PSYCHOMETRIC AND PSYCHOPHYSICAL HUE DISCRIMINATION FUNCTIONS FOR THE PIGEON

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Psychophysical researchers have traditionally employed four approaches in attempting to determine the underlying processes of color vision (Boynton, 1963): (1) color discrimination; (2) color mixture; (3) chromatic adaptation; (4) spectral sensitivity. Data on color discrimination contribute to our understanding of color vision because those spectral regions where color discrimination is best identify regions where the relative contributions of the underlying processes of color vision must be changing most rapidly (Wright, 1947). Wright (1947) in a volume summarizing 20 years of his research on normal and defective color vision said about the hue discrimination function:

The curves as a whole have the characteristics that might be anticipated from a qualitative examination of the spectrum. The part of the spectrum where a minimum exists must obviously occur where there is a rapid change of hue; thus in the yellow where the colour turns redder on one side and greener on the other, in the blue-green where it turns bluer on one side and greener on the other, in the violet where it becomes redder or bluer, minimum steps would be expected.

The hue discrimination function may thus locate interhue transition points, and identify the number of hues the organism perceives.

The present experiment was conducted to obtain a hue discrimination function for the pigeon and to determine whether or not minima of the hue discrimination function would coincide with those spectral regions of hue transition identified from slopes of wavelength generalization gradients (Guttman and Kalish, 1956; Blough, 1961) and from the intersection of the pigeon’s color naming functions (Wright and Cumming, 1971). If the relation between color naming and hue discrimination is found to be the same for other organisms as for humans, minima of hue discrimination functions can be assumed to mark transitions between hues in organisms for which color naming data are not available.

Related to the question of whether or not discrimination is best at color boundaries is the question of whether or not discrimination is the inverse process of generalization. Do subjects generalize their responses to the degree that they cannot discriminate among the stimuli?

Guttman and Kalish (1956) obtained wavelength generalization gradients from pigeons and compared them to the pigeon’s hue discrimination function (Hamilton and Coleman,

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Regions of the spectrum where there was least generalization did not correspond to spectral regions of best hue discrimination.

Transition points between pigeon hues, as determined from color naming functions (Wright and Cumming, 1971) and from slopes of generalization gradients (Guttman and Kalish, 1956; Blough, 1961), were likewise not those spectral regions where the pigeon was shown to have best hue discrimination (Hamilton and Coleman, 1933). As Blough (1961) has said, "... the need for more discriminability data is pressing".

METHOD

Subjects

Subjects were four white Carneaux pigeons (Columbia livia) from the Palmetto Pigeon Plant, Sumter, South Carolina. Birds 285 and 287 were 7 years old, bird 286 was 8 yrs old, and bird 53 was 11 years old at the beginning of the experiment. Bird 53 had previous experience matching monochromatic stimuli (Wright and Cumming, 1971); the other subjects were experimentally naive. Experimental sessions were conducted seven days per week if the subjects were 77-83 per cent of their free-feeding weight.

Apparatus

Optical system. The optical system which produced the bipartite stimulus is shown in Fig. 1. The light source (1) was an Osram XBO 150 W/1 xenon arc lamp. Two beams of light were taken from the source to form the separate halves of the bipartite stimulus. Light from the source passed through infra-red reflectors (2,2') and heat absorbing glasses (3,3'). It was then collimated (4,4') to form separate beams of light. After being reflected from front surface mirrors (5,5'), these collimated beams of light passed through filter boxes (6,6') containing polarizers, neutral density filters, and blocking filters. Then they passed through Bausch & Lomb series No. 44-78 interference filters (7,9). The resulting monochromatic beams were united by the front surface mirror (10) to form the split field. A solenoid operated device (8, of Fig. 1) allowed the radiance of the right field half to be varied automatically by actuation of individual channels containing Kodak Wratten neutral density filters.

Fig. 1. Schematic of optical system for producing a bipartite stimulus. (1) source, (2,2') infra-red reflectors, (3,3') heat absorbing glasses, (4,4') lenses, (5,5') mirrors, (6,6') filter boxes with polarizers, (7) interference filter for reference wavelength, (8) density filter actuator, (9) interference filter for comparison wavelength, (10) mirror, (11) lens, (12) shutter, (13) lens, (14) screen, (15) aperture.
The collimated light was condensed by lens (11), and the edge of the front surface mirror (10) was focused by a photographic triplet (13) onto the ground glass screen (14). Two pieces of ground glass, placed so that their ground surfaces were adjacent, were used as a screen. Placed against the front of the screen was a 0.2500 in. (6.350 mm) aperture (15) which limited the diameter of the bipartite stimulus. The screen was located 2.93 in. (74.4 mm) behind a color-clear glass pecking key, and the visual angle of the bipartite stimulus was approximately 2\(^\circ\)14\('\) of arc when the pigeon's beak was against the front surface of the pecking key. Distance from the tip of a pigeon's beak to its eye is approximately 1-50 in. (38.1 mm).

Bausch & Lomb series No. 44-78 interference filters passed three modes of energy: one in the infra-red, one in the visible, and one in the ultra-violet. The ultra-violet mode was eliminated by blocking filters placed in the filter boxes. The wavelength of the ultra-violet mode determined which blocking filter (Kodak Wratten No. 2A or No. 15 filter) was used. The infra-red reflectors (222) eliminated the infra-red mode of energy.

Wavelength of monochromatic light was varied by rotating the interference filters. Polarizers were placed in the filter boxes (66) so that large angles of incidence could be employed with no band pass distortion (Heavens, 1965). The interference filter (9) was rotated by joining the mounted interference filter to a precision gear reducer (Planet No. A-113) and the gear reducer to a precision stepping motor (Superior Electric No. H5305E). Backlash in the rotational system was eliminated by a weight applying constant torque counterclockwise to the shaft of the interference filter mount, and by all angular positions being approached by nine steps in a clockwise direction. No variability in wavelength produced by the system could be detected with the calibration equipment available.

Experimental chamber. The subject's portion of the experimental chamber was 12 in. (304.8 mm) long \(\times\) 14 in. (357.9 mm) wide \(\times\) 13 in. (330.5 mm) high. A stimulus panel formed one wall to which was attached a grain feeder with a 2 \(\times\) 2 in. (50.8 \(\times\) 50.8 mm) opening located 5.8 in. (146.1 mm) below the center key. Also on the stimulus panel were three horizontally aligned color-clear glass pigeon pecking keys (modified Lehigh Valley No. 121-16), 9.8 in. (247-6 mm) from the chamber floor and spaced 2.50 in. (63.5 mm) as measured from center to center. The pecking keys were positioned behind 1 in. dia. holes in the stimulus panel. In order to close the microswitch of each pecking key, 20 g of force had to be applied through a distance of 1 mm. The side key stimuli were 0.50 in. (12.7 mm) achromatic circles from IEE in-line units positioned 3.50 in. (88.9 mm) behind the color-clear glass pecking keys. The chamber was lighted by four GE No. 1820 bulbs mounted in the ceiling. A 6 \(\times\) 6 \(\times\) 6 in. (152 \(\times\) 152 mm) piece of opal glass diffused the light from the bulbs and produced an illuminance of 0.63 ft-L. (2.16 cd/m\(^2\)) on the gray chamber walls as calibrated with an Ilford SEI photometer.

A fan mounted in the chamber wall opposite the entrance door provided ventilation and masking noise. The calibration instruments could be positioned in front of the bipartite stimulus by removing the chamber wall opposite the stimulus panel.

Calibration of the bipartite stimulus

Wavelength calibrations. An Edgerton, Germeshausen & Grier 580-585 spectroradiometer was used to calibrate wavelengths. The stimulus panel and ground glass screen were removed during wavelength calibrations and a platform positioned the spectroradiometer in front of the stimulus.

A scanning method was used to determine peak wavelength for each position of the interference filter (9). The peak wavelength was defined as the monochromator setting (\(\pm 0.1\) nm) which produced the greatest response. Four determinations of peak wavelength were made at each position; two of them by rotating the monochromator grating in a clockwise direction, and two of them by rotating it counterclockwise. These individual determinations were usually within \(\pm 0.1\) nm of each other. Peak wavelengths were calibrated before and after data collection at each reference wavelength. The means from the two calibrations typically were equal within the resolution (\(\pm 0.1\) nm) of the calibration equipment. Means from the two calibrations contributed equally to the final estimate of peak wavelength.

Mean wave-number was the mean of the reciprocals for the individual wavelength calibrations. Slight differences between the wave-number shown for a particular peak wavelength and the reciprocal of that peak wavelength might occur because the mean of the reciprocals is not equal to the reciprocal of the mean.

Wavelengths of the two field halves were equalized by moving the interference filter (9) in discrete steps until its wavelength was as close as possible to the desired reference wavelength. Then the wavelength of filter (7) was adjusted to equal the particular value of (9). Interference filter (7) was mounted on a Mico (640-A) rotary table and its adjustment was continuous, as opposed to (9) which was adjusted in discrete steps. When monochromatic light from filter (7) was calibrated, the front surface mirror (10) was moved by its rack-and-pinion mount so that the only light incident upon the spectroradiometer came from this filter. As an added precaution, the collimated light beam to filter (9) was blocked as well. In a like manner during calibrations of monochromatic light from filter (9), mirror (10) was moved out of the beam passed by filter (9) and the light to filter (7) was blocked. Being able to move mirror (10) was particularly useful when calibrating radiance; otherwise the value of radiance would depend on the accuracy to which the split field could be divided.

Radiance calibrations. The radiance of each part of the bipartite stimulus was calibrated with an Edgerton,
Germeshausen & Grier 580 radiometer. A platform was used to position the radiometer precisely 4’75 in. (120-6 mm) in front of the ground glass screen. The stimulus panel was removed from the chamber and a 0-50 in. (12-7 mm) aperture was placed in front of the ground glass screen. Mirror (10) was positioned so that only one-half of the bipartite stimulus was incident upon the screen at any one time. Radiance calibrations were performed each time wavelength calibrations were made.

The stimuli were calibrated and adjusted with Kodak Wratten neutral density filters to be photometrically equal (for the pigeon) to a 560 nm stimulus at 2-40 × 10⁻⁴W/cm². This value of irradiant power is specific to the position of the radiometer from the diffusing screen. The 560 nm stimulus, at 2-40 × 10⁻⁴W/cm², was 8-6

mL (27-2 cd/m²) as calibrated with an Ilford SEI photometer. Desired radiometer readings for other to-be-corrected wavelengths were then computed. The radiometer reading at the 560 nm reference was corrected for the spectral response of the radiometer and for the light adapted pigeon (BLOUGH, 1957). The corrected 560 nm reading was set equal to the radiometer reading (unknown) at the to-be-corrected wavelength, multiplied by the spectral response of the radiometer and the coefficient for the light adapted pigeon (BLOUGH, 1957) at this to-be-corrected wavelength. The equation was then solved for the unknown radiometer reading. Next, the radiometer was placed in front of the stimulus and density (Kodak Wratten neutral density filters) was added to the light beam until the desired radiometer reading was obtained. The obtained radiance was at least within ± 0.02 log units of the desired value. Wavelength differences of one or two nanometers were frequently used during the experiment; at these small wavelength differences, photometric equality is identical to radiometric equality. Therefore, at small wavelength differences the accuracy to which brightness of stimuli was equated depended upon the accuracy of calibration equipment and not the pigeon’s luminosity coefficients.

Density needed to equate several stimuli photometrically was compared to the density indicated by a variant of a more traditional procedure. The Edgerton, Germeshausen and Grier 580–585 spectroradiometer was used to calibrate successive 5-0 nm bands of the monochromatic stimulus. Slit widths of the spectroradiometer were set for a 3-0 nm band pass. These calibrations were adjusted for the spectral response of the spectroradiometer and for photopic sensitivity of the pigeon (BLOUGH, 1957). The resulting energies were then summed, using a trapezoidal rule. Density values for the two methods were similar, but the former method of "looking in" with the radiometer and recording the gross response of the system was found to be more reliable.

The split field was halved by moving the mirror (10) until the field appeared to be equally divided. A rack-and-pinion drive moved mirror (10) along its axis so that it did not change its angle to the light beam. The angle of mirror (10) to the light beam from filter (7) was set so that the two halves of the split field were separated by a thin dark line 0-5 mm wide, as calibrated with an optical comparator (Edmund Scientific No. 30,585 6×).

**PROCEDURE**

**Final procedure**

The subjects’ task and the scheduled consequences are diagrammed in Fig. 2. A trial began with the onset of the 0-25 in. (6-4 mm) bipartite stimulus. A peck on the glass disk in front of the bipartite stimulus closed a microswitch, turned on side key stimuli, and allowed side key pecks to produce 3 sec access to grain or an 8 sec intertrial interval. Right side key pecks were correct when the two field halves differed in wavelength, and left side key pecks were correct when the two halves were of equal wavelength. Correct side key choices were occasionally followed by access to grain; reinforcement probabilities generally were changed from session to session to manipulate side key bias. Unreinforced correct side key pecks were followed by a 0-41 sec flash of the feeder light. Reinforcement or feedback (feeder light flash) was followed by an 8 sec intertrial interval. All incorrect side key pecks (either right or left) were followed by a 0-38 sec extinction of the overhead chamber light, and then an 8 sec intertrial interval. Generally, reinforcement probabilities for the two side keys were varied so that their sum was 0-40. Reinforcement probabilities were programmed by tape readers, one for each side key. The sequence for each probability was drawn from a random number table (RAND, 1955) and run lengths were adjusted according to binomial probabilities to yield geometric distributions.

Each of the six bipartite stimuli shown in Fig. 2 was presented for 100 trials in mixed order within a session. The comparison wavelength was either shorter than the reference
wavelength, or equal to it. Wavelengths of the comparison stimuli depended upon the subjects' performance. At each shift to a new reference wavelength, differences were made initially very large, then progressively reduced within the first few sessions. After performance stabilized, the largest difference selected was one where the subject's performance was just short of perfect, and the smallest difference was one where performance was just above chance.

Fifteen sessions were usually conducted at each reference wavelength. Data from the first five sessions were not used in the analysis. During the last two sessions, the radiance of one comparison stimulus was varied; in the next to the last session it was increased 0.3 of a density unit, and in the final session it was decreased by 0.3 of a density unit.

Discrimination performance was determined every 10 nm. The reference wavelength was initially 570 nm. It was increased in 10 nm steps to 660 nm, changed back to 570 nm, and then decreased in 10 nm steps to 470 nm.

**Preliminary procedure**

Before data presented for this experiment was collected, the subjects had been given extended discrimination training. Approximately 350 preliminary sessions were conducted with each subject. Initially only two comparison stimuli were used at a reference wavelength of 555-0 nm. In the presence of the bipartite stimulus 555-0-555-0 nm, right key (different) responses were correct. In the presence of the bipartite stimulus 555-0-555-0 nm, left key (same) responses were correct. Fifty trials of each type constituted a session. The subjects were reinforced for each correct side key choice; they were blacked-out (all chamber lights off) for each incorrect side key choice, and all trials were separated with a 15 sec intertrial interval. After approximately 30 sessions, reinforcement was made intermittently available for correct choices ($p = 0.20$), the intertrial interval was reduced to 8 sec, and the session was lengthened to 500 trials.

Preliminary assessment of discrimination performance was made at reference wavelengths of 555-0, 540-0, 525-0 and 570-0 nm. At 555-0 and 540-0 nm discrimination performance was determined for wavelength differences presented singly within a session and in combinations of five. Performance when only one wavelength difference was presented within a single session was found to be comparable to performance to the same differences when five of them were presented within the same session.

Twelve subjects were initially trained. Eight were eliminated from the experiment before the final procedure; six subjects never acquired appropriate identification of the stimuli, and two were inordinately slow to reacquire performance at new reference wavelengths.
RESULTS

Analytic method

Wavelength discrimination was assessed by manipulating bias and extracting a bias free discrimination index (d') with the analytic methods of signal detection theory. Bias was manipulated by changing the reinforcement probabilities. An increase in reinforcement probability for correct left-key “same” responses relative to correct right-key “different” responses would increase the subject’s bias toward making “same” responses. Such bias change would be shown by the data points being closer to A’ along A–A’ in Fig. 3. For an easier discrimination, one where the difference in wavelength was greater, manipulation of the bias might map out the function from B to B’ in Fig. 3. When data from such bias manipulations are plotted on normal-normal coordinates (as in the lower panel of Fig. 3), the resulting functions are usually linear (Clarke, Birdsell and Tanner, 1959).

The discrimination index d' can be computed for each data point by subtracting the normal deviate value of p (“different”/wavelength difference) from the normal deviate value.

Fig. 3. Hypothetical isosensitivity curves for a difficult discrimination A–A’, and for an easier one B–B’. They are plotted on linear coordinates in the upper panel and on normal-normal coordinates in the lower panel.
of \( p \) ("different"/no wavelength difference). If the linear function (on normal-normal coordinates) is of unit slope, then the value of \( d' \) at all points along the line will be equal. It is not uncommon, however, to find isosensitivity functions with slopes less than one (Green and Swets, 1966). For functions which are not of unit slope, \( d' \) will vary depending upon the particular point selected. When a point must be chosen to compute the discrimination index (\( d' \)) the one frequently chosen (and the one used in this study) is that point where the linear function crosses the negatively sloping diagonal (Clarke et al., 1959; Egan, Schuman and Greenberg, 1961; Pollack, 1959). Egan and Clarke (1966) have noted that day-to-day variability in isosensitivity functions is manifested by changes in slope, while the index \( d' \) at the negative diagonal remains relatively constant.

**Iosensitivity functions**

Figure 4 is a typical example of isosensitivity functions obtained from this experiment. Figure 4 shows five isosensitivity functions (from bird 287) plotted on normal-normal

![Image](image-url)

**Fig. 4.** Iosensitivity functions for bird 287 for five comparison stimuli at a reference wavelength of 640-4 nm. Arrows over data points indicate 100 per cent correct. Unfilled square is for a decrease of 0.3 density unit of the 629-6 nm comparison stimulus. Unfilled triangle is for an increase of 0.3 density unit of the 629-6 nm comparison stimulus. Unfilled circles are from sessions where the only wavelength difference was produced by a comparison stimulus of 631-4 nm.

\(^3\) A limited number of copies of isosensitivity functions at each reference wavelength together with the raw data in tabular form are available upon request to the author.
coordinates. In all five cases the reference stimulus was 640·4 nm. The most difficult discrimination is shown in the upper left hand panel for the 635·4 nm comparison stimulus to be discriminated from the 640·4 nm reference stimulus. The easiest discrimination is shown in the lower right hand panel for the 627·8 nm comparison stimulus to be discriminated from the 640·4 nm reference stimulus. One point in each of the five panels was obtained from each session. The proportion of incorrect right key choices is necessarily the same for all five wavelength differences and so the data points from each individual session have the same abscissa value.

Discrimination data for radience changes in the 629·6 nm comparison stimulus are shown in Fig. 4 by the unfilled triangle and the unfilled square. Changing the radience by

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**Fig. 5.** Psychometric hue discrimination functions for birds 53, and 287. The discrimination index (d') for each data point is a measure of the subject's ability to detect the difference between that comparison wave-number (reciprocal of wavelength) and the reference wave-number.


Psychometric and Psychophysical Hue Discrimination Functions for the Pigeon

0.3 density units did not affect discrimination performance (at 640.4 nm reference wavelength) which suggests that at 640.4 nm discriminations were not being made on the bases of brightness differences.

Filled data points in each panel of Fig. 4 were fitted by straight lines drawn by eye. Generally the closeness of fit to the straight line diminishes somewhat for increasing ease of discrimination. This is not an unexpected finding; the binomial variance, an underestimation of the actual variance (Green and Swets, 1966), increases with closer approximations to the upper left hand corner of the normal-normal square.

Once discrimination performance to the five comparison stimuli was tested (filled data points), six sessions were conducted where the bipartite stimulus was either 640.4–640.4 nm or 640.4–631.4 nm. The unfilled circles are within the range of the filled ones, indicating that there were no prominent interaction effects from testing discrimination performance to all five comparison stimuli in the same session.

Following hue discrimination testing at the first reference wavelength (569.4 nm), it was progressively increased in 10 nm steps to 660 nm. It was then changed back to 569.4 nm, and discrimination performance retested. Birds 287, 286 and 53 showed no change in discrimination performance over the 11 month period, suggesting that their discrimination performance was probably asymptotic. Bird 285 showed a slight improvement over the 11 month period.

Psychometric discrimination functions

The discrimination index (d') was calculated for the point where each isosensitivity function intersected the negative diagonal. The normal deviate value of the horizontal projection was subtracted from the normal deviate value of the vertical projection (Egan and Clarke, 1966).

Each d' value was then plotted as a function of the stimulus difference used to generate the isosensitivity function. One such function per reference wavelength was obtained for each subject as shown in Figs. 5 and 6. Lines were fitted to data points in Figs. 5 and 6 by a least squares method. Straight lines appear to provide a good fit to the data, and the correlation coefficients (r) were usually greater than 0.99. The slope of the lines indicates the rate at which discrimination changes with changes in wave-number difference between the two halves of the split field. A steep slope, e.g. at 600 nm, means that discrimination increases very rapidly for increases in wave-number difference between the two field halves. At 660 nm, the relatively shallow slope means that discrimination increases only slowly with increases in wave-number difference between the two field halves.

Differences between the reference stimulus and the comparison stimulus are scaled in wave-number difference units rather than in the more conventional scale of wavelength difference (∆λ). A scale of wave-number differences was chosen because wave-number, which is a constant proportion of light frequency, is invariant over all media whereas wavelength changes.\footnote{Frequency (ν) and wavelength (λ) are related by their product being equal to the speed of light (c): $νλ = c$. As light enters denser media, its speed decreases, and so the product (νλ) must also decrease. Either λ must decrease, or ν must decrease, or both must decrease. Frequency invariance is dictated by the energy relations of light. The energy (ε) per quantum is equal to Planck's constant (h) times the frequency (ν): $ε = hν$. If the frequency of light were to change upon entering each new medium, then the energy per quantum would also have to vary according to the medium. This obviously is not the case. Frequency cannot be directly measured, it must be calculated by dividing light speed by wavelength. But light speed cannot be determined as accurately as wavelength, and the resolution of frequency needed for most applications would involve more than the possible number of significant digits. Therefore it is more pragmatic to use the reciprocal of wavelength, wave-number, rather than frequency.}
Fig. 6. Psychometric hue discrimination functions for birds 286 and 285. The discrimination index ($d'$) for each data point is a measure of the subject's ability to detect the difference between that comparison wave-number (reciprocal of wavelength) and the reference wave-number.

**Psychophysical discrimination functions: constant $d'$ contours**

The linear functions of Figs. 5 and 6 were intersected at $d' = 2.0$, and the wave-number differences at these intersection points were plotted in the lowest panel of Fig. 7 at the reference wave-number. The dot-dashed line connects the mean points at each reference wavelength; at 590, 600, and 610 nm only the data from birds 287, 286, and 285 contributed to the mean.

These psychophysical functions in the lower panel of Fig. 7 are equal discriminability contours because the wave-number differences are those differences which, if presented to the subject, would result in the same discrimination index ($d'$). The functions for the four
Fig. 7. Psychophysical hue discrimination functions: intercepts of the wave-number difference axis (upper panel), slopes of the psychometric hue discrimination functions (middle panel), and equal $d'$ contours (lower panel).

Subjects are of the same absolute value and of the same general shape. Troughs (or dips) in the function (600, 540 and 500 nm) indicate relatively good discriminability. Bird 286 (filled squares) shows the most accentuated peaks and troughs with clearly defined minima at 500, 550 and 600 nm. Bird 287 (filled triangles) with a very smooth function shows the same trends and locations of the minima as does bird 286, although the trough to peak differences are less than they are for bird 286. Bird 285's function (filled diamonds) is more irregular than is 286's or 287's, and the 530 maximum is questionable as it is an isolated, elevated point. Bird 53's function (filled circles) stops at 510 nm because this (12-year-old) subject developed a cataract. The anomalous points for 590, 600 and 610 nm seem to be due to a progressive deterioration of bird 53's performance at these spectral points, in spite of the precautions to provide conditions conducive to reacquisition at new reference wavelengths. Reacquisition at 620 nm was possible by making the wavelength difference initially very much larger for bird 53 than for the other subjects.

The slopes of the psychometric functions are shown in the middle panel of Fig. 7, and are plotted as a function of reference wave-number. The slopes are plotted on a descending scale, so that dips in the slope function will correspond to dips in the equal $d'$ function (lowest panel of Fig. 7). The slope function shows virtually a one-to-one correspondence to the equal $d'$ function. One difference is that the slope function shows a minimum in the 550 nm region as opposed to the 540 nm region. There is less variability among subjects.
hue discrimination function from Hamilton and Coleman (1933) shows a minimum (best discrimination) at 570–580 nm region, which is the spectral point where there is a maximum in the function from the present experiment. Hamilton and Coleman's function shows a rather broad maximum in the 540 nm region, which is the spectral point where there is a minimum in the function from the present experiment. Only for short wavelengths (<510 nm) do the two functions show general agreement with each other. Several peculiar aspects of Hamilton and Coleman's (1933) data may indicate reasons for the discrepancy between their results and the results from the present experiment.

Hamilton and Coleman (1933) trained three pigeons in a Lashley jumping stand with two doors transilluminated with monochromatic light from a prism monochromator. Radiance was adjusted for sensitivity of the pigeon's eye according to pupillary measurements (Laurens, 1923). Two pigeons were trained to jump to the door of shorter wavelength, the third to the door of longer wavelength. Jumps to the correct door allowed the pigeon to enter; jumps to the incorrect door resulted in no entry and the pigeon fell into a net. The wavelength difference between the two doors was initially very large and was reduced progressively by increasing the shorter wavelength until the pigeon made an incorrect choice. The wavelength difference to which the incorrect choice was made was the discriminable step ($\Delta \lambda$), plotted as a function of the reference wavelength (the longer of the two wavelengths). The authors summarized their procedure for exploring the wavelength continuum as follows:

The spectrum was gone over 'continuously' that is, if the pigeon were just able to distinguish between 670 and 620 nm (nm), one would begin at 620 nm (nm) determine the next least perceptible difference between 620 and 600 nm (nm), say, and the next between 600 and 590 nm (nm), etc. Thus all parts of the spectrum between the points 700 and 460 nm (nm) were surveyed. (Hamilton and Coleman, 1933).

Discussing their results, Hamilton and Coleman (1933) noted:

A bird (Nos. 1 and 3) which had been jumping to the shorter of two lights consistently at all wavelengths above 530 nm (nm) will, when presented discriminable wavelengths below 530 nm (nm) jump at the longer. The second pigeon, trained oppositely, reversed his behavior in an analogous fashion at the pair (500–490 nm).

This peculiar result cannot be easily reconciled with the subjects' hue discrimination function. If the pigeons, trained to jump to the shorter of the two wavelengths, "consistently" jumped to the longer one at wavelengths below 530 nm, then at wavelengths of 530 nm or less the subjects should be "consistently" incorrect, and hence their discriminable step should be infinitely large. But the discriminable step is not infinitely large. In fact, for wavelengths somewhat shorter than 530 nm, the discriminable step decreases and discrimination is shown to improve. It is not clear whether the experimenters redefined a correct response as the longer of the two wavelengths, or whether there might have been a prolonged reacquisition phase so that the subjects would once again "consistently" jump to the shorter wavelength. In any case, it is the subjects' reversal at 530 nm which is of interest.

Another peculiarity of the Hamilton and Coleman (1933) discrimination function is found by computing the value of the comparison wavelength for reference wavelengths 620–700 nm. Computation reveals that the comparison wavelength remained the same (608–612 nm) for all of the reference wavelengths in the range 620–700 nm. This means that discrimination was independent of the wavelength value of the reference stimulus.

Hamilton and Coleman's (1933) procedure did not allow the subjects to make a "same color" versus "different color" response as did the procedure in the present experiment. Rather, the subjects were trained to jump to the shorter wavelength door. But what
does it mean to select the shorter of two wavelengths? It is only from a knowledge of the physical nature of light that yellow is shorter than red, or green is shorter than yellow.Hamilton and Coleman (1933) may simply have trained their subjects to jump to a particular hue. When the wavelength of the comparison stimulus was increased above 600 nm, the subjects made errors. When the wavelength of the reference stimulus was decreased below 540 nm, the subjects made errors. Thus, either the reference stimulus or comparison stimulus (or both) had to be in the range 540–600 nm for the subjects to play the game correctly. These wavelengths 540 and 600 nm may be the boundaries of a pigeon hue. These are the boundaries of a hue identified by Wright and Cumming (1971) from the pigeon’s color-naming functions.

Wright and Cumming (1971) trained pigeons to match-to-sample. In matching-to-sample the subject’s task is to select the side key stimulus which is identical to the center key stimulus. The subjects were tested by presenting test wavelengths on the center key and allowing the subjects to choose between two of the training stimuli on the side keys. For each test wavelength the proportion of choices to each of two possible training wavelengths was tabulated, and the mean proportions for the six subjects in the experiment are shown as filled data points in Fig. 8. Test wavelengths are shown on the abscissa, and wavelengths of the three training stimuli are indicated in Fig. 8 by filled arrows below the abscissa.

For a second test, training wavelengths were changed as shown by the position of the unfilled arrows below the abscissa in Fig. 8. Intersection of these gradients (unfilled data points) occur at the same spectral points (600 and 540 nm) as did the intersection of the gradients from the first test.

If the subjects were matching the stimuli per se, then a change in the wavelength values of the training stimuli (e.g., a uniform decrease of 20 nm) ought to result in intersection points some nanometers less than the former ones. Changing the training wavelengths, however, did not result in a change in intersection points. The subjects seem to have been matching hues rather than wavelengths, and 540 and 600 nm are the transition points between three pigeon hues. These hue transition points are essentially two of the three minima (600, 550–540 and 500 nm) of the hue discrimination function from this experiment. The correspondence of hue transition points to the minima of the hue discrimination function corroborates the conjecture by Wright (1947) that the part of the spectrum where a minimum exits “must obviously occur where there is a rapid change of hue.”

Color naming functions are generalization gradients where presumably the color name generalizes freely within a hue, but very little across hue boundaries. It was suggested (Lasley and Wade, 1946; Guttmann and Kalish, 1956) that subjects’ responses generalize to stimuli to the degree that they cannot discriminate among them, that generalization is the inverse process of discrimination. Guttmann and Kalish (1956) trained pigeons to peck a disk transilluminated with monochromatic light, and conducted generalization tests in extinction. They compared the slopes of the resulting generalization gradients to Hamilton and Coleman’s (1933) hue discrimination function, but they found no simple relation between the slopes of their gradients and minima of the hue discrimination function. If subjects generalize their responses to the degree that they cannot discriminate among the stimuli (inverse hypothesis) then steepest slopes of the generalization gradients (least generalization) should have occurred at those spectral points where hue discrimination was best.

5 No intersection point is shown corresponding to the 500 nm minimum of the hue discrimination function. For an intersection point at 500 nm one training stimulus should be located in the 500–540 nm wavelength range and another in the < 500 nm range. This was not the case for either test 1 or test 2.
It seems that controversy over the validity of the inverse hypothesis has been perpetuated through a dearth of adequate data on the pigeon's hue discrimi


cinability. Spectral regions where the slopes of Guttmann and Kalish's (1956) and Blough's (1961) generalization gradients were steepest are those regions (500, 540 and 600 nm) where hue discrimination was shown (this experiment) to be best. So it seems that the present experiment, together with the experiments of Wright and Cumming (1971), Blough (1961) and Guttmann and Kalish (1956), are in agreement that the regions of 500, 540–550 and 600 nm probably contain hue transitions (color boundaries) for the pigeon.

The inverse hypothesis has, in some cases, been accepted as a "given" rather than a theory to be validated. Graham (1962) used the human hue discrimination function to derive hypothetical color naming functions. This derivation was based upon the inverse hypothesis; regions of best hue discriminability were hypothesized to be regions where generalization of color names would be least. The general features of Graham's (1962) color naming functions have since been confirmed by Beare (1963); Boynton, Schafer and Neun (1964); Boynton and Gordon (1965); Sternheim and Boynton (1966); Beare and Siegel (1967); Luria (1967). The comparison between human data and pigeon data is particularly interesting because the boundary between two pigeon hues in the 540 nm region is located in the middle of a human hue. For increasing wavelength, the human color spectrum changes from blue to green at about 495 nm, and from green to yellow at about 565 nm (Beare, 1963). The 600 nm transition point for pigeons, likewise, does not correspond to the transition point from human yellow to human red, but there are several factors which make this distinction less clear: (1) It is questionable whether orange should be given a status independent from red; (2) Yellow is a narrow hue in terms of its wavelength range (565–585 nm); (3) The minimum of the human hue discrimination function is rather broad for this spectral region (Laurens and Hamilton, 1923; Wright, 1947; Weale, 1951; Bedford and Wyszecki, 1958).

Researches relevant to the physiology of the pigeon's color vision are not in close agreement with one another. There is little agreement as to the spectral characteristics of pigeon cone pigments (Wald, 1958; Bridges, 1962), and there is even some doubt (Sillman, 1969) that they exist. One of the complicating factors is that pigeons (like most saupropoda) have colored oil droplets in the outer segments of the cones. Any attempt to construct a unifying picture of the physiological mechanisms of the pigeon's color vision will have to take into account the role of these oil droplets.

There is somewhat more agreement among the results from microelectrode recording studies than those for photopigments. Donner (1953) recorded the massed discharge of the pigeon's retinal ganglion cells, and those units which gave relatively narrow-band spectral responses (modulators) tended to be of one of three types: (1) Peak response at 480 nm; (2) Peak response at 540 nm; (3) Peak response at 600 nm. As pointed out by Wright and Cumming (1971) the peaks of these response functions correspond to the intersection points of the color naming functions, rather than to the peaks of them. In a recent experiment examining single units of the nucleus rotundus of pigeon's thalamus Granda and Yazulla (1971) found that those units which did not have a peak response at 500 nm, generally showed peaks centered at 540 and 600 nm. These experimenters have recently (personal communication) isolated opponent units, where 500 and 540 nm represent

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6 See Shephard's (1965) analysis of the experiments by Guttmann and Kalish (1956) and Blough (1961).
crossover points in the spectrum between wavelengths that excite the unit and those that inhibit the unit.

It is hoped that the relationships among functions for the pigeon, obtained through various approaches to color vision, will indicate which relationships among functions reported for humans are fortuitous, and which have functional significance. The ability to separate the functional relationships from the fortuitous ones will help advance our understanding of the underlying mechanisms of color vision. The pigeon is particularly interesting as a color vision subject, because its hues do not correspond to human hues. The present experiment has shown pigeon’s hue discrimination to be best at its hue boundaries, corroborating the same finding for human subjects.

REFERENCES


Abstract—Four pigeons were trained on a "yes-no" signal detection procedure to detect the presence or absence of hue difference in a split field. Response bias was manipulated by varying reinforcement probability. Discrimination indices (d'), computed for each reference wave-number (1/λ), were linearly related to wave-number difference, and were shown to be a ratio scale of wave-number difference. Intersection of these functions at d' = 2.0 yielded a hue discrimination function. This psychophysical hue discrimination function and the slopes of the psychometric functions showed that hue discrimination was best at 500, 540–550 and 600 nm spectral regions.

Résumé—On dresse quatre pigeons à une technique de détection par "oui-non" pour décider de la présence ou de l'absence d'une différence de tonalité dans un champ à deux plages. On manipulait les réponses en modifiant la probabilité de renforcement. Les indices de discrimination (d') calculés en fonction du nombre d'ondes (1/λ) sont liés linéairement à la différence des nombres d'onde. L'intersection de ces fonctions à d' = 2.0 donne une fonction de discrimination de tonalité. Cette fonction psychophysique ainsi que les pentes des fonctions psychométriques montrent que la meilleure discrimination tonale est dans les régions spectrales 500, 540–550 et 600 nm.


Резюме.—Четыре голубя были натренированы обнаруживать наличие или отсутствие различий в цветовом тоне в поле зрения разделенном на две половины. Использовалась т. н. "да-нет"—процедура обнаружения сигнала. На реакцию оказывалось влияние с помощью манипулирования различными возможностями "усиления" (reinforcement). Показатели различий (d²), обработанные компьютером для каждого исследованного волнового числа (1/λ), были линейно соотнесены к различию в волновом числе и была получена шкала отношения к различию в волновом числе. Пересечение этих функций при d² = 2.0 давало основание для расчета функции различения цветового тона. Эта психофизическая функция различения цветового тона и ход психометрических функций показывают, что различение цветового тона является наилучшим в спектральных областях 500, 540, 550 и 600 нм.