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# EVIDENCE OF COMPLEMENTARY AFTERIMAGES IN THE PIGEON[1]

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Key pecking of pigeons was reinforced on a variable-interval schedule when ambient illumination came from a green light, but not when it came from a red, yellow, or white light. The different hues were randomly presented for periods of 30 sec each, with the restriction that white never followed red. After discriminative control was established, the pigeons were tested with the same procedure used during training, except that white sometimes followed red. Significantly more responses were made during white-following-red than during white following either green or yellow. These findings indicate that, in changing from red to white, complementary afterimages can be induced in pigeons for a brief period of time. By providing behavioral evidence for afterimages in the pigeon, this technique may be useful to research in comparative neurophysiology, animal discrimination learning, and theories of color vision.

If a human fixates on a stimulus of a particular hue for a period of time and then views an achromatic surface, he typically reports an afterimage of the complementary hue. In order to understand the processes responsible for complementary afterimages, a number of investigators have conducted electroneurophysiological experiments with animals (DeValois, 1960; Graham, 1966; Granit, 1962; Svaetichin and MacNichol, 1958; Wagner, MacNichol, and Wolbarsht, 1960). Although the results of these studies support the opponent theory of color vision (Hering, 1925), no behavioral experiments have been reported demonstrating complementary afterimages in animal subjects.

The present paper describes a procedure for obtaining behavioral data from animals concerning their possible perception of afterimages. The pigeon was used for this research because of its known sensitivity to variations in wavelength (Blough, 1957) and also because it is an excellent subject for carefully controlled, operant research.

## METHOD

### Subjects

Three experimentally naive, male, White Carneaux pigeons, 3 to 4 yr old, were used.

### Apparatus

A key-pecking apparatus (Grason-Stadler E1184JA), measuring 25.4 cm wide, 30.5 cm long, and 30.5 cm high, was employed. The walls and floor were painted flat white and the ceiling was made of translucent plastic. On the upper portion of the front wall was a white key, mounted 9 cm from the right-hand wall and 24 cm from the floor, and operable by pecks of force greater than 0.14 N. Directly below the key was an opening through which the birds had access to food (Purina Pigeon Food) for 2-sec periods during each reinforcement cycle. The food magazine was illuminated with a 4-W bulb whenever the food dispenser was raised. The complete unit was placed inside a light-tight, sound-insulated chest made of plywood and painted flat black on the inside.

The only sources of illumination in the box were five 150-W flood lamps (General Electric). Two of the lamps were red (R40, 150 FL/R), one green (R40, 150 FL/G), one yel-

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low (R40, 150 FL/Y), and one white (R40, 150 FL/W). The lamps were mounted on the ceiling of the insulated chest and were adjusted to illuminate the entire box with a relatively uniform intensity. The two red lamps were wired in series. Measurements of luminance were obtained inside the chamber by means of a Bausch and Lomb luminance meter. The luminance of each of the lamps was 1860 lumens. During the experiment, two levels of brightness (100% and 70% of the original luminance) were obtained by wiring the lamps to separate rheostats.

Grason-Stadler control panels and interval timers scheduled lamp presentations and reinforcements. Pecks were automatically recorded by a Gerbrands cumulative recorder.

*Procedure*

Throughout the experiment, water was available in the home cages. After 10 days of free feeding, a stable weight level was established for each subject and food deprivation was then imposed until each bird's weight was within 70 to 75% of its free-feeding weight. All subjects were maintained at this level for the remainder of the experiment.

After five days of magazine training and shaping the key-peck response, there were seven daily sessions in which every response in the presence of the green light was reinforced with food. Then, the birds were trained for seven days on variable-interval schedules of increasing parameter value: a 5-sec variable-interval schedule (VI 5-sec), a VI 10-sec, a VI 15-sec, and a VI 20-sec schedule. The VI 20-sec schedule was studied for an additional five sessions.

In the next phase, the birds were presented with hues other than the green training stimulus. During each session, subjects were given 30-sec presentations of each hue, but only responses emitted during the green stimulus were reinforced according to the VI 20-sec schedule. Each series of 11 stimulus presentations consisted of two bright and two dim presentations of white, two bright and one dim presentation of green, and one bright and one dim presentation each of red and yellow. Four presentations of white were given because white represented the critical stimulus during the subsequent testing phase, and three presentations of green were given in order to provide a sufficient number of reinforcements to maintain responding. The order of stimulus presentations was randomized except that within each series red never preceded the white stimulus. An example of one of the stimulus series is bright green, dim white, bright red, dim green, dim white, dim yellow, bright white, dim red, bright yellow, bright green, and bright white.

Each training session involved the presentation of 10 series of stimuli for a total of 55 min.

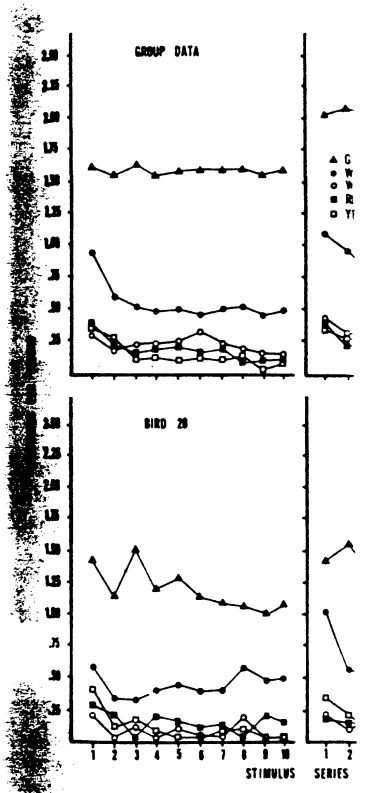
After each bird reached a criterion of responding at least five times more frequently in green than in any of the other stimuli, testing began. The testing procedure was identical to the training phase except that, within each series, one bright and one dim presentation of white was preceded by red; the other two white presentations were preceded by green and yellow. Testing was done in a single session, consisting of 10 series of 11 stimuli each, and reinforcement was scheduled under VI 20-sec during the green stimulus.

Following the test session (Test 1), each bird received five retraining sessions, with the white stimulus never preceding the red stimulus. Then, subjects were again tested (Test 2), as before, with the white stimulus following red on two trials.

## RESULTS AND DISCUSSION

Since the results of Test 1 were consistent with those of Test 2, the data obtained from both tests were combined. The mean response rates (responses per second) for all three pigeons to each of the stimuli, during the 10 consecutive series, are presented in the upper left-hand panel of Figure 1. A relatively high rate of pecking occurred during the green stimulus, when responses were reinforced under VI 20-sec, and there was no decrease in responding over the test series. Response rates during presentations of red, yellow, or white when white did not follow red, were relatively low. On the other hand, there was considerable responding during white-following-red. The difference in responding during the two conditions of white persisted throughout all 10 series and was significant at the 0.01 level when tested with a Wilcoxon test for matched pairs (Seigel, 1957). Furthermore, the rate of responding to white-following-red consistently decreased during testing.



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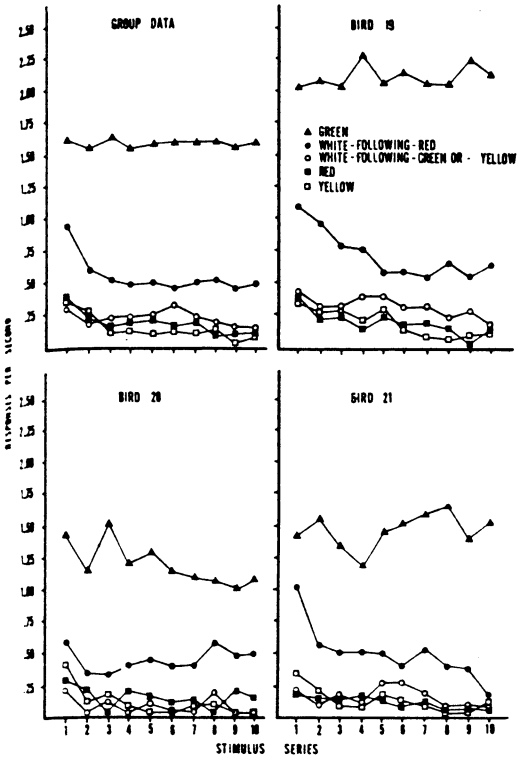


Fig. 1. Mean number of responses per second to ch stimulus for the 10 stimulus series.

The other panels of Figure 1 show the re-onse rate during the stimuli for each of the ree pigeons. The individual data are essen-lly the same as the group results, and the Wilcoxon tests revealed significant ($p < 0.05$) fferences in responding between the two con-itions of white for each of the birds.

The top panel of Figure 2 shows the mean mber of responses per second emitted by ird 19 during each successive 5-sec period of e 30-sec presentation of white-following-d. The data of this bird, which were typical the other subjects, indicate that virtually the responses to white-following-red oc-rred during the first and second 5-sec eriods.

Because responding to white-following-red eared to be relatively transitory, the test sults were reexamined in terms of the prob-lity that at least one response was emitted ing the first 5 sec of each stimulus. The an probabilities were computed for Series o 5 and Series 6 to 10 for each bird. The ttom panel of Figure 2 shows the results of st 1 and 2 combined for all birds. The

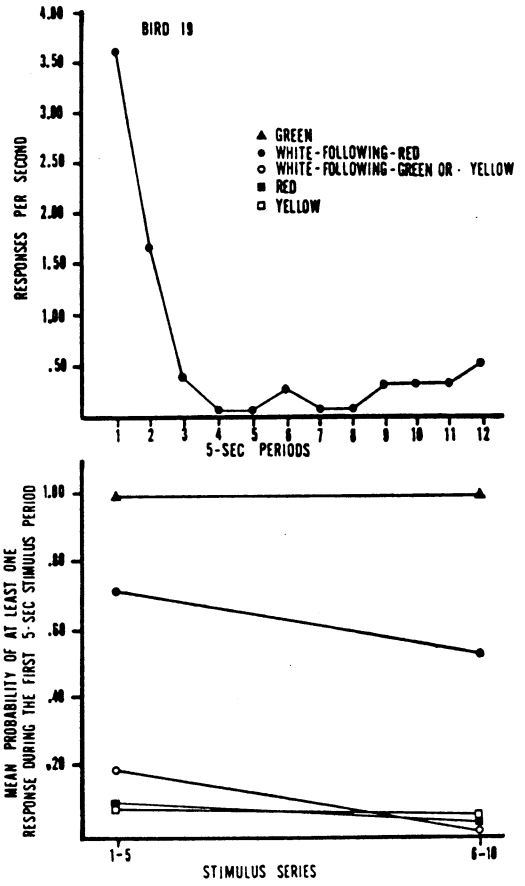


Fig. 2. Top: responses per second emitted by Bird 19 during successive 5-sec periods of white-following-red. Bottom: mean probability of at least one response being made during the first 5-sec period of each stimulus condition for Series 1 to 6 and Series 6 to 10.

mean probability of at least one response occurring in the first 5 sec was greatest for green, next for white-following-red, and least for the three remaining stimulus conditions. The difference in response probabilities between the two conditions of white (following red *versus* not following red) was found to be statistically significant ($p < 0.01$) when tested with a Wilcoxon test. Figure 2 also shows that the probability of responding to white-following-red decreased considerably from Series 1 to 5 to Series 6 to 10. The above findings were observed when examining the response probability data of each of the three birds.

On the basis of both dependent-response measures, rate and response probabilities, it seems evident that if pigeons are trained to respond to green they will also emit responses to the onset of a white stimulus following

red. This finding suggests there is stimulation comparable to what is called in humans a complementary afterimage when exposure to white illumination follows that of red. To demonstrate that the pigeon experiences other afterimages, it would be necessary to replicate the study using different pairs of training and inducing stimuli (*e.g.*, training on red, testing with green changing to white; training with blue, testing with yellow changing to white; *etc.*). That pigeons have stimulation similar to that of afterimages is particularly relevant to the vast amount of operant research on discrimination learning and stimulus generalization. In these studies, various hues are often presented successively on a pecking key. If the stimuli are fairly bright and presented for a period of 10 sec or longer, the birds might experience an afterimage stimulation that could affect their rates of responding.

The decrease in response rate during continued testing, and in the mean probability of responding to white-following-red, may have been the result of the pigeon's gradual discrimination between the stimulation from the "green afterimage" and the stimulation from an actual green stimulus. An important factor that might have controlled the difference in responding to actual green and "afterimage green" is the difference between their saturation.

The major contribution of the present experiment is that it provides a method of obtaining behavioral data that are in agreement with the electrophysiological evidence indicating that opponent or antagonistic processes are found in the visual systems of some animals (DeValois, 1960; and others). With some modification, this procedure could also be used to determine if complementary afterimages are experienced by other species. Such research would produce more knowledge about the comparative neurophysiology of color vision. Furthermore, animal research concerned with complementary afterimages might permit the study of variables that cannot be feasibly investigated with humans.

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