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Scotopic vision in colour-blinds

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Abstract

Alleles causing colour-blindness are present in humans at non-negligible levels, and it is not yet understood how colour-blindness is maintained, since colour-vision probably provides a selective advantage, e.g. when foraging. We show that after dark-adaptation colour-blinds had lower light perception thresholds than colour-normals (0.44 log-units), which may give a selective advantage under scotopic conditions, which may offset the disadvantage that colour-blinds suffer during foraging. © 1998 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Old world monkeys, apes and man have trichromatic colour vision which provides a selective advantage over dichromatism, e.g. when foraging for fruit [1–3]. Nevertheless, alleles causing colour-blindness are present in humans at non-negligible levels (approximately 8% of caucasian males), and it is not yet understood how colour-blindness is maintained in the face of the selection for trichromatic colour vision [4,5]. Morgan et al. [4] showed that human dichromats were better able to detect texture camouflaged by colour than colour normal trichromats, and suggest that ‘the ability to penetrate camouflage, combined with frequency dependent selection, could account for the maintenance of dichromacy’. In this paper we test the hypothesis that colour-blinds have enhanced scotopic vision, which would give a further selective advantage to colour-blinds under scotopic conditions, for example because this makes it easier to detect nocturnal predators, and to forage in low light conditions.

The ability to see colours varies widely between species, and trying to understand this diversity is one of the classic themes in vision research. Although our primary aim is to shed light on the puzzling maintenance of colour-blindness in human populations, infor-

mation regarding the intraspecific relationship between visual performance under different conditions and variation in colour vision ability can potentially help to provide a functional explanation of the large interspecific variation in colour vision.

2. Methods

To test our hypothesis that luminance-thresholds differ between colour-normals and colour-blinds we carried out a retrospective analysis of dark adaptation curves of 326 subjects which were measured in student-practicals designed to study dark-adaptation. Hence both students and supervisors were naive with respect to the hypothesis tested in this report. Groups of two to three students ($n = 326$) in animal-physiology courses in the years 1991–1996 measured each other’s dark adaptation curves, alternating as experimenter and subject. With Ishihara-plates subjects were categorised as colour-normal ($n = 313$), protans ($n = 7$) or deutans ($n = 6$). Of all subjects 4% were colour-blind (2/146 females, 11/180 males). Subjects were seated in a dark room, and light-adapted by gazing for 2 min at a back-lit white filter paper (luminance ca. 1000 cd/m²) at nose-length distance. Subsequently, they viewed an opening in the door (9 × 9 cm) from 80 cm, which was covered by a Kodak Wratten filter (six different types,

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Fig. 1), and thresholds for binocular vision were measured each minute for 30 min using incandescent light. The same filter was used throughout a 30-min session. Luminance was reduced by adding white paper sheets (85% transmission) until the subject reported loss of light perception. Subjects were free to optimise their viewing orientation. Establishing the threshold took approximately 15–20 s, and no light was shown between tests.

Threshold values, measured in number of sheets, were converted to log luminance values. Data used in the analyses are the means of the thresholds at the last 3 min of each test. We pooled data per subject to avoid pseudo-replication, by standardising thresholds for each filter (transformation to distribution with $\bar{x} = 0$ and S.D. = 1), and calculating averages across filters for each subject. Sexes were pooled because male and female colour-normals did not differ in standardised threshold (ANOVA $F_{1,311} = 0.4$, $P = 0.5$).

We estimated the asymptote of the scotopic light adaptation curve with an iterative curve-fitting algorithm, using the data collected throughout the test (F.W. Maes, unpublished). This procedure minimised the residual sum of squares. The fitted asymptote was on average 0.1 log-unit lower than the observed threshold in the last minutes of the test-period, but this deviation did not differ between colour-blinds and colour-normals (t -test, $P = 0.3$). Furthermore, replacing the observations with these estimates did not change the results of the analysis.

3. Results

Colour-blinds had lower light perception thresholds than colour-normals at each of the six colour filters used (on average 0.44 log-units), and this difference was significant at two filters (Fig. 1A). The effect of colour-blindness on light perception threshold showed no significant variation between filters (ANOVA $F_{5,874} = 0.56$, $P = 0.7$). Each subject was tested at 2–3 filters, and to pool the data we averaged the data per subject (see Methods). The standardised threshold was significantly lower in colour-blinds (Fig. 1B; ANOVA $F_{1,324} = 13.42$, $P < 0.001$). Sexes were pooled in this analysis, but the difference between colour-blinds and colour-normals is also significant when the analysis is restricted to males (ANOVA $F_{1,178} = 8.6$, $P < 0.004$).

Colour-blinds, aware of their vision-deficiency, could for psychological reasons be more inclined to report that they can still see the test-area, while in fact they cannot. This would also result in lower light perception thresholds in colour-blinds. However, such behaviour would yield more irregular dark-adaptation curves. The residual sum of squares (RSS) of the fitted dark-adaptation curves provides a measure of the (ir)regularity of the dark-adaptation process in each 30-min test, and we used this to investigate whether colour-blinds behaved differently during these tests. The data (RSS) were pooled per subject following the same procedure as for threshold luminance. This measure of fit was equally good for colour-blinds and colour-normals (ANOVA $F_{1,324} = 0.41$, $P > 0.5$), suggesting that the difference in light perception thresholds between colour-normals and colour-blinds can be attributed to variation in light sensitivity, and not to different behaviour during the tests.

4. Discussion

In our study colour-blinds had enhanced scotopic vision as compared with colour-normals, which suggests colour-blinds can see better at under scotopic conditions, such as dusk, dawn and moonlit nights.

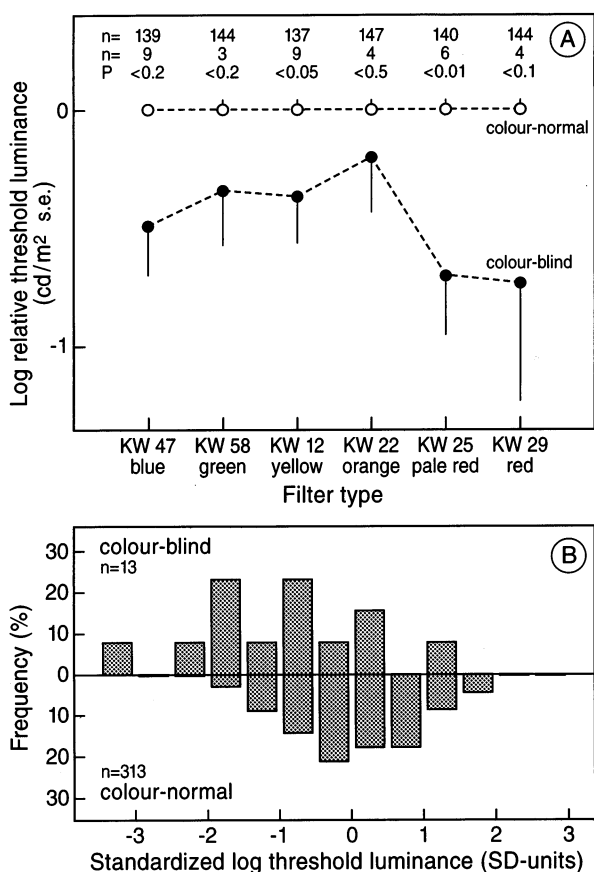


Fig. 1. (A) Relative light perception thresholds (in log units, + S.E.) after dark adaptation of colour-blinds and colour-normals at different filters. Mean log threshold of colour-normals was set to zero for each filter to facilitate within-filter comparison (threshold of colour-normals was on average $10^{-5.8}$ cd/m^2 (S.E. of exponent = 0.04)). P-values are results of two-tailed Mann-Whitney U -tests. Numbers above symbols indicate corresponding sample size (top: colour-normals, bottom: colour-blinds). (B) Frequency distribution of standardized threshold luminance of colour-blinds and colour-normals.

This is likely to provide a selective advantage, for example because enhanced scotopic vision makes it easier to detect nocturnal predators, and to forage or fight in low light conditions. This advantage, together with the earlier finding that colour-blinds are better at detecting colour camouflaged objects [4], could offset the disadvantage that colour-blinds suffer at other times (for example, when foraging).

However, as pointed out by Morgan et al. [4], the finding that colour-blinds are in some way at a selective advantage is not in itself sufficient to explain the maintenance of this trait in human populations. Although enhanced scotopic vision (together with being better able to detect colour camouflaged objects) may go some way in compensating for the disadvantage suffered by colour-blinds at other times, it seems unlikely that these benefits of colour blindness would make this trait exactly selectively neutral.

Humans are group-living animals who benefit from each other's success in finding food and detecting predators. It seems plausible that such cooperation through reciprocal altruism is more profitable when group-members differ in their talents (at least when those talents are traded-off against each other, which precludes that an individual can simultaneously possess all talents at maximum level). Thus the value of an individual to its group-members, and hence its own success in cooperation, will depend on the frequency of its genotype in the population, in the sense that it pays to be rare. Our study suggests that scotopic and photopic vision can be considered two 'talents' which trade off against each other, suggesting that colour-blindness may then be a trait on which selection is frequency dependent (as was also suggested by Morgan et al. [4]), which could explain the maintenance of its polymorphism in human populations.

A polymorphism with respect to colour vision has also been found in new world monkeys [6,7]. Of these species females which are heterozygous with respect to an X-linked gene are trichromatic, while homozygous females and all males are dichromatic. It seems possible that a scotopic advantage of dichromats has also played a role in the evolution of this fascinating system, but this remains to be investigated.

In our study we did not distinguish between dichromats and anomalous trichromats. It is conceivable that a trade-off between scotopic and photopic vision plays a role not only in the maintenance of colour-blindness per se, but also in the maintenance of variation between colour blinds in their ability to see colours. If this were true we would expect scotopic vision of anomalous trichromats to be intermediate to dichromats and colour-normals, but further study is required to test this hypothesis.

The physiological processes giving rise to enhanced scotopic vision in colour-blinds remain to be elucidated.

In principle such an effect could be caused by differential neuronal processing of the information provided by the photoreceptors, or by increased sensitivity of the whole retina to light in colour-blinds. Pupil size and pre-retinal absorption are other factors of potential importance. The light sensitivity of the retina is in part determined by the rod:cone ratio. This ratio is higher in nocturnal birds [8] and mammals [2] than in diurnal species, and deep-sea fishes have more rods in their retinas than species living closer to the water surface [9]. It is usually argued that species living in dark environments have fewer cones because there is insufficient light for them to be useful [5]. Alternatively, diurnal animals may have acquired the ability to see colours at the expense of the light sensitivity of their retinas. Unfortunately, to our knowledge no data are available to investigate whether variation in the rod:cone ratio explains the difference in scotopic vision between colour-blind and colour-normal subjects.

5. Conclusion

In conclusion, scotopic vision is enhanced in colour-blinds, which could explain the maintenance of this colour vision polymorphism in human populations. Viewed in this way, colour blindness is not necessarily a vision deficiency, but rather a different evolutionary solution to the trade-off between photopic and scotopic vision. This trade-off can potentially help to generate a more general understanding of the astounding interspecific variation in the ability to see colours.

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