

Visual Ecology: Coloured Fruit is What the Eye Sees Best

Dispatch

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Trichromatic vision may have evolved as an aid to frugivory. This hypothesis is supported by the recent demonstration that the spatial characteristics of pictures containing fruit are particularly well matched to the abilities of the human visual system.

Most mammals are dichromats and can only distinguish between two dimensions of colour: bright versus dark and blue versus yellow [1]. In contrast, humans are trichromats, our extra class of photoreceptor enabling us to discriminate between reds and greens which would otherwise appear identical. However, this ostensibly modest improvement in our visual capabilities has hidden costs: the increased sparsity of each type-specific cone matrix may theoretically reduce visual spatial acuity, and colour-anomalous ('colour-blind') humans, whose visual world is akin to that of dichromats, can sometimes see features camouflaged by red–green patterns that trichromats cannot detect [2]. Nonetheless, trichromacy is highly conserved in those few primate species that have evolved it. Of over 3,200 old-world monkeys and apes surveyed, inherited colour-anomalous vision has only ever been found in three closely related individuals [3,4], though on an evolutionary timescale such transmissible deficits are likely to have arisen spontaneously many times over. What tips the evolutionary balance so decisively in favour of trichromats?

Several explanations for the evolution of colour vision have been put forward [5]. Colour might serve as a cue for object recognition; animals may use colour to assess the health of other members of their species; and colour could aid image segmentation. But the hypothesis that has attracted the most attention is that trichromacy evolved as an aid to frugivory [6]. This notion is particularly attractive, as many fruits gradually turn yellow, red or orange during ripening. These colours are strikingly visible to trichromats, but dichromats have difficulty distinguishing them from a dappled background of green leaves [5] (Figure 1). Furthermore, fruit is an important component of most modern primate diets, and fossil [7] and physiological [8] evidence suggests that this was also true of early primates. As reported recently in *Current Biology*, Párraga *et al.* [9] have now demonstrated that the spatial characteristics of human red–green vision are better matched to scenes containing fruit than they are to natural scenes chosen at random (Figure 1).

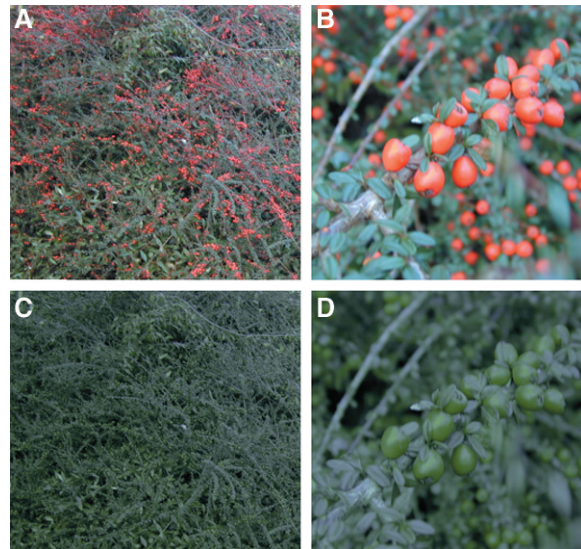


Figure 1: Fruits viewed close up and at a distance.

The top two scenes show in full colour (A) a distant picture of ripe fruit against a leafy background, and (B) a close-up of the same fruits. To remove any advantage in seeing fruit conferred by trichromacy, (C) and (D) on the bottom have had all red–green variation filtered out, but are otherwise identical to pictures (A) and (B). The fruit in (C) is less salient to dichromatic observers. In (D), individual fruits are easily visible, but colour cues to ripeness are weakened.

Previous tests of the trichromacy–frugivory hypothesis have been based on the observation that all trichromatic primate species investigated so far have remarkably similar photoreceptor spectral sensitivities [10]. This is notable because photopigments may undergo rapid evolution [11,12], and because they determine the regions of the spectrum our colour vision is most sensitive to. Alas, it looks increasingly unlikely that photoreceptor ecology will be able to address this particular question. Trichromacy may make it easier to detect fruit against green foliage [13] and to discriminate between ripe and unripe fruit [14], but our photoreceptors are probably optimised to see anything that is not leaf [13], rather than any particular class of object.

The experimental approach of Párraga *et al.* [9] is wholly different, and is founded on the study of image power spectra. In the same way as a graphic equaliser indicates whether a piece of music contains more high than low notes, subjecting an image to Fourier analysis shows how much of its detail occurs on a fine or a coarse spatial scale. The power spectra of luminance (bright–dark) and chromatic contrasts are similarly shaped for a wide range of natural scenes viewed from any distance [15], and there is good evidence that human luminance vision is optimised for such scenes [16]. But measurements of human contrast sensitivity functions suggest that our chromatic vision should have different biases from those of luminance

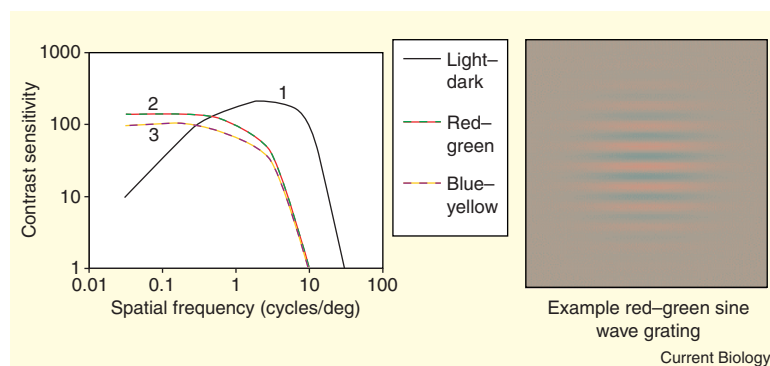


Figure 2. Sensitivity to sine-wave gratings of different spatial frequencies.

Sensitivity was measured by determining the threshold contrast required for each centrally fixated grating to become visible (after [19]). The curve for luminance vision, coloured black (1), shows that it is more sensitive to high spatial frequencies than chromatic vision — red-green (2) and blue-yellow (3) lines — but that we cannot detect variations in luminance if they subtend a sufficiently large visual angle. Sensitivity is still relatively high at low spatial frequencies for both the red-green and the blue-yellow chromatic axes.

vision. Both the red-green and blue-yellow chromatic axes are disproportionately concerned with low spatial frequencies (coarse detail) compared to the bright-dark axis, which is most sensitive to high spatial frequencies (fine detail; see Figure 2).

The main finding reported by Párraga *et al.* [9] is that, compared to the power spectra of previously measured sets of randomly chosen natural images, the power spectra of close-ups of reddish fruit are biased towards low spatial frequencies along the red-green axis. Thus, their shapes more closely match those that our vision finds optimal, and the most parsimonious explanation for why this should be is that natural selection optimised our red-green colour vision for scenes such as these. However, this conclusion rests on the premises that our contrast sensitivity functions are innately determined — and that if they are, this reflects ancient evolutionary pressures rather than physiological constraints. These assumptions may not be justifiable. We know that contrast sensitivity can be influenced by developmental environment [17], and that the low acuity of blue-yellow vision is in part due to chromatic aberration. On the other hand, the shapes of infant chromatic contrast sensitivity functions are probably similar to those of adults [18].

The secondary finding is that there is still a mismatch between the blue-yellow power spectrum of these fruit scenes and the spatial sensitivity of the blue-yellow colour system. Perhaps this should not come as too great a surprise: although blue-yellow colour vision doubtless aids identification of different fruits and ripeness discrimination [13,14], it is probably more useful for other tasks. We might not yet know what these tasks are, but there are certainly many non-frugivorous non-primates with dichromatic vision, who survive in a multiplicity of habitats [1]. Indeed, some trichromats such as gorillas and howler monkeys, are not predominantly frugivorous. Párraga *et al.* [9] argue that their result for the red-green axis may be valid for other classes of scenes, such as reddish faces against a leafy background, but this requires further investigation.

The red-green shift towards low spatial frequencies is only found if the camera is placed sufficiently close to the fruits. Párraga *et al.* [9] conclude their paper by estimating the viewing distance for which their scenes best match human contrast sensitivity functions,

calculating that 0.4 metres is roughly optimal. This is similar to the reach of many primate species, and so is arguably the distance one might expect. Yet anecdotal reports suggest that human dichromats have difficulty detecting the presence of fruit in distant trees, but are able to use form to segment out individual items at closer range [5] (see Figure 1). Perhaps we need a better understanding of what visual tasks a frugivorous trichromat performs, before we can investigate links between trichromacy and frugivory further. Hypothetically, a primate coveting a single item of fruit might approach it closely, fixate the fruit centrally and use colour cues to estimate its ripeness. A second primate searching for a plush fruit tree would probably make more use of its peripheral vision, surveying many trees from afar. Tasks as disparate as these make very different demands of an animal's visual system, a fact that may ultimately be reflected in its make-up.

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