

corvid brain that are structurally, as well as functionally, analogous to the ventromedial prefrontal cortex of humans. This hypothesis remains to be tested.

Avian intelligence is not an oxymoron

Some birds are capable of cognitive feats which put most mammals to shame. In the rainforests of New Caledonia and Mare, New Caledonian crows use and construct a number of different tools which are used to gain access to large grubs found in the crevices of trees. These tools are crafted from raw materials (sticks and *Pandanus* leaves), and there is a suggestion that, like chimpanzees, crow tool use is a form of culture. In the laboratory, New Caledonian crows are equally impressive, demonstrating some understanding of 'folk physics' (the common sense view of how the world works). Perhaps the best demonstration of this is Betty the crow, who appeared to spontaneously bend a piece of wire into a hook to gain access to out-of-reach food.

Other corvids are equally impressive, providing evidence of cognitive abilities thought to be uniquely human. Western scrub-jays, for example, are the first non-human animals to demonstrate episodic-like memory — the ability to remember the 'what, where and when' of a specific past event. In these studies, jays cache different types of food which decay at different rates in specific locations. In order to recover food that is still fresh and edible, the jays had to remember 'what' type of food they cached, 'where' they cached and 'when' they cached it. Scrub-jays are also extremely wary of the presence of conspecifics during caching. If an observer is watching when scrub-jays cache, the storers come back later when alone and move their caches to new places that the observer does not know. Interestingly, storers only do this if they have been thieves themselves in the past. This suggests that experienced scrub-jays may

attribute others with the intention of pilfering, and so implement strategies to reduce this possibility in the future. Scrub-jays also protect their caches by reducing the amount of information available to an observer at the time of caching, by hiding caches behind barriers, in the shade or as far from an observer as possible. All this suggests that western scrub-jays may demonstrate another supposedly unique form of human cognition: theory of mind. Parrots, such as Alex the African grey, have also demonstrated intellectual abilities which rival primates, such as understanding whether objects are the same or different, their number (including zero), their colour and shape.

Our new appreciation of the complexity of the avian brain is closely tied with a new appreciation of the complexity of the avian mind, particularly with respect to corvids and parrots. It is now the job of behavioural biologists, comparative psychologists and neuroscientists to determine how one translates into the other.

Further reading

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Multidimensional scaling reveals a color dimension unique to 'color-deficient' observers

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Normal color vision depends on the relative rates at which photons are absorbed in three types of retinal cone: short-wave (S), middle-wave (M) and long-wave (L) cones, maximally sensitive near 430, 530 and 560 nm, respectively. But 6% of men exhibit an X-linked variant form of color vision called deuteranomaly [1]. Their color vision is thought to depend on S cones and two forms of long-wave cone (L, L') [2,3]. The two types of L cone contain photopigments that are maximally sensitive near 560 nm, but their spectral sensitivities are different enough that the ratio of their activations gives a useful chromatic signal. Like color-normal observers, deuteranomalous observers are formally trichromatic, in that they need three primary lights if they are to match all possible spectral power distributions, but the matches they make are different from those of the normal. Here we use multidimensional scaling (MDS) [4,5] to reveal the color dimension that is private to the deuteranomalous observer.

For both normal and anomalous observers, MDS has previously been used to reconstruct subjective color spaces (for example [6,7]). The input to the scaling program is a matrix of the judged similarities of all possible pairs in a set of stimuli; and the output is a map of the stimuli that minimizes the differences between the input proximities and the corresponding proximities in the derived space. The length of the vector between any two stimuli in the output space indicates how

dissimilar they appeared to the subject, while its direction may allow an interpretation of the dimensions that guided the subject's judgment.

MDS studies of anomalous trichromats have, however, always had a phenotypic bias: stimuli have been selected to be discriminable for the normal observer and the anomalous space has typically been found to be contracted compared to the normal. Such results reinforce the categorization of anomalous trichromats as 'color deficient', but this represents the viewpoint of the majority phenotype. Because anomalous observers have a different set of retinal photopigments from normal, there exist pairs of natural stimuli that appear distinct to them but are indistinguishable ('metameric') for the normal [8]: such pairs produce the same triplet of photon catches in the cones of the normal eye but distinguishable triplets in the anomalous eye. We designed an MDS test that favors the minority phenotype of deuteranomaly.

Our stimuli were disks of 40 mm diameter, each painted with a mixture of two single-pigment acrylics and subtending $\sim 4.5^\circ$ at a typical viewing distance. To the normal eye, these stimuli appeared desaturated greens, varying along a yellow-blue axis. We included pairs of samples with spectral power distributions that were near-metamers for normals but were calculated to be distinguishable by a model deuteranomalous observer (Figure 1). Thus we used two distinct subsets of stimuli: one, labeled X, was made from mixtures of Cadmium Yellow and Cobalt Blue, and the other, labeled Y, from mixtures of Yellow Oxide and Ultramarine Blue.

In selecting suitable stimuli, we modeled the photon catches of individual photoreceptor types when exposed to light from a given stimulus under the experimental illuminant (a broadband amber). Using a spectroradiometer at the position of the observer's eye, we measured the spectral power distribution ($E(\lambda)$), and multiplied it in turn by the spectral sensitivities [9] of short-wave, middle-wave and two classes of long-wave

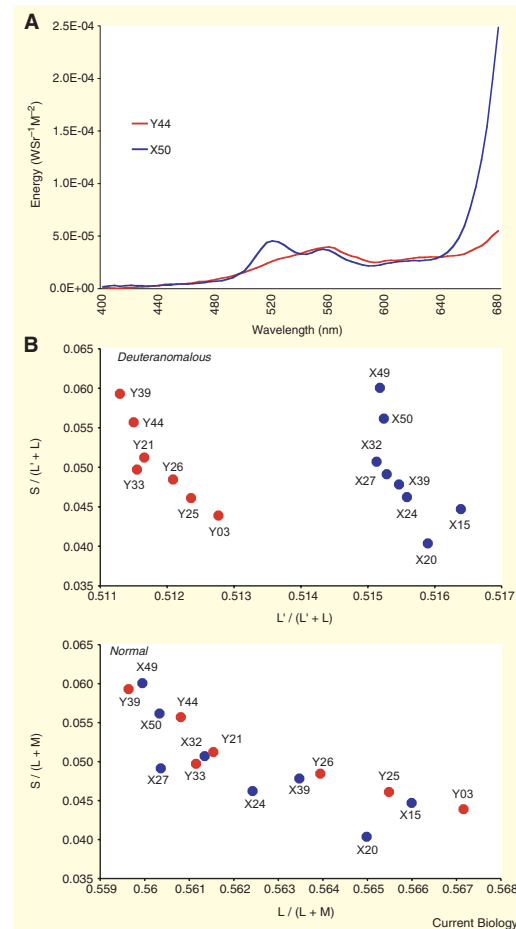


Figure 1. Experimental stimuli.

(A) Spectral power distributions of a pair of our stimuli that are near-metamers for the normal trichromat. (B) Positions of the chromaticities of the 15 stimuli in MacLeod-Boynton space for the normal observer (below) and in an equivalent space for the deuteranomalous observer (above). The X (blue points) and Y (red points) stimulus subsets are separated on the deuteranomalous dimension $L'/(L'+L)$, but intermingled on the normal dimension $L/(L+M)$.

cone: $\Phi_S(\lambda)$, $\Phi_M(\lambda)$, $\Phi_L(\lambda)$ and $\Phi_{L'}(\lambda)$. Integrating each product between 400 and 700 nm gave the photon catches in the four classes of cone. The chromatic signals available to a normal and to a deuteranomalous observer were then modeled as ratios of cone activations, for example $(\int \Phi_M(\lambda) \cdot E(\lambda) \delta\lambda) / (\int \Phi_L(\lambda) \cdot E(\lambda) \delta\lambda)$. Hereafter, we refer to photon catch ratios of this kind as M/L etc. The 15 stimuli chosen for the final set included pairs varying in the unique dimension of the model deuteranomalous observer (L'/L), but nearly matching in the normal dimensions of luminance ($L+M$) and chromaticity ($S/(L+M)$ and M/L). Figure 1B, bottom shows the coordinates of the stimuli in the MacLeod-Boynton chromaticity diagram [10] for normal vision: the samples predominantly fall along a single line and X and Y stimuli are intermingled. In an analogous diagram for the deuteranomalous eye, the X and Y subsets are clearly separated (Figure 1B, top).

Subjects were asked to rate the color difference between each stimulus pair on a scale of 0 to 10. Non-metric MDS was used to reconstruct a subjective space from the matrix of dissimilarity judgments for each observer.

Figure 2 shows two-dimensional solutions for 3 deuteranomalous and 3 (from a total sample of 7) normal observers. The upper panels reveal a subjective color dimension unique to the deuteranomalous. The first dimension for each of these observers shows a clear separation of the X and Y stimulus subsets, a separation not present in the normals' spaces.

For each observer, we correlated the ranks of the stimuli along the modeled dimensions with those along their subjective dimensions revealed by MDS. For the deuteranomalous subjects, the first MDS dimension correlated significantly with L'/L (Spearman's r varied from 0.821 to 0.950) and the second with $S/(L'+L)$ ($0.700 \leq r_s$

