

21. Hill, G. E. Plumage coloration is a sexually selected indicator of male quality. *Nature* **350**, 337–339 (1991).
22. Cuthill, I. C., Bennett, A. T. D., Partridge, J. C. & Maier, E. J. Plumage reflectance and the objective assessment of avian sexual dichromatism. *Am. Nat.* **160**, 183–200 (1999).
23. Andersson, S. Morphology of UV reflectance in a whistling-thrush: implications for the study of structural colour signalling in birds. *J. Avian Biol.* **30**, 193–204 (1999).
24. Keyser, A. J. & Hill, G. E. Condition-dependent variation in the blue-ultraviolet coloration of a structurally based plumage ornament. *Proc. R. Soc. Lond. B* **266**, 771–777 (1999).
25. Krackow, S. Potential mechanisms for sex ratio adjustment in mammals and birds. *Biol. Rev.* **70**, 225–241 (1995).
26. Komdeur, J., Daan, S., Tinbergen, J. & Mateman, A. C. Extreme adaptive modification of the sex ratio of the Seychelles warbler's eggs. *Nature* **385**, 522–525 (1997).
27. Kilner, R. Primary and secondary sex ratio manipulation by zebra finches. *Anim. Behav.* **56**, 155–164 (1998).
28. Nager, R. G., Monaghan, P., Griffiths, R., Houston, D. C. & Dawson, R. Experimental demonstration that offspring sex ratio varies with maternal condition. *Proc. Natl Acad. Sci. USA* **96**, 570–573 (1999).
29. Emlen, S. T. When mothers prefer daughters over sons. *Trends Ecol. Evol.* **12**, 291–292 (1997).
30. Griffiths, R., Double, M. C., Orr, K. & Dawson, R. J. G. A DNA test to sex most birds. *Mol. Ecol.* **7**, 1071–1075 (1998).

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Perception of three-dimensional shape influences colour perception through mutual illumination

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Objects in the natural world possess different visual attributes, including shape, colour, surface texture and motion. Previous perceptual studies have assumed that the brain analyses the colour of a surface independently of its three-dimensional shape and viewing geometry^{1,2}, although there are neural connections between colour and two-dimensional form processing early in the visual pathway^{3,4}. Here we show that colour perception is strongly influenced by three-dimensional shape perception in a novel, chromatic version of the Mach Card—a concave folded card with one side made of magenta paper and the other of white paper. The light reflected from the magenta paper casts a pinkish glow on the white side. The perceived colour of the white side changes from pale pink to deep magenta when the perceived shape of the card flips from concave to convex. The effect demonstrates that the human visual system incorporates knowledge of mutual illumination—the physics of light reflection between surfaces—at an early stage in colour perception.

To quantify this phenomenon, we constructed a concave card with trapezoidal sides which appeared rectangular when viewed from a distance (Fig. 1a). We painted the left side of the card magenta, the right white. Mutual illumination between the two sides generated a strong chromatic gradient across the white side, so that its measured chromaticity varied from deep pink near the crease to pale pink at its outer edge (Fig. 1b). By diluting the magenta paint with increasing amounts of white paint, we created a set of 23 alternative matching colours on small chips, densely

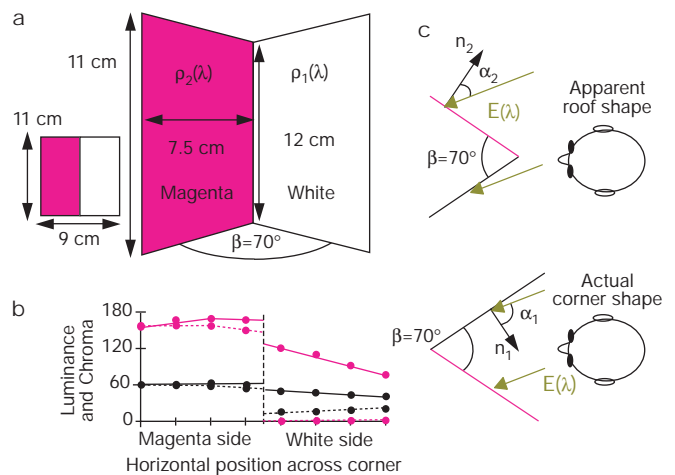


Figure 1 The experimental stimulus. **a**, The chromatic Mach card. The large drawing gives its actual dimensions, with exaggerated perspective cues; the small drawing shows its actual appearance. Average luminance and chromaticity values: 56.58, 0.49, 0.52 (magenta side) and 42.43, 0.45, 0.52 (white side) (CIE 1976 $L^*u^*v^*$ coordinates). **b**, Solid lines, measured variation in chroma (magenta line) and lightness (black line) horizontally and centrally across the card (see Methods). Dashed lines, measurements without mutual illumination (obtained by replacing alternate sides with black paper). **c**, Plan views of the stimulus, illustrating the inversion of the card under pseudoscopic viewing, and the approximate direction of the light source E .

sampling a rough line from magenta to white in uniform colour space (inset, Fig. 2). The card was attached to the back wall of a black box (the stimulus box) and illuminated by a hidden incandescent lamp regulated by a dimmer. A panel containing the coloured chips was attached to the back of a second black box (the matching box) and illuminated by two hidden incandescent bulbs. The illumination in each box was adjusted to produce the same chromaticity and luminance from a central white card, which was removed prior to the experiment.

In the ‘roof’ condition, observers viewed the card through a pseudoscope, a binocular viewing stand fitted with Dove prisms. The prisms invert the image in each eye from left to right, thereby reversing binocular stereo disparities and with them, the depths of objects in the image. The card therefore appeared convex. In the ‘corner’ condition, observers viewed the card through empty but otherwise identical viewing tubes. The card now appeared concave, its true shape. In the roof condition, the white side of the card appeared on the left; in the corner condition, the white side appeared on the right (Fig. 1c). Because the contour cues indicated a flat card and there were no visible shadows in the black stimulus box, the primary cue to the card’s three-dimensional shape was from binocular disparities. Observers were instructed to match the colour of the left (roof) or right (corner) side by selecting from the matching panel a chip identical in colour appearance (see Methods). In the control condition, observers followed the same procedure to match the colour of an unfolded, pink card, viewed with and without the pseudoscope.

The results (shown for 23 observers in Fig. 2) demonstrate a significant shift in perceived colour of the white side from a desaturated pink in the corner condition to a more saturated magenta in the roof condition. There is no shift in perceived colour of the flat control card under the two viewing conditions (Fig. 3a; the two distributions are statistically indistinguishable [$F(1, 90) = 0.05$ at $P = 0.8$]).

The effect cannot be explained in the same way as the classical Mach Card effect. The original Mach Card is a convex folded grey card, one side brightly illuminated and the other in shadow⁵. When the card is perceived correctly to be convex (roof), the two sides

appear the same grey; when perceived to be an inward-pointing corner, the shaded side appears to be painted a darker grey than the lit side. Mach concluded that the human visual system assumes that the direction of illumination is the same for both configurations, so that in the roof, the dark side is turned away from the light source, but not in the corner. In a quantitative demonstration of the phenomenon, Beck⁶ confirmed that observers' assumptions about the number and positions of light sources illuminating the card did indeed influence their lightness matches to both sides. Other studies support the explanation that implicit knowledge about light source and scene geometries or perceived surface layout may directly influence surface lightness perception^{7–11,23}.

The chromatic effect we report here cannot be explained by the above lightness effects, for two reasons. Firstly, in our setup, the light source is deliberately hidden, so that observers cannot be certain of any fixed direction of illumination. In fact, under these conditions, the classical Mach Card effect does not obtain, as we have shown in another experiment¹². Secondly, even if observers were to deduce the approximate location of the light source, they would conclude that the white side received more direct illumination in the corner shape than in the roof shape, because of the inversion induced by pseudoscopic viewing (Fig. 1c). Mach's explanation would therefore predict that the white side should appear darker in the corner than in the roof. This prediction cannot account for our results, because the less saturated matching chips neither are nor appear darker, as we demonstrated in a separate ranking experiment under the same illumination conditions.

Instead, the chromatic effect appears to depend on an inbuilt, perceptual understanding of the laws of mutual illumination. Mutual illumination—the indirect illumination created by light reflected from surfaces onto each other, as opposed to direct illumination from the primary light source—has largely been neglected in analyses of surface colour and shape perception, with a few exceptions^{13,14}. Recent analyses have shown that the chromatic component of mutual illumination may provide cues to the intrinsic surface reflectance of participating surfaces, and therefore enhance colour constancy¹⁵. Psychophysical studies of colour constancy in real^{16,17} and computer-simulated scenes¹⁸ suggest that the human visual system may indeed exploit the information that mutual illumination conveys to recover constant surface colours.

Our present study demonstrates that surface colour perception is contingent on three-dimensional shape perception. A simple model based on bayesian inference¹⁹ demonstrates that this shape–colour

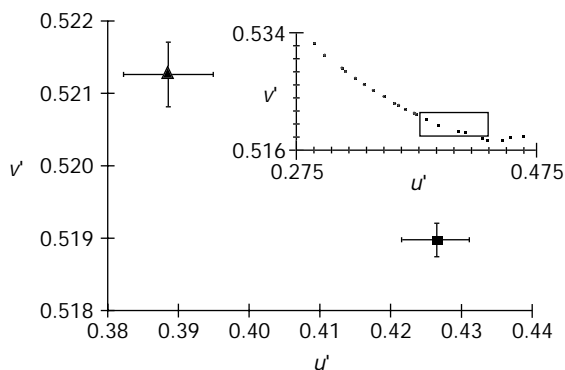


Figure 2 Average (u' , v') coordinates of the matches selected for the white side of the card. Data is shown when seen as a corner, without pseudoscope (triangles), and as a roof, with pseudoscope (squares). Error bars show s.e.m. ($n = 24$ corner, $n = 20$ roof). The difference between the roof and corner average matches is approximately ten times larger than threshold. Inset, the distribution of u' and v' chromaticity coordinates (CIE 1976 $L^*u'v'$) of the 23 matching chips under the illumination conditions used during the experiment. The rectangle indicates the area represented in the main graph.

contingency arises because the human visual system must intrinsically understand the effects of mutual illumination.

The model computes how an ideal observer would perform when asked to select the paper most likely to constitute the 'white' side under the two conditions. The ideal observer is limited only by the internal matching noise and is provided with the following physical information for the task: (1) an understanding of the physics of light reflection, and specifically of mutual illumination; (2) an *a priori* assumption of a single light source and independent knowledge of its energy spectrum; (3) independent knowledge of the card's shape; and (4) independent knowledge of the surface reflectance function of the magenta side, as well as of the matching chips (see Methods). This information determines the likelihood that the surface reflectance of a particular chip would give rise to the observed colour of the 'white' side; this likelihood determines the probability that the ideal observer selects that chip.

The predicted colour of the 'white' side for a particular surface reflectance varies with the direction of the light source. For the model we assume that each direction is equally probable, and integrate over all light source directions to obtain the *a posteriori* probability for each matching chip. This calculation is equivalent to the "generic view" method²⁰, using the direction of the incident illumination as the generic variable. The only difference between the calculation of the predicted match for the corner and roof configurations is that mutual illumination is allowed in the former but not in the latter.

This single feature—the presence or absence of mutual illumination—is necessary and sufficient to make the predicted probability distributions significantly different for the roof and corner configurations (Fig. 3b). Furthermore, the behaviour of the ideal observer predicts the crucial features of the observed matches: the difference

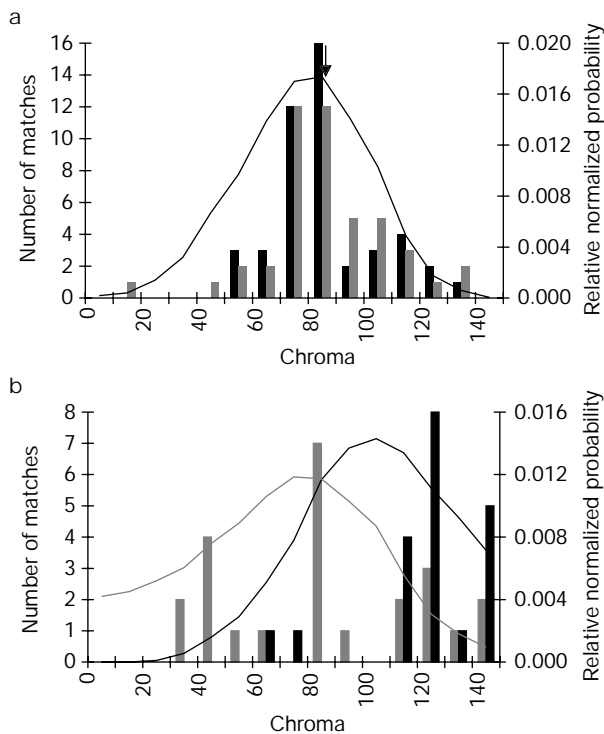


Figure 3 Observed matches and model predictions. **a**, Distribution in chroma of matches to flat control card with (black bars) and without (grey bars) pseudoscope, for 46 total matches by 23 observers, for each condition. Bin size 10; the magenta chip (number 23) has chroma 149. Arrow indicates actual chroma (86) of control card. **b**, Distribution in chroma of matches to the white side of the chromatic Mach card. Grey bars, corner shape, without pseudoscope ($n = 24$). Black bars, roof shape, with pseudoscope ($n = 20$). Overlaid curves show the predicted probability distributions as described in Methods.

between their means (31 chroma units, statistically indistinguishable from the observed mean difference of 35 ± 17), and the spread and overlap of the non-normal distributions (standard deviations of 26 versus observed 22 ± 10 , and 32 versus observed 35 ± 7 , for the roof and corner conditions, respectively; see Methods).

The model predictions demonstrate that the real observer behaves close to the ideal, and, in particular, that the real observer's visual system incorporates accurate knowledge of the effects of mutual illumination. The systematic shift in the absolute values of the observed means compared with the predicted means (Fig. 3b) suggests that the real observer lacks the ideal observer's access to accurate and complete physical measurements, in particular the illuminant spectrum.

It is important to emphasize that the real observer's task was to match the colour of the 'white' side, a direct sensory match, not to match the paper from which it was most likely to be constructed, an indirect match requiring a judgement of surface identity¹. The observer perceives two different colours from the same retinal stimulus under the two different configurations. The model performs a high-level, indirect match, and yet predicts the observed difference in low-level, direct matches. This fact suggests that there is a top-down influence of surface recognition on colour perception, similar to the reported effects of lightness judgements on perceived brightness in the achromatic domain¹¹. This influence is mediated by an in-built knowledge of the chromatic effects of mutual illumination, which dictates that the perception of surface colour and three-dimensional shape are fundamentally linked. □

Methods

Matching procedure

After securing a fused image of a test circle against a grid through the pseudoscope, the observer viewed the folded test card or flat control card in the stimulus box for at least 10 seconds, at a viewing distance of 57 cm. The observer reported whether the folded card was a 'roof' or 'corner' shape. He then moved to the adjacent matching box where the matching chips (each 3 degrees square) were displayed in a 5 × 5 array with 1-degree-wide gaps, against a black background. Each of four such panels, each with a different random arrangement of chips, was displayed in one of four different rotational positions, randomised across trials, to yield a total of 16 different matching displays. The observer selected the chip (by marking its equivalent position on a paper grid) that best matched the specified left or right side of the card. For each change in stimulus, the experimenter drew a black cloth across the front of the stimulus box, so that the observer's view of the card was always through the viewing tubes. Observers were randomly assigned to one of two groups: corner or roof condition first, with the control conditions interleaved between two trials of the same condition. Matches are reported for the first-viewing-only conditions.

Calculation of lightness and chroma

The lightness (L^*) of a surface it is relative brightness compared to a white surface under the same illumination. Chroma (C) is defined as the colourfulness of a surface judged as a proportion of the brightness of a similarly illuminated surface that appears white. Their numerical correlates are calculated as:

$$L^* = 116 \left(\frac{Y}{Y_n} \right)^{\frac{1}{3}} - 16$$

$$C = \sqrt{(u^*)^2 + (v^*)^2}$$

$$u^* = 13L^*(u' - u'_n)$$

$$v^* = 13L^*(v' - v'_n)$$

where Y_n , u_n and v_n are the chromaticity coordinates of a flat white reference paper ($C = 0$ and $L^* = 100$) under the illumination conditions of the stimulus box, in CIE $L^*u'v'$ colour space²¹.

Ideal observer model

For the corner configuration, a vertically infinite surface of reflectance $\rho_2(\lambda)$ forms an angle β of 70 degrees with another of reflectance $\rho_1(\lambda)$. The illuminant $E(\lambda)$ forms angles α_2 and α_1 with the two surface normals, respectively (see Fig. 1). The one-bounce model of mutual illumination¹⁵ yields the intensity equation for surface 1: $I_1(\lambda, x) = E(\lambda)\rho_1(\lambda) [\cos \alpha_1 + f_{21}(x)\rho_2(\lambda) \cos \alpha_2]$, where the first term represents the direct illumination and the second term represents indirect (mutual) illumination due to light reflected from surface 2. $f_{21}(x)$ is the β -dependent form factor describing the extent to which surface 2 reflects light onto surface 1 at distance x from the vertex. $\rho_2(\lambda)$ is specified as the measured reflectance function of chip 23 (identical to the magenta side of the card). $E(\lambda)$ is a

tungsten illuminant spectrum reconstructed from the measured chromaticity values of a white reference paper under the illumination conditions in the stimulus box, using the Cohen basis functions²¹. The surface reflectance $\rho_1^i(\lambda)$ is the measured surface reflectance of the i th matching chip ($i = 1, 2, \dots, 23$). Reflectance functions and the illuminant spectrum are specified in 10-nm steps. For the corner shape, surface 1 receives direct illumination for values of α_1 between 0 (normal to surface 1) and 90 degrees, and indirect illumination for α_1 from 20 to 110 degrees (normal to surface 2). For each value of α_1 between 0 and 110 degrees, in 1-degree steps, and for each surface reflectance $\rho_1^i(\lambda)$, the predicted light intensity $I_1^i(\lambda, x)$, at each of four positions x on surface 1, is computed according to the above formula. From $I_1^i(\lambda, x)$, the predicted luminance, hue and chroma of the 'white' side is computed using the CIE 1964 supplementary standard colorimetric observer and standard colorimetric formulae—the predicted colour of the 'white' side if its surface reflectance were $\rho_1^i(\lambda)$ and it participated in mutual illumination with the magenta side. The differences between the predicted chroma $C(\alpha_1, x)$ and the measured chroma $C_{obs}(x)$ at each position x on the 'white' side are computed and converted to an *a posteriori* probability P for the i th matching chip, by summing over all (110) illuminant directions α_1 and all four sample positions x , and normalizing areas under the curves to unity: $P(\rho_1^i | C_{obs}) = (1/k) \sum_{\alpha_1} \sum_x \exp - (|C_{obs} - C(\alpha_1, x)|^2 / (2\sigma^2))$, where k is the normalizing constant. Here σ is the only free parameter, representing the internal observation error; it is therefore chosen as the value that best predicts the distribution of chroma matches to the flat control card (that is, $\sigma = 20.36$).

For the roof configuration, the intensity equation for surface 1 is $I_1(\lambda) = E(\lambda)\rho_1(\lambda) \cos \alpha_1$. Because surface 1 receives neither direct nor indirect illumination for values of α_1 between 90 and 110 degrees, in this computation α_1 is allowed to vary only from 0 to 90 degrees. Otherwise, the calculation is the same as for the corner configuration.

Calculation of observed mean and standard deviation errors

The 95% confidence intervals for the standard deviations and differences between roof and corner means were estimated by resampling²².

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1. Arend, L. E. & Reeves, A. Simultaneous color constancy. *J. Opt. Soc. Am.* **3**, 1743–1751 (1986).
2. Troost, J. M. in *Perceptual Constancy—Why Things Look As They Do* (eds. Walsh, V. & Kulikowski, J.) (Cambridge University Press, 1998).
3. Gegenfurtner, K. R., Kiper, D. C. & Fenstermaker, S. B. Processing of color, form and motion in macaque area V2. *Vis. Neurosci.* **13**, 161–172 (1996).
4. Zeki, S. & Shipp, S. Modular Connections between areas V2 and V4 of macaque monkey visual cortex. *Eur. J. Neurosci.* **1**, 494–506 (1989).
5. Mach, E. *The Analysis of Sensations* (Dover, New York, 1886/1959).
6. Beck, J. Apparent spatial position and the perception of lightness. *J. Exp. Psychol.* **69**, 170–179 (1965).
7. Gilchrist, A. L. Perceived lightness depends on perceived spatial arrangement. *Science* **195**, 185 (1977).
8. Gilchrist, A., Delman, S. & Jacobsen, A. The classification and integration of edges as critical to the perception of reflectance and illumination. *Percept. Psychophys.* **33**, 425–436 (1983).
9. Ramachandran, V. S. Perception of shape from shading. *Nature* **331**, 163–166 (1988).
10. Knill, D. C. & Kersten, D. Apparent surface curvature affects lightness perception. *Nature* **351**, 228–230 (1991).
11. Adelson, E. H. Perceptual organization and the judgement of brightness. *Science* **262**, 2042–2044 (1993).
12. Bloj, M. G. & Hurlbert, A. C. The influence of shape and illuminant position cues on surface lightness perception. *Invest. Ophthalmol. Vis. Sci.* **40**, S981 (1999).
13. Forsyth, D. & Zisserman, A. Shape from shading in the light of mutual illumination. *Image Vision Comput.* **8**, 42–49 (1990).
14. Nayar, S. K., Ikeuchi, K. & Kanade, T. Shape from interreflections. *Int. J. Comput. Vis.* **6**, 173–195 (1991).
15. Funt, B., Drew, M. & Ho, J. Color constancy from mutual reflection. *Int. J. Comput. Vis.* **6**, 5–24 (1991).
16. Nuberg, N. D., Bongard, M. M. & Nikolaev, P. P. I. On constant perception of colour. *Biophysika* **16**, 285–293 (1971).
17. Kraft, J. M. & Brainard, D. H. Mechanisms of colour constancy under nearly natural viewing. *Proc. Natl Acad. Sci. USA* **96**, 307–312 (1999).
18. Bloj, M. G. & Hurlbert, A. C. Does mutual illumination improve human colour constancy? *Invest. Ophthalmol. Vis. Sci.* **36**, S639 (1995).
19. Knill, D. C. & Richards, W. *Perception as Bayesian Inference* (Cambridge University Press, 1996).
20. Freeman, W. T. The generic viewpoint assumption in a framework for visual perception. *Nature* **368**, 542–545 (1994).
21. Wyszecki, G. & Stiles, W. S. *Color Science: Concepts and Methods, Quantitative Data and Formulae* (Wiley, New York, 1982).
22. Efron, B. & Tibshirani, R. *An Introduction to the Bootstrap* (Chapman & Hall, New York, 1993).
23. Williams, S. M., McCoy, A. N. & Purves, D. The influence of depicted illumination on brightness. *Proc. Natl Acad. Sci., USA* **95**, 13296–13300 (1998).

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A Trapezoidal Chromatic Mach Card

3D shape perception influences colour perception via mutual illumination.

Our original study, reported in Nature (Bloj, Kersten, & Hurlbert, December 23, 1999), used a pseudoscope to reverse the apparent depth relief in a folded card. You can experience a similar reversal by making a trapezoidal card.

Stimulus preparation. 1. Print out this page on a color printer. 2. Cut out the figure on the right with a scissors. 3. Fold it in half along the mid-line (A) so that the red panel faces the white panel. 4. Fold again (lines B and B') so that the two black panels face outward.

Demonstration. Set the folded card on a flat surface as shown below. Orient the card so that the red panel receives direct lighting from a lamp or window. The red side should thus reflect a little pinkish light onto the white side. You may have to pinch crease A to make the angle between the red and white sides small enough. The concave corner A should be farther from you than convex corners B or B'. The idea is the perspective is opposite to what you are used to - the longer edge (A) is further (rather than nearer) from you than from B or B'. This perspective trick can now be used to make the card *appear* as though the red side is facing *away* from the white card. View the card steadily with one eye until the card's geometry appears to change and A seems to be closer to you than B or B'. I.e. crease A goes from appearing concave to convex (like looking down on the "roof" of a house). At this point, you should also see that the white panel appears to change from pinkish white to magenta.

