assimilative processing. Accordingly, we predicted better recall for material encoded in a positive emotional context, a prediction confirmed by our data.

What does that mean for the interpretation of our results? Remember that the SME is defined according to performance in the retrieval task. We do argue that our results are partly due to the fact that we used free recall. If we had used a passive recognition task we would have obtained different behavioural results (different retrieval rates, no advantage for positive context) and thus also a different SME. Evidence for this assumption comes from a follow up study (unpublished data) in which we used a recognition instead of a recall task. In this study, we obtained a much higher rate for recognized words. Furthermore, mood did not affect memory performance, exactly as in the Maratos *et al.* study [5] and as predicted by Fiedler's model [4]. and first analyses of the functional data show different results for the SME from our previous study.

What does it mean for further investigations of mood-memory interactions? It means that results will be partly determined by the kind of retrieval procedure and its associated cognitive style. In line with Fiedler [4] we suggest that memory performance is maximal when stimuli are pleasant (content) *and* mood is positive (context) *and* the task is an active, productive one (cognitive style). Moreover, these three factors can be manipulated at encoding as well as during retrieval. As memory performance determines SME, the cognitive style triggered by the emotional context (mood) as well as the type of encoding and retrieval tasks should be taken into account in future experiments.

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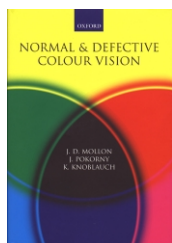
Book Review

Understanding colour

Normal and Defective Colour Vision edited by J.D. Mollon, J. Pokorny and K. Knoblauch, OUP, 2003. £59.50 (422 pages)
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The simplicity and ease with which we perceive the visual world often hides the true complexity of the visual mechanisms involved and this is particularly true of colour vision. *Normal and Defective Colour Vision* is a beautiful example of how diverse and challenging techniques can provide the information needed to understand colour vision.

There are few other subjects that are more varied and demanding. The study of colour vision combines many disciplines ranging from genetics and crystallography to physiology and psychology, and there is a forum – the International Colour Vision Society – that plays an important role in promoting this multidisciplinary research. The editors of the book have brought together a number of excellent contributions on stimulating topics.

The material presented describes the current level of understanding and also addresses unanswered questions concerning normal and defective colour vision.

The book begins very appropriately with John Mollon's outstanding historical introduction to the trichromatic theory of colour vision. Through critical, historical exposition of the gradual scientific progress that led to the trichromatic theory of colour vision, John Mollon manages effortlessly to inform both the newcomer and expert of the key stages involved in colour vision. This introduction serves as preparation for the more challenging contributions that follow. These nine sections of the book each deal with a number of related topics. They include: photoreceptors and retinal processes, the molecular genetics of colour deficiency, colour spaces and their variation, spatial and temporal aspects of colour vision, colour constancy and natural scenes and methods of examining and quantifying the loss of chromatic sensitivity in inherited and acquired colour deficiency. It is not

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possible to do justice to each contribution in this short review. Instead, I propose to discuss some aspects of normal and deficient colour vision that are acknowledged frequently in many of the contributions. Of particular interest is the large variation in the chromatic sensitivity of trichromats and how this relates to the properties of photoreceptors in the eye. These properties include the optical density of photopigments, the wavelength of maximum light absorption, the relative numerocities of long-wavelength and middle-wavelength sensitive cones, both at the fovea and in more distant parts of the retina, and finally the accurate, reciprocal adjustments of cone photoreceptor sensitivity through light adaptation and contrast gain.

In this book we learn that all information present in the retinal image is coded as spatial modulations of either intensity and/or spectral content that can also change over time. It is the job of the four detectors of light in the retina to extract both types of information, so that they can later be used to form the representation of spatially structured objects. At the lowest light levels, only rod photoreceptors have significant sensitivity to capture the very few photons available and to produce a signal that is above noise. Colour vision is not possible at extremely low light levels since signals from a single detector cannot be used to differentiate between spectral and intensity modulations. At higher light levels, three different classes of cone photoreceptor respond selectively to photons in different regions of the visual spectrum and are labelled as short-wavelength (blue or S-), middle wavelength (green or M-) and long-wavelength (red or L-) cones. Comparison of L- and M-cone signals forms a chromatic channel that mediates red-green (RG) discrimination. A second, blue-yellow (BY) channel is achieved from the comparison of S-cone signals against some combination of L- and M-cone signals. These two chromatic channels mediate detection of colour signals selectively, in the red-green and blue-yellow directions. Chromatic sensitivity is often quantified by measuring thresholds for detection of a colour-defined stimulus when its wavelength composition is changed towards the various colours of the spectrum. The resulting threshold curve is often described as a MacAdam ellipse [1], and when used appropriately, it provides a measure of RG and BY chromatic sensitivity. Using such techniques one finds that intersubject differences are small, particularly when colour discrimination is mediated by the RG channel. Functionally this is an amazing achievement that enables us to discriminate colours and, therefore, perceive similar chromatic differences, in spite of significant variation in L:M cone ratios and also in spite of random distribution of L- and M-cones in the retina [2,3]. The mechanisms that make this possible are discussed in several chapters of this book (Chapters 5, 21, 31 and 32). As pointed out by MacLeod (in Chapter 21), light adaptation can provide accurate adjustments of sensitivity in the different classes of cone photoreceptor [4,5]. Selective change of cone-receptor signal strength can in principle minimize the effects of large variations in L:M cone ratio. This could be achieved, either through changes in optical

density which can also cause a small change in spectral responsivity [6,7], or through gain control mechanisms that precede the generation of the colour opponent signal. This problem becomes more interesting when chromatic thresholds are measured in the periphery of the visual field. Current data show that, in general, normal trichromats can exhibit deuteranomalous-like thresholds in the far periphery, even when at the fovea the thresholds are completely normal. The sharp increase in L:M cone ratio measured at more peripheral locations in the visual field [8], when measured in the same subject, is consistent with the observed peripheral deuteranomaly. These findings suggest that the mechanisms that manage so successfully to minimise the effects of large intersubject variation in L:M cone ratio on chromatic sensitivity in central vision are either absent or are made less effective at more peripheral locations by the poor level of chromatic opponency associated with the larger receptive fields of ganglion cells.

Chromatic discrimination is generally poorer when the wavelength separation between the cone pigment sensitivities is decreased. This occurs as a result of L/M or M/L hybrid genes that cause the generation of cone photopigments with anomalous sensitivity [9]. The poor chromatic discrimination is usually reflected in the parameters of the Rayleigh match [10]. In this test the subject is required to match a small spectral yellow field with a mixture of red and green primary lights. Normal trichromats choose a unique red/green combination and can only accept small differences in the red/green mixture ratio as a match to the spectral yellow field.

Anomalous trichromats, on the other hand, can accept a wider range of red/green mixtures and require more green primary when deuteranomalous (i.e. an M-cone shifted pigment) and more red primary when protanomalous (i.e. an L-cone shifted pigment). Examination of a large population of anomalous trichromats does, however, reveal considerable variation in both the mid-point and size of the matching red/green range (Chapter 32), with some subjects showing extreme anomaly for which protan/deutan classification is inappropriate (Chapter 38).

There are other mysteries in the Rayleigh match that have remained so for over 50 years [11]. Some subjects that require either significantly more green or more red in their matches, compared to normal trichromats (an observation consistent with the presence of abnormal hybrid pigments) exhibit very small ranges, often smaller than the mean range for a normal trichromat (Chapter 32). Such findings emphasize the importance of other factors that contribute to chromatic sensitivity, in addition to the spectral separation between the normal and the anomalous photopigment. Changes in pigment optical density or gain control mechanisms that precede the generation of the colour opponent signal might play an important role in making chromatic discrimination thresholds less dependent on the spectral separation between normal and hybrid pigments (Chapter 31).

Several chapters in the book examine the genetics of normal and anomalous colour vision and attempt to explain how the heterogeneous distribution of gene-type

and numbers of genes, and also the ordering of genes in the arrays, determine the colour vision phenotype. The results indicate that, in general, genetic analysis can predict the type and severity of colour deficiency, but exceptions have been found when different genotypes yield the same phenotype and vice versa. Much remains to be done to establish an exact relationship between sequence variations in hybrid genes, the expression into anomalous photopigments that exhibit differences in optical density and spectral shifts and the corresponding effects on colour vision.

Current progress in retinal research and molecular genetics, together with a better understanding of how changes in the properties of cone photopigments can affect the generation of chromatic signals, are likely to advance rapidly our knowledge of normal and defective colour vision. Progress in this field requires integration of useful information from diverse, interdisciplinary studies, a problem that should not be underestimated. *Normal and Defective Colour Vision* addresses this problem and succeeds both in strengthening our understanding of existing findings and in identifying gaps in our knowledge of chromatic processes that can be addressed in future studies. In this respect, the book as a whole is significantly more valuable than the sum of its constituent parts and is

therefore a 'must' for both students and researchers in this field.

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Letter

Prometheus to Proust: the case for behavioural criteria for 'mental time travel'

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Suddendorf and Busby [1] claim that only humans are capable of mental time travel (MTT), either backwards to recollect specific past episodes (episodic memory), or forwards to anticipate future events (future planning). Although western scrub-jays remember the what-where-and-when of specific past events [2], Suddendorf and Busby argue that this result does not provide convincing evidence for episodic-like memory, and raise several points in support of this claim. We will respond to each of these in turn.

(1) *Animals should be able to declare their memories, through pantomime or other behavioural expression, ...'even if we cannot establish "the feel", i.e. autozoetic consciousness'.*

First, we have already demonstrated that our jays' episodic-like memories are declarative in character [3]. We have focused on perhaps the principal criteria of declarative memory – flexibility and integration – and have

shown that the jays' memories for caching episodes are strikingly flexible [4]. Other behavioural indices, such a pantomime, might provide converging evidence for the declarative nature of the memory, but such incidental behavioural markers do not seem as important to us as the core notion that declarative information is represented in a form that supports flexible deployment.

(2) *The memory should be shown to use a generative, reconstructive process at retrieval.*

Contemporary explanations of episodic retrieval, such as Tulving's encoding specificity hypothesis, do not insist upon reconstructive processes [5]. Reconstructive processes certainly played no part in Proust's classic tale of episodic recall, when the taste of a crumb of Madeleine cake retrieved Marcel's childhood memory of a Sunday morning in his aunt's bedroom in Combray [6]. Although humans might resort to such reconstructive generative processes when faced with retrieval failure, we do not understand why this should be a *necessary* criterion for episodic memory. Suddendorf and Busby argue that

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