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.

References

1 MacAdam, D.L. (1942) Visual sensitivities to color differences in daylight. *J. Opt. Soc. Am. A.* 32, 247–274
2 Roorda, A. and Williams, D.R. (1999) The arrangement of the three cone classes in the living human eye. *Nature* 397, 520–522
3 Brainard, D.H. *et al.* (2000) Functional consequences of the relative numbers of L and M cones. *J. Opt. Soc. Am. A.* 17, 607–614
4 Dacey, D.M. *et al.* (1996) Horizontal cells of the primate retina: cone specificity without spectral opponency. *Science* 271, 656–659
5 MacLeod, D.I.A. *et al.* (1992) A visual nonlinearity fed by single cones. *Vision Res.* 32, 347–363
6 Pokorny, J. and Smith, V.C. (1976) Effect of field size on red-green color mixture equations. *J. Opt. Soc. Am. A.* 66, 705–708
7 He, J.C. and Shevell, S.K. (1994) Individual differences in cone photopigments of normal trichromats measured by dual Rayleigh-type color matches. *Vision Res.* 34, 367–376
8 Yamaguchi, T. *et al.* (1997) Visual pigment gene structure and expression in human retinae. *Hum. Mol. Genet.* 6, 981–990
9 Sharpe, L.T. *et al.* (1999) L, M and L–M hybrid cone photopigments in man: deriving lambda max from flicker photometric spectral sensitivities. *Vision Res.* 39, 3513–3525
10 Rayleigh, L.S.R.J. (1881) Experiments on colour. *Nature* 25, 64–66
11 Wright, W.D. (1946) *Researches on Normal and Defective Colour Vision*, Henry Kimpton, London

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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. autonoetic 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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'accuracy is not imperative'. Certainly human episodic memory is prone to error. But would it be more convincing if our jays' memories were less accurate?

(3) *Episodic memory requires metarepresentation.*

We do not understand why the ability to metarepresent the episodic content should be a necessary feature of this form of memory. Nonetheless, there is some evidence that our birds do represent the content of other minds, based on their own social experiences [7]. Furthermore, the birds can differentiate between a conspecific and a mirror image of themselves (Dally, Clayton and Emery, unpublished observations).

(4) *Episodic memory can be used to construct future plans.*

We have a great deal of sympathy with this claim, and are currently pursuing this aspect of MTT in ongoing experiments in our laboratory. Current work demonstrates that our jays can use past experiences of recovering food to inform their future caching strategies (Clayton *et al.*, unpublished observations). Whether episodic memory and future planning ability *must* co-occur, and whether they share similar mechanisms and neural substrates is, however, an issue for future research.

In the absence of these critieria, Suddendorf and Busby suggest that we should refer to our birds' caching memories as 'www-memory' rather than as episodic-like memory. But even without the demonstration of autonoetic consciousness, our conception of episodic-like memory encompasses more than merely what, where and when. We have proposed three behavioural criteria for episodic-like memory, namely content, structure and flexibility [8]. 'What, where and when' satisfies only one of these criteria, namely the content criterion. In our opinion, Suddendorf and Busby's characterization of our approach as 'Characteriz[ing] episodic memory in terms of the information encoded' (Option 2) therefore captures only one aspect of episodic-like memory.

In summary, we argue that the concept of episodic-like memory, as defined by behavioural criteria, makes a worthwhile contribution to the analysis of comparative cognition in general, and episodic-like memory and future planning in particular. Although we are reassured by the convergence between the analysis of MTT offered by Suddendorf and Busby and our own research programme with western scrub-jays, we caution against grounding the concept of episodic-like memory in the phenomenology of the modern human mind, rather than in terms of core cognitive capacities.

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References

1 Suddendorf, T. and Busby, J. (2003) Mental time travel in animals? *Trends Cogn. Sci.* 7, 391–396
2 Clayton, N.S. and Dickinson, A. (1998) Episodic-like memory during cache recovery by scrub jays. *Nature* 395, 272–278
3 Griffiths, D.P. Dickinson, A. and Clayton, N.S. (1999) Declarative and episodic memory: what can animals remember about their past? *Trends Cogn. Sci.* 3, 74–80
4 Clayton, N.S. Yu, K.S. and Dickinson, A. (2003) Interacting cache memories: evidence of flexible memory use by scrub jays. *J. Exp. Psychol. Anim. Behav. Process.* 29, 14–22
5 Tulving, E. (1983) *Elements of Episodic Memory*, Oxford University Press
6 Proust, M. (1922) *Swann's Way: Part One Remembrance of Things Past* (Vol. 1), Chatto and Windus
7 Emery, N.J. and Clayton, N.S. (2001) Effects of experience and social context on prospective caching strategies in scrub jays. *Nature* 414, 443–446
8 Clayton, N.S. Bussey, T.J. and Dickinson, A. (2003) Can animals recall the past and plan for the future? *Nat. Rev. Neurosci.* 4, 685–691

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Letter Response

Like it or not? The mental time travel debate: Reply to Clayton *et al.*

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In response to our recent paper on mental time travel (MTT) in animals [1], Clayton *et al.* [2] defend their own case for episodic-like memory in scrub jays. Other than suggesting an alternative label, 'www-memory', that we thought less likely to conjure up unwanted notions of human phenomenology, we did not actually argue with their case. Contrary to their reading, we did not question the evidence for episodic-like memory, nor did we list new necessary criteria for it. Scrub jays demonstrate episodic-like memory. After all, the term episodic-like memory was coined by Clayton and Dickinson [3] to describe their findings with scrub jays (and they have since expanded their definition to incorporate new findings of integration and flexibility [4]).

We do not dispute their conclusion that 'the concept of episodic-like memory…makes a worthwhile contribution to…episodic-like memory and future planning…' [2]. What we did question [1], however, is whether episodic-like memory is anything like MTT into the past (i.e. episodic memory in Tulving's later sense of the word). We point out, for example, that semantic knowledge of, say, your own

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