parameters of their reactions, including the concentrations of the iridium catalyst, the enzyme and the enzyme's cofactor. They developed a system that reduces mixtures of (*E*)- and (*Z*)-isomers of alkenes to form a single stereoisomer, in multi-milligram quantities (Fig. 1a). The authors went on to convert the stereoisomer into a variety of biologically active molecules and key intermediates that have been used to prepare such molecules, thereby highlighting the potential application of their chemistry for preparative organic synthesis.

As Litman *et al.* point out, photocatalytic reactions typically occur at or near to room temperature, which makes them compatible with the thermal requirements of enzymatic systems. Photocatalysts also often work through mechanisms (such as outer-sphere electron transfer and energy transfer) that generate intermediates that are stable in the presence of water and tolerant of the chemical groups found in enzymes. Therefore, photocatalysts in general might be particularly suitable for being combined with enzymes for synthetic reactions.

This compatibility of photo- and enzymatic processes has been exploited in two other studies published earlier this year. In the first[6], a water-soluble iridium catalyst was combined with the enzyme monoamine oxidase (MAO-N) to convert racemic mixtures (one-to-one mixtures of mirror-image stereoisomers known as enantiomers) of amine compounds into a single enantiomer (Fig. 1b). This process begins by generating a highly reactive free radical from a starting material (an imine). The radical is then converted *in situ* to a racemic mixture of amines. MAO-N recycles only one of the enantiomers back into the imine, and the whole process repeats until all of the imine has been converted into the enantiomer that is not the substrate for MAO-N. In the second study[7], a photocatalytic reaction of thiols with enones was used to generate ketone intermediates that were reduced *in situ* with a ketoreductase enzyme, yielding products known as mercaptoalkanols enantioselectively (Fig. 1c).

As with all enzymatic systems, the reaction scope and scalability of Litman and colleagues' transformation will determine the extent to which it finds practical applications. For example, the alkene substrates reported in the paper are linear molecules that bear aryl groups (structural units that contain benzene rings; a substrate bearing an aryl group known as a pyridine ring is also reported). It will be interesting to see whether the chemistry can be extended to cyclic and non-aryl-bearing substrates. Moreover, the concentration of substrates used in the reactions is currently lower than would be needed for industrial processes. It remains to be seen whether the photocatalyst and enzyme will work at industrially useful substrate concentrations.

Even if the enzyme does not work under conditions demanded by industry, or for a broad range of substrates, all is not lost. Techniques such as protein engineering and directed evolution are increasingly being used to rapidly optimize the characteristics of enzymes (such as their substrate scope, stability and selectivity) to make them compatible with industrial processes[8]. Indeed, enzymes are the ultimate tunable catalysts, and will therefore surely be combined with many other chemical catalysts in the future. ■

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VISION

Birds perceive colours in categories

Humans perceive colours in categories such as red, even though we can discern red hues including ruby and crimson. It emerges that birds also categorize colours and this affects their colour-discrimination ability. SEE LETTER P.365

ALMUT KELBER

The amount of information reaching our sensory organs every second would be overwhelming if it were not for our ability to categorize it. Colour perception is a good example of this phenomenon. When we pick strawberries, we can easily discriminate between unripe fruit and fruit of the many different shades of red that indicate ripeness. Caves *et al.*[1] report on page 365 that zebra finches (*Taeniopygia guttata*) can also perceive a continuum of colours as belonging to distinct categories, a phenomenon that affects birds' ability to distinguish similar colours.

Although we can easily discriminate between the different shades of ripe strawberries, we tend to generalize and treat these shades as being equivalent. When comparing colours, if the differences between them are on the same scale of separation, our ability to perceive differences between colours from two separate categories, say 'red' and 'orange', is enhanced compared with our ability to perceive differences in colours that are both within one of these categories[2,3]. This enhanced ability to distinguish between colours if the colours are in separate categories is called categorical colour perception.

The preconditions necessary for the ability to perceive colours in distinct categories had already been demonstrated in birds. Humans and our close relatives have evolved to have three types of colour-sensing cone cell in the eye, and birds have evolved to have four types[4,5]. Birds have impressive colour-discrimination abilities[4], including the capacity to perceive the ultraviolet range of the spectrum. A remarkable earlier study[5] provided clear evidence that birds can generalize among certain colours, and thus divide the continuum of the colours that they perceive into discrete categories. But it was not known whether this ability affects how birds perceive similar colours and whether it helps them to spot key colour differences. Caves and colleagues investigated whether birds' ability to categorize colours affects their colour-discrimination abilities, and thus whether these animals have categorical colour perception.

"Birds are the only animals, besides primates, in which categorical colour perception has now been demonstrated."

The authors created an ingenious experimental set-up. Female zebra finches were presented with a device in which food was hidden beneath coloured discs. Food was present beneath bicoloured discs and absent below discs composed of a single colour. This training scheme allowed the authors to test how well the birds recognized colour differences by their ability to identify bicoloured discs when searching for food.

The authors studied a range of colours from orange to red, evenly dividing this part of the spectrum into eight shades of colour. Caves and colleagues made great efforts, using physiological models of bird colour vision, to make all of the steps between the shades equivalently

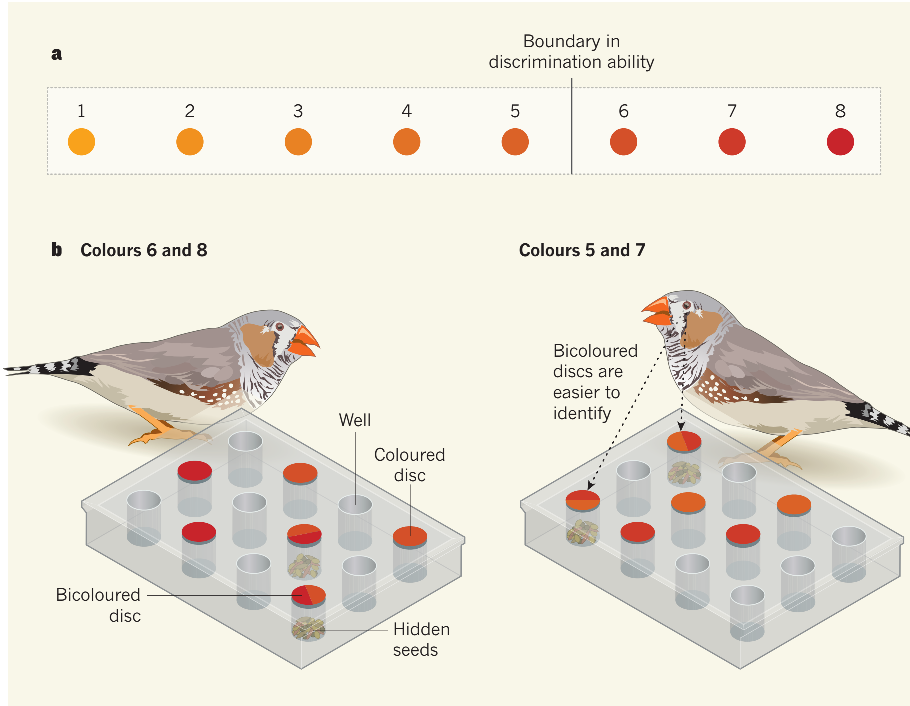

Figure 1 | Categorical colour perception in birds. Caves *et al.*[1] investigated colour perception in zebra finches (*Taeniopygia guttata*). The authors found that, like humans, the birds group colours into categories and this affects their colour-discrimination ability — a phenomenon called categorical colour perception. **a**, The authors tested birds' ability to distinguish between neighbouring colour pairs in eight evenly separated shades on the orange to red spectrum. Birds were substantially better at discriminating between shades 5 and 6 than between other pairs, suggesting that this represents a colour-category boundary. **b**, To test whether birds have the capacity for categorical colour perception, the authors presented birds with a device that had been designed so that the ability to distinguish between two colours and identify bicoloured discs enabled birds to access a food reward. The wells of the device contained seeds covered with bicoloured discs and empty wells that were either uncovered or covered by single-coloured discs of each of the colours on the bicoloured discs. The finches were less successful at identifying bicoloured discs if the colours were on the same side of the 5/6 category boundary (such as colours 6 and 8) than if the colours were in different categories (5 and 7).

sized on the birds' colour scale. These colours are worthy of attention because the zebra finch beak is red or orange. Beak colour depends on the amount of astaxanthin pigment deposited, which reflects the health of an individual's immune system[4], hence these colours might provide information about an individual's fitness. Females seem to be able to discriminate not only between males that have red or orange beaks, but also between males that have beaks of differing red shades[6]. However, whether female preference for males depends on male beak shade is debated[6].

Caves and colleagues first tested the finches using neighbouring pairs of shades from their eight-step colour scale and observed that birds distinguished between two of the shades better than between any other pair of neighbouring hues. This suggests that a putative border is present between the red and orange shades. The authors then investigated whether the birds were better at discriminating between pairs of colours of a similar level of shade separation that cross the proposed category boundary, compared with their ability to discriminate between colour pairs from one side of the category boundary (Fig. 1). Zebra finches passed this key test, demonstrating their capacity for categorical colour perception.

This result is fascinating and thought-provoking for many reasons. Birds are the only animals, besides primates[2,3], in which categorical colour perception has now been demonstrated. More work should be done to investigate whether other aspects of colour, such as intensity and spectral purity, influence categorical perception in birds. It would also be interesting to determine whether zebra finches' ability to group colours into 'red' and 'orange' has relevance for mate choice. However, this could be difficult to test because mate selection might depend on a range of male characteristics, such as the rate of male courtship displays[7], rather than only beak colour.

The work also has implications for our understanding of human colour perception. There is an ongoing debate about whether language — including colour terms such as red, blue, green and yellow — influences colour perception. One school of thought holds that colour categories have a cultural and linguistic basis[2]. The hallmark of categorical perception — faster and more-accurate discrimination of colours in different colour categories — is seen only if a subject's language has names for the specific colour categories being compared[2].

The other school of thought contends that colour perception has a biological basis that is not dependent on cultural and linguistic influences. Evidence to support this viewpoint includes the observation that terms for specific colours cluster around the same hues across different languages[3], and the fact that infants can discriminate between red, green, blue, yellow and purple before they have learnt the words for these colours[3]. Caves and colleagues' finding that birds have the capacity for categorical colour perception adds more evidence to support the biological basis of this phenomenon.

Why might categorization be important, and how does it fit into the broader context of signal perception? The term 'categorical perception' was coined to describe the human ability to distinguish sounds in discrete units, called phonemes, that help to discriminate one word from another (such as the sounds 'd', 't', 'b' and 'p' in the English words bad, bat, pad and pat[8]). Perception of phoneme-like elements also occurs in other animals, including birds[9]. Categorical perception could be described as a top-down mechanism to focus on key sensory cues by separating such signals from the enormous volume of irrelevant information. Another way to achieve this separation is a bottom-up approach termed 'matched filter', a concept which proposes that many animals' sensory organs are designed as filters that perceive only the range of information that is relevant to the organism[10]. These two approaches could together enable animals to handle the vast amount of sensory input that is needed to inform their choices and behaviours.

The level of contribution of these processes, and how they evolved in different animal clades, are topics worthy of further study. Caves and colleagues' work on zebra finches might be the start of a wider survey of categorical perception of colour in other animals. ■

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