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13. The concentration of rhodamine was approximately 1 percent in 2 to 4 ml of urine. Portions of urine (approximately 1 ml) were drawn from each urine-containing vial.
14. Male guinea pigs were allowed access to female urine on three glass plates (7.5 by 15.0 cm) for 4 minutes per plate, with a 30-second pause between plates. For females, the male urine was placed on the rim of their food bowl or presented on cotton swabs saturated with the dyed urine. The females were allowed access to the stimulus for less than 5 minutes. We have no evidence that the different modes of stimulus presentation influenced the results.
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17. Broadband excitation of about 450 to 490 nm, with emission wavelength $\gtrsim 515$ nm, was obtained with a Leitz Orthoplan fitted with an I2 filter combination (FITC). A Leitz M2 filter combination yielded a maximum excitation wavelength of about 546 nm, with a half-bandwidth of 14 nm and emission at $\gtrsim 580$ nm (rhodamine). At other times, a Zeiss Standard was fitted with filters BP 450-490, FT 510, LP 520 for broadband excitation of 450 to 490 nm and emission at $\gtrsim 520$ nm (FITC); or with BP 546/12, FT 580, LP 590 for a maximum excitation wavelength of about 546 nm, with half-bandwidth of 12 nm and emission at $\gtrsim 590$ nm. When viewed with the FITC filters, the vomeronasal organ of each subject, regardless of experimental manipulation, exhibited considerable autofluorescence. Without preliminary treatment of the tissue, the medial sensory epithelium contained a scattered array of colored points not seen in the lateral respiratory-like (nonsensory) epithelium. Also, a band of elastin lateral to the respiratory-like epithelium exhibited an intense green fluorescence. The source of this autofluorescence is not known.
18. With the rhodamine filters, autofluorescence was seen in the deep cartilagenous and bony tissues of the olfactory organ (but not the neuroepithelium) of every guinea pig surveyed, regardless of the experimental group assignment.
19. A Plexiglas tube (outside diameter, 10.0 mm; inside diameter, 6.5 mm) was cut to an approximate length of 7.0 mm and sealed at one end with a flat sheet of Plexiglas. A 1.5 by 2.5 mm hole was punched in the tube near the closed end. The open end of the tube was affixed to the rhinarium with glue.
20. Prior to the presentation of dyed urine, six females and one male had undergone one of a variety of surgical attempts to block the nasopalatine duct unilaterally. None of the attempts were a complete success. Patency, albeit slight in some cases, was observed in each instance. However, in the male and in four of the females, the gross amount of rhodamine fluorescence was less in the vomeronasal organ ipsilateral to the damaged duct than in the organ contralateral to the damage.
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Filter-Mediated Color Vision with One Visual Pigment

Abstract. *The compound eye of the grasshopper* Phlaeoba *has alternating bands that appear clear or brown. Electroretinograms recorded from the individual bands have different action spectra: The spectrum of the clear band peaks at 525 nanometers and that of the brown band at 545 nanometers. Spectrally selective whole-eye adaptation with light of either long or short wavelength yields identical action spectra. This evidence suggests that this eye has only one visual pigment, whose spectrum is altered in the brown bands by a screening pigment. In behavioral tests of spontaneous choices between stimuli that appear green to the normal human and those that appear red, the green stimuli are preferred even when the relative intensity is varied by 0.9 log units around the equal-brightness level (determined by the electroretinogram). When some red light is mixed with the green light, the preference for the mixture is less than for the green light alone, even though the mixture is more intense. True color vision therefore seems to exist. Painting the bands shows that behavioral color vision requires the presence of both types. These data suggest that* Phlaeoba *has true color vision mediated by one visual pigment and suitable optical filters.*

True color vision requires at least two receptor types with different action spectra. The receptor action spectra usually differ because they contain different visual pigments (*1*). However, a receptor's spectrum is also modified by ocular screening materials that selectively filter incident light (*2*) and thereby modify color vision. The colored oil droplets found in some birds and the corneal filters found in some flies have therefore been thought to play a role in color vision (*3*). But direct experimental evidence is lacking, and there has been some controversy (*4*) about the significance of these filters. Nevertheless, it is possible for true color vision to exist, even in organisms that have only a single visual pigment, if suitable optical filters exist. We now report data from the grasshopper *Phlaeoba* sp. (native to Hong Kong; common name, "kan chow" or "choose nest"); these data provide what is, to our knowledge, the first evidence for filter-mediated true color vision. Three lines of evidence lead to this conclusion. (i) Physiological studies show that the eye of *Phlaeoba* is organized for filter-mediated color vision; (ii) behavioral studies show that *Phlaeoba* exhibits true color vision; and (iii) this behavior depends on the integrity of the optical filter system.

The compound eye is strikingly divided into brown and clear bands (*5*) by screening pigments (Fig. 1). Such screens modify the action spectra of other insect and invertebrate eyes (*2, 6, 7*); their functions are to shield the eye from strong light and to improve visual acuity. Electroretinographic (ERG) action

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spectra were obtained by conventional techniques (*6, 8*). The band action spectra were measured by placing the active electrode over one band's center after masking the remainder of the eye with thick black paint (*9*). The clear band spectrum was taken from either band 2 or band 4; it is shown with a dashed line representing Dartnall's nomogram for a visual pigment (*10*) in Fig. 2A. (For clarity, the data from the clear band have been raised by 0.3 log units.) The clear band spectrum is somewhat narrower than the nomogram. This is not unusual for spectra obtained from single invertebrate photoreceptors (*11*). The spectrum taken from brown band 3 peaks near 545 nm (Fig. 2A). The sensitivity difference between the clear and brown bands (or the effective screen) is also shown with an arbitrary vertical location. The screen peaks near 500 nm, and its spectrum is much flatter than the spectrum of a visual pigment. These data suggest, but do not prove, that this eye contains a single rhodopsin-like visual pigment and that the brown bands also contain a stable screening pigment. But small amounts of visual pigments with peak absorptions at other wavelengths might still exist.

This possibility was tested by chromatically adapting the whole eye with either short- (Wratten 47B) or long-wavelength (Wratten 25) light. Light-adapted spectra could not be taken from individual bands because the signals were then too weak. Accordingly, whole-eye action spectra were measured in both dark and light adaptation (Fig. 2A). The active electrode was placed on the boundary between bands 2 and 3. Even though both types of light adaptation reduced sensitivity by more than 1 log unit, the dark- and light-adapted spectra are virtually the same, and both can be well fitted by the average of the clear and brown band spectra. More importantly, the short- and long-wavelength adapting lights each produced virtually the same light-adapted spectrum (Fig. 2A). If other visual pigments existed, we would have found other peaks in the chromatically adapted spectra. The chromatic adaptation evidence, taken together with the evidence from the nomogram, make it likely that this eye contains only one visual pigment.

The screening pigment in the bands therefore provides a possible physiological basis for filter-mediated color vision; these animals have the receptors needed to discriminate midwavelength lights from other stimuli. This is the kind of discrimination that these animals must make in order to locate the vegetation of their preferred habitat. But do these animals show a behavioral color preference for stimuli that appear green to humans? To answer this question, animals were placed between two targets (Fig. 2B). One target was illuminated with light that appears red to us (Wratten 24). The other was illuminated with light that appears green to us (Wratten 58). The animals responded by hopping or walking toward either target. The stimuli were calibrated by placing a grasshopper on each target so that the light fell directly on an eye and recording ERG's. The intensities of the red and green lights that would be of equal brightness were taken as those giving the same ERG response. The intensity of the green light was varied relative to the red light around the equal brightness point. At all intensity ratios, green was preferred significantly ($P < .05$ or better) more often than chance and, at equal ERG brightness, the animals prefer green 82 percent of the time ($N = 200$, $z = 9.05$, $P < .001$) (Fig. 2C). To determine whether an artifact had caused this preference independently of the color, the Wratten filters were removed and the two targets were illuminated with white lights of equal intensity. The resulting response ratio was 55:45 ($N = 107$, $z = 1.03$, $P > .05$), which does not differ from chance. When one of the white targets was attenuated by 0.6 log units, the response ratio was 72:28 ($N = 117$, $z = 4.76$, $P < .001$). These results suggest that the animals do prefer green to red, but they also show that the animals prefer brighter lights. This is critical, for, however unlikely, a calibration error might have occurred in this experiment. Such an error (if it were large enough) could have made a preference for different colors that is based only on brightness seem like a true color preference that is also modulated by brightness.

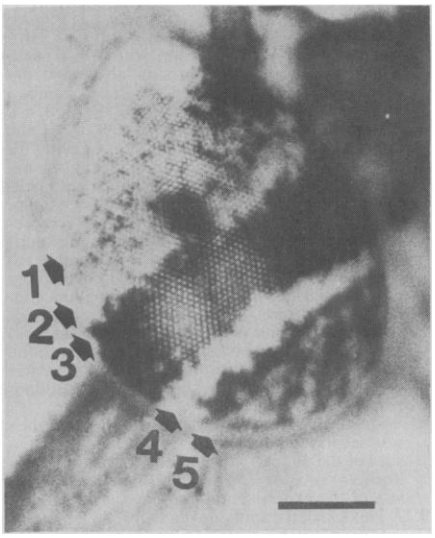

Fig. 1. The compound eye of the grasshopper *Phlaeoba* sp. with the bands identified. The calibration marker is 0.5 mm. The dark spot in the middle of band 2 is the pseudopupil.

A second behavioral experiment was therefore conducted according to procedures immune to calibration errors. The targets were initially illuminated by green- or red-appearing lights of equal ERG brightness ($N = 210$). A third light source then projected red light onto the green target; the amount of red light in the mixture was varied, keeping the green constant. If the animals respond only to brightness, the added red light should increase the response to the mixture side regardless of the quality of the calibration. On the other hand, if the animals really prefer green as a color while also preferring brighter stimuli, then adding some red light to the mixture should first reduce the preference for the mixture side (as the color difference between the targets disappears). Further additions of red light should increase the mixture preference once the targets are similar in color because of the brightness preference. This is a severe test of the color vision hypothesis: A positive result can be obtained only if a color preference not only exists but if it is also more powerful than the brightness preference. The results of this experiment are shown in Fig. 2D. The initial reduction ($N = 210$) in the preference for the mixture side is statistically significant ($z = 2.52$, $P < .02$) as is the final upswing ($N = 200$) that occurs when there is more red than green light in the mixture ($z = 3.35$, $P < .001$) (*12*).

Phlaeoba therefore appears to have true color vision. But is this color vision really mediated by the band system, or did our ERG experiments miss the presence of a second receptor population (*13*) with a retinal distribution unrelated to the banding? This question was answered by overpainting the bands. Because subjects tend to stop responding after repeated testing, and because of the difficulty of painting the eyes, these experiments were each done at a single arbitrarily chosen green:red ratio. As a control, six subjects had their eyes painted to leave a slit that was the same size as the central brown band but perpendicular to the bands (and hence exposed both band types). These subjects preferred green and the difference in the preference for green before and after painting was not significant, indicating that handling and painting did not affect the behavioral preference (log ratio = −0.6: green preference, 62 percent, $N = 103$ unpainted; 66 percent, $N = 104$ painted: $z = 0.63$, $P > .05$).

Then we masked the clear bands of 12 animals originally used in the first behavioral experiment. Under these conditions, the preference for green disappeared and the responses fell to a level consistent with the intensity ratio (log ratio = −0.3: green preference, 77 percent N = 200 unpainted; 41 percent, N = 150 painted: z = 6.79, $P < .001$). Another nine animals were first tested with unpainted eyes, and then the whole eye was masked except for band 4. The clear-cut preference for green exhibited in the unpainted condition changed to a brightness-only response after painting (log ratio = 0.0: green preference, 79 percent, N = 126 unpainted; 53 percent, N = 125 painted: z = 4.45, $P < .001$). These results strongly associate behavioral color vision with the bands, ruling out the possibility that a second visual pigment is distributed independently of the bands. The necessary and sufficient condition for color vision in these animals is the presence of both band types.

Phlaeoba thus has the physiological equipment needed for filter-mediated color vision and exhibits behavioral evidence for true color vision, color vision that exists if and only if light is permitted to stimulate both band types. It may seem strange that evolution has produced a color vision system that at best permits only a very coarse color discrimination, as the alternating bands do not share identical visual fields. These animals probably cannot perceive the colors of small stationary targets. (Indeed, we were unable to obtain reliable behavioral discriminations with point-source stimuli.) However, the system does facilitate the perception of large, uniformly colored stimuli, such as patches of vegetation. Discrimination may also be improved by scanning during movement. This hypothesis is supported by the fact that the bands are oriented differentially in different grasshopper species. Small

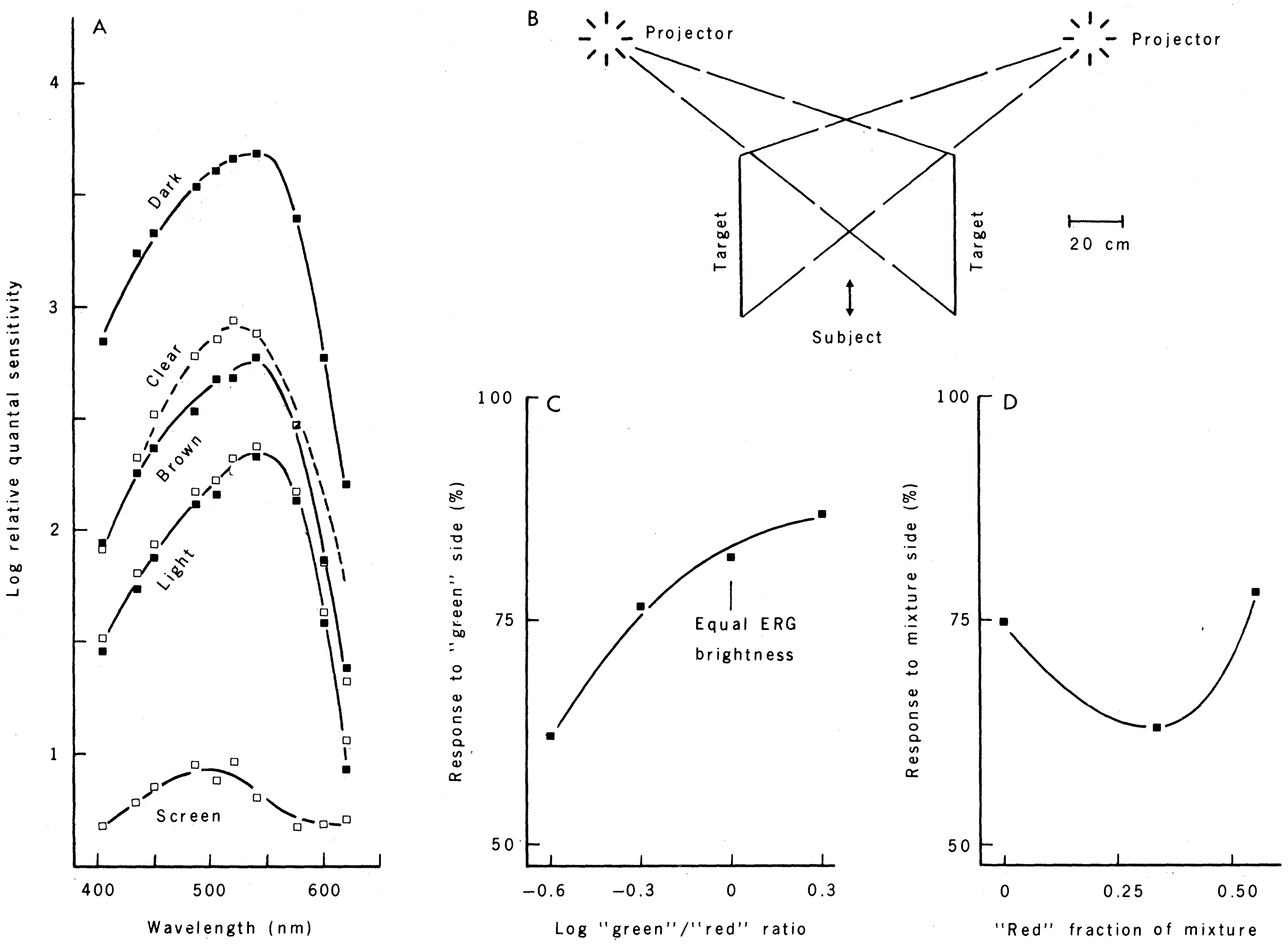

Fig. 2. (A) Examples of ERG action spectra showing the relative number of quanta required at each wavelength to elicit a 1.5-mV criterion response to a 100-msec flash. Each point represents an average of 12 measurements from three subjects except for the dark-adapted whole eye spectrum, which is based on ten observations at each wavelength. Error bars are not shown because they were about the size of the data points and were fairly consistent. (The average standard error was 0.035 log units.) The interaction effect between the brown and clear band spectra was significant [$F(9, 90) = 51.06$, $P < .001$). The light-adapted spectra produced by adapting lights of short (open squares) and long (filled squares) wavelengths were virtually the same. (B) Top view of the behavioral apparatus. The targets were made of white drawing paper standing on a base painted flat black. The projectors were Kodak Carousels. At the start of each trial, a subject was placed with its long axis parallel to and midway between the two targets; the subject could see the targets but not the light source. The direction in which the grasshopper faced was rotated 180° on successive trials. In the initial experiments, the entire appratus was rotated 180° on successive sessions, but this cumbersome procedure was abandoned when it became apparent that the apparatus orientation had no effect. Each subject contributed at least ten trials in a single session. Subjects were retrieved immediately after landing on a target in order to prevent the direct light from adapting one of the eyes, thus biasing subsequent choices. (C) Behavioral results when one target was illuminated with long-wavelength light ("red") and the other target was illuminated with medium-wavelength light ("green"). The frequency of responses to the green side are plotted as a function of the logarithm of the ratio of green to red. (The subjects run at the highest ratio were tested at a different time.) Each point is based on 200 trials. (D) Effect of adding red light to the green target when the ERG brightnesses were initially equated. The frequency of responses to the mixture side is shown as a function of the fraction of red added to the mixture.

grasshoppers such as *Phlaeoba*, whose locomotion has a large vertical component, have their bands oriented horizontally, while larger migratory and flying species have their bands oriented vertically. (The latter typically have finer bands than the former.)

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Hummingbirds See Near Ultraviolet Light

Abstract. *Three species of hummingbird (*Archilochus alexandri, Lampornis clemenciae, *and* Eugenes fulgens*) were trained to make visual discriminations between lights of different spectral content. On the basis of initial choices of feeders following a period of conditioning, birds of all three species were able to distinguish near ultraviolet (370 nanometers, 20-nanometer half bandwidth) from darkness (unilluminated viewing screen) or from the small amount of far red light that leaked through the ultraviolet-transmitting glass filter. A human observer was unable to make either discrimination. The birds were also able to distinguish white lights lacking wavelengths shorter than 400 nanometers from the full spectrum of the quartz-halogen bulbs. One can infer that the cone oil droplets, which have been lost from the retinas of most mammals, provide a potentially more flexible system for restricting the short wavelength end of the visible spectrum than does the filtering action of lens and macula that serves this function in the human eye.*

The visible spectrum for the human eye does not extend into the near ultraviolet (UV). The physical reason is that the lens absorbs wavelengths shorter than about 400 nm and the central area of the retina contains a yellow patch of carotenoid-containing cells, the macula lutea, which also filters out the violet rays (*1*). These features are generally believed to be evolutionary answers to the inevitable problem of chromatic aberration in the refractile elements of the eye. Because chromatic aberration becomes increasingly severe as wavelength decreases, visual acuity is significantly enhanced by the presence of these short wavelength absorbing filters (*2*). The modest price is a sacrifice in sensitivity to the shortest wavelengths available in the terrestrial solar spectrum. For insects, in contrast, whose eyes are assembled on a different optical principle, chromatic aberration is not a problem, and receptors specifically sensitive to near UV are frequently present (*3*).

Among the lower vertebrates, restrictions on sensitivity to short wavelengths appear common, at least in diurnal forms. Yellow lenses are common (*4*), and the densely colored cone oil droplets that are such prominent features of the retinas of birds and reptiles have often been interpreted as long-pass filters that reduce the effects of chromatic aberration (*5, 6*). Until recently there has been little evidence that the eyes of vertebrates are normally sensitive to near UV light, but reports exist for toads (*7*), newts (*8*), and lizards (*9*). The ocular media of chickens and pigeons are transparent to much of the near UV (*10*), and pigeons (*Columba livia*) see in this spectral region (*11, 12*). The action spectrum reported by Kreithen and Eisner (*12*) is noteworthy because the threshold in the UV is lower than the peak in the visible range and cannot therefore be attributed to fluorescence or absorption by a rhodopsin *cis* peak.

I now report behavioral experiments demonstrating sensitivity of hummingbirds to near UV light (*13*). The experiments exploit the fact that hummingbirds can be attracted readily to artificial feeders and can be taught by differential reinforcement to make discriminations between feeders. The experiments were done in the Chiricahua Mountains in southeastern Arizona, on three species of hummingbird: the black-chinned (*Archilochus alexandri*), the blue throated (*Lampornis clemenciae*), and magnificent or Rivoli's (*Eugenes fulgens*). By netting and marking individual birds, the population size of *A. alexandri* was estimated to be about 90, and the frequencies of visitation of individual birds was measured (*14*). The visiting population can be retrained to a new discrimination in less than 1 day, and in making discriminations, hue is demonstrably more important than brightness (*14*).

Four feeders were mounted on photographic tripods at a height of about 1 m and in a row about 0.6 m apart. Each consisted of a matte black metal box (20 by 18 by 25 cm) containing a 500-watt quartz-halogen projector lamp run from a stabilized power supply, heat and neutral density filters, collimating lenses, and filters to alter the spectral composition of the light. At each feeder, the light irradiated a 22-mm ground glass disk on the front of the box, located about 1.5 cm behind the stem of a plastic feeding bottle. The birds viewed this luminous disk both while approaching the feeder and while hovering to drink. Sugar solution (30 percent sucrose) was supplied at two of the feeders (training light) and 0.5*M* NaCl at the others (test light) (*15*). Test and training lights appeared at alternate positions in the array of four feeders, and the positions were interchanged at regular intervals to prevent the birds from locating the correct feeder by position rather than spectral content of the light.

Near UV light was generated with a Corning CS 7-37 filter, which transmits a broad band of wavelengths (λ) with a maximum at 360 nm. Because of the emission characteristics of the lamps, the maximum in the spectral distribution

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