

THE INFLUENCE OF ULTRAVIOLET RADIATION ON THE PIGEON'S COLOR DISCRIMINATION¹

ANTHONY A. WRIGHT

COLUMBIA UNIVERSITY

Two experiments demonstrated the pigeon's sensitivity to ultraviolet light. In Experiment I, pigeons' responses were reinforced on a multiple schedule with a variable-interval reinforcement schedule in one component and extinction in the other component. Response rates were quite different in the two components where the 520-nm stimuli signaling each component differed only in that one of them contained a 366-nm ultraviolet component. In Experiment II, pigeons were trained to peck one side key when two halves of a split field were of different wavelength and to peck another side key when they were of the same wavelength. Initially, field halves contained both "visible" and ultraviolet components of energy. Discrimination performance improved when the ultraviolet component was removed from one field half. It was argued that the critical change in the stimulus was a color change, rather than a brightness one, or a fluorescence of structures in the pigeon's eye.

During a series of generalization tests, it was discovered accidentally that pigeons were sensitive to ultraviolet radiation. The experiment had been designed to determine whether changes in response rates or in reinforcement densities would produce behavioral contrast. In one component (S1) of the multiple schedule, responses were reinforced on a variable-interval schedule, and in a second component (S2), fulfillment of a rate requirement was reinforced on a variable-interval schedule. Following training on each combination of a rate requirement and a variable-interval schedule in the second component, a generalization test was conducted. The results for two (of five) subjects are shown in Figure 1.

All of the subjects' gradients for the first three tests showed a lack of responding to 534- and 547-nanometer (nm) test wavelengths. Inspection of the spectral characteristics of the filters revealed that all of the filters, except 534 and 547 nm, passed a prominent ultraviolet (UV) mode of energy and a less-prominent infrared one. Spectral characteristics of the 547-nm, 534-nm, S1 and S2 stimuli are shown in

Figure 2. Following the third generalization test, a blocking filter (see the bottom panel in Figure 2) was inserted in the light beam to remove UV components. Subjects were trained to S1 and S2 with the UV components removed and the generalization gradients following this training (GT 4) were smooth and no longer showed discontinuities at 534 and 547 nm. During generalization tests 1, 2, and 3, it seems that the absence of a UV component from the 534- and 547-nm test stimuli altered their apparent color to such an extent that they were not even on the same generalization gradient as the other test stimuli. This was an unexpected finding because human observers reported that there was no color change when the UV component was removed from the stimuli.

In order to test the pigeon's sensitivity to ultraviolet radiation, two experiments were conducted: (1) A free-operant discrimination where reinforcement occurred in only one component of a multiple schedule; the difference between the light stimuli associated with the two components was the presence or absence of a UV component. (2) A psychophysical discrimination where pigeons were trained to detect hue differences between two halves of a bipartite stimulus. Tests were conducted by removing a UV component from one half of the field to determine its effect upon discriminability.

¹This research was partially supported by Mental Health grant #MH 18624 to John A. Nevin, principal investigator. The author is grateful to Professor Nevin for his encouragement and comments in preparing this paper. Reprints may be obtained from the author, University of Texas Graduate School of Biomedical Sciences, 6420 Lamar Fleming Blvd., Texas Medical Center, Houston, Texas 77025.

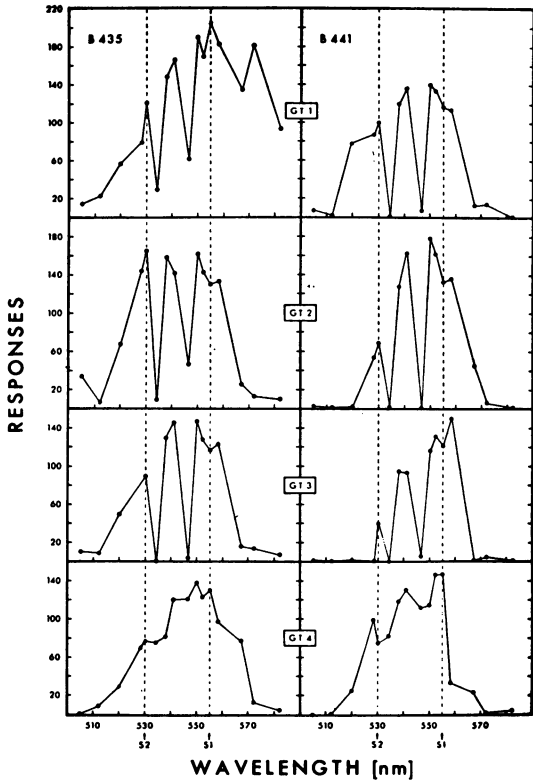


Fig. 1. Generalization gradients for two birds with an ultraviolet component present in all the stimuli except for 534 nm and 547 nm (GT 1, 2, and 3), and with ultraviolet components absent from all stimuli (GT 4).

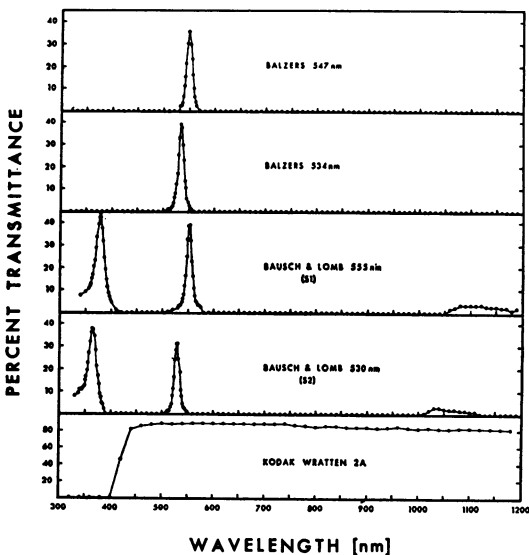


Fig. 2. Transmission characteristics of four stimuli before removing the ultraviolet components with a blocking filter (lowest panel).

EXPERIMENT 1

Subjects

Four White Carneaux pigeons (*Columba livia*), obtained from the Palmetto Pigeon Plant, Sumter, South Carolina, were experimentally naive and 6 yr old. Daily sessions were conducted if the subjects were within the range 77% to 83% of their free-feeding weights.

Apparatus

The experimental chamber was a converted picnic ice box. The subject's portion was rectangular and measured 12 in. (30.5 cm) long by 14.8 in. (37.5 cm) wide by 12 in. (30.5 cm) high. A stimulus panel formed one wall, and on it was a pigeon pecking key (Lehigh Valley #121-16 with a Polacoat plastic "lenscreen") located 9.8 in. (24.7 cm) from the chamber floor, and a 2 by 2 in. (5 by 5 cm) grain feeder opening 5.8 in. (14.6 cm) below the pecking key. An exhaust fan, located on the wall opposite the stimulus panel, provided ventilation and masking noise.

Collimated light from a Sylvania 150 Q/c1 quartz iodine lamp was filtered by a 520-nm Bausch and Lomb series #44-78 interference filter and a Liberty Mirror special #436 interference coating, and then was projected onto the pecking key. The 520-nm interference filter passed three modes of light energy: (1) a "visible" component of 520-nm peak wavelength, (2) an UV component of 366-nm peak wavelength, (3) an infrared component that was removed by the #436 filter permanently placed in the light beam. Wavelength calibrations were made with an Edgerton, Germeshausen, and Grier #580-585 spectroradiometer.

An Edgerton, Germeshausen, and Grier #580 radiometer was used to calibrate the intensity of the stimuli. There was 15.25×10^{-8} watts/cm² in the bimodal stimulus composed of the 520-nm "visible" component and the 366-nm UV component, and 13.75×10^{-8} watts/cm² in the 520-nm "visible" component when the UV component was removed. These energies were obtained with the diffuser of the radiometer placed 4.75 in. (10.4 cm) from the pecking key.

To obtain an estimate of the energy in the stimulus composed of both the "visible" and the UV component, it was necessary to obtain estimates of the energy in the "visible" and UV

components separately and then add them. Energy in the "visible" component of the bimodal stimulus could not be calibrated directly because the Kodak Wratten #2A filter used to remove the UV component also removed a small portion of the "visible" component. Therefore, it was necessary to perform the calibrations in several steps: (1.) Two blocking filters (Kodak Wratten #2A) were placed in the light beam passed by the interference filter and the intensity calibrated. (2.) One blocking filter was removed and the intensity calibrated; this is the intensity of the "visible" component with the UV component removed. (Note that there is still another blocking filter in the system that continues to block out the UV component.) (3.) The percent increase of (2) relative to (1) was calculated, and then the same percent increase was applied to (2) to determine the intensity of the "visible" component alone without any blocking filters. (4.) The second blocking filter was removed and the increase in intensity calibrated. (5.) The intensity in the UV component (0.67×10^{-8} watts/cm²) was then calculated by subtracting the calculated increase in intensity of (3) from the calibrated intensity in (4). (6.) Energy calculations of steps (5) and (3) were added to obtain the estimate of the bimodal stimulus composed of the 520-nm "visible" component and the 366-nm UV component. The Edgerton, Gernshausen, and Grier #580 radiometer was particularly well suited to calibrating the small increases in intensity of (2) and (4) because the radiometer compensator allowed the ambient light to be nulled out, so that small changes could be calibrated on sensitive scales.

The experiment was arranged, and data were collected by a system of relays, timers, and counters.

Procedure

The subjects' key pecks were shaped to an attenuated white light, and then were given multiple schedule training. In one component of the multiple schedule (S^D), key pecks were reinforced on a variable-interval schedule of reinforcement; in the other component (S^A), they were never reinforced (extinction). The S^D for Birds 362 and 363 was the unblocked 520-nm Bausch and Lomb interference filter containing two modes of energy, one in the

"visible" (520 nm) and one in the UV (366 nm). The S^A for Birds 362 and 363 was produced by the same interference filter, but with a Kodak Wratten #2A filter inserted in the light beam to block out the UV component. The S^D for Birds 364 and 365 was the same stimulus as the S^A for Birds 362 and 363; the S^A for Birds 364 and 365 was the same stimulus as the S^D for Birds 362 and 363.

Each session consisted of 21 presentations of S^D intermixed with 21 presentations of S^A. Each presentation of S^D or S^A was 56 sec in duration. Four different sequences were available; the particular one selected varied from session to session. The interval between stimulus presentations was 4 sec. The reinforcement schedule was VI 15-sec for the first day of training, VI 30-sec for the second day, and VI 1-min thereafter. The reinforcement interval was 2.5 sec of free access to mixed grain.

After 25 days of multiple schedule training (VI 1-min in S^D), light from the unblocked interference filter ("visible" plus UV) was attenuated in 0.1 density unit steps from 0.1 to 0.6 and in 0.2 density unit steps from 0.6 to 1.0.

RESULTS

The separation of response rates in Figure 3 shows that the subjects rapidly learned to identify the presence or absence of ultraviolet light in stimuli that were otherwise identical. This discrimination was maintained throughout the final 14 sessions when the intensity of the unblocked stimulus was attenuated. Discrimination was thus shown to be independent of any brightness differences between the two stimuli.

A procedural error was made in the second session. Stimuli and reinforcement dependencies were reversed for Bird 364, and this subject was presented with the S^D and S^A appropriate for Birds 362 and 363. This error may account for the somewhat slower acquisition for this subject.

DISCUSSION

Experiment I demonstrated that a discrimination could be formed between two stimuli that differed only in that one of them contained a UV component. The most probable basis for the discrimination was a difference in apparent color between the stimuli. The ultraviolet component probably mixes with the

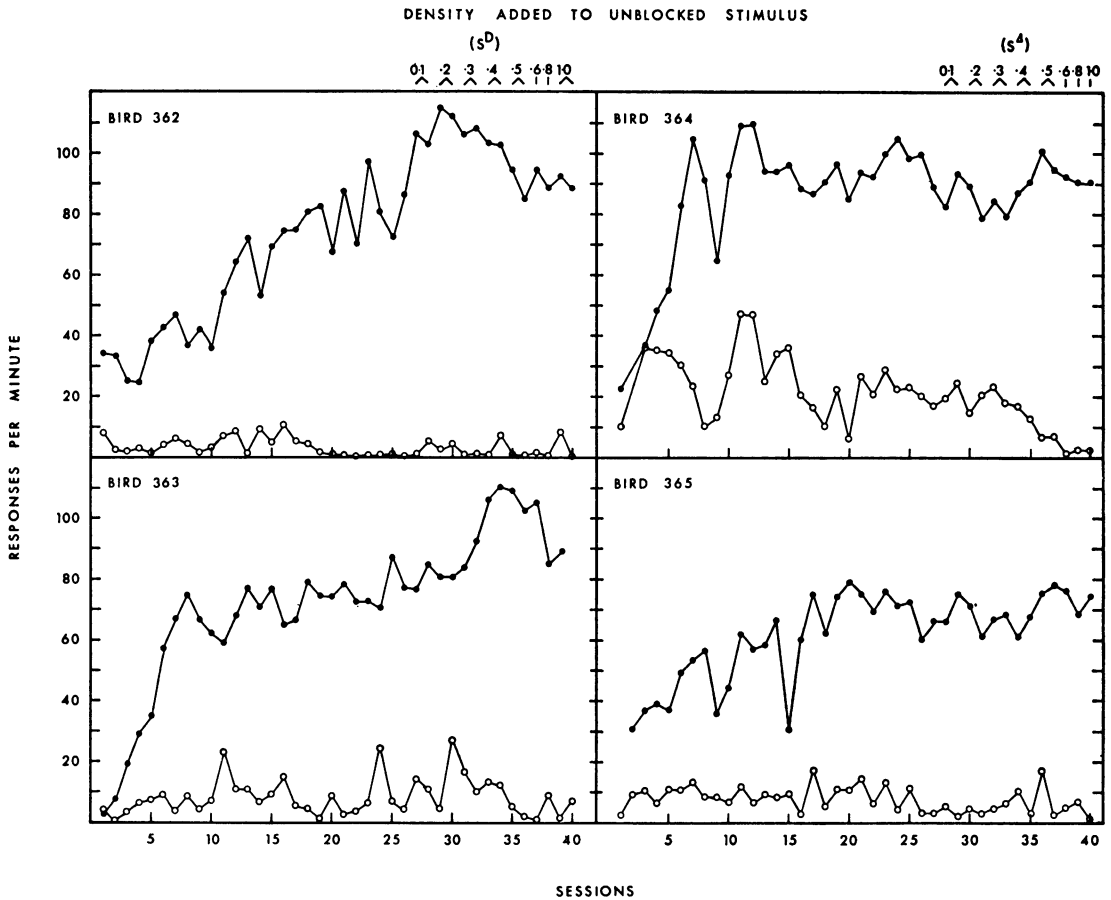


Fig. 3. Response rates of four birds in a VI 1-min multiple schedule component (filled data points) and in an extinction component (unfilled data points). The stimulus in which reinforcement occurred for the two birds on the right contained the UV component. For those on the left, the UV component was blocked from the stimulus in which reinforcement occurred.

“visible” one and the dominant wavelength of the mixture shifts according to whatever color mixture relationships for the pigeon might be involved.

An alternate possibility is that UV radiation may cause one or more structures of the pigeon’s eye (*e.g.*, the lens) to fluoresce. This fluorescence might alter the character of the stimulus sufficiently to enable the pigeon to base its discrimination on the presence or absence of fluorescence.

It is unlikely that the discrimination could have been based on brightness differences; despite the greater energy in the unblocked stimulus, the photometric difference between the stimuli was negligible. The unblocked stimulus had a UV component and also contained more energy in the 520-nm component than the blocked one. If the logarithm of the energy of the blocked stimulus is subtracted

from the logarithm of the sum of the energies of the UV component and the unblocked 520-nm component, the remainder is 0.063. This is the density needed to equate the stimuli radiometrically. When the sensitivity of the pigeon’s eye is considered (Blough, 1957), the density required is even less, approximately 0.030 density units.² Maintained discrimination during attenuation of the unblocked stimulus confirmed that the discrimination was not based upon brightness differences.

EXPERIMENT II

Experiment II was also designed to test the pigeon’s sensitivity to UV light. Experiment

²The luminosity coefficient for 380 nm (Blough, 1957) was used to adjust the intensity of the UV component in accordance with the sensitivity of the pigeon’s eye; a coefficient for 366 nm was unavailable.

II tested the possibility (raised in the discussion of Experiment I) that the pigeon's sensitivity to UV radiation may be indirect, that UV radiation may fluoresce structures in the pigeon's eye; the fluorescence producing a visual sensation. Unlike Experiment I, Experiment II was conducted in a psychophysical setting where the stimuli to be discriminated were juxtaposed on a split field so that they could be simultaneously compared. Choices were made on each trial; right-side key choices were correct when the two field halves differed in wavelength and left ones when they were of identical wavelength. The discrimination was established with a "visible" and UV component displayed on each half of the bipartite stimulus. Ultraviolet sensitivity was tested by eliminating the UV component from one field half and observing whether or not the subject's discrimination performance would change. Any performance changes would not be due to fluorescence of structures in the pigeon's eye (or changes there of), because fluorescence from the UV of the remaining field half would spread over the retinal images of both field halves. Structures of the eye, e.g., the lens, are not focused on the retina.

METHOD

Subjects

Four White Carneaux pigeons (*Columba livia*), obtained from the Palmetto Pigeon Plant, Sumter, South Carolina, were 7- to 11-yr old at the beginning of the experiment. One subject, Bird 53, had had previous experience matching monochromatic stimuli (Wright and Cumming, 1971); the others were experimentally naive. Experimental sessions were conducted seven days per week if the subjects were 77 to 83% of their free-feeding weights.

Optical System

The optical system that produced the bipartite stimulus is shown in Figure 4. 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 infrared 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 and neutral density filters. Then they passed through Bausch and Lomb series #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 Figure 4) allowed the radiance of the right-field to be varied automatically by actuation of individual channels containing Kodak Wratten neutral density filters.

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 0.25-in. (0.6-cm) aperture (15) that limited the diameter of the bipartite stimulus. The screen was located 2.9 in. (7.5 cm) behind a color-clear glass pecking key, and the visual angle of the bipartite stimulus was approximately 3 degrees 14 min 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 1.5 in. (3.8 cm).

Wavelength of monochromatic light was varied by rotating the interference filters. Polarizers were placed in the filter boxes (6,6') so that large angles of incidence could be employed with no band-pass distortion (Heavens, 1965). The interference filter (9) was rotated

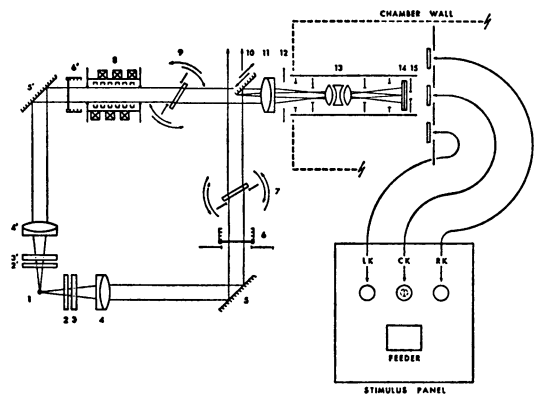


Fig. 4. Schematic of optical system for producing a bipartite stimulus. (1) source, (2,2') infrared reflectors, (3,3') heat absorbing glasses, (4,4') lenses, (5,5') mirrors, (6,6') filter boxes with polarizers, (7) interference filter for reference wavelength, (8) density filter actuator, (9) interference filter for comparison wavelength, (10) mirror, (11) lens, (12) shutter, (13) lens, (14) screen, (15) aperture.

by joining the mounted interference filter to a precision gear reducer (Planet #A-113) and the gear reducer to a precision stepping motor (Superior Electric #HS50E). 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 measured 12 in. (30.5 cm) long by 14.8 in. (37.5 cm) wide by 13.8 in. (35 cm) high. A stimulus panel formed one wall to which was attached a grain feeder with a 2 by 2 in. (5 by 5 cm) opening located 5.8 in. (14.6 cm) below the center key. Also on the stimulus panel were three horizontally aligned color-clear glass pigeon pecking keys located 9.8 in. (24.8 cm) from the chamber floor and spaced 2.5 in. (6.4 cm) center to center. The pecking keys were positioned behind 1-in. (2.5 cm) diameter holes in the stimulus panel. In order to close the microswitch of each pecking key, 20 g (0.20N) of force had to be applied through a distance of 1 mm. The side key stimuli were 0.5 in. (1.3 cm) achromatic circles from IEE in-line units positioned 3.5 in. (8.9 cm) behind the color-clear glass pecking keys. The chamber was lighted by four GE #1820 bulbs mounted in the ceiling. A 6.0 by 6.0 in. (15.2 by 15.2 cm) piece of opal glass diffused the light from the bulbs and produced an illuminance of 0.63 foot-lamberts (2.16 cd/m²) on the gray chamber walls as measured with an Ilford SEI photometer.

A fan mounted in the chamber wall opposite to 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 to the stimulus panel.

Wavelength Calibrations

An Edgerton, Germeshausen, and 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 (± 0.1 nm) that 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 ± 0.1 nm of each other. Peak wavelengths of the "visible" stimuli followed by their ultraviolet peak wavelengths in parenthesis are as follows: (1) reference, 570 nm (393 nm); (2) comparisons, 566.4 nm (390 nm), 563.9 nm (388 nm), 562.1 nm (386 nm), 559.9 nm (384.3 nm), 555.5 nm (381 nm).

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, and Grier 580 radiometer. A platform was used to position the radiometer precisely 4.75 in. (12.1 cm) in front of the ground glass screen. The stimulus panel was removed from the chamber and a 0.5 in. (1.3 cm) 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.

A radiance of 3.19×10^{-8} watts/cm² at 555.0 nm was used as the reference. Desired radiometer readings for other to-be-corrected wavelengths were then computed. The radiometer reading at the 555-nm reference was corrected for the spectral response of the radiometer and for the light-adapted pigeon (Blough, 1957). The corrected reading was equated to the radiometer reading (unknown) at the to-be-corrected wavelength, also corrected for the spectral response of the radiometer and the light-adapted pigeon. The equation was then solved for the unknown radiometer reading. Next, the radiometer was placed in front of the stimulus and Kodak Wratten neutral density filters were placed in 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, and with the small wavelength differences used radiometric equality is not very different from photometric equality.

The stimuli were adjusted to be equally bright for the pigeon with both the "visible" component and the UV component present. Therefore, brightness settings will be in error to the extent that the UV component affects them differentially.

The method used in Experiment I to determine the intensity of the various components of energy was also used in Experiment II. The irradiant power of the visible component at 570.0 nm when present in conjunction with the UV component was 2.67×10^{-8} watts/cm². The power in the UV component was 0.52×10^{-8} watts/cm², and in the 570.0-nm "visible" component with no UV present was 2.45×10^{-8} watts/cm². Relative values for the other stimuli are equivalent. The difference between the logarithms for the unblocked (570-nm) stimulus and the blocked one (570-nm) is 0.12, which is the density one should add to the unblocked stimulus to make it radiometrically equivalent to the blocked one. When the irradiant powers are weighted by Blough's (1957) photopic luminosity coefficients (separately for the UV component and the 570-nm "visible" component), the difference between the unblocked stimulus and the blocked one is only 0.04 log units. This is the density value for the loss by reflection

(4%) at each surface of the blocking filter. Therefore, when weighted by the luminosity coefficients, the UV component is contributing a negligible amount toward the intensity of the stimulus.

As calibrated with an Ilford SEI photometer, the blocked 570-nm stimulus was 8.6 millilamberts (27.2 cd/m²).

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 adjusted 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 #30,585 6X).

Procedure

The subjects' task and the scheduled consequences are diagrammed in Figure 5.³ A

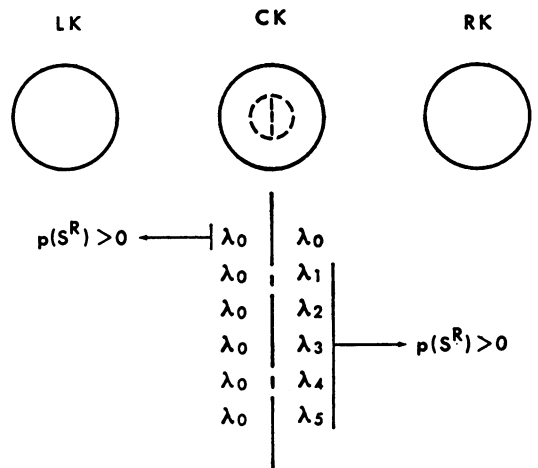


Fig. 5. Schematic of response options and reinforcement conditions for hue discrimination procedure. λ_0 is the reference wavelength and $\lambda_1 - \lambda_5$ are comparison wavelengths that are shorter than the reference wavelength.

trial began with the onset of the 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-

³A variant of this procedure was used to obtain a hue discrimination function for the pigeon. See Wright, A. A. Psychometric and psychophysical hue discrimination functions for the pigeon. *Vision Research*, (in press).

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 a 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-key choices were varied so that their sum was 0.40. Reinforcement probabilities were arranged 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 a geometric distribution.

Each of the six bipartite stimuli shown in Figure 5 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. Wavelength values of the comparison stimuli depended upon each subject's performance. The largest difference was selected where the subject's performance was just short of perfect, and the smallest difference was one where performance was just above chance.

Ten baseline sessions were conducted where the stimulus on each half of the split field contained a UV component and a "visible" component. During the ninth baseline session, the radiance of 563.9-nm comparison stimulus was increased by removing 0.3 density units from the comparison channel whenever this comparison stimulus was presented. During the tenth baseline session, the radiance of the 563.9-nm comparison stimulus was decreased by adding 0.3 density units to the comparison channel whenever this comparison stimulus was presented.

Following these baseline sessions, four test sessions were conducted to test the subjects' sensitivity to UV radiation. The UV component was removed from the 563.9-nm compar-

ison stimulus during the first test session, from the 563.9- and 566.4-nm comparison stimuli during the second test session, from the 563.9 and 566.4-nm comparison stimuli and the 570-nm reference stimulus during the third test session, and from all comparison stimuli and the reference stimulus during the fourth test session.

RESULTS

Analytic Method

Wavelength discrimination was assessed by manipulating bias and employing analytic

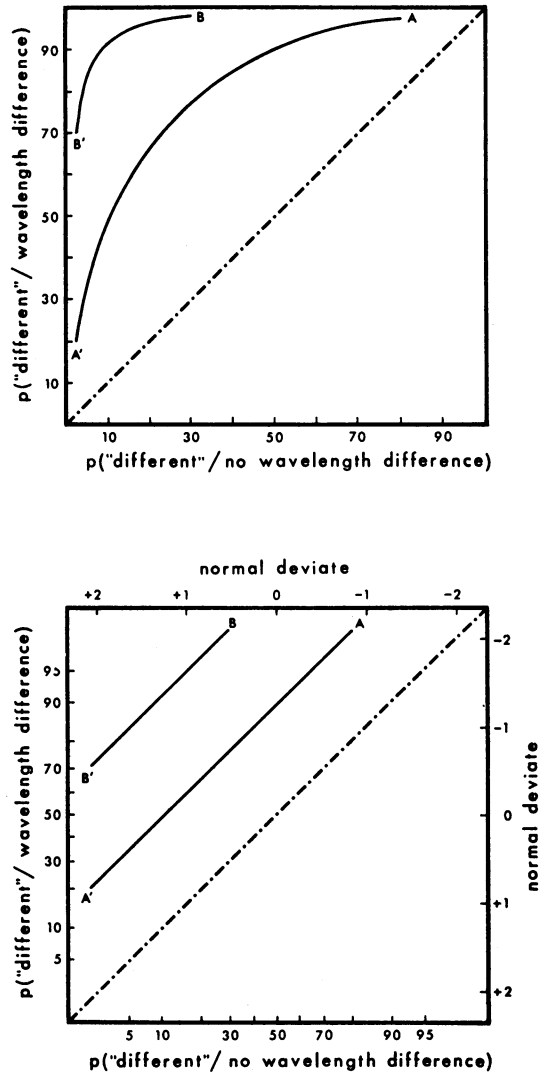


Fig. 6. Hypothetical isosensitivity curves for a difficult discrimination A-A', and for an easier one B-B'. They are plotted on linear coordinates in the upper panel and on normal-normal coordinates in the lower panel.

methods from signal detection theory. 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 the line A-A' in Figure 6. 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'. When data from such bias manipulations are plotted on normal-normal coordinates (as in the lower panel of Figure 6), the resulting functions are usually linear. "Almost all ROC curves (certainly all of those which have appeared in the literature) are fit very well by a straight line." (Clarke, Birdsall, and Tanner, 1959.) Linear functions facilitate extraction of discrimination indices, and levels of discrimination can be assessed at a glance. As the discrimination becomes easier, the lines are simply displaced further from the chance line. In Figure 6, the chance line is the dot-dashed positive sloping diagonal.

Wavelength Discrimination

Discrimination data for a representative subject (Bird #286) are shown in Figure 7. Data for the five wavelength differences are plotted in separate panels. Each session yielded five data points, one for each of the five wavelength differences. The proportion of right-key choices when the two field halves were equal (570 nm) was necessarily the same for all five wavelength differences. This proportion of incorrect right-key choices obtained during each session is shown in Table 1 so that the individual data points from each session can be identified. The most difficult discrimination is shown in the lower, right-hand panel where 566.4 nm was to be discriminated from 570 nm. The unfilled circles, which comprise the baseline data, are distributed in a linear fashion on the normal-normal plot. For progressively easier discriminations (shown in other panels), the linear array of unfilled data points moves further and further away from the dot-dashed, chance line.

Discrimination data for radiance changes in the 563.9-nm comparison stimulus are indicated in Figure 7 by arrows. Changing the radiance by ± 0.3 density units did not effect discrimination performance. This suggests

Table 1

Reinforcement probabilities and proportion of incorrect right key choices for bird 286.

Session	$P(S^R)$ right correct	$p(S^R)$ left correct	P (incorrect right key choices)
Baseline			
1	0.05	0.35	0.04
2	0.15	0.25	0.26
3	0.20	0.20	0.77
4	0.10	0.30	0.66
5	0.10	0.30	0.05
6	0.15	0.25	0.18
7	0.20	0.20	0.50
8	0.15	0.25	0.45
9	0.15	0.25	0.56
10	0.10	0.30	0.13
Test			
1	0.15	0.25	0.43
2	0.05	0.35	0.20
3	0.05	0.35	0.12
4	0.05	0.35	0.31

that discriminations were not based on brightness differences.

The legend in the upper, right-hand corner of Figure 7 shows the stimulus conditions for each test session. During successive test sessions, ultraviolet components were progressively removed from the stimuli and the data from these test sessions are plotted as filled data points in Figure 7. The baseline data (unfilled circles) serve as the basis for assessing performance changes that resulted from removal of the ultraviolet components.

The left-hand column of the legend in Figure 7 shows the stimulus conditions for the first test session. The 570-nm reference wavelength, which always appeared on the left field half, is shown to the left of the dividing line while the comparison wavelengths are shown to the right of it. The line through the 563.9-nm comparison wavelength in the first column of the legend indicates that the UV component was removed from this stimulus. Removing the ultraviolet component from 563.9 nm markedly improved the subject's discrimination performance, as shown by the filled circle in the upper right-hand panel labelled 563.9 nm. The arrow above the data point signifies that out of 100 trials when this comparison stimulus appeared, the subject was 100% correct in its choices. Filled circles for other comparison wavelengths were obtained during the same session, and they are, in each

NORMAL DEVIATE

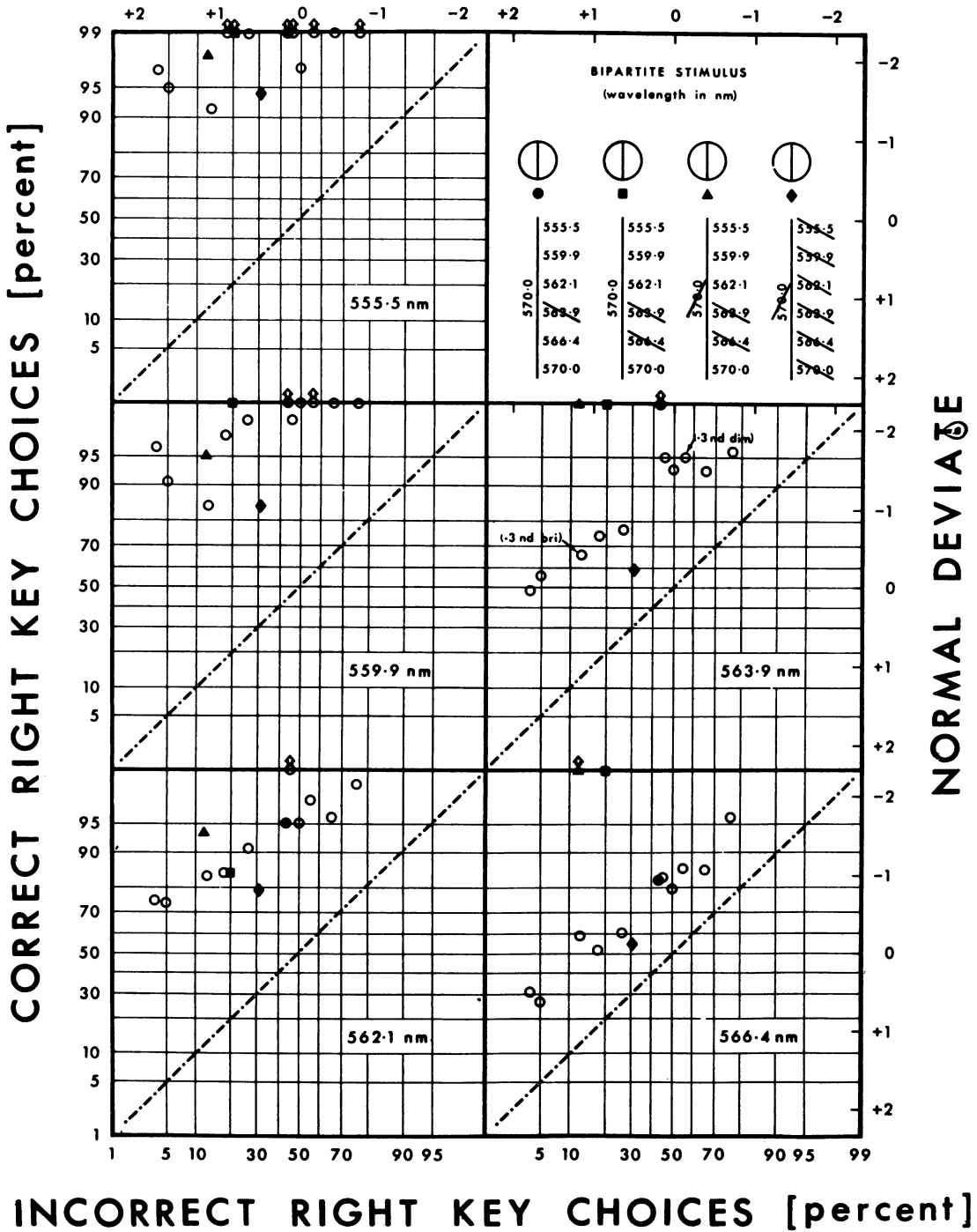


Fig. 7. Isosensitivity functions for Bird 286 for five comparison stimuli with a 570 nm reference stimulus. Slashes through wavelength values indicate removal of ultraviolet components.

case, within their array of the baseline discrimination data (unfilled circles).

During the second test session, the ultraviolet component was removed from the 566.4-nm stimulus as well as from the 563.9-nm stimulus. These removals are shown by slashes in the second column of the legend in Figure 7, and the resulting discrimination performance is plotted as filled squares. Removing the ultraviolet component from 566.4 and 563.9 nm markedly improved the subject's discrimination of these wavelengths from the 570-nm reference stimulus, as shown by the position of the filled squares relative to the unfilled circles for these comparison wavelengths. Performance to stimuli (555.5, 559.9, 562.1 nm) with ultraviolet components was maintained as before.

During the third test session, the ultraviolet component was removed from the reference stimulus appearing on the left field half as well as from the two previously deleted stimuli (563.9 and 566.4 nm) appearing on the right field half. Position of the filled triangles for the third test session indicates that discrimination performance relative to the second test session was generally not affected. It is possible that discrimination performance improved slightly to the 562.1-nm stimulus as the filled triangle in the lower, left-hand, panel is somewhat further from the chance line than the baseline data (unfilled circles).

Elimination of the ultraviolet component from all of the stimuli in the fourth test session, generally depressed discriminability, as shown by the relative proximity of the filled diamonds to the dot-dashed chance line.

DISCUSSION

The subjects' discrimination performance improved considerably when the ultraviolet component was removed from one half of the split field. Removing the ultraviolet component may have affected the appearance of the stimulus in one of several ways, thus providing the basis for the improved performance. The evidence seems to indicate that a change in apparent color between the two halves of the split field was responsible for the improved performance, rather than a change in brightness or a change in fluorescence of one or more structures in the pigeon's eye.

A change in the brightness between the two

halves of the field is unlikely to have caused the improved discrimination performance because the ultraviolet component accounted for only a small proportion of the intensity of the stimulus. There was approximately 0.10 log unit change in intensity when the UV component was removed, but this value was only 0.04 log unit when the photopic sensitivity (Blough, 1957) of the pigeon's eye was considered. This is a small intensity change, equivalent to inserting a clear-glass cover slip into the light beam. Furthermore, before the ultraviolet component was removed, the subjects were tested to determine the degree to which their discriminations were based on brightness differences between the two halves of the split field. The subjects were not basing their discriminations on brightness differences. During the last two days of baseline training, Bird 286's discrimination performance was not affected by doubling (or halving) the percent transmittance of the 563.9-nm comparison stimulus. (Likewise, the other subjects did not show changes in their discrimination performance when the intensity of one comparison stimulus was altered.)

It is also unlikely that a change in fluorescence of structures in the eye could have caused the improved discrimination performance when the UV component was removed. In Experiment II, a split field was used and presence or absence of a wavelength difference between the two halves of the field dictated which side key choice would be reinforced. If a difference in fluorescence between the two field halves was the basis for the discrimination (during the baseline sessions), then any difference in fluorescence would have to be confined to the image of the split field on the retina. This is unlikely because structures in the eye are not focused on the retina. Thus, any difference in fluorescence, from a difference in UV light between the two field halves, would be intermixed by the time the fluorescence impinged upon the retina. Likewise, during testing, fluorescence from the unblocked reference wavelength would be spread across the retinal image of both field halves.

The ultraviolet component most likely changed the apparent color of the stimulus. The color of the unblocked stimuli probably resulted from a simple mixture of the "visible" component and the ultraviolet compo-

nent, similar possibly to the way in which a mixture of green and red produce a human yellow. Although there is little energy in the UV stimulus either of a radiometric nature or of a photometric one, probably the coloring power (for pigeons) of UV light is much greater than for longer wavelengths. Short wavelengths have more coloring power for humans than long ones, “. . . when a white test stimulus is matched, the luminosity of B may be only about 1/20th of that of G in the match although, since white may be regarded as neutral in colour, the colouring powers of R, G, and B in their proportions in the match may be regarded as approximately the same.” (W. D. Wright, 1947.) Like the “gain” mechanism for human short wavelength blue stimuli, pigeons may have a “gain” mechanism operating on short wavelength UV stimuli.

Pigeons are more sensitive to short wavelengths than are humans. Figure 8 shows the pigeon's photopic luminosity function (Blough, 1957), as compared to the human photopic luminosity function (CIE, 1924). The pigeon's function shows that there is even slightly increasing sensitivity to short wavelengths. Pigeons require only 10 times as much energy at 380 nm than at 560 nm to detect the stimulus, whereas, humans require 10,000 times as much energy at 380 nm than at 560 nm to detect the visual stimulus. This difference is probably due to the absorption of ultraviolet light by the human lens. Aphakic

humans (with lenses removed) are more sensitive to short wavelengths (Wald, 1945) than normal subjects (CIE, 1924), and their sensitivity at 380 nm relative to 560 nm is similar to that of the pigeon's (Blough, 1957).

Data on the photopic sensitivity of the pigeon (Blough, 1957; Granit, 1942; Donner, 1953; Ikeda, 1965) do not show values for wavelengths as short as 366 nm, the peak of the UV component used in Experiment I. The increase of the pigeon's photopic sensitivity function (Figure 8) for very short wavelengths may be the precursor of a second hump in the function. Iodopsin, which Wald (1958) claims to have extracted from the pigeon eye, shows two peaks in its absorption spectrum, one at 560 nm and the other at 370 nm (Wald, 1955).

Light generated by grating monochromators, interference wedges, and interference filters, all commonly used in stimulus control research, is composed of several harmonics of energy. If the specified wavelength (L) is of the first order, then there will be other harmonics of energy with peaks at 1/2 L, 1/3 L, 1/4 L. . . . Fortunately, most grating monochromators, and some interference filters and wedges are supplied with blocking filters that remove these commonly neglected harmonics. If an experimental report does not mention that the ultraviolet components were removed, then the manufacturer can be consulted to determine if the components were supplied as standard with blocking filters.

Because pigeons are sensitive to ultraviolet light, experimenters should take precautions to eliminate these lower harmonics of energy. Otherwise it will be difficult, if not impossible, to evaluate the results.

REFERENCES

Blough, D. S. Spectral sensitivity in the pigeon. *Journal of the Optical Society of America*, 1957, 47, 827-833.
 CIE Proc. 1924, p. 67. Cambridge: Cambridge University Press, 1926.
 Clarke, F. R., Birdsall, T. G., and Tanner, W. P., Jr. Two types of ROC curves and definitions of parameters. *Journal of the Acoustical Society of America*, 1959, 31, 629-630.
 Donner, K. O. The spectral sensitivity of the pigeon's retinal elements, *Journal of Physiology (London)*, 1953, 122, 524-537.
 Granit, R. The photopic spectrum of the pigeon. *Acta physiology Scandinavia*, 1942, 4, 118-124.
 Heavens, O. S. *Optical properties of thin solid films*. New York: Dover, 1965.

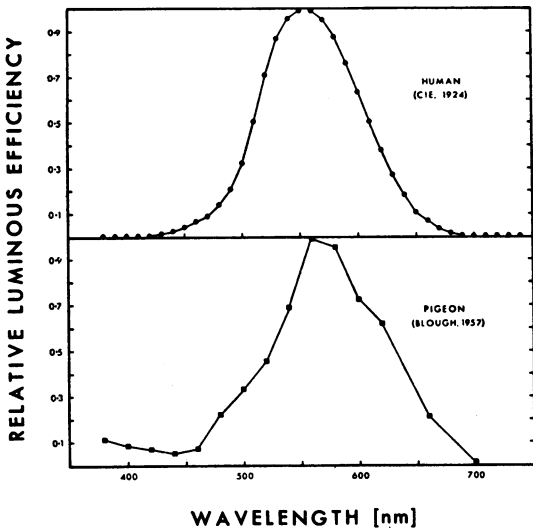


Fig. 8. Spectral sensitivity for the human (upper panel), and for the pigeon (lower panel).

- Ikeda, H. The spectral sensitivity of the pigeon (*Columba livia*). *Vision Research*, 1965, 5, 19-36.
- The Rand Corporation. *A million random digits with 100,000 normal deviates*. Glencoe, Ill.: Free Press, 1955.
- Wald, G. Human vision and the spectrum. *Science*, 1945, 101, 653-658.
- Wald, G., Brown, P. K., and Smith, H. P. Iodopsin. *Journal of General Physiology*, 1955, 38, 623-681.
- Wald, G. Retinal chemistry and the physiology of vision. In *Visual problems of color*. Symposium No. 8. National Physical Laboratory (U.K.). London: H.M.S.O., 1958. Pp. 7-61.
- Wright, W. D. *Researches on normal and defective colour vision*. St. Louis: Mosby, 1947.
- Wright, A. A. and Cumming, W. W. Color-naming functions for the pigeon. *Journal of the Experimental Analysis of Behavior*, 1971, 15, 7-17.

Received 18 February 1971.

(Final acceptance 24 January 1972.)