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Color vision in the dog

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Abstract

The color vision of three domestic dogs was examined in a series of behavioral discrimination experiments. Measurements of increment-threshold spectral sensitivity functions and direct tests of color matching indicate that the dog retina contains two classes of cone photopigment. These two pigments are computed to have spectral peaks of about 429 nm and 555 nm. The results of the color vision tests are all consistent with the conclusion that dogs have dichromatic color vision.

Keywords: Dogs, *Canis familiaris*, Comparative color vision, Dichromacy, Cone Pigments

Introduction

Although keen color vision has long been considered an important sensory capacity of primates, the summary view has often been offered that members of other mammalian orders tend to lack color vision (Walls, 1942; Tansley, 1965; Ali & Klyne, 1985). According to Tansley (1965, p. 98), for instance, "On the whole mammals appear not to have color vision except for the primates." Contrary to this assertion, there is in fact evidence to indicate that at least the presence of color vision can be established in quite a number of nonprimate mammalian species (Jacobs, 1981). The major problem in deriving any generalizations about color vision in mammals is that appropriate tests have only been conducted on a relatively small number of mammalian species. Striking among the gaps in our knowledge is a lack of compelling information about color vision in any of the canids (Jacobs, 1981). This is particularly surprising in the case of the domestic dog (*Canis familiaris*) for two reasons. First, of course, the dog enjoys a unique status as a favored companion and able assistant to our species, the latter role often requiring the use of good vision. Second, dogs are subject to a variety of retinal degenerative diseases and in recent years this fate has made the species a frequent subject of ophthalmological studies (Aguirre et al., 1982; Schmidt & Aguirre, 1985; Schmidt et al., 1986).

The structure of the dog retina clearly suggests the possibility for color vision. In particular, there are abundant numbers of cones that comprise as many as 20% of all of the receptors in the central portion of the retina (Parry, 1953). In addition, there is both electrophysiological (Aguirre, 1978; Odom et al., 1983) and behavioral (Coile, 1982) evidence that these cones provide robust signals under classically defined, photopic test conditions. Despite these facts, behavioral studies have to date not yielded any concensus conclusion about dog color vision. Twenty years ago, Rosengren (1969) reviewed the studies published up to that time. Of the 16 studies she found in the literature, roughly half had concluded that dogs had some color vision; the remaining studies had either yielded negative conclusions or were ambiguous in outcome. Rosengren (1969) ran several simple color vision tests on four cocker spaniels and concluded that they had the capacity to make some color discriminations. There do not appear to have been any subsequent studies of dog color vision. None of the studies in this early literature would be considered as very compelling relative to modern standards for investigations of color vision. Accordingly, we have reexamined this issue and here report results that establish the presence of color vision in the dog, characterize the nature of this capacity, and provide an estimate of the spectral properties of the cone pigments of this animal.

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Methods

Subjects

The subjects were three adult, purebred dogs. Two of these were Italian greyhounds—a female (here designated as GY) and a male (FL). The third subject was a female toy poodle (RE). The dogs were tested daily. As their performances were rewarded with highly palatable food pellets, no deprivation measures were required.

Apparatus

Both the apparatus and general procedures were developed for studies of monkey color vision and they are described in detail elsewhere (Jacobs, 1983, 1984). Briefly, dogs were tested in a three-alternative, forced-choice discrimination. The subjects viewed three small, circular stimulus panels (diameter = 2.5 cm) mounted in a line (center-to-center = 5.0 cm) along one wall of

a test chamber. These translucent panels were illuminated by a two-beam optical system located outside of the chamber. Two of the panels were identically illuminated; the third received different illumination. The dogs were trained to select the uniquely illuminated panel, indicating their choice by touching the panel with their nose. A correct choice resulted in the automatic delivery of a 97-mg beef and cheese-flavored pellet (Noyes; Lancaster, NH). An incorrect choice resulted in a new test trial with the location of the positive panel and its radiance/wavelength composition determined by the experimental protocol. Each trial was marked for the subject by the occurrence of a cueing tone. The light reaching the positive panel originated from either a monochromator (Instruments SA Model H-10) or from a color mixer. The latter was made up of two monochromatic filters (Ditric, half-energy passband = 10 nm); these were mounted side-by-side on a linear positioner such that movement of the positioner changed the proportion of a light beam that passed through the two filters. Light reaching the two negative panels was drawn from a tungsten-halogen lamp. Light reaching all three panels was passed through diffusing spheres and the exit ports of these diffusers were the stimulus panels. The wavelength of the monochromator and the position of the color mixer were controlled through the use of stepper motors. High-speed electromagnetic shutters were located in each test beam, as were variable neutral density filters. All of the details of stimulus selection and timing, as well as the delivery of reinforcement and the recording of responses, were computer controlled. The interior of the test chamber was ambiently illuminated (100 lux) throughout all experiments.

Procedure

Using conventional shaping procedures, dogs were first trained to select a single brightly illuminated panel from among the three. Once the subjects made the correct selection nearly all the time, the discrimination tests were initiated. Several different experiments were run.

1. Increment-threshold spectral sensitivity

For determination of these spectral sensitivity functions, the three stimulus panels were continuously and equally illuminated with achromatic light (4800 K). On each trial, monochromatic light was added to one of the three stimulus panels and the subject's ability to detect the presence of this light was determined as described above. The test trial terminated when the animal responded or after 7 s; the intertrial time was 2 s. Both of these values were selected empirically as a result of early tests so as to maximize the performance of these subjects. Over trials and daily test sessions, both the radiance of the light and its wavelength were varied so that detection performance could be measured; the former was changed every five trials in steps of 0.2 log unit from a level where detection was near perfect down to levels where the dog performed at chance levels (33% correct). Stimulus wavelength was varied in steps of 10 nm from 440–650 nm. Following an extensive period of initial training, a final sample of discrimination performance was recorded (24 trials per wavelength/radiance combination) and from these psychometric functions were drawn. Spectral sensitivity functions were derived by determining the radiance required to detect each of the test wavelengths at a level significantly better than chance performance ($P = 0.05$). Complete spectral sensitivity functions were determined at two steady panel luminances—9 and 27 cd/m^2.

2. Neutral point test

The intent of this experiment was to see if dogs could discriminate between various monochromatic lights and a fixed achromatic light (4800 K; luminance = 5 cd/m^2). On each trial, the two negative panels were illuminated with achromatic light while the positive panel was illuminated from the monochromator. As a result of the outcome of experiment 1, most of the testing involved monochromatic lights drawn from the 460–500 nm portion of the spectrum; this range was covered in steps of 2 or 3 nm. In addition, several longer wavelength lights were tested for one of the three subjects. The classical problem in color tests with nonhuman subjects is to assure that discrimination performance reflects the use of color cues only. A variety of strategies may be used to accomplish this goal (Jacobs, 1981). One approach is to first measure a V_λ spectral-luminosity function and then use that information in conjunction with direct brightness matches between the to-be-discriminated stimuli. Since the results of experiment 1 indicated that the V_λ function for the dog should be quite similar to that for the normal human, we employed the alternate procedure of randomly varying the radiance of the monochromatic light (in blocks of 5 trials each) over a large range—from ± 0.6 to ± 1.0 around the level at which a normal human trichromat judged each monochromatic/achromatic pair to be equal in brightness. The radiance variation was accomplished in steps of 0.2 log unit. Other details of the test were identical to those used to measure increment-threshold spectral sensitivity.

3. Short-wavelength color matching

This experiment sought to determine the equation values for a short-wavelength color match. The two primary lights, 440 nm and 500 nm, were obtained from the color mixer. The standard light illuminated the two negative panels; it had a wavelength value of 480 nm. The training procedure and the method for obviating brightness cues were the same as those of experiment 2. Other details were the same as for experiment 1.

4. Wavelength discrimination

Wavelength discrimination was measured at each of five spectral points—440, 460, 480, 500, and 520 nm. In each case, the positive light (the variable wavelength in classical terms) came from the monochromator while the negative lights (the standards) were obtained by passing the second beam through an interference filter (Ditric, half-energy passband = 10 nm). At each test wavelength, the subject was first trained with the test light set, alternately, substantially (15–40 nm depending on the test wavelength) to the long and short wavelength sides of the standard. After extended training, the wavelength of the test light was progressively changed toward that of the standard in steps of 6 nm. The luminances of the standard lights varied slightly across wavelength in the range of 1.4–2.1 cd/m^2. The control procedure used to eliminate brightness as a potential cue for discrimination was the same as that described above for experiment 2.

Results

Although there was some variation among the three subjects, each rather quickly learned to make the visual discriminations

required of the present experiments. Once trained, the dogs completed 200–400 trials in each test session.

Increment-threshold spectral sensitivity functions were derived from psychometric functions constructed from the asymptotic discrimination data obtained at each test wavelength. The spectral sensitivity functions for the three dogs obtained on a 9-cd/m^2 background are shown at the top of Fig. 1. In that figure, the functions for the three subjects have been shifted along the vertical axis so that they best superimpose. In terms of absolute sensitivity, the results for GY and FL were indiscriminable; both of these subjects were on average about 0.3 log unit less sensitive than the poodle, RE. It is apparent that there are no significant differences in the shapes of the spectral sensitivity functions for the three subjects. The dog increment-threshold spectral sensitivity function has two locations of peak sensitivity—one at about 440 nm and a second in the range from 530–570 nm. A prominent feature of these functions is a sharply defined zone of much lowered sensitivity located at about 480 nm.

For subject RE, a second complete spectral sensitivity function was obtained when the three panels were illuminated with a considerably brighter steady light (27 cd/m^2). That function is shown at the bottom of Fig. 1 (open circles). The spectral sensitivity function obtained at the lower adaptation level from this same animal is also shown at the bottom of Fig. 1 (solid circles). Note that the form of the spectral sensitivity function is essentially unchanged for these two adaptation levels. The functions of Fig. 1 define photopic spectral sensitivity for the dog as determined at increment threshold.

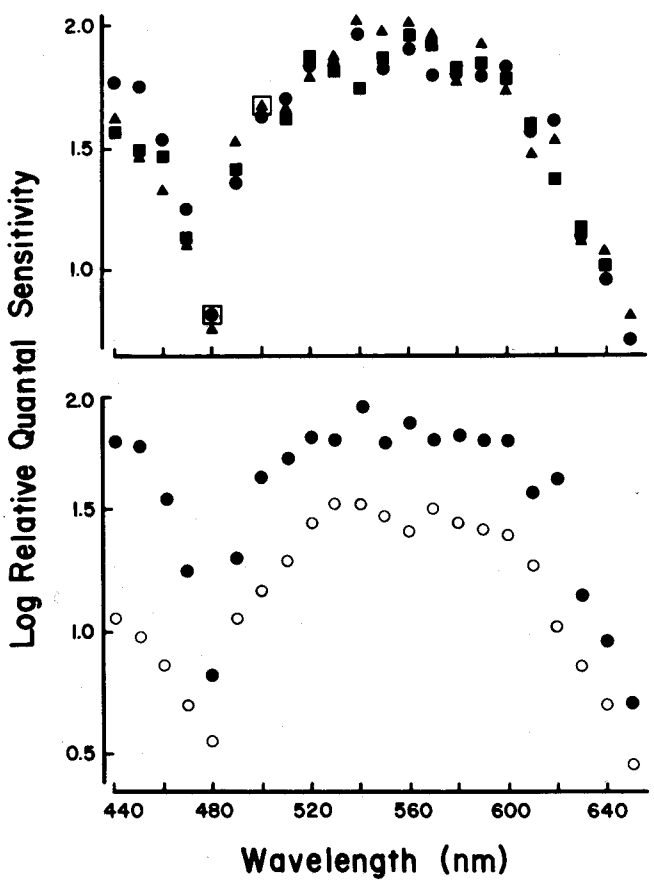

Fig. 1. Increment-threshold spectral sensitivity functions obtained from dogs. Results for individual subjects are coded as follows: circles (RE), squares (FL), triangles (GY). The results shown in the top panel were obtained with a background luminance of 9 cd/m^2. The functions for the three subjects have been slid vertically so that they best superimpose. The two functions shown in the bottom panel were obtained from subject RE. The open symbols are for a background luminance of 27 cd/m^2; the closed symbols show thresholds obtained on a 9-cd/m^2 background. Absolute differences in sensitivity at these two background levels are preserved.

Spectral sensitivity functions measured under conditions such as those for Fig. 1 are classically interpreted as indexing contributions to behavior from neural mechanisms whose outputs reflect subtractive interactions between multiples classes of cone types (Harwerth & Sperling, 1971; King-Smith & Carden, 1976). The most reasonable interpretation of Fig. 1 is that there are at least two types of cones in the dog eye; this conclusion provided the motivation for undertaking several direct tests of color vision.

The spectral sensitivity functions of Fig. 1 suggested that dogs might have dichromatic color vision. Unlike trichomats, dichromats would be expected to be able to match perfectly a monochromatic light to some equally bright achromatic lights. The forms of the functions of Fig. 1 would predict that if such a match would be possible, it would be for some monochromatic light in the vicinity of 480 nm. We explored this by seeing if the dogs could discriminate various monochromatic lights in this part of the spectrum from equally bright achromatic lights, i.e. if they had a spectral neutral point (Pokorny et al., 1979).

Each subject first received extensive training (>4000 trials) during which they were required to attempt to discriminate each of the test wavelength/radiance combinations (see Procedure) from the achromatic light many times. At the point where discrimination performance showed no further change, an additional 24 trials were run for each of the discrimination pairs. In this test, there are two possible cues to allow correct discrimination: brightness differences and color differences between the positive and negative stimulus. Variations in test light radiance at any given test wavelength would presumably have little effect on the presence or magnitude of any potential color cue, but they should greatly alter the magnitude of any potential brightness cue and, presuming the radiance range was correctly selected, at some radiance the brightness difference should be eliminated entirely, i.e. a pure color discrimination would be required.

The results of this test are illustrated for subject RE in Fig. 2; the other two subjects gave very similar results. Shown there are the asymptotic levels of performance achieved at each test wavelength from 460–500 nm at each of several test light radiances. Note that at most wavelengths this subject correctly discriminated all radiance values of the test light from the achromatic light. At each wavelength, some of these radiance values (covering a range of ± 0.6 to ± 1.0 log unit around equal brightness values for a human trichromat) must have included settings where the two stimuli were equally bright. This result thus demonstrates that dogs indeed have color vision. Note also in Fig. 2 that the animal fails to make the discrimination for a narrow band of test wavelengths. Since these wavelengths must have also included some radiance settings where the achromatic and chromatic light were equally bright, these regions define a color match, in this case a neutral point.

Figure 3A summarizes the neutral point test results for all

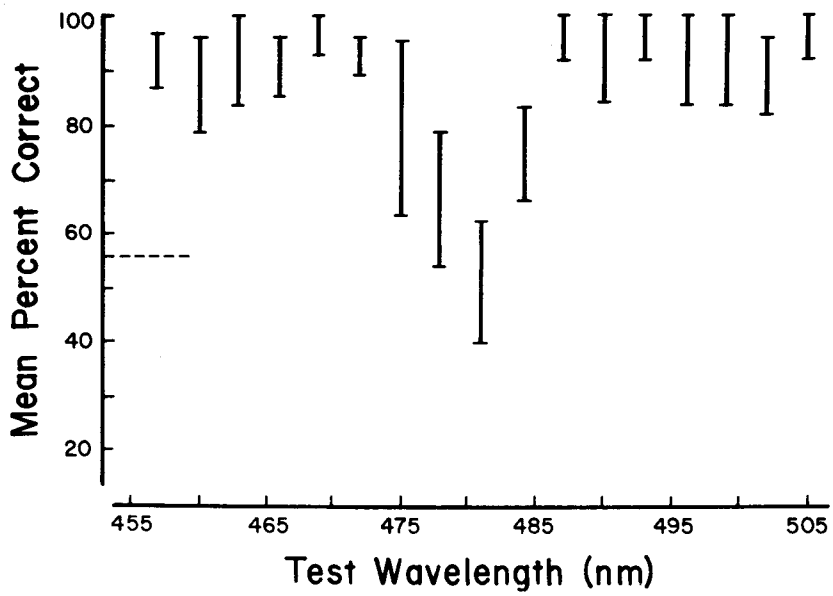

Fig. 2. Neutral-point test results. The vertical bars at each test wavelength enclose the total range of discrimination performance at all of the intensity settings. The horizontal dashed line at the left indicates the level of performance required to reach the 95% level of confidence. Subject: RE.

three dogs. For each test wavelength, we have plotted the poorest performance for any of the test light radiances. As explained above, the assumption is that these points represent the values closest to the point where test and negative lights were equally bright. Although RE was, overall, somewhat better at this task, the essential result is the same for all three subjects. Each of the animals could successfully discriminate a large number of different monochromatic lights from the achromatic light, but all of them failed to discriminate the monochromatic light when its wavelength was set at or near 480 nm. This pattern of outcome indicates that dogs have dichromatic color vision. Note (Fig. 3A) that one of the dogs, RE, was additionally tested at some relatively long test wavelengths and that she showed little difficulty in also making those color discriminations.

The dichromatic color vision of the dog implied by the results in Fig. 3A predicts that they should be able to perfectly match the appearance of a mixture of two monochromatic lights, one of which lies on either side of 480 nm, to a single light of some intermediate wavelength. This prediction was examined in a second color vision experiment in which the dogs were required to discriminate various mixtures of 440- and 500-nm light from a steady 480-nm light. The asymptotic performance of one subject, RE, is shown in Fig. 3B. The results there indicate that she successfully discriminated all mixture proportions (440 nm + 500 nm) from 480-nm light except for those lying in a narrow range of mixture proportions. A second subject, GY, gave very similar results. As noted above, the production of such a color match verifies the conclusion that dogs have dichromatic color vision.

In a final experiment, we obtained an index of the acuteness of dog color vision by measuring wavelength discrimination at five spectral locations. The complete wavelength-discrimination function for RE is shown in Fig. 3C. For the dog, color vision is relatively acute in a single part of the spectrum (at 480 nm RE was able to discriminate a wavelength difference of approximately 4 nm), but color discrimination ability falls off drastically for spectral regions much removed from this location. The result is that wavelength discrimination becomes effectively impossible for standard wavelengths of longer than about 520 nm. The falloff in this capacity to the short wavelength side of the best location is smaller, but also impressive.

Discussion

These experiments lead to the straightforward conclusion that dogs have color vision, and that it is dichromatic in character. That behavior is predicated on the presence of two classes of cone photopigment. The spectral sensitivity functions of Fig. 1 and the results from the short-wavelength color matching test (Fig. 3B) allow an estimation of the spectra of these two photopigments. On the assumption that only one of these two photopigments has significant absorbance in the long wavelengths (e.g. a photopigment having a λ_{max} of about 430 nm is more than 4 log units down from its sensitivity peak at 580 nm—Baylor et al., 1987), we best fit the sensitivity values from Fig. 1 for test wavelengths from 580–650 nm to wavelength-dependent visual pigment nomograms (Ebrey & Honig, 1977) using an iterative procedure (Neitz & Jacobs, 1984). In this procedure, a computer was used to determine the spectral peak (to the nearest nanometer) of the nomogram that gave the best fit to the array of sensitivity values. This exercise yielded a predicted spectral peak (λ_{max}) for the long wavelength cone of 555 nm.

Given that 555 nm is an appropriate estimate for the long wavelength cone, and that the shape of dog cone photopigment spectra are accurately captured by wavelength-dependent visual pigment nomograms, the data from the color match of Fig. 3B can be used to obtain an estimate of the spectral peak of the other (short wavelength) cone pigment of the dog. This was accomplished as follows. From the quantal value of the 500 nm/440 nm ratio at the match in Fig. 3B, the spectral position

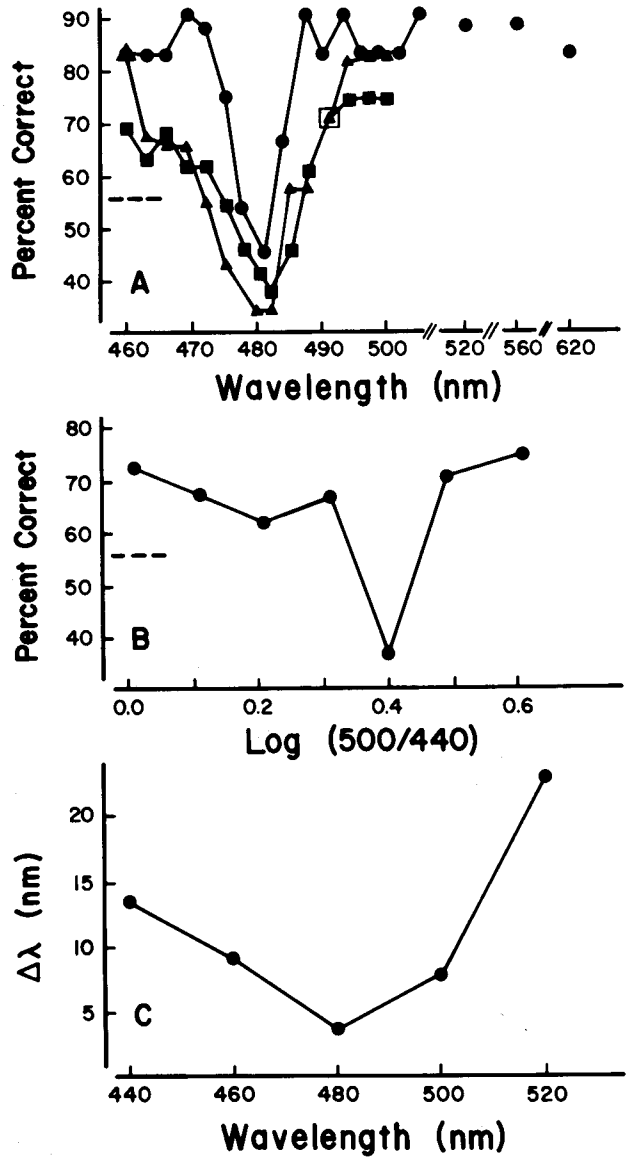

Fig. 3. Results from three tests of dog color vision. The results for individual subjects are coded as in Fig. 1. A, in this color matching test, dogs were required to discriminate various monochromatic test lights (abscissa values) from achromatic light. Several values of the latter were tested at each wavelength. The data points reflect those discriminations presumed to be at the brightness matched values (see text). The horizontal dashed line (left) shows the level of performance required to reach the 95% level of confidence. B, results from a second test of color matching. In this case, dogs were required to discriminate various mixtures of two monochromatic lights (500 nm and 440 nm) from an equally bright 480-nm light. Data shown for RE. Other conventions as noted above. C, wavelength discrimination function for RE. The data points give the change in wavelength required ($\Delta\lambda$) to discriminate ($P < 0.05$) the test light from each of five standard wavelengths (440, 460, 480, 500, and 520 nm). For the 460-, 480-, and 500-nm standards, the values are averages for wavelength change in both spectral directions; for the 440-nm and 520-nm standards, the difference thresholds could only be measured for longer and shorter wavelengths, respectively.

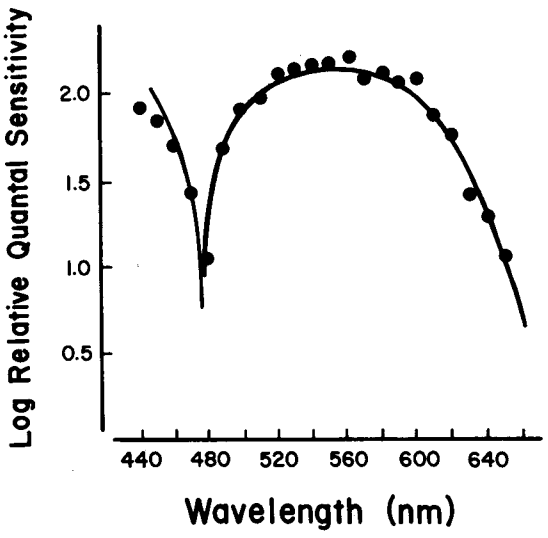

Fig. 4. Increment-threshold spectral sensitivity function for the dog. The data points are average sensitivity values for three subjects. The line drawn through the data points represents the best-fitting subtractive combination of the two presumed photopigments of the dog, i.e. those having λ_{max} values of 429 nm and 555 nm. This best fit combines these two pigments in the proportions of 55% (429 nm) and 45% (555 nm).

of the peak absorption for the putative short-wavelength cone was computed by solving simultaneously the color matching equations and the polynomial expression for a wavelength-dependent visual pigment nomogram appropriate for the short wavelengths (Dawis, 1981). In making this computation, we further assumed (1) that there is no significant differential absorption by the lens over the wavelengths of interest, and (2) that dog cones have a pigment optical density of 0.2. The λ_{max} value for the short-wavelength cone of the dog as derived by this method is 429 nm.

Some idea of the adequacy of these estimates of the dog cone pigments can be obtained by seeing how well they account for the increment-threshold spectral sensitivity functions of Fig. 1. The data points in Fig. 4 are the average spectral sensitivity values for the three dogs as determined on a 9-cd/m^2 background. The continuous curves in that figure are best fits obtained based on the assumption that dog cone pigments have λ_{max} values of 555 nm and 429 nm, respectively, and that the outputs from these pigments are combined in a subtractive fashion to yield the increment-threshold spectral sensitivity functions. This subtractive procedure has previously been used to account for increment-threshold data of other dichromatic subjects (Jacobs & Neitz, 1986). The generally good fit of these curves to the data points suggests that the derived estimates for the dog cone pigments are probably reasonable.

Although the results of the several tests of color vision allow a formal classification of the nature of dog color vision, they fail to provide an indication of how useful this capacity might be. Although not totally compelling, there are two aspects of the results that suggest that color is a salient feature of the dog's visual world. The first is that it was relatively easy to train dogs to make color discriminations: almost from the first day of training each of the three subjects gave evidence that they could

make pure-color discriminations. This is in striking contrast to the number of other animals that have dichromatic color vision that we have tested in the same situation and with the same paradigm. A second factor is evident from Fig. 2. Note that subject RE failed to significantly discriminate virtually all of the test lights in the region of her neutral point despite the fact that some of these must have been greatly different in brightness from the achromatic comparison light. This suggests that, once trained to make a color discrimination, this subject tended to ignore obvious brightness cues. Again, this behavior is quite different from what we have seen in other dichromatic subjects comparably tested. Both of these facts suggest that color vision for the dog is not simply a laboratory curiosity, but rather may provide a useful source of environmental information.

That dogs have dichromatic color vision should not be too surprising—this arrangement appears not to be uncommon among mammals. For instance, among the nonprimate species recently examined, dichromacy has been found to characterize several species of ground-dwelling sciurid (Jacobs, 1978), the tree squirrel (Blakeslee et al., 1988), the tree shrew (Jacobs & Neitz, 1986), the pig (Neitz & Jacobs, 1989), and probably, although not certainly, the cat (Loop et al., 1987). If there is an emerging generalization to be found, it is that trichromacy does not appear to be present in any mammalian species other than the primates. However, the number of mammalian species, about whose color vision we remain ignorant, is still so large that it would be foolhardy to pretend that the situation is even approximately characterized.

There are several dichromatic types whose color vision appears similar to that of the dog. The most obvious is the human deuteranope. The increment-threshold spectral sensitivity function for the dog is very similar to that of the human deuteranope (Zrenner, 1983) and the spectral positioning of both the long- and short-wavelength cones in the human deuteranope (average values of 558 nm and 427 nm, respectively—Mollon et al., 1984) is close to that of the estimates given above for the dog. Furthermore, the dog wavelength-discrimination function of Fig. 3C is similar to that classically measured for the human deuteranope (Wright, 1946). The average neutral point for the human deuteuranope (Hurvich & Jameson, 1974; Massof & Bailey, 1976) is centered at a somewhat longer wavelength than that for the dog (about 505 nm *vs* 480 nm), but that difference could be partially accounted for by differences in lens density (and thus the effective spectral character of the achromatic comparison light) in the two species.

Over the years, the selective breeding of *C. familiaris* has led to a long list of different breeds with strikingly different morphological and behavioral characteristics. The three subjects here were drawn from two of the six breed groups recognized by the American Kennel Club. We found no differences in color vision among the three animals, suggesting that the same cone pigment types and nervous system connections necessary for color vision are probably common to all members of this species.

In sum, the experiments whose results are reported here show the dog to have dichromatic color vision. These results predict that dogs should be capable of making color discriminations between stimuli whose predominant spectral energies lie, respectively, to the short and long sides of 480 nm; these results also indicate that color discriminations between stimuli whose spectral energies fall on only one side of this value would be expected to vary from easy to impossible as a function of how greatly these two depart from 480 nm.

Acknowledgments

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