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WAVELENGTH CATEGORIZATION BY GOLDFISH *(CARASSIUS AURATUS)*

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ABSTRACT: Goldfish pressed a paddle for intermittent food reinforcement in the presence of one of seven different monochromatic wavelengths. Wavelengths in 20 nm steps from 430 to 690 nm, matched for "brightness," were then presented for 20 days during which food maintained responding to the training stimulus. Generalization gradients calculated from the final four days were asymmetric. A long wavelength gradient showed maintained responding above 630 nm; at short wavelengths responding generalized below 490 nm; four middle wavelength gradients could indicate two groupings having maximum responses at around 510 and 570 nm.

The physiology of the goldfish visual system has been extensively described (Wheeler, 1982). The three cone pigments are maximally sensitive to wavelengths of 455, 530, and 625 nm (Marks, 1965; Harosi and MacNichol, 1974). In the subsequent stages of retinal processing there are cells which respond in an opponent fashion. Some horizontal cells hyperpolarize and depolarize to different wavelengths (MacNichol and Svaetichin, 1958; Tomita, 1965); many bipolar and amacrine cells are color-coded (Kaneko, 1973); there are ganglion cells with double-opponent receptive fields (Daw, 1968; Spekreijse, Wagner, and Wolbarst, 1972; Beauchamp and Lovasik, 1973; Mackintosh, Bilotta, and Abramov, 1987); and single cells in the optic tectum of the goldfish respond in an opponent manner (Jacobson, 1964). In addition to these physiological descriptions, what is needed is an understanding of how this information is integrated and used by the fish.

This paper examines how the various wavelengths are grouped together by the goldfish. This issue has been explored in nonhuman animals in two ways: matching-to-sample and generalization gradients. Wright and Cumming (1971) described "color-naming" gradients for pigeons using a matching-to-sample technique. After the pi-

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geons were matching three different wavelengths with 90% accuracy, sample probes of wavelengths in between the original training stimuli were presented. The pigeons had to respond to nonmatching hues on the side keys as if they were a match. The three functions derived from the data had transition points at 540 and 595 nm. These groupings are different from human color naming functions where transitions occur around 492, 561, and 605 nm (Boynton and Gordon, 1965). The application of this method to goldfish is complicated by the fact that on matching-to-sample tasks goldfish do not reach the high levels of accuracy needed for reliable assessment of "color-naming" transition values (Goldman and Shapiro, 1979).

Generalization gradients are obtained by presenting a series of unreinforced wavelengths after the animal has been trained to respond to one wavelength. Usually the animal is reinforced on a variable interval schedule during training to ensure a steady response rate. If tested in extinction, the animal gradually stops responding during a single session so that few responses are made to stimuli presented at the end. To maintain responding during the testing phase, Blough (1961) obtained steady state generalization gradients from his pigeons by reinforcing responses during four of the six presentations of the training stimulus which were interposed among many other unreinforced wavelengths. The reinforced stimulus was changed every few days so that over the course of the study each bird was successively tested for generalization to a number of different wavelengths. Although the results showed the effects of previously reinforced wavelengths and individual idiosyncracies, Blough found consistent asymmetries in the shapes of the gradients. A symmetrical gradient shows responses tapering off equally at both higher and lower wavelengths around the training stimulus, suggesting that the training stimulus is located in the middle of a color category. An asymmetrical gradient shows a rapid decline in responding on one side of a specific training stimulus and a more gradual decline on the other side, suggesting that the training stimulus is located closer to one color boundary. For all of Blough's birds, a rapid decline occurred at 540 nm, in agreement with the data from Wright and Cumming, while two out of four birds showed a steep gradient at 590 nm. Emmerton (1983) has summarized results from wavelength discrimination experiments on pigeons and has shown a high degree of correspondence among data obtained with steady state generalization gradients, matching-to-sample, and hue discrimination procedures.

Two wavelength generalization gradients have been obtained from goldfish by Yarczower and Bitterman (1965) without controlling for "brightness." One curve shows an almost symmetrical gradient around a 550 nm training stimulus with responses slowing at 490 and 610 nm. The other curve is an asymmetrical gradient around a 580

nm training stimulus where the peak is shifted to 560 nm, responding is still high at 520 nm, and there is a steep decline at 620 nm. The small number of gradients and the narrow range of spectral values explored make it difficult to assess color categorization in the goldfish. In the present experiment the fish were tested using a reinforced generalization procedure similar to Blough's, but more training and testing sessions were added to try to lessen the effects of previous wavelength training. We used seven different training wavelengths equated for "brightness" and the testing stimuli ranged from 430 to 690 nm to explore more of the spectrum.

METHOD

Subjects

Ten goldfish, 8-12 cm standard length, purchased from a local pet store, were housed individually in 9.6 liter tanks (31 × 16.5 × 20.5 cm) continuously aerated through plastic filters. The room temperature was maintained at 21° C. Fluorescent room lights were on for 18 h, beginning at 7 am, and off for 6 h. The fish were fed once daily during testing.

Apparatus

The fish tank, with filter removed and debris siphoned, was placed into a black Plexiglas chamber through a hinged side door along the 31 cm side. A single Plexiglas disc, 3.1 cm in diameter, suspended on a steel rod could be lowered into the tank in front of a single hole in one 16.5 cm wall by closing a top lid. The steel rod was suspended from a mechanical relay contact. A sheet of painted black metal extended 8.5 cm below the lid to prevent the fish from hitting the rod. Food pellets were delivered from a tube by a Gerbrands feeder through a 2.5 cm hole 4.75 cm from the black sheet. Mouth press responses to the Plexiglas disc closed the relay contact and were recorded on relay equipment.

Light from a GE tungsten ribbon filament 6 volt bulb passed through heat absorbing glass and was then projected through a Diffraction Products Czerny-Turner grating monochrometer. The monochromatic output could be intercepted by a shutter mounted on an electromechanical positioning motor, which controlled the presentation of the visual stimuli with onset and offset of less than 100 ms. The unblocked monochrometer output was brought to a focus. A Kodak continuous 15 cm diameter circular neutral density absorbing wedge with a mechanical compass along the outer edge was placed in

the focal plane so that the intensity values could be set manually. Light passing through the filter was focused on a ground glass mounted in front of the 3 cm circular hole at the end of the experimental chamber. Fourteen wavelengths (half-band width = 16 nm) ranging from 430 to 690 nm in 20 nm steps were used in testing. These values were manually adjusted between stimulus presentations.

Calibration

The wavelength vernier of the monochrometer was calibrated several times during the course of the experiment with a mercury vapor lamp at 546 and 579 nm. Stimulus intensity values were determined based on an average relative spectral sensitivity function as determined for Yager's (1967) data for light adapted goldfish. The points were connected and interpolated values for the wavelengths used were determined. Stimulus value determinations and calibrations were done with an EG and G Model 580/585 radiometer with a photomultiplier head. A computer program determined the radiometric output inversely weighted by the fish sensitivity function (taking into account the spectral sensitivity of the photomultiplier as calibrated by EG and G against a National Bureau of Standards standard). Given the relatively high fish sensitivity in the blue spectral region and the lower output of the tungsten source in that region, an attempt was made to achieve the highest intensity output possible from the system with all stimuli equated for the fish sensitivity. A maximum intensity output was determined for the lowest wavelength value used and the computer determined the outputs required for all other wavelengths. These values were manually set by positioning the wedge to produce the closest approximation to the computer value within accuracies of 3 percent. Radiometric energy levels at 450, 530, and 630 nm were 11.5, 12.0, and 12.2 log quanta/s/square centimeter respectively. These values are comparable to those used by Powers (1978).

Procedure

Each fish was shaped to press the lighted disc with its mouth for Noyes formula "J" 20 mg fish pellets. The disc was transilluminated with one of the testing wavelengths at the appropriate intensity setting. Three fish were initially trained in the presence of 450 nm, three with 530 nm, three with 570 nm, and one with 630 nm. This monochromatic light was the only illumination in the box. After shaping, a random interval (RI) schedule of food reinforcement was instituted and the mean time interval was gradually lengthened until

its final average value of RI 133 s. In this schedule, the first mouth press in a 2 s repeating time period has a .015 probability of earning a Noyes pellet. Subsequent responses in that period are not reinforced. Stimulus light on periods were gradually reduced from 10 min to 2 min. A 15 s blackout followed all stimulus presentations. By the end of approximately 40 days of training, each fish responded at a steady rate throughout the hour and earned about 20 food pellets. Generalization testing involved 2 min presentations of the 14 different stimuli so that each stimulus was presented three times over two days. Reinforcement was programmed to occur on an RI 27 s schedule during six additional presentations of the training stimulus on each day. This schedule permitted approximately the same daily number of food pellets as in the final training conditions. Thus, an example of one day's testing would be 27 light on periods which included 6 of the training stimulus with reinforcement possible, one or two with the training stimulus and no reinforcement possible, and the other 19 periods with the other 13 stimuli presented once or twice, without reinforcement possible. The order of stimulus presentation was determined by random permutation. In the second half of the experiment, a constraint was added that a given wavelength could not follow the reinforcement period more than once. Testing continued for either 20 or 25 days, after which most of the fish were reinforced on an RI 133 s schedule for responding to a new training stimulus. This second training stimulus was presented alone for 10 or 20 days before the generalization testing phase was begun and carried out in the same manner as described for the first training stimulus. After generalization testing, some of the fish were trained and tested on a third stimulus. The following sequences of training stimuli were used for different groups of fish: 450, 530, 630 nm; 530, 590, 490 nm; 570, 510 nm; and one fish was trained to only 630 nm to replace an animal from the first group that had died. For the groups begun with 530 and 570 nm, training time to the second and third stimulus was reduced from 20 days to 10 and testing time for all stimuli was reduced from 25 days to 20 because the shorter time was sufficient to obtain peaked gradients.

RESULTS

The first gradients obtained after single stimulus training to 450 nm, 530 nm, and 630 nm were flat across the wavelength spectrum. The fish trained to 570 nm and one fish trained to 450 nm showed peaked gradients from the first two generalization sessions. Many of the first gradients for the second and third training stimuli showed responses to the previous stimuli. By the 15th to 20th generalization

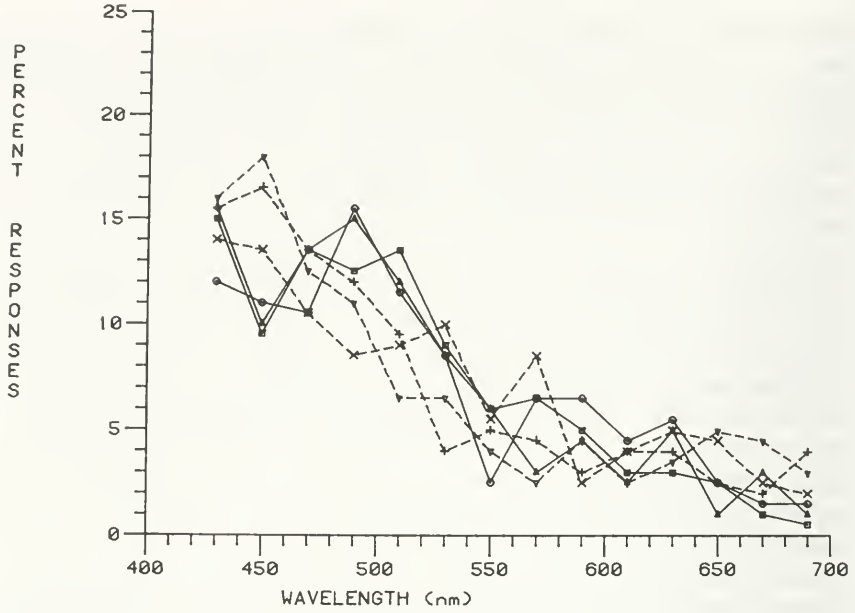

FIGURE 1. Generalization gradients after training to 450 nm (dashed lines) and 490 nm (solid lines) for six different fish from testing days 18-21 (450 nm) or 17-20 (490 nm).

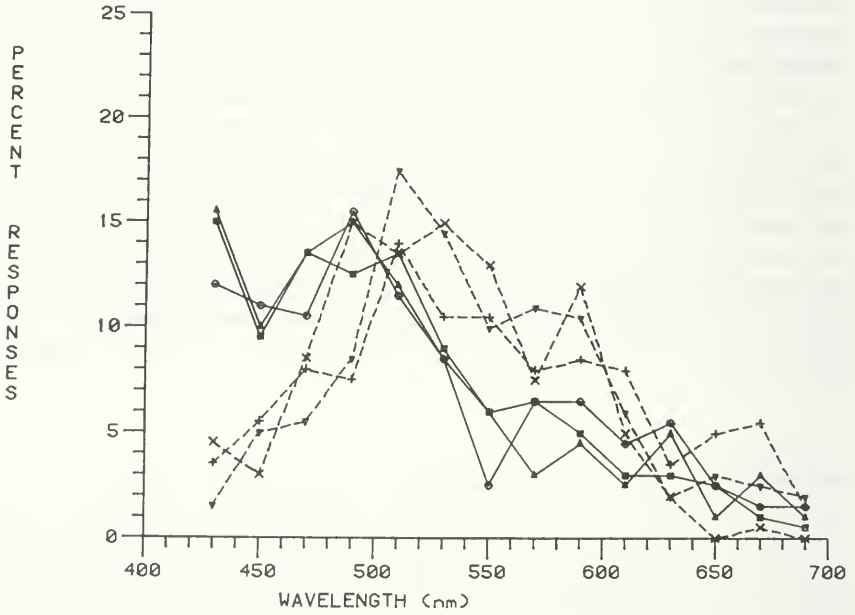

FIGURE 2. Generalization gradients after training to 490 nm (solid lines) and 510 nm (dashed lines) for six different fish from testing days 17-20.

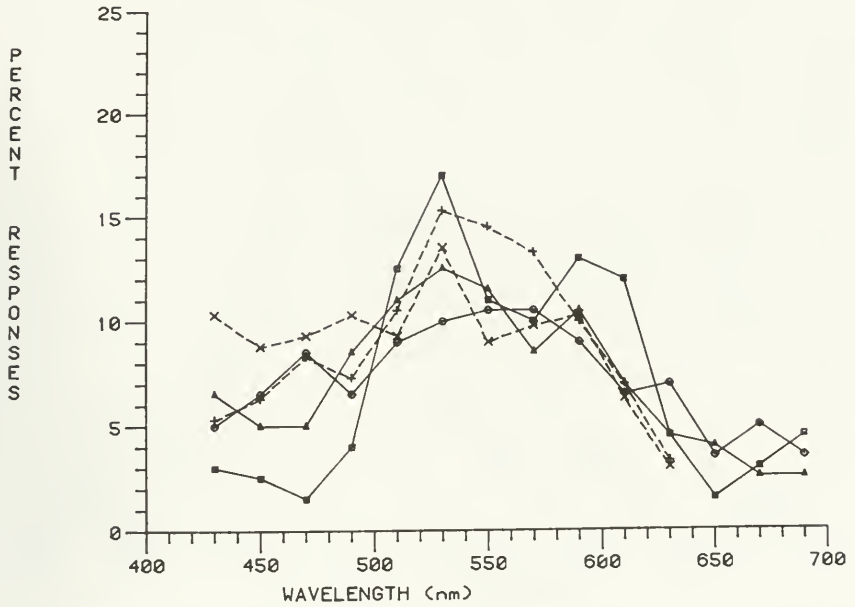

FIGURE 3. Generalization gradients after training to 530 nm from testing days 17-20 for five fish. The dashed gradients are from two fish for which 530 nm was the second training stimulus; the solid gradients are from three fish for which 530 nm was the first training stimulus.

testing session, the gradients peaked at the current training stimulus.

For consistency of comparison across the experimental conditions, the data from sessions 17-20 (or 18-21) for stimulus presentations without reinforcement will be presented. The animals first trained to 450 nm were given a single generalization session with a restricted range of wavelengths, to see how flat the initial gradient would be. Subsequent generalization sessions produced two day gradients, thus necessitating the use of days 18-21 for compatibility. Each two day gradient was computed by dividing the sum of the responses in the three unreinforced presentations of each wavelength by the total number of responses to stimuli without reinforcement on those days. The last two gradients, days 17/18 and 19/20, were then averaged and are presented in Figures 1-5. Figures 1, 2, and 5 each show individual generalization gradients for six different fish; Figure 4 shows gradients for the same three fish after training to one wavelength, obtaining a gradient, and retraining to a second.

The data from all three fish trained to respond to a 450 nm light transilluminating the Plexiglas disc and all three fish trained to a 490 nm light are presented in Figure 1. Although the functions peak

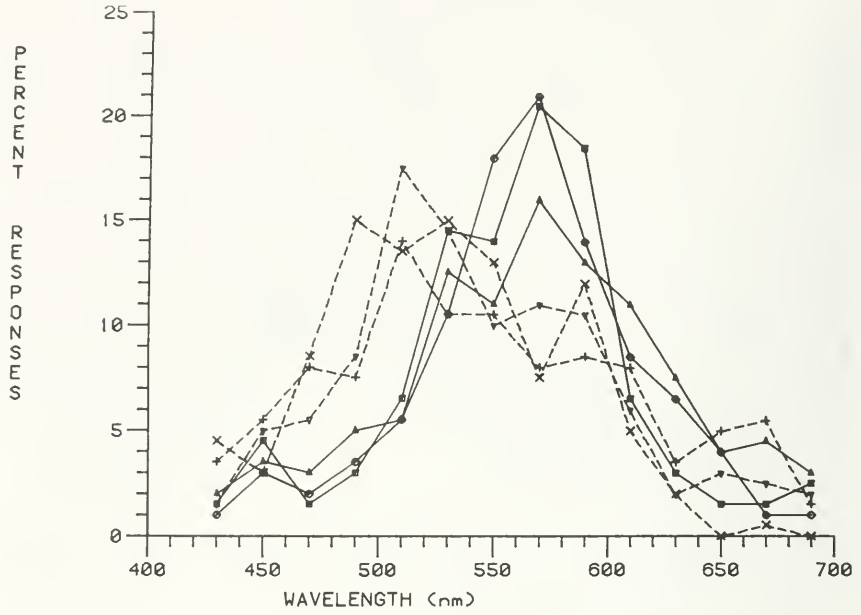

FIGURE 4. Generalization gradients after training to 510 nm (dashed lines) and 570 nm (solid lines) for the same three fish from testing days 17-20.

around their respective training stimuli, they have essentially the same shape; the animals respond to wavelengths lower than 490 nm. At wavelengths above 510 nm responding decreases and after 610 nm stays below five percent. This similarity occurs even though 490 nm was the third training stimulus after 530 nm and 590 nm for one group of fish, while 450 nm was the first training stimulus for the other fish.

Figure 2 shows the same three gradients to the 490 nm training stimulus together with gradients from all three fish trained to respond to a light of 510 nm. There is a clear separation of the 490 nm and 510 nm functions. At wavelengths below 470 nm responding by fish trained to 510 nm declines below five percent, while responding by the fish trained to 490 nm remains around 10-15 percent of total. Even the fish that generalized to 490 nm from the 510 nm training stimulus shows a steep decline in responses below 490 nm. The responding of the 490 nm animals declines to wavelengths above 510 nm, including one fish that generalized to 510 nm. The animals trained to 510 nm show generalization to all wavelengths between 530 and 590 nm. Two of these fish had secondary peaks around 570 and 590 nm, which could have been residual responding from previous 570 nm training.

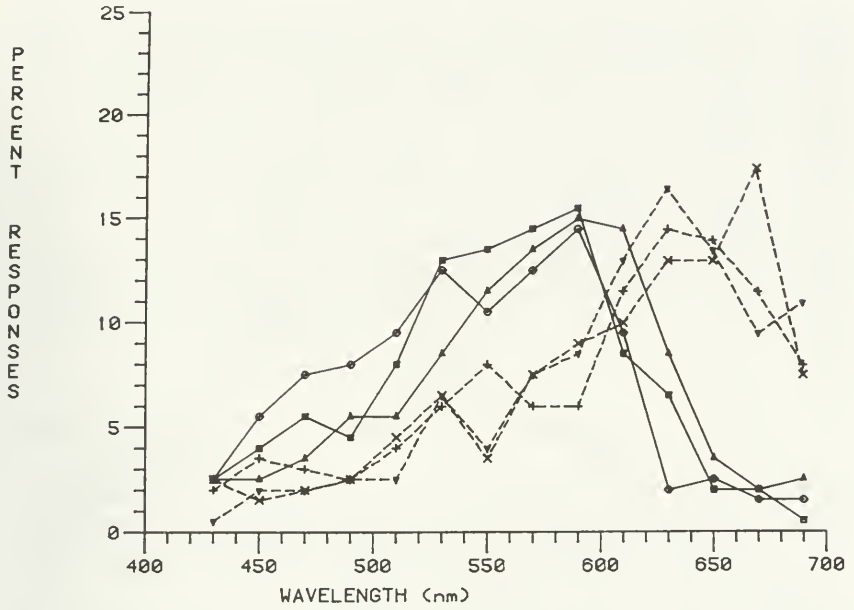

FIGURE 5. Generalization gradients after training to 590 nm (solid lines) and 630 nm (dashed lines) for six different fish from testing days 17-20.

Figure 3 shows the generalization gradients from all five fish trained to respond to a light of 530 nm. The two fish trained to 530 nm after 450 nm (dashed lines) seemed to show some residual responding below 490 nm and had some responding to all wavelengths lower than 630 nm, yielding a flat gradient; so a new group of three fish were given 530 nm as their initial training stimulus. Their three gradients (solid lines) also are rather broad and flat between 490 and 610 nm. Two of the new fish had responses above five percent between 430 and 490 nm. Two of the gradients display a secondary peak around 570 and 590 nm as did the gradients from the fish trained to 510 nm, even though those fish trained to 530 nm had not been reinforced at any other wavelength.

In contrast to the 530 nm gradients, the gradients from all three fish trained to respond to 570 nm are clearly peaked at the 570 nm stimulus. These are the solid lines in Figure 4, shown along with the gradients from the same fish to the 510 nm training stimulus (dashed lines) which were already presented in Figure 2. The 570 nm gradients have steep drops to below five percent responding for wavelengths both below 490 nm and above 650 nm. Both sets of gradients decline similarly on the long wavelength side, above 610 nm, while on the short wavelength side they are separated.

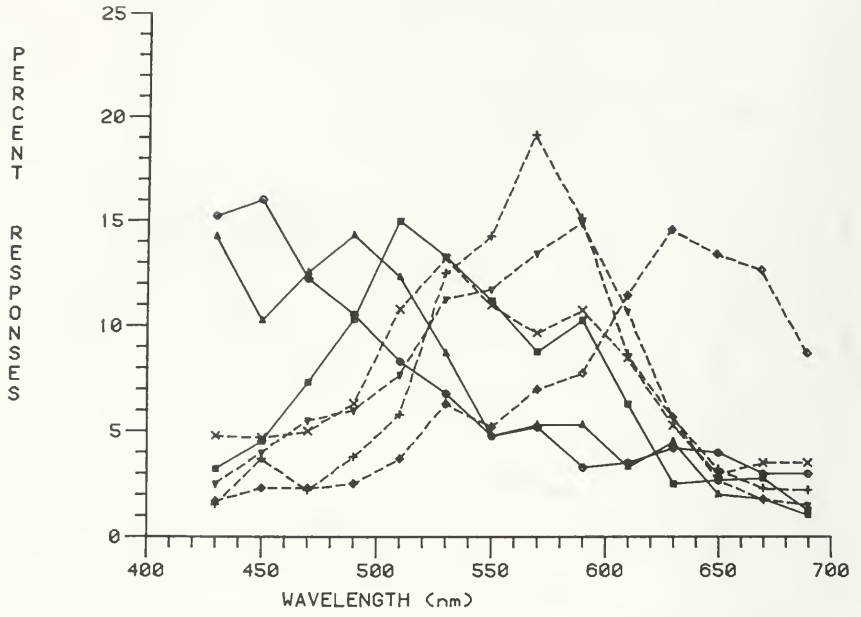

FIGURE 6. Generalization gradients from testing days 17-20 (18-21 for 450 nm) averaged from data for three animals. The gradients around 490, 530, and 590 nm are from the same three animals; a different group of three produced the 510 and 570 nm gradients; and the 630 nm gradient includes data from two fish from the 450 nm group.

Figure 5 shows the generalization gradients from all three fish trained to respond to 590 nm along with the gradients from all three different fish trained to a 630 nm light. The gradients around 590 nm are similar in shape to the 570 nm gradients although not as peaked. They have steep declines in responding to wavelengths above 590 nm (the training stimulus). The decline in responding to shorter wavelengths is very slight between 590 and 530 nm. The gradients to the 630 nm training stimulus are clearly different. Responding drops below ten percent at wavelengths of 590 nm and shorter, whereas there is more responding to wavelengths of 610 nm and above. All three gradients to 630 nm are alike even though 630 nm was the third training stimulus given to two of the fish and the only training stimulus for the third fish.

The data from the three fish trained at each wavelength were averaged and plotted on the same axes in Figure 6. As demonstrated in Figure 1, the gradients for the 450 and 490 nm training stimuli, on the left of Figure 6, show generalized responding to wavelengths below 490 nm and low levels of responding, below five percent, to wave-

lengths above 550 nm. On the right in Figure 6, the gradient to the 630 nm stimulus is different from any other gradient, with responding maintained to wavelengths longer than 610 nm, decreased responding to 590 nm and shorter wavelengths, and very little responding below 510 nm. The four middle curves show considerable overlap. All four have decreased responding between 590 and 630 nm. The curves for 510 and 530 nm have secondary peaks at 590 nm, while the curves for 570 and 590 nm have steeper declines below 530 nm than between 530 nm and the training stimuli. The largest separation is between the curves from the 510 and the 570 nm training stimuli as demonstrated in Figure 4.

DISCUSSION

The shape of the generalization gradients along the wavelength continuum indicates the way an organism groups wavelengths into color categories. There should be more generalization within a category, indicated by high peaks or flat slopes, and minimal generalization between categories, with steep slopes at the color boundaries. The question asked here is how many color categories do goldfish demonstrate. When the aforementioned rules are applied to Figure 6 there is clearly only one gradient for the long wavelengths above 610 nm. The peaks of the functions are all found at the training stimuli. Around 630 nm there is a gradual decline to 670 nm, and a steeper drop to 570 nm, with low responding to 510 nm and few responses at shorter wavelengths. Similarly, the gradients around 490 and 450 nm show generalization to 430 nm, steeper declines to 530 nm, and minimal responding above 590 nm. Figure 1 displays the closeness of the individual gradients to 450 and 490 nm, suggesting that they represent a single short wave function below 490 nm. These gradients also demonstrate the absence of generalization between the "blue" and "red" ends of the spectrum found in data from pigeons (Wright and Cumming, 1971) and humans (Boynton and Gordon, 1965). The lack of wraparound in the goldfish functions may be a result of the goldfish's sensitivity to ultraviolet, which extends the visible spectrum to short wavelengths below 400 nm (Hawryshyn and Beauchamp, 1985), where there is probably an additional color category.

The question remaining is whether the four middle wavelength functions represent one category or two broadly overlapping categories. All four curves have steep slopes above 590 nm, flatter slopes between 590 and 530 nm, and another steep drop below 530 or 510 nm. The close proximity of the long wavelength sides and the unexpected secondary peaks (without any previous training in the 530 and 570 nm groups) support a single category hypothesis. On the other

hand, the separation of the 510 and 570 nm functions on the short wavelength side, the distinctiveness of the 570-590 nm peaks from the 510-530 nm peaks, and the flatness of the 530 nm functions, support a dual category hypothesis. The flatness of the gradient around 530 nm was a surprise because flatness indicates a lot of generalization and 530 nm is the peak of one cone's spectral absorption function. The stimuli (450, 530, 630 nm) presented to the first group of fish were chosen to be close to the maximal absorption of the goldfish cones. The gradients to 530 nm, the second training stimulus, appeared to have so much residual responding to the shorter wavelengths around 450 nm that a new group of fish was given 530 nm as their initial training stimulus. As shown in Figure 3, although there was somewhat less responding to the shorter wavelengths, these three fish also gave very flat gradients. Therefore, some residual responding from previously trained stimuli did not alter the gradients' shapes dramatically. The flat gradients to 530 nm may thus indicate confusion between two color categories because it is near the crossover point for two separate middle wavelength functions.

A comparison of these functions with the physiological data of Jacobson (1964) from the optic tectum supports the two category hypothesis. Tectal units, which were classified by Jacobson into three types: red-green, red-blue, and yellow-blue, had maxima in four spectral locations; 448-476 nm, 497-517 nm, 552-584 nm, and 605-651 nm. Jacobson emphasized that none of his units had a maximum response at 530 nm. These results support the four category hypothesis and fit well with the current functions around 450, 510, 570, and 630 nm. Neutral points were found by Jacobson between 497 and 517 nm, 517 and 552 nm, and 552 and 584 nm. The first neutral point is close to our crossovers between 490 and 525 nm, the second agrees with the hypothesized 530 nm crossing point, but the third is clearly different from the 595-608 nm crossovers from the current data. These 595-608 nm crossing points are closer to the transitions found by Beare (1973) in the ganglion cells, although she thought they represented "yellow" while our data clearly indicate that there is no color category at these wavelengths. Jacobson's neutral points between 552 and 584 nm from his "R-G" cells and a few of Beare's neutral points at 570 and 580 nm are more likely to be the "yellow" crossovers as the current data suggest a color category within this range.

Comparison with Yarczower and Bitterman's (1965) frequency gradients from their Experiment II yields some interesting similarities, in spite of the different methodologies. Their data are from testing days during which the stimuli, not matched for "brightness," were presented for 30 s with a 10 s inter-trial interval. The animals were reinforced for responses to the training stimulus before and after testing on each day. Yarczower and Bitterman's 580 nm curve has

a peak at 560 nm and a steep drop to 620 nm, similar to the 570 nm gradient of the present study; their 550 nm curve is broader than their 580 nm curve, as is our 530 nm curve. The almost symmetrical decrease in responses to 510 and 610 nm places the 550 nm gradient right in the middle of our middle wavelength group; but the departures from symmetry suggest that it is more similar to their 580 nm and our 570 nm functions because the decrease in responding to the shorter wavelengths is steeper than the decline in responding to longer wavelengths.

Yarczower and Bitterman compared their generalization gradients to a wavelength discrimination function to test the inverse hypothesis: the theory that areas of greatest generalization are those in which discrimination is the poorest and areas of least generalization should correspond to those wavelengths where discrimination is the best. Our data can be compared to a more recent wavelength discrimination function which covers the entire spectrum from 400 to 650 nm with the stimuli matched for "brightness" (Neumeyer, 1986). The area of good discrimination at 600-610 nm is right at our 595-610 crossover points and we also have some crossovers around 500 nm, the region of the best discrimination, thus supporting the inverse hypothesis. Given the range of crossing points in the present study, comparison of the goldfish gradients with those from pigeons and humans shows a remarkable correspondence of good discrimination and little generalization in the 595-605 nm region. This agreement occurs in spite of differences in the peaks in the cone spectra for these groups. Pigeons have a definite crossover at 540 nm; humans do not; goldfish show a tendency toward broad generalization in this spectral region. Both humans and goldfish have good discrimination and crossovers in the 490-500 nm region. Our study therefore extends comparison of behavioral wavelength categorization to show consistencies between the goldfish data and those from other animal groups. Perhaps, as Neumeyer (1986) suggests, the convergence of processes from diverse groups of animals relates to the daylight spectrum of the sun.

The present data were obtained with stimuli photopically equated based on data by Yager (1967) for the freely swimming fish. Other photopic sensitivity functions have been suggested in the literature (Beauchamp, 1978; Powers, 1978; Neumeyer, 1984). The variations in the shapes and peak sensitivities of these functions are related to differences in the task and adaptation conditions. Yager's data, obtained with freely moving fish, were chosen as the closest procedurally to our training conditions (Yager, 1970). Although the fish in the present study were in the dark between stimulus presentations, the stimuli were presented above photopic threshold. This 15 s dark interval was needed for the experimenter to change stimulus conditions and is not sufficient for dark adaptation to occur. The sim-

ilarity of our data to Yarczower and Bitterman's may reflect the robustness of the wavelength generalization procedure in spite of intensity differences.

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