THE PIGEON'S PERCEPTION OF SATURATION¹

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Three experiments used similar methods to investigate the pigeon's perception of saturation of monochromatic lights. This trial-wise procedure consisted of brief presentations of positive and negative stimuli in random sequence. Pecks to the positive stimuli were occasionally reinforced on a low fixed-ratio schedule. The first study determined absolute thresholds for "white" and monochromatic lights by establishing a discrimination between lights of various radiances and a dark key. Experiment II investigated generalization from a white light to various monochromatic lights under conditions that minimized the use of luminance as a cue. The third experiment examined discrimination of various monochromatic lights along a colorimetric purity continuum; responses to white light were reinforced, while responses to lights that combined white and monochromatic lights in various proportions were not. The results indicated that lights of different wavelength differ in saturation, but that all are discriminable from white. Wavelengths between 550 and 600 nm are least saturated for the pigeon, and saturation increases markedly as wavelength decreases below this region of the spectrum.

Key words: color saturation, animal psychophysics, maintained generalization, vision, pigeon

Studies of visual discrimination with pigeons make frequent use of colored stimuli, and the skill with which these birds learn such discriminations has contributed to their reputation as a species possessing excellent color vision. In recent years, published research has filled in some of the detail concerning the pigeon's sensitivity to the various components of this complex dimension. The shape of the photopic spectral sensitivity curve has been described by D. S. Blough (1957), Graf (1969) and, more recently, by Yager and Romeskie (1975). Studies of wavelength discrimination by P. M. Blough (1972), Riggs, Blough, and Shafer (1972), and Wright (1972) indicate that the pigeon is most sensitive to wavelength differences in the 600-nm and the 525- to 540-nm regions of the spectrum.

Less research is available regarding the third color dimension, saturation. Studies with humans typically use a colorimetric purity

continuum to investigate this attribute; monochromatic lights are mixed in various proportions with a "white" light, and the subjects scale these stimuli with respect to their differences from a "white" standard (*e.g.*, Onley, Klingberg, Dainoff, and Rollman, 1963). The results of such studies indicate that, for humans, some monochromatic lights are more similar to white than are others. A comprehensive color theory must account for the details of these data along with those of wavelength discrimination and spectral sensitivity.

Data concerning the pigeon's discrimination of saturation would help to fill in the currently incomplete picture of its color psychophysics. Such a picture would increase the feasibility of examining the applicability of modern color theory to the bird's unique visual system. The pigeon's central visual pathways appear to be organized differently from those of primate species, and color-coded cells have been found in a thalamic nucleus whose comparability to primate structures is unclear (Karten and Hodos, 1970; Yazulla and Granda, 1973). The retina also has a markedly different structure. It is relatively thick, contains a high proportion of cones throughout, and is characterized by the presence of colored oil droplets.

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Since light must pass through these droplets before reaching the cones, it is clear that they must act as color filters, but the way in which the oil droplets and any cone pigment or pigments interact to yield cones of varying spectral sensitivity is unknown. Thus, the extent to which a modern color theory (*e.g.*, Hurvich and Jameson, 1957) applies to pigeon data would be an excellent test of the theory's generality.

The experiments described below explored the pigeon's saturation perception with three related techniques. An initial investigation (Experiment I) determined thresholds for "white" and monochromatic lights, so that their luminances could be equated in subsequent experiments. A generalization experiment (Experiment II) examined the extent to which pigeons generalized from white light to monochromatic lights of various wavelengths. The final study (Experiment III) used a related discrimination technique to examine the discriminability of lights of varying colorimetric purity.

METHOD

Apparatus

A two-channel optical system provided stimuli that were adjustable in luminance, wavelength, and colorimetric purity. A Sylvania DNF tungsten-halogen 150-W bulb operated at 6.6 A was the source of light for both channels. For the white path, light from this source passed through a system of lenses and mirrors and was focussed on a neutral density wedge; it was then collimated and refocussed at a beam-splitter, where it joined the second channel. Just beyond the beam-splitter was a tube containing the ends of three fiber-optics cables. Each cable ended behind the glass response key in one of the three experimental chambers. The spectral emission characteristics of the light from this channel approximated those of a 3050° K blackbody radiator. To form a second, monochromatic path, light from the common source entered a Bausch and Lomb 250-mm grating monochromator. The monochromator's entrance and exit slits were set at 3 mm; nominal half-band width was 9.9 nm. Light from the monochromator passed through a balancing wedge and was focussed on a second neutral density wedge; it then passed through its own system of lenses and

mirrors to the beam splitter, where its path joined that of the white path. An image of the monochromator's grating was focussed on the ends of the fiber-optics cables. Each channel had its own shutter, located just in front of the neutral density wedge.

The experimental chambers were the single-key, Grayson-Stadler pigeon boxes described in an earlier report (P. M. Blough, 1972). White noise in each box served to mask cues based on apparatus noises. The light spot on each response key was 2 mm in diameter; the rest of the key was blackened. In place of the regular houselight, two tungsten 6-W bulbs were mounted on the front panel to either side and slightly above the response key. A metal housing enclosed each bulb; windows in the housing consisted of Wratten 78AA ("daylight") filter material. Thus, light incident on the front panel, painted white, had a flatter energy distribution than is the case with an unfiltered tungsten illuminant. The panel's luminance in the area of the response key was approximately 31.8 cd/m².

The procedure for adjusting monochromatic lights so that they have equal luminance for the pigeon has been described previously (P. M. Blough, 1972). A threshold procedure (Experiment I below) provided data by which white and monochromatic lights could be equated. Readings from a MacBeth Illuminometer provided reference luminances for both channels. Because the light spots on the keys were too small to measure directly, a large surround was first adjusted so that it appeared equal in luminance to that of the spot on the key and then MacBeth readings were taken on the surround.

A LINC computer (Clark and Molnar, 1964) provided on-line control for these experiments. In addition to operating the shutters, wedges, houselights, and food magazines, it sensed responses, performed timing operations, and reduced and stored data.

EXPERIMENT I: THRESHOLDS FOR WHITE AND MONOCHROMATIC LIGHT

In Experiments II and III of this study, it was necessary to adjust white and monochromatic lights so that they would be equal in luminance to each other for the pigeon. The D. S. Blough (1957) and the Yager and

Romeskie (1975) spectral sensitivity functions provide a basis by which monochromatic lights of differing wavelength can be equated. It would be difficult, however, to use these data to equate monochromatic lights to a broad band light such as that supplied by the tungsten source along the "white" path described above. The present experiment helped to make this equation by assessing absolute thresholds for the white light and for a monochromatic light of 540 nm. An assumption of this procedure is that lights of "threshold" luminance are equal in luminance to each other.

Subjects

Six White Carneaux pigeons, six months to 2 yr in age, served. For three birds, 680, 683, and 686, the stimulus light was the unfiltered tungsten source. These birds were experimentally naive at the beginning of the study. For the other three subjects, 541, 553, and 649, the stimulus was a monochromatic light of 540 nm. These birds had served in a wavelength discrimination study (P. M. Blough, 1972). The data for only two birds in each group are presented below; the other two birds did not meet the performance criteria to be described.

Procedure

Preliminary key training was accomplished for the naive birds (680, 683, 686) by an auto-shaping procedure in which variable-time presentations of the stimulus lights, each 8 sec in duration, were followed by food presentation. For the experimental birds 541, 553, and 649, a small amount of hand-shaping re-established the response.

When the pecking response was established, regular sessions on the basic threshold-assessment program began. This program consisted of 2-sec presentations of the stimulus light interspersed with intertrial intervals (ITIs) whose variable duration ranged from 4 to 12 sec. During the ITI, the houselights were on, the response key was dark, and pecks delayed stimulus onset by 2 sec. During stimulus presentation, the houselights went out. Stimuli included S+ values of variable luminance and a "zero" luminance condition (S-) during which the houselights went out, the shutter operated, but light was blocked by an opaque portion of the neutral density wedge.

Pecks to S- delayed onset of the ITI by 2 sec; pecks to all other stimulus conditions were reinforced according to the schedule described below.

Positive stimulus (S+) luminances, differing from each other by 0.2 log cd/m², were chosen to yield a broad range of response probabilities. These values occurred in a randomized block design. Early in training, only one relatively high luminance was presented. As training progressed, lower values were added, and final data were based on a set of 12 S+ luminances. In addition to these 12 values, each block included four presentations of the S- condition. Altogether, a single block consisted of 16 randomized stimulus presentations that included 12 lights of varying luminance and four "zero luminance" presentations. A session consisted of several such blocks, the exact number depending on reinforcement probability.

Reinforcement probability and key-peck requirements were adjusted as training progressed. Initially, one peck per trial was defined as a "response"; later, the number of pecks required per trial increased such that a "response" was defined as a set of key pecks that had to be emitted within the 2.0-sec trial. This requirement was set individually for each bird at values that yielded a relatively high response probability to the brightest stimulus light and that seemed at the same time to maintain a minimal response probability to S-. Thus, for Bird 680 a "response" consisted of two pecks emitted within the 2-sec trial period, and for Bird 683 ten pecks were required. The peck ratio for the other subjects was three. An incomplete ratio was cancelled at the end of the trial; the pecks were not carried over to the next trial, a response was not recorded, and a scheduled reinforcement was not delivered. If a bird exceeded its ratio on a trial, the additional pecks were ignored; that is, no more than one response was recorded or reinforced in a single trial.

Reinforcement probability was the same for all S+s and decreased over the course of training from a probability of 1.0 to one of 0.25 during final data-collection sessions. An additional restriction on the reinforcement schedule prevented long sequences of unreinforced trials; during final sessions, a reinforced trial would be arranged whenever a series of eight unreinforced S+ presentations had occurred.

The number of trials in a session varied with reinforcement probability so that total reinforcements per day stayed constant at about 60. Magazine time was adjusted for individual birds so that the food consumed during the experiment was approximately the amount that maintained each subject at its 80% weight. For Bird 649, food presentation lasted for 2.5 sec; for the other birds, magazine time was 3.0 sec. Sessions were conducted almost daily for about two months.

RESULTS

Figure 1 shows, for four birds, the relation between response probability and stimulus luminance for the two stimuli used. Responses to the dark key are not shown. The data points, shown individually by sessions, are from the final two or three sessions for each bird. A session consisted of 20 blocks of trials; thus, each session contained 20 presentations of the 12 S+ luminances and 80 S- trials.

Sessions were terminated when the bird's behavior had appeared to stabilize and when at least two successive sessions yielded functions that did not differ systematically from each other. The graphs in Figure 1 show results only for those four birds that responded to S- 10% or less of the presentations. For the other two birds, the per cent of responses to S- was relatively high; thus, the function relating response probability to stimulus luminance covered a relatively narrow range, making threshold assessment difficult.

Threshold values were derived from lines fitted by eye to the functions shown in Figure 1. A frequently used criterion for "threshold" is a probability of 0.5 of detecting the stimulus. In the present case, this criterion corresponds to the occurrence of a response on one half of the S+ presentations or, since there were 20 presentations in a session, to the occurrence of 10 responses. Interpolation at the value 10 on the y-axes in Figure 1 yielded, for

Fig. 1. Probability of the key-peck response as a function of luminance. All luminances had an equal probability of reinforcement; each value occurred 20 times in a session. Pecks in S- (dark key) are not shown here.

unfiltered tungsten, thresholds of $-3.20 \log \text{cd/m}^2$ for Bird 680 and $-3.25 \log \text{cd/m}^2$ for Bird 686. For the 540-nm monochromatic light, thresholds were $-2.60 \log \text{cd/m}^2$ for Bird 541 and $-2.75 \log \text{cd/m}^2$ for Bird 649. The relative thresholds for the white and 540-nm lights were used in the following experiments as a basis for equating monochromatic and white lights in the manner described in the following section.

EXPERIMENT II: GENERALIZATION FROM WHITE TO MONOCHROMATIC LIGHTS

The attribute of "saturation" may be described roughly in terms of the similarity of a given light to a "white" light. In operant research, it is common to use the generalization paradigm to assess similarities among stimuli. Experiment II used a modification of this paradigm to consider for the pigeon the extent to which various monochromatic lights were similar to the white provided by the tungsten source.

Subjects

Of three White Carneaux pigeons, six months to 2 yr of age, two, 487 and 676, were experimentally naive. The third, Bird 680, had served in Experiment I.

Procedure

The two naive birds were key trained by a combination of autoshaping and hand-shaping techniques. A training program resembling the threshold program described in Experiment I then began. In this procedure, the positive stimuli (S+) were all white lights provided by the tungsten source described earlier and having luminances well above threshold. There were four luminances, covering an 0.8 log-unit range in 0.2 log-unit steps, and having a median luminance of $-2.48 \log \text{cd/m}^2$. For Bird 680 there was also an S-, a dark key, that occurred with a probability of 0.5. The other two subjects had no S- presentations during the training procedure. Stimulus presentations lasted 2 sec and were accompanied by offset of the houselights. During the 2-sec ITI, houselights were on and pecks delayed stimulus presentation. Stimulus values were prevented in quasirandom order; all S+ luminances had equal probability of reinforcement.

Reinforcement probability, initially set at 1.0, decreased as training progressed to a final value of 0.063. As reinforcement probability decreased, trials per session increased to a final value of 697. Magazine time was again adjusted individually so that the birds would maintain their weights during experimental sessions. These durations were 3 sec for Birds 487 and 680 and 4 sec for Bird 676. Number of pecks defined as a "response" was two for Bird 680 and three for the other two subjects. Training on this task was considered complete when the birds responded on almost every trial at the 0.063 reinforcement probability. Altogether, Bird 680 had nine training sessions, and Birds 487 and 676 had 17.

A maintained procedure tested for generalization to monochromatic lights of varying wavelength. Two-second presentations of the single white S+ and of 16 monochromatic stimuli occurred in a randomized block design. No reinforcement was scheduled for any of these presentations. Superimposed on this design, however, were occasional reinforced presentations of the S+. These presentations occurred at random with a probability of 0.063 but with the restriction that a maximum of 32 consecutive unreinforced stimulus presentations could occur. Their luminances varied over the same range as in training. Again, the offset of the houselight accompanied stimulus presentation, and pecks during the ITI postponed the onset of the stimulus presentation by 2 sec. A single key peck constituted a "response", and only one response was counted during a single stimulus presentation.

Monochromatic wavelengths ranged in 10-nm steps from 480 to 630 nm. On the basis of D. S. Blough's (1957) spectral sensitivity data,² these lights were set equal in luminance to the value selected for the 540-nm stimulus. The 540-nm light in turn was equated to the median luminance of the white S+ values in terms of their ratios to the thresholds determined in Experiment I.

Testing occurred over several days, with a total of 40 unreinforced presentations of each stimulus in a single daily session. Bird 680 had only two test sessions. For Birds 487 and 676, testing continued until responding to the monochromatic stimuli appeared minimal. For

²The Yager and Romeskie (1975) spectral sensitivity data were not available at the time of this study.

these birds, an additional session tested generalization to a new set of wavelengths, ranging from 540 to 615 nm in 5-nm steps. These lights were also equated in luminance to the white light and to each other in the manner described above.

RESULTS

Figure 2 summarizes the data from this experiment. Note that the response measure is per cent of responses to the S+, but the actual S+ responses are not shown on the function. No position on the x-axis corresponds to the complex wavelength composition of the tungsten light.

Two features of these data are of special interest. First, responding to the monochromatic test stimuli decreased over sessions and, for two of the birds, fell to values below 10% at all wavelengths. When new, intermediate monochromatic stimuli were introduced for these birds, S- responding remained low. Since the maintained generalization procedure is in effect a discrimination method (P. M. Blough, 1972), the data in Figure 2 indicate that Birds 487 and 676 learned to discriminate all monochromatic lights tested here from the white S+. Although test sessions for Bird 680 lasted only two days, the data for Day 2 already show marked differential responding.

The ability to discriminate all monochromatic lights from white light is characteristic of species with trichromatic color vision (Hsia and Graham, 1965). Although the present study did not explore the entire visible spectrum, our findings indicate that pigeons discriminate white from all of a broad range of monochromatic values. Thus, the present findings support other data indicating that the pigeon has at least three hue receptor systems. (e.g., Riggs *et al.*, 1972; Wright, 1972).

The second point of interest concerns the shapes of these functions, especially early in testing. All birds tended to generalize more to wavelengths in the regions between 550 and 580 nm than they did to shorter and longer values, but there was a greater tendency to generalize to longer wavelengths than to shorter ones. These findings suggest that, for the pigeon, lights in the middle of the spectrum appear more like the white used here than do lights at the extremes. To the extent that these data are acceptable as judgments of the "whiteness" of various colored lights,

the functions in Figure 2 describe saturation estimates for the various test stimuli.

One additional remark concerns the performances of Bird 680. As the data indicate, this pigeon tended to generalize less to all wavelengths than did the others, even on the first day of testing. Since this bird had participated in the threshold experiment, and since its training program included an S-, it had had much more experience with discrimination problems than did the other two subjects. Although the discrimination required in the present procedure was along a different continuum than in the threshold study, it is possible that the earlier experience contributed to the more rapid acquisition of this new discrimination. The extent to which pigeons transfer among various discrimination tasks is a matter of some controversy (e.g., Cumming and Berryman, 1961; Honig, 1965).

EXPERIMENT III: DISCRIMINATION ALONG A COLORIMETRIC PURITY CONTINUUM

In human studies of saturation discrimination, the physical dimension most frequently manipulated is that of colorimetric purity (e.g., Onley *et al.*, 1963). Stimuli varying along a colorimetric purity dimension include combinations of monochromatic and white lights in varying proportions. Lights of low colorimetric purity, usually judged by humans as relatively desaturated, contain a relatively high proportion of white, while a saturated light consists principally of the monochromatic component. The discriminability of lights on a colorimetric purity dimension is different for different wavelengths; *i.e.*, for some wavelengths, more monochromatic light must be added to produce a given change than is true for other wavelengths. This experiment examined discriminability along the colorimetric purity continuum in pigeons.

Subjects

The same three birds that participated in Experiment II served, but Bird 680 was used on only six of the seven conditions, and none of this bird's functions was replicated.

Procedure

This experiment examined the discrimination of colorimetric purity at a number of dif-

Fig. 2. Probability of responding to lights of various wavelength, all S- values, in terms of per cent total responses to S+. There were 40 presentations of each stimulus in a daily session. S+ was a "white" light; responding to it was maintained by reinforcement both before and during sessions that included the S- values shown here. The various curves describe data collected on the first day that the monochromatic lights were introduced and on several subsequent days.

ferent wavelengths. Its general program was similar to the test phase of Experiment II. The positive stimulus was a "white" light, supplied by the tungsten source described earlier. Its median luminance was approximately $-0.86 \log \text{ cd/m}^2$, but the actual luminance of the reinforced presentations varied over an 0.8 log-unit range around this value. Nonreinforced presentations of the $-0.86 \log \text{ cd/m}^2$ white light were mixed with nonreinforced presentations of 15 test stimuli varying along a colorimetric purity dimension. These test stimuli were a mixture of white and monochromatic lights; stimuli that were relatively high in colorimetric purity contained a greater proportion of monochromatic light than those of low purity. For each wavelength, the range of colorimetric purity values was adjusted such that one extreme corresponded to a response probability near zero and the opposite extreme, to a probability similar to that for the white positive stimulus. Within this range, the energy of the monochromatic light varied in 0.1 log-unit steps. The amount of white added to this mixture was adjusted for each stimulus so that the total luminance was approximately constant.³

As in the preceding two experiments, unreinforced stimuli occurred in a randomized block design. A single block included 16 stimuli, including the 15 test stimuli and an unreinforced presentation of the S+. Superimposed on this design were reinforced presentations of the S+, occurring at first with a probability of 0.125, and eventually with a probability of 0.063. Data-collection sessions consisted of 41 presentations of each test stimulus. However, the final results omitted the first block and thus included the final 40 presentations of each of the 16 test values, including the unreinforced presentations of the S+. Each trial, signalled by the offset of the houselights, lasted 2 sec; a constant 8-sec ITI

with houselights on separated these presentations.

In this fashion, the discrimination of colorimetric purity was assessed for seven monochromatic lights, ranging from 500 to 650 nm. A series of sessions examined the response function to a single wavelength; each series was terminated when three consecutive sessions yielded functions that did not appear to differ from each other in a consistent fashion. For Birds 487 and 676, sets of sessions investigated first responses to 500 nm, then to 550, 600, 650, 624, 574, and 524 nm, in that order. The procedure then repeated, beginning again with 500 nm, but following with 524, 550, 574, 600, 624, and 650 nm in that order. Sessions with Bird 680 did not begin until part way through this portion of the study. The order of testing for this bird was 600, 624, 650, 500, and 524 nm.

For each bird, the key-peck ratio constituting a "response" was adjusted to minimize responses to relatively saturated stimuli and at the same time to maximize response probability to the S+. These ratios were 15, 7, and 1 for Birds 487, 676, and 680 respectively. Pecks exceeding this ratio on a given trial were ignored. Magazine times were 3.0, 4.0, and 2.5 sec respectively for Birds 487, 676, and 680.

RESULTS

Figure 3 shows sample psychophysical functions, describing the relation between response probability and colorimetric purity of the stimulus mixtures. Since the white stimulus is off the continuum represented by the x-axis, these functions do not include responses to the S+. The graphs show separately the data points obtained on the first and second series. When there appeared to be a significant difference between the two functions, separate curves were fitted. These data describe the relation between the energy of the added monochromatic light and the discriminability of that stimulus from white. Thus, when a function is displaced toward lower energy values, less monochromatic light was required to obtain the desired performance.

For Bird 487, the data for the first and second wavelength series are similar enough in all but the 600-nm case that a single function seemed to fit all the data. For Bird 676, however, the functions were consistently displaced to the right on replication. In cases

³According to Abney's Law, when lights of different colors are mixed, the luminance of the mixture is equal to the arithmetic sum of the component luminances (Graham, 1965). Our rule for holding luminance constant depended on the applicability of this law, and, as in Experiment II, of D. S. Blough's (1957) spectral sensitivity curve and our present threshold data (Experiment I). Although it is not certain that the resulting mixtures did indeed have equal luminance for the pigeons, the use of varying S+ luminance appeared to discourage effectively the use of luminance cues.

Fig. 3. Sample psychophysical functions illustrating discrimination along a colorimetric purity continuum. Shown here are data obtained at 500 and 600 nm for each bird. When first and second sets of data did not replicate well, separate functions were fit. Each data point represents a combination of white and monochromatic light, all S- values. S+ was pure "white" light. Values on the y-axis indicate the total number of responses to 120 trials. Values on the x-axis are the energy of the added monochromatic light relative to values read from a Photovolt photomultiplier. Average probability of response to S+ was 0.91.

where the two sets of data required separate smooth curves, the interpolated threshold values were averaged.

Functions like those shown in Figure 3 are the basis of the threshold data to be described. Threshold values were determined by interpolating at the value 60 on the y-axis; this value indicates a response probability of 0.5, since each data point is based on 120 trials. Thresholds assessed in this manner are shown in the bottom portion of Figure 4. These three functions show, for each bird separately, the way in which these thresholds varied with the wavelength that constituted the monochromatic portion of the mixture. Although the exact shape of these functions differs among birds, there is a consistent trend for thresholds to rise, fall, and rise again with increasing test wavelength. The averaging procedure used with the data of Bird 676 appeared to have little effect on the shape of this bird's function. Note that these functions are expressed in terms of relative energy; that is, the measure is uncorrected for the pigeon's changing sensitivity to different portions of the wavelength continuum.

The functions at the top of Figure 4 describe the pigeon's sensitivity to various wavelengths. The two functions are from separate studies. Because further data analysis depends on one's choice of a spectral sensitivity function, the D. S. Blough (1957) and the Yager and Romeskie (1975) data are presented here. In the analysis below, the Yager and Romeskie curve was used because the present adapting and stimulating conditions were more similar to those used in their study than they were to D. S. Blough's.

To arrive at a more conventional expression of saturation, the energy data from Figures 3 and 4 must be expressed in terms of luminance. Colorimetric purity is usually expressed as the ratio between the luminance of the monochromatic component and the total luminance of the test field (Graham, 1965). Since the test field luminance was constant in this study, colorimetric purity was directly proportional to the luminance of the added monochromatic light. Figure 5 combines the energy and spectral sensitivity functions of Figure 4 to express the colorimetric purity data in this way. The broken-line functions show, at each wavelength, the relative luminance of the lights associated with threshold performance.

These luminance values were derived from the data shown in Figure 4, since the luminance of a light is simply the sum of its energy and the associated spectral sensitivity value when expressed in logarithmic terms. Plotted with these functions are solid curves showing the first day's generalization data from Experiment II. There are intuitive similarities between the tasks represented by the two functions, because both relate to the "whiteness" or saturation of monochromatic lights. The functions agree in suggesting that saturation is lowest in the mid-portion of the wavelength range used here, that it increases somewhat toward the longer wavelengths, and especially that there is a pronounced increase in saturation as wavelength decreases below 550 nm. In some details, however, the two functions differ; perhaps the most obvious difference is the location of the least saturated wavelength. The generalization data indicate that saturation is minimal between 550 and 575 nm; the colorimetric purity data suggest a less pronounced locus of minimal saturation in the region between 575 and 625 nm.

DISCUSSION

The three studies described here used a single response ("go/no-go") paradigm and the presentation in single sessions of a large number of stimuli along the dimension to be investigated. This method was efficient, since it required a simple response and just one stimulus field for each bird and because it allowed a large number of trials at each stimulus value in each session. Since presentations were randomized, this procedure avoided possible effects of sequential stimulus ordering.

There are special considerations that apply to this method's use as a psychophysical technique, however. One concerns the extent to which the birds may have been biased by non-stimulus variables. In the go/no-go paradigm, asymmetrical reinforcement contingencies tend to bias the subject toward the measured response. The emission of this response in S+ is strengthened by reinforcement, but reinforcement is not available for withholding the response in S- (Terman and Terman, 1972). Thus, these contingencies may favor responses in S- ("false alarms"). Such a bias, in the present study, would tend to raise the threshold for colorimetric purity, since the pecking re-

Fig. 4. The three lower functions describe, for each bird, energy of monochromatic light required to produce a threshold response to colorimetric purity as a function of wavelength. The upper functions are previously published spectral sensitivity data. Yager and Romeskie used daylight adaptation and on-key targets, while D. S. Blough's curve was acquired for above-key targets during partially dark-adapted conditions.

sponse indicates that there is no detectable monochromatic component to the stimulus.

On the other hand, applications to animals of signal-detection theory (*e.g.*, Terman and

Terman, 1972; Wright, 1972) predict that the probability of S+ and of reinforcement also affects response bias. As the relative frequency of these events increases, for example, false

Fig. 5. Comparison of the results from Experiments II and III. The solid lines are the generalization functions obtained the first day of testing in Experiment II (left-hand y-axis). The dashed curves describe the luminance of the monochromatic light that yielded threshold response on the colorimetric purity continuum in Experiment III (right-hand y-axis).

alarms become more likely, and failures to respond to a stimulus decrease. In Experiment III, the probability of S+ and of reinforcement were both very low, and there was no problem in maintaining a low response probability to S- values of relatively high purity. In Experiment I, however, where reinforcement and S+ probabilities were relatively high, false alarms presented an annoying prob-

lem, necessitating the delay contingency and the selection of data.

In the absence of a more complete investigation from the detectability viewpoint, it is impossible to assess the amounts of bias yielded by the various applications of this procedure. It is hoped, however, that, when basic parameters are constant, the technique yields a good estimate of relative sensitivity across a set of

conditions. An earlier study (P. M. Blough, 1972) was encouraging in this respect, since a similar method yielded wavelength discriminability data that agreed well with data obtained by other procedures.

The findings of Experiments II and III indicate convincingly that, for the pigeon, lights of different wavelengths have different saturations. These studies agree to some extent on the shape of the saturation-perception function. According to the theory of Hurvich and Jameson (1957), the saturation effect arises from differential activity of two separate color processing systems, one that processes luminance and a second that processes hue. The balance between the activities of these two systems is wavelength dependent. Thus, for a highly saturated wavelength, the activity of the hue-processing system is large relative to that of the luminance-processing system. For a less saturated wavelength, the activity of the hue-processing system is relatively small. The predictions that stem from Hurvich and Jameson's approach agree well with human psychophysical data, and DeValois and Marrocco (1973) have described associated electrophysiological findings for monkeys.

The extent to which this analysis applies to the uniquely organized avian brain is at present unclear. A recent study of Romeskie and Yager (1975) has made a beginning, however. This research reports, for the pigeon, the relation between wavelength and photochromatic interval, a range of low photopic luminances at which colored lights are discriminable from darkness, but not from "white". This range varies with wavelength, and in humans its size has an inverse relation to saturation. Romeskie and Yager account for their data in terms of the Hurvich and Jameson theory by postulating a set of receptor color mechanisms and a processing system similar to the one suggested for primates.

Comparisons among saturation perception studies must be qualified, because so-called "white" lights may differ from each other in their spectral emission characteristics. The data from the present Experiment III agree moderately well with those of Romeskie and Yager, although Romeskie and Yager used a 4800° K "white". The function describing the size of the photochromatic interval rises from the short wavelengths to a maximum at about 600 nm, where it begins to fall again.

The decline in photochromatic interval beyond 600 nm is sharp relative to the change in the present colorimetric purity data in that region, but both sets agree in suggesting that the most desaturated wavelengths are those around 600 nm. In humans, saturation is least in the region of best wavelength discrimination, a relation that appears to hold true in this case also, since for pigeons the region of best wavelength discrimination appears also to be around 600 nm (P. M. Blough, 1972; Wright, 1972). A possible explanation of this relationship may be that saturation is uncontrolled in wavelength discrimination experiments; thus, monochromatic lights are changing rapidly in saturation as well as in hue when the 600-nm region is explored.

The data of Experiment II, however, are more consistent with those reported by Schneider (1972). Schneider examined the probability with which birds reported that lights of various wavelengths were the same or different from each other. A white light with spectral emission characteristics similar to our own was included in the stimulus set. The probability of a "same" response was higher when white was paired with lights ranging from 542 to 568 nm than when it was paired with other wavelengths. The data of Experiment II are close to Schneider's in indicating that monochromatic lights in the mid 500-nm range are most similar to white.

The present experiments suggest that training pigeons to respond to a "white" positive stimulus will raise the strength of the response to some hues more than it will to others. Thus, stimulus control studies that use wavelength as a dimension should avoid the use of "white light" as an independent or orthogonal dimension.

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