

cryospheric components, including snow cover, permafrost and ice sheets, together with temperature data, to help detect the fingerprints⁹ of greenhouse global warming.

Ola M. Johannessen*

Martin Miles

Einar Bjørge

Nansen Environmental and Remote Sensing Center,

Edvard Griegsvei 3a,

5037 Solheimsvik/Bergen, Norway

*Also at Geophysical Institute, University of Bergen, 5007 Bergen, Norway.

What do colour-blind people see?

SIR — Most human observers enjoy trichromatic vision: a three-dimensional colour space represents all the light that they can discriminate¹. Two per cent of the male population are dichromats, that is, they lack one class of photopigment and have a colour gamut that can be represented in a two-dimensional space. Here we offer to the normal trichromat a simulation of the reduced colour gamut seen by the dichromat. Our algorithm incorporates a strictly colorimetric transformation, but must also make explicit assumptions about the residual sensations experienced by dichromats.

For the normal trichromat, all discriminable light can be represented in three-dimensional space, with axes corresponding to the signals of the long-wave (L), middle-wave (M) and short-wave (S) cones²⁻⁵. Protanopes, deuteranopes and tritanopes lack L, M and S photopigments, respectively⁶. They confuse lights that differ only in the excitation of the missing class of cones; one of the three vector components is physiologically undetermined. In this simulation, we treat dichromatic vision as a reduction of the vision of the average normal observer, although both normal and dichromatic vision are known to be polymorphic⁷ and refinements of our algorithm could simulate alternative forms of, say, deuteranopia for alternative types of normal.

For the physiologically undetermined component, we choose values so as to imitate, for a normal observer, the appearance of colours for the dichromat. To this end, we make the following assumptions based on the colour perceptions reported by unilateral dichromats. First, we assume that neutral colours for normal observers are perceived as neutrals by dichromats. Accordingly, neutral stimuli, including any metamer, are not changed by the simulation and define the achromatic axis in the LMS colour space for both the dichromat and the normal. Second, we assume that the achromatic axis divides the surface of reduced



Reproduction of the video monitor display that simulates the reduced colour gamut of dichromatic colour-defective observers. *a*, Photograph of the 'Jardin des Plantes' (photo: Jean Le Rohellec; Grande Galerie, FNAC). The contrast was reduced to allow for all three projections onto the reduced stimuli surfaces to exist. *b*, *c*, *d*, Simulations of how *a* is seen by a protanope, deuteranope and tritanope, respectively. (A colorimetrically exact reproduction of the video display cannot be guaranteed in the printed version.)

stimuli into two half-planes, each corresponding to a single hue. Third, we assume that a stimulus of 575 nm is perceived as the same yellow, and a stimulus of 475 nm as the same blue, by trichromats as by protanopes or deuteranopes⁸. In a case of unilateral acquired tritanopia, the corresponding two hues were a red–pink at a dominant wavelength of 660 nm, and a blue–green at a dominant wavelength of about 485 nm (ref. 9).

Each half-plane of reduced stimuli in LMS space encompasses the achromatic axis and is anchored on a point specifying the invariant monochromatic radiation. Given the LMS specification of a stimulus, the algorithm replaces the undetermined component by the value corresponding to the projection of the original stimulus on the reduced stimuli surface, parallel to the direction of the missing fundamental axis.

The figure presents our simulation of the reduced colour gamut seen by each class of dichromat, after transformation of each pixel of a digitized picture. The L, M and S tri-stimulus values of each of the red, green and blue primary colours of the video monitor were determined by weighting their measured radiance spectra by the L, M and S sensitivities⁵. A protanope and a deuteranope were each satisfied with the match between the original image and the transformation corresponding to their particular deficiency, but they discriminated the original from the other transformations.

These responses of dichromats serve as a necessary check on our colorimetry; however, for any given image there are an

infinite number of alternative reductions that are metameric images for a particular type of dichromat. In using the rare cases of unilateral dichromacy to infer the residual sensations of the ordinary daltonian, we have followed an established tradition⁸. We do, however, recognize that the existence of unilateral dichromacy in male observers still lacks a genetic explanation and that the 'good' eye in such cases is seldom entirely normal¹⁰. There is one positive advantage in the particular wavelengths we have chosen to represent the residual sensations of protanopes and deuteranopes. At 575 nm, the Abney effect is minimized, that is, there is little change of hue at this dominant wavelength as the purity of the stimulus changes¹¹. At 475 nm, the loci of constant hue are curved, but mainly when they approach the spectrum locus¹². Within the colour gamut achievable on a video screen, stimuli within each half-plane of

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reduced stimuli look uniform in hue to a colour-normal observer, as they are assumed to look to a dichromat.

The availability of computer-controlled colour displays has allowed us to develop something that has often been asked for by nonspecialists — a simulation of how the dichromat perceives a complex coloured scene. Our algorithm should be of value to those who prepare display screens and colour-coding systems for use by the public. Although the quality of another's sensations can never fully be known, the present simulation illustrates, for the normal observer, the range of the daltonian's colour experience.

F. Viénot

H. Brettel*

Muséum National d'Histoire Naturelle,
CNRS UPR 257, 43 rue Cuvier,
75005 Paris, France

L. Ott

A. Ben M'Barek

Ecole Nationale Supérieure de
l'Electronique et de ses Applications,
95014 Cergy-Pontoise, France

J. D. Mollon

Department of Experimental Psychology,
University of Cambridge,
Cambridge CB2 3EB, UK

*Present address: CNRS URA 820, Département Images,
ENST, 46 rue Barrault, 75013 Paris, France.

How 'bad genes' survive

SIR — Wilcockson *et al.*¹ report the results of a study of genetic variance of body size in the seaweed fly (*Coelopa frigida*); large males are preferred by females in mating. Most of the genetic variance is expressed in males and is located in the $\alpha\beta$ heterotic-inversion system. The authors state, "Because heterotypic larvae exhibit superior viability, mate preferences based on size could generate fitter offspring, a slightly unusual type of 'good genes' female choice."

The fact that there is considerable additive genetic variance for size indicates that large size itself is not heterotic, and the authors do not say this. The suggestion of some kind of female choice in a heterotic system does, however, highlight a problem with the 'good genes' theory. The question is: what maintains the genetic variation from which the females choose? Why are 'bad genes' present to be rejected? Ewens² has shown that, at equilibrium, for a range of selection regimes there is no additive genetic variance for fitness. Charlesworth³ has discussed this in relation to the 'female choice' problem.

For the two-allele heterosis case, it is easy to show that, at equilibrium, with random mating the fitness of the offspring mated to the superior heterozygous males is the same as that of females mated to

FITNESS OF THE OFFSPRING OF FEMALES
MATED TO MALES BEARING ALLELES
A1 AND/OR A2

	A1A1 males	A1A2 males	A2A2 males
Female offspring	0.6775	0.6770	0.6740
Male offspring	0.6084	0.6101	0.6117

either one of the two inferior homozygotes and is equal to $1 - s/(s+t)$, where s and t are the selection coefficients against the two homozygotes relative to the heterozygote. If females choose to mate with the superior heterozygous males, then there is additional sex-limited heterosis in the males. This case cannot be solved analytically, but is amenable to simulations. For example, if the relative viabilities of the three genotypes in both sexes are 0.3, 1 and 0.4 and the relative mating successes of the male genotypes are 0.5, 1 and 0.7, the equilibrium frequencies of the three adult genotypes are 0.0938, 0.7339 and 0.1720. The table shows the mean fitness, at equilibrium, of the offspring of the females depending on the males to which they mate. The male offspring fitnesses include their future mating success and are lower because of the increased selection against the homozygotes relative to heterozygotes.

A survey of parameters involving more or less intense selection and symmetric as opposed to asymmetric selection on homozygotes gives the same result of essentially equal offspring fitnesses. The extremely slight differences in offspring fitness always show the offspring of preferred heterozygous males as being intermediate.

We emphasize that this is not meant to be a model of the seaweed fly system which is more complicated, including polygenic variation. We do propose, however, that the same problem applies when variation is maintained by simple balancing selection. The purpose of this simple exercise is to provide a reminder of a theoretical conundrum posed by the cause of variation in 'good genes' theories. Charlesworth³ and others have suggested solutions to this problem, such as cycling variation, migration, antagonistic pleiotropy and mutation selection equilibrium; these possibilities should be pursued when female choice is encountered.

Timothy Prout

Norman Eaton

Center for Population Biology,
University of California,
Davis, California 95616, USA

WILCOCKSON ET AL. REPLY — 'Good genes' sexual selection usually refers to the selection of mates with high genetic quality, and the subsequent production of progeny of high fitness. In spite of the general acceptance of good genes as an explanation for female mate choice (particularly outside the specialist genetic literature and in

popular television programmes), there are serious difficulties in understanding exactly how it could work as an evolutionary process³. The problem is that classical population-genetic theory predicts that no additive genetic variation of fitness should exist at equilibrium; and yet we have demonstrated high heritability for a sexually selected character, male size¹. This apparent contradiction is resolved if it is recognized that fitness is a theoretical concept of which experimental biologists can only measure components. In addition, Pomiankowski and Møller⁴ have recently provided a theoretical basis for understanding how genetic variability in sexually selected traits could be maintained.

We suggested that in seaweed flies there exists a "slightly unusual type of good genes female choice". If females prefer to mate, not with males of high viability as in the model of Prout and Eaton, but with the less viable homozygotes (strictly speaking, homokaryotypes), and if females mate disassortatively, then the progeny produced are indeed fitter⁵. In heterotic systems, homozygous females mating with males homozygous for a different allele produce heterozygous offspring with the highest viability. The mating preferences of heterozygous females are of little consequence in terms of offspring viability. Observations on some, though not all, natural populations of seaweed flies suggest that females do exhibit such a pattern of mating⁶. This means that males cannot be said to have 'good' or 'bad' genes; it is the complementarity of sperm and eggs that is important.

In seaweed flies, beauty is in the eye of the beholder, and is judged on the basis of size. Although size itself is not heterotic, its major genetic determinant, a polymorphic chromosomal inversion system, is. Furthermore, the genes determining female preference may well be in linkage disequilibrium with this same inversion system^{7,8}. It will be interesting to see if heterotic systems in other species are subject to 'good genes' sexual selection of this sort. Perhaps we shall be proved wrong in saying that mate choice in female seaweed flies is of an unusual type.

Ray Wilcockson

Caroline Crean

Tom Day

Department of Genetics,
University of Nottingham,
Nottingham NG7 2UH, UK

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