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An adaptation of the Cambridge Colour Test for use with animals

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Abstract

Recently, molecular biological techniques have presented new opportunities for addressing questions concerning the neural mechanisms involved in color coding, thereby rousing renewed interest in animal color vision testing. We have modified a computer-based assessment tool, the Cambridge Colour Test, to make it suitable for use with animals. Here, the validity and reliability of the testing method were evaluated using squirrel monkeys. Because the chromatic stimuli and the achromatic backgrounds of the test consist of dots that vary in lightness, the stimulus parameters can be adjusted so that animals are not able to use luminance differences to make correct discriminations. Thus, in contrast to methods used previously, this test does not require that time be spent equating the luminance of each chromatic stimulus examined. Furthermore, the computer video-display based design of the testing apparatus can be easily replicated and adapted for use with many species in a variety of settings. In the present experiments, the squirrel monkeys' behavioral results agreed with the predictions for their color vision based on genetic analysis and electroretinography (ERG) spectral sensitivity data. Repeated measurements were highly consistent. Thus, an adaptation of the Cambridge Colour Test provides a valid and reliable method for testing color vision in animals.

Keywords: Color vision, Animal vision testing, Color vision deficiency, Protanopia

Introduction

Animal color vision testing has been used to assess the presence of color vision, to determine its dimensionality and acuteness, and to yield inferences about its biological basis and functional utility (Jacobs, 2004). There is a large range of differences both between and within species. Among placental mammals, color vision varies from monochromatic to trichromatic, with the latter occurring only in primates (Jacobs, 1993). While trichromacy is the norm for the catarrhines (Old World monkeys, apes, and humans), widespread within-species variation is characteristic among many platyrrhines (New World monkeys) (Jacobs, 1998).

In the past, color vision tests involving operant behavior were frequently performed on nonhuman primates using an apparatus in which the stimulus panels were transilluminated by an optical system (Jacobs, 1984). All chromatic stimuli needed to be carefully adjusted in order to be equally luminant for the animal. This was done by a combination of ascertaining an animal's sensitivity to various spectral stimuli and testing a range of luminance differences for each pair of test lights to determine if the animal could make a discrimination based on wavelength differences alone (Jacobs, 1981). In the present experiments, we used a modified version of the Cambridge Colour Test, a cathode ray tube– (CRT-) based assessment tool, in which the stimuli resemble the plates of a traditional pseudoisochromatic test. Because the chromatic stimuli and the achromatic backgrounds consist of small dots that vary in lightness, the parameters can be set so that animals are not able to use luminance differences to make correct discriminations, thus eliminating the need to test every chromatic stimulus individually over a range of intensity values. Modified Ishihara pseudoisochromatic plates have recently been used to evaluate color vision in chimpanzees (Saito et al., 2003). In this case, the stimuli were printed on glossy paper and placed in front of the animal's cage. The advantages of a CRT-based test over printed plates are that a computer program automatically generates the chromaticity and relative position of successive stimuli and the saturation level of each chromaticity can readily be varied. Overall, the CRT-based testing system allows for detailed and efficient assessment of color vision capacity, and it can be quickly adapted for use with a wide range of species and conditions.

Results from molecular genetics have renewed interest in animal color vision testing. Recent studies investigating the photopigment genes among macaques (Hanazawa et al., 2001) and chimpanzees (Saito et al., 2003) have yielded individuals who are predicted to be color defective, despite the trend for routine trichromacy among these species. Another genetic study identified one species of New World monkey, the howler monkey, which has

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the photopigment basis for trichromacy similar to that of the Old World monkeys (Jacobs et al., 1996*a*). However, whether this genetic potential is realized as a capacity for red-green color vision has not yet been determined. Modern molecular techniques have also presented new opportunities for addressing questions concerning the neural mechanisms involved in color coding. For example, we are currently using gene therapy to determine whether adding an additional photopigment will be sufficient to transform a dichromatic squirrel monkey into a trichromat. Comparing both pre- and posttherapy color vision profiles will be necessary for evaluating the effects of the treatment. Here we describe experiments that fulfill the dual purpose of collecting pretherapy color vision data for squirrel monkeys and assessing the validity and reliability of a modified version of the Cambridge Colour Test when used with nonhuman primates.

Materials and methods

Subjects

Squirrel monkeys of Guyanian origin were obtained from Osage Research Primates, Osage Beach, Missouri. Osage provided blood samples from several male monkeys, and animals that were predicted to be protanopic, based on the photopigment gene found on their X chromosome, were selected from the colony. Animals were approximately three years old when behavioral testing began. A protanopic human was also tested for comparison.

Molecular genetics

DNA was extracted from blood samples obtained from 13 male squirrel monkeys. The polymerase chain reaction (PCR) was used to amplify and sequence the coding region of the X-linked photopigment gene in order to identify animals with a pigment of spectral peak near 532 nm. Exon 5 of the photopigment gene was amplified using a forward primer with the sequence 5′GTG GCAAAGCAGCAGAAAG and a reverse primer with the sequence 5′CTGCCGGTTCATAAAGACATAG. The sequences of the forward and reverse primers for exon 3 were 5′GGATCA CGGGTCTCTGGTC and 5′CTGCTCCAACCAAAGATGG, respectively. For each exon, the forward and reverse primers lie near the 5′ and 3′ ends of the exon being amplified. PCR products were directly sequenced with the Big Dye Terminator Sequencing kit (Applied Biosystems, Foster City, CA) and analyzed on an ABI Prism 310.

Flicker-photometric ERG

Electroreginograms (ERGs) were differentially recorded using a Burian-Allen contact lens electrode. Animals were anesthetized using ketamine hydrochloride (15 mg/kg) and xylazine (2 mg/kg). Atropine (0.05 mg/kg) was also administered intramuscularly. 1% tropicamide was used for dilation, and 0.5% proparacaine hydrochloride was used as a local anesthetic. Goniosol (2.5% hydroxypropyl methylcellulose) was placed underneath the contact lens electrode. Details on the ERG procedure have been published (Neitz & Jacobs, 1984; Jacobs et al., 1996*b*; Carroll et al., 2000). A three-channel Maxwellian view optical system produces the stimuli for ERG flicker photometry that are distributed over a 70-deg patch of retina. High-speed electromagnetic shutters were used to alternately present the reference and test lights at 31.25 Hz. The intensity of the reference light remained constant while the intensity of the test light was adjusted to produce a null of minimum ERG signal amplitude. This null is taken as the point when the effectiveness of the test light equals that of the fixed reference light. Null points were determined at 10-nm increments over a range of 450–670 nm. Spectral sensitivities were determined from the average of two complete runs. Spectral sensitivity data were best fit to a vitamin-A_1 visual pigment template by allowing the λ_{max} to vary (Carroll et al., 2000). The human spectra were corrected for preretinal absorption by the lens (Pokorny et al., 1987), while the squirrel monkey spectra were not.

Apparatus

During testing the unrestrained monkey stood on a perch that was positioned in front of a 19.5 cm × 9 cm transparent, touch-sensitive stimulus panel through which it viewed a computer monitor that produced the test stimuli. A feeding well connected to a peristaltic pump (Gilson, Inc., Middleton, WI; Model MP1 Minipuls) was located directly below each of the three positive stimulus positions of the panel. White grape juice was used for reinforcement. The ceiling of the apparatus consisted of a fluorescent light box that provided ambient illumination of *ca.* 100 lux. A speaker in the chamber provided reinforcing tones, and one-way mirrored windows permitted direct observation of the animal subjects.

The task was a modified version of the Cambridge Colour Test, which was originally developed for human subjects (Reffin et al., 1991; Regan et al., 1994). Cambridge Research Systems (CRS) (Rochester, UK) generously provided the source code for the test, and we altered it for use in this application. During testing, the animal viewed a background of size- and luminance-varying gray disks that filled the area of the touch-sensitive viewing panel described above. The disks varied in diameter from 4 mm to 12 mm, and their luminance varied over six levels between 8 and 18 cd/m^2. The modified task was a three-alternative, forced-choice discrimination in which a roughly 50 mm × 50 mm colored patch of disks appeared in one of three randomly chosen, evenly spaced positions across the panel. The colored patch of disks, which also varied in size and luminance according to the parameters listed above, subtended about 35 deg to 50 deg of visual angle depending on the position of the animal. When the animal chose the colored target, he received a small amount of juice from the corresponding feeding well and heard a positive tone. If the animal touched the incorrect part of the panel, no juice was delivered, and a negative tone sounded. During each session the position, chromaticity, and saturation of the targets were randomly changed by the computer program.

Procedure

The animals were housed in individual cages in a temperature- and humidity-controlled room and maintained under a 12:12 h light-:dark cycle. They were allowed food and water ad lib following their morning training session each day. Through a shaping procedure, they were first trained to touch the stimulus panel at any location for a juice reward. Once this behavior was learned, they were next trained to select the section of the stimulus panel that appeared different from the other two sections. Discrimination thresholds were tested for each of 16 different hues *vs.* gray. The saturation, or the distance from gray, was varied from a minimum vector length (Euclidean distance) of 0.01 to a maximum of 0.11

in CIE (1976) u', v' color space, so as to span a performance range from chance (33% correct) to the vector length that either yielded nearly 100% correct or corresponded to the highest possible saturation. The monkey was given an unlimited amount of time to respond to each stimulus presentation. Incorrect responses were followed by a penalty time interval of 2 s before the next presentation would appear. A complete color vision test consisted of a minimum of 60 trials at each vector length for all 16 hues. The modified test used the method of constant stimuli to obtain complete psychometric functions, examples of which are shown in Fig. 1. Each psychometric function was least-squares best fit to a cumulative Gaussian function, and the threshold value was determined based on the saturation, or color purity, of the target that would be required to support discrimination at a level of 57% correct. This threshold criterion corresponds to the proportion of correct responses required to exceed that predicted from chance performance alone ($P = 0.05$). All procedures were done in accordance with the principles regarding the care and use of animals adopted by the American Physiological Society and the Society for Neuroscience. Tests involving human protanopes were done in accordance with the principles embodied in the Declaration of Helsinki.

Light measurements and calibration of the CRT used in behavioral testing

The stimuli for the Cambridge Colour Test are produced by a CRS visual stimulus generator (VSG), which provides 14-bit color and luminance control. The system was calibrated regularly using the ColorCAL, a high-performance colorimeter that is made to CRS specifications by Minolta (Osaka, Japan). The ColorCAL measures the phosphor colors in terms of CIE coordinates as well as their luminances. Because the CRS VSG systems have 14-bit output resolution, the Cambridge Colour Test can provide a finely graded measurement of discrimination and allow small changes to be monitored over time.

Even though the ColorCAL was used to initially calibrate and maintain consistency of chromatic stimuli produced by the computer monitor, all the final u', v' CIE coordinates used in reporting and interpreting the data were calculated from spectroradiometric measurements obtained directly from the stimulus panel. The International Light RPS 380 Portable Spectroradiometer was used. The RPS380 is calibrated (National Institute of Standards and Technology [NIST] traceable) from 380 to 780 nm, and it is capable of displaying chromaticity as well as spectral radiance. The CIE system is appropriate for specifying and reporting the properties of the lights for squirrel monkeys because the photopigments underlying the monkeys' vision are similar to those of humans. The CIE specifications would not be appropriate for an animal with photopigments and preretinal filters that are significantly different than a human's. In such cases, spectroradiometric measurements could be used to specify the CRT-generated color stimuli in terms that are appropriate for the species.

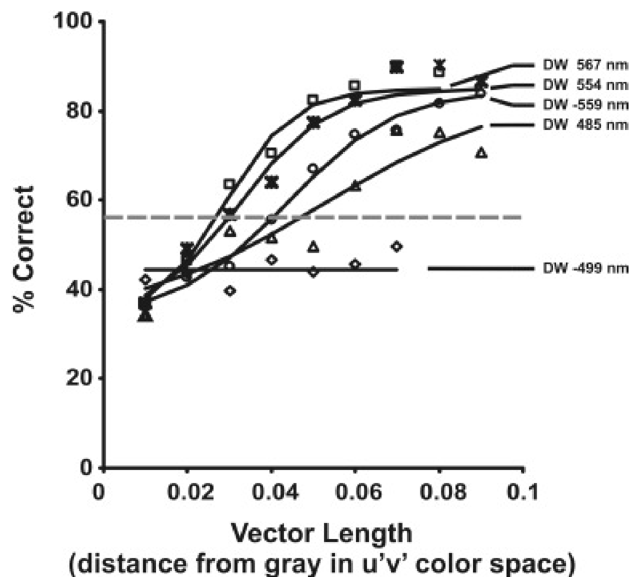

Fig. 1. Example psychometric functions for five different chromatic stimuli. Threshold values were determined based on the vector length (i.e. saturation) of the target that was necessary to support discrimination at 57% correct (gray dashed line). Specified in terms of DW, the five different colors are as follows: squares = DW 567 nm; X's = DW 554 nm; circles = DW −559 nm; triangles = DW 485 nm; diamonds = DW −499 nm (see text).

Results

Molecular genetics

There are three different alleles for the gene that encodes the middle-to-long-wavelength-sensitive photopigment in squirrel monkeys. The peak spectral sensitivities of these pigments are 561 nm, similar to the human L pigment (λ_{max} = 560 nm); 532 nm, similar to the human M photopigment (λ_{max} = 530 nm); and 547 nm, intermediate to the human L and M pigments. Spectral sensitivity differences between the monkey pigments are determined by amino acids found at three positions: 180, 277, and 285 (Neitz et al., 1991). The amino acid combinations that specify each class of photopigment are listed in Table 1. Three animals (1, 2, and 3) whose X-chromosome visual pigment genes specified alanine at position 180, phenylalanine at position 277, and alanine at position

Table 1. *Analysis of X-encoded pigment genes and predicted spectral sensitivities*[a]

Monkey	Animal ID	Amino Acid Position			Predicted λ_{max} (nm)
		180	277	285	
1	67Cf17C	A	F	A	532
2	A580D19	A	F	A	532
3	2657050	A	F	A	532
4	F73661F	A	F	A	532
5	1382B28	A	F	T	547
6	1572B76	A	F	T	547
7	2333E58	A	F	T	547
8	3011F00	A	F	T	547
9	F7C397B	A	F	T	547
10	2454271	S	Y	T	561
11	2557c08	S	Y	T	561
12	D304543	S	Y	T	561
13	702285F	S	Y	T	561

[a]Single-letter amino acid code: A = alanine, F = phenylalanine, S = serine, T = threonine, Y = tyrosine.

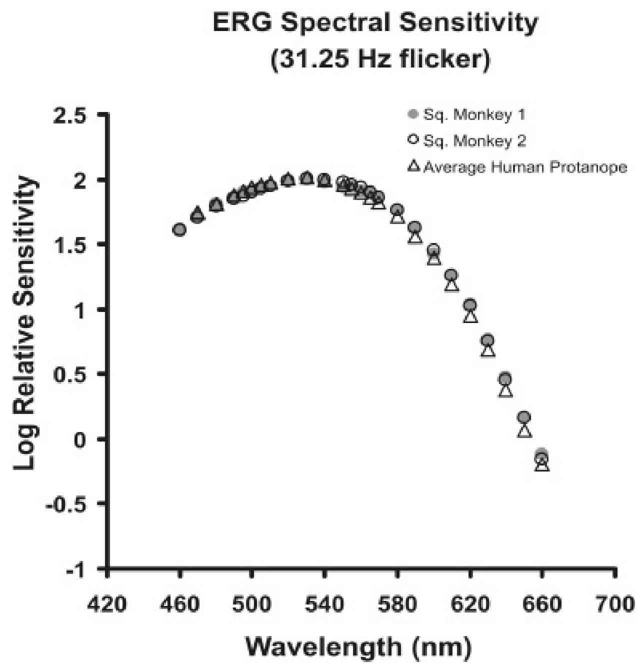

Fig. 2. Flicker photometric ERG spectral sensitivity curves of squirrel monkeys 1 and 2 (solid dots and open circles, respectively) compared to the average of 10 protanopic humans (open triangles).

285 were purchased. The X-encoded cone photopigment in these animals is predicted to have a spectral peak of 532 nm.

Flicker-photometric ERG

Fig. 2 shows the ERG flicker-photometric spectral sensitivity functions for 2 of the protanopic squirrel monkeys, compared to the average of 10 human protanopes (Carroll et al., 2000). The visual pigment template that best fits the human curve has a spectral peak of 530 nm. The monkey curves had spectral peaks of 532.50 nm and 532.71 nm. The average λ_{max} value for the monkeys' M pigments is very slightly different than the average human protanope; however, the monkey values fall within the range of variation reported for human protanopes (Carroll et al., 2002). Thus, these animals provide an ideal model of human protanopia.

Color vision thresholds

Color vision was characterized extensively for two squirrel monkeys (1 and 2), and a complete set of thresholds for each animal is shown in Fig. 3. Data obtained from a human protanope tested in the animal apparatus is also shown for comparison (Fig. 3, bottom). Here, thresholds determined from the cumulative Gaussian that best fit each psychometric function have been plotted in the CIE (1976) u', v' diagram. Plotted points that lie near the center of the graph indicate hues for which the subject has low thresholds; that is, the chromatic stimulus did not have to be very saturated in order to be distinguished from the achromatic background. If a subject had great difficulty discriminating a particular colored stimulus, the extrapolated threshold for that color plotted outside the limit of the gamut available on the computer monitor. In some cases, subjects were not able to reliably distinguish a particular

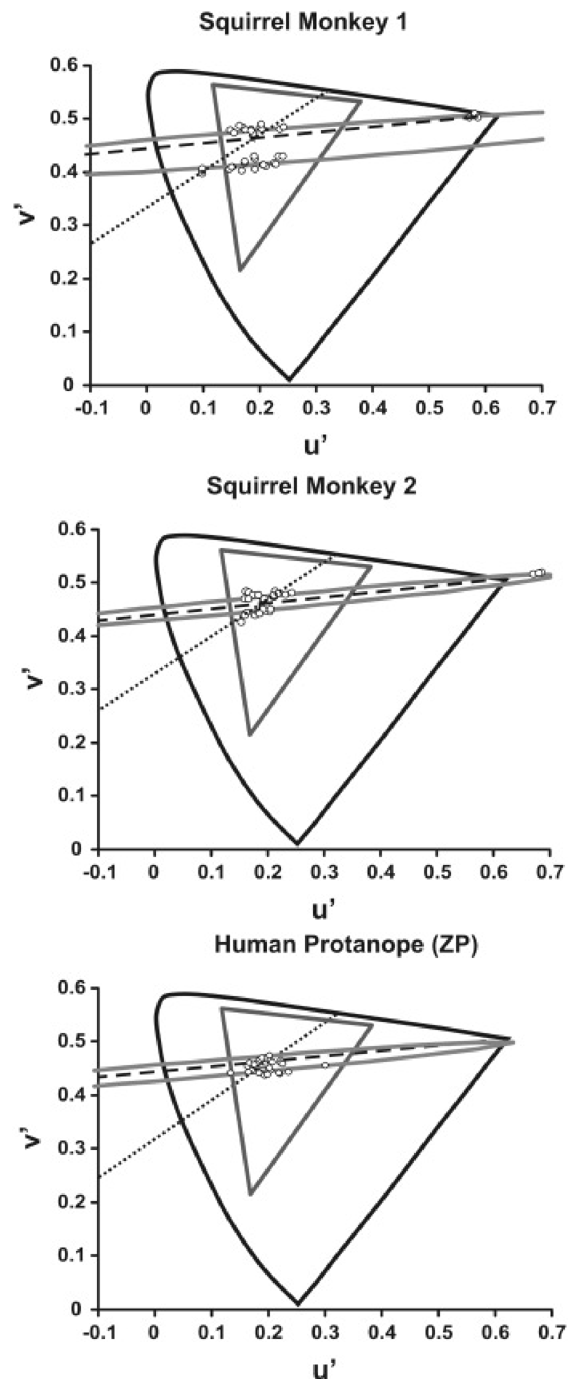

Fig. 3. Color vision thresholds plotted in CIE (1976) u', v' color space. The top and middle graphs contain thresholds from monkeys 1 and 2, respectively; the bottom graph contains data from a human protanope. Lines that were drawn through the typical human protan and deutan confusion points are shown for comparison (dashed and dotted lines, respectively). The triangle in each graph represents the limit of the gamut of hues available on the computer monitor. The measured discrimination ellipses of each subject are shown in light gray. The coordinates of the neutral gray background of the test are located at $u' = 0.1888$, $v' = 0.4607$.

hue from the gray background at any of the available levels of spectral purity, and the extrapolated thresholds for these colors approached infinity, producing the open-ended appearance of the ellipses shown in Fig. 3.

Reliability of the modified test

Three separate color vision tests were completed by each of the two monkeys. In Fig. 4, thresholds obtained for animals 1 and 2 have been plotted in x, y graphs in which the x-axis shows the 16 different hues that were tested and the y-axis shows the corresponding thresholds for each hue. Plotting the thresholds in this way allows them to be displayed at higher resolution than is possible in the CIE diagrams of Fig. 3. In Fig. 4, the directions in color space of each of the 16 hues are specified in terms of the dominant wavelength (DW) of the most saturated color tested for that hue. The separate curves in each plot correspond to individual threshold sets. The time required to test all 16 hues in a monkey is about 2–4 months. In Fig. 4, the three different tests shown were obtained consecutively, and the evaluation of all 16 hues in one test was complete before the next began. Thus, the results represent color vision testing that was conducted over the majority of a year for each animal. The results are highly repeatable, and there is no improvement in performance between the first complete test and the third test.

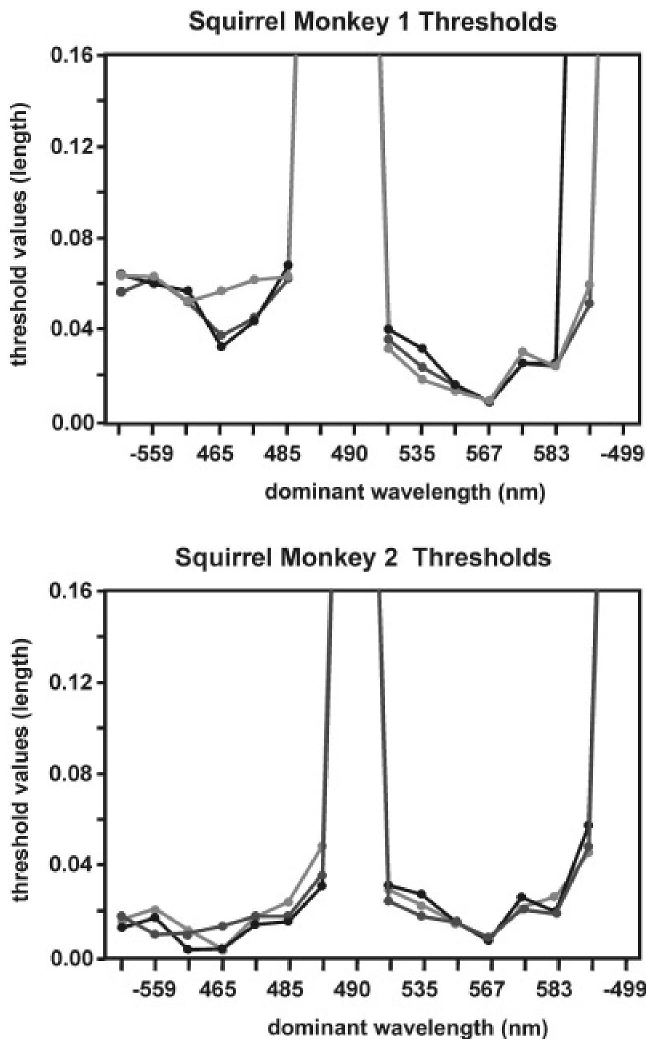

Fig. 4. Results from three separate complete color vision tests performed on squirrel monkey 1 (top) and 2 (bottom). The separate curves in each plot correspond to individual threshold sets of 16 colors each.

Discussion

The validity of a modified version of the Cambridge Colour Test was evaluated using squirrel monkeys whose middle-to-long-wavelength-sensitive photopigments had been characterized both genetically and physiologically. The results of genetic analysis revealed that the X-chromosome photopigment gene of the animals specifies a middle-wavelength-sensitive photopigment with a λ_{max} of 532 nm. Furthermore, the flicker photometric ERG spectral sensitivity obtained for each monkey was similar to the averaged spectral sensitivities of 10 human protanopes. Together, the genetic and ERG data indicated that these animals would have dichromatic color vision behavior, indistinguishable from that of a human protanope.

There are two dominant wavelengths that a dichromat cannot discriminate from gray. Accordingly, the color vision thresholds for a dichromat produce an elliptical plot in CIE u', v' color space, in which the long axis of the ellipse defines a confusion line along which all colors are indistinguishable for the individual. In each graph of Fig. 3, a dashed line was drawn through the coordinates of the neutral gray background of the test ($u' = 0.1888$, $v' = 0.4607$) and the typical coordinates of the human protan confusion point, $u' = 0.678$, $v' = 0.501$; a dotted line was drawn through the gray point and the typical coordinates of the human deutan confusion point, $u' = -1.271$, $v' = 0.782$. When the monkey thresholds were best fit to an ellipse, the long axis was closely oriented along the line drawn through the human protan confusion point, indicating that the animals' color vision behavior corresponds to that of a human protanope. These results demonstrate that the modified version of the Cambridge Colour Test not only is a valid method for determining the presence or absence of color vision in animals, but it also provides information about the spectral identities of the underlying photopigments. This test reliably distinguishes protan and deutan (and tritan) types of color deficiency and provides information about the severity of each, as discussed further below.

The thresholds obtained in three separate complete color vision tests for monkeys 1 and 2 are shown in Fig. 4. Repeated measurements of color vision behavior on individual animals were highly consistent. In practice, all chromatic stimuli are specified in terms of their CIE coordinates; however, in Fig. 4 the vectors are listed according to the DW value in nanometers of the most saturated color for that vector. This labeling system seems more intuitive for the reader than using CIE coordinates; however, it is used here with the reminder that metamerism between the colors produced by the phosphors of a CRT monitor as compared to pure spectral lights holds only for eyes with the same properties as a human's. For the squirrel monkeys, any discrepancies between results using monochromatic lights compared to DWs measured from the CRT are estimated to be small. In our test, the monkeys perform no better than chance for two stimuli that lie on the human protan confusion line, DW = -499 nm and DW = 490 nm. The latter value is nearly identical to the average wavelength of the spectral neutral point measured for human protanopes, 496.5 nm (Hecht & Shlaer, 1936). The dichromatic monkeys have the lowest thresholds for colors around DW = 567 nm and DW = 465 nm, and their thresholds progressively increase as the stimulus chromaticity is varied from those they discriminate most easily to the ones they cannot distinguish from gray. Because this test provides a quantitative measure of the animals' color discrimination, it will be possible to accurately track the course of any changes that may occur during future experiments.

While previous tests of animal color vision were often directed at determining the type of color vision (e.g. dichromatic *vs.* trichromatic) and the underlying photopigment basis, less has been done to determine the magnitude of the chromatic signal, or acuity of the color capacity. A commonly used test to evaluate color vision in animals has been the neutral point test. In this test, the subject's ability to discriminate between equiluminant monochromatic and achromatic lights is measured to determine if there is a band of wavelengths at which the animal's performance drops to chance. If such a spectral neutral point is identified, then the animal is considered dichromatic. Because only saturated test lights are used, while the neutral point test can distinguish dichromats from trichromats, it is not able to detect differences that might exist in the quality of red-green color vision between trichromats. For example, the discrimination failures shown by anomalous trichromats to desaturated lights would not be exposed with the neutral point test, and anomalous trichromats would not be distinguished from normals as a result. Fig. 5 illustrates that the Cambridge Colour Test provides comparable information to that of the neutral point test. The great advantage, however, is that because the Cambridge test provides the ability to determine saturation thresholds, it can be used to measure gradations in color vision capacity among trichromats, including the difference between anomalous trichromats and normal trichromats.

In conclusion, the adapted version of the Cambridge Colour Test is more efficient than conventional methods that have been used previously because it eliminates the need to equate the luminance of each chromaticity tested, and it provides the ability to continuously measure an animal's response to all possible saturations of the stimulus. This method will allow the color capacity of additional species to be characterized with great detail, and it is also sensitive enough to quantitatively monitor changes in an animal's color vision over time.

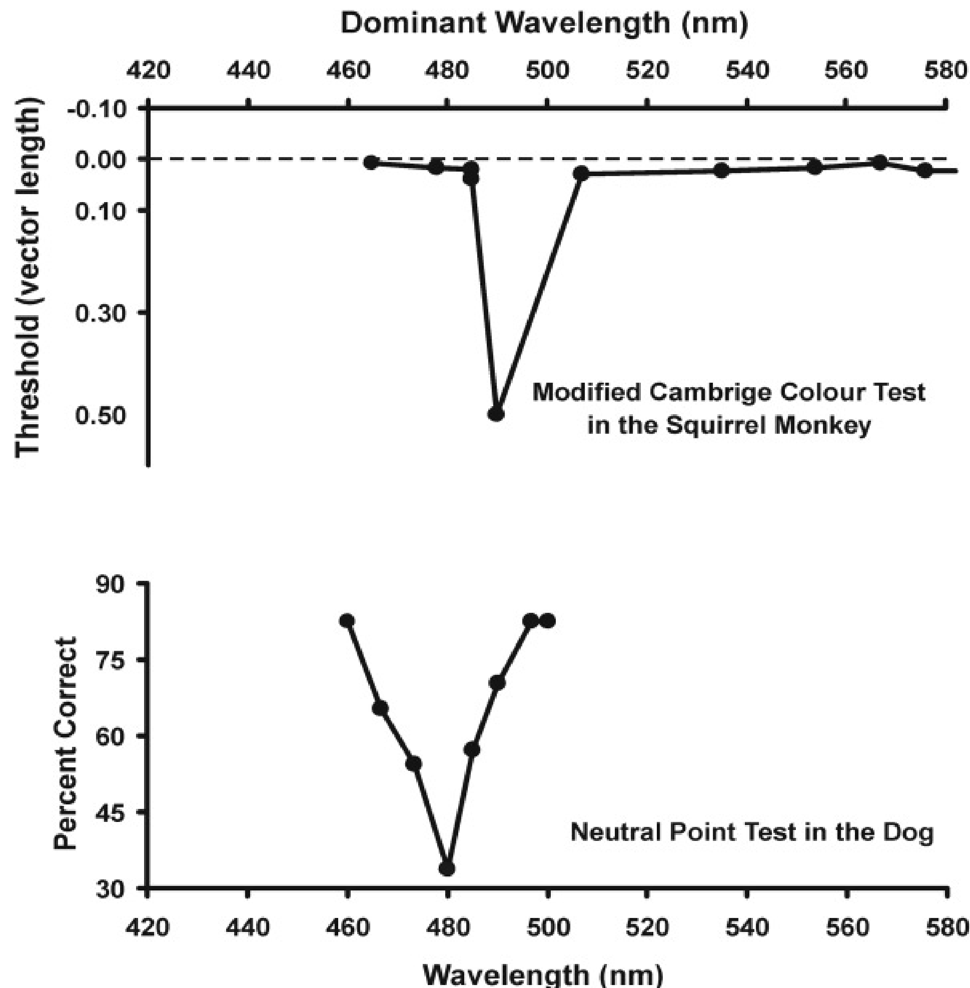

Fig. 5. Discrimination threshold analysis in a squirrel monkey compared to the neutral point test in a dog. The upper part of the graph corresponds to averaged color vision data from squirrel monkey 2, in which the horizontal axis plots the DW of the chromatic stimuli that were tested and the vertical axis shows the corresponding thresholds. The lower part of the graph corresponds to data obtained from a dog using the neutral point test (Neitz et al., 1989). The *x*-axis plots the wavelength of the test light, while the *y*-axis shows the percentage correct. Both tests can discriminate a dichromat from a trichromat by identifying a saturated color that is indistinguishable from gray for the dichromat. However, results of a neutral point test cannot be used to distinguish anomalous trichromats from normals. An advantage of the Cambridge Colour Test is that it provides the ability to measure saturation thresholds and is therefore sensitive enough to provide detailed information about the relative quality of trichromatic color vision.

Acknowledgments

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