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A Wavelength Discrimination Function for the Hummingbird *Archilochus alexandri*

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Summary. Free-flying black-chinned hummingbirds (*Archilochus alexandri*) at a site in southeastern Arizona were attracted to artificial feeders displaying narrow spectral bands of light (7 nm half band width). The birds were taught to discriminate between pairs of wavelengths of approximately equal brightness but with a spectral separation of 10 nm. After training, performance of the birds was not significantly changed by alterations in the relative intensities of the two lights. Moreover, when the spectral composition of the test and training lights was made identical, the birds did not learn to make a discrimination on the basis of intensity differences of 0.5 or 1 log unit. In the learned foraging behavior of these hummingbirds, the salience of brightness is therefore inconsequential relative to hue.

Discrimination scores for a constant 10 nm separation of test and training wavelengths were determined between 410 and 650 nm. This measure of the spectral dependence of wavelength discrimination shows a deterioration of performance at the red end of the spectrum but not in the blue and violet. Moreover, the minima at 585 and 555 nm indicate more structure than is present in this region of the spectrum in the human hue discrimination curve, and are similar but not identical to data on pigeon. These results are consistent with a growing body of evidence suggesting that the color space of birds may be more than three dimensional.

Introduction

In a previous study (Goldsmith and Goldsmith 1979) wild black-chinned hummingbirds (*Archilochus alexandri*) were trained at artificial feeders to discriminate between narrow bands of wavelengths. In general, their performance became poorer as the wavelength interval between the test and training lights was made smaller. From this work it appeared that the general shape of the wavelength discrimination function could be found by measuring the birds' ability to discriminate two wavelengths of constant separation as a function of position in the spectrum. In other words, when test and training wavelengths are separated by 10 nm, in a spectral region of good hue discrimination the birds should show fewer errors than in another part of the spectrum where their capacity for hue discrimination is poorer. A plot of performance vs wavelength should therefore serve to define the number and spectral positions of the minima in the wavelength discrimination curve, although it will not provide any information on the minimum $\Delta\lambda$ that can be perceived.

We have measured a wavelength discrimination curve for *A. alexandri* by this method. It has more structure in the green region of the spectrum than the human hue discrimination curve, and it suggests a rich color vision in the violet.

Methods

The feeders and experimental methods have been described in detail previously (Goldsmith and Goldsmith 1979); this account is therefore limited to a summary of the essential information.

Location. During May of 1978 and 1979 experiments were done on a population of wild birds at the Southwestern Research Station of the American Museum of Natural History near Portal, Arizona. About 70% of the experiments were done in May-June, 1980 at Aguila-Rancho, home of the Walter Spoffords, about 5 miles down the canyon from the first site.

Feeders. Four feeders were mounted on photographic tripods at a height of about 1 m and with lateral separation of about 0.7 m. At each feeder assembly the birds drew solution from the stem of a 125 ml plastic wash bottle mounted in an inverted position in front of a ground glass disk (22 mm diameter) which was illuminated from behind with narrow wavelength bands of light. Energies were measured with a calibrated photodiode, and fluxes lay within

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the range 9×10^{14}–1.2×10^{16} photons $\mathrm{sec}^{-1}\ \mathrm{cm}^{-2}$ in a plane behind the feeding tube and just in front of the luminous ground glass disk. Feeder and viewing port were kept shaded by an adjustable awning mounted on each feeder assembly. Unless specified otherwise, lights were adjusted for equal photopic brightness for the pigeon (Goldsmith and Goldsmith 1979); this is an arbitrary choice that has no bearing on the outcome, as demonstrated in detail in the section of Results devoted to brightness effects.

Scoring of Visits and Analysis of Data. The feeders were viewed from the side from a distance of about 10 m with 7× binoculars, which enabled us to see whether a bird that paused in front of a feeder actually inserted its tongue or bill into the feeding tube. During the 1980 experiments, the feeders were under constant observation from about an hour after dawn until feeding stopped at dusk. In so far as possible, only the initial visit of a bird was scored as it arrived at the feeders.

The available information on population size and stability has been reported (Goldsmith and Goldsmith 1979).

Frequency distributions were analyzed by the X^2 test; probabilities that observed differences are due to chance are given in the text and with several of the figures.

Procedure. Training and test wavelengths were drawn from interference filters (7 ± 2 nm half bandwidth) whose transmission maxima were separated by 10 nm. The bottles at the training light contained solutions of 25% sucrose; those at the test light, only water. The birds' final performance was scored following 6–8 h training, by which time performance had optimized. Learning curves are presented in Goldsmith and Goldsmith (1979). Throughout both training and testing the lights appeared alternately across the array of four feeders, thus the training color at A and C and the test wavelength at B and D, or vice versa. The two configurations were interchanged after every 25 counts, which prevented the birds from associating the sugar solutions with static positions in the array. The results presented in Figs. 4 and 5 represent nearly 5,000 counts, taken after performance of the birds had reached a plateau; several times that many visits were logged during training.

Results

An Example Discrimination of Two Wavelengths 10 nm Apart

The outcome of a typical discrimination experiment is illustrated in Fig. 1. The birds were provided sugar at the feeders in front of the 490 nm viewing ports but only water at 480 nm. Following several hours of training, a count of 100 visits showed 74% correct choices. As during training, the count of 100 visits took place in alternating blocks of 25, in which the sugar appeared first at positions A and C, then at B and D, and so forth. Test and training lights were therefore time-randomized across the array. One end of the array of feeders was preferred by the birds, irrespective of color, as can be seen by the distribution of total visits (small open circles, broken curve). This position effect is the baseline distribution against which effects of wavelength must be measured. The distribution of visits for the two blocks of 25 counts in which 490 nm appeared at feeders A and C is shown in the left half of Fig. 1. The birds clearly favored positions A and C, and the probability that this departure from the position effect could occur by chance is less than 0.01. Similarly, when the sugar and 490 nm appeared at B and D, these feeders were visited more frequently (Fig. 1, right half).

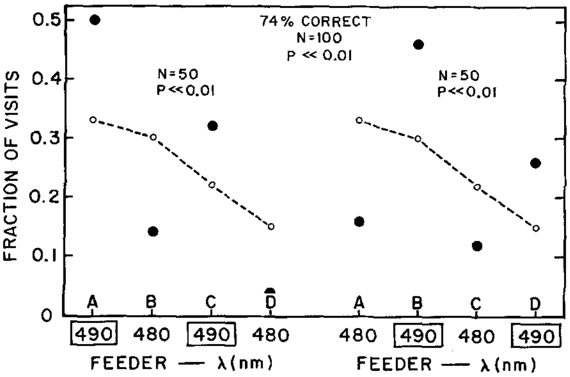

Fig. 1. A sample experiment showing the distribution of visits to the four feeders following sucrose reinforcement at one wavelength (490 nm) with only water at a comparison wavelength displaced by 10 nm (480 nm). Training wavelength shown by enclosing in a rectangle. The feeder positions were alternated on a regular basis to prevent learning of position (see the text). Small open circles and broken line: fraction of total visits ($n = 100$) to each feeder position, wavelength-randomized, showing that during the period of these observations the birds were favoring the feeders at the left end of the array (A, B). Large filled circles: fraction of visits at each feeder position for the two configurations (right and left halves of the figure) of test and training lights. Deviation of the large filled circles from the small open circles and broken line shows the degree to which the test and training wavelengths were discriminated. Note that following training the birds were able to locate the training color 74% of the time, and that with both configuration of lights the distribution of visits by wavelength is highly significantly different from the measured position effect. Each data point in Fig. 4 is based on an experiment similar to this

Some position bias is almost always present, but it changes with time and is frequently not as large as the example in Fig. 1 (see also Goldsmith and Goldsmith 1979). The results of every experiment were measured against the position effect that prevailed at the time.

What Do the Birds Learn?

Discriminations Are Based on Properties of the Lights. A measure of wavelength discrimination requires that the results not be influenced by cues that may be unrecognized by the experimenter. In previous investigations we have shown that when $\Delta\lambda$ is reduced to zero, the birds are unable to distinguish between the test and training lights. This experiment has been done in the red, green (Goldsmith and Goldsmith 1979) and near UV (Goldsmith 1980) regions of the spectrum, and we have repeated it again in the blue. Following training to 470 nm against a 460 nm test light, the birds chose the 470 nm light 75% of the time. When the 460 nm test light was shifted to 470 nm, performance fell to chance (52% correct, $N=125$, $P=0.53$). These several experiments, done at two sites over three seasons, provide an important internal control, for they demonstrate that discriminations are based on differences in the lights and not some spurious cue that the birds are recognizing but we are not. Furthermore, they demonstrate that the alternations of test and training positions after every 25 counts is frequent enough to prevent the birds from learning the positions of the sugar bottles.

Discriminations Are Not Based on Brightness Differences. The matter of brightness is critical. It is well known from human psychophysics that failure to equalize luminosities will invalidate quantitative judgements of hue discrimination, and appropriate caution permeates animal psychophysics. Against this background, our findings about the role of intensity differences are both simple and surprising.

In the behavioral paradigm we are using, which exploits the natural feeding behavior of hummingbirds, the birds' selections of feeder are not measurably influenced by intensity differences. This observation is so at variance with the usual expectations that we have taken some pains to establish the point. The evidence is as follows.

In the first experiments with this equipment (Goldsmith and Goldsmith 1979), the test and training lights were adjusted for equal photopic brightness for the pigeon. Following training, the discrimination of 620 nm from 546 nm was not significantly altered over a 30-fold change in luminosity of one of the lights. A similar experiment involving two wavelengths only 20 nm apart and a 0.5 log unit change in luminosity gave the same result.

One might argue that as $\Delta\lambda$ becomes smaller and the discrimination more difficult, brightness differences between the test and training lights would become a more important cue. We have therefore performed several experiments designed to reveal the role of brightness differences with smaller $\Delta\lambda$, directing our attention to the blue and violet regions of the spectrum where photopic luminosity might be more steeply dependent on wavelength. Birds were trained to discriminate λ from $\lambda \pm 10$ nm, with the longer wavelength of the pair 0–0.2 log units less intense (on the basis of quantum flux). When performance was stable, the intensity of the longer member of the pair (which was usually the training wavelength, λ) was attenuated 0.5 log units, and performance was remeasured. Positions of the feeders were alternated after blocks of 25 counts in order to prevent the learning of position, as described in Methods. The measurement of performance continued for 50 or 100 counts, the original intensity relationships were restored, and the process repeated until 200 visits had been tabulated. Scores for the two intensities were then compared. The results of six experiments are summarized in Table 1. Altering the intensity of one of the lights was accompanied by small changes, either increases or decreases, in the fraction of choices that were correct, and in only one of the six cases was the change in performance statistically significant. This result confirms and extends our earlier observation that following a period of training, changes in relative brightness of the two lights do not alter the birds' scores in selecting the sugar-containing feeders.

Table 1. Insensitivity of wavelength discrimination scores to changes of relative intensity of one of the lights

Task (nm)	Pattern of intensity alternation[a]	Score (fraction correct)[b]	Δscore after reducing[c]		Probability of observing this difference by chance
			I_{test}	I_{train}	
450 vs 460	100/100	0.72	–	+0.04	0.37
450 vs 460	50/50/50/50	0.65	–	−0.01	0.84
450 vs 460	50/50/50/50	0.74	–	−0.06	0.20
450 vs 460	50/50/50/50	0.70	–	+0.03	0.51
450 vs 440	100/100	0.78	–	−0.11	0.03
430 vs 440	100/100	0.78	+0.03	–	0.47

[a] After a period of training, the intensity of either the training light or the test light (see fourth and fifth columns of table) was reduced 0.5 log units. Feeder positions were interchanged after blocks of 25 counts, but intensity changes were made in alternating sets of either 50 or 100 counts, as designated in this column

[b] Fraction of visits to the training color when test and training lights had the intensity relation of the training period

[c] Change in the fraction of correct choices associated with reduction in intensity of one of the lights by 0.5 log units. In some experiments successive sets of 100 visits were compared; in others alternating sets of 50 visits were tabulated for a total of 200 (see column 2)

A second kind of experiment was done in which, following training, only one of the two training lights was reduced 0.5 log units in intensity. As measurement continued, the two training lights in the feeder array therefore simultaneously bore two different intensity relationships to the test wavelength, which was present at a single intensity at the other two feeders. The cycle of four feeder configurations (I–IV) is shown in the upper half of Fig. 2; feeders were shifted after every 25 counts, and following 100 counts each of the two training intensities had appeared at each of the four feeder positions (A–D) for an equivalent period.

The distribution of correct visits at the full (unshaded box) and attenuated intensity (shaded box) is shown in the lower part of Fig. 2. About 55%

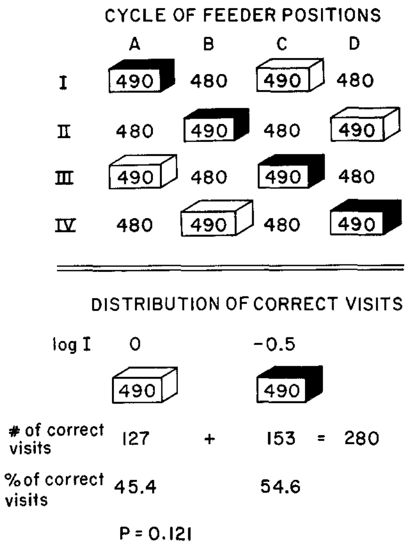

Fig. 2. Upper half: design of an experiment to examine the role of relative brightness. Following training to 490 nm (boxes) vs 480 nm, the intensity of one of the 490 nm lights was reduced 0.5 log units (shaded box) and tabulation of visits continued. The feeder positions were shifted after every 25 counts, as shown by the four rows (I–IV), and counting extended for a total of 400 visits. Lower half: of the 280 correct, position-randomized choices, 153 (54.6%) occurred at the 490 nm feeders where the intensity had been reduced 0.5 log units. This deviation from 50:50 is not significant by the usual criteria ($P=0.121$)

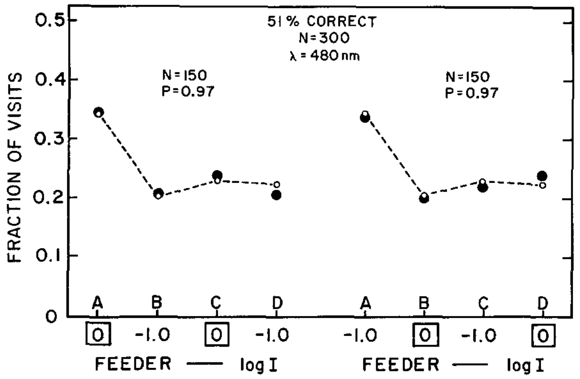

Fig. 3. Efforts to train the hummingbirds to an intensity difference of 1 log unit with 480 nm at all feeders were unsuccessful. After 6 h of training, which is sufficient for the birds to master a wavelength discrimination, they were performing no better than chance. Further details in the caption to Fig. 1 and the text

of the 280 correct visits occurred at the training light that had been reduced 0.5 log units in intensity. This is not a convincing departure from 50:50, however, for the probability of this deviation occurring by change is 0.12. This experiment therefore reinforces the conclusion that the birds select feeders primarily on the basis of differences in wavelength.

Table 2

Training (nm)	Test (nm)	Fraction correct	
		Immediate testing	Final average
430 vs 440	430 vs 420	0.85	0.83
450 vs 460	450 vs 440	0.78	0.78
470 vs 480	470 vs 460	0.75	0.76
560 vs 570	560 vs 550	0.78	0.77
550 vs 560	550 vs 540	0.70	0.72
540 vs 550	540 vs 530	0.69	0.67

As a third approach, we have attempted to train the birds to brightness differences while all feeders were displaying the same wavelength, i.e. $\Delta\lambda=0$, no differences in wavelength present. The result of this experiment is remarkable. For the first several hours the birds were offered sugar at lights 0.5 log units more intense than at the test feeders. As they showed no learning during this period, the intensity difference was increased to 1 log unit and measurement continued. The distribution of the final 300 counts of this experiment is shown in Fig. 3. Even with a 10-fold difference in intensity, the birds did no better than chance in finding the correct feeder. In short, in the training times employed in the wavelength discrimination experiments the birds are *totally unable* to master discriminations based solely on brightness. We therefore feel confident that the wavelength discrimination data we have obtained are not contaminated by luminosity differences between the test and training lights. In the Discussion we suggest a reason why this is so.

Discriminations Are Based on an Absolute Judgement of Spectral Position. We have shown that following training to λ vs $\lambda \pm \Delta\lambda$, if Δ is subsequently made 0, the birds are unable to distinguish the test and training lights. Put together with the evidence that brightness differences do not play a role in making the discriminations, we can conclude that the birds are learning wavelength differences. Two possibilities exist. They might be learning to recognize the longer (or shorter) of a wavelength pair, or they could be learning some absolute quality of the training wavelength, enabling them to distinguish it not only from the test light, but also from wavelengths displaced in the other direction in the spectrum. The latter is the case. Table 2 shows the results of six experiments. In each case the fraction of correct visits recorded immediately after introducing the new test light was high, and was not improved with additional experience. These observations lead us to conclude that during training the birds acquire some absolute measure of the spectral position of the training wavelength in the sense that their judgement of its color is independent of whether the comparison wavelength lies at +10 nm or −10 nm.

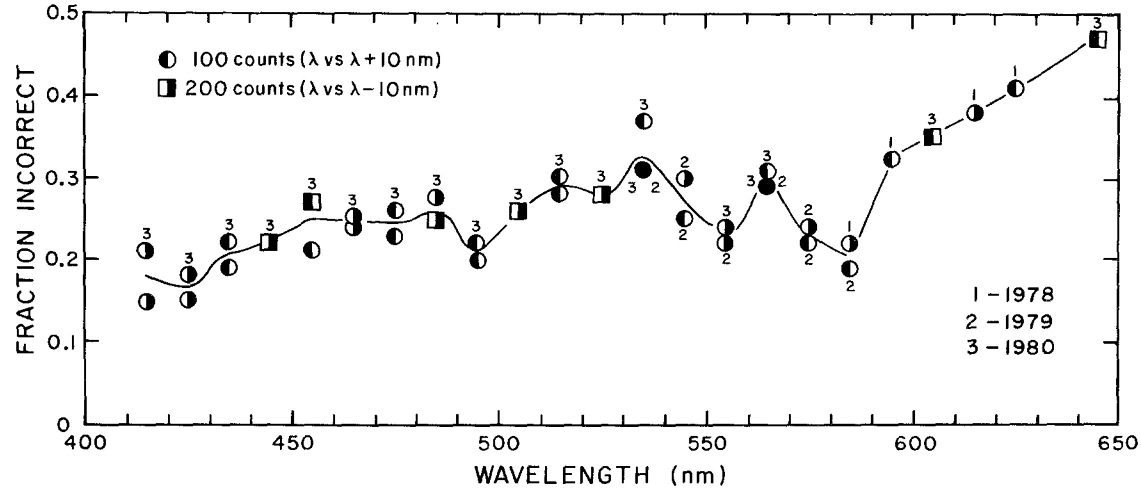

Fig. 4. Spectral variation of wavelength discrimination as measured by the fraction of incorrect choices for $\Delta\lambda = 10$ nm. Each data point is based on a count of 100 (circles) or 200 (squares), performed as shown in Fig. 1. The 1–3 best scores achieved in a day are shown in this figure, and the points are plotted on the abscissa midway between the test and training wavelengths. The training wavelength lay 5 nm to the shaded side of the data symbol. The experiments were conducted during May-June of three successive years, and the variation between years is no greater than the variation within a single day. The variations in performance that are statistically significant are considered in the text

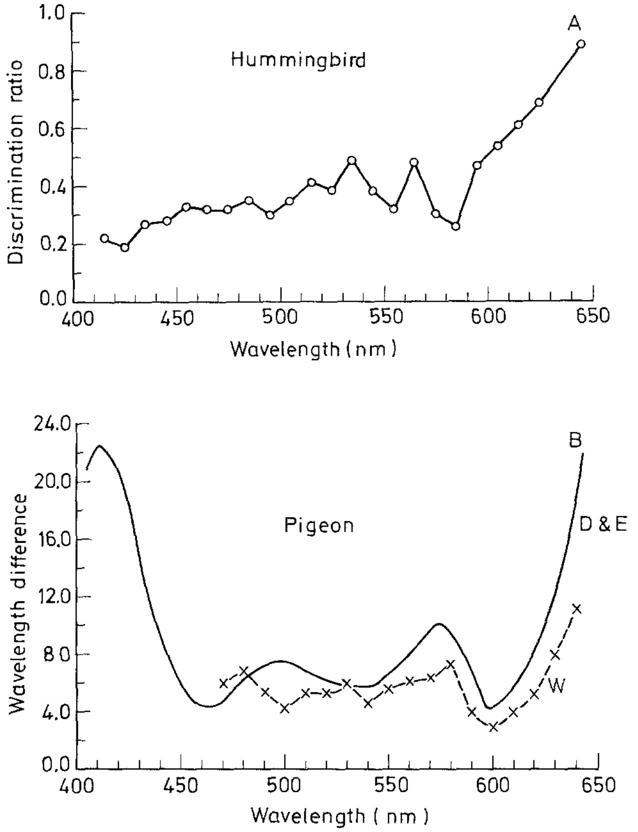

Fig. 5. A Average data from Fig. 4 plotted as the discrimination ratio – fraction incorrect:fraction correct. Performance at 565 nm is significantly poorer than at the two wavelengths to either side, as confirmed by the experiment of Fig. 6. **B** Wavelength discrimination functions for the pigeon as measured by Wright (1972) (X's) and Delius and Emmerton (1979) (dotted curve)

Wavelength Discrimination

The results of an extensive series of experiments involving pairs of wavelengths are shown in Fig. 4. Each of the 42 data points represents a count of 100 (circles) or more (usually 200, squares), representing the birds' best performances following training of 6–8 h and based on analyses similar to that in Fig. 1. (For learning curves, see Goldsmith and Goldsmith 1979). Test and training wavelengths were 10 nm apart, and the fraction incorrect is plotted at a wavelength half way between. The training wavelength lay in the direction of the filled side of the symbol. These experiments were conducted during May and early June of 1978–80, and the variation between years falls within the variation measured during a single day. Second, there is no tendency for performance to be better with the training wavelength either the longer or shorter member of the pair. All of the scores in Fig. 4 are significantly different from 0.5 except the point at 645 nm.

The averages are replotted in Fig. 5A as the discrimination ratio – fraction incorrect/fraction correct – a treatment that expands the ordinate somewhat and emphasizes the features of the curve we believe to be significant. For comparison, Fig. 5B also includes the hue discrimination data of Wright (1972, 1979) and Delius and Emmerton (1979) for the pigeon, obtained by operant conditioning. The precise relationship between discrimination ratio and the minimum $\Delta\lambda$ that can be detected is not known, so our discussion will focus on the number and spectral

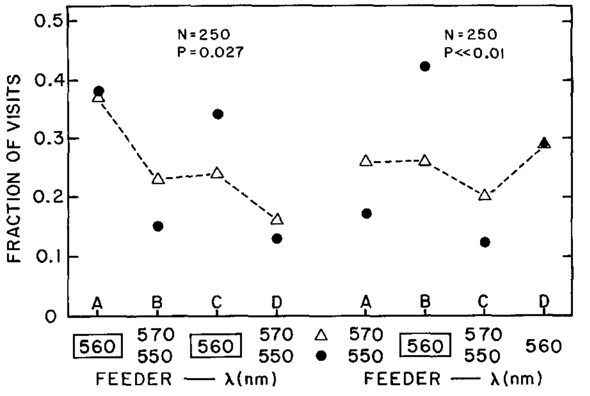

Fig. 6. Analysis of an experiment showing that *Archilochus* makes significantly fewer errors in discrimination 560 from 550 nm than 560 from 570 nm. Birds were trained to 560 nm and tested against 550 and 570 nm in alternating series of 50 counts for a total of 500 counts. As in all experiments, the positions of the training and test lights were alternated after every 25 counts. Open triangles and dashed curve: distributions of visits for the 560 vs 570 nm discrimination. (Note that the wavelength-randomized position effect is not shown). Filled circles: distribution of visits for the 560 vs 550 nm discrimination. For both spatial configurations of the feeder array, the birds did somewhat better in tracking the 560 nm light in the 550/560 discrimination and this difference is statistically significant (X test: $P<0.05$, left; and $P<0.01$, right)

positions of the minima in the curve for the hummingbird. Comparison with the pigeon is made in the Discussion.

Discrimination is poorest in the red and improves at all shorter wavelengths in the visible spectrum. There are minima at 585, 555, possibly at 490, and in the violet near 425 nm. The maximum at 565 nm is real, but because it is defined by a point at a single wavelength, and because the scatter for the 560 vs 570 nm discrimination was greater than for any other pair of wavelengths, an experiment was designed to verify its reality. Birds were trained to 560 nm, and tested at 550 and 570 in consecutive, alternating runs of 50 counts, for a total of 500 counts. (As usual, feeder positions were interchanged every 25 counts). The results, which are not included in Figs. 4 and 5, are shown in Fig. 6, where the frequency distribution of visits for the 560 vs 550 discrimination (filled circles) is compared with the distribution for the 560 vs 570 discrimination (triangles). As can be seem from the P values in the figure, these distributions are significantly different from each other. We therefore conclude that hue discrimination is significantly better in the region 550–560 nm than it is at 560–570 nm.

The shallow minimum at 495 nm is significantly lower than the peak at 535 nm, and the curve drops still further in the violet region of the spectrum. This result was so unexpected that we rechecked discriminations at longer wavelengths to be certain that there had not been a systematic and general improvement in performance. There had not. Throughout most of the spectral region we were using, we were able, with varying ease, to distinguish the test and training hues while standing in front of the feeders. For the shortest wavelength pairs tested however, where the birds' performance was its best, we were hard pressed to distinguish one light from the other. We conclude that the ability of hummingbirds to discriminate wavelengths in the violet region of the spectrum is almost certainly better than ours.

A Negative Experiment with Polarized Light

The feeders were fitted with polarizing filters and the lamps set for 480 nm and equal intensity. There was no measurable change in intensity on rotating the polarizing filters. An effort was made to train the birds to horizontal vs vertical e-vector, with no success. After 8 h of training, over a count of 200 visits the birds found the feeders with the sugar only 51% of the time.

Discussion

Significance of the Hummingbirds' Failure to Learn Brightness Differences

The facility with which hummingbirds learn to make wavelength discriminations contrasts sharply with their refractoriness to intensity cues, and this result will likely be understood only in the context of their natural feeding behavior. Hummingbirds exploit a variety of nectar sources through a season, and they are always ready to explore novel objects that represent new sources. At the same time, they can show fidelity to the richest sources currently available, at the expense of objects that experience has shown to be relatively unproductive, a tactic that makes the best use of the available energy supplies. Vision is the most important sensory modality in making these choices; color, as well as shape and location, are excellent cues, but brightness (and polarization pattern of reflected light) are unreliable. The amount of light reflected from a flower will vary with the illumination in unpredictable ways, as will the brightness contrast.

One possible interpretation of our experimental results is that the foraging experience of individual birds has greatly reduced the 'salience' of brightness cues relative to hue. If this is the explanation, the effect is profound; within the time frame of our experiments it appears that the salience of brightness cues is so low that the birds have learned not only to ignore, but not to learn even when reinforced. *Archilochus* seldom, if ever, draws sustenance from bright green objects, but can be taught to associate sugar with green lights as readily as with red (Goldsmith and Goldsmith 1979). Lack of experience with a particular hue therefore has no significant effect on the ease with which these hummingbirds can learn color-food associations. An argument that brightness has little salience therefore carries with it the additional inference that all visual cues that experience has shown to have low predictive value are not handled identically.

A somewhat broader class of explanation recognizes that evolutionary history can mold the associative process in species-specific ways, leaving animals prepared, unprepared, or even counter prepared to deal with specific learning tasks (Seligman 1970). Pigeons, for example, whose feeding is visually directed, are readily taught to make visual discriminations in an operant, key pecking paradigm with food as reinforcement, but fail to learn pitch discriminations with the same procedures (Delius and Emmerton 1979). The different degrees to which hummingbird feeding behavior is influenced by wavelength and intensity differences does not mean that the birds cannot make brightness discriminations; only that a more appropriate paradigm must be found to study their sensitivity to luminance differences. Likewise, it will be necessary to study the ontogeny of hummingbird foraging behavior in a controlled environment to ascertain what ultimately constrains their use of luminance cues in feeding. For example, it is conceivable that brightness/food associations are made with difficulty even by birds that have not had experience with the unpredictability of natural brightness cues.

A similar argument can be advanced with regard to our failure to demonstrate a sensitivity to the orientation of the plane of polarization. Hummingbirds, like pigeons (Kreithen and Keeton 1974; Delius et al. 1976), may possess this sensory capacity, and their failure to exhibit it in these experiments could be due either to the adaptational irrelevancy of the association they were asked to learn, or to the fact that only the part of the eye that normally views the sky is equipped for polarization analysis, and other regions of the retina are used for viewing the illuminated ports on the feeder boxes (Delius et al. 1976; Delius and Emmerton 1979).

Table 3. Visual pigments of avian cones

Species	Wavelengths of λmax (nm)				Method	Author
Pigeon chicken	413	467	507	562	Selective bleaching of early receptor potential	Govardovskii and Zueva (1977)
Pigeon	–	461	514	567	Microspectrophotometry	Bowmaker (1977)
Chicken	417	449	–	560	Detergent extracts	Fager and Fager (1981)

Visual Pigments of Birds

Recent evidence indicates the chicken and pigeon have four cone pigments (Table 3). Moreover, electrophysiological or behavioral correlates of the blue- and violet-sensitive visual pigments have been measured in both chicken and pigeon (Graf and Norren 1974; Norren 1975; Graf 1979) as well as the daw *Corvus monedula* (Wessels 1974; Norren 1975). These studies suggest a tetrachromatic color vision and demonstrate the presence of receptors for good hue discrimination at the short wavelength end of the spectrum. The relationship of these receptors to the ultraviolet sensitivity of pigeons (Kreithen and Eisner 1978) and hummingbirds (Huth and Burkhardt 1972; Goldsmith 1980), as well as the role of the cone oil droplets and the similarities and differences to other species of birds remain to be analysed.

Wavelength Discrimination Function of Pigeon and Hummingbird

Two wavelength discrimination functions for the pigeon are shown in Fig. 5B. They were measured in different laboratories by instrumental conditioning procedures, and, unlike our function for the hummingbird, the ordinate is the minimum perceptible $\Delta\lambda$. The curves are similar to each other in showing minima at about 600 and 540 nm, and a maximum at 570–580 nm. There are fewer data and there is less agreement at shorter wavelengths.

The curve for the hummingbird is qualitatively similar at the long wavelength end of the spectrum, with minima at 585 and 555 nm and a maximum at 565 nm. Although the spectral positions are somewhat displaced, the same pattern is thus present in the data for both species. The pattern shows more structure than occurs in this region of the spectrum in the human hue discrimination curve (Wright and Pitt 1934).

The wavelength discrimination curve for the hummingbird has a second maximum at 535 nm, and most interestingly, continued good performance at wavelengths shorter than 485 nm. In this latter respect it appears to differ from the hue discrimination curves for both pigeon and human, although the presence of pigeon cone pigments with λ_{max} at 480 and 415 nm (Table 3) should support good hue discrimination in this region of the spectrum. At this writing we have no knowledge of the numbers or spectral properties of hummingbird cones, but we know their visual sensitivity extends into the near ultraviolet (Huth and Burkhardt 1972; Goldsmith 1980).

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