Is Color Vision Deficiency an Advantage under Scotopic Conditions?

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Purpose. To examine experimentally whether color vision deficiency confers a selective advantage under scotopic conditions.

Methods. Red-green color-deficient subjects, monochromats, and age-matched color-normal control subjects were examined. In each subject the time course of dark adaptation, scotopic visual field sensitivity, and performance on a scotopic perceptual task were measured.

Results. No significant differences were found between red-green color-deficient subjects and control subjects on any of the three tests. Our small sample of monochromats had higher absolute thresholds than the corresponding control subjects, but their performance at the scotopic visual field test and perceptual task did not differ significantly from that of color-normal subjects.

Conclusions. No evidence was found that red-green color deficiency or monochromatism confers a selective advantage under scotopic conditions. (*Invest Ophthalmol Vis Sci.* 2001; 42:3357–3364)

Congenital red-green color deficiency—daltonism—leads to difficulty in certain natural tasks, such as detecting fruit among foliage,[1] and yet the condition affects as many as 8% of white males.[2] Why then is daltonism so prevalent? One possible explanation is that daltonism confers a selective advantage at other tasks. For example, it has been shown that daltonians can break camouflage that defeats color-normal subjects.[3] A further possibility is that daltonians have an advantage in night vision. In 1998, this hypothesis was put forward by Verhulst and Maes[4] who reported that daltonians had significantly lower absolute thresholds than color-normal subjects.[4] Their findings came from a retrospective analysis of the data collected in an undergraduate practical class that measured dark-adapted thresholds. Although their data were not collected in closely standardized conditions, their study has the advantage that the original experimenters were unaware of the hypothesis that would later be tested. Verhulst and Maes' report has prompted us to examine sensory and perceptual aspects of scotopic vision in a population of color-deficient observers and matched control subjects.

The report of Verhulst and Maes has in fact many antecedents. A daltonian described by Nicholl in 1818[5] gave this account of his experience:

> *The only advantage I have observed from this peculiar vision is, that I see objects at a greater distance and more distinctly in the dark than any one I recollect to have met with; this I discovered many years before I was aware of my defective vision in colours. . . .*

A popular theory of daltonism in the first half of the 20th century held that protan defects arise from overactive, or oversensitive, rods and deutan defects from underactive, or insensitive, rods.[6,7] This led these investigators to expect corresponding differences in dark-adaptation functions and scotopic thresholds. In fact, experimental tests of dark-adapted vision in daltonians have produced distinctly mixed results. Some investigators claim to find no difference between daltonians and normal subjects,[8–10] whereas others claim that an advantage accrues only to certain classes of daltonian.[11,12] Karma[13] claims that protanopes have elevated scotopic thresholds, whereas other types of daltonian are indistinguishable from normal subjects. Chapanis[14,15] and Hecht and Hsia[16] reported that protans are less sensitive than normal subjects to long-wavelength stimuli at scotopic levels. The latter finding can be accounted for merely by considering the differences in the spectral sensitivity functions of protans and color-normal subjects.

If we accept the recent claim of Verhulst and Maes,[4] how might the daltonian achieve lower scotopic thresholds than the color-normal person? We outline four possibilities:

1. In the case of dichromats, the missing class of cones may be replaced by rods, thus increasing scotopic sensitivity.
2. The night vision of daltonians may be enhanced by an alteration in cone–rod interaction, either because an active inhibition of rods by cones is reduced or because there is less noise originating in dark-adapted cones. The suppressive effect of rods on cone vision is known to be absent in protanopes.[17]
3. Daltonians may differ from normal subjects in some ocular parameter, such as pupil size or the optical density of the crystalline lens pigment(s).[4]
4. Daltonians may be more attentive to small differences of luminance and so may perform better than normal subjects under the colorless conditions of scotopic vision.

It is also possible that daltonians may enjoy superior mesopic vision, as well as or alternatively to, possessing superior scotopic vision. A hypothesis of this kind was advanced by Reimchen[18] in 1987 to explain the positive correlation between latitude and the incidence of daltonism. In the experiments reported herein, we have concentrated only on the issue of scotopic vision.

A further question concerns scotopic vision in monochromats. Sacks[19] has observed that the monochromats of the Pacific Island of Pingelap are particularly adept at night fishing, leading him to hypothesize that they may actually see better at night than those with normal cone vision.[19] It is generally thought that monochromats have normal dark-adapted sensitivity.[20,21] However, Frey et al.[20] claimed that monochromats have absolute thresholds that are actually higher than those of color-normal subjects, although they themselves point out that this finding may be a consequence of having used inappropri-

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ate control subjects.[22] Reports differ as to whether the time course of adaptation is abnormal in monochromats. There are claims that adaptation is slower than in normal subjects,[23] that it is more rapid than in normal subjects,[24–27] and that there is no difference between monochromats and normal subjects.[28,29] However, the genotypic variation among monochromats is now better understood, and we might therefore expect corresponding variation in scotopic visual function.[30]

In addition to the four potential explanations of superior scotopic vision that we have outlined for the case of daltonians, we may add three that apply only to monochromats:

5. Monochromats may use a superior fixation strategy under scotopic conditions. The monochromat typically fixates eccentrically, whereas the normal subject may use foveal fixation under scotopic conditions. Because the fovea contains no rods, a foveal fixation strategy is disadvantageous at low light levels.
6. The light-avoidance behavior of monochromats may lead them to be less adapted to bleaching lights in experimental studies of dark adaptation.[29] Their same photophobia in everyday life may change their scotopic sensitivity in the medium or the long term—for example, by protecting the crystalline lens from yellowing or by protecting the retina from other forms of light damage.
7. Because the monochromat has no foveal receptors, it is possible that the part of the visual cortex normally devoted to processing input from the fovea (and ultimately from cones) is devoted instead to processing input from extrafoveal regions and ultimately from rods.

We set out to test the hypotheses that daltonians and monochromats have scotopic vision superior to color-normal subjects. Because these hypotheses have arisen in part from subjective reports that daltonians and monochromats enjoy superior perception at night, it is important to examine scotopic perceptual ability as well as sensitivity. Our tests therefore comprised both classic sensitivity measurements (dark-adaptation curves and scotopic thresholds) and measurements on a more cognitive, perceptual test (in which subjects use their dark-adapted vision to describe what they perceive).

Methods

Subjects

Twenty subjects with color-defective vision took part in the experiment: 16 daltonians (2 protanopes, 2 extreme protanomals, 2 protanomals, 3 deuteranopes, 4 extreme deuteranomals, and 3 deuteranomals, as diagnosed by the Nagel anomaloscope), and 4 subjects with a clinical and electrophysiological diagnosis of autosomal recessive monochromatism. Subjects with this latter condition (which affects approximately 1 in 60,000) have no observable cone ERG but have a normal rod ERG and are sometimes described as rod monochromats. However, most patients with a clinical diagnosis of autosomal recessive monochromatism can be shown to have residual color discrimination.[31,32]

As control subjects for the color-defectives, we recruited 20 age-matched color-normals. To control for extraneous variables that could influence performance at our scotopic perceptual task, each normal control subject was either a friend or relative recruited individually by each daltonian or monochromat. The mean age of the daltonian group was 22 years (range, 16–31), and the mean age of their control subjects was 22 years (range, 13–33). The mean age of the monochromats was 15.8 years (range, 9–31), and the mean age of their control subjects was 18 years (range 10–39). All normal and daltonian subjects had acuities of 6/6 or better, and all had normal fundi. No subject was taking any medication known to affect vision or had any systemic condition known to affect vision.

We made three experimental measurements for each subject: the time course of dark adaptation; scotopic visual field sensitivities; and a test of scotopic perceptual efficiency.

Dark-Adaptation Curves

We measured dark-adaptation curves using a modified visual field analyzer (Humphrey Instruments, San Leandro, CA) controlled by a computer. Using one eye (generally the right eye, unless there was a strong left-eye dominance), subjects fixated a dim red point in the center of the perimeter bowl. Short-wavelength circular test flashes (480 nm, 10-nm bandwidth) were presented 15° below this fixation point: The subjects' task was to press a response button when they detected a flash. The duration of the test flashes was 200 msec, and two stimulus diameters were used: 0.4° (Goldmann size III) and 1.7° (Goldmann size V).

At the beginning of the session, subjects were given 5 minutes' practice at the task, to familiarize them with the procedure. Next, they were subjected to a white bleaching light of moderate intensity (1472 scotopic candelas [cd]/m^2) for 10 minutes, to achieve a controlled level of light adaptation. The bleaching light was provided by two incandescent lamps placed as close as possible to the original background light sources of the field analyzer. An infrared blocking filter and a diffuser were placed in filter slots directly in front of each lamp.

After light adaptation, we measured the course of dark adaptation for 40 minutes. Testing began by determining the threshold for 0.4° test flashes. The Humphrey visual field analyzer measures threshold on a decibel scale, with a maximum test flash intensity of 60 dB, corresponding to 3.2 scotopic cd/m^2. For the first threshold measurement, the test flash intensity was set to 25 dB and was increased in 5-dB steps until the subject saw the flash. The intensity at this point was taken as the initial threshold. The initial threshold was then estimated in the same manner for 1.7° test flashes. After these initial measurements, thresholds were repeatedly estimated for the two stimulus sizes in alternation. As soon as threshold had been set for one stimulus size, testing continued with the other stimulus size. On the second and third pairs of threshold measurement, the test flash intensity began 7 dB below the previous threshold estimate and was increased in steps of 1 dB until the subject saw the flash. On the fourth and subsequent pairs of threshold measurement, the test flash intensity began 3 dB below the previous threshold estimate and was increased in 1-dB steps until the subject saw the flash.

Scotopic Visual Field Sensitivities

Once the measurement of dark-adaptation curves was complete, subjects were given 5 to 10 minutes' rest in complete darkness, before scotopic visual field sensitivity was estimated. For these measurements, the same visual field analyser was used, with the same stimulus wavelength as before (480 nm), but only the 1.7° test flashes were presented. As before, subjects fixated a dim red point with one eye. They were told that test flashes could now appear anywhere in the visual field, and they were instructed to press a button whenever they thought they had seen a flash. During dark adaptation and scotopic field testing, fixation was monitored. An infrared camera mounted in the perimeter bowl relayed an image of the subject's eye to a video screen on the side of the instrument. If the experimenter noticed that the subject was not fixating properly, the subject was reminded to keep looking directly at the fixation point.

Sensitivity was probed at 52 points in the visual field. The points tested were arranged in a grid pattern, with adjacent points separated by 6° along the horizontal and vertical. At the beginning of the test, sensitivity was determined for four primary stimulus positions (in degrees away from fixation along the vertical and horizontal meridians, these positions were [+9°, +9°]; [+9°, −9°]; [−9°, +9°]; and [−9°, −9°]). The sensitivity measured for a primary point was used to calculate the expected hill of vision[33] for each of its eight adjacent secondary stimulus positions. The sensitivities at the secondary positions were in turn used to calculate the hill of vision for the remaining

FIGURE 1. *Hudibras Beats Sidrophel and His Man Whacum* (William Hogarth, 1726).

tertiary stimulus positions. At the secondary and tertiary stimulus positions, the starting points of the staircases used for determining sensitivity were set to 4 dB below the sensitivity expected from the estimated hill of vision. At each eccentricity, sensitivity was determined by the rapid staircase procedure first described by Bebie et al. in 1976.[34] If the subject could see the test stimulus at the intensity set as the starting point for the staircase, then the intensity was decreased in 4-dB steps on successive trials, until the subject could no longer see the test stimulus. The intensity was then increased in 2-dB steps until the subject again saw the stimulus. If the subject could not see the test stimulus at the intensity set as the starting point, then the procedure was performed in reverse. In either case, the sensitivity was taken as the last intensity to which the subject made a response. On each trial, the computer chose one of the eccentricities to be tested at random, maintaining a separate staircase for each point.

If the sensitivity measured at any point differed from the sensitivity predicted from the estimated hill of vision by more than 4 dB, a second measurement of sensitivity was made at that point, and the two sensitivity estimates were averaged.

Scotopic Perceptual Efficiency Test

The final task demanded of our subjects was a test of scotopic perceptual efficiency. This test, originally intended to identify normal individuals with superior night vision, was developed during the second World War for selecting military personnel. It is described in a Medical Research Council report by Pirenne et al.[35]

In our version of the test, we closely followed the method used by Pirenne et al. Our subjects were seated in a dark room and viewed, binocularly, a photographic copy of the monochrome engraving (Fig. 1), *Hudibras Beats Sidrophel, and His Man Whacum* (William Hogarth, 1726). We refer to this test as the Hudibras test. The picture measured 58 × 38 cm and was viewed from a distance of 90 cm. It was dimly illuminated by an incandescent light source, the light being attenuated by neutral-density filters so that the luminance of the table cloth in the picture was 4.8×10^{-4} scotopic cd/m^2 (the spectral radiance distribution of the table cloth was measured with a spectroradiometer (model PR650; Photo Research, Chatsworth, CA) before the neutral-density filters were put in place, and the luminance was then calculated from the known absorption properties of the filters). Subjects were read the following instructions:

You are sitting in front of a picture of the inside of a magician's room. I want you to describe to me in your own words what you see within the picture. Try to be as accurate as possible with your description, as though you're giving a report in a law court; give a description of where on the picture you see any objects and if possible, what they are. Try to avoid vague statements like "I see a light patch over here." The picture is an old picture, so you won't find anything specifically modern within it, though as I said, the picture is of the inside of a magician's room, and so you should expect to see people, animals or other objects within it.

Subjects were asked if they understood the instructions, before making their responses. Their responses were recorded using a cassette recorder and later transcribed. Each record was then numbered randomly and given in counterbalanced order to two independent markers (JDM and BCR). Our marking system was based on the scheme of Pirenne et al.,[35] which was as follows:

TABLE 1. Summary of Results in Daltonians

ID	Age (y)	Diagnosis	SS (dB)	R Score	M Score	R+ Score	M+ Score	$V_{0_{III}}$ (dB)	τ_{III} (min)	V_{0_V} (dB)	τ_V (min)
DER	28	P	52.5	15	9.5	16	12.5	17.8	2.6	8.2	2.9
RF	31	P	53.8	17.5	16	22.5	16.5	17.3	7.2	7.1	6.3
RW	16	EPA	48.9	10.5	5	12.5	12.5	18.1	8.6	9.3	9.8
LW	17	EPA	48.7	0	2	2	2.5	16.0	7.4	6.3	7.3
JW	18	PA	49.2	6	−1	8	5	16.9	5.6	7.3	5.4
DR	27	PA	47.9	6.5	3	8.5	8	20.3	4.0	10.7	4.5
MM	26	D	49.2	14	8.5	15	12.5	14.2	5.8	6.2	6.1
GS	23	D	50.7	2.5	−1	5.5	3	17.0	4.6	6.8	5.2
MN	25	D	49.7	3	0.5	7	5	15.7	5.6	6.7	5.5
SK	19	EDA	44.5	10.5	9	11.5	8.5	20.0	6.9	11.9	5.2
BK	21	EDA	49.8	5	4.5	11	10.5	15.7	6.6	6.9	5.7
KH	17	EDA	47.1	4	1	5	5	18.9	6.8	10.3	6.9
SV	24	EDA	49.2	10.5	6.5	13.5	10	17.3	6.2	8.1	5.6
SS	18	DA	48.6	10.5	5	12.5	8.5	15.7	5.3	6.5	6.2
TN	20	DA	51.2	4	4	8	8.5	20.6	8.3	11.8	8.3
PvE	22	DA	49.0	2.5	3.5	2.5	3.5	18.5	7.9	8.6	7.5

Diagnosis shows the classification of type of daltonism in each subject: P, protanopia; EPA, extreme protanomaly; PA, protanomaly; D, deuteranopia; EDA, extreme deuteranomaly; DA, deuteranomaly. SS, average scotopic sensitivity for the central visual field. R, R+, M, and M+ are scores on the Hudibras test awarded by the markers (BCR and JDM), using the negative (R and M, respectively) and positive (R+ and M+, respectively) marking schemes. $V_{0_{III}}$, final threshold estimated from the best-fitting exponential to the rod portion of the dark-adaptation curve for a Goldmann size III (0.4°) target; τ_{III}, time constant for dark adaptation estimated from the best-fitting exponential to the rod portion of the dark-adaptation curve for a Goldmann size III (0.4°) target; V_{0_V}, final threshold estimated from the best-fitting exponential to the rod portion of the dark-adaptation curve for a Goldmann size V (0.4°) target; τ_V, time constant for dark adaptation estimated from the best-fitting exponential to the rod portion of the dark-adaptation curve for a Goldmann size V (1.7°) target.

(a) A mark was given for each correct statement made in the description of the picture and a mark was deducted for every wrong statement.
(b) Some statements were considered to consist of several statements and were given several marks. Thus, "human figure," was given 2 marks; "a man," that is a male human figure, was given 3 marks. If a man was described as a woman, 2 marks were given for human figure, which is a correct statement and 1 mark was deducted for "female" which is a wrong statement; thus the final score was 2 − 1 = 1 mark.
(c) Some vague statements were given half a mark—for example, the statement, "a long horizontal object hanging from the ceiling" for the stuffed crocodile.

In fact, we used two slightly different versions of this scheme: Negative marking, in which incorrect statements attracted the loss of a mark, exactly as scored by Pirenne et al.,[35] and positive marking, in which deductions were not made for incorrect statements. The latter marking scheme was introduced to avoid awarding low marks to subjects who had been able to perceive a great deal of the picture, but who had also been overenthusiastic in their responses.

Each subject's response was marked twice by each marker: once according to the negative marking scheme and once according to the positive marking scheme. The markers were given copies of the marking system of Pirenne et al.[35] as set out herein, as well as sample reports from the subjects of Pirenne et al., with their corresponding scores. The responses were marked blind, so that the markers did not know which responses were from daltonians or monochromats and which were from control subjects.

The research followed the tenets of the Declaration of Helsinki. Informed written consent was obtained from the subjects after the nature of the study was explained to them. The research was approved by the Research Ethics Committee, Cambridge Health Authority.

RESULTS

Tables 1, 2, and 3 summarize the results on each of our tests for daltonians, monochromats, and their normal control subjects, respectively.

Dark-Adaptation Curves

Dark–adaptation functions were plotted for each subject and the rod portions were fitted with the following exponential function:

$$V = V_0 + A \cdot e^{-t/\tau}$$

where V is threshold, V_0 is final threshold, A is a constant, t is time, and τ is the time constant of adaptation. The smaller the τ value in the fitted exponential, the more rapid the recovery of sensitivity. The τ and V_0 obtained from our subjects are given in Tables 1, 2, and 3, for the two different stimulus sizes. Dark-adaptation curves for daltonians and their control sub-

TABLE 2. Summary of Results in Monochromats

Name	Age (y)	SS (dB)	R Score	M Score	R+ Score	M+ Score	$V_{0_{III}}$ (dB)	τ_{III} (min)	V_{0_V} (dB)	τ_V (min)
DB	9	46.5	−4	−2	0	0	20.8	2.7	11.3	3.9
KP	10	46.6	3	3	4	3	21.1	5.5	11.9	5.2
SB	13	47.3	2	0	4	4	18.1	10.2	10.4	7.9
PM	31	45.9	2.5	1.5	2.5	2	21.9	6.9	11.4	9.3

See Table 1 for explanation of data.

TABLE 3. Summary of Results in Normal Control Subjects

ID	Age (y)	Control for (ID)	SS (dB)	R Score	M Score	R+ Score	M+ Score	$V_{0_{III}}$ (dB)	τ_{III} (min)	V_{0_V} (dB)	τ_V (min)
SB	10	DB	52.9	5	4.5	6	6	15.4	5.1	5.5	5.7
GP	10	KP	49.2	−2	−2	0	0	16.7	6.0	6.1	6.2
AC	13	SB	46.1	1	−1	6	3	17.5	4.6	9.2	5.3
TM	39	PM	46.9	0.5	−0.5	0.5	0	18.3	5.8	10.4	6.2
PS	24	DER	49.3	12.5	11	15.5	12	16.2	6.1	6.2	6.3
RY	33	RF	52.5	14	10	17	13	17.7	6.2	8.9	5.8
GW	13	RW	50.9	17	16.5	18	17.5	16.8	5.8	8.4	5.4
TM	17	LW	48.8	2.5	2	5.5	5	24.0	7.6	15.8	5.9
NG	19	JW	47.5	3.5	2	4.5	3	18.0	5.7	8.3	7.1
PD	29	DR	45.9	2	−3	3	1.5	17.6	4.4	8.8	4.5
KK	24	MM	51.3	3	2	4	3	13.6	5.0	5.3	4.9
MS	27	GS	50.5	8.5	5	9.5	5.5	15.7	4.4	7.6	3.2
KM	22	MN	51.5	5.5	−1	8.5	5	16.5	6.7	7.5	6.1
CW	21	SK	51.3	8.5	1	5	8	16.4	4.8	6.7	5.9
LC	19	BK	48.5	−2	0	1	2	18.6	5.7	10.3	5.9
NS	18	KH	49.1	9.5	6.5	11.5	9	17.9	8.7	9.4	7.1
AA	24	SV	49.3	4.5	−0.5	6.5	2	15.5	6.0	6.7	6.6
PDS	19	SS	48.2	8	4	12	9	20.4	4.8	9.5	8.1
RC	21	TN	51.1	2	−1	2	2	15.4	5.6	6.4	5.5
FG	22	PvE	51.1	5.5	0.5	7.5	4.5	18.1	3.6	8.5	4.2

See Table 1 for explanation of data.

jects are shown in Figure 2 and for monochromats and their control subjects in Figure 3.

Neither the time constant of dark adaptation, τ, nor the final threshold, V_0 (both averaged for the two stimulus sizes), differed significantly between daltonians and their normal control subjects (robust rank-order test, $\acute{U}$ = 0.73 and 0.22, respectively). We also compared specific types of daltonism with the control subjects, but we found no significant differences between dichromats and control subjects ($\acute{U}$ = −0.70 and −1.44 for τ and V_0, respectively), between anomalous trichromats and control subjects ($\acute{U}$ = 1.45 and 0.99), between protans and control subjects ($\acute{U}$ = 0.26 and 0.37), or between deutans and control subjects ($\acute{U}$ = 0.81 and 0.05).

The dark-adaptation curves for monochromats intersect the ordinate at a point approximately 10 dB lower than the curves for their control subjects, suggesting that the monochromats may have recovered sensitivity more rapidly at the beginning of dark adaptation. However, this may be because the mono-

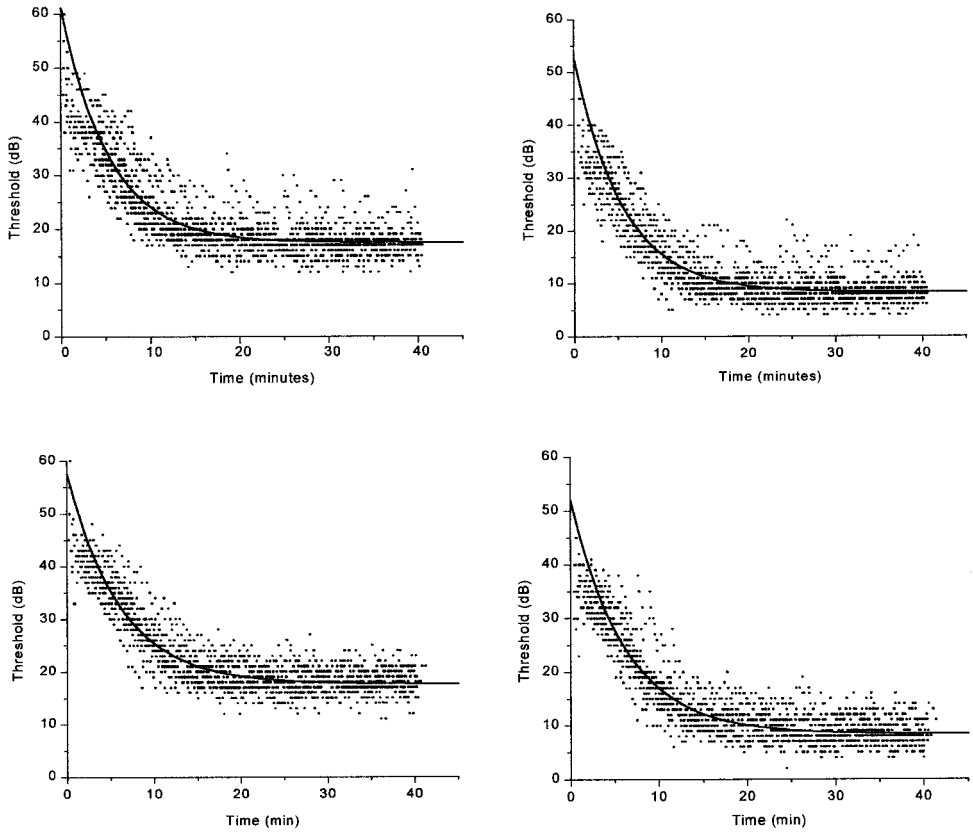

FIGURE 2. Dark-adaptation data of normal control subjects (*top*) and daltonian subjects (*bottom*). *Left*: data for Goldmann size III (0.4°) stimulus; *right*: data for Goldmann size V (1.7°) stimulus. The rod portion of each plot has been fitted with an exponential curve.

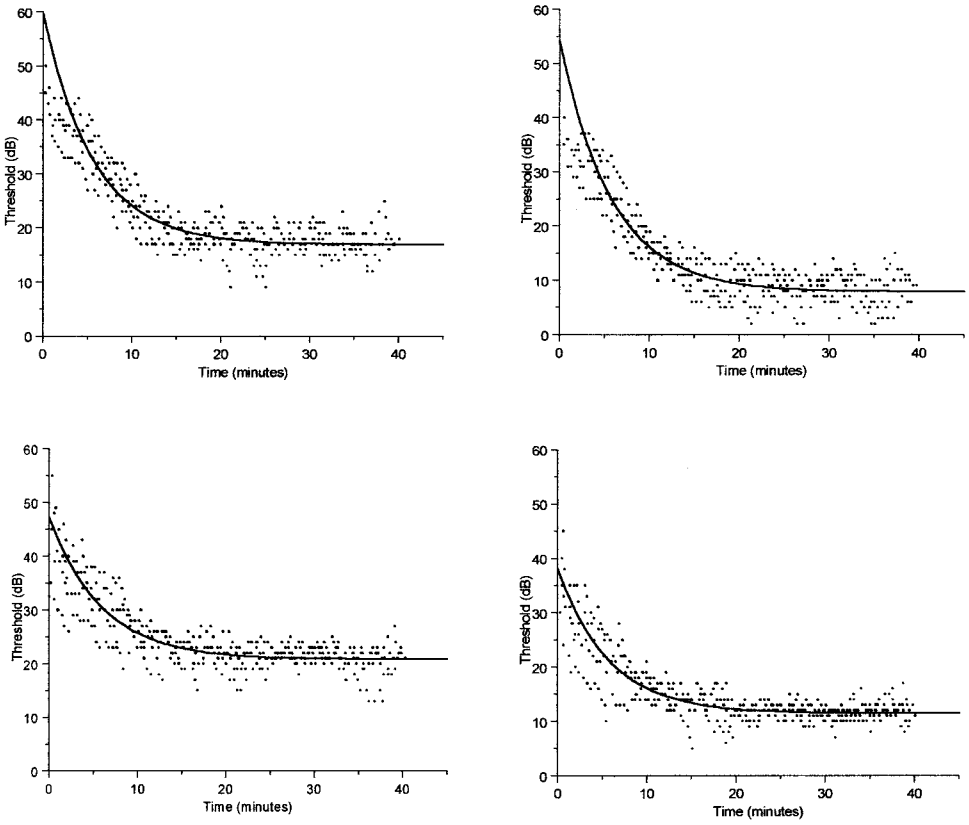

FIGURE 3. Dark-adaptation data of normal control subjects (*top*) and monochromats (*bottom*). Data are presented as described in Figure 2.

chromats found the bleaching light uncomfortable and blinked more frequently during the bleaching phase than the normal subjects, thus undergoing less light adaptation. Comparing the time constants of dark adaptation (τ) for monochromats and their control subjects revealed no significant difference between the two groups ($\acute{U} = 0.24$). This supports the idea that the apparent difference between monochromats and normal subjects arose because the two groups did not begin dark adaptation from the same initial adaptation state. As Sharpe and Nordby[29] emphasize, such an explanation may account for the frequent finding that monochromats adapt more rapidly to the dark than normal observers.[25–27,29] The final thresholds for monochromats were found to be elevated when compared with those of normal subjects, with the difference reaching statistical significance ($\acute{U} = 4.48$).

Scotopic Visual Field Sensitivities

For each subject, scotopic sensitivity measurements were converted into matrices using the Kriging method.[36] The mean scotopic sensitivity for each class of subject is plotted as a three-dimensional grid in Figure 4.

There was one notable difference between the scotopic field plot for monochromats and the scotopic field plot for other subjects: The monochromats did not show the sharp decline in sensitivity found in other subjects around the blind spot. This is because the monochromats used eccentric viewing; thus, the location of the blind spot was blurred over several eccentricities. There were no other systematic differences between the field plots for different types of subject.

For each subject, we made an estimate of absolute scotopic sensitivity by discarding the poorest threshold (corresponding to the blind spot) and taking the mean threshold across the remaining 51 points. These mean scotopic sensitivities are shown in Table 1. We found no significant differences between the average scotopic sensitivity of daltonians and that of their normal control subjects ($\acute{U} = -0.75$), or between monochromats and their control subjects ($\acute{U} = -1.21$). The latter result does not necessarily contradict the finding that monochromats had significantly elevated final thresholds. When the sensitivities for the two points closest to that examined in the dark-adaptation phase of the experiment were averaged, it was found that the sensitivities in monochromats and normal subjects were significantly different. This is possibly the result of the monochromats' eccentric fixation. It may be that this point corresponded to a less sensitive portion of their visual fields. Considering the different groups of daltonians individually, we found no differences between dichromats and their control subjects ($\acute{U} = 1.26$), anomalous trichromats and control subjects ($\acute{U} = -1.88$), protans and control subjects ($\acute{U} = 0.03$), or deutans and control subjects ($\acute{U} = -1.15$).

Hudibras Test

The scores awarded for this test ranged from -4 to 17.5 under the negative marking scheme, and from 0 to 22.5 under the positive marking scheme. The scores awarded by the two markers correlated well: Spearman's rank-order correlation coefficient was highly significant for both negative ($r = 0.81$, $P < 0.001$) and positive ($r = 0.93$, $P < 0.001$) marking schemes. Because the scores correlated well, we took the mean of the scores given by the two markers for further analysis.

We found no significant differences between daltonians and normal control subjects on this test (robust rank-order test, $\acute{U} = 0.89$ and 1.25 for negative and positive marking, respectively), or between dichromats and their control subjects ($\acute{U} = 0.67$ and 1.47), anomalous trichromats and their control subjects ($\acute{U} = 0.72$ and 0.80), protans and their control subjects ($\acute{U} = 1.00$ and 1.28), or deutans and their control subjects ($\acute{U} = 0.55$ and 0.85).

We also found no difference between the scores of monochromats and their control subjects ($\acute{U} = 0.24$ and -0.37).

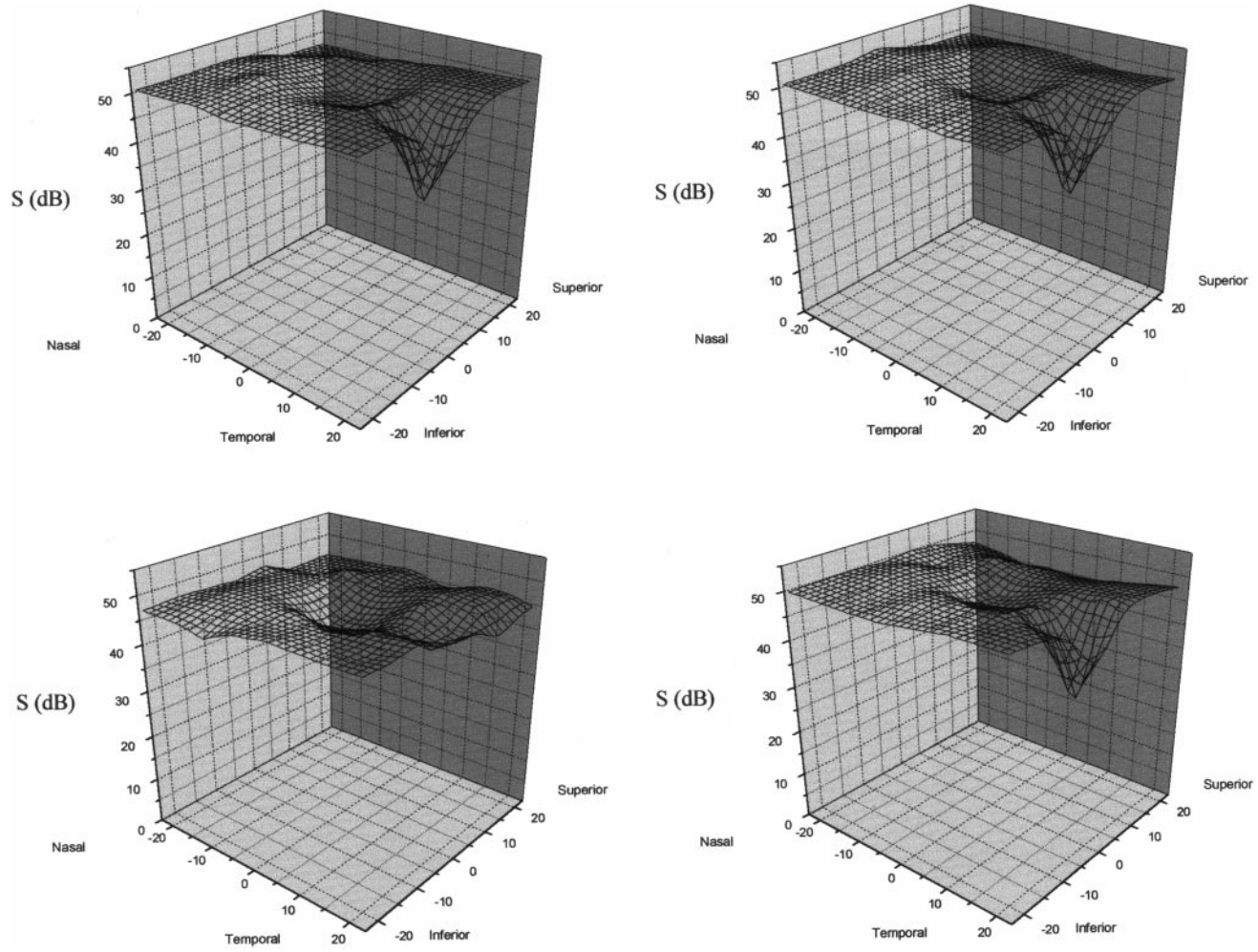

FIGURE 4. Averaged scotopic field plots for daltonians and matched normal control subjects (*top left* and *right*, respectively) and for monochromats and their control subjects (*bottom left* and *right*, respectively). *Horizontal plane*: the position in the visual field (in degrees); *vertical axis*: sensitivity (in decibels).

In addition, we have compared our subjects' performance on tests of scotopic sensory efficiency and scotopic perceptual efficiency. In Figure 5, the scores obtained in the Hudibras test are plotted against scotopic sensitivity. Data points from those subjects with the best night vision fall in the top righthand corner and from those with the poorest night vision in the lower lefthand corner. There is a significant correlation between the two data sets: Spearman's $r = 0.40$ ($P < 0.01$) for negative-marked scores on the Hudibras test and $r = 0.44$ ($P < 0.01$) for positive marking.

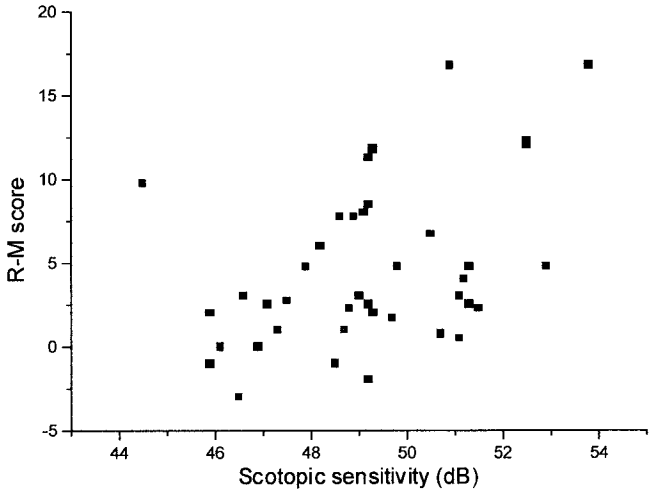

FIGURE 5. Averaged scores on the Hudibras test for markers BCR and JDM plotted against averaged scotopic field sensitivity.

DISCUSSION

Our results contradict the findings of Verhulst and Maes.[4] We found no significant differences in scotopic visual performance between daltonians and color-normal subjects, either on sensory or on perceptual measures. We were also unable to find any evidence to support the suggestion of Sacks[19] that monochromats might see better in the dark. Our monochromats displayed absolute thresholds that were in fact significantly higher than those of our normal control subjects; this suggests that they have inferior scotopic vision.

An interesting finding was the positive correlation between performance at the Hudibras test and scotopic sensitivity. This finding supports the report of Pirenne et al.,[35] but it contradicts the claims of Craik and Vernon,[37] who also compared absolute thresholds with performance on relatively simple scotopic perceptual tasks. (Reanalysis of the data of Craik and

Vernon shows that there is in fact a significant correlation between the scotopic threshold and the luminance required to identify the silhouette [Spearman's $r = 0.67$, $P < 0.005$] for one subset of their stimuli: clock faces, for which correct identification meant identifying the orientation of the hands). The assertion of Pirenne et al. that performance on their test should be limited by threshold seems sound. We should not expect someone with a high sensory threshold to perform well on a perceptual test of scotopic vision.

In conclusion, we are able to suggest no advantages to daltonism beyond the documented superiority of daltonians at breaking camouflage.[3] It is nevertheless possible that daltonians would exhibit some superiority of vision under mesopic conditions, as proposed by Reimchen,[18] and this is a possibility that warrants further investigation. Similarly, we find no evidence that monochromatism conveys an advantage under scotopic conditions; in fact, our subjects exhibited increased absolute thresholds.

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