Winter 1981

SIMPLE AND CONTINGENT CHROMATIC AFTEREFFECTS IN PIGEONS

JEAN ROBERTS ATAK

Recommended Citation

ATAK, JEAN ROBERTS, "SIMPLE AND CONTINGENT CHROMATIC AFTEREFFECTS IN PIGEONS" (1981). *Doctoral Dissertations*. 1300.
https://scholars.unh.edu/dissertation/1300

INFORMATION TO USERS

This was produced from a copy of a document sent to us for microfilming. While the most advanced technological means to photograph and reproduce this document have been used, the quality is heavily dependent upon the quality of the material submitted.

The following explanation of techniques is provided to help you understand markings or notations which may appear on this reproduction.

1. The sign or "target" for pages apparently lacking from the document photographed is "Missing Page(s)". If it was possible to obtain the missing page(s) or section, they are spliced into the film along with adjacent pages. This may have necessitated cutting through an image and duplicating adjacent pages to assure you of complete continuity.

2. When an image on the film is obliterated with a round black mark it is an indication that the film inspector noticed either blurred copy because of movement during exposure, or duplicate copy. Unless we meant to delete copyrighted materials that should not have been filmed, you will find a good image of the page in the adjacent frame. If copyrighted materials were deleted you will find a target note listing the pages in the adjacent frame.

3. When a map, drawing or chart, etc., is part of the material being photographed the photographer has followed a definite method in "sectioning" the material. It is customary to begin filming at the upper left hand corner of a large sheet and to continue from left to right in equal sections with small overlaps. If necessary, sectioning is continued again—beginning below the first row and continuing on until complete.

4. For any illustrations that cannot be reproduced satisfactorily by xerography, photographic prints can be purchased at additional cost and tipped into your xerographic copy. Requests can be made to our Dissertations Customer Services Department.

5. Some pages in any document may have indistinct print. In all cases we have filmed the best available copy.

University
Microfilms
International

300 N. ZEEB RD., ANN ARBOR, MI 48106

8212778

ATAK, JEAN ROBERTS

SIMPLE AND CONTINGENT CHROMATIC AFTEREFFECTS IN PIGEONS

University of New Hampshire PH.D. 1981

University
Microfilms
International 300 N. Zeeb Road, Ann Arbor, MI 48106

SIMPLE AND CONTINGENT CHROMATIC AFTEREFFECTS IN PIGEONS

BY

Jean Roberts Atak
B.A., Northwestern University, 1968
M.A., Columbia University, 1970

DISSERTATION

Submitted to the University of New Hampshire
in Partial Fulfillment of
the Requirements for the Degree of

Doctor of Philosophy
in
Psychology

December, 1981

This dissertation has been examined and approved.

John A. Nevin

Dissertation director, John A. Nevin
Professor of Psychology

James R. Davis, Professor Psychology

Kenneth Fuld

Kenneth Fuld, Assistant Professor of Psychology

Robert A. Smith

Robert A. Smith, Research Associate

Marty J. Schmidt

Marty J. Schmidt, Ph.D.
New York Association for the Blind

Winsor H. Watson

Winsor H. Watson III, Assistant Professor of Zoology

November 20, 1981

Date

ACKNOWLEDGMENTS

I would like, first and foremost, to thank Tony Nevin, who was tolerant enough to let me tackle an unusual and rather risky problem, generous with both time and grant money, ready to bend unimportant rules but never his standards of excellence, and always enthusiastic. His subtle influence pervades both this thesis and my view of psychology generally, and his manner of teaching serves as an example to strive to follow.

The other members of my committee, too, have been extremely helpful in guiding my thinking, from specific criticisms of the dissertation research to more general insights and ways of looking at the problem. I thank each one.

More specifically, I would like to thank the Central University Research Fund for a grant (#S-64) which paritally funded this endeavor, the University of New Hampshire Graduate School, which granted me a Dissertation Fellowship for Semester II of the 1980-81 academic year, and Dr. Kenneth Andersen for helping me perform spectral analyses of slides.

On a more personal level, I would like to thank my husband, Baris, who insisted I pursue the Ph. D. and provided support and encouragement when I needed it most. This, in addition to the many concrete favors, such as

xeroxing proposals and spending an uncomfortable hour serving as a subject, is much appreciated. My parents, too, deserve my gratitude for their constant support on many levels, both during my studies at U. N. H. and throughout my academic career. Besides support, they provided fine role models of persistence, care, and striving for excellence.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

SIMPLE AND CONTINGENT CHROMATIC AFTEREFFECTS IN PIGEONS

by

Jean Roberts Atak

University of New Hampshire, December, 1981

In order to assess whether pigeons acquire simple and contingent chromatic aftereffects, four White Carneaux pigeons were trained to discriminate between colored and achromatic slides: Right and left key-pecks were reinforced following exposure to colored and achromatic slides, respectively. The chromatic set included slides of six different hues, added sequentially. Behavior on the first day each new color was added and on two transfer tests involving novel stimuli indicated that a 'chromaticity' concept had been acquired by all four birds.

In Experiment II, an attempt was made to demonstrate the McCollough effect (ME). In five procedures, various conditions known to produce a maximally strong ME in humans were arranged for the pigeons. In each case, various slides, including achromatic ME test stimuli, were presented following adaptation. As compared with control achromatic slides, no increase in right key-pecks following test stimuli was observed. Thus, no evidence for the ME was obtained.

In Experiment III, evidence of simple chromatic adaptaion in the pigeons was obtained. Six-min components alternated in which the experimental chamber was illuminated with either a green floodlamp or a "white" bulb. The proportion of right key-pecks following achromatic slides was much higher during green than during white components, indicating that the achromatic slides appeared more like the chromatic slides.

Because the chromatic and achromatic slides differed in film type (Kodachrome, Panatomic-X), some dimension other than the chromaticity of the object photographed might have controlled the birds' behavior. In Experiment IV, two tests separated these two potential sources of stimulus control by presenting "achromatic" Kodachrome slides and Panatomic-X slides with spots of color. Film type, not object chromaticity, was found to control the birds' behavior at this time. Spectral analyses of the two types of slides showed that they differed chromatically, and a further test revealed that this difference controlled the birds' behavior: When color-correcting green filters of varying saturation were sandwiched with Panatomic-X slides, the proportion of right key-pecks increased as a function of filter saturation. The results of this experiment demonstrate the difficulty of "communicating" with non-verbal creatures and make the results of Experiment II difficult to interpret.

INTRODUCTION

In 1965, Celeste McCollough reported a chromatic aftereffect (AE) which has since been intensively investigated in humans (see Skowbo, Timney, Gentry, & Morant, 1975, and Stromeyer, 1978, for reviews). Following alternating inspection of vertical and horizontal grids superimposed upon blue and orange backgrounds, respectively, subjects reported that achromatic vertical and horizontal grids appeared colored. The chromatic AE associated with each stimulus orientation was approximately the complement of its background hue during inspection. The major goal of the research described herein was to demonstrate this so-called McCollough effect (ME) in the pigeon.

The study of visual AEs has a long history, and has contributed a great deal to our understanding of human visual processes. Perhaps the best-known AE is the familiar negative afterimage (early systematic investigations include those of Fechner, 1840, and Helmholtz, 1866), in which inspection of a colored light subsequently leads to the perception of its complement upon an achromatic field. A wide variety of other visual AEs has also been reported, such as motion AEs (Hunter, 1914), threshold elevation (Blakemore & Campbell, 1969), spatial frequency shifts (Blakemore & Sutton, 1969), tilt AEs (Gibson & Radner, 1937) and other "figural AEs" (Osgood & Heyer, 1952), and depth AEs (Blakemore & Julesz, 1971). More recently, a class of AEs known as contingent aftereffects (CAEs) has been reported; the ME is the most intensively studied of this class. In CAEs, the AE occurs only in the presence of a specific value along some other stimulus dimension. In the ME, for example, chromatic AEs are contingent upon the orientation of the test lines. Thus, the ME is an orientation-contingent color AE. Other CAEs include, for example, color-contingent tilt AEs and motion-contingent color AEs (Mayhew & Anstis, 1972).

The demonstration of a CAE such as the ME in the pigeon would be of value for several reasons. First of all, it would add to the growing literature studying the visual capacities and processes of the pigeon (see Granda & Maxwell, 1979, for representative examples). This literature includes both physiological studies (e.g. Maturana, 1962) and psychophysical studies (e.g. Blough, 1956). A second contribution of such a demonstration would be to the field of comparative psychology. Both psychophysical and physiological comparisons have been made between the vision and visual systems of primates and birds, which possess what may be the two most highly developed visual senses found in nature. Many similarities between the two systems have been described (see Chapter 2 for examples), and a demonstration of the ME in pigeons would add yet another. Furthermore, such a demonstration might have implications bearing on the evolutionary relationship between the avian and mammalian nervous systems and/or (if homologues cannot be identified) on mechanisms by which each system may have evolved from that of their common reptilian ancestors. Finally, a demonstration of the ME in pigeons might contribute to the understanding of the ME itself. Although a demonstration of the effect in pigeons probably would not shed light upon its mechanism directly, further studies, especially ones employing physiological manipulations (obviously impossible with human subjects) would become feasible. Indeed, Shute has recently suggested that studying the ME in "an experimental animal with good colour vision ... and ... looking for changes in the activity of colour-coded cells..." is perhaps the best direction to take in advancing our understanding of the ME (Shute, 1979, p. 133).

Is it possible to predict whether or not the pigeon should be expected to acquire the ME? In order to answer this question, theories of the mechanism and functional significance of the ME are first reviewed in Chapter 1. In Chapter 2, current knowledge about avian vision and its neural substrate is summarized and compared with that of the primate. Finally, in Chapter 3, the question of whether or not the pigeon should be expected to acquire the ME will be evaluated in the light of Chapters 1 and 2.

Chapter 4 describes the general research strategy which was adopted in attempting to demonstrate the ME in pigeons. The subsequent four chapters describe the research which was performed: In Chapter 5, acquisition of the 'chromaticity' concept in pigeons is described; in Chapter 6, attempts to demonstrate the ME in pigeons are described; in Chapter 7, evidence of a simple chromatic AE is presented; and in Chapter 8, further analyses of the stimulus control of the birds' behavior are presented. In Chapter 9, the research is summarized and its implications are discussed.

CHAPTER 1

THEORIES OF THE McCOLLOUGH EFFECT

The contingent aftereffects, which have received so much attention in the last 15 years (the extensive literature, especially on the ME, has been reviewed by Anstis, 1975; Skowbo, Timney, Gentry, & Morant, 1975; Stromeyer, 1978; and Harris, 1980), have actually been known for some time. James Gibson (1933), for example, reported that straight vertical lines appeared curved and tinged with color following the prolonged wearing of prisms. Both of these are negative AEs, since they are the opposite of the distortions seen while first wearing the prisms. The color fringes, at least, are also clearly contingent AEs, since their hue depends upon whether an edge faces right or left. This contingent feature of many prism (and other "goggle") AEs was perhaps first noted by Ivo Köhler (1951/1964, 1962), who described the color fringe AEs as "situational color adaptation" (1962) and spoke of the various AEs as "'conditioned' after-effect(s)" (1951). As Held (1980) has suggested, it seems likely that the "rediscovery" of and present intense interest in these CAEs is due to the availability of new formulations about how the nervous system encodes and processes sensory "features," which seemed to be directly involved in the CAEs. These theoretical formulations have resulted in part from receptive field mappings of single cells in the visual system (e.g. Hubel & Wiesel, 1959), which have been interpreted, for example, as "feature detectors." Caution is often prescribed in drawing parallels between the neurophysiological and psychophysical data (e.g. Keith White, 1978, has called this approach to the study of sensory coding "heuristic neuromythology"). Yet the belief that the two taken together might reveal something important about how the visual world is perceived is clearly the major impetus for the serious interest now taken in CAEs. Recently, it has been suggested that this class of phenomena may also tell us something about how creatures learn.

In this section, we will first summarize the theoretical mechanisms which have been proposed as explanations of the ME. Second, possible functions of the effect will be discussed.

Theoretical Models of the McCollough Effect

Harris (1980) has recently delineated two general classes of models which have been offered as explanations of the ME: (a) adaptation or fatigue models and (b) association models. Most of these models are fairly general, although more formal models of the phenomenon have begun to appear (Montalvo, 1976; Kruger, 1979; Grossberg, 1980).

Adaptation Models

The simplest (though not the first-offered) model of the ME is that it is due to simple afterimages. This would seem to be ruled out since the hue of the AE depends upon spatial characteristics of the pattern which is not the case for afterimages, but Harris and Gibson (1968) pointed out that if subjects tended to fixate consistently upon an edge of the adaptation grids, a red and green plaid afterimage would result. If the test gratings were also subject to biased fixation, one of the afterimage colors would be covered by each of the vertical and horizontal black test gratings. Assuming that the "edges" of the colored afterimages would blur, the typical ME appearance would thus occur. Harris and Gibson tested this model by tachistoscopically presenting each adaptation pattern in each of two positions 180°out of phase, such that any red and green afterimages that might occur would completely cancel each other out. Since subjects still reported the ME, the afterimage model was ruled out. These authors offered, however, what they considered to be the simplest type of neural mechanism which could account for the effect: dipoles. Dipoles are mechanisms which respond to an intensity difference between two particular retinal sites. Harris and Gibson suggested that some of these would respond and thus red-adapt to one grating orientation while others would respond and green-adapt to the other grating orientation. When the achromatic test gratings are subsequently presented, they would be processed by the chromatically adapted dipoles: Those which were red-adapted would have relatively less red input than usual so that the grating would appear greenish, and similarly for the green-adapted dipoles.

The dipole model is actually very similar to the one originally offered by McCollough (1965). McCollough postulated that the effect was due to chromatic adaptation of "edge-detectors" which differ from dipoles only in being more pattern specific. Harris (1980) has suggested that the degree of pattern-specificity of the ME might be the only way to distinguish between the dipole and edge-detector models. Although both fairly narrow (Fidell, 1970) and broad (Ellis, 1977) orientation tuning curves have been reported, Lovegrove and Over (1972) have argued that the degree of spatial frequency specificity (roughly an octave) which they found was similar to that of monkey and cat cortical edge-detectors measured through single cell recording techniques. The latter result, then, supports the edge-detector model over the dipole model.

A variant of the adapted edge-detector model posited mechanisms tuned not only to spatial orientation (and/or frequency) but also to color: so-called double-duty channels. In this model, for example, mechanisms specific to vertically oriented red edges would be fatigued by the adaptation procedure, so that vertical-green detectors would dominate when the achromatic test pattern was subsequently observed. This model dominated the early ME literature (e.g. Fidell, 1970; Held & Shattuck, 1971; Breitmeyer & Cooper, 1972; Lovegrove & Over, 1972; May, 1972; Coltheart, 1973). The neurons responsible for the effect were thought to be located at an early cortical level: cortical because of the spatial specificity and early cortical because of the color specificity and the monocularity implied by the lack of interocular transfer first noted by McCollough. Harris (1980) claims that recent neurophysiological findings are more in line with the double-duty than the single-duty (chromatic adaptation of edge detector) model, but it is not clear that these findings are established well enough to support one view over the other: Both general types of neurons have been described, and there is a fair amount of latitude possible in interpreting the neurophysiology. Sharpe and Tees (1978), for example, have noted that the very same neurophysiological data have been interpreted as supportive of each of two particular competing models by different experimenters!

A final adaptation-type model which has been proposed (Hirsch & Murch, 1972; Murch, 1972; Shattuck & Held, 1975; Ambler & Foreit, 1978) suggests that the effect occurs in two stages, with a color stage (at the LGN?) "feeding into" a (cortical) level which is specific to spatial aspects of the pattern. An example of a finding used as evidence for such a view is the independence of the simple spatial frequency shift and spatial frequency contingent chromatic AE resulting from the same adaptation conditions (Murch, 1972). Specifically, the former effect decays more rapidly than the latter and only the former shows interocular transfer. The suggestion is that the color information is processed at a lower level (and thus does not transfer interocularly) and then "feeds into" higher level mechanisms processing spatial information. Riggs, White, and Eimas (1974) also claim that the complex form of the ME acquisition and decay functions favor at least a two-stage model.

Association Models

The adaptation models described above have increasingly been perceived as inadequate; in their place learning or association models have been offered. The most important arguments against a simple fatigue or adaptation model concern the decay of the ME.

First of all, the decay of the ME has an extremely long time course. Jones and Holding (1975), for example, reported a measurable effect at up to three months following adaptation and their decay curve extrapolated to zero at six to nine months. Such a long-lasting effect seems incompatible with fatigue models; most simple AEs decay within minutes. Second, the course of decay has been shown to depend upon the type of visual stimulation intervening between adaptation and test. For example, viewing achromatic gratings hastens decay (Riggs et al., 1974; Holding & Jones, 1976; Skowbo & Clynes, 1977) while sleep or darkness arrests it (D. M. MacKay & MacKay, 1975b). Again, these results are incompatible with a simple fatigue model.

The second most commonly cited criticism of the adaptation models is that they lack parsimony (e.g. Leppman, 1973; Murch, 1974; Harris, 1980). An adaptation model would necessitate the positing of another type of double-duty mechanism (e.g. sensitive to direction of motion and spatial frequency, or to binocular disparity and color) for each new CAE demonstrated, and additional CAEs seemed to be reported with alarming frequency (see Mayhew & Anstis, 1972; Wyatt, 1974; Skowbo et al., 1975; Stromeyer, 1978). While this is a common criticism of the adaptation models, it is a rather weak argument given the complexity of the nervous system, and many researchers do not seem to find such complexity disturbing (e.g. R. A. Smith, 1976; Virsu & Haapasalo, 1973).

Most association models which have been proposed have been fairly general, suggesting some sort of association process between spatial and color aspescts of a stimulus. For example, Creutzfeldt (1973) suggested that the effect might be due to "...selective functional connections between color sensitive cells and achromatic edge detectors within cortical columns"; Leppman (1973) proposed it was due to an association "between spatial aspects and an opponent colour response" in a process "analogous to classical conditioning"; D. M. MacKay and MacKay suggested "...cooperative changes at a synaptic or subsynaptic level throughout an 'association network'..." (1974) or "...something like associative habituation of synaptic couplings..." (1975b). Shute (1979) also favors an association model, perversely calling the mechanism a "forgetting" process.

A classical conditioning model, where the grating serves as conditional stimulus (CS), color as unconditional stimulus (US), and the unconditional (UR) and conditional response (CR) is a change in spectral sensitivity, has been proposed by Murch (1976, 1977). The most frequently mentioned similarity between the ME and classical conditioning is the fact that repeated exposure to achromatic grids produces faster ME decay, just as repeated exposure to a CS produces extinction of a CR in classical conditioning. Other similarities include the following: (a) An increase in ME strength between two temporally spaced testings is sometimes reported (Mayhew & Anstis, 1972; Skowbo & Clynes, 1977), just as "spontaneous recovery" of a CR occurs if a delay follows extinction (Pavlov, 1927). (b) Using two pattern-color pairings rather one produces narrower "tuning curves" (Wyatt, 1974; Murch, 1976; V. MacKay & MacKay, 1977), just as discrimination training leads to steeper generalization gradients (Liu, 1971; Tomie, Davitt, & Engberg, 1976). (c) A ME can be produced when the pattern and color are temporally (Murch, 1976; Schmidt, Pinette, & Finke, 1978) or spatially (Schmidt et al., 1978) separated, just as is typically the case of the CS and US in classical conditioning. (d) As acquisition of the ME is repeated, fewer trials are necessary to produce a given level of strength (Schmidt, et al., 1978), just as the reacquisition of a CR after its prior extinction is rapid. (e) Inspecting achromatic grids before ME adaptation reduces subsequent ME strength (White & Graves, 1976, cited by Skowbo & Clynes, 1977) just as prior exposure to a CS alone impedes acquisition of a CR when the CS is later paired with a US, a phenomenon known as "latent inhibition" (e.g. Lubow & Moore, 1959).

To the above list of similarities which have been noted between classical conditioning and the ME, I would add the following four points: First, other cases of conditioned perceptual responses have been reported, including conditioned afterimages with a tone as CS (Davies, 1976). Displacement aftereffects following adaptation to prisms have also been interpreted as cases of classical conditioning, following Taylor's (1962) work.[1] Taylor developed what amounts to a discrimination procedure in which the AE can be made contingent upon goggle-wearing (Kravitz, 1972) or even the occurrence of a tone (Kravitz & Yaffe, 1972). Second, if two orientations (V. MacKay & MacKay, 1977) or two spatial frequencies (Lovegrove & Over, 1972) are used as the adaptation/test gratings, the strongest ME may occur at an orientation or spatial frequency which is different from the adaptation value, shifted in a direction away from the other value, and the degree of this "peak shift" increases as the two adaptation stimuli are more similar to each other (V. MacKay & MacKay, 1977). An analogous phenomenon, known as the "peak shift,"

---

[1] Taylor's model is actually more an operant conditioning model, but subsequent investigators have largely described the prism situation in Pavlovian terms in cases where the distinction is made.

also occurs in classical conditioning[1] (Hupka, Liu, & Moore, 1969; Moore, 1972; Bushnell & Weiss, 1980) with generalization testing following discrimination training on two CS's differing along some stimulus dimension (where one CS is paired with the US and the other is not). Third, Shute (1979) has reported a finding which is consistent with the conditioning literature. Specifically, the usual ME was built up with red and green paired with vertical and horizontal gratings, respectively, and the subject then wore a red filter for 36 minutes following a single test measuring the strength of the ME. Upon removal of the red filter it was found that the red component of the ME was slightly higher than immediately after adaptation but decayed faster than usual, while the green component was

---

[1] The peak shift is not nearly so robust a finding for classical conditioning as it is for operant conditioning (e.g. Spence, 1937; Hanson, 1959). Bushnell and Weiss (1980), for example, demonstrated the phenomenon with autoshpaing in only 1/6 birds, and for the rabbit's nictitating membrane response it has been observed with auditory stimuli only when the CS- is higher in frequency than the CS+ (Hupka, Liu, & Moore, 1969; Liu, 1971; Moore, 1972). In all of the above cases, however, an area shift was demonstrated, which suggests that inhibition due to the CS- is present but not always large enough to produce a peak shift. It should be noted that in the typical ME procedure the "CS-" is not associated with extinction (absence of US) as in the usual discrimination procedure, but with another US which elicits a UR (say, green AE) incompatible with and opposite to the other UR (say, red AE). One would expect, in this case, a much larger "inhibitory" influence and thus a greater peak shift. It would be interesting to look for a peak shift with the direct analogue of the discrimination procedure (e.g. one orientation paried with red and another with white).

maintained at roughly the same level and decayed at the usual rate.[1] Shute explained these results in terms of inhibitory effects of opponent color mechanisms, but it might also be considered in the light of the conditioning model. If colors serve as US's (US-R and US-G) and grid orientation as CS's (CS-V and CS-H), Shute's experiment would be equivalent to removing the contingency in one CS/US pair:[2] Since the US-R occurs at all times it is independent of the presence/absence of the CS's (i.e., $p(\text{US-R}/\text{CS-V}) = p(\text{US-R}/\overline{\text{CS-V}}) = 1.0$). Whereas removing the CS-US contingency leads to extinction of the CR (Rescorla, 1967), Epstein and Skinner (1980) have recently reported that autoshaped key pecks (CR's) in pigeons show a "resurgence" when a dot (CS) is presented following extinction of the previously conditioned response through removal of the CS-US contingency. (This is not the exact analogue of Shute's experiment since the p(US) in the Epstein and Skinner extinction procedure was somewhere

---

[1] Shute's match method of measuring ME strength actually only measures the red component. My description above of what happened to the green component following red-flooding is what Shute found with respesct to the red component following green-flooding.

[2] A contingency is said to exist between a CS and a US if $p(\text{US}/\text{CS}) \neq p(\text{US}/\overline{\text{CS}})$, where $p(\text{US}/\text{CS})$ and $p(\text{US}/\overline{\text{CS}})$ are conditional probabilities that the US occurs given that the CS is or is not presented, respectively (Rescorla, 1967; Gibbon, Berryman, & Thompson, 1974).

between 0 and 1.0.) The authors suggested various possible explanations of the effect. For our purposes, it is enough to note that the effect occurs and is analogous to Shute's findings, at least on a qualitative level. Finally, Wyatt (1974) has demonstrated two types of "doubly contingent" AEs, one of which is reminiscent of another classical conditioning procedure. Wyatt's subjects were exposed to two adaptation procedures, one in which vertical gratings of two spatial frequencies were illuminated in either red or green to produce a frequency-contingent chromatic AE. In the second adaptation period gratings of the same two spatial frequencies were tilted to the right or left, to produce an orientation-contingent spatial frequency shift. In a final test phase, gratings of intermediate and equal spatial frequency were tilted to the right or left, but appeared shifted in spatial frequency and colored pink or green. Wyatt pointed out that the data could be interpreted in terms of adapted triple-duty information channels or a sequential model in which the output of one stage (spatial frequency shift) served as the input for the next (orientation --> spatial frequency shift, spatial frequency --> color AE). The latter "stage" model can be compared with higher order conditioning, in which a stimulus, CS1, is paired with a US, and then another stimulus, CS2, is paired with CS1, with the result that CS2 elicits a CR without having been directly paired with the US (Pavlov, 1927). In

Wyatt's experiment, the colors would be analogous to the US, the different spatial frequencies CS1's, and the orientations CS2's.

Various criticisms have been made, both of association models in general and of Murch's (1976) classical conditioning model in particular. The following points are especially relevant to the latter. (a) It was pointed out fairly early (e.g. Riggs et al., 1974) that the ME involved different colors than those demanded by a classical conditioning model, since a CR is generally similar to the UR. That is, pairing red with a vertical grid should result in a red, not green, AE associated with vertical grids. This is typically no longer seen as problematic (e.g. Harris, 1980), since the "neutralizing response" rather than the perception is viewed as the CR. Other cases of a CR being opposite in direction from a UR have also been described, such as heart rate changes with shock as the US (Black, 1971) and conditioned drug tolerance with morphine as the US (Siegel, 1975). It seems likely that characteristics of a CR will depend upon whether or not the nervous system initiates some sort of homeostasis-maintaining mechanism. (b) Holding and Jones (1976) have noted that a single "extinction" trial is enough to initiate a predictable, and seemingly invariant, decay course. Extinction in classical conditioning typically necessitates several trials in which the CS occurs without the US, and depends on the number of such occurrences rather than time. It might be noted, on the other hand, that a decay-like decline in learned behavior over time has been reported, although investigated but little (see Mackintosh, 1974). (c) Presenting the color before the pattern would be the analogue of backwards conditioning (where US precedes CS) in the Pavlovian paradigm, which typically leads to little if any learning (see, for example, Mackintosh, 1974, pp. 58-60). In the case of the ME, however, the result is a "reversed ME" where the same color as preceded the pattern is reported when the achromatic pattern is viewed (Murch & Hirsch, 1972; Murch, 1976; Schmidt, et al., 1978). While Murch has interpreted this as a case where the chromatic afterimage served as the CS, Schmidt et al. (1978) point out that this makes little sense and would require that the afterimage itself elicit another neutralizing response. On the other hand, there is evidence in the conditioning literature that a backward conditioning procedure may produce inhibitory conditioning (e.g. Kamin, 1963). If for an opponent-process color mechanism "inhibition" might translate into "complement" then perhaps these results are consistent with a classical conditioning paradigm after all. (d) Various miscellaneous differences between the ME and accepted instances of classical conditioning have been pointed out by McCarter and Silver (1977), such as the fact that an effective US typically has motivational qualities and that simultaneous conditioning is generally poor for classical conditioning but optimal for the ME. Most of these criticisms, however, have been adequately defended by Murch (1977), and in my opinion are not major obstacles to the model. (e) Wyatt (1974) noted that when subjects were exposed to adaptation with, say, red narrow grids alternating with green wide grids, both spatial frequency-contingent color AEs and color-contingent spatial frequency shifts were reported with the appropriate test stimuli. That is, each stimulus dimension was simultaneously functioning as both CS and US. Although a given stimulus can function as either CS or US depending upon its temporal location and strength relative to the other stimulus (e.g. Pavlov, 1927; Jones, 1924), I know of no case analogous to Wyatt's in the conditioning literature.

Other criticisms apply equally to the classical conditioning and general association models. First of all, several authors have noted that ME generalization may be unlike what one might expect based upon association analogues (Foreit & Ambler, 1978; Sharpe & Tees, 1978; Harris, 1980). For example, if interrupted or blurred lines are used during adaptation, maximal MEs are observed on complete or sharply focussed test lines rather than on lines identical to the adaptation stimuli (Sharpe & Tees, 1978). Secondly, it has been noted that it is not possible to use any arbitrary pattern to induce the ME (Mayhew & Anstis, 1972; Foreit & Ambler, 1978; Stromeyer, 1978); Mayhew and Anstis have suggested that only patterns which produce simple AEs can serve. Harris (1978), on the other hand, has suggested that the ME might be a case of non-arbitrary learning, such as has been noted in the learning literature where certain specific stimuli having special ecological adaptive significance are more easily associated with a given US than are others. In the case of conditioned taste aversion, for example, taste stimuli are especially easily conditioned to illness in the rat, whereas associations between visual or tactile stimuli and illness typically do not occur (Rozin & Kalat, 1971). By analogy, it may be that chromatic AEs can only be conditioned to a specific set of stimuli. This is an appealing notion; however it seems odd that the ME should be so specific while afterimages (Davies, 1976) and prismatic displacement (Kravitz & Jaffe, 1972) have been conditioned with an auditory CS. (According to Riggs, Note 5, White has been unable to demonstrate a ME-type phenomenon using an auditory stimulus in place of the usual grids.)

The most troublesome criticism which has been made of an association model calls into question the notion that a long time-course of decay is in fact unique to the CAEs. Specifically, it has been suggested that simple AEs may also be long-lasting (see Harris, 1980). If this is so, an adaptation model of the ME would become much more acceptable. The cases of long-lasting simple AEs which have been reported or noted in this regard, however, involve either prolonged (Gibson, 1933; Masland, 1969; Kalfin & Locke, 1972; Frome, Harris, & Levinson, 1975) or repeated (Yachzel & Lackner, 1977; Hansel & Mahmud, 1978) adaptation, which suggests that some sort of learning may be taking place. Furthermore, they may be interpreted (some more easily than others) as instances of CAEs. Indeed, this has been pointed out in some of the above reports (Masland, 1969; Hansel & Mahmud, 1978). On the other hand, long-lasting inhibitory processes have been reported at a neural level in moluscs (Tauc, 1969), and Creutzfeld (1973) has suggested that a similar process may be involved in the ME.

Recently, several relatively formal models of the ME have been offered (Montalvo, 1976; Kruger, 1979; Grossberg, 1980). Montalvo's model is a computer simulation in which neurons' receptive field characteristics are assumed to change as a result of sensory input. Creutzfeld and Haggeland (1975) have indeed shown that characteristics of adult cat receptive fields can be modified by visual input. Grossberg's model makes use of the notions of feed-back and feed-forward, and is mathematically more specific than is Montalvo's; neither of these, however, specify particular neural sites or mechanisms for their proposed processes. Kruger's model is more physiologically specific, and relies upon inhibitory processes taking place in opponent-process neurons with center-surround receptive fields in the LGN. The long duration of the ME is explained by postulating that metabolites are depleted more at particular synaptic endings within a particular neuron, while newly-manufactured metabolites are distributed equally to all endings, so that a relative metabolite imbalance is maintained. All these models are presented as associative models, and yet share some characteristics of the adaptation models. As White (1978) has suggested, "...at some point in the nervous system, the distinction between receptive fields underlying pattern vision and neural substrates of learning or memory becomes less pronounced...." (p. 268).

The Functional Significance of the McCollough Effect

In this section, we shall consider three possibilities regarding the functional role which might be played by the process underlying the ME. The most common suggestion (Mayhew & Anstis, 1972; Hohmann & von der Malsburg, 1978; Held, 1980) is that it would be useful in bringing one's perception of the world more in line with external stimulus attributes by "editing out" constant sensations which would likely have their origin in optical imperfections in the eye. Hohmann and von der Malsburg (1978), for example, have demonstrated that cylindrical lenses (with distortions such as might cause astigmatism) cause color effects due to chromatic aberration which are specific to line orientation and perceptually similar to the ME. The mechanism underlying the ME, then, might function to counteract these distortions due to an imperfect optical system. Held (1980) has made a similar suggestion, and has pointed out that the independence of the two eyes demonstrated with the ME[1] is consistent with this interpretation, since the two eyes often differ in the type and degree of optical distortion present. Montalvo (1976) has made a somewhat different suggestion along these same lines in connection with his model of changing receptive field characteristics, or a dynamic "visual metric": "Such a metric would have obvious adaptive ... value by precisely specifying frequent features and suppressing irrelevant features, such as the suppression of colored fringes produced by prism glasses...." (p. 50).

It should be noted that the type of functional role of the ME described above is similar in many respects to that frequently proposed for other types of "perceptual learning," such as adaptation to displaced or otherwise rearranged vision (see, e.g., Held, 1965; Rock & Harris, 1967). In these cases, vision must be recorrelated with

---

[1] Minimal binocular interaction occurs with the ME. Independent and opposite MEs can be induced in the two eyes simultaneously and interocular transfer does not readily occur (McCollough, 1965). Some binocular interaction has been reported (D. M. MacKay & MacKay, 1975a; Vidyasagar, 1976; White, et al., 1978; Shute, 1979), but it occurs only under special conditions and may be opposite in color to the AE in the adapted eye.

other modes of sensory information such as touch, whereas for the ME the correlation takes place within one sense modality. The suggestion is often made, in connection with sensory-motor rearrangement studies, that the process underlying adaptation is the same as that at work developmentally.

Anstis (1975) accepts the function of the process underlying the ME described above, but has proposed in addition a second possibility. He notes that in addition to the "optical cross talk" produced by chromatic aberration as described above, there may also be "neural cross talk." The latter might arise in the visual system as it progresses toward units responding to increasingly specific input. The suggestion is that in moving from double-feature (e.g. color and form) to single-feature units, imperfect divergence or "cross talk" may occur.

> Such correlation errors could be removed by CAE adaptation, which would thus play a valuable internal housekeeping role in automatically editing out cross talk.... The persistent correlations imposed artificially in experiments on CAEs are presumably indistinguishable from spurious correlations caused by neural transmission errors, and they lead to the same processes of adaptation. (Anstis, 1975, p. 281.)

A final point which must be made regarding the question of CAE function is the possibility that the ME and other CAEs have no functional role whatsoever. It is possible, for example, that their mechanism is genetically linked to some other process which is, indeed, functionally significant. Indeed, cases of non-functional organs, etc., have historically played a prominent role as evidence in support of evolutionary theory (see Gould, 1980, for some interesting instances of this). On the other hand, other mechanisms which down-play constancies and enhance change recur in organisms at various levels of organization (e.g. habituation, blocking, perceptual constancies, visual nystagmus and the fading stabilized retinal image, lateral inhibition and Mach bands, etc.). If species typically evolve by adapting a process that works for one problem to solving another, as Jerison (1973) has suggested for the case of distance senses in primates, then the fact that the ME is yet another example of a process which minimizes constancies might suggest that it does, indeed, carry functional significance. Perhaps this question can only be solved after the mechanism underlying the ME has been understood, at which time it might be possible to investigate the behavioral effects of tampering with that mechanism.

CHAPTER 2

VISION AND THE VISUAL SYSTEM IN THE PIGEON

In the previous chapter, we reviewed current theories of the mechanism and function of the ME. Clearly, no consensus exists with regard to these questions, and yet we now have some idea of the sorts of things to look for in the pigeon which might suggest whether or not this creature should be expected to acquire a ME. In this chapter, relevant aspects of avian vision and its substrate in the nervous system will be summarized (see Donavan, 1978, and Blough, 1979, for reviews). Particular note will be made of similarities and differences which exist between bird and mammal in general and between pigeon and primate in particular.

Pigeon Vision

With its laterally situated large eyes,[1] the pigeon enjoys a 340° panoramic visual field (Chard & Gundlach, 1938). Most of the behavioral research which has been

---

[1] By weight, the pigeon's eyes constitute fully one-half of its entire brain (Chard & Gundlach, 1938). The lateral placement is more common among vertebrates in general than the frontal placement typical of primates. Frontal eyes are especially common among nocturnal predators, who can afford to give up the panoramic field important in the survival of prey animals in favor of the increased efficiency in low illumination and improved image quality and depth perception afforded by frontal eyes. It is likely that the earliest primates were nocturnal predators (Allman, 1977).

carried out with the pigeon has dealt only with the frontal 24° binocular field (Chard & Gundlach, 1938) which is relatively myopic (Catania, 1964; Blough, 1973). The pigeon's acuity is good and comparable to that of the human both in the frontal field (e.g. Nye, 1968; Blough, 1973; Hodos, Leibowitz, & Bonbright, 1975; Hodos & Leibowitz, 1977) and in the lateral, slightly hyperopic field (Gundlach, 1933; Hamilton & Goldstein, 1933; Chard, 1939; Blough, 1971; Blough, 1973). Good discrimination of small changes of orientation of bar stimuli has also been reported (Mulvanny, 1979).

The pigeon has excellent color vision, similar in many ways to that of humans (see A. A. Wright, 1979, for a review). Various aspects of color vision have been studied in this creature, including spectral sensitivity (Blough, 1957; Graf, 1969; Blough, Riggs, & Schafer, 1972; Graf & Norren, 1974; Yager & Romeskie, 1975; Romeskie & Yager, 1976a), color difference scaling (B. Schneider, 1972), saturation (Blough, 1975), the photochromatic interval function (Romeskie & Yager, 1976b), color naming functions (A. A. Wright, 1976), and color mixing (Cohen, 1967; Jitsumori, 1976). In most respects, the color vision of pigeon and person are very similar; the following are the most striking differences which have been reported: (a) The pigeon can discriminate light of differing polarization planes (Delius & Emmerton, 1979; Kreithen, 1979) and is sensitive to light in the ultraviolet range (A. A. Wright, 1972; Delius & Emmerton, 1979; Kreithen, 1979), capacities which the human lacks.[1] (b) the cut-off points between hues or color names differ for the two species (A. A. Wright & Cumming, 1971). (c) The pigeon is probably tetrachromatic (Jitsumori, 1976; Govardovskii & Zueva, 1977; Graf, 1979) in contrast to the trichromatic human (e.g. W. D. Wright, 1928-29). (d) Spectral sensitivity differs slightly at different retinal loci of the pigeon (Yager & Romeskie, 1975; Martin & Muntz, 1979), probably due to the influence of differing distributions of the several pigmented oil droplets associated with the cones (Bowmaker, 1977, 1979; Wallman, 1979).[2] (e) The pigeon may be able to analyze mixed wavelengths as well as synthesize them (Cohen, 1967); humans can only achieve the latter.

---

[1] Humans can see ultraviolet light, but only if their lens, which absorbs ultraviolet light, has been removed (Wolbarsht, 1976). The perceived hues of these short wavelengths "go back" around the color circle (red beyond the blue, etc.), but are less saturated (Tan, 1971, cited in Wolbarsht, 1976).

[2] While some five types of colored oil droplets (Bowmaker, 1977) undoubtedly modify the pigeon's color vision, Wallman (1979) has shown that color discrimination still occurs in quails whose oil droplet pigments have been eliminated through special diet.

The Pigeon Visual System

Until fairly recently the avian and mammalian visual systems were thought to be radically different. Each was thought to consist of one main pathway, going from retina to thalamus to visual cortex in mammals and from retina to optic tectum in birds. The major visual area for mammals, then, was in the cortex, while for birds it was in the midbrain. As Karten (1979) has pointed out, however, modern research has drastically changed our understanding of both the mammalian and the avian visual systems. On the one hand, a second major mammalian pathway through the superior colliculus has been identified (e.g. G. E. Schneider, 1967; Trevarthen, 1968; Gordon, 1972; Diamond, 1973). On the other, a second major pathway going from retina to thalamus to telencephalon ("visual Wulst") has been identified in birds (Karten, 1969, 1979; Nauta & Karten, 1970; Webster, 1973, 1974). Figure 2.1 outlines the major pathways in mammals and in birds. Especially clear in this diagram is the general similarity between the visual systems of these two classes of organisms. The diagrams are, of course, simplified: Other structures receive visual input and other connections between the structures have been described besides the major ones indicated here.

In this section, current knowledge on the avian visual system will be summarized. Again, special note will be made

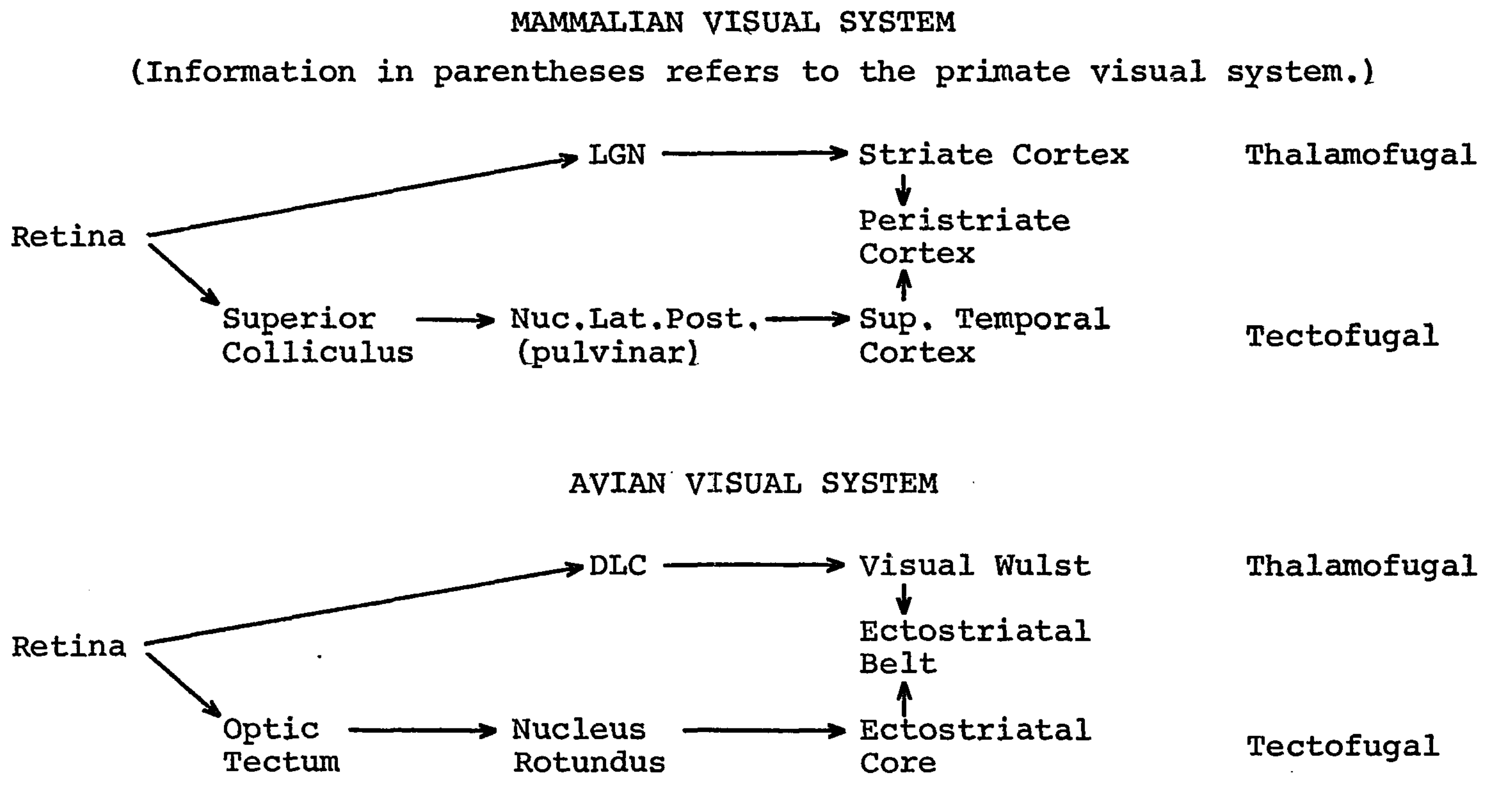


Figure 2.1. Schematic representation of the thalamofugal and tectofugal pathways in the mammalian and avian visual systems. Pathways which cross completely (cc) or partially (cp) to the contralateral hemisphere are so labelled. Abbreviations include: DLC, dorso-lateral complex; LGN, lateral geniculate nucleus; Nuc. Lat. Post, nucleus lateralis posterior; and Sup., superior.

of similarities and differences between primate and pigeon and of mechanisms which might potentially be involved in producing a ME. The two major pathways, the tectofugal and thalamofugal, will be described separately.

Tectofugal Pathway

The tectofugal pathway is the major visual pathway in birds, in the sense that the majority of retinal neurons proceed to the optic tectum rather than to structures of the thalamofugal pathway. This represents a difference between birds and primates; of the two pathways, the thalamofugal is the larger in primates. The tectofugal pathways of bird and mammal are similar in proceeding from retina to tectum to thalamus to telencephalon. Furthermore, the largest structures of each pathway, the mammalian superior colliculus and the avian optic tectum, are recognized as being homologous. That is, they are believed to have evolved from the same structure in a common ancestor, presumably the reptile-like cotylosaur (Romer, 1933; Campbell & Hodos, 1970).

Many of the retinal neurons in the pigeon have complex receptive fields, selective to direction of movement or to line orientation, for example (Maturana, 1962; Maturana & Frenk, 1963). These neurons are thought to project only to sites in the tectofugal pathway (Holden, 1977).[1] This degree of stimulus specificity is not found at the retinal level in primates, but it does occur in some mammals such as rabbits (Barlow, Hill, & Levick, 1964) and to a lesser degree in the ground squirrel (Michael, 1968).

Retinal fibers in the avian tectofugal pathway cross completely at the optic chiasm, terminating in the optic tectum. Complete cross-over at this point of the thalamo-striate pathway is also typical in mammals, but partial cross-over is the rule in primates (Allman, 1977). In birds, the major group of efferent fibers from the optic tectum [2] projects to both the ipsilateral and the contralateral nucleus rotundus of the thalamus, which projects to the ectostriatum and thence to the peri-ectostriatal belt of the telencephalon. Anatomical topographical organization is evident at all levels of this system in both birds and mammals.

One of the most universal findings of single-cell

---

[1] This pattern of different functional types of retinal neurons projecting to separate visual pathways has also been reported to occur in frog and ground squirrel (Michael, 1970, 1972).

[2] Some fibers project to the isthmo-optic nucleus, and thence in a feedback loop back to the retina. Such "centrifugal fibers" have only been proven to exist in birds and are thought to increase general sensitivity (Shortess, 1978; other possible functions which have been proposed are also enumerated).

recording studies is that as one progresses through the tectofugal pathway, receptive fields become larger and larger. This trend has been reported in rabbits, rats, monkeys and cats as well as in birds (Revzin, 1970, 1979; Gordon, 1972). In the pigeon, by the time the nucleus rotundus is reached, 75-80% of the neurons have receptive fields 140-180°in diameter (Revzin, 1970) while some 95% of the units in the ectostriatum are "wide-field units" (Revzin, 1970; Kimberly, Holden, & Bamborough, 1971). Most researchers agree, therefore, that this pathway is not likely to be involved in fine spatial and pattern vision (e.g. Revzin, 1970; Mulvanny, 1979; Maxwell & Granda, 1979). It would seem that the progression in this pathway is from a very high to a low degree of spatial specificity.[1]

Another dominant receptive field characteristic, which has been observed at all levels in the avian tectofugal pathway, is sensitivity to motion. Many neurons in this system are selective to direction and/or velocity of movement (e.g. Revzin, 1970, 1979; Kimberly et al., 1971; Maxwell & Granda, 1979). Motion has also been reported to be an important stimulus parameter in units of the mammalian tectofugal pathway (e.g. Sterling & Wickelgren, 1969).

A major difference between bird and mammal is that color information seems to be processed in the avian

---

[1] Although the receptive fields are large, pattern specificity is sometimes reported (e.g. Revzin, 1979).

tectofugal system, but not in the mammalian system. Yazulla and Granda (1979) have identified units with opponent-color characteristics in the optic tectum and nucleus rotundus but not in structures of the thalamofugal pathway in pigeons. Mammalian opponent-color cells, on the other hand, are associated with the geniculo-striate pathway (e.g. DeValois, 1965).[1]

Studies of behavioral deficits following lesions in the tectofugal pathway have generally supported the notion that this system is primarily involved in the spatial localization of visual cues rather than in pattern discrimination (G. E. Schneider, 1967; Trevarthen, 1978). This has been most clearly demonstrated among mammals. Hamsters with ablation of the superior colliculus have difficulty in locating but not in identifying (discriminating among) stimuli (G. E. Schneider, 1967). Pattern recognition is thus attributed to the geniculo-striate system. Such functional separation in the two pathways may not be as complete in birds, since analogous deficits have not been reported for birds with optic tectum lesions. However, essentially complete

---

[1] Neurons with differing spectral sensitivities have been reported to occur in the superior colliculus of cats (Ingvar, 1959) and squirrel monkeys (Wolin, 1966). These reports are, however, the exception, and macques have been shown to be color-blind following ablation of primary visual cortex (Klüver, 1942). It would appear that further research is needed to clarify the issue.

recovery to preoperative levels of accuracy on various discrimination problems has been reported for the pigeon following tectal ablations (Hodos & Karten, 1966, 1974; Hodos, 1969; Pritz, Mead, & Northcutt, 1970), indicating that the tectum is probably not important (or at least not alone) in the processing of pattern and luminance information. Given the importance of motion found in the single-cell studies, it has been suggested that the avian tectofugal pathway is important in flight (Kimberly et al., 1971) or in signalling approaching stimuli (Revzin, 1970); these functions are certainly consistent with the spatial localization and orientation functions attributed to the mammalian tectofugal pathway.

Thalamofugal Pathway

As Figure 2.1 shows, the avain thalamofugal pathway is very similar to that of mammals in proceeding from retina to thalamus to telencephalon. The "higher centers" beyond the thalamus of each pathway, the mammalian visual cortex and the avian visual Wulst and ectostriatum, are probably not homologous, however. Although Karten (1969) and Nauta and Karten (1970) have argued convincingly that the avian ectostriatum should not be considered as homologous with the mammalian striatum,[1] there are problems in considering it to be homologous with the mammalian visual cortex (Webster, 1974). It has been suggested that only certain populations of neurons within the avian Wulst and ectostriatum should be considered as homologous with the mammalian visual cortex (Nauta & Karten, 1970; Allman, 1977). In sum, the phylogenetic relationship between avian and mammalian versions of this pathway is presently the subject of much debate.

In the pigeon, a relatively small number of retinal neurons has been identified which have the concentric antagonistic center-surround receptive fields typical of most mammalian retinal units (Holden, 1977); these are thought to be part of the thalamofugal visual pathway. Fibers in this pathway originate in the retina and cross completely to the contralateral dorso-lateral complex (DLC) (Karten & Nauta, 1968) which is composed of three major thalamic nuclei. Efferents from the DLC partially deccusate (Miceli, Gioanni, Reperant, & Peyrichoux, 1979) and project to both the ipsilateral and the contralateral visual Wulst in the telencephalon (Revzin, 1969; Perisic, Mihailovic, & Cuenod, 1971). The Wulst in turn projects to the peri-ectostriatal belt (Karten, 1969), as well as rostrally

---

[1] If comparisons are made in terms of chemical composition and anatomical connections, only the internal striatum of birds is similar to the mammalian striatum (comprised of caudo-putamen and globus pallidus).

to both the optic tectum and DLC (Miceli, et al., 1979).

Single-cell recording studies have shown that the progression in the avian thalamofugal pathway is from a low to a high degree of stimulus specificity, just the opposite of the the progression evident in the tectofugal pathway. Receptive fields of most DLC units have concentric center-surround organization (Jassik-Gerschenfeld, Teulon, & Hardy; Maxwell & Granda, 1979), whereas many units in the viual Wulst have been reported to have complex response requirements, such as specificity to orientation, direction or velocity of motion (O'Flaherty & Invernizzi, 1972; Pettigrew & Konishi, 1976; Miceli, et al., 1979).[1] The similarity of this progression to that in the mammalian geniculo-striate pathway has been noted by virtually every experimenter cited in this section.

Other physiological differences between the avian tectofugal and thalamofugal pathways include the following: (a) Receptive fields of DLC units are smaller than those in the nucleus rotundus, being on the average one-third as large (De Britto, Brunelli, Francesconi, & Magni, 1975; Maxwell & Granda, 1979). (b) The majority of DLC units respond to stationary spots, although some respond best to movement (Jassik-Gerschenfeld, Teulon, & Ropert, 1976).

---

[1] Units specific to binocular disparity have also been reported for the owl, which has frontal eyes and a very highly developed Wulst (Pettigrew & Konishi, 1976).

Units responsive to movement are frequently direction-specific (De Britto, et al., 1975; Maxwell & Granda, 1979). (c) Wavelength information is not differentially coded in the DLC; all units there respond maximally to light of 540 nm (Maxwell & Granda, 1979). The first two, but not the third of these differences are also characteristic of mammals (see previous section).

Studies of behavioral deficits following lesions in the thalamofugal system are particularly instructive, since they exemplify how language can sometimes hinder our understanding of human perception, and how the results from animal studies can instruct experimenters on how to pose questions to human subjects. In mammals, ablation of visual cortex produces large visual deficits, but a great deal of recovery is typically observed, especially if retraining is provided. This has been demonstrated for rats, hamsters, squirrels, rabbits, hedgehogs, cats, bush babies, tree shrews, and monkeys (see Spear, 1979, for a review). The only apparent exception was with humans, who reported blindness or scotoma with cortical damage, with no recovery. Weiskrantz (1980), however, recently demonstrated residual vision in humans with coritcal lesions within their "blind" areas when a forced-choice procedure was employed. As with other mammals, discriminations were possible based upon cues other than differences in total luminous flux, and explicit training seemed necessary for recovery to proceed. Choices were sometimes 90-100% correct despite the subjects' continued insistence that they saw nothing.

In birds, lesions in the thalamofugal pathway have a much less pronounced effect upon visual discrimination than is the case with primates (see Hodos & Karten, 1966, 1974; Hodos, 1969; Pritz, Mean, & Northcutt, 1970). In fact psychophysical techniques are necessary to detect these deficits. The decreased sensitivity that has been reported does not, however, recover as quickly as it does following lesions in the tectofugal pathway. This has been demonstrated for intensity difference thresholds (Hodos & Bonbright, 1974) and for orientation difference thresholds (Mulvanny, 1970). Compared with mammals, we see a lesser deficit with thalamofugal pathway lesions in birds, suggesting that the two pathways may be more functionally redundant than is the case for mammals. Those deficits which do occur in both classes of organisms, however, would seem to support the notion that the thalamofugal pathway is important in the processing of pattern information.

CHAPTER 3

PREDICTING A McCOLLOUGH EFFECT IN PIGEONS

Given its excellent color and pattern vision, including a high degree of sensitivity to line orientation (Mulvanny, 1979), the pigeon seems a prime candidate for a creature who might be expected to acquire a ME. Based upon our knowledge of the ME in humans and of the pigeon's visual system, however, can we now make a more clear prediction of this occurring? Such a result would depend at least upon the following: (a) the mechanism of the ME in the human visual system, (b) the function of the mechanism underlying the ME in humans, (c) the existence (or lack thereof) in the pigeon visual system of mechanisms which are homologous or analagous to those underlying the human ME, and (d) the importance (or lack thereof) for the pigeon of the function (if any) underlying the human ME. As we have seen in the preceding sections, most of the above issues have not been resolved, so a unique clear prediction cannot be made. However, conditional predictions based upon assumptions related to the above issues can perhaps be made.

Two different species might share a given behavioral or perceptual phenomenon by either one of two general routes. First, the phenomenon might be the result of the same mechanism in either homologous or analogous neural structures. In this case, the phenomenon might either itself function in enhancing the survival of the species or it might be a byproduct of some other phenomenon which is of evolutionary significance; these functions could conceivably differ for the two species. Secondly, on the other hand, two species might share a behavioral phenomenon which is the result of entirely different mechanisms in the two cases. If this were the case, it seems unlikely that the phenomenon would have independently arisen in the two species unless it had some function of biological significance.

Let us suppose, first of all, that if pigeons are able to acquire a ME, it will be due to the same type of underlying mechanism as that in humans. Let us first consider what we should expect if the human ME is due to an adaptation or fatigue-type process. If, in this case, the mechanism is located in homologous neural structures we should look in the pigeon's thalamofugal pathway, which is certainly generally similar to the primate geniculo-striate pathway (in which the process producing the human ME is always assumed to dwell) if it is not in fact homologous to it. We have seen that neural units with orientation-specificity are to be found at various levels of this pathway: some are found in the DLC (De Britto et al., 1975) and many are found in the Wulst (e.g. Miceli et al., 1979). Color-coding, however, has not been found in this pathway (Maxwell & Granda, 1979). Thus, if the ME is due to adaptation of double-duty channels then the pigeon should not acquire a ME (unless such units exist in the ectostriatal belt, which has not yet been studied physiologically). On the other hand, if the effect is due to chromatic adaptation of edge detectors then the pigeon should acquire a ME. The two-stage process in which color information (at the primate LGN) "feeds into" orientation-specific units could not occur for the pigeon, unless it occurred at the ecstostriatal belt with color information coming from the tectofugal pathway and converging onto spatial information coming from the thalamofugal pathway.

If we allow our adaptation mechanism to be located in the tectofugal pathway, then neurons at the retinal level would seem the most likely candidates for producing a ME: certainly the necessary spatial specificity is found there. Donner (1953) found retinal units sensitive to different wavelengths (though not opponent-process type), so that double-duty units might be available to produce a ME at this level. Certainly a chromatic-adaptation-of-edge-detector mechanism would be feasible. At other levels of the tectofugal pathway the necessary color specificity is there, but the pattern specificity probably is not.[1] On the other

---

[1] Maxwell and Granda (1979) and Revzin (1979) have speculated about the presence of such pattern-specific units. However, if they exist they would have receptive fields which would be too large to produce a ME such as occurs in humans, which is specific to retinal location (Stromeyer, 1972a).

hand, Maxwell and Granda (1979) have described units in the nucleus rotundus which would qualify as Harris-and-Gibson-type "dipoles".

Still assuming that a ME in pigeons should occur via the same type of mechanism as produces that in humans, let us consider what we should expect if the latter is an association-type process. The only model of this type specific enough to allow a clear prediction is that of Krüger (1979), which relies on inhibitory processes in LGN opponent-process neurons with center-surround receptive fields. If this model is correct, then the pigeon clearly should not acquire a ME, since such neurons are not found in its thalamofugal pathway. Other less formal association models do not allow for such a clear prediction. On the one hand, pigeons obviously do learn, including, specifically, via classical conditioning (e.g. Brown & Jenkins, 1968). On the other hand, when it comes to "perceptual learning," birds (along with other creatures with lateral eyes)[1] are often described as lacking plasticity (e.g. K. U. Smith & Smith, 1962; Taub, 1968). Adult chickens, for example, do not adapt to optical rearrangement (Pfister, 1955, cited by

---

[1] Blakemore (1974) suggested that only creatures with frontal eyes needed to "tune" receptive fields of the two eyes to produce stereopsis, and that therefore only such species would exhibit sensory and neural plasticity (see also Mitchell, 1980).

Taub, 1968).[1] If the pigeon, too, lacks this "plasticity" then it should not be expected to acquire a ME.

Let us now consider the second major route by which pigeon and person might share a phenomenon such as the ME. Suppose, that is, that the effect is due to different underlying mechanisms. If this is so, then a specific function should be identifiable which would contribute to the survival of both species. In Chapter 2, we noted two functions which have been proposed for the ME in humans. One (Anstis, 1975) suggested that it might function to edit out neural cross talk occurring as color and pattern information diverged into separate channels. For the pigeon, this function may be carried out by the separation of color and pattern information into different pathways. If so, it would not need another mechanism such as would produce a ME. The second proposed function of the ME (e.g. Held, 1980) was to adapt to chromatic aberration such as might be produced by the optics of the eye. Certainly, if anything this would be even more of a problem for the pigeon than for the primate, since chromatic aberration increases with eccentricity and the pigeon probably has good acuity

---

[1] Rossi (1968, 1969, 1971, 1972) has reported evidence that newly hatched chicks do adapt to prismatic displacement, although the effect depends upon such variables as the number of other chicks present and the density of scattered grain during adaptation. Thus, the effect would appear to be quite fragile, and probably only occurs during some sensitive period.

over much of its retina (Blough, 1979). On the other hand, one of the functions which has been proposed for the colored oil droplets of the pigeon retina is to eliminate blur due to chromatic aberration (Walls & Judd, 1933; Wolbarsht, 1976). Again, this function may be carried out in the pigeon another way.

Should the pigeon acquire the ME? "Maybe" seems to be about the best we can do. On the other hand, a demonstration of the presence or absence of this perceptual phenomenon might render some models of the ME in humans more or less plausible and might modify our conception of the pigeon's nervous system and its relationship to that of the primate.

CHAPTER 4

RESEARCH STRATEGY

In order to attempt to demonstrate the McCollough effect in pigeons, the following strategy was adopted: (a) the subjects were first taught to "report" on their relevant visual experiences, and (b) in testing for the ME, parameters were employed that would maximize the chances of finding the effect if it exists.

Reporting Perceived Colors

One of the most exciting applications of the operant techniques developed by Skinner (1938) and others is in assessing the sensory capacities and perceptual experiences of non-verbal organisms. This branch of the experimental analysis of behavior is generally known as "stimulus control" and has been applied to creatures as different as the octopus (Sutherland, Mackintosh, & Mackintosh, 1963) and the human infant (Bower, 1964). These techniques are especially exquisite when combined with psychophysical methods (e.g. Blough, 1956), and indeed most of the research cited earlier on pigeon vision made use of this marriage of methods.

As Gleitman (1974) has pointed out, the fact that non-verbal creatures cannot directly communicate their experiences to us may in fact be an advantage in disguise.

For example, an adult human who is red-green color blind may insist that a given object appears green. He, like other adult humans, has been reinforced by the verbal community for calling certain items "green," but the stimulus dimension upon which his judgments are based is almost certainly different from that employed by normal trichromates. In Chapter 2, we saw in the work of Weiskrantz (1980) a clear example of how reliance upon subjects' verbal reports can lead to problems of interpretation. When an experimenter cannot rely upon a past reinforcement history of verbal behavior, as is the case when the subject of investigation is not human, reinforcement contingencies must be devised specifically for use in a given study. Since these contingencies are explicit, potential problems of interpretation may be more obvious than when relying upon verbal communication. (See, however, Chapters 8 and 9.)

In the present research, pigeons were "instructed" to report whether a given stimulus was colored or achromatic by arranging that reinforcement be contingent upon one response (a peck to a key located on the right side of the chamber) if the stimulus was in fact colored, and upon another response (a left key peck) if it was achromatic. Once a high level of accuracy was achieved, reinforcement was programmed for only a proportion of the correct responses. Novel stimuli could then be presented without providing reinforcement for the bird's subsequent responses. In this case, a right key peck could be interpreted as a report of perceived color and a left key peck as a report of no perceived color, without providing feedback (reinforcement) which might "instruct" the creature on how to classify a given stimulus in the future.

Pigeons were trained to report on color in general, rather than on some particular color (such as red or green). The main reason for this was the inability to predict precisely what the hue of a ME might be for the pigeon, since it is not known what hues are complementary for this creature. Since differences exist between human and pigeon hue boundaries (A. A. Wright & Cumming, 1971) and anomalies have been reported in the limited color-mixing studies which have been performed with the pigeon (Cohen, 1967; Jitsumori, 1976), it seems safer not to assume anything about the specific characteristics a ME might take on for the pigeon.

In order to insure that the subjects' behavior was under the control of chromaticity rather than specific hues, intensities, or saturations of stimuli, training stimuli varied considerably on all these dimensions. The attempt, then, was to teach the pigeons the abstract concept of chromaticity.

Maximizing the Probability of ME Detection

In testing for the presence of the ME, parameters were chosen which have been demonstrated to increase the strength of the ME in humans. These included: (a) prior dark adaptation (Stromeyer, 1978); (b) lengthy ME adaptation (White, 1978); (c) bright adaptation stimuli (White, 1976) with highly saturated colors (White, 1978); (d) adaptation colors roughly opposite from each other (and thus, perhaps, complementary) on the pigeon color space (B. Schneider, 1972): although it is not mandatory to use complementary colors during adaptation, some investigators have suggested that they may enhance ME strength (Riggs et al., 1974); (e) test stimuli of the same spatial frequency as the adaptation stimuli (Teft & Clark, 1968; Stromeyer, 1972b); (f) test stimuli with both orientations present simultaneously, which enhances the ME through color contrast (Stromeyer, 1978); (g) test stimuli of high contrast (Stromeyer, 1978) and relatively low intensity (Stromeyer, 1971; White, 1976); (h) maintaining relatively constant head position of the subjects during testing (McCollough, 1965); and (i) including adaptation/test sessions in which the subjects were injected with scopolamine (Shute, 1979).

CHAPTER 5

EXPERIMENT I. THE CHROMATICITY CONCEPT IN PIGEONS

The purpose of this phase, as described in the previous section, was to teach a general chromaticity concept to the subjects, so that they might "report" their experience of color following ME adaptation. The demonstration of an abstract concept such as chromaticity in pigeons is also of some interest in its own right, however. Pigeons have been shown capable of acquiring various concepts, including so-called "natural" concepts such as "person" (Herrnstein & Loveland, 1964) and "tree" (Herrnstein, 1979), as well as less concrete concepts such as "A" (Morgan, Fitch, Holman, & Lea, 1976) and "symmetrical" (Delius & Habers, 1978). Premack (1978), however, has questioned the generality and abstractness of many of these demonstrated concepts, and has specifically suggested that pigeons should be incapable of acquiring the concept of "chromaticity." Premack argues that generalization will occur, but that "true" conceptual behavior, such as that demonstrated in his chimps, will not.

> Perhaps the simplest way to show that the pigeon does not have the human concept of color would be to train it to peck the left key in the presence of certain chromatic values and right key in the presence of certain achromatic ones. To say that the bird makes the human distinction, in effect, "knows what kind of thing a color is" -- and therefore accepts blue, red or green as instances of color no less than the yellow on which it was trained -- requires that the bird peck the left key to all chromatic values and the right key to all achromatic ones. But will the bird respond in the

> categorical manner required by the human distinction between colored and not colored? Or will it simply generate gradients around the training stimuli? (Premack, 1978, p. 436.)

Fortuitously, the procedure employed in this study is nearly identical to that required in Premack's test.

Conceptual behavior may be defined as generalization within a stimulus class and discrimination between stimulus classes (Keller & Schoenfeld, 1950) and is demonstrated by transfer to novel instances of the classes. In this study it was possible to assess the existence and generality of a chromaticity concept in two ways. First, hues were introduced and added to the chromatic set one at a time, so that the birds' performance on the first day that a hue was added could indicate whether the new colored stimuli were already classified in the same way as previously encountered colored stimuli. Secondly, two transfer tests employing novel stimuli were included.

Methods

Subjects

Five White Carneaux pigeons (23, 24, 230, 37 and 40) served as subjects. Three of these (23, 24 and 230) had experimental histories including a red-white discrimination. Bird 24 died during the experiment, whereupon birds 37 and 40 were added. Their experimental histories included discriminative autoshaping using colored CS's, and a study employing an auditory discrimination. The data for bird 24 are not reported, being incomplete.

Apparatus

The 30.5 x 32 x 35 cm experimental chamber, illustrated in Figure 5.1, included three manipulanda: two standard pigeon keys positioned 18 cm apart and 20 cm above the floor, and a rectangular sleeve, 5 x 5 cm at the opening and 12.5 cm long, into which the pigeon could insert its head. A back-projection screen was located at the end of the sleeve, and a photocell placed 3 cm beyond the sleeve opening allowed detection of the bird's head in the sleeve. A grain magazine was mounted directly below the opening to the sleeve and 5.5 cm from the floor. A house light was positioned 4 cm above the sleeve opening.

The above chamber was housed in a larger 60 x 60 x 90 cm insulated box equipped with a fan. An 8 x 10.5 cm hole in the box allowed the beam from a Kodak Ektagraphic Carousel projector to enter, a shutter being positioned 9 cm behind the hole and 15.5 cm from the back projection screen. Two photocells were positioned at the level of the shutter, which allowed the coded slides to be read as (a) colored or black-and-white, and (b) training or test stimuli (test stimuli will be described in Chapter 6).

Stimuli

The stimuli consisted of colored or black-and-white slides, the former processed from Kodachrome or Ektachrome

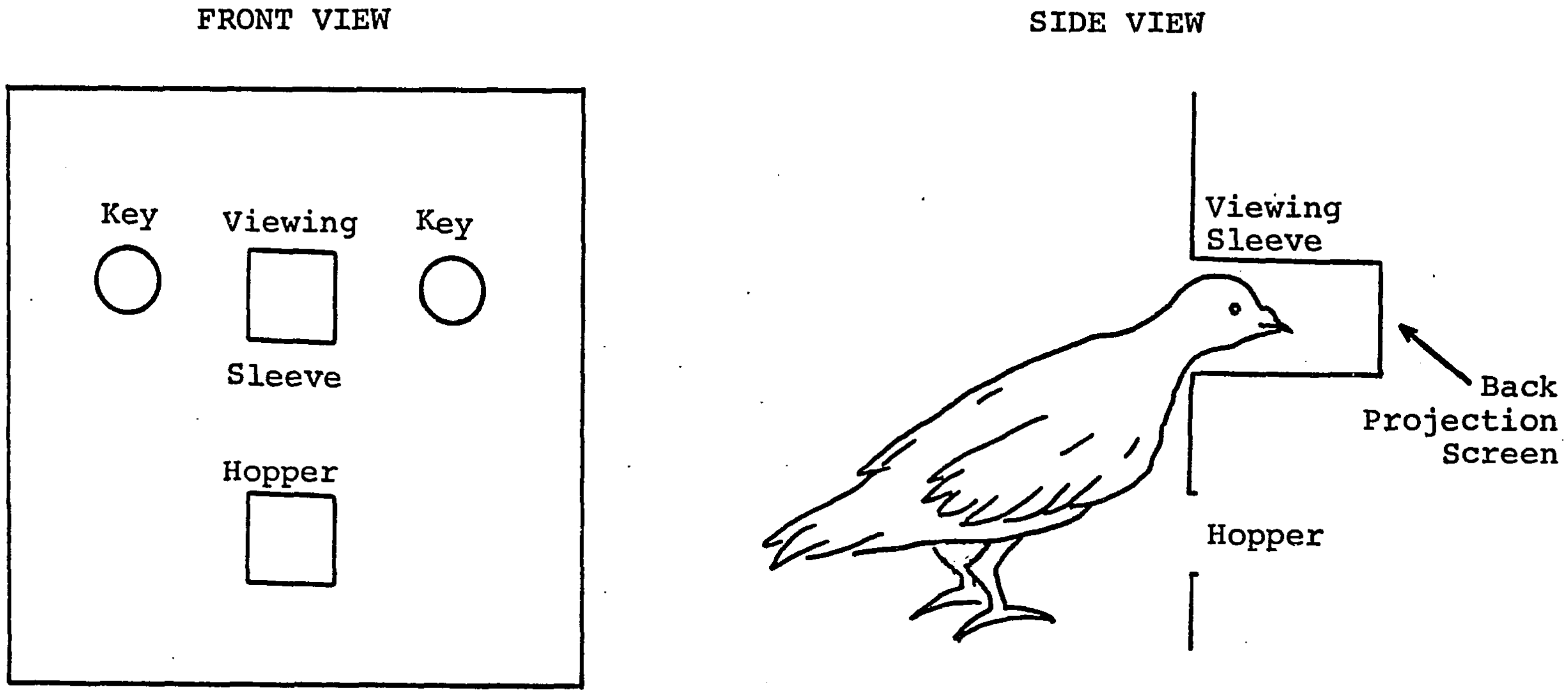


Figure 5.1 Schematic diagram (not to scale) of the apparatus employed in Experiment I. Shown are diagrams of the control panel located inside the chamber. The front view (left) shows the relative location of the response keys, viewing sleeve and hopper. The side view (right) shows the location of the back projection screen at the end of the viewing sleeve, and the position required of the birds during the first link of the chained schedule.

film and the latter from Kodak direct positive Panatomic-X film. All slides used in the training phase included various patterns (grids, circles, triangles, letters, or no pattern), and were photographed over a 3 f-stop range in order to vary the intensity or brightness of the slides. Colored slides were made either by photographing the patterns through one or more colored filters (Kodak Wratten 58, 59, 25, 29, CC50R, CC10M, CC05M; or orange, yellow, aqua, violet plastic) or by photographing colored cut-outs on a white background or black or white cut-outs placed on colored paper. When measured with a Sears and Roebuck model 376.80510 light meter, the intensities of the chromatic set ranged from 6.3 to 11 units, while the intensities of the achromatic set ranged from 5 to 10.5 units.

The chromatic slides in each training set included stimuli which varied in apparent saturation, dominant wavelength, and intensity, but of the same basic (human) hue. Circular slide trays holding 80 or 140 (for Transfer Test 1) slides were used, with equal numbers of colored and achromatic stimuli being used. The order of slides was block randomized, with no more than three in succession of either type. The slide orders were changed when a new color was added and occasionally at other times.

The chromatic stimuli for the first transfer test utilized combinations of 16 new and 6 old colors with 16 new and 9 old patterns. The characteristics of the 140 stimuli used are summarized in Table 6.1. The second transfer test consisted of photographs of magazine pictures, Degas and Van Gogh paintings, book jackets, etc., with each of the 40 stimuli photographed both in color and in black-and-white.

Procedure

Preliminary Training

The birds were maintained at 80% of their free feeding weights. They were first trained to peck a white lit key, being presented with only one of the two keys at a time. Next, the birds were shaped to insert their head into the sleeve, after which the following contingencies were instituted: Inserting the head into the sleeve opened the shutter. If the head were kept in the sleeve for some minimum amount of time the shutter would close and a side key would come on which, when pecked once, extinguished and was followed by 4 sec access to grain. If the head were held in the sleeve for less than the minimum time required, the shutter would close but the keys would remain dark. The head-in time requirement was gradually increased to 4.2 sec, and a 5 sec black-out, in which the house light was turned off and head-ins had no scheduled consequences, was added contingent on shorter head-in times. A 5 sec inter-trial interval with house light off was also added following each key peck to allow time for slides to advance in the next phase.

Table 5.1

Transfer Test 1 Stimuli:

Number of Slides Employed of Various Types

	New Color[a]	Old Color	Achromatic
New Pattern	26	12	38
Old Pattern	17	0	32
Two Colors (no pattern)	8	7	--

[a] Filters (aqua, yellow + aqua, magenta + violet, magenta + yellow, magenta) or construction paper (pink, dark green, yellow-green, orange, brown, gold, dark purple, blue, light blue, light violet, muddy violet).

Discrimination Training

The above procedure was modified such that both keys were lit after the bird had held its head in the sleeve for the required amount of time. Furthermore, a peck on the right key was only reinforced if a colored slide had just been presented, whereas a left key peck was reinforced following presentation of an achromatic stimulus. The slide advanced during the inter-trial interval whether the response had been correct or not. A schematic summary of the procedure is presented in Figure 6.2. A session consisted of 100 trials, so that one-quarter of the 30 slides were presented twice within a session. The first slide presented varied from day to day.

A given set of stimuli was presented until the seven-day median accuracy level of all birds was 70% or better and the next set of stimuli was ready. The accuracy level actually attained was above 85% except for one case (bird 37 with its first color), and above 90% in every case but four (first color for 23, 37, and 40; second color for 230). At that time, the new color was added to the previous chromatic set, so that the second discrimination, for example, was red or green versus achromatic. At the last addition, the chromatic set consisted of 6 or 7 slides of each of six colors. Colors were added to the chromatic set in the following orders: For birds 23, 24, and 230, red (R), green (G), orange (O), yellow (Y), violet (V), blue

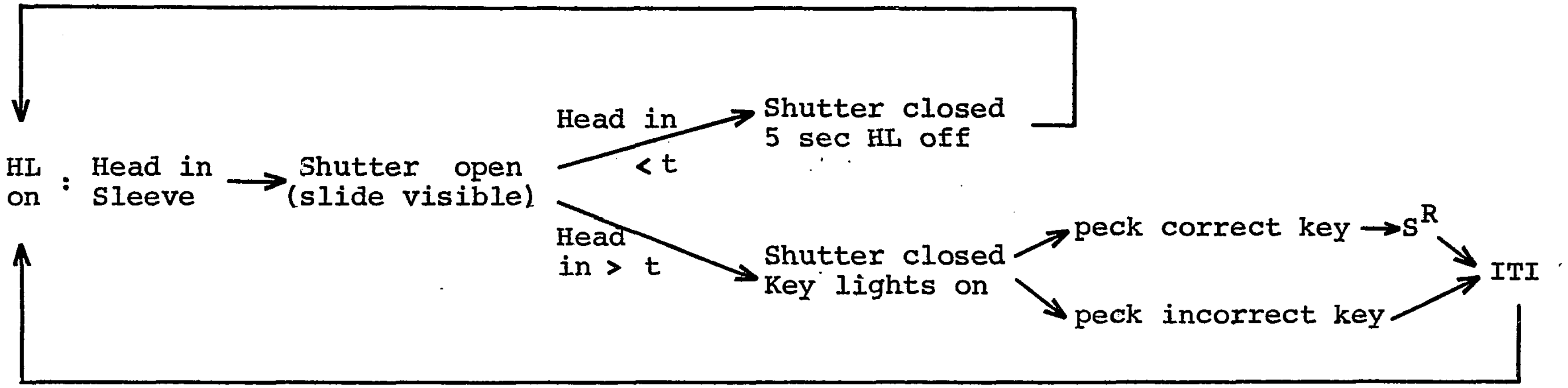


Figure 5.2. Schematic diagram of the procedure employed in Experiment I. The correct key is defined as the right key following a colored slide or the left key following an achromatic slide, while the incorrect key is defined as the left key following a colored slide or the right key following an achromatic slide. During the inter-trial interval (ITI), the house light (HL) and key lights go off the the slide advances. The minimum head-in time required is t; S^R is the reinforcer (access to grain).

(B); for birds 37 and 40, G, R, O, B, V, Y.

Reinforcement for correct responses was shifted to a partial schedule after the addition of the fourth color, with the probability of reinforcement being gradually decreased to .45. This schedule of reinforcement was also in effect during the transfer tests.

Transfer Tests

Following the above training, the four birds were tested with new slides, as described above. Each of the 140 stimuli of the first transfer test was presented but once in a session, while some of the 80 stimuli of the second test were presented twice in a session, as with the training stimuli.

Results

Training

Of primary interest is the birds' behavior during the first session that a new color was added. More specifically the accuracy level of the new color as compared with that of the old color would indicate whether the subject had acquired a more or less general chromaticity concept (if the accuracy on the new color were above chance and more or less similar in level to that on the old color) or whether the bird had merely learned a set of stimulus-response rules,or, alternatively, a relatively narrow concept such as "red" (if the accuracy on the new color were at the chance level).

Figures 5.3 through 5.6 show the percentage of right key responses on the first session when each new color was added for each bird. Complete acquisition data over the first 7 to 12 sessions following each new color addition are presented in Appendix A. Performance levels are indicated separately for the new color, old color(s), and achromatic stimuli, except with the first new color for birds 23 and 230, when only data for achromatic and all colored stimuli combined are available. Note that a right key peck is correct following colored stimuli and incorrect following achromatic stimuli. The first striking feature of these data is that in only three cases was first day responding to new colors at chance or below:[1] namely, for birds 23 and 230 when B was added, and for bird 37 when O was added. Although each individual presentation of the new color would afford an opportunity for learning to take place (at least with the first three additions when a continuous schedule of reinforcement was in effect), there is some suggestion that the chromaticity concept was already present following training with only one exemplar.

A second result indicated in these figures is that, in all but five cases, the accuracy level with the new color is lower than with the old color(s). The exceptions occur

---

[1] Responding may have been at chance for 23 and 230 when G was added. Responses to R and G were not recorded separately at that time.

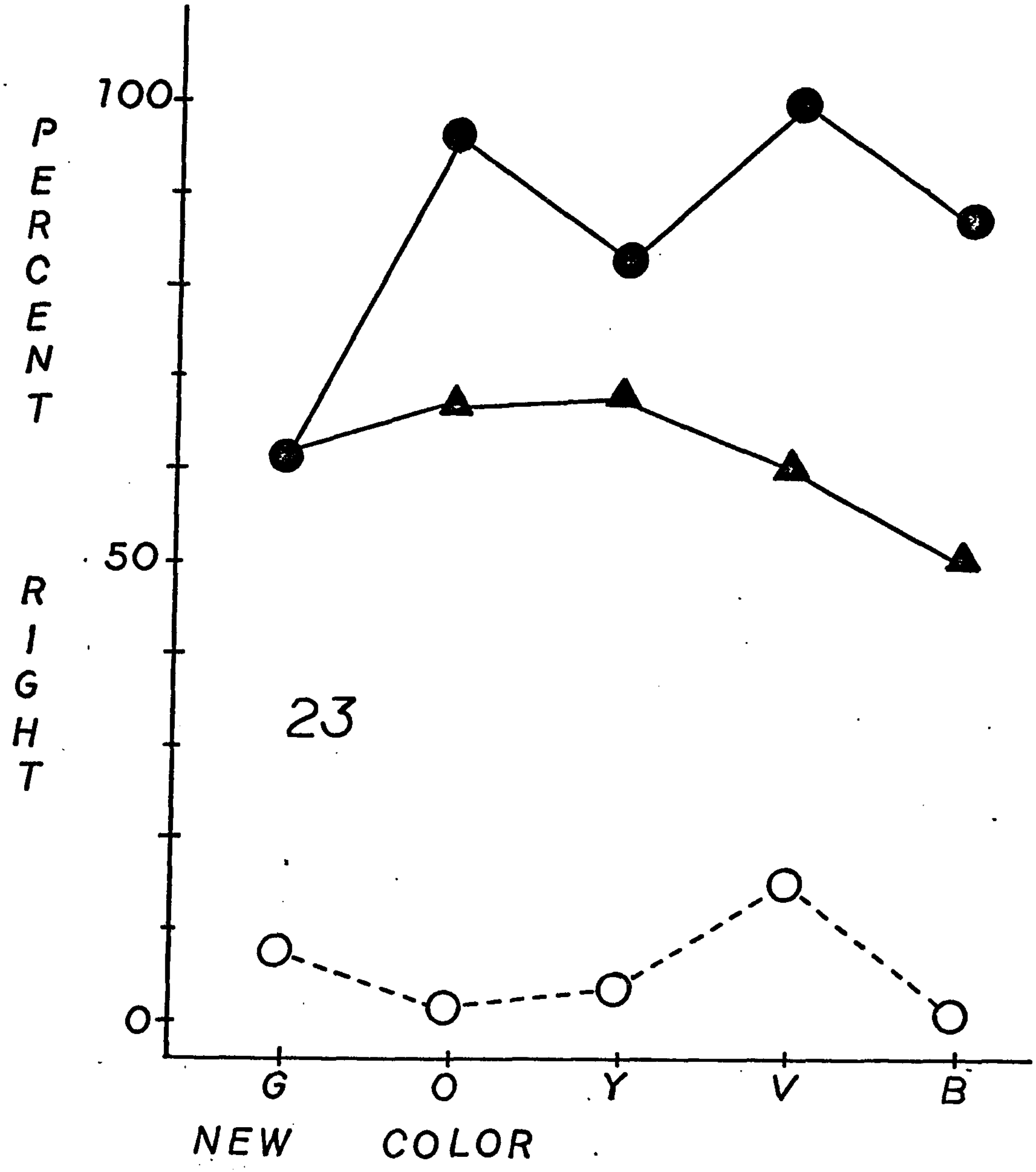


Figure 5.3. Percentage of right key pecks on the first day each new color was added for bird 23. Filled symbols are for colored stimuli: triangles for the new color (green, G; orange, O; yellow, Y; violet, V; blue, B), circles for the old colors (or for both new and old colors combined for G). Open circles are for achromatic stimuli.

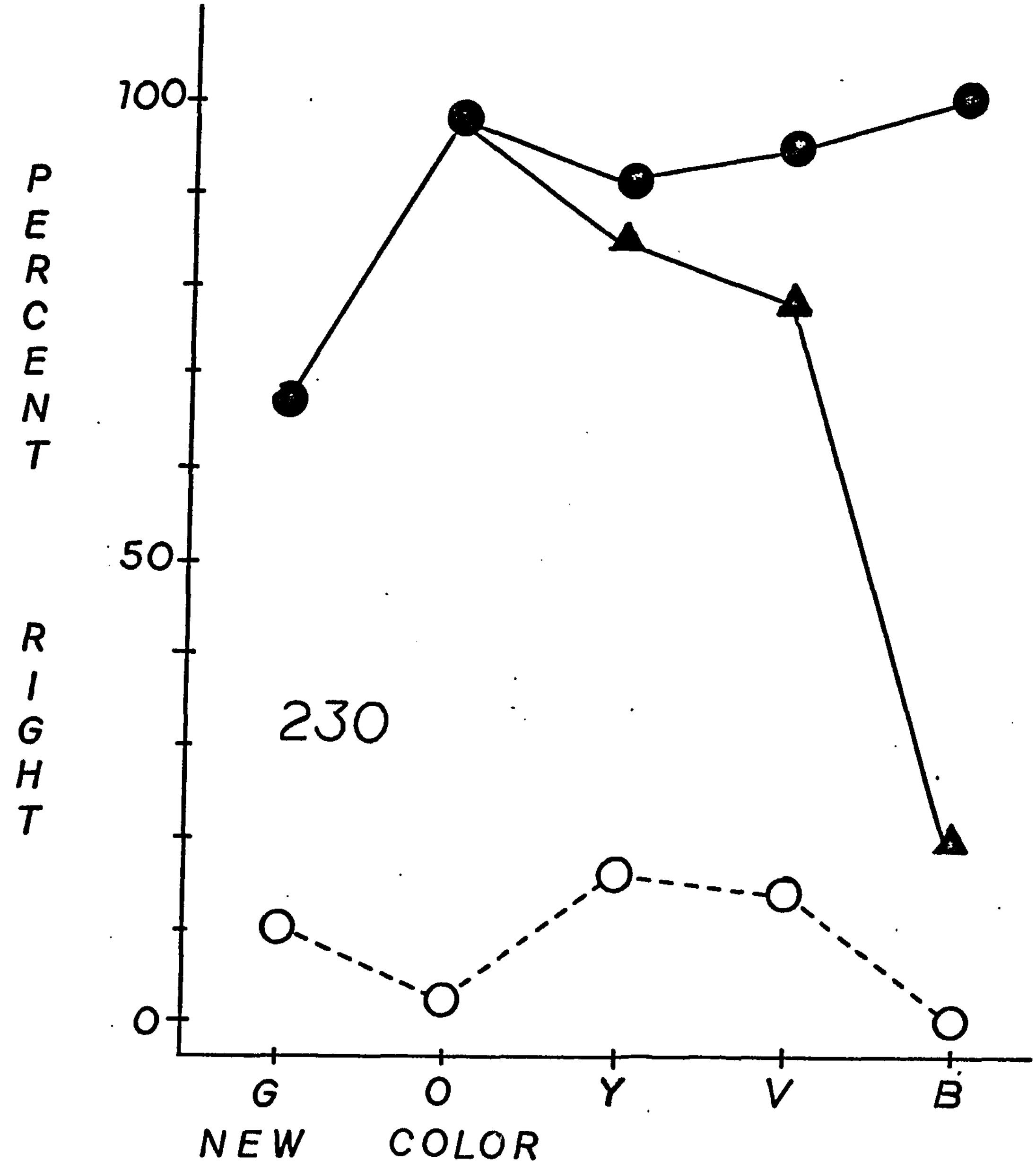


Figure 5.4. Percentage of right key pecks on the first day each new color was added for bird 230. See the legend of Figure 6.3 for details.

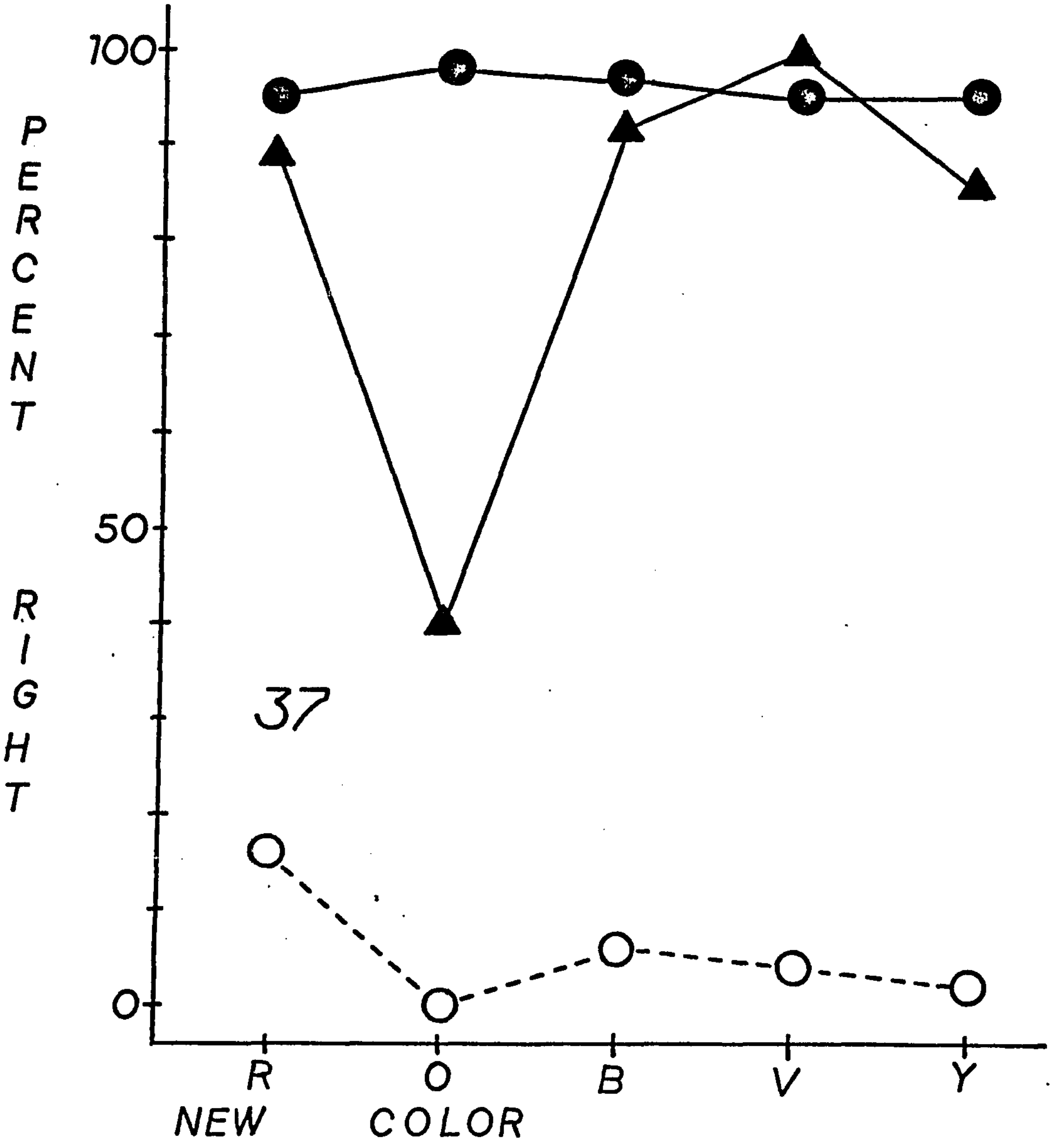


Figure 5.5. Percentage of right key pecks on the first day each new color was added for bird 37. See legend of Figure 6.3 for details.

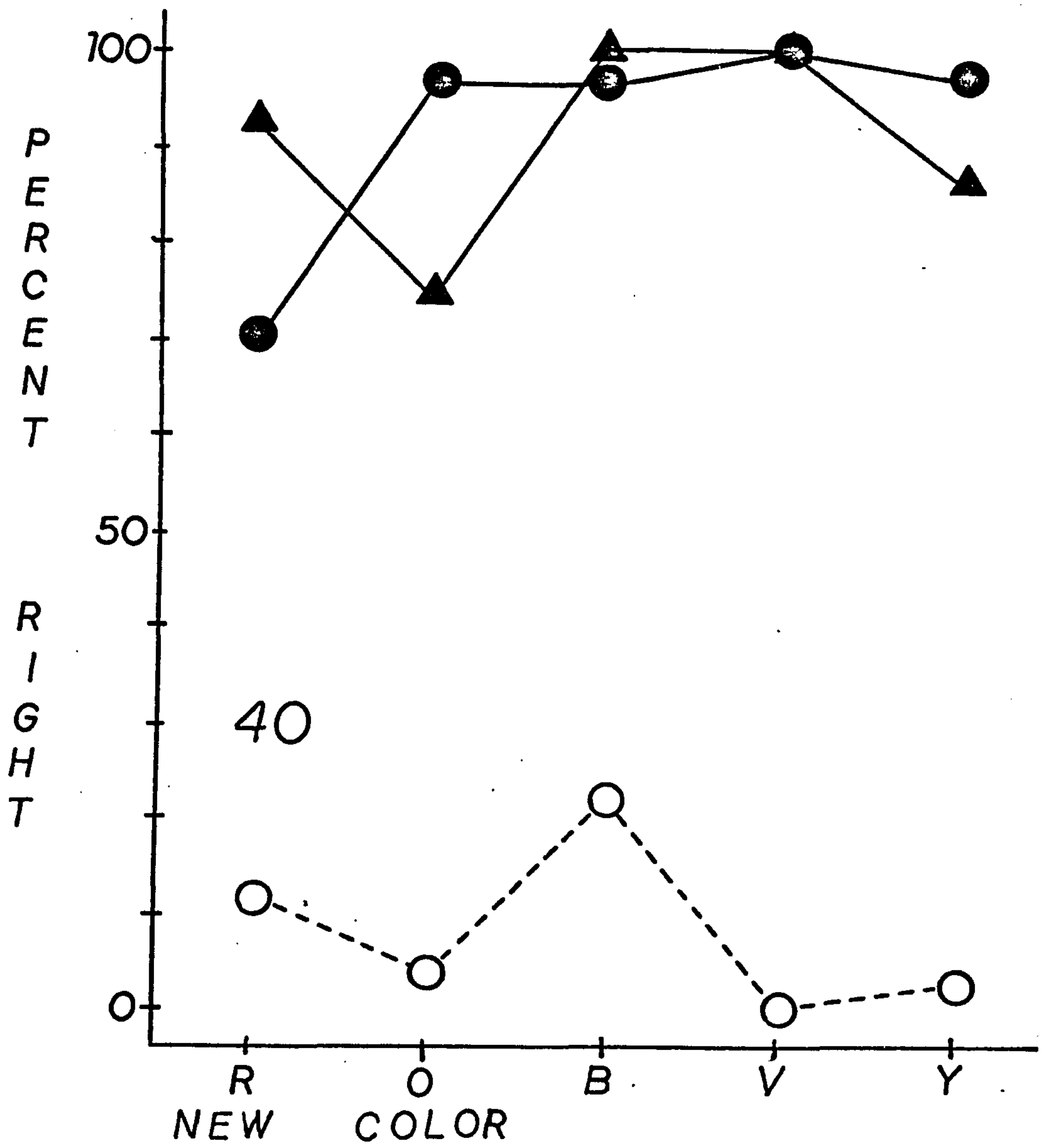


Figure 5.6. Percentage of right key pecks on the first day each new color was added for bird 40. See legend of Figure 6.3 for details.

mostly with bird 40, with additions of R, B, and V; bird 37 also did better on the new color when V was added, while bird 230 did equally well on new and old colors when O was added. This might suggest that the chromaticity concept acquired was not perfectly general (i.e., some generalization decrement occurred), with the possible exception of bird 40.

Table 5.2 summarizes the birds' behavior on the first day a new color was added relative to their previous seven-day range of accuracy. A difference between the behavior of birds 23 and 230 and birds 37 and 40 is apparent, with the former pair showing much more disruption of behavior than the latter, particularly with the new color. It might be argued that birds 23 and 230 exhibited generalization decrements with the novel colors, whereas birds 37 and 40 seem to have already acquired a general chromaticity concept following training with only one exemplar, such that behavior with new and old colors was highly similar. A clear exception for the latter two two birds is with the addition of O, which disrupted both birds' behavior considerably.

Table 5.2 also shows a tendency for birds 23 and 230 to become disrupted on familiar stimuli as well as on the new color: This occurred on 4 to 6 (depending upon whether behavior when G was added is assumed to have affected both new and old colors or new colors only) of the 9 occasions

Table 5.2

Accuracy Relative to Baseline on First Session of Each New Color

		Below Baseline Range			Within Baseline Range		
Bird	NC	NC[a]	OC[a]	A[a]	NC	OC	A
23	G	X[b]					X
	O	X				X	X
	Y	X	X				X
	V	X		X		X	
	B	X				X	X
230	G	X[b]					X
	O				X	X	X
	Y	X	X	X			
	V	X		X		X	
	B	X				X	X
37	R				X	X	X
	O	X				X	X
	B				X	X	X
	V				X	X	X
	Y	X				X	X
40	R				X	X	X
	O	X				X	X
	B			X	X	X	
	V				X	X	X
	Y	X				X	X

[a] NC = New Color, OC = Old Color(s), A = Achromatic.

[b] Accuracy on all colored stimuli combined. Separate data for NC and OC unavailable.

when new stimulus behavior was below baseline. This tendency is absent for the other two birds. It might be argued that a portion of these birds' performance decrement was non-specific, and should perhaps be attributed to exposure to novelty rather than to generalization decrement along the wavelength dimension.

Table 5.3 summarizes the birds' early behavior on the new color stimuli. Once again, birds 37 and 40 exhibit superior performance as compared with birds 23 and 230. Except for the first new addition for bird 37, the former birds responded correctly on every first exposure to a new color; 23 and 230 did so on only half of the occasions when those data were available. On the first five exposures to a new color, birds 37 and 40 averaged 92 and 84 percent correct, respectively, while birds 23 and 230 averaged 60 and 65 percent correct, respectively. All of these mean levels are above chance, and only when B was added for 23 and 230 was any one of these below the chance level.

No consistent learning-to-learn trend is evident for any of the birds as shown in Table 5.3. This is true with respect to percent correct on new stimulus trials 1-5, percent correct on new color for the first session, and with respect to number of sessions to various criteria of

Table 5.3

Accuracy Levels on New Colors

Bird	New Color	Trial 1	% Correct Trials 1-5	% Correct First day	Sessions to Criterion 70%	Sessions to Criterion 80%	Sessions to Criterion 90%
23	G	a	a	a	a	a	a
	O	Correct	80	68	2	2	2
	Y	Correct	60	68	2	6	8
	V	Incorrect	60	60	2	2	2
	B	Incorrect	40	50	2	2	12
230	G	a	a	a	a	a	a
	O	Correct	100	97	1	1	1
	Y	Correct	100	83	1	1	5
	V	Incorrect	60	78	1	2	2
	B	Incorrect	0	20	3	4	5
37	R	Incorrect	80	89	1	1	5
	O	Correct	80	62	12	13	13
	B	Correct	100	92	1	1	1
	V	Correct	100	100	1	1	1
	Y	Correct	100	86	1	1	4
40	R	Correct	80	93	1	1	1
	O	Correct	60	75	1	12	13
	B	Correct	100	100	1	1	1
	V	Correct	100	100	1	1	1
	Y	Correct	80	86	1	1	2

[a] Information not available.

accuracy.[1]

Transfer Tests

Figures 5.7 through 5.10 show the results of the first transfer test, in which new and old colors and patterns were combined (see Table 5.1). Each session represents one exposure to each the 140 stimuli. The figures show the percentage of right key responses for each of the following classes of stimuli: (a) achromatic stimuli with new patterns, (b) achromatic stimuli with old patterns, (c) new colors, and (d) old colors. Pattern had no consistent effect, so all new colors were pooled, as were all old colors. Following the second day of this transfer test with birds 23 and 230, the newly-processed achromatic stimuli were compared with the old ones, since bird 230 behaved increasingly as though they were colored. It was found that, in comparison with the older slides, the new ones had a slight greenish tinge. The slides were therefore reprocessed until they appeared similar to the old slides. Birds 37 and 40 were exposed only to the reprocessed stimuli.

Excluding 230's responses to the new "achromatic"

---

[1] Note that sessions include fewer exposures to the new stimuli as more colors are added. When the data are considered in terms of the number of novel stimulus trials (rather than sessions) to criterion, consistent learning-to-learn trends are still absent. These data are presented in Appendix A.

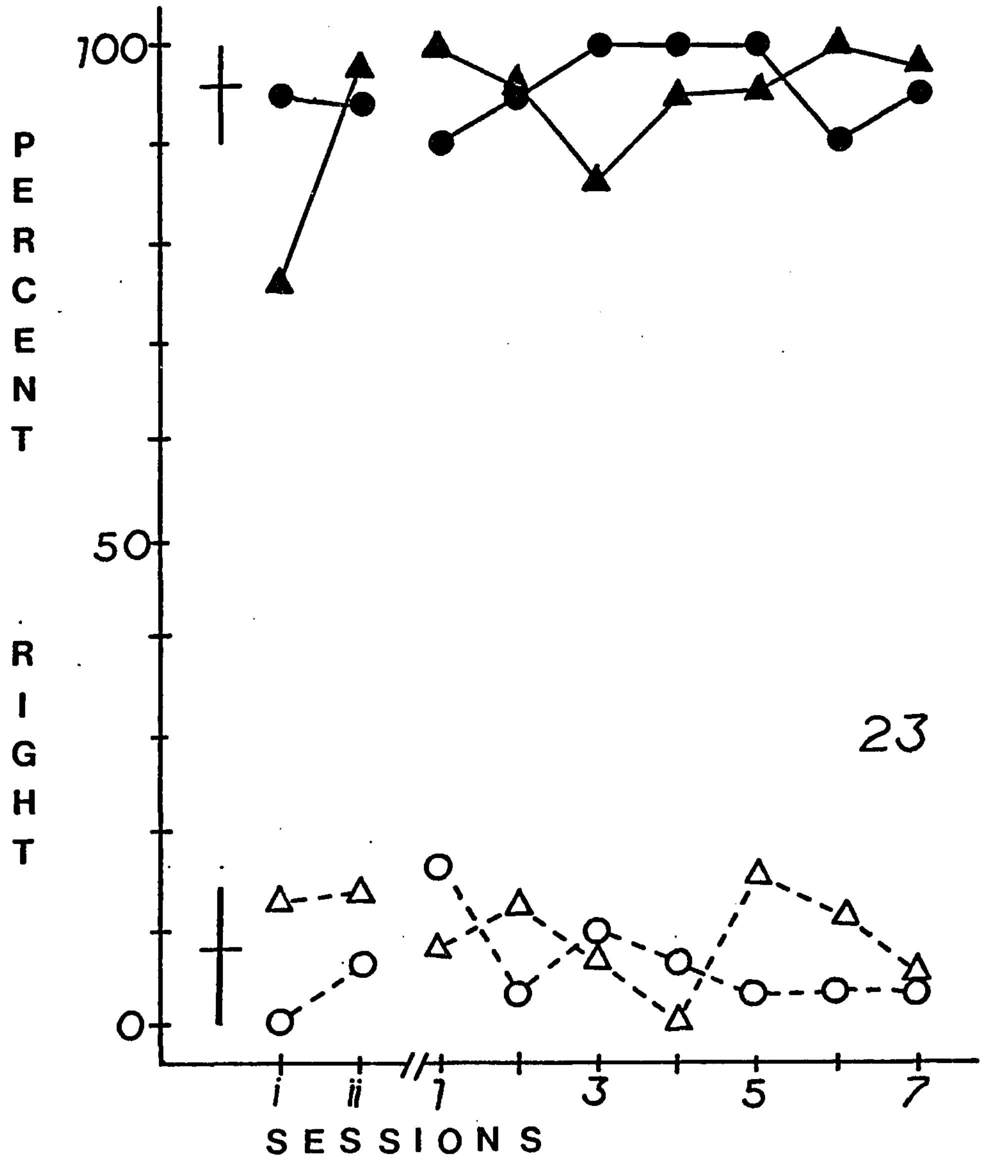


Figure 5.7. Percentage of right key pecks during the first several sessions of Transfer Test 1 for bird 23. Filled symbols are for colored stimuli: circles, old slides; triangles, new slides. Open symbols are for achromatic stimuli: circles, old slides; triangles, new slides. Sessions i and ii occurred before reprocessing of new stimuli. Bars at left show the previous seven-day range for colored (above) and achromatic (below) stimuli; the seven-day median is indicated with a horizontal line.

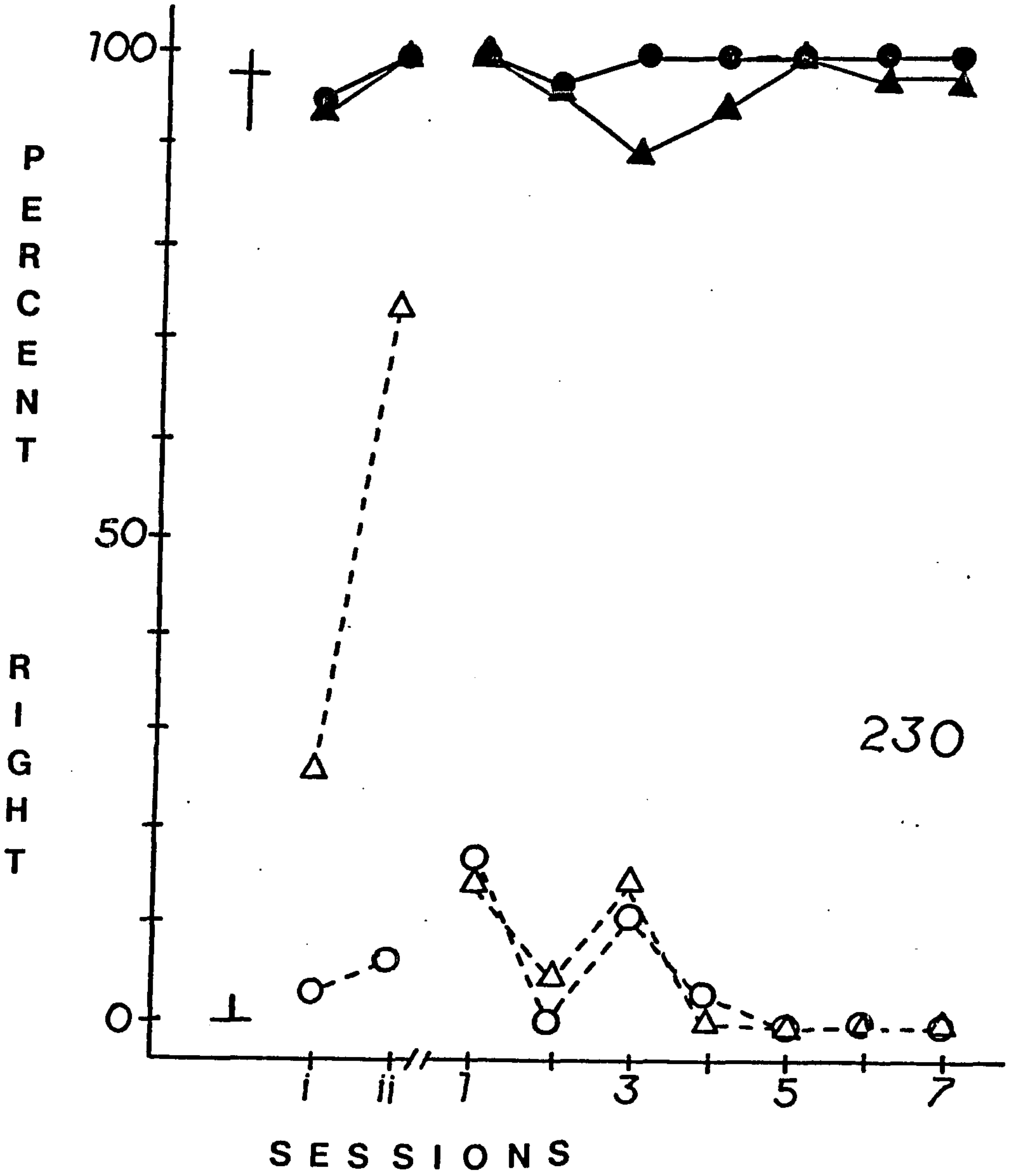


Figure 5.8. Percentage of right key pecks during the first several sessions of Transfer Test 1 for bird 230. See legend of Figure 6.7 for details.

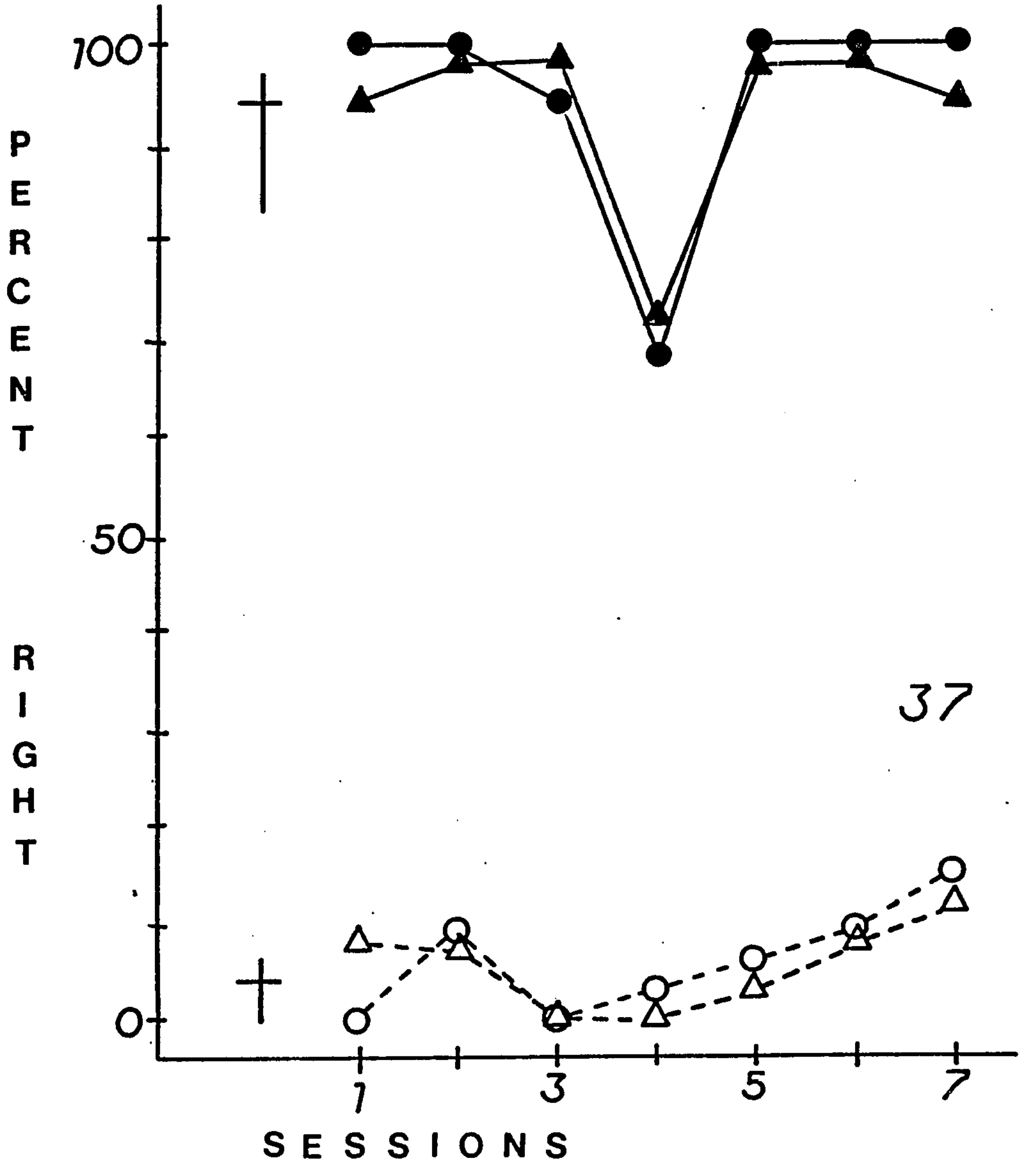


Figure 5.9. Percentage of right key pecks during the first several sessions of Transfer Test 1 for bird 37. See legend of Figure 6.7 for details.

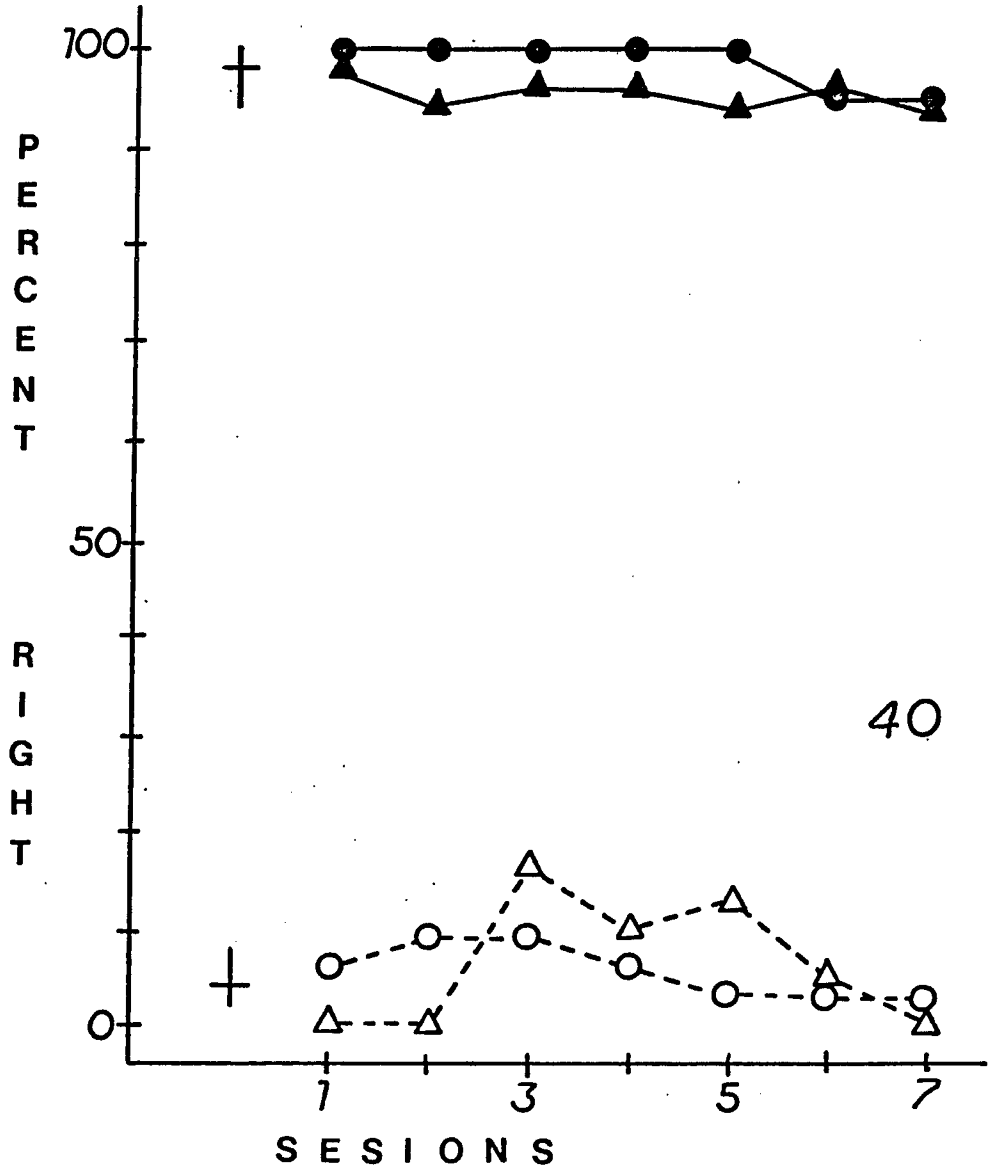


Figure 5.10. Percentage of right key pecks during the first several sessions of Transfer Test 1 for bird 40. See legend of Figure 6.7 for details.

stimuli on the first two test days, responses to all types of stimuli were above 90% correct for three of the four birds; only bird 23 performed below this level with both types of novel stimuli. On subsequent sessions, performance levels fluctuate, but in most cases accuracy levels with new and old stimuli covary. In general, these results provide good evidence for the acquisition of the chromaticity concept. Evidence for a sharp difference between birds 23/230 and birds 37/40, as seen during training, is absent here.

Figures 5.11 through 5.14 present the results of the second transfer test, which consisted of complex stimuli, each represented in both chromatic and achromatic form. The birds' performance here is again somewhat variable from day to day. However, accuracy is consistently well above chance, and performance on the first day is above 90% correct for birds 23 and 37. Birds 230 and 40 exhibit a similar high level of accuracy on the chromatic stimuli, but a lower level on the achromatic stimuli. Again, as with the first transfer test, a chromaticity concept is indicated, with no evidence for the differences in concept generality among birds which was evident during training.

Discussion

The following points summarize the major results of this experiment: (a) Across training, no consistent

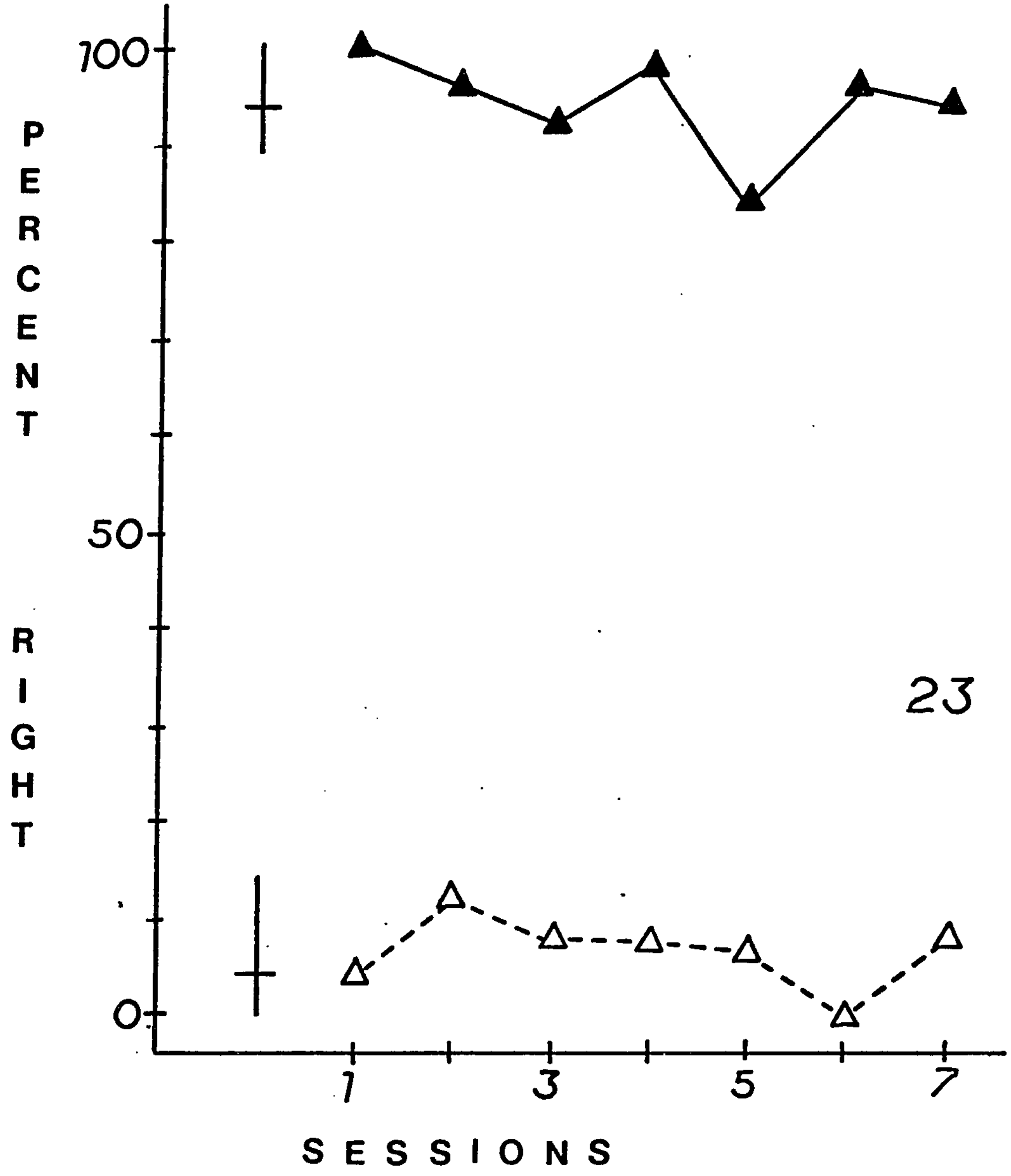


Figure 5.11. Percentage of right key pecks during the first seven sessions of Transfer Test 2 for bird 23. Filled triangles are for colored stimuli; open triangles for achromatic stimuli. The previous seven-day range and median are shown at left for colored (above) and achromatic (below) stimuli.

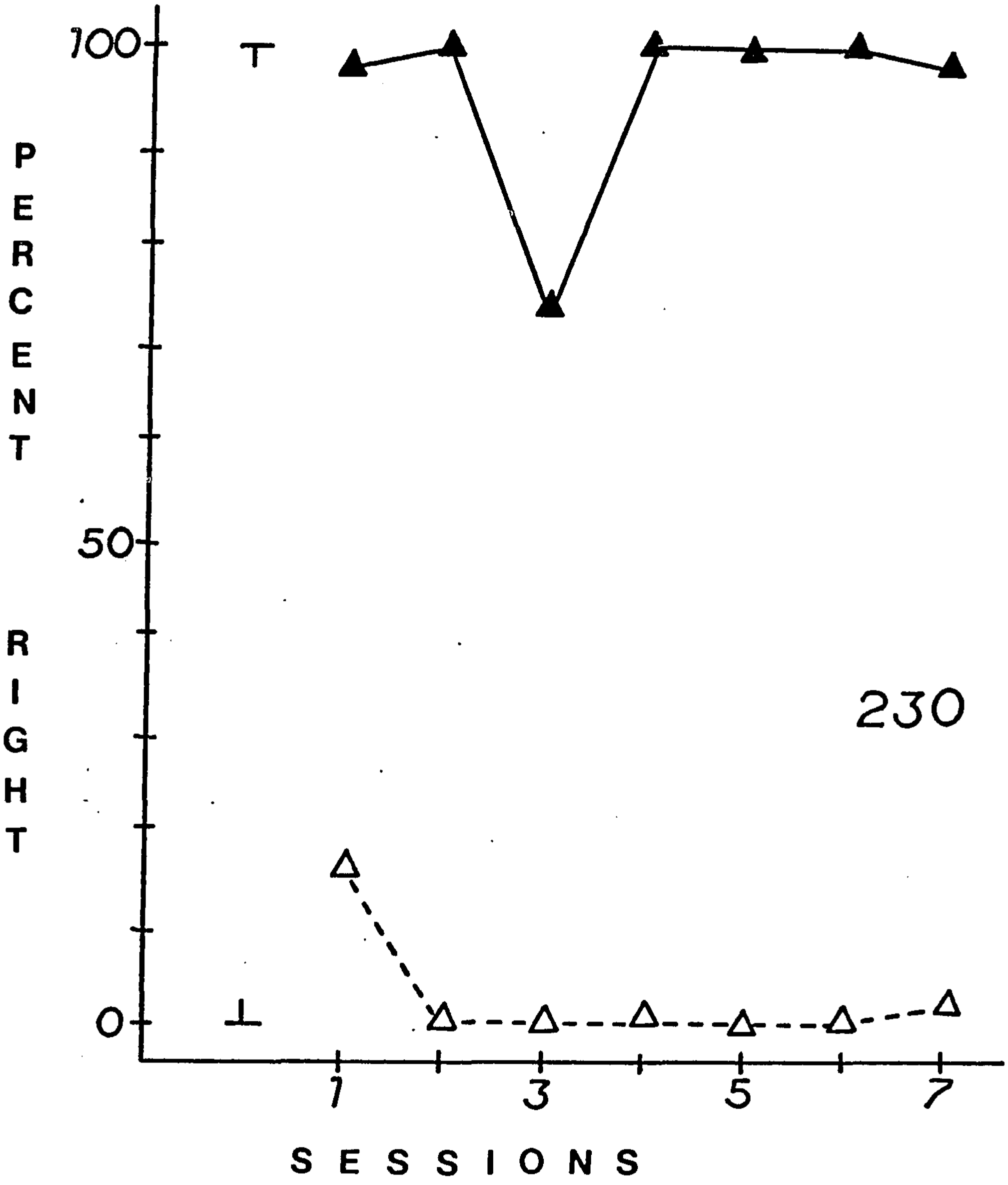


Figure 5.12. Percentage of right key pecks during the first seven sessions of Transfer Test 2 for bird 230. See legend of Figure 6.11 for details.

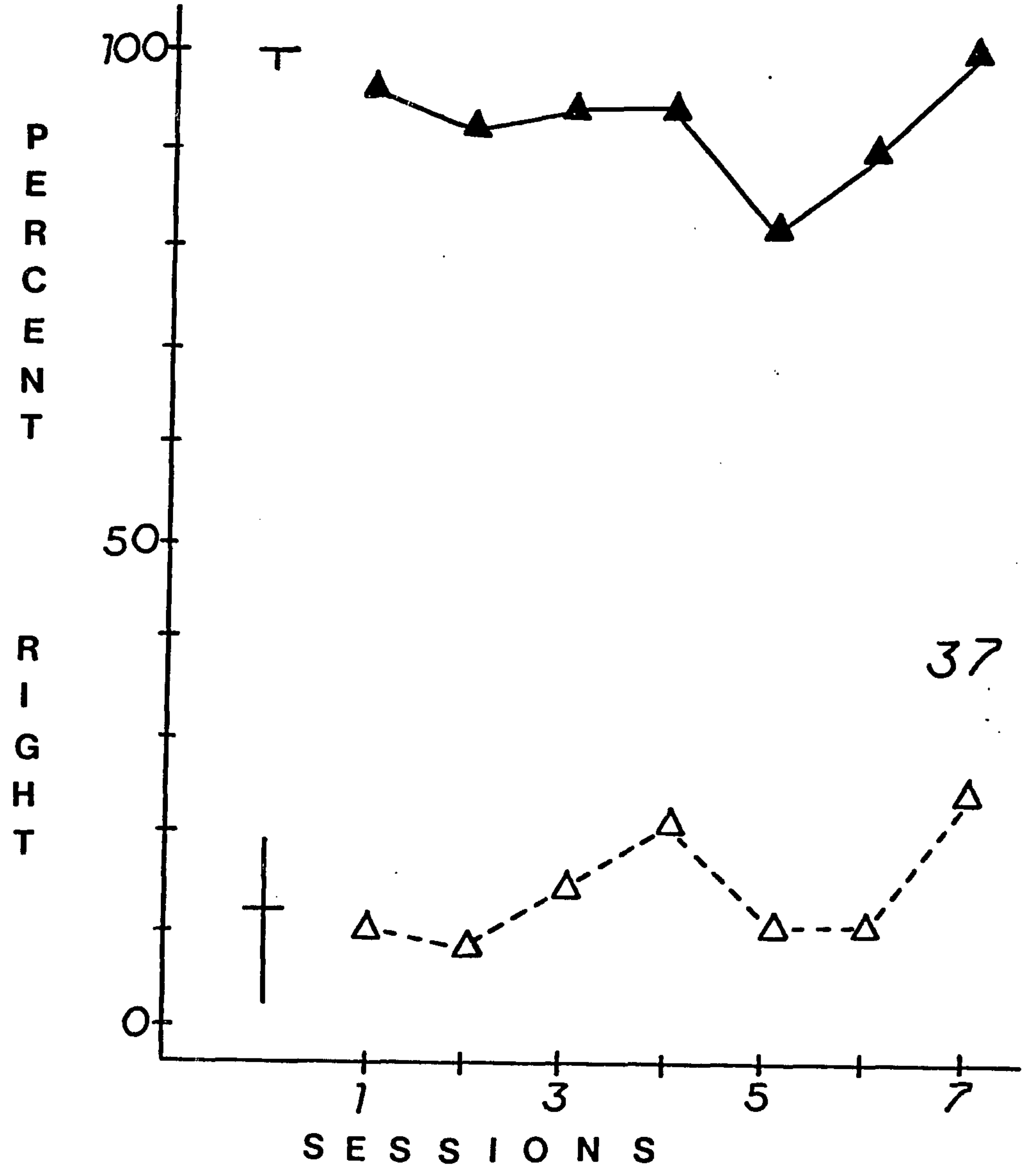


Figure 5.13. Percentage of right key pecks during the first seven sessions of Transfer Test 2 for bird 37. See legend of Figure 6.11 for details.

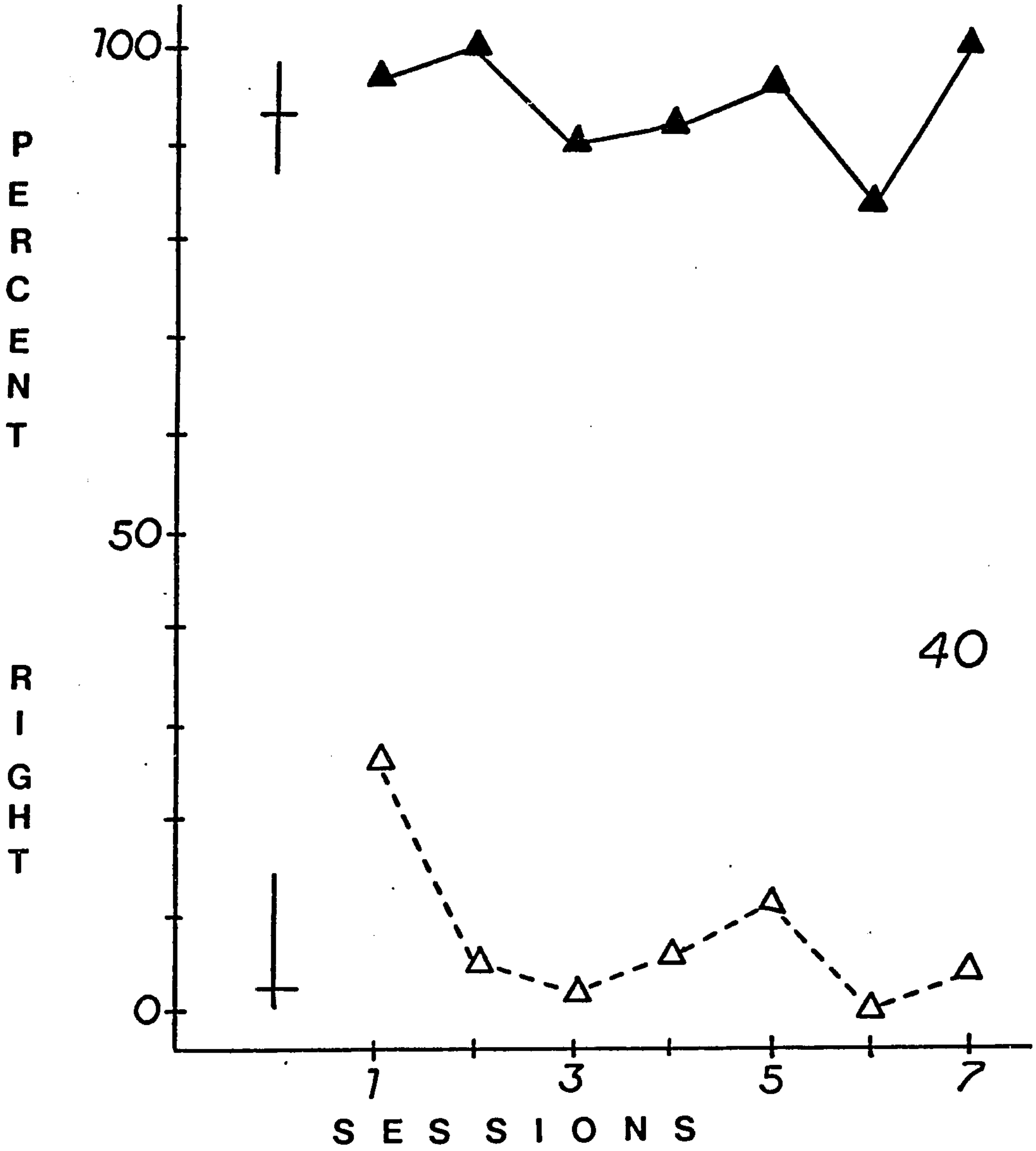


Figure 5.14. Percentage of right key pecks during the first seven sessions of Transfer Test 2 for bird 40. See legend of Figure 6.11 for details.

improvement on first-day new-color performance was evident. That is, no learning set was acquired. (b) First day accuracy on new colors was above chance in 17 out of 20 cases, but below old color accuracy in 16/20 cases. The three new color transfer failures occurred with orange following green and red training for bird 37 and with blue following training on red, green, orange, yellow and violet for birds 23 and 230. (c) With the first new color addition, birds 37 and 40 performed above 80% correct. On 6/10 of all new color additions for these birds , first-day accuracy was above 90%. The other two birds did this well in only 1/10 cases. (d) Accuracy on the first five new color trials following training on three hues was 100% for all birds but 23, with 60% correct. (e) On the first transfer test, first-day performance for birds 37 and 40 was above 90% correct for each type of stimulus. Slight disruption on new colors for bird 23 and on white for 230 was evident, but no accuracy level was below 75%. (f) On the second transfer test, first-day accuracy for birds 23 and 37 was above 90% on each stimulus type. Birds 230 and 40 showed slight disruption on white, with 84% and 74% correct, respectively.

If conceptual behavior is defined in terms of generalization within a stimulus class and discrimination between stimulus classes with novel stimuli (Keller & Schoenfeld, 1950), all four birds in this study clearly exhibited the concept of chromaticity. Premack (1978) would ask, however, whether the birds had acquired a "true" (categorical) concept or had "merely" generalized about the training stimuli. The relatively poorer performance on new colors as compared with old colors does, indeed, suggest some generalization decrement. However, the decrement was typically small. Furthermore, cases of transfer failure would argue against the "mere" generalization hypothesis. For example, the behavior of bird 37 was disrupted the most when orange was added, even though this followed training on red. In contrast, his performance on red following training on green was excellent. Clearly, these levels of accuracy should have been reversed if generalization had been at work.

Premack's analysis of "true" conceptual behavior has been justifiably criticized by Johnson (Note 3). Premack's insistence upon an all-or-none categorization of stimuli, in particular, is not consistent with the nature of most concepts. Both Rosch (1973) and Posner and Keele (1968) have pointed out that most if not all concepts have "fuzzy" boundaries, and that while a "prototypical" example of a class may exist (e.g. the sparrow for the class of birds), borderline cases (e.g. penguins) and various gradations in between exist as well. Even for the concept focussed upon by Premack, "same," one might expect graded behavior in cases where two stimuli are similar, though not identical.

This characterization of concepts becomes indistinguishable from the generalization/discrimination model. In both cases some stimuli are more likely to be included within a class than are others, and whether this is called a generalization gradient or fuzzy boundaries seems unimportant.

Perhaps one could distinguish between conceptual behavior and generalization in a way suggested by the work of Posner and Keele (1968). In their research, human subjects were more likely to include within a class a "prototypical," but novel, stimulus than "boundary," but familiar, stimuli, where the "boundary" stimuli were constructed by making geometric transformations of the "prototype." One might distinguish, then, between generalizing around a prototype and generalizing around training stimuli, and only count the former as an instance of "true" conceptual behavior. To distinguish between these models in the present instance one would need to identify some stimulus (a "prototype") which was more likely to be included within the set than any training stimulus. Furthermore, one would need to identify some dimension (saturation?) along which stimuli could be ordered, with decreasing likelihood of class inclusion as one deviated from the prototype as distinct from a training stimulus. The data from the present research cannot easily address this issue. However, the cases of transfer failure discussed above clearly do not show generalization about training stimuli along the wavelength dimension.

In a matching-to-sample procedure, Premack (1978) found that his chimps were able to exhibit conceptual behavior ("same/different") after training on only three exemplars. Specifically, all four subjects responded correctly on the first trial of a transfer test employing novel stimuli and at the 90% level on the first five trials.[1] Accuracy levels of the pigeons in this study compare favorably with Premack's chimps: Following training on three colors, all four birds responded correctly to the first instance of the new color, and 3/4 were 100% correct on the first five trials. (But see discussion of the prior histories of birds 37 and 40 below.) Certainly this does not mesh with Premack's cut-off between primates and non-primates in their ability to abstract a concept following exposure to a small number of exemplars. An even more impressive case of rapid concept formation in birds was reported by Cerella (1979). In one study, pigeons were reinforced for pecking a single silhouette of a white oak leaf, with no explicit S- provided

---

[1] This must be an average across subjects, since 90% correct is not possible out of five trials. Note that 90% is not 100%, so even these primates do not meet Premack's own rigid all-or-none criterion of "true" conceptual behavior!

other than a dark screen.[1] Yet the birds generalized to new cases of oak leaves (varying considerably in number of lobes, etc.) but not to non-oak leaves: Mean response rates to the training stimulus, new oak leaves and non-oaks were 51, 48 and 8 responses per min, respectively. Although Premack might argue that oak leaves are an innate category for pigeons, he would certainly not do so in the case of the present chromaticity category.

As Johnson (Note 3) has pointed out, it may not be fruitful to characterize conceptual behavior as species-specific (as Premack, 1978, has done) or innate (as Herrnstein, 1976, 1979, has done),[2] as such notions can only gain support through negative findings, and may discourage further analysis. Certainly merely to demonstrate or fail to demonstrate that a particular concept can be acquired by members of a particular species obscures

---

[1] An S- is a stimulus correlated with non-reinforcement of a response. For example in another experiment described in the same paper, Cerella (1979) presented non-oak leaves as S-'s during training: in their presence, pecks were not followed by food.

[2] Herrnstein (1980) has recently modified his view to suggest that the concepts which his pigeons have acquired are probably not innate. Rather, he suggests that a creature's perceptual system has evolved to generalize along the same (not easily specified, multi-faceted) dimensions along which naturally-occurring categories of objects (i.e., species of plants and animals) vary. This view puts conceptual behavior in the same class as generalization, which, as Herrnstein admits, is itself not well understood.

the importance of analyzing the controlling stimulus dimension and of the particulars of the training procedure. For example, Lea and Ryan (Note 4) were able to specify certain stimulus dimensions which were important in pigeons' concept of "A." Similarly, Johnson (Note 3) proposed that the manner in which training stimuli are introduced might affect concept acquisition. Specifically, she suggested that constant variation of the stimuli presented during training ("bombardment" procedure) would result in faster concept acquisition than successive presentation of fixed sets of training stimuli ("learning set" procedure). Although Johnson was unable to demonstrate such an effect in acquisition of the chromaticity concept, Herrnstein and de Villiers (1980) have recently shown that less generalization occurs for the concept "fish" following training with a fixed set of training stimuli than following a procedure in which training stimuli were changed daily.[1]

Another approach to the question of the innateness of categories might, perhaps, be more meaningful than that of merely demonstrating/failing to demonstrate that a concept can be acquired. If one can show that categorization is

---

[1] Clearly, this experiment is not the ideal test of Johnson's "learning set" versus "bombardment" hypothesis since Herrnstein and de Villiers' analogue of the "bombardment" birds had three times as many total training stimuli as their "learning set" birds. However, the results are not inconsistent with Johnson's hypothesis, and suggest that further work along these lines would be fruitful.

invariant across a variety of training procedures, then one is perhaps justified in pointing to evolutionary (as opposed to learning) principles as being responsible for the way in which the world is partitioned. Two examples of this approach come to mind. Wright and Cumming (1971) trained pigeons in a three-key matching-to-sample paradigm with two of three training colors always appearing as the comparison stimuli. When the wavelength of the sample was varied during unreinforced probe trials, the wavelength at which 50% of the responses were made to each comparison stimulus remained invariant across three experiments in which the particular trio of comparison colors was varied. That is, the boundary between color categories remained the same regardless of which particular example of two neighboring categories was chosen; two such pigeon hue boundaries (at 540 nm and 595 nm) were identified and interpreted as typical of the species. A second example of this approach is Rosch's (1973) research on human hue categorization. Rosch's subjects spoke a language (Dani) which possesses only two color words (one meaning "dark," the other "light"), so that hue categorization could not be attributed to learning in the form of language training. The subjects were required to associate one of eight clan names with each of three colors (24 color stimuli altogether). It was found that acquisition was faster when the colors to be associated with each term fell within the center of a hue category (as determined by other cross-cultural human color-naming data) than when they fell near the edge of a category or, worst of all, straddled two categories. Rosch suggested, then, that color categories, like other "perceptual" categories[1] such as form, are innately determined by the human visual system, and thus invariant across humans speaking varying languages.

Birds 37 and 40 showed better transfer behavior than birds 23 and 230, at least during training. Indeed, they appeared to have acquired the chromaticity concept after only one exemplar. It seems likely, however, that this superiority should be attributed to their prior reinforcement history. Specifically, 37 and 40 both served in a series of studies (Jenkins, 1979) which included a "resistance to reinforcement" procedure in which seven chromatic stimuli (with dominant wavelengths ranging from 538 to 597 nm) were paired with food. (Each stimulus was presented six times per session for four sessions.) One can perhaps think of this procedure as training the birds to treat all hues as equivalent. (It should be noted, however, that bird 37 failed to peck the key at all during Jenkin's entire experiment, so that any "learning" in this bird would have to have been "latent.") If this training transferred to

---

[1] Rosch claims that "nonperceptual" categories, such as "bird" or "crime" are learned rather than innate, and that the "prototypes" of such categories are abstracted through some sort of averaging process, as in Posner and Keele's (1968) model.

the situation in the present study, it could account for their apparent extremely rapid acquisition of the chromaticity concept. It should be noted that neither red nor blue were included among the stimuli in the Jenkins study, but that a reddish yellow (dominant wavelength of 597 nm) was included. This cannot account for the pattern of transfer success/failure for these birds.

One fact casts doubt upon whether these birds had, in fact, acquired the concept of chromaticity: The two categories of stimuli were prepared with different types of film, black-and-white and color. It is thus possible that the birds' behavior was under the control of some stimulus dimension other than chromaticity which was also correlated with the two stimulus types. This possibility is further explored in Chapters 8 and 9. At this point, however, it was deemed most likely that the behavior of all four birds was under the control of chromaticity. Thus, the stage was set for an attempt to demonstrate the ME in these subjects.

CHAPTER 6

EXPERIMENT II. THE McCOLLOUGH EFFECT IN PIGEONS

In human subjects, exposure to vertical grids with a red background in alternation with horizontal grids with a green background for 5 or 10 min typically produces the report of the fairly desaturated colors contingent upon grid orientation known as the ME. In this attempt to demonstrate the ME in the pigeon, the same basic procedure was employed as in Experiment I, such that right key pecks were interpreted as reports of color and left key pecks as reports of no color. An attempt was made to maximize the chances of demonstrating the ME if it in fact occurs for the pigeon (see Chapter 4).

Methods

Subjects

The same pigeons were employed as served in Experiment I. In addition, three humans served as control subjects. Subjects KH and DY were naive with respect to the ME, while BA had heard of the effect, but not experienced it.

Apparatus and Basic Procedure

The same apparatus and general procedure as was employed in Experiment I were used in this study.

Stimuli

The following were added to the pool of stimuli employed in Experiment I: (a) additional desaturated chromatic stimuli; (b) additional chromatic stimuli with only relatively small patches of color; (c) ME induction stimuli, consisting of vertically oriented square-wave grids (spatial frequency is .6 cycles per degree of visual angle, assuming the birds viewed the stimuli from a distance of 8 cm) on a red background (Wratten filter 25, dominant wavelength 617.2 nm) and horizontally oriented grids on a green background (Wratten filter 58, dominant wavelength 538.2 nm); (d) ME test stimuli, consisting of achromatic stimuli with juxtaposed areas of horizontal and vertical lines of the same spatial frequency as those of the induction stimuli; (e) ME-test control slides, consisting of the same patterns as the test stimuli but oriented at 45°; (f) "psuedo-ME" control slides, identical to the above control slides, but colored faintly to resemble the appearance of a human ME.

Procedure

Following additional training with the stimuli described in categories (a) and (b) above, six procedures were employed in an attempt to demonstrate the ME. In all cases, the birds were first dark adapted for 30 min. During testing, reinforcement was never available for responses following test stimuli.

<u>Procedure 1</u>: In this procedure, both adaptation and test stimuli were presented in the usual way in the experimental chamber. First, slides including the adaptation stimuli were presented daily for ten days. Specifically, 300 trials of a set of 60 slides (36 ME adaptation slides, 4 desaturated color slides, and 20 achromatic slides) were presented. This yields a minumum of 180 presentations or 13.5 min total exposure time to the ME adaptation stimuli per day. Schmidt et al. (1979) demonstrated that over the course of several series of adaptation stimulus presentations, progressively fewer trials were necessary to reach a criterion of ME acquisition in humans. It was reasoned, therefore, that the effect might be more likely to occur after several acquisition sessions. On the test day, the above procedure was repeated until the adaptation stimuli had been presented for a total of approximately 10 min, at which time three ME test stimuli were added to the slide tray. Two test sessions were carried out with this procedure.

<u>Procedure 2</u>: It was felt that in procedure 1 there may not have been enough presentations of the ME adaptation stimuli and that these may have been too widely separated temporally, since the subjects proceeded at their own rate. Therefore, in procedure 2, ME adaptation took place outside of the experimental chamber and was controlled by the

experimenter. The birds were restrained from the neck down by being placed in a plastic pitcher with a hole for the head. Rear vision was blocked, and flat black barriers (25 cm high) were placed on either side of the pigeon's head (10 cm apart). These barriers extended for 25 cm beyond the bird's eye-level, ending at the wall, on which a white piece of paper was affixed. The latter served as the screen on which the ME adaptation slides were projected. Care was taken to ensure that the projected image was of the same spatial frequency as when viewed by the pigeon within the experimental chamber. During adaptation, the two stimuli were alternated at 3- to 5-sec intervals for 30 min. Testing was carried out in the experimental chamber with the usual procedure and a set of 72 slides. Specifically, these consisted of 36 ME adaptation stimuli, 9 desaturated colored stimuli (to ensure continued "reports" of desaturated colors), 9 test stimuli, 9 ME-test control stimuli and 9 other achromatic stimuli. Thus, a total of 45 colored and 27 achromatic stimuli was used; these 72 slides were presented for 200 trials (about 25 test trials per session). The procedure was repeated three times, with a minimum of five baseline sessions intervening.

ME control: In this session, procedure 2 was duplicated, except that the test stimuli were replaced with the pseudo-ME control slides.

Procedure 3: It was felt that the failure to demonstrate the ME in procedure 2 may have been because the birds did not look at the stimuli during adaptation, although on the occasions when the experimenter observed the birds, their heads usually were oriented toward the stimuli. In this procedure, therefore, following adaptation as in procedure 2, additional adaptation took place in the experimental chamber, where reinforcement was contingent upon stimulus observation (the first link in a chain ending with a key peck). To increase the number and density of trials possible, the head-in time requirement was reduced to 1.5 sec and the inter-trial interval was decreased to 1 sec. During the second, within-chamber, adaptation phase of a session, ME adaptation slides only were presented until approximately 10 min total exposure time had occurred. Testing was then carried out as in procedure 2. This procedure was carried out once.

Procedure 4: Another possible reason why the birds may not have acquired the ME in procedure 2 is that they may have been viewing the stimuli with their lateral visual fields during adaptation: This was occasionally observed to occur. (A greater viewing distance from the adaptation screen than from the testing screen was necessary so that the birds would not block the projector light path). Thus, in this procedure the birds were placed, restrained as in procedure 2, inside the experimental chamber and directly in front of the viewing sleeve. The back projection screen was moved closer to the bird (8 cm away, or approximately the viewing distance during testing) with the spatial frequency of the image held constant. Adaption stimuli were then presented as in procedure 2. For testing, the stimulus set was altered slightly, such that the first 8 slides in the carousel were ME adaptation slides. Thereafter, 12 sets of 5 slides were presented, with each set composed of one desaturated colored slide, one pseudo-ME slide, one test slide, one ME-test control slide and one other achromatic slide. Within a five-slide set, the order was randomized. These 68 slides were each presented three times.

Procedure 5: Shute (1979) has reported that the drug scopolamine enhances the ME, and that even subjects who normally acquired very little if any ME exhibited a strong ME following the ingestion of 0.6 mg ("twice the clinically effective dose") of the drug. Thus, in this procedure, .1 mg/kg of scopolamine dissolved in physiological saline was injected i.m. into the birds 30 min before ME adaptation, the wait coinciding with the dark adaptation period. All other aspects of this procedure were the same as in procedure 4. The procedure was carried out at least twice, since organisms often behave ideosyncratically with their first exposure to a drug.

This dosage level was chosen because, first, it is roughly in the middle of the range which has been used with pigeons in the literature: Ksir and McKearney (1978) used doses ranging from .006 to .05 mg/kg, while Osborne, Rysberg and Killeen (1977) used a range of .2 to 1.6 mg/kg. Second, .1 mg/kg is somewhat more than twice the effective dose, at least in the Ksir and McKearney (1978) situation. Third, a larger dose might degrade discrimination performance (Milar, Halgren, & Heise, 1978).

Human controls: Three humans were subjected to a situation roughly equivalent to procedure 4 above. Only 20 min of dark adaptation were required. Subject BA viewed the adaptation and test stimuli lying down with his head in the experimental pigeon chamber. The ME adaptation phase lasted for 25 min for this subject. Subjects KH and DY viewed the stimuli projected on the wall while sitting at a distance such that the grids were approximately the same spatial frequency as for the birds. Adaptation times for these subjects were 10 min and 5 min, respectively.

The instructions prior to adaption were as follows: "I'll be showing you some slides. You may move your head and eyes as you wish, but don't move from your chair." The instructions prior to testing were as follows: "Now I'll show you some more slides. Please tell me after each presentation whether the slide was colored or black-and-white." No feedback was given during testing.

Results

Figures 6.1 through 6.4 indicate the percentage of right key pecks for various types of slides during ME test

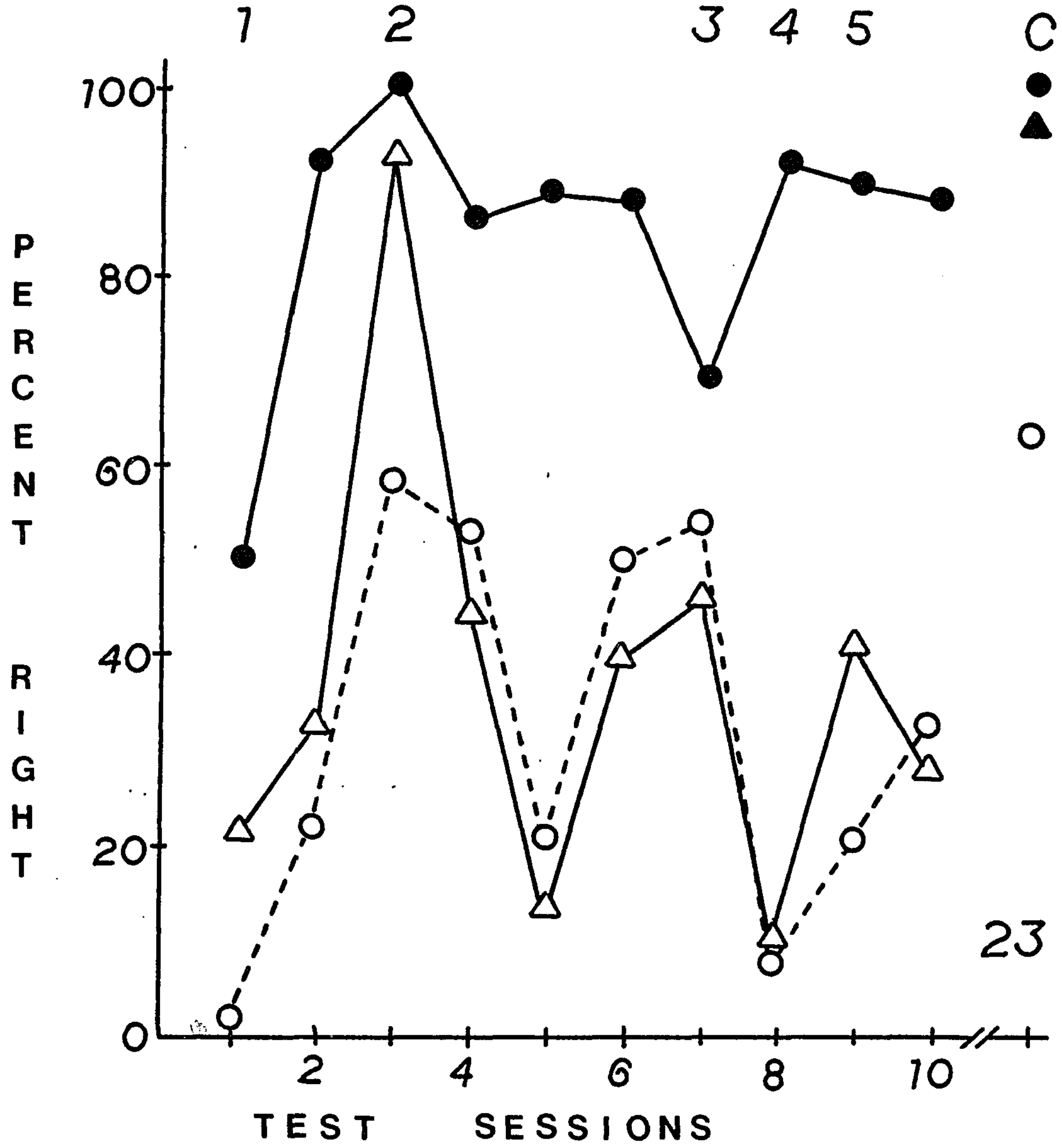


Figure 6.1. Percentage of right key pecks during ME test sessions for bird 23. Filled circles are for colored slides, open circles for achromatic slides, and open triangles for ME test slides. Filled triangles are for pseudo-ME test slides during the control (C) session. Numbers along the top indicate the induction and test procedure used.

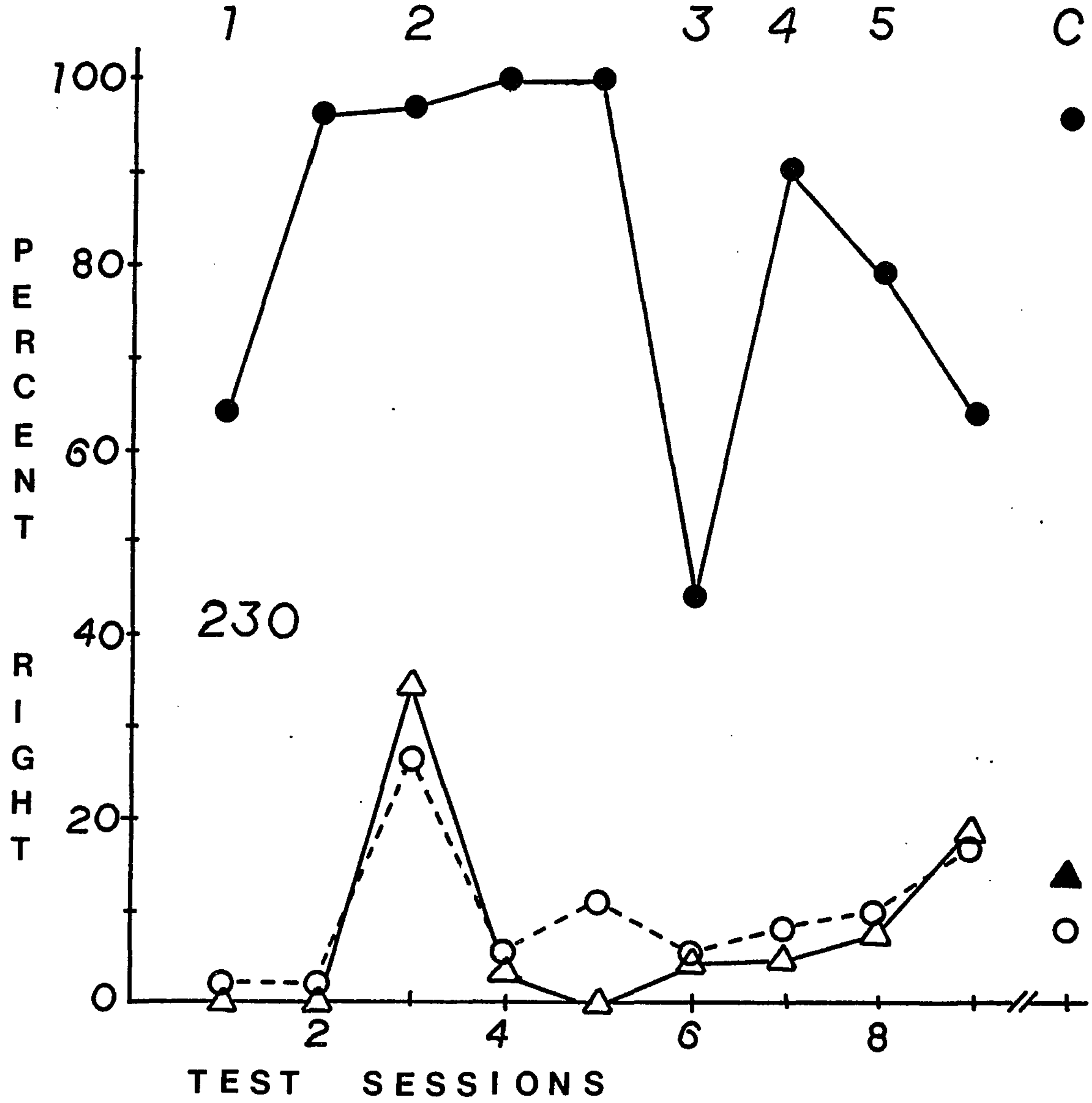


Figure 6.2. Percentage of right key pecks during ME test sessions for bird 230. See legend of Figure 7.1 for details.

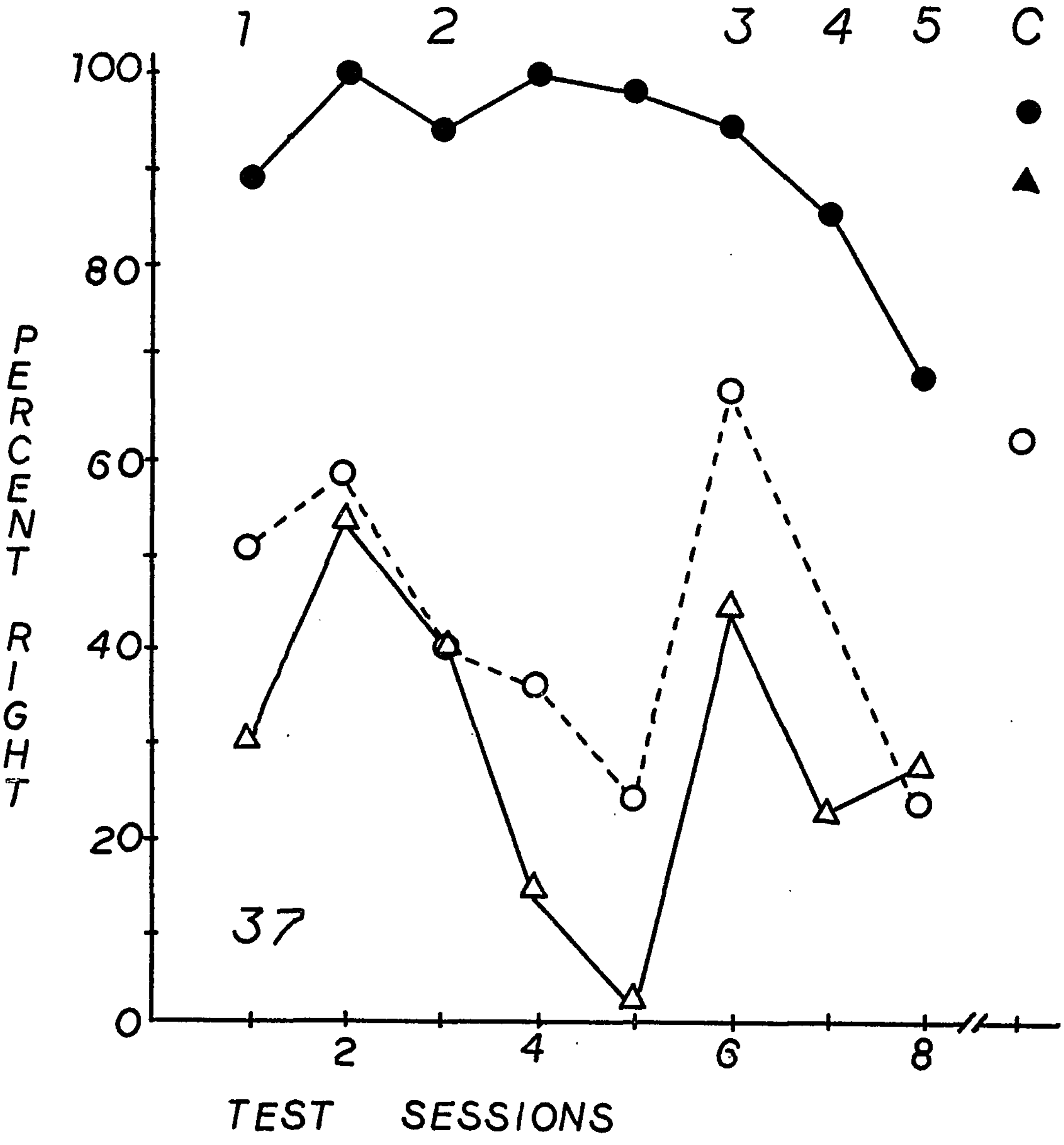


Figure 6.3. Percentage of right key pecks during ME test sessions for bird 37. See legend of Figure 7.1 for details.

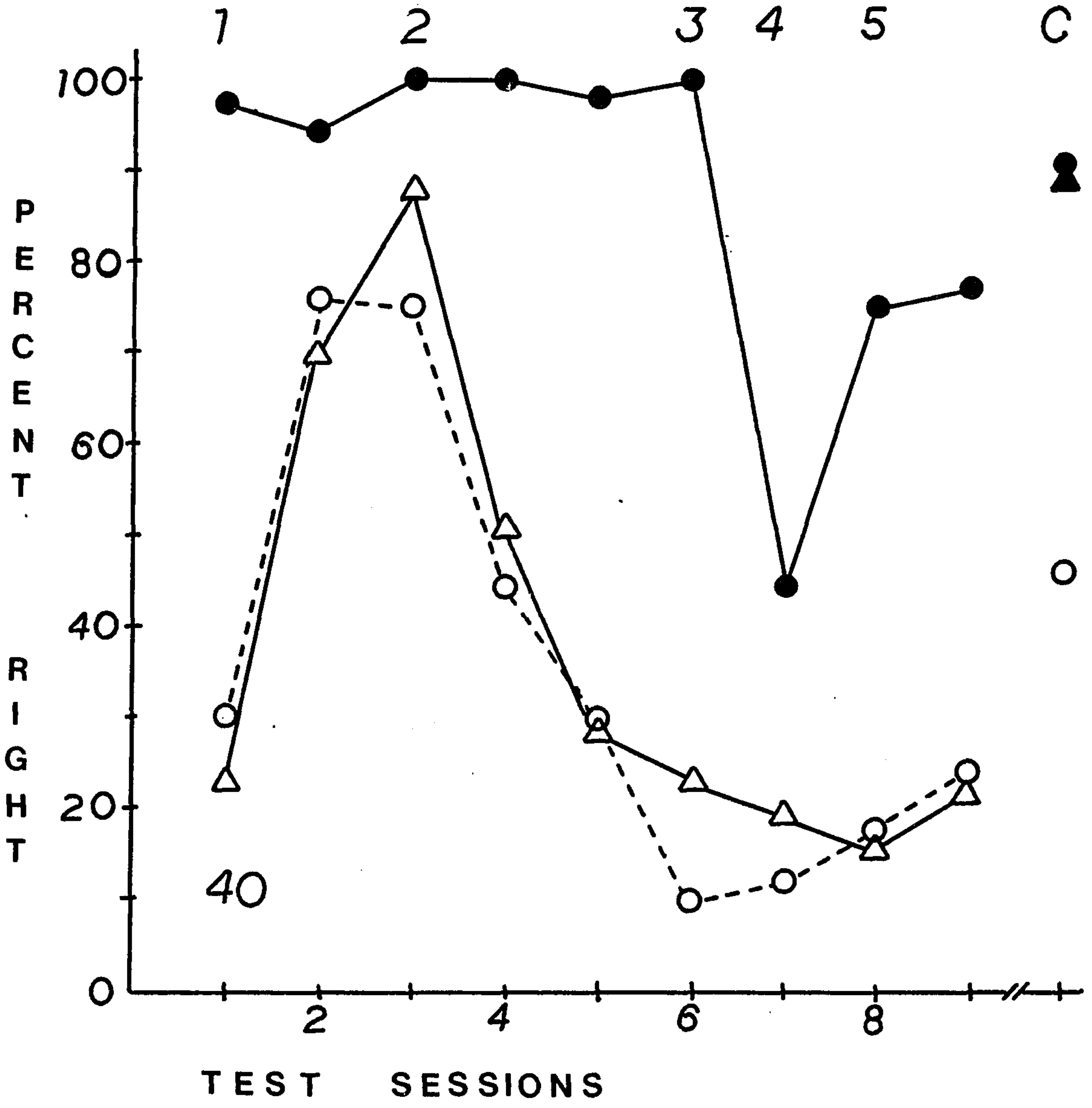


Figure 6.4. Percentage of right key pecks during ME test sessions for bird 40. See legend of Figure 7.1 for details.

sessions for birds 23, 230, 37 and 40, respectively. Note that right key pecks are correct for the colored slides, incorrect for achromatic slides, and are to be expected following test slides only if a ME has been acquired. The data for the colored stimuli include only the desaturated slides, while all achromatic stimuli have been pooled since no systematic differences occurred for ME-control slides compared with other achromatic slides. The fluctuations from session to session evident in the figures reflect, in large part, changes in response bias.[1] In general these figures show little difference between behavior following test and achromatic stimuli, indicating that no ME had been acquired. Instances of proportionately greater right-key responses on test than on achromatic stimuli did occur; see especially birds 23 and 40. However, the differences are typically of the same magnitude as those in the other direction and seem unrelated to adaptation procedure across birds. The lack of evidence for acquisition of the ME holds generally for all five adaptation procedures. The

---

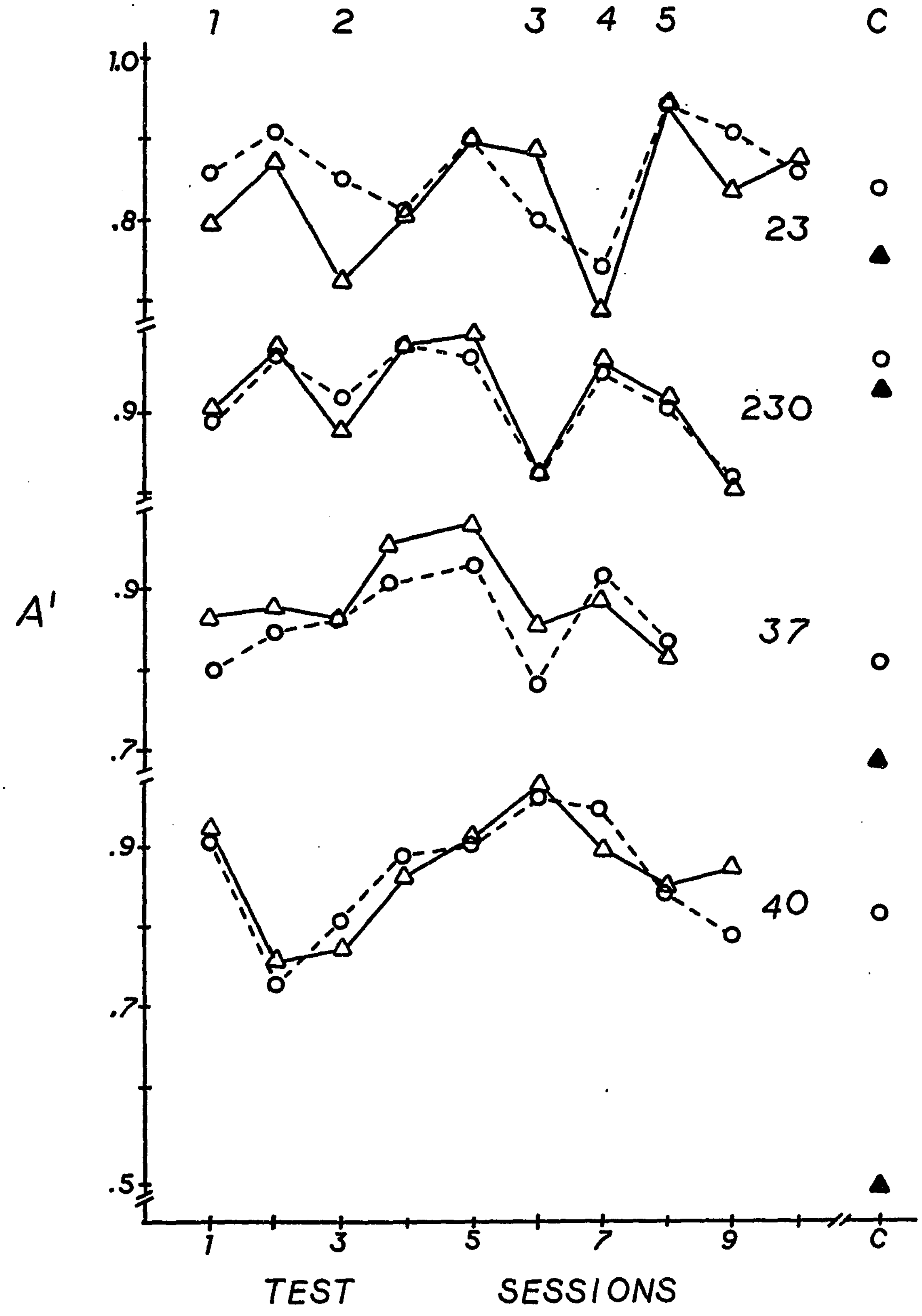
[1] In some cases response bias was actually manipulated by arranging that the probability of reinforcement be greater for correct responses following colored than following achromatic stimuli. This was done because it might be more likely for a weak ME to be "reported" with a larger right-key bias. Whether such a bias would be expected to have a greater effect on test than other achromatic stimuli, however, would depend upon certain assumptions, such as the form of the underlying "signal" and "noise" distributions. No relationship between bias and likelihood of pecking right following test versus achromatic stimuli was found.

percentage of right pecks following the pseudo-ME stimuli was substantially higher than that following achromatic stimuli for all birds except 230.

Figure 6.5 shows values of A' over ME test sessions for each of the four birds. A' is a nonparametric measure of the "discriminabilty" of two classes of stimuli corrected for response bias (Pollack & Norman, 1964) and is analogous to d' in the theory of signal detectability. A' varies between .5 (indicating the stimuli are indiscriminable) and 1.0 (indicating perfect discriminability). Figure 6.5 shows A's (a) for colored versus achromatic stimuli and (b) for colored versus test stimuli. If a ME were acquired, these values should differ, with test stimuli being less discriminable from colored stimuli than are achromatic stimuli. Once again, the patterns in the figure generally indicate that the ME was not acquired. On the other hand, lower values of A' were found for the pseudo-ME control versus colored stimuli in all cases except for bird 230, indicating that these stimuli were less discriminable from colored stimuli than were achromatic stimuli.

Figures 6.6 and 6.7 show the results of the three human control subjects. Figure 6.6 shows data analogous to that shown for the birds in Figures 6.1 through 6.4, as a function of ME adaptation time. The most striking aspect of this figure is the steep increase in the percentage of test stimuli called "colored" with increasing adaptation time, as

Figure 6.5. Discriminability index, A', during ME test sessions for birds 23, 230, 37 and 40. Open circles show the discriminability of achromatic from colored stimuli, and open triangles of ME test stimuli from colored stimuli; filled triangles show that of pseudo-ME from colored stimuli during the control (C) session. Numbers along the top of the figure indicate the induction and test procedure used.


1
2
3
4
5
C
1.0
.8
.9
.9
.7
.9
.7
.5
A'
23
230
37
40
1
3
5
7
9
C
TEST SESSIONS

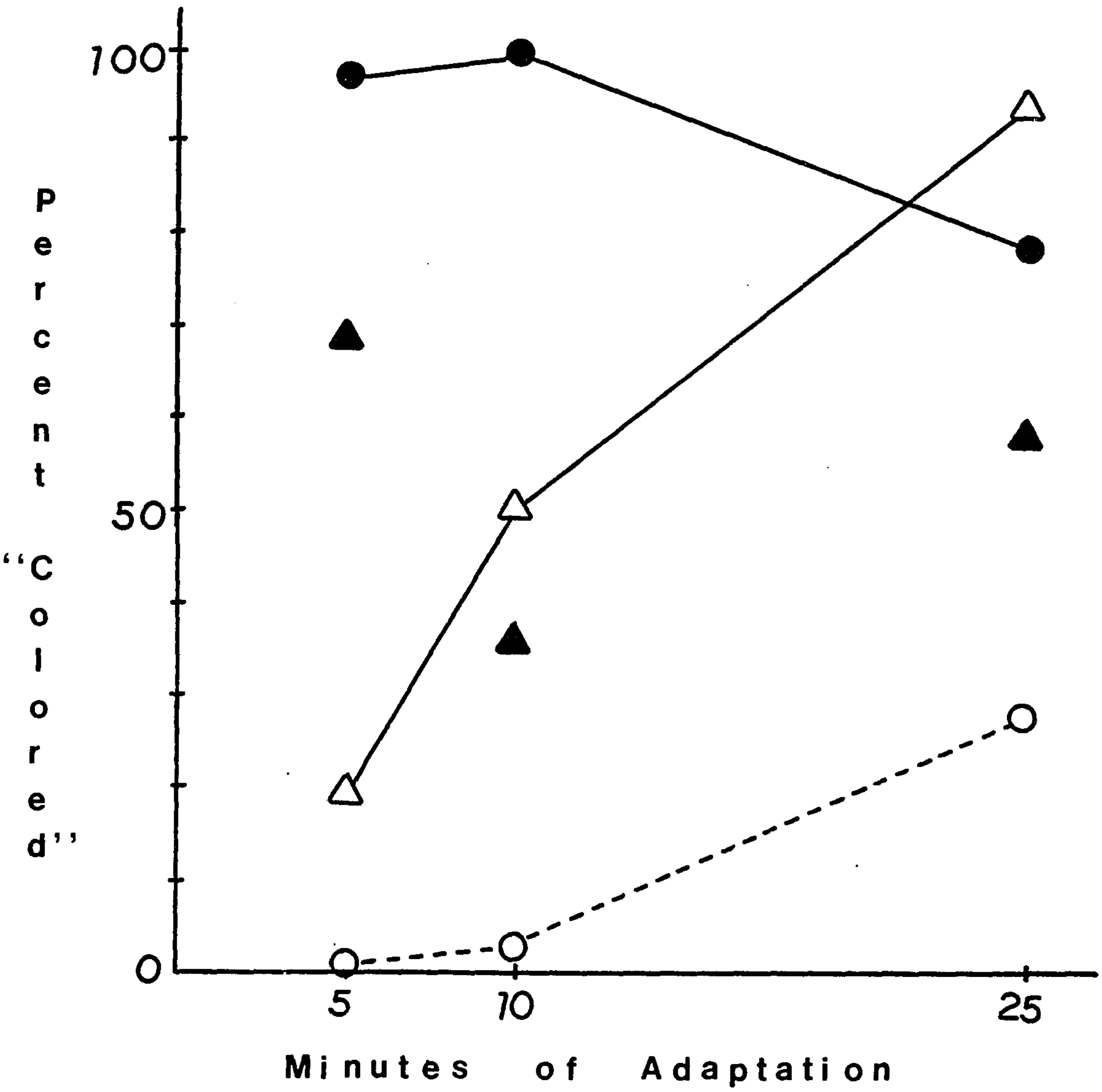


Figure 6.6. Percentage of stimuli called "colored" by the human control subjects as a function of adaptation time. Filled symbols are for colored stimuli: triangles for pseudo-ME, and circles for other chromatic stimuli. Unfilled symbols are for achromatic stimuli: triangles for ME test, and circles for other achromatic stimuli.

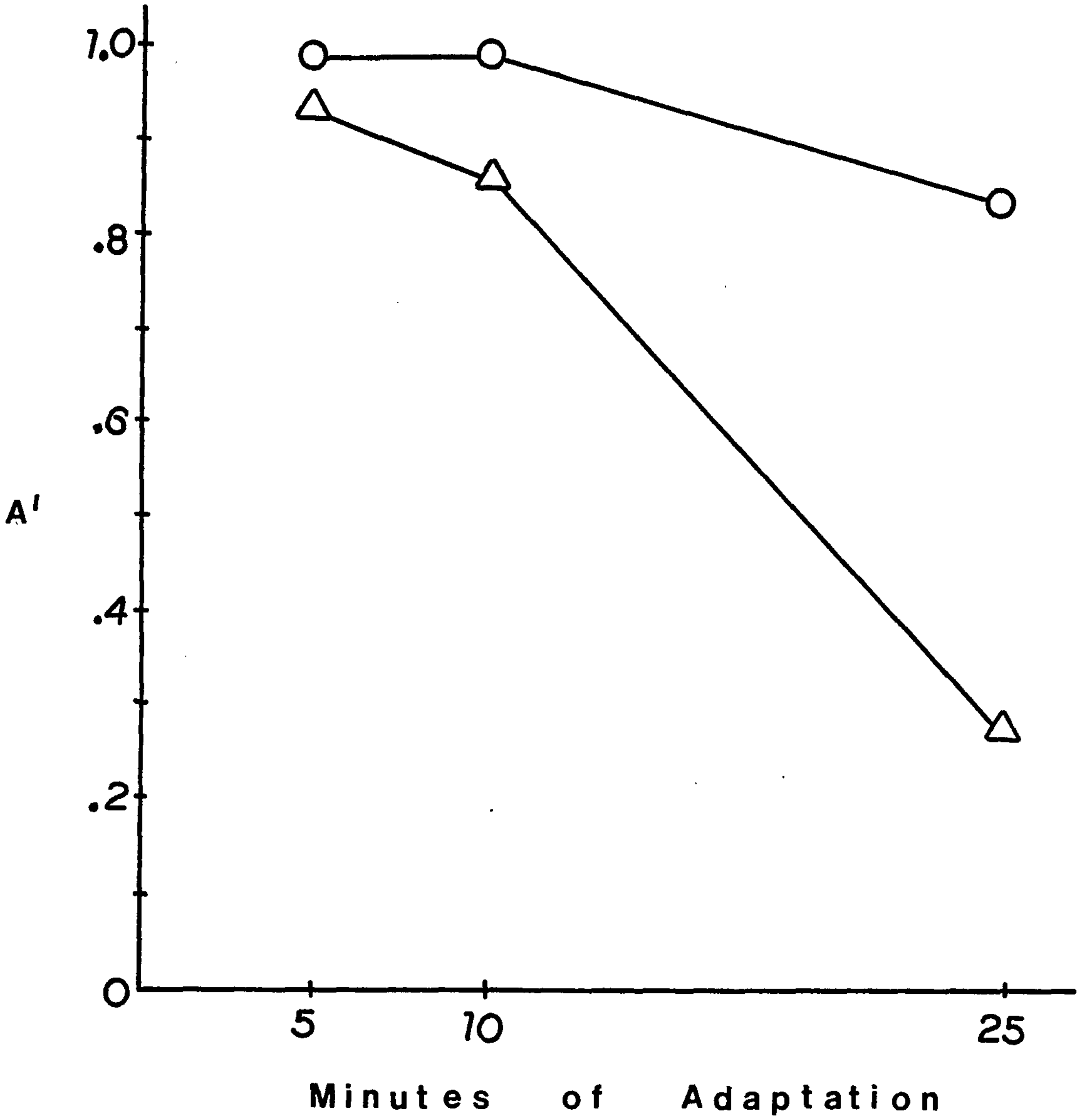


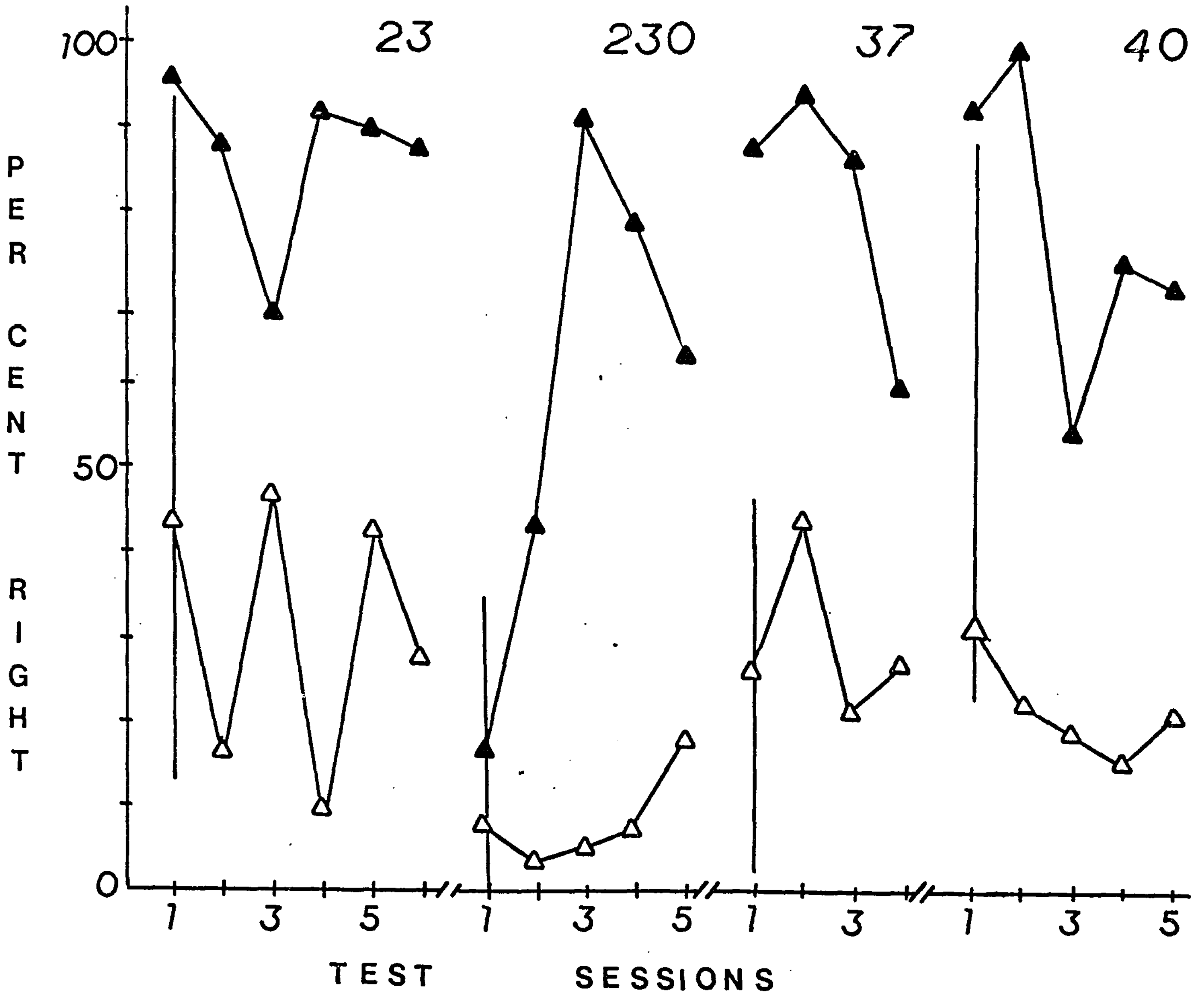
Figure 6.7. Discriminability index, A', for the human control subjects as a function of adaptation time. Open circles show the discriminability of achromatic from colored stimuli, and open triangles of ME test stimuli from colored stimuli.

would be expected since longer adaptation produces stronger MEs. The three subjects exhibited different levels of accuracy on colored, achromatic, and pseudo-ME control stimuli. This might be due either to different levels of response bias (that is, different criteria as to what constitutes chromaticity), or to different color sensitivities on the part of the three subjects. Figure 6.7 shows the data corrected for response bias, plotting values of A' analogous to those for the birds in Figure 6.5. The same general pattern is seen in Figure 6.7 as in Figure 6.6, with larger differences between the two A's with longer adaptation time.

One interesting feature of Figure 6.6 is the relation between percent "colored" on test and pseudo-ME control stimuli. After 5 min of adaptation the pseudo-ME control stimuli were called "colored" more often than were the test stimuli, while the reverse is true following 10 or 25 min of adaptation. This relationship was substantiated in another way. Following the testing procedure, each subject was shown a test stimulus and a pseudo-ME stimulus which had been reported as "colored" at least once, and was asked to indicate which of the two was "more colored." Subject DY, who had adapted for 5 min, indicated that the pseudo-ME stimulus was more colored, while the other two subjects indicated that the test stimulus was more colored.

It would be of some interest to look at the relationship between the birds' behavior following test and pseudo-ME control stimuli, as was done with the human subjects. Figure 6.8 shows the percentage of right key pecks for these two types of stimuli in those test sessions where both were included. The first pair of points for each bird compares the performance on the pseudo-ME stimuli during the control session (which was the first exposure the birds had had to the latter stimuli) with the median performance level on ME test stimuli for the seven previous ME test sessions. (Note that no reinforcement was provided for responses to the pseudo-ME stimuli during the control session, but that it was during other subsequent sessions.) The other pairs of points represent data within individual test sessions with procedures 4-6. This figure shows that in every case where a comparison is possible, the pseudo-ME control stimuli were more likely to be classified as "colored" than were the test stimuli. This may not be true for bird 230's first pair of points: the percent right following pseudo-ME stimuli was within the range of percent right following test stimuli for the five test sessions contributing to the median value shown. For this bird, a clear learning trend is evident over the following two test sessions with reinforced exposure to the pseudo-ME stimuli. Certainly in the case of the other three birds, however, the pseudo-ME stimuli were consistently reported as "colored" much more frequently than were the test stimuli. Comparing

Figure 6.8. Percentage of right key pecks following pseudo-ME (filled triangles) and ME test (open triangles) stimuli during test sessions for birds 23, 230, 37 and 40. The first "session" compares responses to pseudo-ME stimuli during the control session with the median performance level to ME test stimuli during the previous seven ME test sessions. The bars indicate the ranges for these seven sessions for each bird. Sessions two through five compare responses within individual ME test sessions.


PER CENT RIGHT
100
50
0
23
230
37
40
1
3
5
1
3
5
1
3
1
3
5
TEST SESSIONS

this with the human data, any ME which might have been acquired by the birds must have been of strength comparable to that acquired by a human with less than ten minutes' adaptation time.

Discussion

Although all three human subjects showed evidence of acquiring a ME in a situation analogous to that experienced by the pigeon subjects, no clear evidence was found that any of the birds had acquired a ME. Given that three out of the four birds did respond appropriately to the pseudo-ME stimuli when first exposed to them, it seems unlikely that the failure to demonstrate the phenomenon can be attributed to the birds' having had a bias towards calling desaturated colors "achromatic." It is difficult to rule out inattention to the adaptation stimuli as a reason for the failure to demonstrate the phenomenon. However, in procedures which required the birds to respond to these stimuli (procedures 1 and 3), responses to the test stimuli were not systematically different from the analogous behavior with the other adaptation procedures. Furthermore, if a pigeon-ME had a similar course of acquisition as a human-ME, the birds should have shown evidence of acquiring the effect even if they had only attended to the adaptation stimuli for between 1/6 and 1/3 of the time (i.e., for 5 to 10 out of the 30 min of adaptation time).

It is likely that the spatial frequency of the gratings used in the present experiment was not optimal. Stromeyer (1972b) found that adaptation and test square-wave gratings (of equal spatial frequency) of 5 c/deg typically produced a stronger ME than various other spatial frequencies, over a range of 1-20 c/deg. This might perhaps reflect the human spatial frequency sensitivity, which for sinusoidal gratings peaks at around 6 c/deg (e.g. Davidson, 1968). An optimal spatial frequency for ME acquisition in the pigeon, then, might be at around 4 c/deg, which is the pigeon's peak sensitivity for sinusoidal gratings (Nye, 1968). This is a substantially higher frequency than the .6 c/deg employed in the present study. It should be noted that Stromeyer's data indicated that a difference in spatial frequency between adaptation and test gratings had a larger effect on ME strength than did the spatial frequency of both adaptation and test gratings when equal. Also, note that the human subjects acquired the ME in the present study with these low-frequency gratings.

Aside from the possibility mentioned at the close of Chapter 5 that the birds' behavior was under the control of some stimulus dimension other than chromaticity, one further explanation of these negative findings seems worth exploring: It is possible, if unlikely, that the pigeons had acquired a ME in this experiment, but were somehow able to discriminate between such "illusory" color and "true" color, and thus behaved differently in the two cases. If these pigeons could be shown, however, to respond with a right key peck to another type of "illusory" color, this argument would be considerably weakened. The study described in the next chapter, then, attempted to demonstrate simple chromatic adaptation in these pigeons.

CHAPTER 7

EXPERIMENT III. SIMPLE CHROMATIC ADAPTATION IN PIGEONS

The previous study failed to demonstrate a contingent chromatic AE (the ME) in pigeons. It seems reasonable, before concluding that pigeons do not acquire such an effect, to ask whether a simple chromatic AE can be demonstrated in this setup and with these birds. There is already evidence that birds experience both afterimages (Swindle, 1916; see Appendix B) and chromatic adaptation (Williams, 1974). Thus a failure to demonstrate a simple AE in the present context would call into question the validity of the procedure employed in this research and thus of any conclusion as to the possibility of birds' acquiring a ME.

In this study, chromatic adaptation was demonstrated in pigeons. Chromatic adaptation consists of changes in spectral sensitivity (Stiles, 1949) and in the apparent hue of objects as a result of a relatively long exposure to colored light. For example, following exposure to a green light, human sensitivity to green declines and other wavelengths appear basically as though green had been subtracted and its complement "disinhibited": e.g. a light formerly appearing to be white looks pink. Williams (1974) has demonstrated a chromatic adaptation aftereffect with pigeons. Specifically, the subjects were trained to peck a key, with reinforcement being provided on a VI schedule only when the ambient illumination (provided by over head lamps) was green. During training, the color of the over head illumination was changed every 30 sec, and was either green, red, yellow or white; white never followed red. After the birds had reached a criterion of response rates in green five times higher than in other components, test sessions in which the red over head illumination preceded white illumination were carried out. Williams found that response rates during white following red, while not as high as during green, were higher than at other times, at least during the first ten sec of the interval. He interpreted this as evidence for "negative afterimages" (which we have called chromatic adaptation), with exposure to red light for 30 sec producing the subsequent experience of green during white illumination.

In this study, the birds were exposed to a situation similar to that used by Williams described above. Specifically, lights, either intense green or white, illuminated the experimental chamber for alternating six-min intervals while the birds were viewing and reporting upon slides in the same procedure as used in Experiments I and II. If the birds experienced chromatic adaptation, it was expected that they would be more likely to report achromatic slides to be "colored" (i.e., peck the right key) during the green periods than during the white periods.

Methods

Subjects

The same four pigeons as served in Experiments I and II.

Apparatus

The same experimental chamber as used in Experiments I and II was employed. One of the walls of this chamber, which served as a door and was constructed of clear Plexiglas, was covered with translucent paper (tracing paper). Two sockets were mounted outside this wall, one of which held a red or green floodlamp (G.E. 100 W, 100PAR/R or 100 PAR/G) or, in preliminary training, a "white" bulb, and the other of which held a "white" bulb (7.5 to 100 W).

Stimuli

A set of slides was selected from the pool employed in Experiments I and II. The chromatic set included slides with fairly desaturated colors including some with a pink or light green background such as might occur as AEs of adaptation to green or red light. A different set of slides was used on baseline and test sessions, and the test pool was changed on the second day of the second series of test sessions (see below).

Procedure

Sessions consisted of eight 6-min intervals, during which one of the two lamps outside the pigeon chamber was illuminated. Specifically, the two lamps were lit in alternation, so that each was illuminated for a total of four 6-min periods. These lights were extinguished whenever a pigeon had its head within the viewing sleeve so as to ensure that the birds continued to respond to the chromaticity of the slides rather than to that of the ambient illumination.

Baseline Sessions. When the outside lights were first introduced the birds' behavior was disrupted, so only very dim lights were used for a time, with more intense lamps being gradually introduced. The final baseline procedure employed alternating 100 and 60 W white lights.

Test Sessions,Series 1. During the first group of test sessions, ten 6-min intervals occurred with the 100 W white bulb being replaced by the green flood lamp. No reinforcement was available for responses following achromatic slides during the periods when the green flood lamp was illuminated. (Due to an apparatus failure, bird 23 received no reinforcement for responses following achromatic stimuli in either component on the first test session.) Four such test sessions were carried out, with 11 to 15 sessions of baseline training intervening.

Control Session. Following the above test sessions, one control session was carried out which was identical to the above test sessions except that the green flood lamp was removed. That is, 6-min periods with white illumination alternated with periods with no external illumination, and no reinforcement for responses following achromatic slides was available during the dark periods.

Test Sessions,Series 2. Following the control session, test sessions were carried out in which the usual reinforcement contingencies were always in effect. That is, left key pecks were occasionally reinforced following the observation of achromatic stimuli. Five such test sesisons were carried out with either a green or red flood lamp being used during half of the 6-min intervals, and with 4 to 13 baseline sessions intervening between successive test sessions.

Results

The results of all test and control sessions in this experiment are shown in Figures 7.1 through 7.4. The percentage of right key pecks is shown for colored and achromatic stimuli during components with either colored or white ambient light. A chromatic AE should be manifest by an increase in the percentage of right responses following achromatic stimuli during the green (red) components, and this is exactly what has occurred for all birds during the first set of test sessions. Bird 37 (and perhaps bird 40) also shows a higher accuracy level on colored slides during green than during white components, which might also be

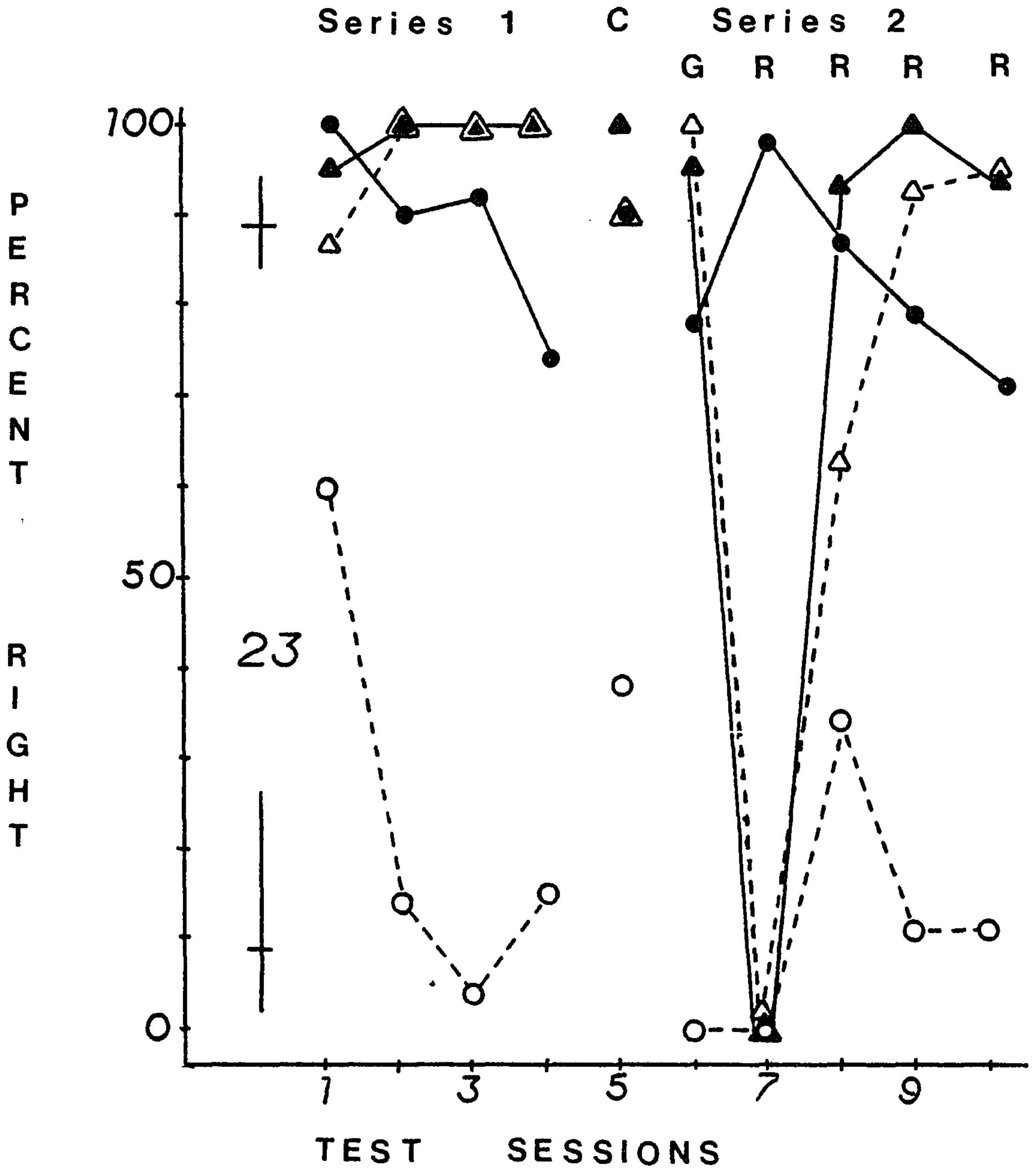


Figure 7.1. Percentage of right key pecks during chromatic adaptation test sessions for bird 23. Filled symbols are for colored and open symbols for achromatic stimuli. Circles are for responses during white components and triangles for responses during colored components. Bars at left show the range and median performance during the baseline sessions prior to each test session for colored (above) and achromatic (below) stimuli. The type of test session (Series 1; control, C; or Series 2), and the color presented during colored components of Series 2 (red, R; green, G) are indicated.

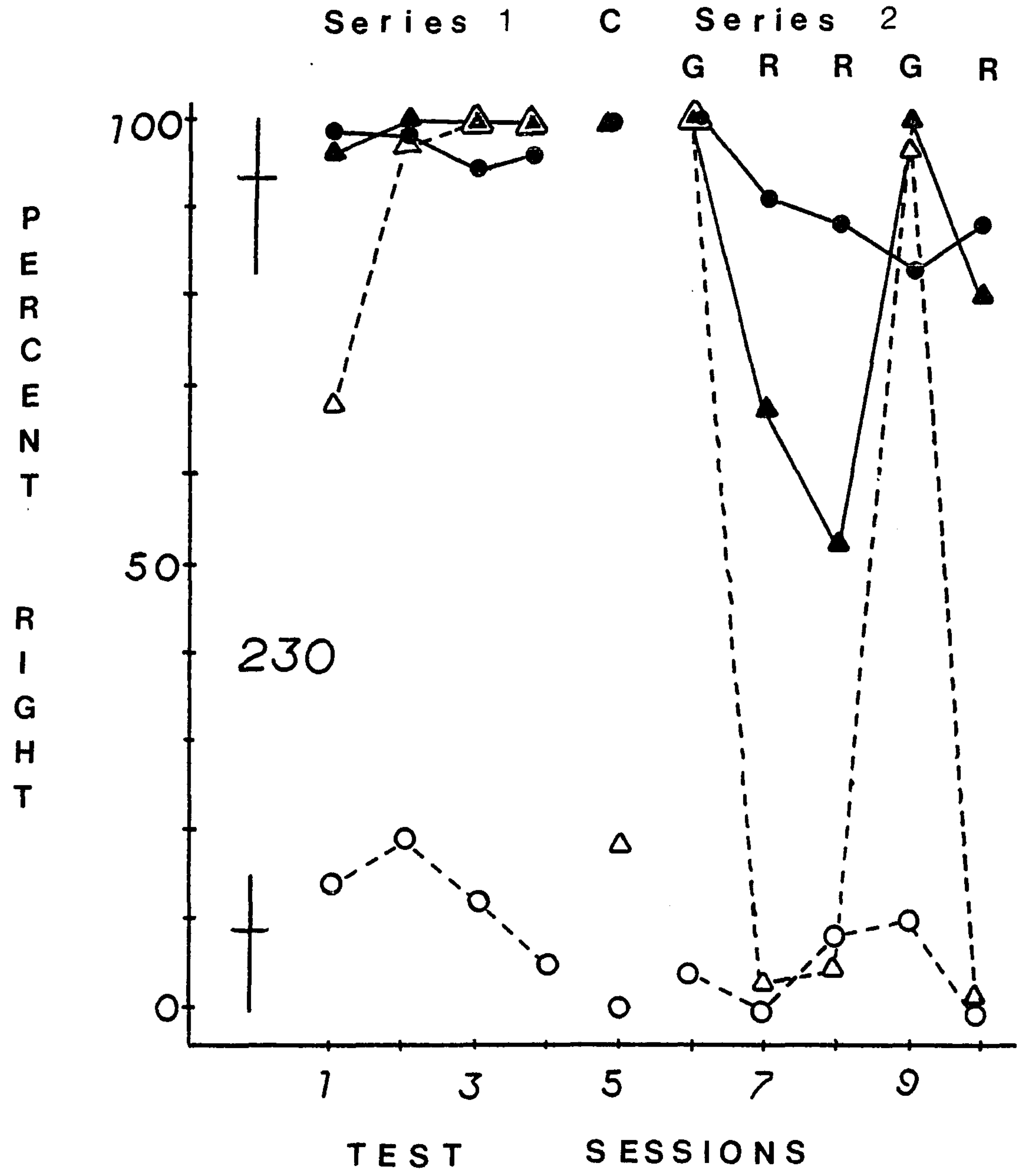


Figure 7.2. Percentage of right key pecks during chromatic adaptation test sessions for bird 230. See legend of Figure 8.1 for details.

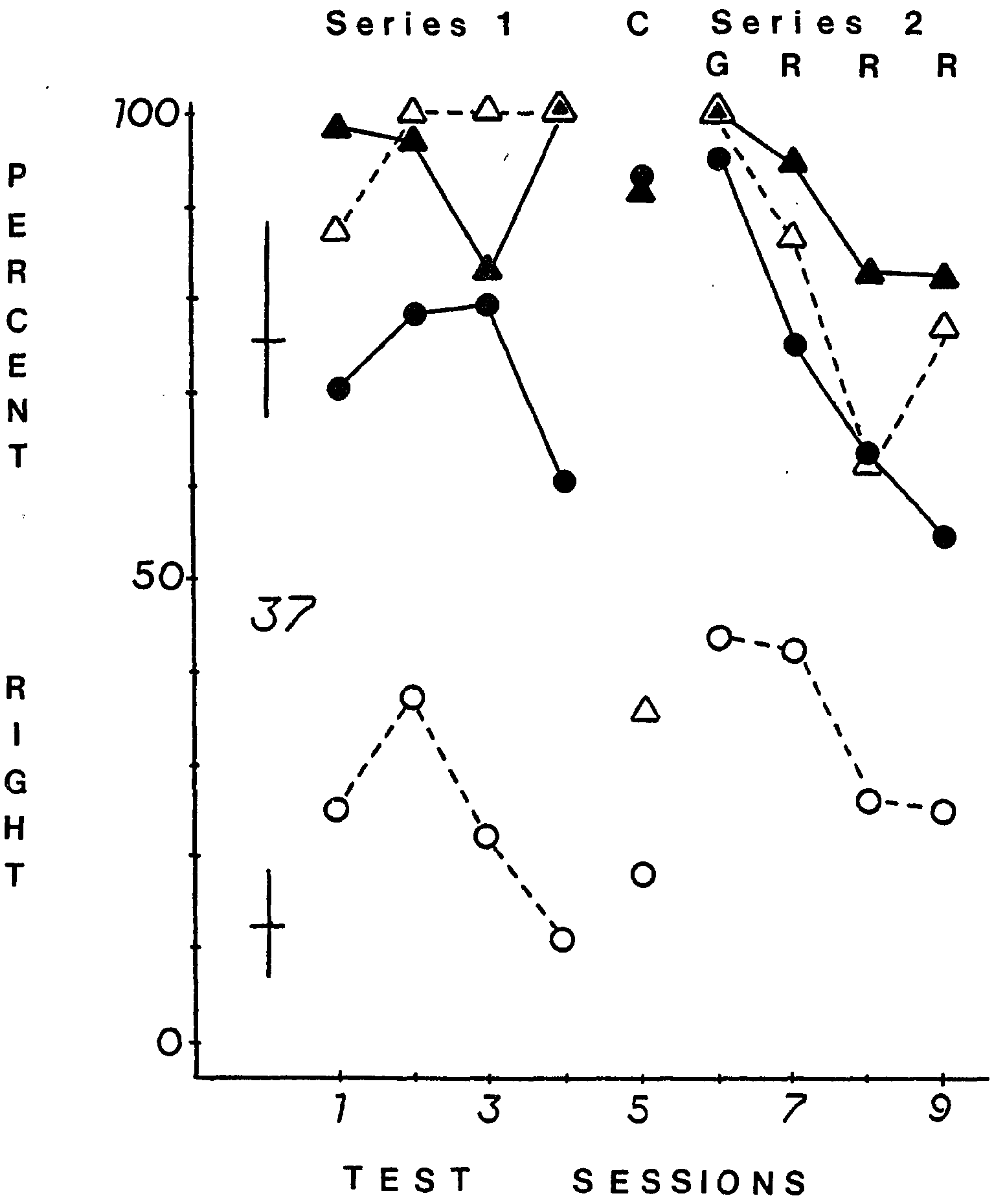


Figure 7.3. Percentage of right key pecks during chromatic adaptation test sessions for bird 37. See legend of Figure 8.1 for details.

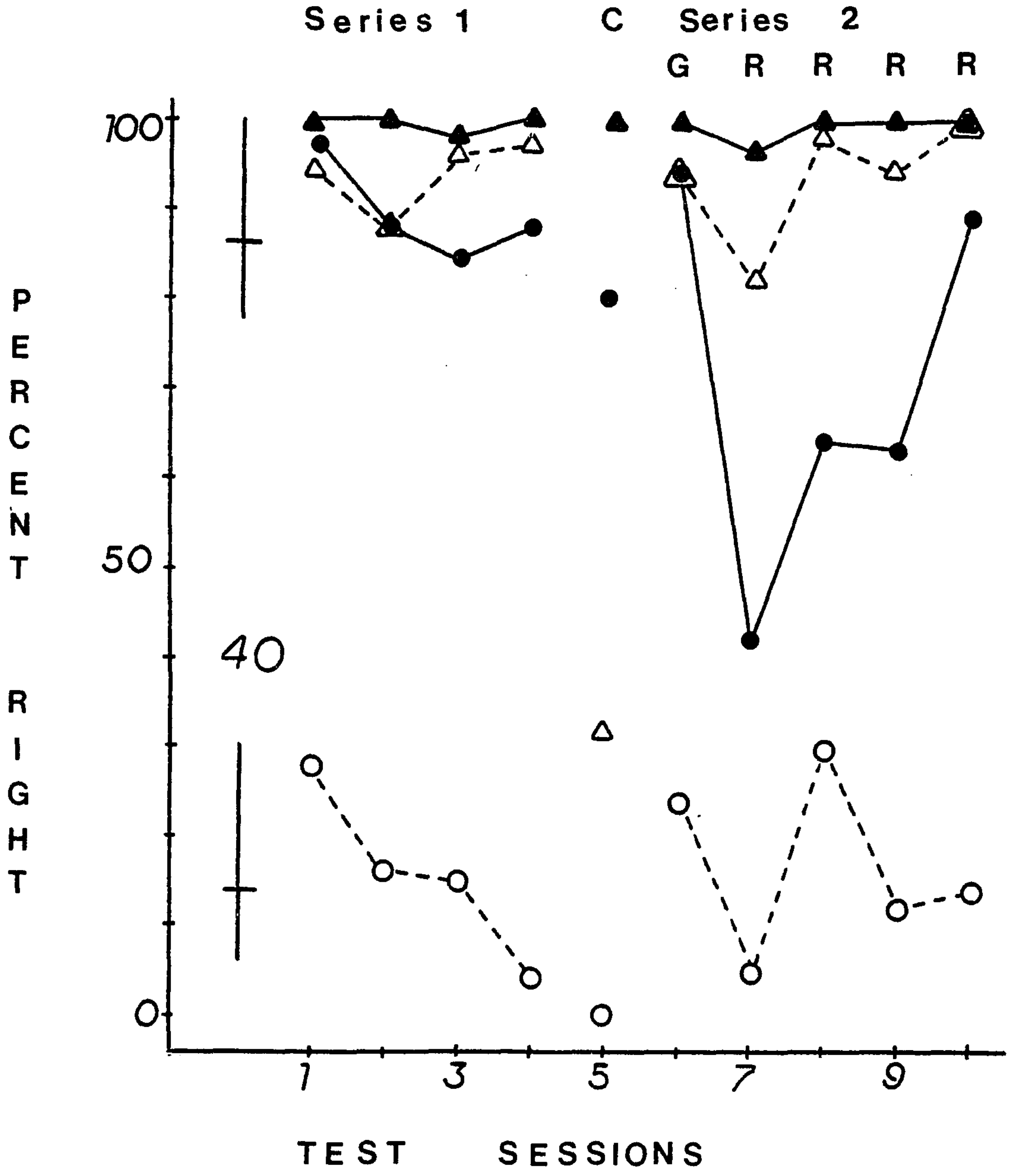


Figure 7.4. Percentage of right key pecks during chromatic adaptation test sessions for bird 40. See legend of Figure 8.1 for details.

expected to result from chromatic adaptation: Many of the desaturated colored slides were pale pink and these should appear even pinker following adaptation to green. (This trend would not be expected to be apparent for birds 23 and 230, since the percentage of right responses following colored stimuli is already near the maximum possible during white components.)

It should be noted that the reinforcement contingencies which were in effect during test sessions might also be expected to lead to right key pecks following achromatic slides during green components. During these sessions, responses following achromatic slides during green were never reinforced and, consequently, only right responses were reinforced during green. If this change in contingencies were detected, it would in effect constitute a change in "instructions" to the birds: "During white components peck right with colored and left with achromatic slides, but during green components always peck right." It was felt that since test sessions were infrequent and the rate of reinforcement was low, the change of contingencies was not likely to be discriminated by the birds. There is evidence, however, that such was not the case for at least two of the birds. First of all, an increase in percent right following achromatic slides is evident over test sessions for birds 23 and 230. It seems unlikely that this is due to a larger AE after the first session. A more reasonable interpretation of this trend is that these birds had come to discriminate the change in contingencies and had adopted a peck-right-during-green strategy. Bird 23 had an especially long exposure to the contingencies due to an apparatus failure (34 components occurred on the first day for this bird). The results of the control session show that all birds were able to discriminate such a change in contingencies within a single session. Here, all birds showed more right responses following achromatic stimuli during the dark components (in which reinforcement was unavailable for left key pecks), as compared with performance during white components. Clearly, this result cannot be explained in terms of any "illusory" colors, but is consistent with the discrimination of the altered reinforcement contingencies. It should be noted that a much smaller percentage of right responses following achromatic stimuli occurred than was observed during green components for any of the previous test sessions, except in the case of bird 23. Thus, it seems that an AE must also have contributed to the observed patterns of behavior, especially on the first test session. The similarity of bird 23's behavior pattern during the control session to that on the previous test sessions suggests that a peck-right strategy may have been under the control of "not white" or "different from baseline" rather than "green." (See also 23's data on the first test session with red, described below.)

During the second set of test sessions, in which the usual baseline reinforcement contingencies were maintained continuously, the effects of chromatic adaptation and of the reinforcement contingencies would be in opposition to each other. Thus, right pecks following achromatic slides during green would be fairly strong evidence of chromatic adaptation. On the first day of this set of test sessions, all birds maintained the behavioral pattern of the first set of test sessions. However, most birds made no contact with the new contingencies of reinforcement: Only bird 40 received any reinforcers for pecking left following an achromatic stimulus during a green component, and even this bird received only one such reinforcer (see Table 7.1). The hue of the colored components was changed from green to red in hopes that the birds would come in contact with the new contingencies. When this was done, two of the birds exhibited ideosyncratic behavioral patterns, again suggesting that they had come under the control of chamber illumination and its associated differential reinforcement contingencies during the first set of test sessions. Bird 23 appeared to show a complete shift in response bias, pecking only the left (rather than the right) key during red components. On the second test session with red for this bird, the left key light was extinguished following some chromatic slides, so that he was "forced" to peck the right key during red components. The data shown include only the

Table 7.1

Number of Reinforcers Obtained During Colored Components of Series 2 Test Sessions

Bird	Color During Colored Components	No. Reinforcers Achromatic Stimuli	No. Reinforcers Colored Stimuli
23	G	0	10
	R	11	0
	R	2	7
	R	1	10
	R	1	11
230	G	0	17
	R	15	5
	R	12	14
	G	0	5
	R	9	5
37	G	0	31
	R	3	13
	R	4	16
	R	1	8
40	G	1	16
	R	1	17
	R	0	16
	R	1	28
	R	0	19

final six components of the session for this bird when no further forced exposure was given. Following this, the behavior pattern returned to that seen during the first set of test sessions, but it is not clear how this should be interpreted. The bird may have merely returned to its previous response bias, although at least one reinforcer was obtained for a left key peck following an achromatic slide during red on each test session.

Bird 230 also seems to have switched its response bias during red components, but not to the same degree as bird 23 did. The pattern here, poorer performance following colored but not achromatic slides during red, is the reverse of what should be expected on the basis of a chromatic adaptation effect. The basis of this bird's behavior pattern is obscure. At any rate, when green was reintroduced during the colored components, 230 reverted to its previous behavior pattern.

Birds 37 and 40 did not show such large changes in behavioral pattern as did 23 and 230 during the second set of test sessions, still making a large number of right responses following achromatic stimuli during the colored components. These birds seem to give the clearest evidence of chromatic adaptation of the four. Continuing to reinforce left responses following achromatic stimuli during red did have some effect upon these birds, however, in the form of poorer discrimination. If the achromatic stimuli appeared colored during red, then this is not surprising, since other research has shown that discrimination worsens when errors are reinforced (Nevin, Olson, Mandell, & Yarensky, 1975).

The fact that both a chromatic AE and the contingencies of reinforcement doubtless influenced the observed patterns of behavior makes it seem important to take a closer look at the data for the first test session, when the contribution from the reinforcement contingencies would be at a minimum. Figures 7.5 through 7.7 show the percentage of right responses during successive 6-min components for this session. (These data are not available for bird 23.) We see here that all three birds clearly showed the increase in right responses following achromatic stimuli during all colored components, including the first one. However, a clear trend is evident starting in the third green component for bird 230, which might be interpreted as the emergence of a new response "stragegy" during colored components. This further supports the notion that the data form birds 23 and 230 may have been more contaminated by the effects of reinforcement contingencies than were those from birds 37 and 40.

The time, relative to the beginning of a component, at which right key pecks following achromatic slides were emitted was recorded during the first set of test sessions.

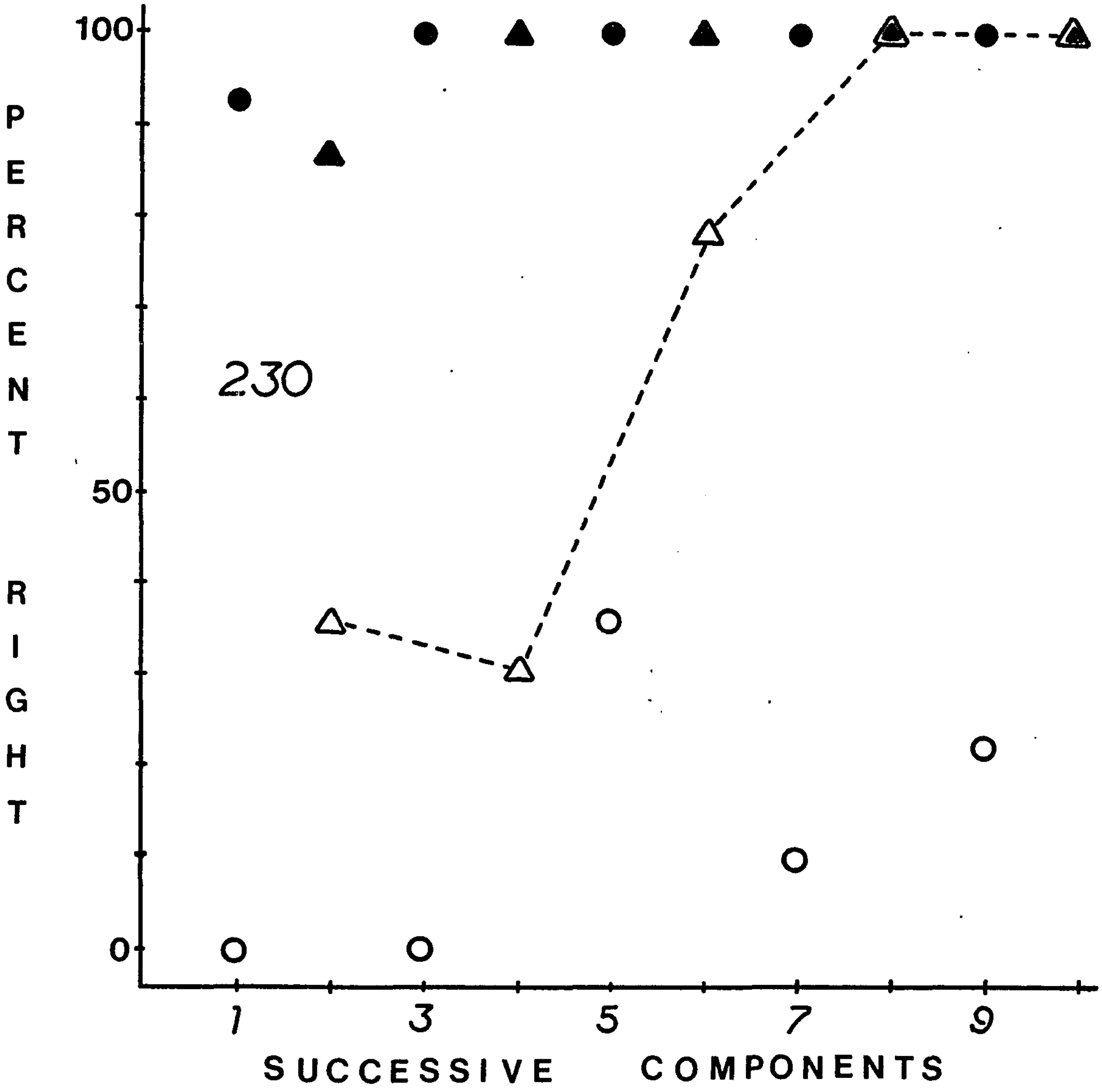


Figure 7.5. Percentage of right key pecks during successive six-min components on the first test session of Series 1 for bird 230. Filled symbols are for colored stimuli, open symbols for achromatic stimuli. Circles are for white (odd-numbered) components, triangles for green (even-numbered) components.

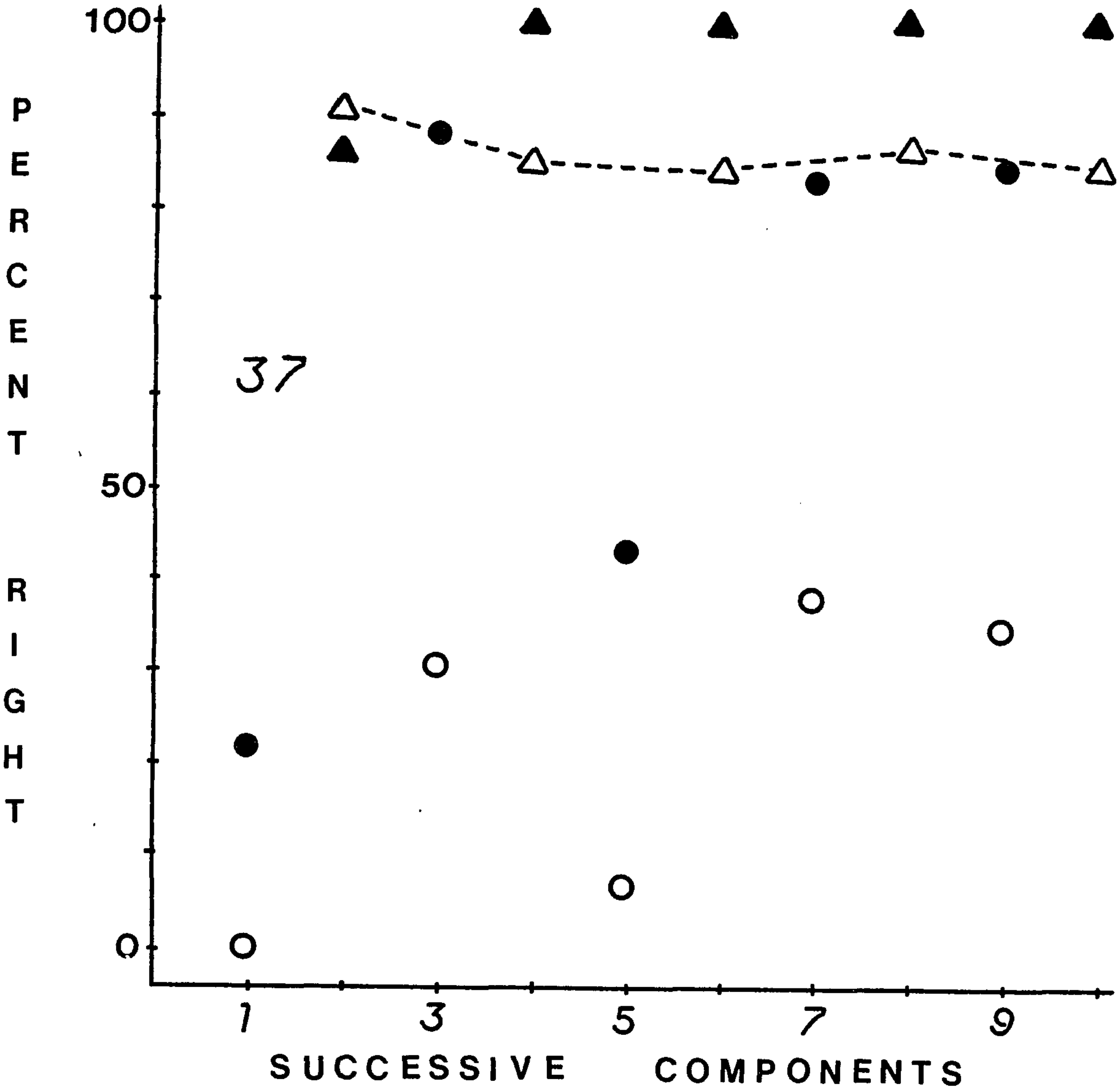


Figure 7.6. Percentage of right key pecks during successive six-min components on the first test session of Series 1 for bird 37. See legend of Figure 8.5 for details.

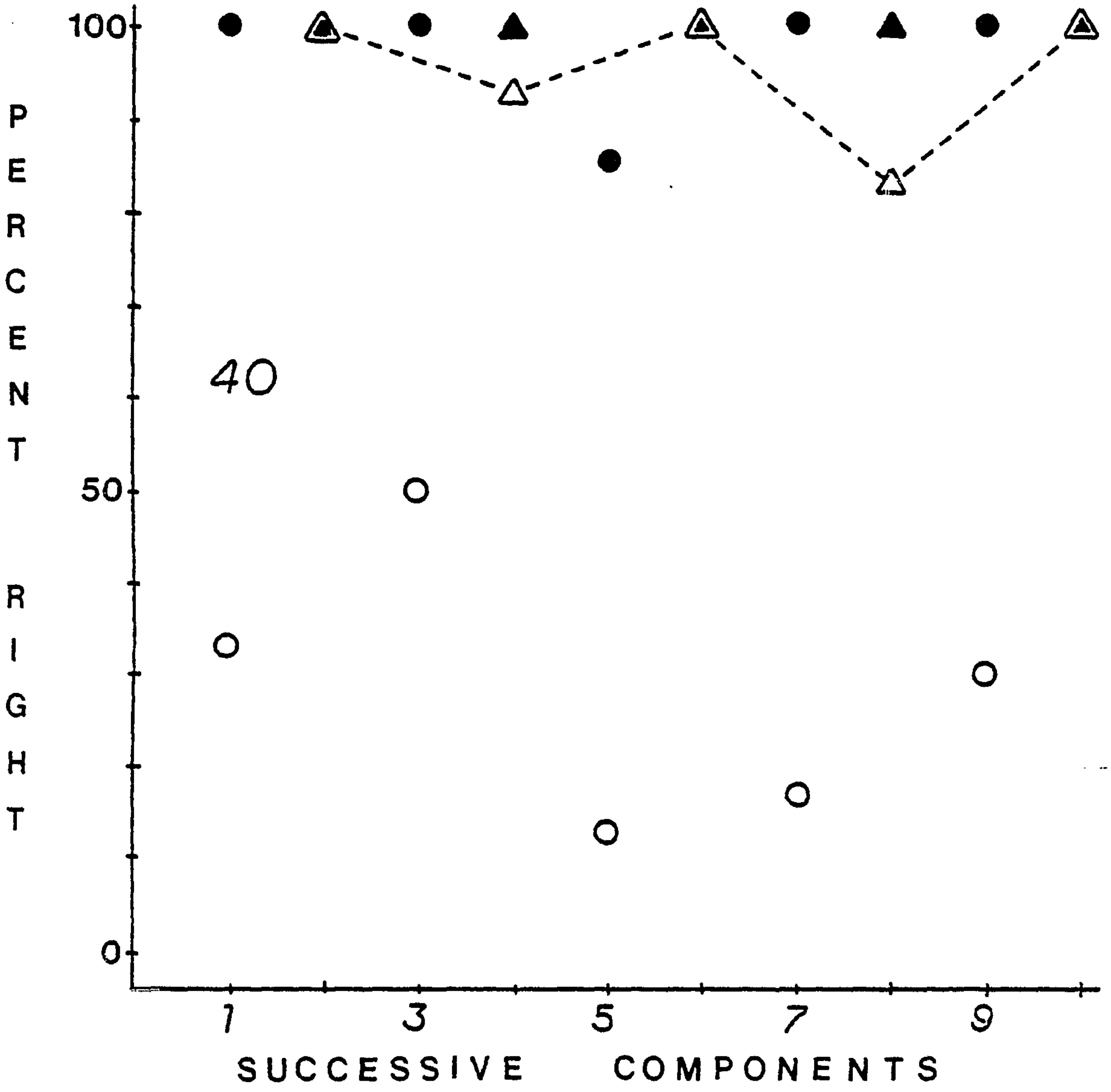


Figure 7.7. Percentage of right key pecks during successive six-min components of the first test session of Series 1 for bird 40. See legend of Figure 8.5 for details.

These data are shown in Figures 7.8 through 7.11, with response frequencies during successive 40-sec intervals of the green and white components plotted separately.[1] Also shown are the data from the first test session (the first ten components of this session for bird 23). If the AEs of chromatic adaptation (a) take some minimum amount of exposure to the colored light to be built up and (b) decay over time after the colored light is extinguished, one might expect to see these processes reflected in the data shown in this figure. Specifically, one might expect to see (a) an increase in the error rate during the green components and (b) a decrease in the error rate during the white components, reflecting the acquisition and decay of the AE, respectively. The functions for the green components are generally quite flat, probably indicating that the time-course of chromatic adaptation is shorter than 40 sec. There seems to be a hint of a decline in the functions for

---

[1] The data from the last 40-sec interval of the 6-min components are not included here. In all cases, a sharp decrease in response frequency was indicated by the data, but this is most likely due to the way in which the apparatus was programmed. The print-out counter recording the time at which a response was made required a long pulse to print. This was achieved by a peck "making" and the next head-in "breaking" a lock-up circuit. The counter did not advance during this period so that each printed time indicated the time since the beginning of the component minus the cumulative time between pecks and head-ins for the responses recorded. This was partially corrected for by adding 4 sec for each response, but longer latencies did occur, which would result in less than 360 sec being accumulated for a 6-min component.

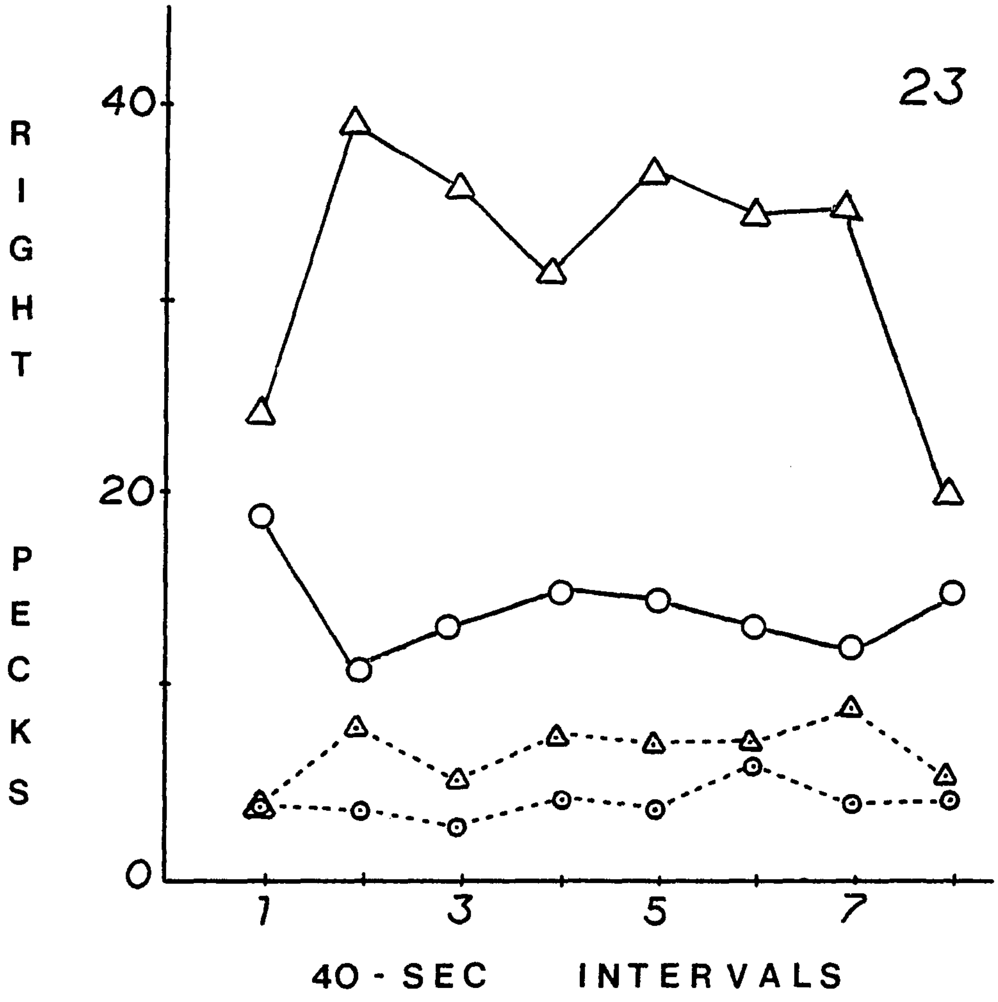


Figure 7.8. Number of right key pecks emitted by bird 23 during successive 40-sec intervals of white (circles) or green (triangles) components for Series 1 test sessions. Large symbols are for the four sessions combined, small symbols with dots are for the first session only.

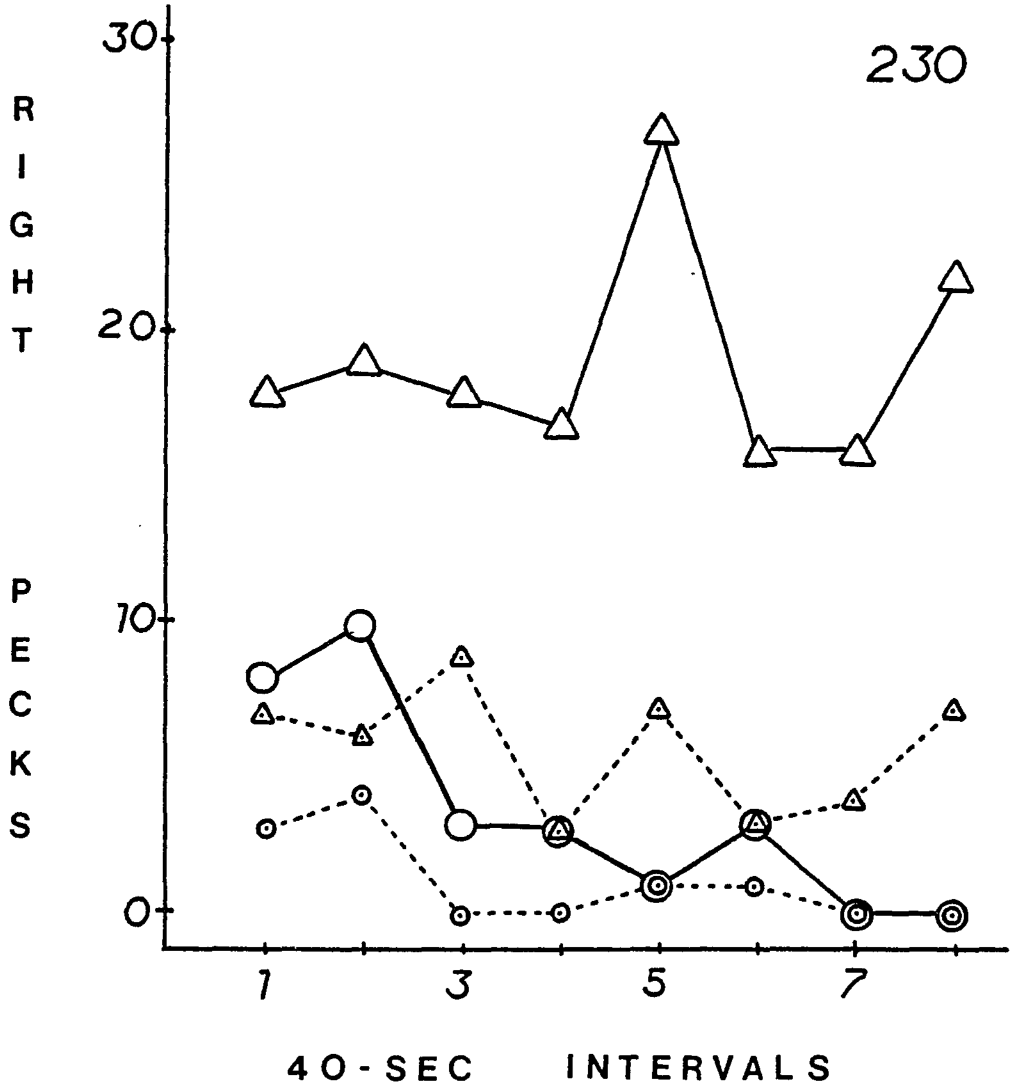


Figure 7.9. Number of right key pecks emitted by bird 230 following achromatic stimuli during successive 40-sec intervals of white or green components for Series 1 test sessions. See legend of Figure 8.8 for details.

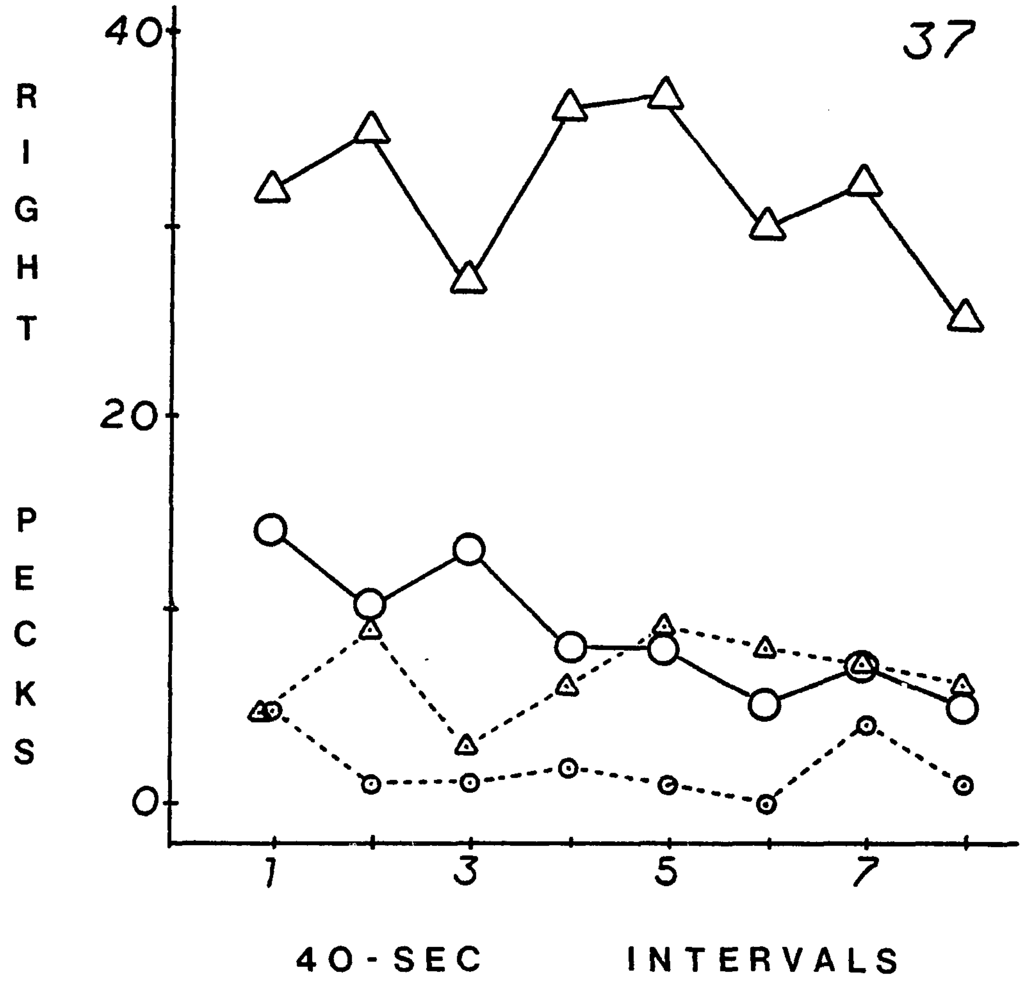


Figure 7.10. Number of right key pecks emitted by bird 37 following achromatic stimuli during successive 40-sec intervals of white or green components for Series 1 test sessions. See legend of Figure 8.8 for details.

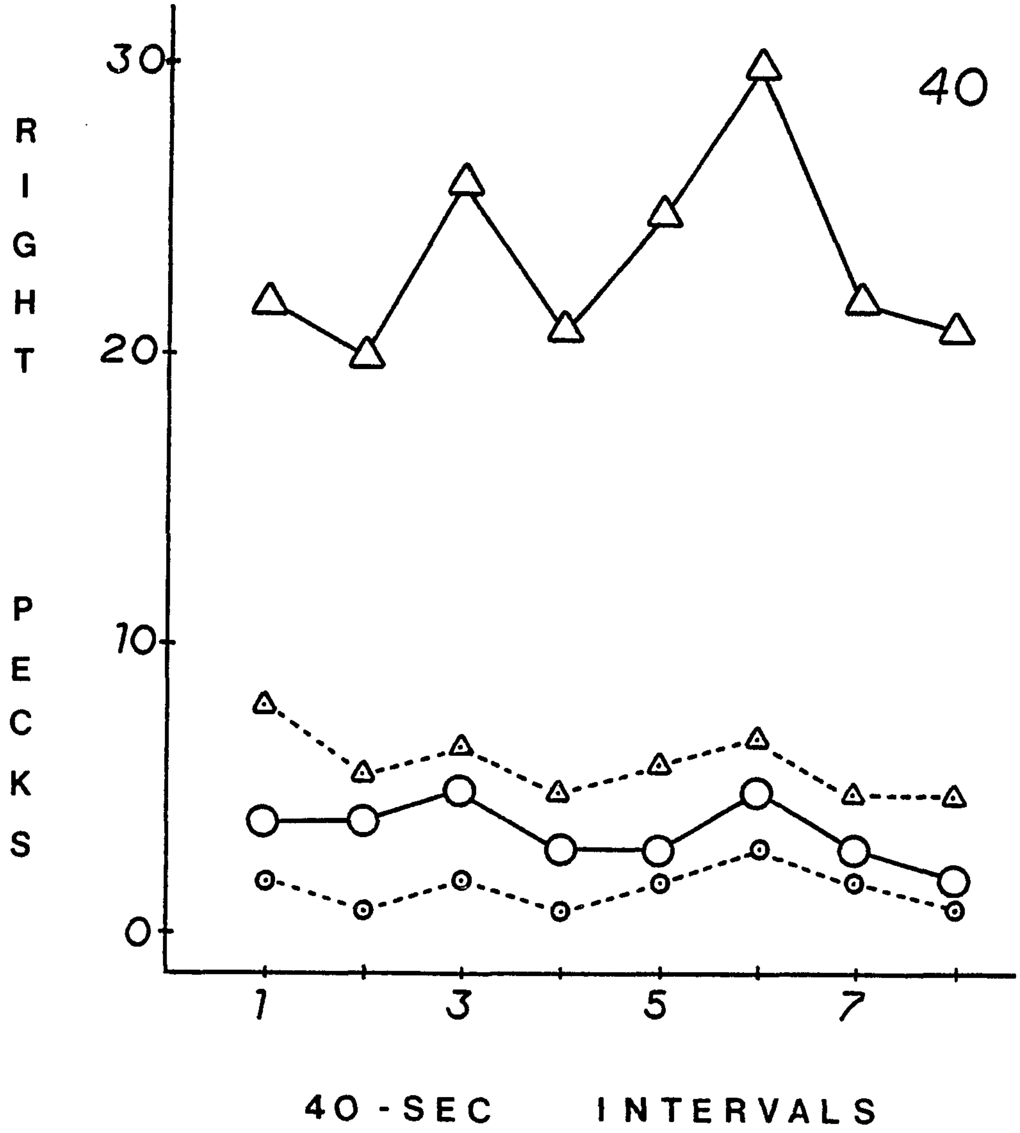


Figure 7.11. Number of right key pecks emitted by bird 40 following achromatic stimuli during successive 40-sec intervals of white or green components for Series 1 test sessions. See legend of Figure 8.8 for details.

the white components for three of the birds, declining sharply after 40 sec and 80 sec for birds 23 and 230, respectively, and gradually over the interval for bird 37. Too much significance probably should not be placed upon these declines, however, due to the small number of responses involved. The initial peak does seem to be present on the first session for birds 230 and 37, but not for bird 23. However, the sampling problem is even more severe for these data.

Discussion

This experiment provided evidence that pigeons experience simple chromatic AEs, as would be expected on the basis of Williams' (1974) data. The fact that these birds reported these "illusory" colors suggests that they should likewise have reported a ME in Experiment II, had they experienced it. (This is assuming, of course, that the birds' behavior was under the control of stimulus chromaticity.)

It is also clear from the results of this experiment that at least some of the birds were quite sensitive to changes in reinforcement contingencies, even with exposure to only one session employing different contingencies. In hind-sight, it may have been wiser to reinforce (with some probability) any response following the observation of achromatic slides during colored components, rather than reinforcing no response in this situation. This may have decreased the likelihood that the birds would detect the change in contingencies.

The data suggested that the aftereffects of chromatic adaptation required less than 40 sec of exposure to the colored light to occur. The time-course of decay of this AE was not clear from the results of this study. Whereas three of the birds showed a decline in errors on achromatic slides after 40 to 80 sec following the beginning of the white component, the declines in most cases were not large, and any trend is difficult to interpret in the light of the small sample of total errors obtained. Williams' birds showed an analogous decline in response rate after only ten sec in white following green periods, which suggests that the AE may have decayed too rapidly to follow its time-course in the present study. As Williams pointed out, however, discrimination of the AE from the training stimuli may have contributed to the decline in response rate evident in his data. Thus, ten sec may have underestimated the decay rate of the AE in his study. It should be noted that individual differences in the subjects' criterion of "chromatic" would also be reflected in different decay rates as estimated from these data. Thus, it is not unreasonable that the birds should have differed in this respect, as for example birds 23 and 230 seem to have done. A further attempt to measure the time-course of decay of a simple chromatic AE, the afterimage, is described in Appendix B.

CHAPTER 8

EXPERIMENT IV. DIMENSIONS OF STIMULUS CONTROL: CHROMATICITY OR FILM TYPE?

In Experiment I, the subjects exhibited conceptual behavior by responding differentially to new instances of the two classes of stimuli, which the experimenter designated as "chromatic" and "achromatic." It is not clear, however, whether the subjects' discrimination performance was under the control of the same stimulus dimension as that of the experimenter, because the two classes of stimuli were prepared with different types of film. Specifically, the "achromatic" set of slides was prepared using black-and-white film (Panatomic-X) whereas the "chromatic" set was prepared using color film (Ektachrome or Kodachrome 40). Because these film types may have differed in a variety of ways other than the chromaticity of the stimulus photographed, such as graininess or background spectral charateristics, the stimulus dimension which actually controlled the pigeons' behavior is an empirical question, one addressed in the present chapter.

When a discriminative stimulus is composed of more than one stimulus attribute, one may determine which aspesct controls behavior by presenting each one separately. For example, following a discrimination training procedure in which pigeons' responses were reinforced in the presence of a triangle on a red background but not in the presence of a circle on a green background, Reynolds (1961) presented each form and color separately. During this test, one pigeon responded almost exclusively to red, while another responded almost exclusively to the triangle. Thus color controlled one bird's behavior, while form controlled the other bird's behavior. Another technique to determine what controls behavior would be to place the potential controlling cues in opposition to each other. For example, Reynolds could have presented green triangles and red circles in the test phase; presumably one of his birds would have pecked the former and the other the latter stimulus. The first test described below used the latter tactic, disassociating object chromaticity from film type by presenting slides of achromatic stimuli photographed with color film or Panatomic-X slides with added color. If object chromaticity controlled behavior, the birds were expected to peck the left key following exposure to the former slides and the right key following exposure to the latter. The reverse would be expected to occur if some other aspect of the slides controlled behavior. In the second test, the stimulus attributes implicated in the first test as controlling behavior were combined, and thus pitted against one another in an attempt to determine whether the center or surround of the slide was more important in controlling behavior. These tests both indicated that some dimension other than object chromaticity controlled the birds' behavior. The third test attempted to test whether this other dimension might be the chromatic differences among the film backgrounds.

General Methods

Subjects

The same four pigeons as served in the previous experiments. Following Experiment III, all birds served in a study (described in Appendix B) designed to measure the time course of after-image decay. This involved the same basic discrimination as the other experiments. Following this, the birds continued to perform the discrimination while being adapted to collars, in preparation for a study which was abandoned due to the results of the present study.

Apparatus

The same experimental chamber as was employed in the previous experiments. Spectral analyses of slides were carried out using a Cary 219 Spectrometer.

Film Base Tests

Methods

Procedure and Stimuli

Film Base Test 1. This test consisted of a single session which included three presentations of each of 70 slides. These included 54 of the previous training slides, half chromatic (in Ektachrome or Kodachrome 40) and half achromatic (in Panatomic-X). Correct responses, as defined previously, continued to be reinforced on a partial reinforcement schedule (probability of reinforcement = .4) following these stimuli. In addition, 16 test slides were included, following which responses were never reinforced. Five types of stimuli were employed: (a) achromatic stimuli photographed with Kodachrome film (4 slides); (b) the same as (a), but from a newly-processed batch of Kodachrome film which appeared to the experimenter chromatically different from the previously processed batch (1 slide); (c) achromatic stimuli photographed with Ektachrome film (4 slides); (d) "pseudo-ME" slides as employed in Experiment II, which consisted of grids associated with desaturated background colors to resemble a human ME, prepared with Ektachrome film (3 slides); (e) "pseudo-ME" slides similar to (d), but prepared by painting Panatomic-X slides (4 slides).

Film Base Test 2. This test, which took place in the session immediately following Film Base Test 1, also consisted of a single session similar to the above test. In this case, six types of test stimuli were employed: (a) A hole was punched (using a standard paper-punch) from each of a Kodachrome and a Panatomic-X slide, the former including achromatic or no stimuli. A circle punched from a

Kodachrome slide was then taped in a hole of a Panatomic-X slide. Three such slides (P-K) were included in the test. (b) Three slides (P-E) were prepared as above, except that a circle from an Ektachrome slide was inserted into a hole in a Panatomic-X slide. (c) On one Panatomic-X slide (P-red), a small hole was cut with a pen-knife, and a small piece of red cellophane was taped over the hole. (d) One slide (K-P) was included in which a circle from a Panatomic-X slide was inserted into a hole in a Kodachrome slide as with P-K and P-E. (e & f) Both types of "pseudo-ME" slides which were presented in Film Base Test 1 (3 each in Ektachrome and Panatomic-X) were again presented. The surrounding areas of the slides were covered with black tape such that only the grids and their associated desaturated colors were visible (P(ME, mask) and E(ME, mask)).

Filters Test 1. During each of three consecutive session, achromatic (Panatomic-X) and chromatic slides were presented with the usual reinforcement contingencies in effect. However, during each session one of three filters was placed over the projector lens, such that the chromaticity of all slides would be affected. The filters used were Kodak Wratten color-correcting filters CC05R, CC10M, and CC10G.

Results

The results of Film Base Test 1 are shown in Table 3.1.

Table 8.1

Percent Right on Film Base Test 1

Type of Stimulus	Approx. No. Presentations	BIRD			
		23	230	37	40
<u>Control</u>:					
Kodachrome[a]	81	80.2	92.8	80.0	70.7
Panatomic-X[a]	81	17.3	11.2	41.0	18.8
<u>Test</u>:					
Kodachrome[b]	12	91.7	83.3	75.0	75.0
K2[c]	3	100.0	100.0	75.0	33.0
Ektachrome[b]	12	63.6	100.0	60.0	69.2
E(ME)[c]	9	77.8	100.0	91.7	62.5
P(ME)[c]	12	8.3	8.3	60.0	0.0

[a] Control Kodachrome and Panatomic-X are the same as "colored" and "achromatic" in previous studies.

[b] Achromatic in terms of stimuli photographed.

[c] See text for description.

The first two rows show the percentage of right responses following exposure to previously presented Kodachrome and Panatomic-X stimuli, and represent the standard to which behavior following the various test stimuli should be compared. The next three rows show the percentage of right responses following achromatic stimuli photographed with color film (K, K2, and E). In general, the birds' responses following these stimuli were similar to those following the control (chromatic) Kodachrome stimuli. In only one case (bird 40 with test stimuli K2) was a bird's behavior more similar to that following the control Panatomic-X stimuli. In fact, in 8 out of 12 cases the percentage of right key pecks following these test stimuli was equal to or higher than that following control Kodachrome stimuli. It appears, then, that the birds' discrimination behavior was controlled not by the chromaticity of the object photographed, but by some aspect of film type. This is even more clear in the last two rows of Table 8.1, which compare the data for pseudo-ME test slides prepared with either Panatomic-X or Ektachrome film. In the case of the E(ME) stimuli, the birds tended to peck the right key, as would be expected given that they had already experienced training with these stimuli. In the case of the P(ME) stimuli, where a colored object occurred on Panatomic-X film, three out of four birds were even less likely to peck the right key than they were following control Panatomic-X stimuli. The only exception is with Bird 37, whose percentage of right key pecks was roughly mid-way between those following the two types of control stimuli.

The results of Film Base Test 2 are presented in Table 8.2. Again, the first two rows represent the control conditions. Presented in the next four rows are the results of test stimuli in which the possible sources of stimulus control suggested by the results of Film Base 1 were combined. With test stimuli P-K and P-E, three out of four birds' behavior was more similar to that exhibited with the control Panatomic-X stimuli, while bird 230 showed the opposite result. This suggests that the surrounding film type, or alternatively the film type covering the largest area, controlled the behavior of most birds. In the case of stimulus P-red, three out of four birds again pecked the left key in most cases. For birds 23 and 230 this tendency was more pronounced than in the case of stimuli P-K and P-E, indicating that the total proportion of Panatomic-X film (which was greater for P-K and P-E than for P-red) may have controlled behavior for these birds. In the case of bird 40, on the other hand, the P-red stimulus was typically followed by a right key-peck, which is consistent with the suggestion that the saturation of the "colored" (non-Panatomic-X) portion of the slide may have contributed to stimulus control. In the case of stimulus K-P, most birds tended to peck the right key, with bird 230 again

Table 8.2

Percent Right on Film Base Test 2

Type of Stimulus	Approx. No. Presentations	BIRD 23	230	37	40
Control[a]					
Kodachrome	81	74.4	93.9	82.7	78.4
Panatomic-X	81	6.1	42.0	27.4	21.2
Test[b]					
P-K	9	25.0	77.8	50.0	11.1
P-E	9	22.2	77.8	33.3	33.3
P-red	3	0.0	33.3	33.3	66.7
K-P	3	100.0	66.7	66.7	100.0
E(ME, mask)	9	33.3	77.8	55.6	77.8
P(ME, mask)	9	0.0	22.2	20.2	0.0

[a] Same as in Film Base Test 1.

[b] See text for description.

being an exception with the proportion of right key pecks falling roughly mid-way between the two control stimulus types. This pattern is generally consistent with the pattern of responses to stimuli P-K, P-E, and P-red which suggested that most birds' behavior was controlled by either the background film type or the film type occupying the largest area.

In test stimuli E(ME, mask) and P(ME, mask), an attempt was made to focus the birds' attention upon the area of the stimuli containing color, independent of film type, by masking the surrounding areas. Surprisingly, this generally had the effect of increasing the likelihood that the birds would peck the left key for both the E(ME, mask) and the P(ME, mask) stimuli, as compared with the results with the E(ME) and P(ME) stimuli from Film Base Test 1. The impliciatons of these results are unclear.

The question arises as to what it might be about the different types of film which could control the pigeons' behavior. A likely candidate, upon casual inspection of the slides, is the different tinge of color present in the film backgrounds. Figure 8.1 shows the spectral characteristics of representative examples of each film type, showing absorptance as a function of wavelength. The Ektachrome and Kodachrome slides chosen were photographs of white, patternless paper. The figure shows that, indeed, there are chromatic differences among the three types of film. The

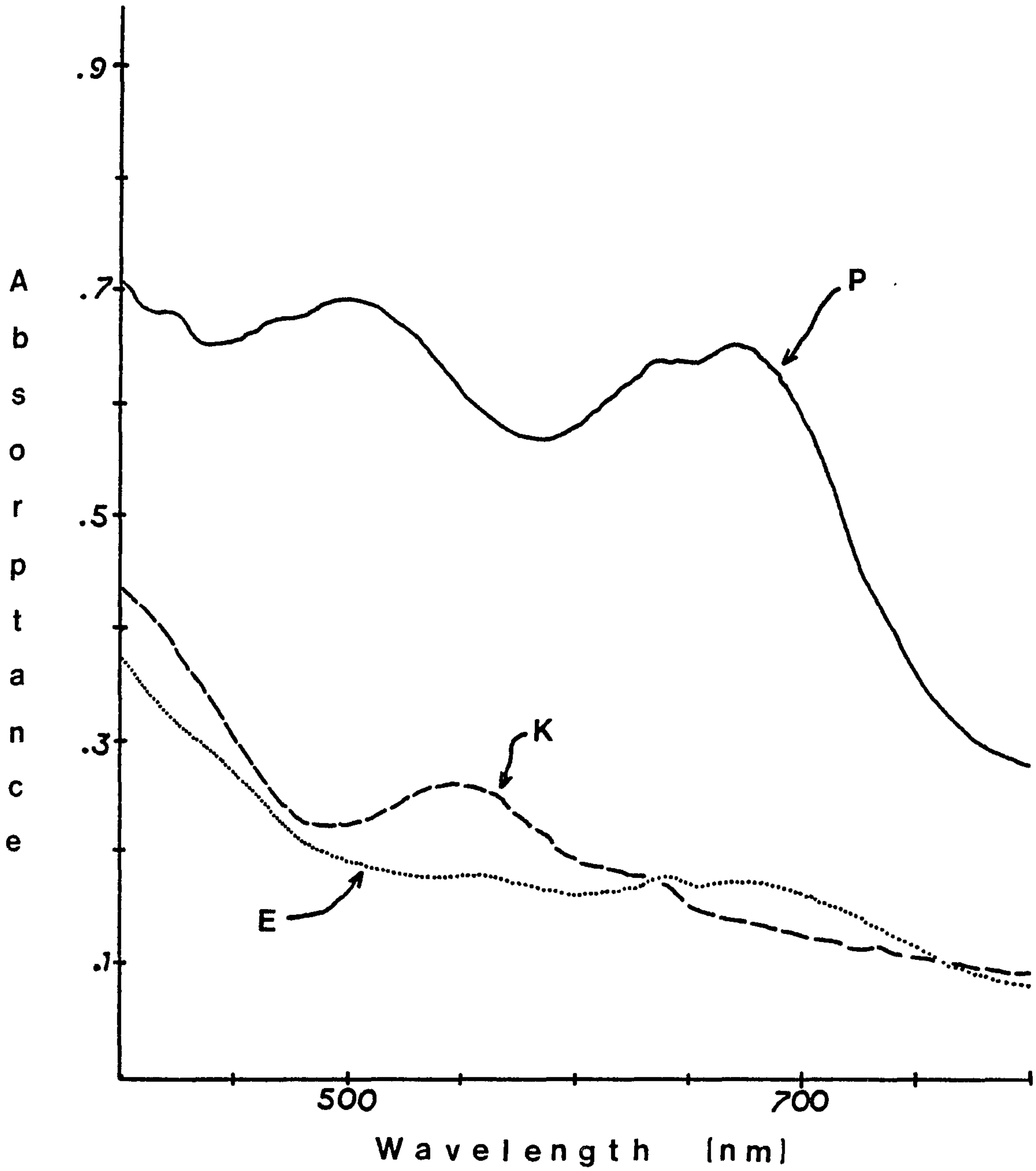


Figure 8.1. Spectral analyses of three "achromatic" slides using Panatomic-X (P), Kodachrome (K) or Ektachrome (E) film.

major differences seem to lie in two regions: 520-600 nm (green and yellow), where Panatomic-X shows a relative decrease in absorptance, and 620-700 nm (red), where Panatomic-X shows a relative increase in absorptance. Another possible area of difference is 480-520 nm (blue-green), where Panatomic-X shows a relative increase in absorptance. If these chromatic differences did, indeed, control the birds' behavior, it would seem reasonable that color filters passing more light in the red or green regions might be expected to disrupt or alter the discrimination performance. Filter Test 1 was thus carried out.

The results of Filters Test 1 are presented in Table 8.3. In 15 out of 23 cases, the percentage of right key pecks following the two classes of stimuli was within the baseline range, suggesting that the filters had little effect upon responding. This might be interpreted as indicating that the discrimination was a relative one such as might be expected if pigeons experience color constancy as do humans. Alternatively, the results might simply indicate that the filters were too weak to make any discriminable difference in the appearance of the slides.

Discussion

The results of the two Film Base Tests indicated that the birds' discrimination behavior was controlled by some aspect of the film types (Panatomic-X versus Kodachrome or

Table 8.3

Percent Right on Filters Test 1

Bird and Film Type	Baseline (7 days) Range	Baseline (7 days) Median	Test Sessions Filter Employed CC05R	CC10M	CC10G
Bird 23					
Kodachrome	84.0- 90.8	88.5	81.0	71.2	92.4
Panatomic-X	7.7- 17.1	9.7	1.1	0.0	7.4
Bird 230					
Kodachrome	93.0-100.0	96.6	96.3	92.3	82.3
Panatomic-X	0.0- 30.0	1.3	3.2	2.4	2.2
Bird 37					
Kodachrome	56.2- 82.5	68.0	79.1	75.3	86.0
Panatomic-X	5.6- 49.1	21.4	7.2	18.1	13.4
Bird 40					
Kodachrome	48.0-100.0	86.3	80.7	59.0	91.8
Panatomic-X	1.8- 31.5	11.6	14.3	2.4	9.3

Ektachrome), rather than by the chromaticity of the object photographed. The spectral analysis of examples of the three types of slides indicated that a potential basis for stimulus control by film type lay in the spectral characteristics of the film backgrounds. The results of Filters Test 1 were not conclusive in implicating this as the basis of stimulus control.

Chromaticity with Film Type Controlled

The results reported above call into question the interpretation of Experiment II. Specifically, the test slides upon which a ME might have appeared were prepared with Panatomic-X film, which we have shown to control left key pecks at a later stage of this research. The responses of the birds following the P(ME) and E(ME) test slides in the preceding study suggest further that any color which might have been apparent on a test slide which was as desaturated as that of a human ME (such as mimicked in the pseudo-ME slides) would have been insufficient to lead to a right key peck. (This problem is discussed further in Chapter 9.) It would appear, then, that in order to correctly test for a ME, the birds would have to be trained to discriminate between presence and absence of color on film of the same type. This was attempted in the following study.

Methods

Stimuli

Sets of colored and achromatic slides were prepared for use as training stimuli, all with Kodachrome 40 film. The slides were similar to those used in previous studies in terms of patterns and colors used. The achromatic set consisted of photographs of black-and-white patterns. Sets of colored and achromatic slides were also prepared for use in a transfer test. These consisted of novel patterns and colors, similar to Transfer Test 1 in Experiment I.

Procedure

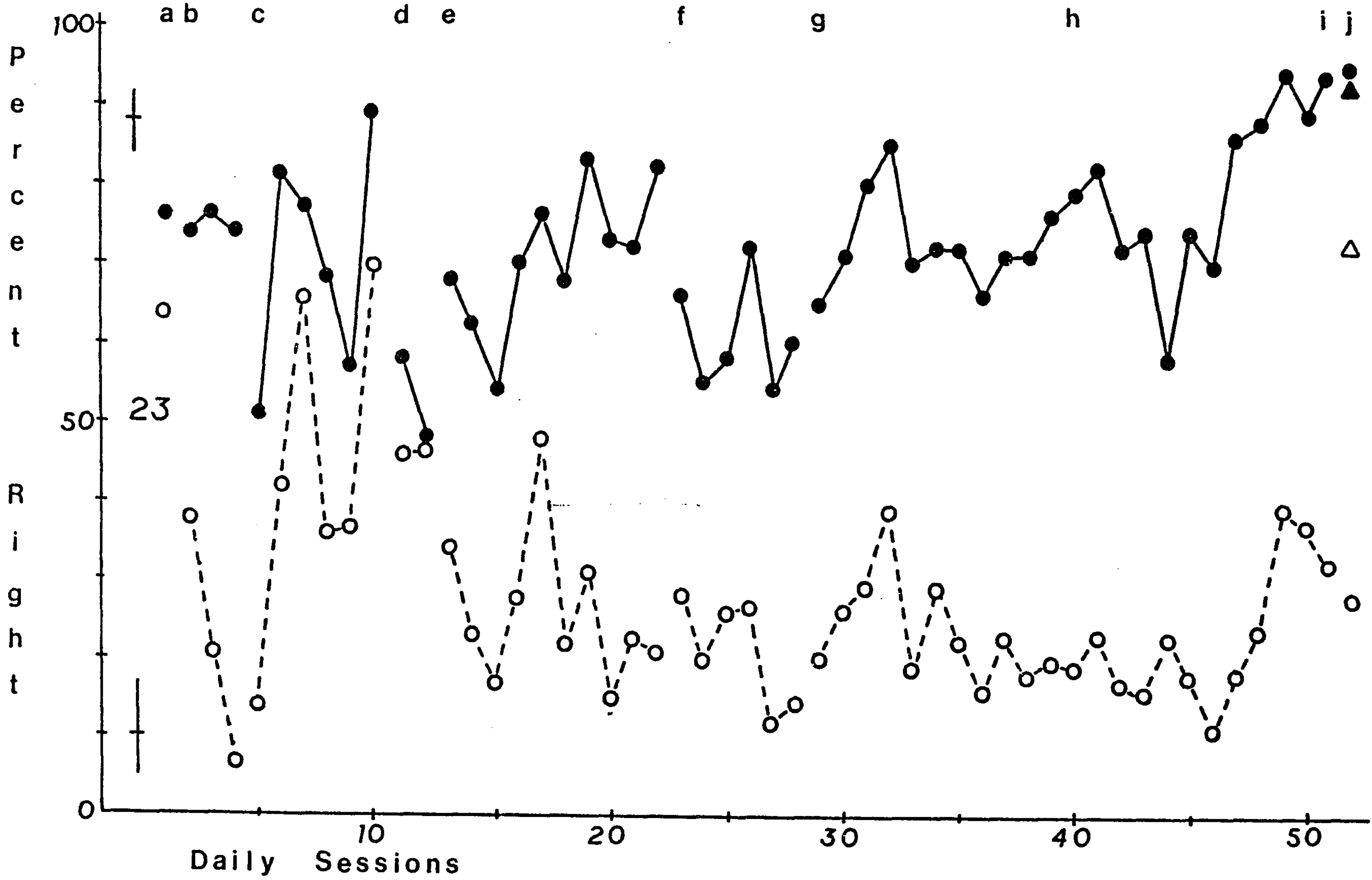
Training. The aim during training was to teach the subjects the new discrimination as quickly as possible. To this end, a number of procedures were introduced, including gradually increasing the difficulty of the discrimination and adding a penalty for incorrect responses. The penalty consisted first of a 30-sec time out during which the house light was extinguished and inserting the head into the sleeve had no scheduled consequences. At a later point, this penalty was signalled by a flashing house light, to make it immediately discriminable from an inter-trial interval. Correction procedures were also sometimes in effect, which consisted either of the slide failing to advance following errors, or of forced exposure to the correct response. In the latter correction procedure, following an error the slide did not advance and only the correct key was lit on the subsequent trial. This procedure is similar to that described by Chase (Note 1). The correction trials were not included in calculating the percentage of right key pecks. These procedures and their order of introduction will be described in detail in the Results section. Approximately 50 daily sessions of training, consisting of 100 to 300 trials, were conducted.

Transfer Test. The transfer test consisted of a single session. Equal numbers of four types of stimuli (20 each) were presented during the test: old colored slides, new colored slides, old achromatic slides, and new achromatic slides. Each slide was presented three times during the session.

Results

The course of acquisition and the results of the transfer test are presented in Figures 8.2 through 8.5, which show the percentage of right key pecks following colored and achromatic stimuli across sessions. On the first day of acquisition (point a in the figures), all novel training stimuli were employed. Here discrimination was generally poor, and two of the birds (37 and 40) actually pecked the right key more following achromatic than following colored stimuli. During the next three sessions (b), the set of colored stimuli consisted of previously-encountered slides with saturated red or green backgrounds; all birds quickly acquired this easier

Figure 8.2. Acquisition of discrimination between colored and achromatic Kodachrome stimuli for bird 23. Filled and open circles are for colored and achromatic stimuli, respectively. Bars at left indicate the seven-day range and median for the previous Kodachrome (upper bar) versus Panatomic-X (lower bar) discrimination. Letters indicate procedural changes, which are described in the text.



a b
c
d e
f
g
h
i j
100
50
0
P
e
r
c
e
n
t
R
i
g
h
t
23
10
20
30
40
50
Daily Sessions

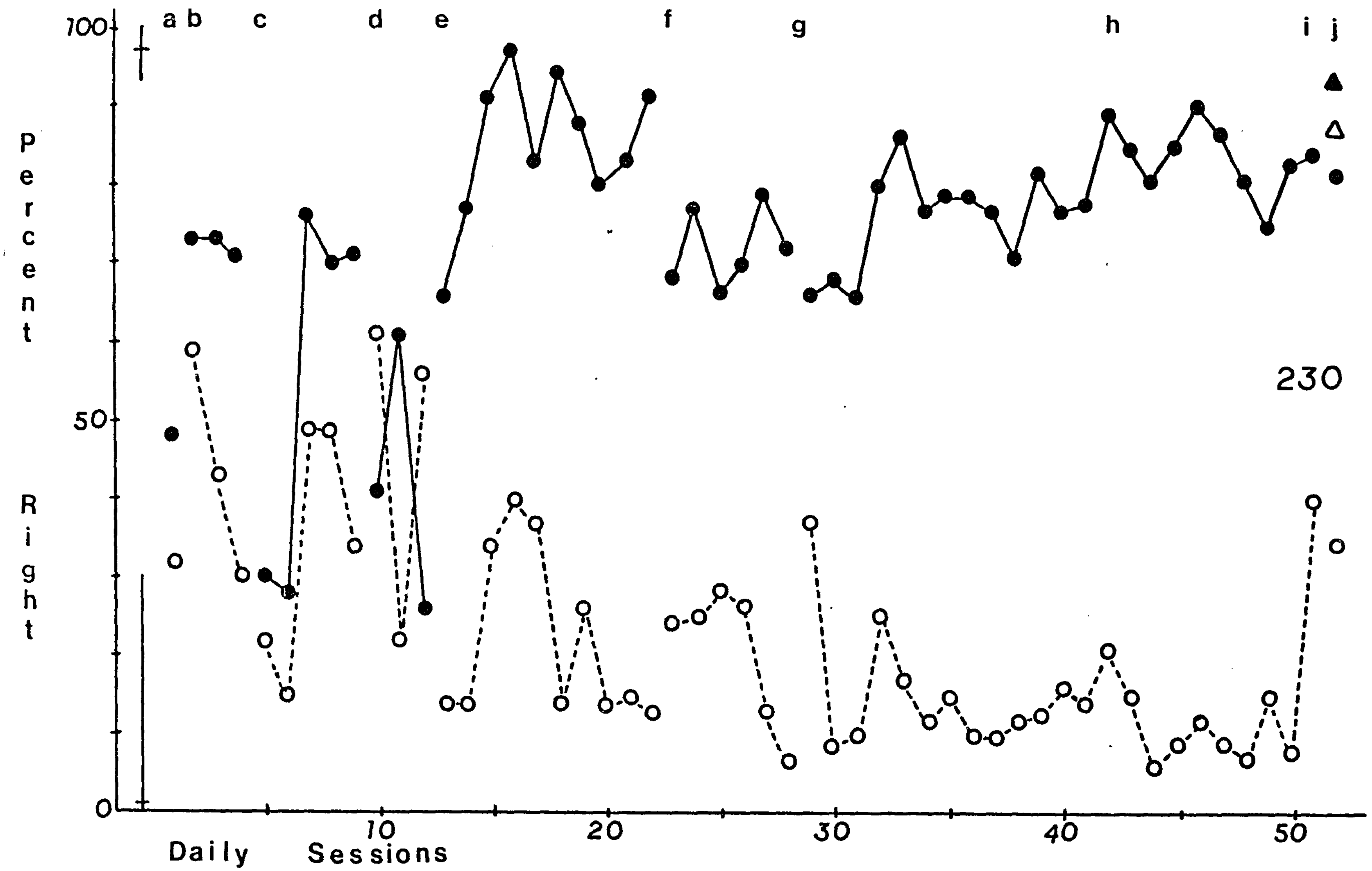


Figure 8.3. Acquisition of discrimination between colored and achromatic Kodachrome stimuli for bird 230. See legend of Figure 9.2 for details.

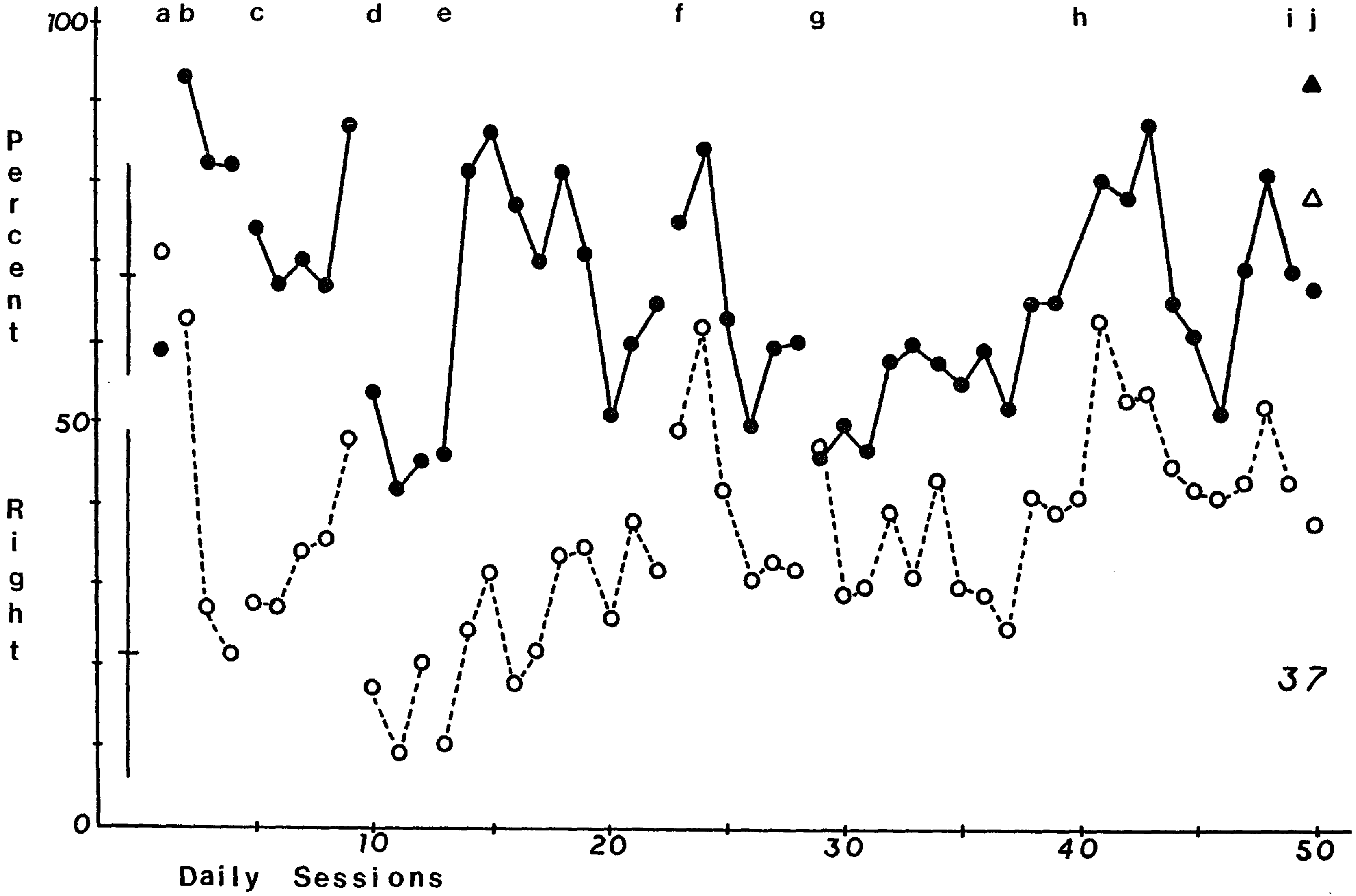


Figure 8.4. Acquisition of discrimination between colored and achromatic Kodachrome stimuli for bird 37. See legend of Figure 9.2 for details.

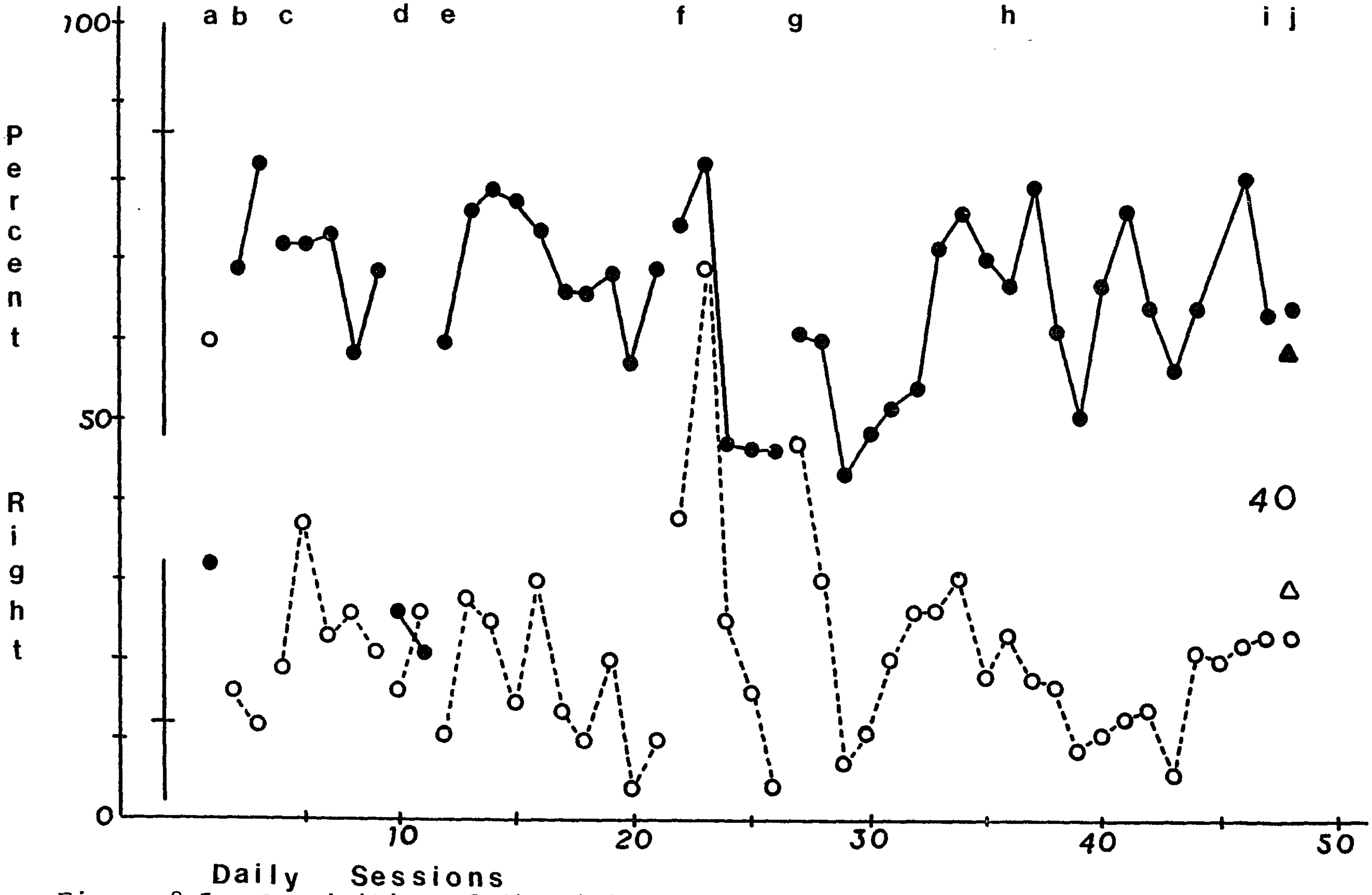


Figure 8.5. Acquisition of discrimination between colored and achromatic Kodachrome stimuli for bird 40. See legend of Figure 9.2 for details.

discrimination. On the fith session (c), half of the easy colored slides were replaced by new stimuli; this set of stimuli was employed for five sessions. Reasonable discrimination behavior was exhibited within the five sessions for all birds except 23. During the next two sessions (d), a cardboard mask was placed over the screen, such that only the central portion of each slide was visible. It was thought that the mask might make the discrimination easier since the colored objects were generally located in that portion of the slides. However, except for bird 37, the birds' discrimination behavior completely fell apart; thus the procedure was abandoned.[1]

Ten additional days of training with the same set of slides (e) was carried out. At this time (f) the penalty for errors was also introduced. On session 23 (g), five additional easy colored slides were removed and replaced by new slides, which proved especially disruptive for birds 37 and 40. After six sessions (h), ten more new colored stimuli were substituted for easier slides; ten of the achromatic slides were also replaced by new stimuli. Twenty-two sessions of training with this set of stimuli were carried out, during which time the flashing house light was also added during penalties for errors. It should be

---

[1] This poor discrimination behavior when the slides were masked might account for the pattern of behavior exhibited following P(ME, mask) and E(ME, mask) test stimuli during Film Base Test 2 if a left key bias were assumed.

noted that although all birds acquired the discrimination, the level of accuracy achieved by each was not as good as his previous baseline, and was especially poor for bird 37.

On session 51 (i), ten new slides (five colored and five achromatic) were again added, and since little disruption occurred the transfer test was carried out the next day (j). The results of this transfer test were not encouraging: Although every bird showed a higher proportion of right key pecks following new colored slides than following new achromatic slides, the separation was much smaller than that between the two types of old slides. Indeed, birds 230 and 37 were more likely to peck the right key following new achromatic slides than following old colored slides, and for bird 23 the proportion of right pecks following new achromatic slides was more similar to that following either type of colored slide than to that following old achromatic slides. Only in the case of bird 40 was reasonable transfer acheived, in the sense that the behavior following new colored and ahcromatic stimuli was similar to that following old colored and achromatic stimuli.

Discussion

Given the vast amount of training that the birds had experienced on the Panatomic-X versus Kodachrome or Ektachrome discrimination, and the likelihood that this discrimination was based upon the chromatic differences between the two classes of stimuli, a potential existed for either positive or negative transfer to the discrimination of the present study. Unfortunately, the latter seemed to predominate. Although the discrimination was acquired to some level of accuracy by all birds, reasonable transfer to novel stimuli was not exhibited by most birds. It thus seems likely that the birds had learned the appropriate response to make in the presence of each slide, rather than acquiring a general concept. Vaughan and Green (Note 6) have recently reported that pigeons are capable of such memorization with up to 400 stimuli randomly assigned to one of two stimulus classes. In their study, discrimination behavior with each new set of 30 slides was typically acquired in only three to five sessions, with two exposures to a slide per session. The birds in the present study obviously acquired the discrimination much more slowly than this. However, Vaughan and Greene employed slides of natural scenes in their study, and their birds had considerably more trouble acquiring a similar discrimination using slides of random shapes: In this case only one of three birds acquired the discrimination after 200 sessions. The stimuli used in the present study are similar to Vaughan and Greene's random shapes, which probably contributed to the relatively slow rate of acquisition of the discrimination.

It would appear, then, that the birds' histories have made it difficult for them to acquire a chromaticity concept, with type of film eliminated as a confounding variable. It would seem that a set of naive birds would be more likely to acquire the concept.[1]

Filters Test 2

It was suggested earlier that a possible basis upon which Panatomic-X slides were discriminated from those made with other types of film was the chromatic difference between them. However, it is still possible that some other aspect of the slides, such as graininess, may have served as the relevant dimension of stimulus control. In the present study, this issue was further explored. Specifically, Kodak Wratten color correcting filters were sandwiched with each type of slide, in an attempt to make Panatomic-X slides appear chromatically similar to Kodachrome, and vice versa.

Methods

Retraining. The birds were given eleven sessions with 250 to 300 trials per session of retraining on the Panatomic-X versus Kodachrome discrimination, in which left and right pecks were reinforced following Panatomic-X and

---

[1] Discrimination training was continued for another 17 sessions with bird 40, who had exhibited the best evidence of having acquired a chromaticity concept on the transfer test, in the hopes that a test for the ME could be performed. His discrimination behavior, however, continued at a low level of accuracy, so training was discontinued.

Kodachrome slides, respectively. The set of Kodachrome slides included both colored slides and slides which had been designated as achromatic in the previous study. Note that the contingencies of reinforcement for the latter type of Kodachrome slide were the opposite of those in effect during the immediately preceding study.

Filters Test. The test consisted of a single session, during which 53 of the retraining (control) stimuli, 26 Kodachrome and 27 Panatomic-X, and 3 each of 9 types of test stimuli were presented, each three times during the session. Responses following control stimuli were reinforced as during retraining; no reinforcement was available for responses following test slides. Five types of test stimuli used Kodachrome slides (achromatic, in terms of object photographed) sandwiched with one of four Kodak Wratten color correcting magenta filters of varying saturation (CC05M, CC10M, CC20M, CC40M) or with no filter. The other four types of test stimuli employed Panatomic-X slides sandwiched with the corresponding Kodak Wratten color correcting green filters (CC05G, CC10G, CC20G, CC40G). Each of the nine types of slides employed one each of three patterns.

Results

Figures 8.6 through 8.9 present the percentage of right key pecks for Kodachrome and Panatomic-X slides during retraining. The traingles indicate performance on those Kodachrome slides previously classified as achromatic, which were to be responded to differently than during the preceding study. By the end of retraining, reasonably good discrimination performance was exhibited by all birds, and their behavior following the achromatic Kodachrome slides was similar to that following other Kodachrome slides.

The results of the filters test are presented in Table 8.4. In all cases, behavior following Kodachrome test slides seemed to be little affected by the addition of the filters. On the other hand, the addition of the two most saturated filters to the Panatomic-X test slides caused behavior to resemble that following the Kodachrome slides.

The data in Table 8.4 are plotted in Figures 8.10 through 8.13 as a function of the filter number used in the test slides. (K and P slides with no added filters are placed at zero.) While saturation of the filters does increase with filter number, this scale should at best be interpreted as an ordinal level scale for the pigeon. The clearest trend evident in these figures is the increase in percent right with increasing filter number on Panatomic-X test slides. Two other features of the data, however, also deserve mention. First, for two or three of the four birds

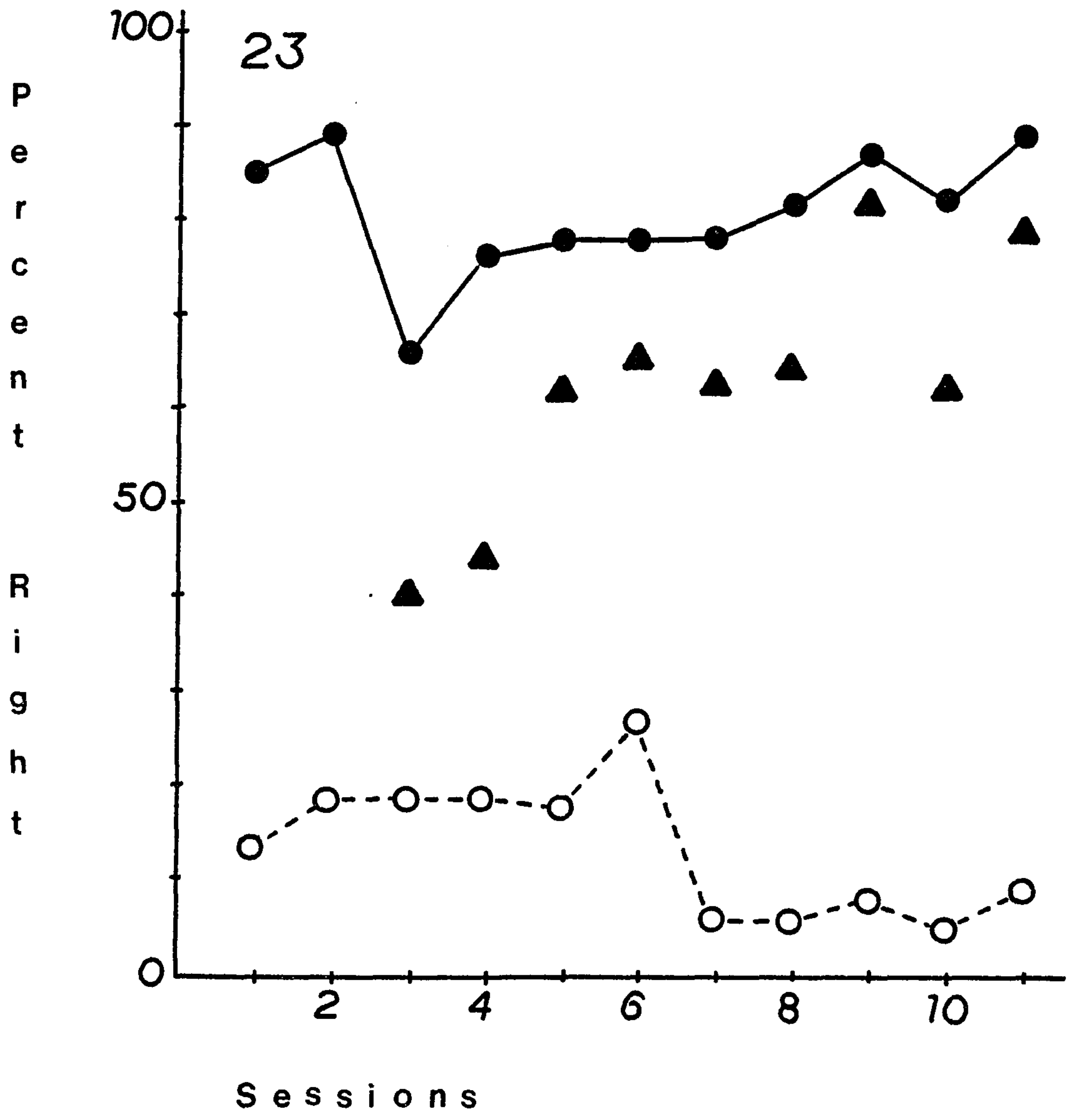


Figure 8.6. Percentage of right key pecks during retraining of the Kodachrome versus Panatomic-X discrimination for bird 23. Filled symbols are for Kodachrome slides: triangles for those designated as "achromatic" in the previous training period, circles for colored stimuli. Open circles are for Panatomic-X slides.

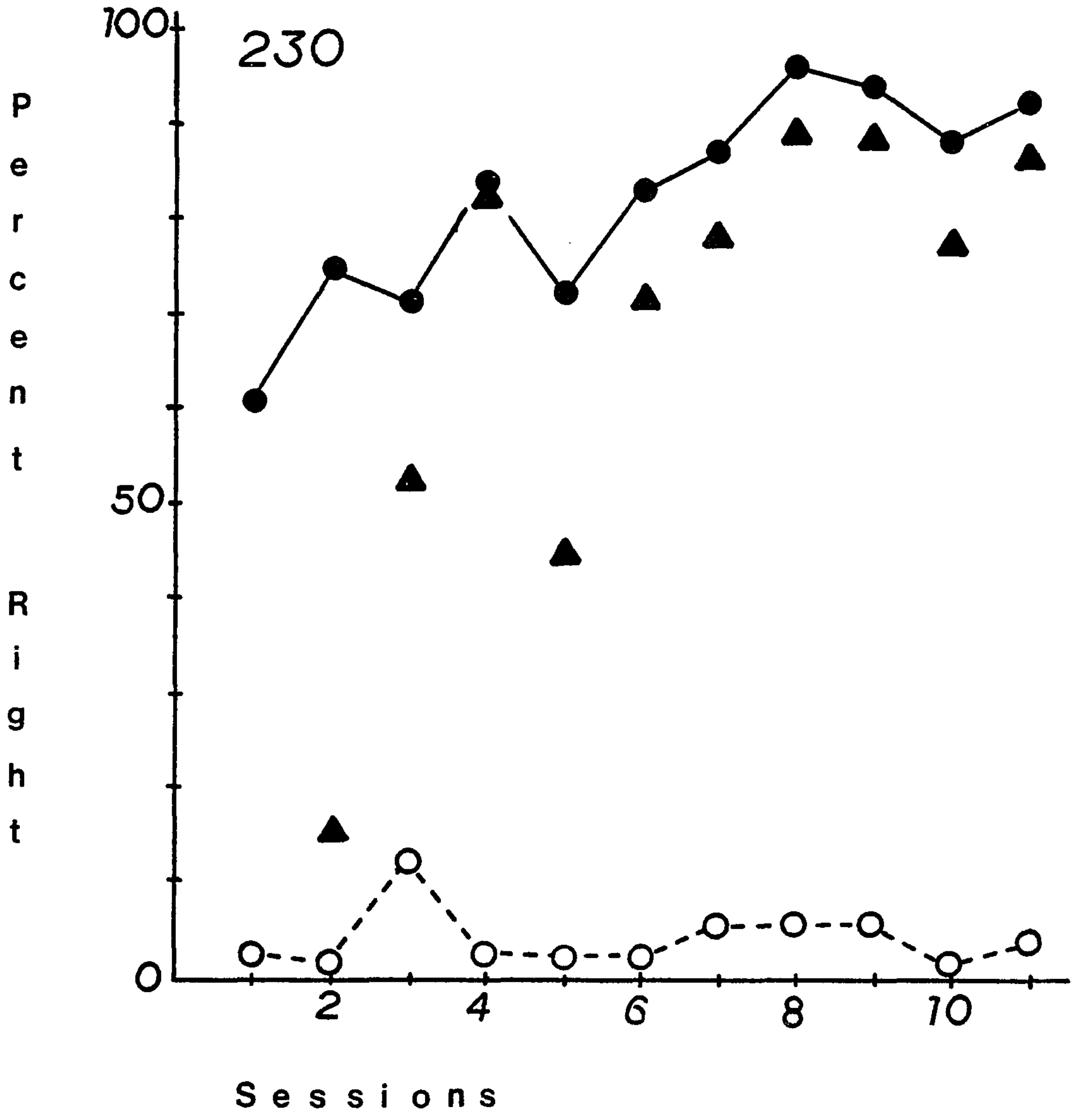


Figure 8.7. Percentage of right key pecks during retraining of the Kodachrome versus Panatomic-X discrimination for bird 230. See legend of Figure 9.6 for details.

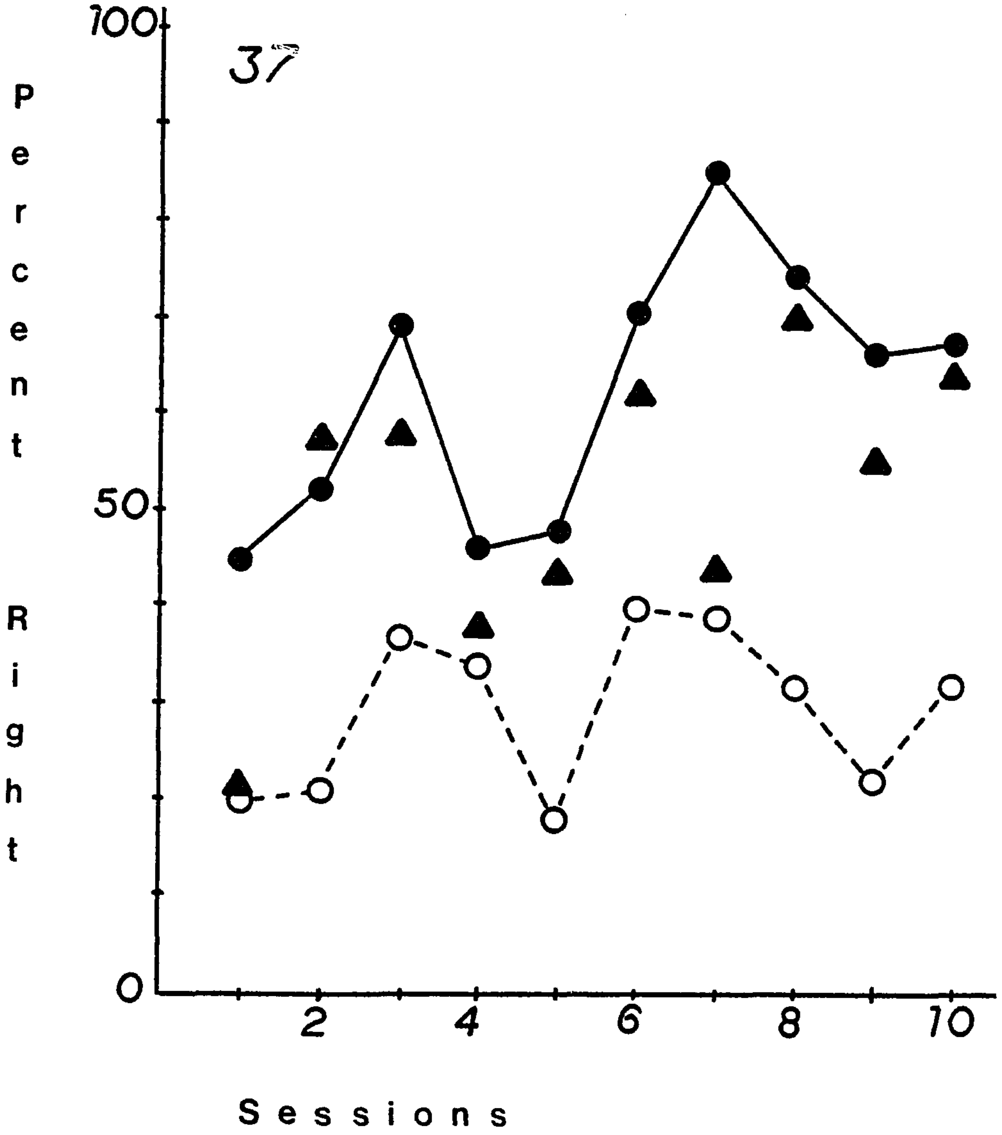


Figure 8.8. Percentage of right key pecks during retraining of the Kodachrome versus Panatomic-X discrimination for bird 37. See legend of Figure 9.6 for details.

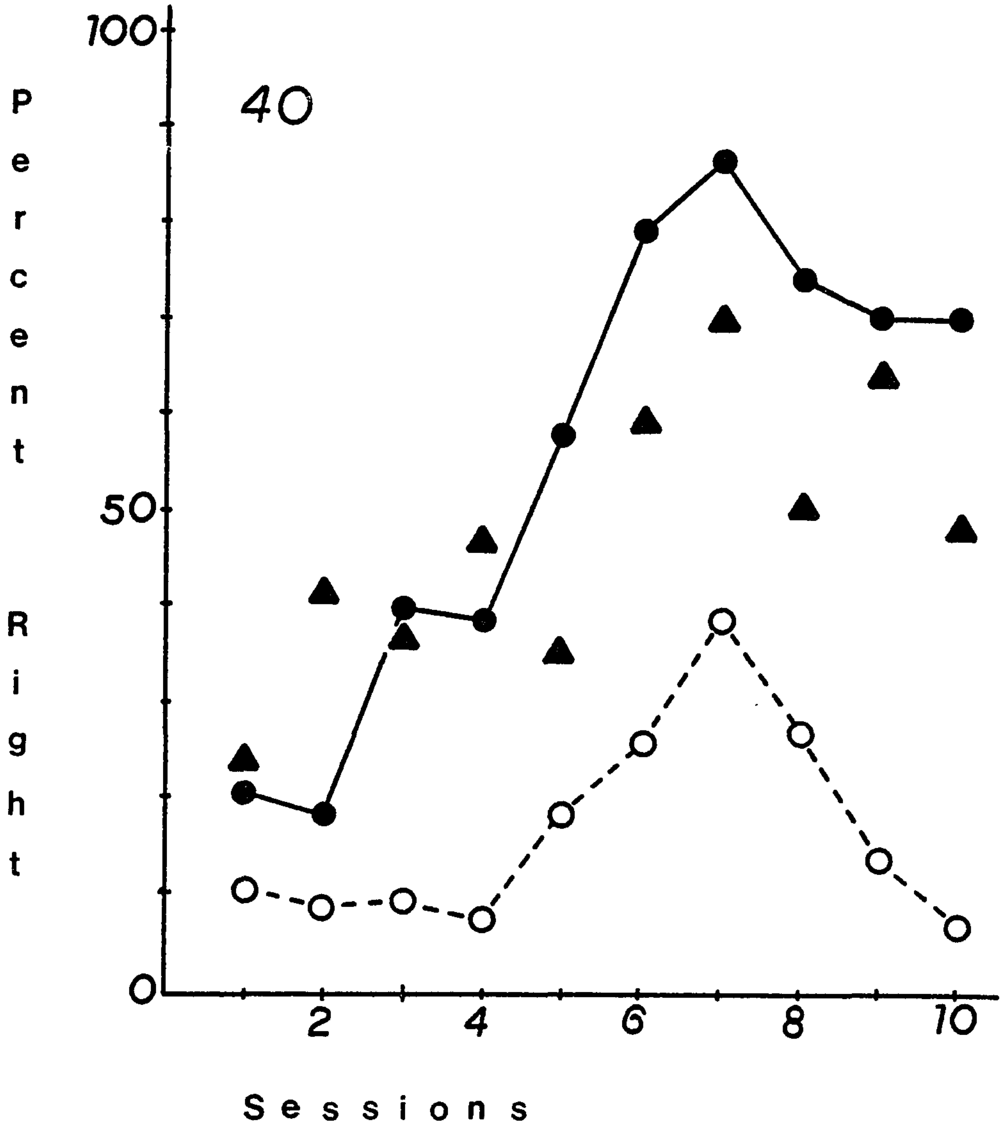


Figure 8.9. Percentage of right key pecks during retraining of the Kodachrome versus Panatomic-X discrimination for bird 40. See legend of Figure 9.6 for details.

Table 8.4

Percent Right During Filters Test 2

Type of Stimulus		Bird 23	 230	 37	 40
Control:	Kodachrome	96.0	85.5	81.4	91.8
	Panatomic-X	12.8	2.4	47.6	20.5
K Test:	no filter	100.0	100.0	88.9	88.9
	CC05M	88.9	77.8	77.8	90.0
	CC10M	100.0	80.0	100.0	77.8
	CC20M	100.0	77.8	88.9	90.0
	CC40M	100.0	88.9	87.5	80.0
P Test:	CC05G	44.4	0.0	55.6	50.0
	CC10G	11.1	0.0	33.3	33.3
	CC20G	66.7	40.0	66.7	77.8
	CC40G	100.0	80.0	77.8	90.0

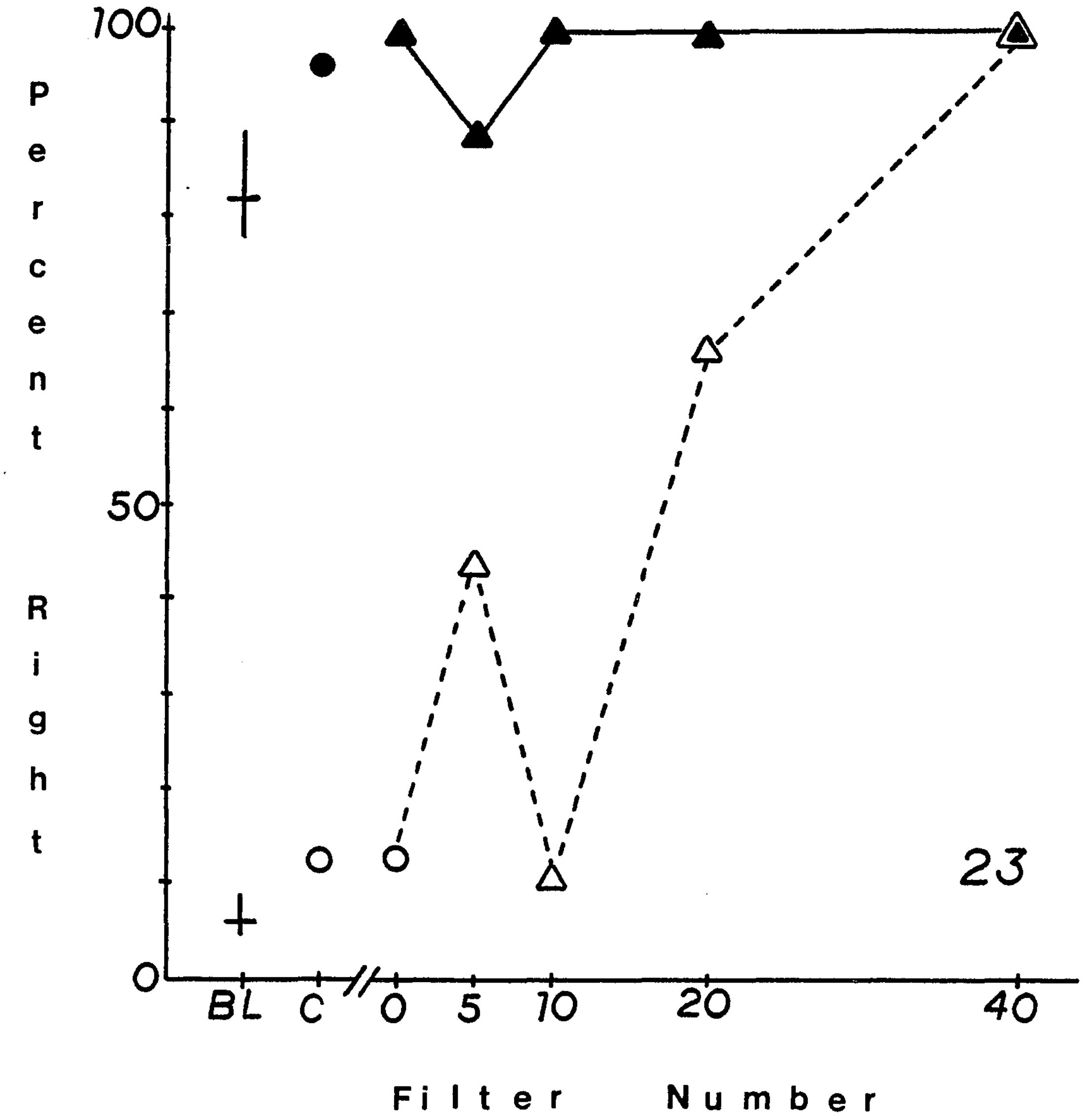


Figure 8.10. Percentage of right key pecks as a function of the filter number used in test slides during Filters Test 2 for bird 23. Filled symbols are for Kodachrome film, open symbols for Panatomic-X film; triangles are for test stimuli, circles for control (C) stimuli. Bars at left show the range and median of the previous seven baseline (BL) sessions for Kodachrome (above) and Panatomic-X (below) stimuli.

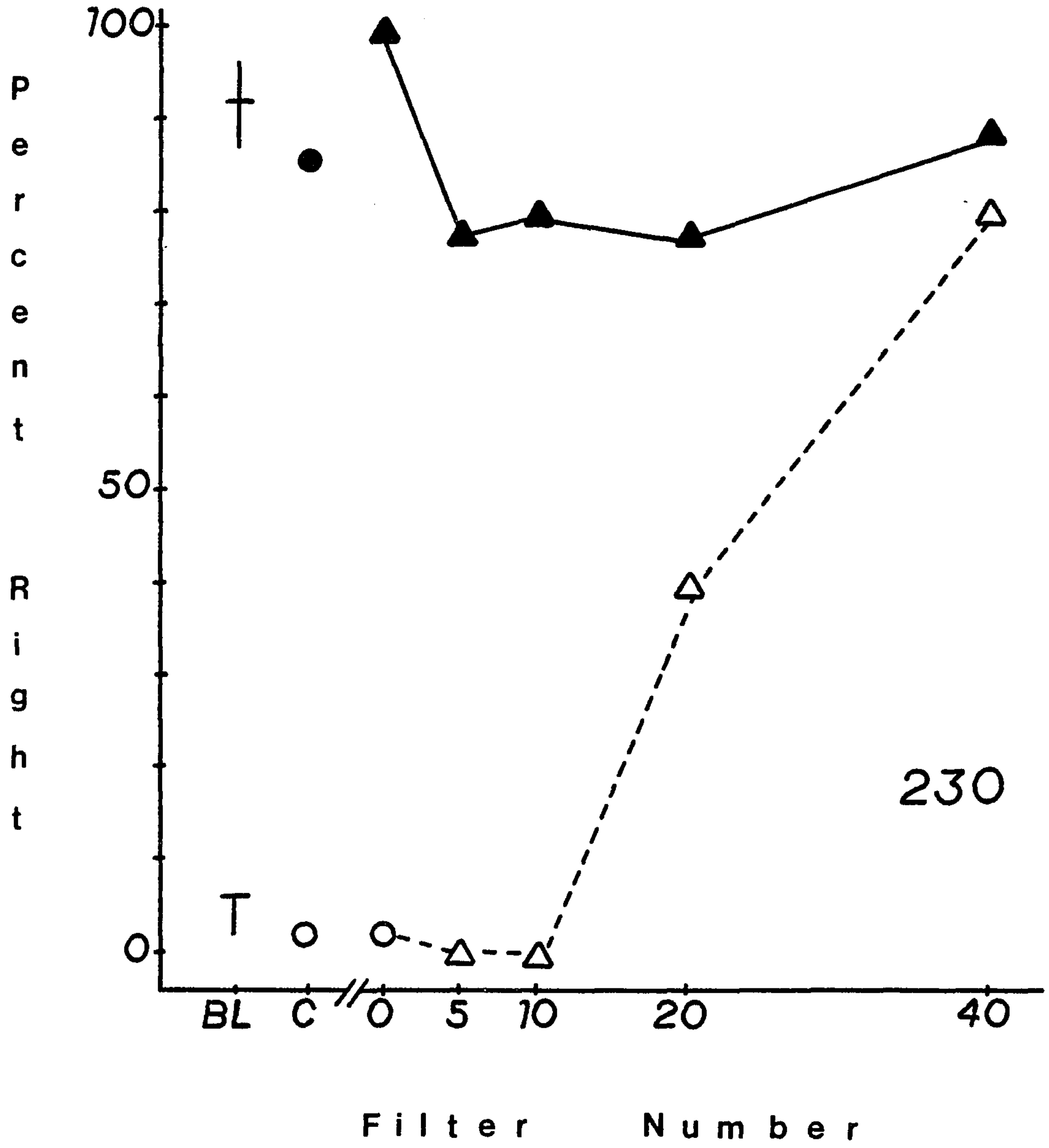


Figure 8.11. Percentage of right key pecks as a function of the filter number used in test slides during Filters Test 2 for bird 230. See legend of Figure 9.10 for details.

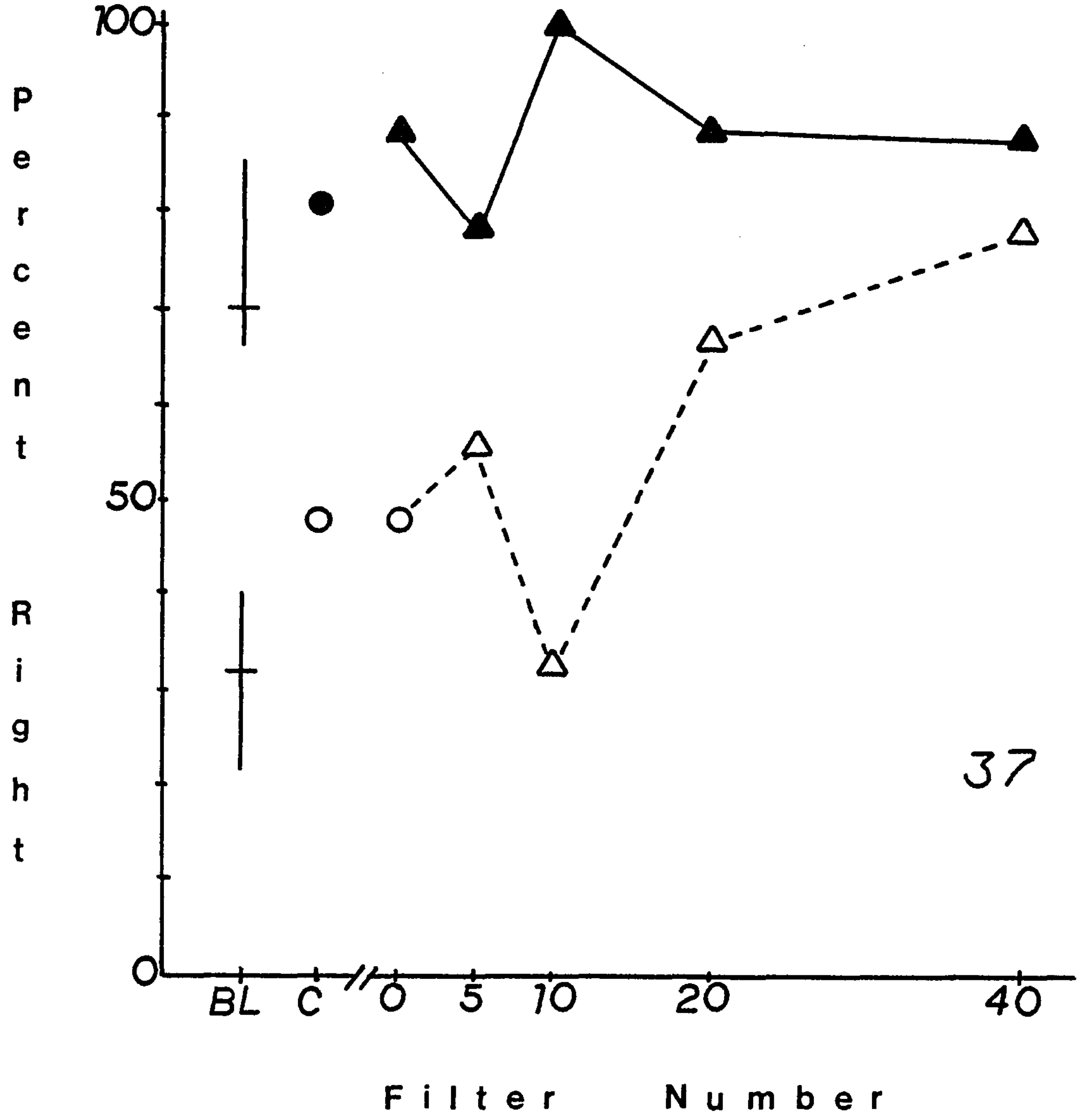


Figure 8.12. Percentage of right key pecks as a function of the filter number used in test slides during Filters Test 2 for bird 37. See legend of Figure 9.10 for details.

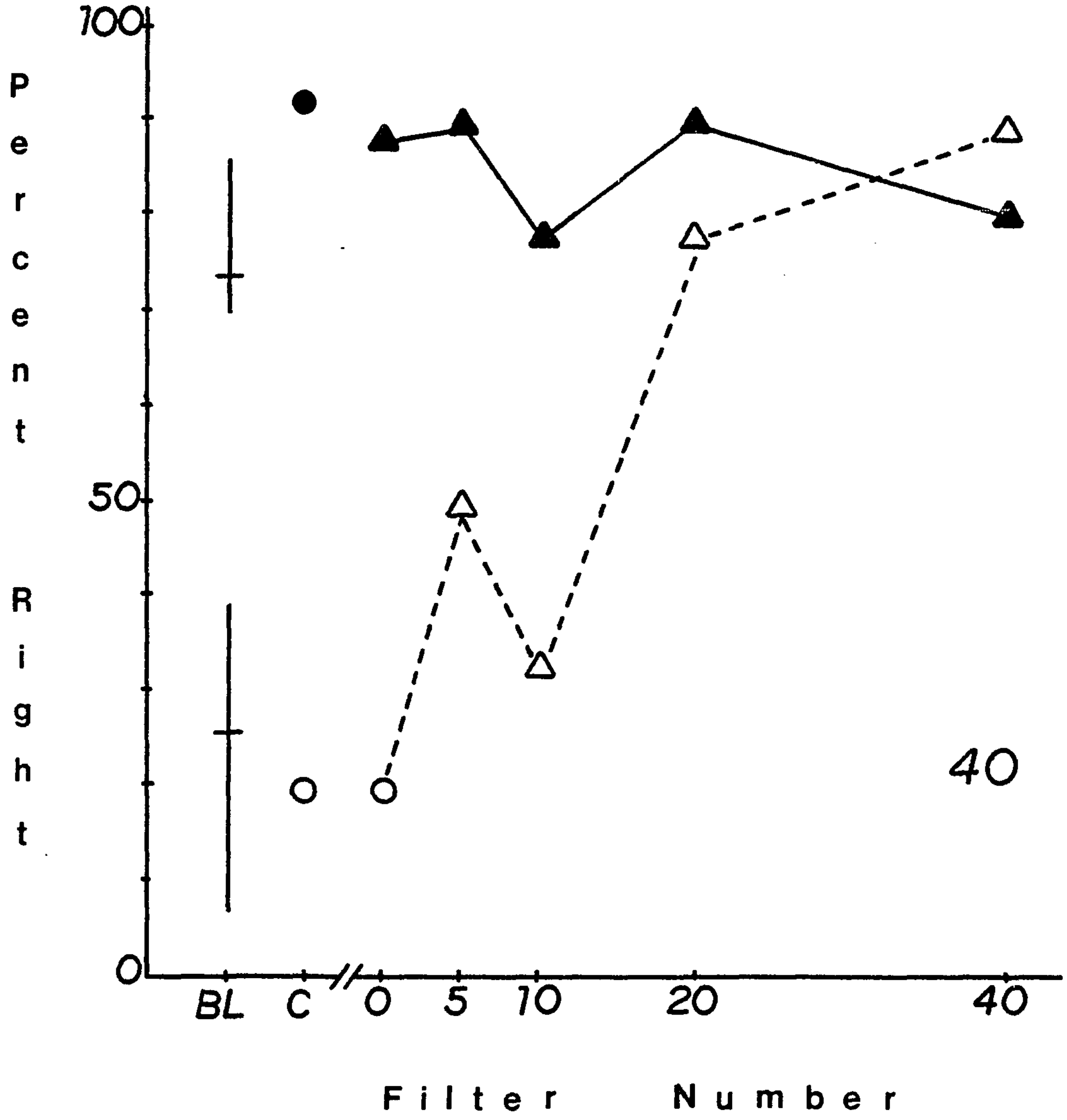


Figure 8.13. Percentage of right key pecks as a function of the filter number used in test slides during Filters Test 2 for bird 40. See legend of Figure 9.10 for details.

(23, 40 and possibly 37) the percentage of right responses is higher following CC05G Panatomic-X test slides than following either CC10G Panatomic-X test slides or Panatomic-X slides with no filter (control slides). Similarly, there is a slight decrement in the percent right for CC05M Kodachrome test slides for three of the birds (the exception is 40). It may be that these two types of test slides were most successful in mimicking (for the pigeon) the background of the achromatic Kodachrome and the Panatomic-X slides, respectively. Comparing spectral analyses of these slides is not especially instructive in interpreting these two reversals (see Appendix C).

Discussion

The results of Filters Test 2 showed that when filters of sufficient saturation were sandwiched with Panatomic-X slides, the pigeons usually responded to the resulting stimuli by pecking the right rather than the left key. This indicates that the pigeons' discrimination behavior was, indeed, controlled by slide chromaticity, rather than by some other aspect of the different types of film.

To determine whether brightness or stimulus intensity, rather than chromaticity, might have controlled the birds' behavior, the intensities of those test slides using added filters were measured using a Sears and Roebuck model 376.80510 light meter. The average readings for the Kodachrome test slides were 8.5, 8.7, 8.2 and 8.5 units for the slides using CC05M, CC10M, CC20M and CC40M filters, respectively. The ranges in intensity showed considerable overlap among these sub-groups, and the slides with CC05M filters spanned the entire range of intensities employed. The average readings for the Panatomic-X slides were 8.5, 8.3, 8.3 and 7.9 units for the slides using CC05G, CC10G and CC40G filters, respectively. Here, a rough correlation between filter number and intensity did exist, with filter number or saturation negatively correlated with brightness. However, the ranges in intensity showed considerable overlap among the sub-classes, and the range of intensities among the slides with CC20M filters encompassed the range of intensities found among the slides with either CC05M or CC10M filters. Thus, it seems highly unlikely that the behavior patterns exhibited by the birds could be explained in terms of stimulus control by brightness. Furthermore, the considerable overlap in the intensity ranges of the training stimuli used in Experiments I-III (6.3 to 11 units and 5 to 10.5 units for the chromatic and achromatic sets, respectively) would have made this stimulus dimension an inconsistent predictor of reinforcement, at best. Note that the rough correlation existing between class membership and intensity within these training stimuli was just the opposite of what might be expected on the basis of the rough correlation existing between intensity and behavior pattern among the Panatomic-X test stimuli. That is, the darker training stimuli tended roughly to be Panatomic-X slides, which controlled left key pecks, while the darker test stimuli tended roughly to control right key pecks. Finally, consider the one case in which two sub-classes of test stimuli showed little overlap in their ranges of intensities, the Panatomic-X slides with CC10G filters and the Kodachrome slides with CC10M filters. Here, the Panatomic-X slides were darker than the Kodachrome slides (except for one of each set of the same brightness), and yet the former controlled left and the latter right key pecks, just the opposite of what would be expected on the basis of the rough correlation between brightness and behavior which existed among the Panatomic-X test stimuli.

It was apparently not possible to obtain a good metameric match of the color of Panatomic-X film for the pigeon by combining color-correcting magenta filters with Kodachrome slides: For all birds, right key pecks predominated following all Kodachrome test slides. The CC05M plus Kodachrome combination may have come closest to this end, however, since most birds showed a small decrease in right key responding with this type of slide.

It seems reasonable that the class "non-Panatomic-X" was chromatically much broader for these birds than the class "Panatomic-X." That is, the class "non-Panatomic-X" might encompass a variety of specific background colors, including "achromatic Kodachrome" (i.e., the background color of photographs of an achromatic stimulus using Kodachrome film). If this is so, then the additon of almost any sufficiently saturated filter to a Panatomic-X slide would probably have succeeded in producing increased right key responding, whether or not the resulting combination appeared similar to "achromatic Kodachrome." The Panatomic-X test slides employing the two most saturated green filters should probably be interpreted in this light. On the other hand, the fact that the Panatomic-X test slide functions in Figures 8.10 and 8.13 (and possibly 8.12) are not monotonic might perhaps indicate that there is something special about the CC05G plus Panatomic-X combination. If this were interpreted as a relatively good match to "achromatic Kodachrome" for these two pigeons, then the CC10G plus Panatomic-X test slides would represent stimuli failing to fall into either the sub-class "achromatic Kodachrome" or "other colors."

CHAPTER 9

GENERAL DISCUSSION

The research described herein began with the question of whether pigeons should be expected to acquire a McCollough effect, and then set out to determine whether they do in fact acquire the effect. The strategy was first to "instruct" the birds to "report" on whether slides contained any color, by teaching them a general chromaticity concept. In Experiment I, then, the birds were trained to peck a right key following exposure to colored slides and to peck a left key following exposure to achromatic slides. This differential behavior was shown to persist when novel colored and achromatic stimuli were presented to the birds. Thus, right key pecks were interpreted as "reports" of color. In Experiment II, the conditions known to produce a ME in humans were arranged for the pigeons, but no evidence of a ME was found: Achromatic test stimuli were still typically followed by left key pecks, whereas pseudo-ME test stimuli, prepared to mimick the faintly colored appearance of a human ME, were typically followed by right key pecks. In Experiment III, one possible explanation of the results of Experiment II was ruled out: Because evidence of chromatic adaptation was obtained, the suggestion that the birds were somehow able to discriminate an "illusory" chromatic AE from "true" colored stimuli, and thus "reported" only the latter to be colored, was shown to be untenable. Experiment IV, however, showed that the birds' behavior may have been misinterpreted: The birds' discrimination behavior was shown at that point to be under the control of subtle differences in the chromatic characteristics of the two classes of film type used in preparing the "colored" and "achromatic" slides, rather than being under the control of the foreground or object chromaticity, as was the case for the experimenter. It seems important, therefore, to take another look at the results of Experiments I-III.

Interpreting Experiments I-III in the Light of Experiment IV

The correct interpretation of Experiment I is now fairly clear: The birds used in the present research certainly did acquire a concept, since their discrimination behavior transferred to novel instances of the two classes of stimuli. However, it now seems inappropriate to call the concept they demonstrated "chromaticity," since their discrimination behavior was later shown to be under the control of film type. On the other hand, Filters Test 2 did indicate that it was, indeed, the chromaticity of the film types that controlled the birds' behavior. Thus, it might be appropriate to call the concept which they demonstrated "the color of Panatomic-X versus all other colors."

It should be pointed out that we cannot determine whether film type controlled the birds' behavior throughout the entire series of experiments, or whether the stimuli controlling their behavior changed at some point. For example, following the first introduction of the pseudo-ME slides, the birds were explicitly trained to include these slides in the "chromatic" set. This may have had the effect of training the birds to attend to the subtle background differences which may have been more salient than the desaturated colors associated with the grids. Note that bird 230 generally pecked the left key when the pseudo-ME slides were first introduced, and only learned to peck the right key in this situation after being reinforced for doing so (see Figures 6.2 and 6.8). Another point at which the stimuli controlling the birds' behavior might have changed was prior to Experiment III. At this time the birds were given fairly extensive explicit training with "colored" slides having quite desaturated hues in the background only. These were intended to mimick the expected appearance of the the "achromatic" slides following chromatic adaptation.

The correct interpretation of Experiment II is not nearly so clear. If the birds' discrimination behavior was under the control of film type throughout the experiment, then we must conclude that we lack any relevant evidence whatsoever as to the existence of the ME in pigeons, for the birds' behavior must be interpreted as "reports" of the type of film of a given test slide rather than of the presence/absence of color. In this case, left key pecks would be expected following the test slides (prepared with Panatomic-X film) regardless of whether a ME had been acquired or not. Again, the fact that the birds pecked the left key following psuedo-ME slides prepared with Panatomic-X film during Film Base Test 1 is telling.

If the stimulus dimension controlling the birds' discrimination behavior changed during the course of this research, as suggested above, it is interesting that the nature of their responses to the ME test stimuli did not. It should be noted that the explicit training with the pseudo-ME slides occurred between ME induction procedures 2 and 3, and that the training preceding Experiment III took place between procedures 3 and 4. Obviously, even if it is suspected that a change in stimulus control occurred during Experiment II, the evidence that this is so is now irretrievable.

The results of Experiment IV do not change our interpretation of Experiment III, unlike in the case of Experiments I and II. Despite the fact that the birds' behavior was most likely under the control of film type at that time, the birds still tended to peck the right key in response to Panatomic-X slides during green or red components. That is, the effect of exposure to the intense colored lights was large enough to alter the chromatic appearance of the Panatomic-X slides.

On the Difficulty of Communicating with Animals

Perhaps the most common source of arguments and disputes among people is the unrecognized failure to use a given word in the same way. Do humans have instincts? Is Albert Bandura a behaviorist? Is Jimmy Carter a liberal? Is socialism good? People may argue such questions for hours or decades, only to find that they mean something quite different than their opponent does by the term "instinct," "behaviorist," "liberal," or "good." In other words, they and their opponent have failed to communicate.

To say that two people "mean" something different when using the same word is, of course, to say that their verbal behavior is under the control of different stimulus characteristics. The potential for such problems in communication exists because in any given situation the stimuli available to gain control over behavior are myriad. The particular aspect of the universe which comes to control emitting the word "socialist" may thus vary for different individuals, particularly if their reinforcement history with respect to uttering the term differs.[1] Even in members of the same species with similar reinforcement histories, however, differences in the "meaning" of a behavior may occur. Reynolds (1961), for example, trained

---

[1] See Skinner (1957) for a discussion of verbal behavior and, e.g., Johnson and Cumming (1968) for an example of how reinforcement history can determine what aspect of the environment gains control over behavior.

two pigeons to discriminate between a triangle with a red background and a circle with a green background by reinforcing pecks to the former stimulus compound. In a subsequent test in which the subjects were presented the patterns and colors separately, one pigeon pecked the triangle and the other the red key almost exclusively. That is, for one pigeon pecking was controlled by color, while for the other pigeon it was controlled by form. We could say that for one pigeon pecking meant "it's red," while for the other it meant "it's a triangle."

The Reynolds results is in fact out of the ordinary: More commonly, given the same reinforcement history, members of the same species tend to come under the control of the same stimulus dimensions. It is said, for example that color is a "salient" cue for birds (Wilcoxon, Dragoin, & Kral, 1971; see also Randich, Klein, & LoLordo, 1978) while taste is "salient" for rats (Revusky & Garcia, 1970). In part, this type of difference across species doubtless reflects differences in sensory equipment.[1] Thus, problems of communication, where a given behavior (be it verbal or otherwise) is under the control of different stimulus dimensions for two individuals, are much more likely to occur between species than within a species. Such a lack of

---

[1] Both behavior (tendency to come under stimulus control of "salient" cues) and physiology doubtless were shaped by the contingencies of survival, to use Skinner's (1974) terms.

communication was dramatically exemplified in Experiment IV, which demonstrated that the behavior of the pigeon subjects was under the control of a different stimulus dimension than was that of the human experimenter.

Greene (Note 2) has recently described a similar case of an interspecies difference in stimulus control, again between pigeons and people. The experimenter sorted slides according to whether or not they contained a picture of a particular person (Steve). The pigeon subjects were reinforced for pecking those slides which contained the person, and exhibited transfer to novel slides also containing pictures of Steve. However, the pigeons also pecked slides of scenes not containing Steve but which had appeared as the background in former training slides in which Steve _had_ appeared. That is, while the experimenter's sorting behavior was under the control of "Steve present," the pigeons' pecking behavior was under the control of something like "Steve or one of his hang-outs present."

In an interesting paper, Gleitman (1974) described a general method for "getting animals to understand the experimenter's instructions" which corresponds very closely to the strategy employed in the present research. Specifically, Gleitman suggested that the animal should first be taught to abstract a particular concept, and that the question of interest might then be posed. The first stage corresponds to the expeimenter's instructing the animal subjects. What must be added to Gleitman's paradigm is the exhortation that the experimenter make sure, in teaching the concept, that <u>only</u> the relevant stimulus dimension be available to control the animal's behavior. Especially in the case of instructing or communicating with another species, the experimenter cannot assume that the animal "won't pay attention to the background" or "won't pay attention to the film type"!

Assessment of Research Strategy:The ME in Pigeons

The research strategy followed in assessing whether pigeons acquire a ME involved first an "instruction" phase, in which the subjects were presumably trained to discriminate "chromatic" from "achromatic" stimuli. The importance of controlling for film type in this initial, "instruction" phase has been clearly demonstrated. However, even if film type were controlled for, how might the resulting conceptual behavior best be characterized? Would the designation "achromatic" (left key peck) "mean" the same thing for pigeon and person? For the human, the concept "achromatic" doubtless has as its basis the appearance of sunlight. Other stimuli categorized as "white" or "achromatic" may not have exactly the same spectral composition, but the human observer does not discriminate among them. Given that the pigeon processes color information differently than the human does (see Chapter 2), it seems unlikely that stimuli with differing spectral characteristics which for the one species "match" will necessarily "match" for members of the other species. In order to determine whether the human concept "achromatic" is isomorphic with the pigeon category "achromatic," one would have to introduce generalization tests including, in addition to novel slides, novel light sources. Again, it seems unlikely that these categories would prove isomorphic for the two species.

If the category "achromatic" were indeed found to differ for pigeon and person, it is important to consider what effect this might have upon the likelihood of demonstrating a ME in the pigeon. Suppose, for example, that an "achromatic" slide appeared to the pigeon not sunlight-like, but as a distinct hue, call it "beyaz." Might the presence of "beyaz" in effect mask a ME even if it had been acquired? A study reported by Murch (1979) suggests that it would not. Subjects were adapted to horizontal and vertical gratings with red or blue backgrounds for 30 min, and then presented with each of a horizontal and vertical test grating containing a central patternless patch. The subjects were required to vary the spectral characteristics of the patch until it matched the appearance of the surrounding area; the difference in settings for patches within horizontal and vertical test gratings served as a measure of the strength of the ME. In three conditions, the test gratings were presented either in "white," broad band green, or narrow band green light; each condition produced equally strong MEs. Furthermore, the subjects reported that the test patterns, when viewed in green light appeared yellowish orange (vertical grid) or bluish green (horizontal grid), so that the effect was great enough to be apparent even without appealing to the more sensitive matching data. Of course, certain hues might be more likely to mask a ME than others. For example, a pink AE might not affect the appearance of a red test grating. On the other hand, as long as the background hue were not too saturated and the test stimuli contained both grating orientations situated adjacent to one another, a contrast between the two areas should be apparent.

The above considerations suggest that the acquisition of a "chromaticity" concept, even if not isomorphic with the human concept, should allow subsequent detection of a ME. However, such a broad and general dichotomy as "chromatic-achromatic" may not be as sensitive as another, "more explicit," set of instructions. Specifically, it is suggested that all training slides contain two or more areas where black stripes are oriented at right angles, as in the case of the ME test slides used in the present research. Two classes of slides would differ in terms of whether the color associated with the stripes in the two different orientations was the same or different. Thus, one class of slides would be chromatically homogeneous, or all one color, while the other class of slides would contain two colors, similar to the pseudo-ME test slides of the present research. After one behavior was reinforced in the presence of one class of stimuli and another in the presence of the other class of stimuli, transfer tests could assess whether or not the abstract concept "one color versus two colors" had been acquired. Following ME adaptation, if properly oriented ME test slides[1] controlled behavior appropriate to the two-color class of stimuli, it would be concluded that pigeons acquire the ME.

This research has unfortunately not been able to offer a solution to the problem originally posed. Additional evidence was provided that pigeons experience simple chromatic AEs, but the more interesting question of whether they acquire a contingent chromatic AE, the ME, remains unanswered. It is hoped, however, that some understanding has been gained of the intricate methods by which this question, and other questions requiring "communication" with animal subjects, may be answered in further research.

---

[1] Adaptation and test stimuli will differ from those used in the present research by using a higher spatial frequency, at 4 to 5 cycles per degree. (See Discussion, Chapter 6.)

LIST OF REFERENCES

REFERENCE NOTES

1. Chase, S. Pigeons and the magical number seven. Paper presented at the Fourth Harvard Symposium on Quantitative Analysis of Behavior: Acquisition Process, Cambridge, June 1981.
2. Greene, S. L. Figure-ground relations in concept formation. Paper presented at the Fourth Harvard Symposium on Quantitative Analysis of Behavior: Acquisition Process, Cambridge, June 1981.
3. Johnson, D. F. Concept formation in pigeons. Unpublished matser's thesis, University of New Hampshire, 1979.
4. Lea, S. E. G., & Ryan, C. M. E. Feature analysis of pigeons' acquisition of discrimination between letters. Paper presented at the Fourth Harvard Symposium on Quantitative Analysis of Behavior: Acquisition Process, Cambridge, June 1981.
5. Riggs, L. A. Personal communication, 1981.
6. Vaughan, Jr., W., & Greene, S. L. Acquisition of absolute discriminations in pigeons. Paper presented at the Fourth Harvard Symposium on Quantitative Analysis of Behavior: Acquisition Process, Cambridge, June 1981.

REFERENCES

Allman, J. Evolution of the visual system in the early primates. In J. M. Sprague & A. N. Epstein (Eds.), Progress in psychobiology and physiological psychology (Vol. 7). New York: Academic Press, 1977.

Alpern, M., & Barr, L. Durations of the afterimages of brief light flashed and the theory of the Broca and Sulzer phenomenon. Journal of the Optical Society of America, 1962, 52, 219-221.

Ambler, B. A., & Foriet, K. G. Induction of the McCollough effect II: Two different mechanisms. Perception and Psychophysics, 1978, 24, 466-470.

Anstis, S. M. What does visual percpetion tell us about visual coding? In M. S. Gazzaniga & C. Blakemore (Eds.), Handbook of psychobiology. New York: Academic Press, 1975.

Barlow, H. B., Hill, R. M., & Levick, W. R. Retinal ganglion cells responding selectively to direction and speed of image motion in the rabbit. Journal of Physiology, 1964, 173, 377-407.

Black, A. H. Autonomic aversive conditoning in infrahuman subjects. In F. R. Brush (Ed.), Aversive conditioning and learning. New York: Academic Press, 1971.

Blakemore, C. Development of functional connexions in the mammalian visual system. British Medical Bulletin, 1974, 30, 152-157.

Blakemore, C., & Julesz, B. Stereoscopic depth aftereffect produced without monocular cues. Science, 1971, 171, 286-288.

Blakemore, C., & Campbell, F. W. On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. Journal of Physiology, 1969, 203, 237-260.

Blakemore, C., & Sutton, P. Size adaptation: A new aftereffect. Science, 1969, 166, 245-247.

Blough, D. S. Dark adaptation in the pigeon. Journal of Comparative and Physiological Psychology, 1956, 49, 425-430.

Blough, D. S. Spectral sensitivity in the pigeon. Journal of the Optical Society of America, 1957, 47, 827-833.

Blough, P. M. The visual acuity of the pigeon for distant targets. Journal of the Experimental Analysis of Behavior, 1971, 15, 57-67.

Blough, P. M. Visual acuity in the pigeon II: Effects of target distance and retinal lesions. Journal of the Experimental Analysis of Behavior, 1973, 20, 333-343.

Blough, P. M. The Pigeon's perception of saturation. Journal of the Experimental Analysis of Behavior, 1975, 24, 135-148.

Blough, P. M. Functional implications of the pigeon's peculiar retinal structure. In A. M. Granda & J. H. Maxwell (Eds.), Neural mechanisms of behavior in the pigeon. New York: Plenum Press, 1979.

Blough, P. M., Riggs, L. A., & Schafer, K. L. Photopic spectral sensitivity determined electroretinographically for the pigeon eye. Vision Research, 1972, 12, 477-485.

Bower, T. G. R. Discrimination of depth in premotor infants. Psychonomic Science, 1964, 1, 368.

Bowmaker, J. K. The visual pigments, oil droplets and spectral sensitivity of the pigeon. Vision Research, 1977, 17, 1129-1138.

Bowmaker, J. K. Visual pigments and oil droplets in the pigeon retina, as measured by microspectrophotometry, and their relationship to spectral sensitivity. In A. M. Granda & J. H. Maxwell (Eds.), Neural mechanisms of behavior in the pigeon. New York: Plenum Press, 1979.

Breitmeyer, B. G., & Cooper, L. A. Frequency-specific color adaptation in the human visual system. Perception and Psychophysics, 1972, 11, 95-96.

Brown, J. L. Afterimages. In C. H. Graham (Ed.), Vision and visual perception. New York: John Wiley & Sons, 1965.

Brown, P., & Jenkins, H. M. Autoshaping of the pigeon's keypeck. Journal of the Experimental Analysis of Behavior, 1968, 11, 1-8.

Bushnell, M. C., & Weiss, S. J. An investigation of peak shift and behavioral contrast for autoshaped and operant behavior. Journal of the Experimental Analysis of Behavior, 1980, 33, 101-118.

Campbell, C. B. G., & Hodos, W. The concept of homology and the evolution of the nervous system. Brain, Behavior & Evolution, 1970, 3, 353-367.

Catania, A. C. On the visual acuity of the pigeon. Journal of the Experimental Analysis of Behavior, 1964, 7, 361-366.

Cerella, J. Visual classes and natural categories in the pigeon.Journal of Experimental Psychology: Human Perception & Performance, 1979, 5, 68-77.

Chard, R. D. Visual acuity in the pigeon. Journal of Experimental Psychology, 1939, 24, 588-608.

Chard, R. D., & Gundlach, R. H. The structure of the eye of the homing pigeon. Journal of Comparative & Physiological Psychology, 1938, 25, 249-272.

Cohen, J. The synthetic-analytic character of color vision in the pigeon. Psychonomic Science, 1967, 9, 429-430.

Coltheart, M. Colour-specificity and monocularity in the visual cortex. Vision Research, 1973, 13, 2595-2598.

Creutzfeld, O. D. Some neurophysiological considerations concerning memory. In H. P. Zippel (Ed.), Memory and transfer of information. New York: Plenum Press, 1973.

Davidson, M. L. Perturbation approach to spatial brightness interaction in human vision. Journal of the Optical Society of America, 1968, 58, 1300-1309.

Davies, P. Conditioning afterimages: A procedure minimizing the extinction effect of normal test trials. British Journal of Psychology, 1976, 67, 181-189.

De Britto, L. R. G., Brunelli, M., Francesconi, W., & Magni, F. Visual response pattern of thalamic neurons in the pigeon. Brain Research, 1975, 97, 337-343.

Delius, J. D., & Emmerton, J. Visual performance of pigeons. In A. M. Granda & J. H. Maxwell (Eds.), Neural Mechanisms of behavior in the pigeon. New York: Plenum Press, 1979.

Delius, J. D., & Habers, G. Symmetry: Can pigeons conceptualize it? Behavioral Biology, 1978, 2, 336-342.

De Valois, R. L. Analysis and coding of colour vision in the primate visual system. Cold Spring Harbor Symposia, 1965, 30, 567-579.

Diamond, I. T. The evolution of the tectal-pulvinar system in mammals: Structural and behavioral studies of the visual system. Symposium of the Zoological Society of London, 1973, 33, 205-233.

Donner, K. O. The spectral sensitivity of the pigeon's retinal elements. Journal of Physiology (London), 1953, 122, 524-537.

Donovan, W. J. Structure and function of the pigeon visual system. Physiological Psychology, 1978, 6, 403-437.

Ellis, S. R. Orientation selectivity of the McCollough effect: Analysis by equivalent contrast transformation. Perception & Psychophysics, 1977, 22, 539-544.

Epstein, R., & Skinner, B. F. Resurgence of responding after the cessation of response-independent reinforcement. Proceedings of the National Academy of Science USA, 1980, 77, 6251-6253.

Fechner, G. T. Ueber die Subjectiven Nachbilder und Nebenbilder. Poggendorf Ann. Phys. Chem., 1840, 50, 193-221, 427-470.

Fidell, L. S. Orientation specificity in chromatic adaptation of human "edge-detectors." Perception & Psychophysics, 1970, 8, 235-237.

Foreit, K. G., & Ambler, B. A. Induction of the McCollough effect I: Figural variables. Perception & Psychophysics, 1978, 24, 295-302.

Frome, F., Harris, C. S., & Levinson, J. Z. Extremely long-lasting shifts in perception of size after adaptation to gratings. Bulletin of the Psychonomic Society, 1975, 6, 433.

Gibbon, J., Berryman, R., & Thompson, R. L. Contingency spaces and measures in classical and instrumental conditioning. Journal of the Experimental Analysis of Behavior, 1974, 21, 585-605.

Gibson, J. J. Adaptation, aftereffect, and contrast in the perception of curved lines. Journal of Experimental Psychology, 1933, 16, 1-31.

Gibson, J. J., & Radner, M. Adaptation, aftereffect and contrast in the perception of tilted lines. Journal of Experimental Psychology, 1937, 20, 453-467.

Gleitman, H. Getting animals to understand the experimenter's instructions. Animal Learning & Behavior, 1974, 2, 1-5.

Gordon, B. The superior colliculus of the brain. Sceintific American, 1972, 227, 72-82.

Gould, S. J. The panda's thumb. New York: W. W. Norton & Co., 1980.

Govardovskii, V. I., & Zueva, L. V. Visual pigments of chicken and pigeon. Vision Research, 1977, 17, 537-543.

Graf, V. A. A spectral luminosity function in the pigeon determined by flicker photometry. Psychonomic Science, 1969, 17, 282-283.

Graf, V. A. Four spectral mechanisms in the pigeon (Columba livia). in A. M. Granda & J. H. Maxwell (Eds.), Neural mechanisms of behavior in the pigeon. New York: Plenum Press, 1979.

Graf, V. A., & Norren, D. V. A blue sensitive mechanism in the pigeon retina: λmax 400 nm. Vision Research, 1974, 14, 1203-1209.

Granda, A. M., & Maxwell, J. H. (Eds.) Neural mechanisms of behavior in the pigeon. New York: Plenum Press, 1979.

Grier, J. B. Nonparametric indexes for sensitivity and bias: Computing formulas. Psychological Bulletin, 1971, 75, 424-429.

Grossberg, S. How does a brain build a cognitive code? Psychological Review, 1980, 87, 1-51.

Gundlach, R. H. The visual acuity of homing pigeons. Journal of Comparative Psychology, 1933, 16, 327-342.

Hamilton, W. F., & Goldstein, J. L. Visual acuity and accomodation in the pigeon. Journal of Comparative Psychology, 1933, 15, 193-197.

Hansel, C. E. M., & Mahmud, S. H. Comparable retention times for the negative colour afterimage and the McCollough effect. Vision Research, 1978, 18, 1601-1605.

Hanson, H. M. Effects of discrimination training on generalization. Journal of Experimental Psychology, 1959, 58, 320-334.

Harris, C. S. Insight or out of sight?: Two examples of perceptual plasticity in the human adult. In C. S. Harris (Ed.), Visual coding and adaptability. Hillsdale, New Jersey: Lawrence Erlbaum Press, 1980.

Harris, C. S., & Gibson, A. R. Is orientation-specific color adaptation in human vision due to edge detectors, afterimages, or "dipoles"? Science, 1968, 162, 1506-1507.

Hay, J. C., Pick, H. L., & Rosser, E. Adaptation to chromatic aberration by the human visual system. Science, 1963, 141, 167-169.

Held, R. Plasticity in sensory-motor systems. Scientific American, 1965, 213, 84-94.

Held, R. The rediscovery of adaptability in the visual system: Effects of extrinsic and intrinsic chromatic dispersion. In C. S. Harris (Ed.), Visual coding and adaptability. Hillsdale, New Jersey: Lawrence Erlbaum Press, 1980.

Held, R., & Shattuck, S. R. Color- and edge-sensitive channels in the human visual system: Tuning for orientation. Science, 1971, 174, 314-316.

Helmholtz, H. von. Handbuch der physiologischen Optik. Hamburg and Leipzig: Voss, 1866.

Herrnstein, R. J. Acquisition, generalization, and discrimination reversal of a natural concept. Journal of Experimental Psychology: Animal Behavior Processes, 1979, 5, 116-129.

Herrnstein, R. J., & de Villiers, P. A. Fish as a natural category for people and pigeons. In G. H. Bower (Ed.), The psychology of learning and motivation (Vol. 14). New York: Academic Press, 1980.

Herrnstein, R. J., & Loveland, D. H. Complex visual concept in the pigeon. Science, 1964, 146, 549-551.

Hess, E. H. Space perception in the chick. Scientific American, 1965, 195, 71-80.

Hirsch, J., & Murch, G. M. Variation in hue of a contour-contingent aftereffect due to color adaptation during inspection of the stimulus patterns. Perception & Psychophysics, 1972, 11, 406-408.

Hodos, W. Color discrimination deficits after lesions of the nucleus rotundus in pigeons. Brain, Behavior & Evolution, 1969, 2, 185-200.

Hodos, W., & Bonbright, J. C., Jr. Intensity difference thresholds in pigeons after lesions of the tectofugal and thalamofugal visual pathways. Journal of Comparative & Physiological Psychology, 1974, 87, 1013-1031.

Hodos, W., & Karten, H. J. Brightness and pattern discrimination deficits in the pigeon after lesions of nucleus rotundus. Experimental Brain Research, 1966, 2, 151-167.

Hodos, W., & Karten, H. J. Visual intensity and pattern discrimination deficits after lesion of the optic lobe in pigeons. Brain, Behavior, & Evolution, 1974, 9, 165-194.

Hodos, W., & Leibowitz, R. W. Near-field visual acuity of pigeons: Effects of scotopic adaptation and wavelength. Vision Research, 1977,17, 463-467.

Hodos, W., Leibowitz, R. W., & Bonbright, J. C., Jr. Near-field visual acuity of pigeons: Effects of head location and stimulus luminance. Journal of the Experimental Analysis of Behavior, 1975, 25, 131-141.

Hohmann, A., & von der Malsburg, C. McCollough effect and eye optics. Perception, 1978, 7, 551-555.

Holden, A. L. Concentric receptive fields of pigeon ganglion cells. Vision Research, 1977, 17, 545-554.

Hubel, D. H., & Wiesel, T. N. Receptive fields of single neurones in the cat's striate cortex. Journal of Physiology, 1959, 148, 574-591.

Hughes, C. P., & Pearlman, A. L. Single unit receptive fields and the cellular layers of the pigeon optic tectum. Brain Research, 1974, 80, 365-377.

Humphrey, N. K., & Weiskrantz, L. Vision in monkeys after removal of the striate cortex. Nature (London), 1967, 215, 595-597.

Hunter, W. S. The after-effect of visual motion. Psychological Review, 1914, 21, 245-277.

Hupka, R. B., Liu, S. S., & Moore, J. W. Auditory differential conditioning of the rabbit nictitating membrane response: V. Stimulus generalization as a function of the position of CS+ and CS- on the frequency dimension. Psychonomic Science, 1969, 15, 129-131.

Ingvar, D. H. Spectral sensitivity as measured in cerebral visual centers. Acta Physiologica Scandinavica Supplementum, 1959, 159, 46-105.

Jassik-Gershenfeld, D., Teulon, J., & Ropert, N. Visual receptive field types in the nucleus dorsolateralis anterior of the pigeon's thalamus. Brain Research, 1976, 108, 295-306.

Jassik-Gerschenfeld, D., Teulon, J., & Hardy, O. Spatial interactions in the visual receptive fields of the nucleus dorsolateralis anterior of the pigeon thalamus. In A. M. Granda & J. H. Maxwell (Eds.), Neural mechanisms of behavior in the pigeon. New York: Plenum Press, 1979.

Jenkins, P. E. Inhibitory dimensional control in the pigeon: The effects of discriminative autoshaping and negative automaintenance procedures. Unpublished doctoral dissertation, University of New Hampshire, 1979.

Jerison, H. J. Evolution of the brain and intelligence. New York: Academic Press, 1973.

Jitsumori, M. Anomaloscope experiment for a study of color mixture in the pigeon. Japanese Psychological Research, 1976, 18, 126-135.

Johnson, D. F., & Cumming, W. W. Some determinants of attention. Journal of the Experimental Analysis of Behavior, 1968, 11, 157-166.

Jones, M. C. The elimination of children's fears. Journal of Experimental Psychology, 1924, 7, 382-390.

Jones, P. D., & Holding, D. H. Extremely long-term persistence of the McCollough effect. Journal of Experimental Psychology: Human Perception & Performance. 1975, 1, 323-327.

Kalfin, K., & Locke, S. Evaluation of long term visual motion after-image following monocular stimulation. Vision Research, 1972, 12, 359-361.

Kamin, L. J. Backward conditioning and the conditioned emotional response. Journal of Comparative & Physiological Psychology, 1963, 56, 517-519.

Karten, H. J. The organization of the avian telencephalon and some speculations on the phylogeny of the amniote telencephalon. Annals of the New York Academy of Science, 1969, 167(1), 164-179.

Karten, H. J. Visual lemniscal pathways in birds. In A. M. Granda & J. H. Maxwell (Eds.), Neural mechanisms of behavior in the pigeon. New York: Plenum Press, 1979.

Karten, H. J., & Nauta, W. J. H. Organization of retinothalamic projections in the pigeon and owl. Anatomical Record, 1968, 160, 373.

Keller, F. S., & Schoenfeld, W. N. Principles of psychology. New York: Appleton-Century-Crofts, 1950.

Kimberly, R. P., Holden, A. L., & Bamborough, P. Response characteristics of pigeon forebrain cells to visual stimuluation. Vision Research, 1971, 11, 475-478.

Klüver, H. Functional significance of the geniculo-striate system. Biological Symposium, 1942, 7, 253-299.

Köhler, I. [The formation and transformation of the visual world.] Psychological Issues, 1964, 3, 28-46, 116-133. (Originally published, 1951.)

Köhler, I. Experiments with goggles. Scientific American, 1962, 206, 62-72.

Kravitz, J. H. Conditioned adapttion to prismatic displacement. Perception & Psychophysics, 1972, 11, 38-42.

Kravitz, J. H., & Yaffe, F. Conditioned adaptation to prismatic displacement with a tone as the conditioned stimulus. Perception & Psychophysics, 1972, 12, 305-308.

Kreithen, M. L. The sensory world of the homing pigeon. In A. M. Granda & J. H. Maxwell (Eds.), Neural mechanisms of behavior in the pigeon. New York: Plenum Press, 1979.

Krüger, J. McCollough effect. A theory based on the anatomy of the lateral geniculate body. *Perception & Psychophysics*, 1979, *25*, 169-179.

Ksir, C., & McKearney, J. W. Penobarbital, promazine, *d*-amphetamine, and scopolamine effects on behavior under multiple and primed schedules of reinforcement. *Psychopharmacologia*, 1978, *59*, 205-207.

Leppmann, P. K. Spatial frequency dependent chromatic after-effects. *Nature*, 1973, *242*, 411-412.

Liu, S. S. Differential conditioning and stimulus generalization of the rabbit's nictitating membrane response. *Journal of Comparative & Physiological Psychology*, 1971, *77*, 136-142.

Lovegrove, W. J., & Over, R. Color adaptation of spatial frequency detectors in the human visual system. *Science*, 1972, *176*, 541-543.

Lubow, R. E., & Moore, A. U. Latent inhibition: The effect of nonreinforced preexposure to the conditioned stimulus. *Journal of Comparative & Physiological Psychology*, 1959, *52*, 415-419.

MacKay, D. M., & MacKay, V. The time course of the McCollough effect and its physiological implications. *Journal of Physiology*, 1974, *237*, 38P-39P.

MacKay, D. M., & MacKay, V. Dichoptic induction of McCollough-type effects. *Quarterly Journal of Experimental Psychology*, 1975a, *27*, 225-233.

MacKay, D. M., & MacKay, V. What causes decay of pattern-contingent chromatic aftereffects? *Vision Research*, 1975b, *15*, 462-464.

MacKay, V., & MacKay, D. M. Multiple orientation-contingent chromatic after-effects. *Quarterly Journal of Experimental Psychology*, 1977, *29*, 203-218.

Maguire, W. M., Meyer, G. E., & Baizer, J. S. The McCollough effect in rhesus monkey. *Investigative Ophtalmology & Visual Science*, 1980, *19*, 321-324.

Mackintosh, N. J. *The psychology of animal learning*. New York: Academic Press, 1974.

Martin, G. R., & Muntz, W. R. A. Retinal oil droplets and vision in the pigeon (*Columba livia*). In A. M. Granda & J. H. Maxwell (Eds.), *Neural mechanisms of behavior in the pigeon*. New York: Plenum Press, 1979.

Maturana, H. R. Functional organization of the pigeon retina. In R. W. Granda & J. W. Duyff (Eds.), Information processing in the nervous system (Vol. 3). Proceedings of the International Union of Physical Scientists, 22nd International Congress, Leiden, 1962.

Maturana, H. R., & Frenk, S. Directional movement and horizontal edge detectors in the pigeon retina. Science, 1963, 142, 977-979.

Masland, R. H. Visual motion perception: Experimental modification. Science, 1969, 165, 819-921.

Maxwell, J. H., & Granda, A. M. Receptive fields of movement-sensitive cells in the pigeon thalamus. In A. M. Granda & J. H. Maxwell (Eds.), Neural mechanisms of behavior in the pigeon. New York: Plenum Press, 1979.

May, J. G. Chromatic adaptation of orientation- and size-specific visual processes in man. Vision Research, 1972, 12, 1509-1517.

Mayhew, J. E. W., & Anstis, S. M. Movement aftereffects contingent on color, intensity, and pattern. Perception & Psychophysics, 1972, 12, 77-85.

McCarter, A., & Silver, A. I. The McCollough effect: A classical conditioning phenomenon? Vision Research, 1977, 17, 317-319.

McCollough, C. Color adaptation of edge-detectors in the human visual system. Science, 1965, 149, 1115-1116.

Miceli, D., Gioanni, H., Reperant, J., & Peyrichoux, J. The avian visual Wulst: I. An anatomical study of afferent and efferent pathways. II. An electrophysiological study of the functional properties of single neurons. In A. M. Granda & J. H. Maxwell (Eds.), Neural mechanisms of behavior in the pigeon. New York: Plenum Press, 1979.

Michael, C. R. Receptive fields of single optic nerve fibers in a mammal with an all-cone retina. II. Directionally selective units. Journal of Neurophysiology, 1968, 31, 257-267.

Michael, C. R. Integration of retinal and cortical information in the superior colliculus of the ground squirrel. Brain, Behavior & Evolution, 1970, 3, 205-209.

Michael, C. R. Visual receptive fields of single neurons in superior colliculus of the ground squirrel. Journal of Neurophysiology, 1972, 35, 815-832.

Milar, K. S., Halgren, C. R., & Heise, G. A. A reappraisal of scopolamine effects on inhibition. Pharmacology, Biochemistry & Behavior, 1978, 9, 307-313.

Mitchell, D. E. The influence of early visual experience on visual perception. In C. S. Harris (Ed.), Visual coding and adaptability. Hillsdale, New Jersey: Lawrence Erlbaum, 1980.

Montalvo, F. S. A neural network model of the McCollough effect. Biological Cybernetics, 1976, 25, 49-56.

Moore, J. W. Stimulus control: Studies of auditory generalization in rabbits. In A. H. Black & W. F. Prokasy (Eds.), Classical conditioning II: Current research and theory. New York: Appleton-Century-Crofts, 1972.

Morgan, J. J., Fitch, M. D., Holman, J. G., & Lea, S. E. G. Pigeons learn the concept of an 'A.' Perception, 1976, 5, 57-66.

Mulvanny, P. Discrimination of line orientation by pigeons after lesions of thalamic visual nuclei. In A. M. Granda & J. H. Maxwell (Eds.), Neural mechanisms of behavior in the pigeon. New York: Plenum Press, 1979.

Murch, G. M. Binocular relationships in a size and color orientation specific aftereffect. Journal of Experimental Psychology, 1972, 93, 30-34.

Murch, G. M. Color-contingent motion aftereffects: Single or multiple levels of processing? Vision Research, 1974, 14, 1181-1184.

Murch, G. M. Classical conditioning of the McCollough effect: Temporal parameters. Vision Research, 1976, 16, 615-619.

Murch, G. M. A reply to McCarter and Silver. Vision Research, 1977, 17, 321-322.

Murch, G. M. The role of test pattern background hue in the McCollough effect. Vision Research, 1979, 19, 939-942.

Murch, G. M., & Hirsch, J. The McCollough effect created by complementary afterimages. American Journal of Psychology, 1972, 85, 241-247.

Nauta, W. J. H., & Karten, H. J. A general profile of the vertebrate brain with sidelights on the ancestry of cerebral cortex. In F. O. Schmitt (Ed.), The neurosciences. Second study program. New York: Rockefeller University Press, 1970.

Nevin, J. A., Olson, K., Mandell, C., & Yarensky, P. Differential reinforcement and signal detection. Journal of the Experimental Analysis of Behavior, 1975, 24, 355-367.

Nye, P. W. The binocular acuity of the pigeon measured in terms of the modulation transfer function. Vision Research, 1968, 8, 1041-1053.

O'Flaherty, J. J., & Invernizzi, G. Functional organization of the receptive fields of single visual units of the "Wulst" in the pigeon. Bollettino della Societa Italiana di Biologia Sperimentale, 1972, 48, 137-139.

Osborne, S. R., Rysberg, J., & Killeen, P. The effects of scopolamine on the temporal control of behavior. Physiology & Behavior, 1977, 19, 79-85.

Osgood, C. E., & Heyer, A. W. A new interpretation of figural after-effects. Psychological Review, 1952, 59, 93-118.

Pavlov, I. P. Conditioned reflexes. (G. V. Anrep, trans.). Oxford: Oxford University Press, 1927.

Perisic, M., Mihailovic, J., & Cuenod, M. Electrophysiology of contralateral and ipsilateral projections to the Wulst in pigeon (Columba livia). International Journal of Neuroscience, 1971, 2, 7-14.

Pettigrew, J. D., & Konishi, M. Neurons selective for orientation and binocular disparity in the visual Wulst of the barn owl (Tyto alba). Science, 1976, 193, 675-678.

Pollack, I., & Norman, D. A. A non-parametric analysis of recognition experiments. Psychonomic Science, 1964, 1, 125-126.

Posner, M. I., & Keele, S. W. On the genesis of abstract ideas. Journal of Experimental Psychology, 1968, 77, 353-363.

Premack, D. On the abstractness of human concepts: Why it would be difficult to talk to a pigeon. In S. H. Hulse, H. Fowler, & W. K. Honig (Eds.), *Cognitive processes in animal behavior*. Hillsdale, New Jersey: Lawrence Erlbaum, 1978.

Pritz, M. B., Mead, W. R., & Northcutt, R. G. The effect of wulst ablation on colour, brightness and pattern discrimination in pigeons (*Columba livia*). *Journal of Comparative Neurology*, 1970, *140*, 81-100.

Randich, A., Klein, R. M., & LoLordo, V. M. Visual dominance in the pigeon. *Journal of the Experimental Analysis of Behavior*, 1978, *30*, 129-137.

Rescorla, R. A. Pavlovian conditioning and its proper control procedures. *Psychological Review*, 1967, *74*, 71-80.

Revusky, S., & Garcia, J. Learned associations over long delays. In G. H. Bower (Ed.), *The psychology of learning and motivation* (Vol. 4). New York: Academic Press, 1970.

Revzin, A. M. A specific visual projection area in the hyperstriatum of the pigeon (*Columba livia*). *Brain Research*, 1969, *15*, 246-249.

Revzin, A. M. Some characteristics of wide-field units in the brain of the pigeon. *Brain, Behavior & Evolution*, 1970, *3*, 195-204.

Revzin, A. M. Functional localization in the nucleus rotundus. In A. M. Granda & J. H. Maxwell (Eds.), *Neural mechanisms of behavior in the pigeon*. New York: Plenum Press, 1979.

Reynolds, G. S. Attention in the pigeon. *Journal of the Experimental Analysis of Behavior*, 1961, *4*, 203-208.

Riggs, L. A., White K. D., & Eimas, P. D. Establishment and decay of orientation-contingent aftereffects of color. *Perception & Psychophysics*, 1974, *16*, 535-542.

Rock, I., & Harris, C. S. Vision and touch. *Scientific American*, 1967, *216*, 96-104.

Romer, A. S. *Vertebrate paleontology*. Chicago: University of Chicago Press, 1933.

Romeskie, M., & Yager, D. Psychophysical studies of pigeon color vision--I. Photopic spectral sensitivity. Vision Research, 1976a, 16, 501-505.

Romeskie, M., & Yager, D. Psychophysical studies of pigeon color vision--II. The spectral photochromatic interval function. Vision Research, 1976b, 16, 507-512.

Rosch, E. H. On the internal structure of perceptual and semantic categories. In T. E. Moore (Ed.), Cognitive development and the acquisition of language. New York: Academic Press, 1973.

Rossi, P. J. Adaptation and negative aftereffect to lateral optical displacement in newly hatched chicks. Science, 1968, 160, 430-432.

Rossi, P. J. Primacy of the negative aftereffect over positive adaptation in prism adaptation with newly hatched chicks. Developmental Psychobiology, 1969, 2, 43-53.

Rossi, P. J. Prism-induced negative aftereffects without food-reinforced feedback in newly hatched chicks. Psychonomic Science, 1971, 24, 141-142.

Rossi, P. J. The influence of population density and food dispersion on the development of prism-induced aftereffects in newly hatched chicks. Developmental Psychobiology, 1972, 5, 239-248.

Rozin, P., & Kalat, J. W. Specific hungers and poison avoidance as adaptive specializations of learning. Psychological Review, 1971, 78, 459-486.

Schmidt, M. J., & Finke, R. A. Contrast and frequency competition for orientation-contingent color aftereffects. Perception & Psychophysics, 1979, 25, 406-412.

Schmidt, M. J., Pinette, P. R., & Finke R. Further evidence for conditioning processes in the McCollough effect. Journal of General Psychology, 1978, 99, 117-132.

Schneider, B. Multidimensional scaling of color difference in the pigeon. Perception & Psychophysics, 1972, 12, 373-378.

Schneider, G. E. Contrasting visuomotor functions of tectum and cortex in the golden hamster. Psychologische Forschung, 1967, 31, 52-62.

Sharpe, L. T., & Tees, R. C. Contour specificity of the McCollough effect. Perception & Psychophysics, 1978, 23, 451-458.

Shattuck, S., & Held, R. Color and edge sensitive channels converge on stereo-depth analyzers. Vision Research, 1975, 15, 309-311.

Shortess, G. K. Some comments on the functional significance of centrifugal fibers to the vertebrate retina. In J. C. Armington, J. Krauskopf, & B. R. Wooten (Eds.), Visual psychophysics and physiology. New York: Academic Press, 1978.

Shute, C. C. D. The McCollough effect. Cambridge: Cambridge University Press, 1979.

Siegel, S. Evidence from rats that morphine tolerance is a learned response. Journal of Comparative & Physiological Psychology, 1975, 89, 498-506.

Skinner, B. F. Behavior of organisms. New York: Appleton-Century-Crofts, 1938.

Skinner, B. F. Verbal behavior. New York: Appleton-Century-Crofts, 1957.

Skinner, B. F. About behaviorism. New York: Alfred A. Knopf, 1974.

Skowbo, D., & Clynes, N. Decline and revival of McCollough effects following inspection of achromatic gratings. Perception & Psychophysics, 1977, 12, 180-182.

Skowbo, D., Timney, B. N., Gentry, T. A., & Morant, R. B. McCollough effects: Experimental findings and theoretical accounts. Psychological Bulletin, 1975, 82, 497-510.

Smith, K. U., & Smith, W. M. Perception and motion. Philadelphia: W. B. Saunders, 1962.

Smith, R. A. The motion/disparity aftereffect: A preliminary study. Vision Research, 1976, 16, 1507-1509.

Spear, P. D. Behavioral and neurophysiological consequences of visual cortex damage: Mechanisms of recovery. In J. M. Sprague & A. N. Epstein (Eds.), Progress in psychobiology and physiological psychology (Vol. 8). New York: Academic Press, 1979.

Spence, K. W. The differential response of animals to stimuli differing within a single dimension. Psychological Review, 1937, 44, 430-444.

Sterling, P., & Wickelgren, B. G. Visual receptive fields in the superior colliculus of the cat. Journal of Neurophysiology, 1969, 32, 1-15.

Stiles, W. S. The determination of the spectral sensitivities of the retinal mechanisms by sensory methods. Nederlands Tijdschrift voor Natuurk., 1949, 15, 125-146.

Stromeyer, C. F. McCollough effect analogs of two-color projections. Vision Research, 1971, 11, 969-978,

Stromeyer, C. F. Contour-contingent color aftereffects: Retinal area specificity. American Journal of Psychology, 1972a, 85, 227-235.

Stromeyer, C. F. Edge-contingent color after effects: Spatial frequency specificity. Vision Research, 1972b, 12, 717-733.

Stromeyer, C. F. Form-color aftereffects in human vision. In R. Held, H. W. Leibowitz, & Hans-Lukas Teuber (Eds.), Handbook of sensory physiology (Vol. 8). Berlin: Springer-Verlag, 1978.

Sutherland, N. S., Mackintosh, N. J., & Mackintosh, J. Simultaneous discrimination training of Octopus and transfer of discrimination along a continuum. Journal of Comparative & Physiological Psychology, 1963, 56, 150-156.

Swindle, P. F. Positive after-images of long duration. Americal Journal of Psychology, 1916, 27, 324-334.

Taub, E. Prism compensation as a learning phenomenon: a phylogenetic perspective. In S. J. Freedman (Ed.), The neuropsychology of spatially oriented behavior. Homewood, Illinois: The Dorsey Press, 1968.

Tauc, L. Polyphasic synaptic activity. Progress in Brain Research, 1969, 31, 247-257.

Taylor, J. G. The behavioral basis of perception. New Haven and London: Yale University Press, 1962.

Teft, L. W., & Clark, F. T. The effects of stimulus density on orientation specific aftereffects of color adaptation. Psychonomic Science, 1968, 11, 265-266.

Tomie, A., Davitt, G. A., & Engberg, L. A. Stimulus generalization of auto-shaped key-pecking following interdimensional and extradimensional training. Learning & Motivation, 1976, 7, 240-253.

Trevarthen, C. B. Two mechanisms of vision in primates. Psychologische Forschung, 1968, 31, 299-337.

Vidyasagar, T. R. Orientation specific colour adaptation at a binocular site. Nature, 1976, 261, 39-40.

Virsu, V., & Haapasalo, S. Relationship between channels for colour and spatial frequency in human vision. Perception, 1973, 2, 31-40.

Wallman, J. Role of the retinal oil droplets in the color vision of Japanese quail. In A. M. Granda, & J. H. Maxwell (Eds.), Neural mechanisms of behavior in the pigeon. New York: Plenum Press, 1979.

Walls, G. L., & Judd, H. D. The intra-ocular colour-filters of vertebrates. British Journal of Ophthalmology, 1933, 17, 641-675, 705-725.

Webster, K. E. Thalamus and basal ganglia in reptiles and birds. Symposium of the Zoological Society of London, 1973, 33, 169-203.

Webster, K. E. Changing concepts of the organization of the central visual pathway in birds. In R. Bellairs & E. G. Gray (Eds.), Essays on the nervous system. Oxford: Clarendon Press, 1974.

Weiskrantz, L. Contour discrimination in a young monkey with striate cortex ablation. Neurophysiologia, 1963, 1, 145-164.

Weiskrantz, L. Varieties of residual experience. Quarterly Journal of Experimental Psychology, 1980, 32, 365-386.

White, K. D. Luminance as a parameter in establishment and testing of the McCollough effect. Vision Research, 1976, 16, 297-302.

White, K. D. Studies of form-contingent color aftereffects. In J. C. Armington, J. Krauskopf, & B. R. Wooten, Visual psychophysics and physiology. New York: Academic Press, 1978.

White, K. D., Petry, Heywood, M., Riggs, L. A., & Miller, J. Binocular interactions during establishment of McCollough effects. Vision Research, 1978, 18, 1201-1215.

Wilcoxon, H. Dragoin, W., & Kral, P. Illness-induced aversions in rat and quail: Relative salience of visual and gustatory cues. *Science*, 1971, *171*, 826-828.

Williams, J. L. Evidence of complementary afterimages in the pigeon. *Journal of the Experimental Analysis of Behavior*, 1974, *21*, 421-424.

Wolbarsht, M. L. The function of intraocular color filters. *Federation Proceedings*, 1976, *35*, 44-50.

Wolin, L. R. Massopust, L. C., Jr., & Meder, J. Differential color responses from superior colliculi of squirrel monkeys. *Vision Research*, 1966, *6*, 637-644.

Wright, A. A. The influence of ultraviolet radiation on the pigeon's colour discrimination. *Journal of the Experimental Analysis of Behavior*, 1972, *17*, 325-337.

Wright, A. A. Bezold-Brücke hue shift functions for the pigeon. *Vision Research*, 1976, *16*, 765-774.

Wright, A. A. Color-vision psychophysics: A comparison of pigeon and human. In A. M. Granda & J. H. Maxwell (Eds.), *Neural mechanisms of behavior in the pigeon*. New York: Plenum Press, 1979.

Wright, A. A., & Cumming, W. W. Color-naming functions for the pigeon. *Journal of the Experimental Analysis of Behavior*, 1971, *15*, 5-17.

Wright, W. D. A re-determination of the trichromatic coefficients of the spectral colours. *Transactions of the Optical Society (London)*, 1928-1929, *30*, 141-164.

Wyatt, H. J. Singly and doubly contingent after-effects involving color, orientation and spatial frequency. *Vision Research*, 1974, *14*, 1185-1193.

Yachzel, B. R., & Lackner, J. R. Adaptation to displaced vision: Evidence for transfer of adaptation and long-lasting aftereffects. *Perception & Psychophysics*, 1977, *22*, 147-151.

Yager, C., & Romeskie, M. On the proper control of luminance cues in pigeon color vision experiments. *Journal of the Experimental Analysis of Behavior*, 1975, *23*, 293-295.

Yazulla, S., & Granda, A. M. Opponent-color units in the thalamus of the pigeon (*Columba livia*). *Vision Research*, 1973, *13*, 1555-1563.

APPENDIXES

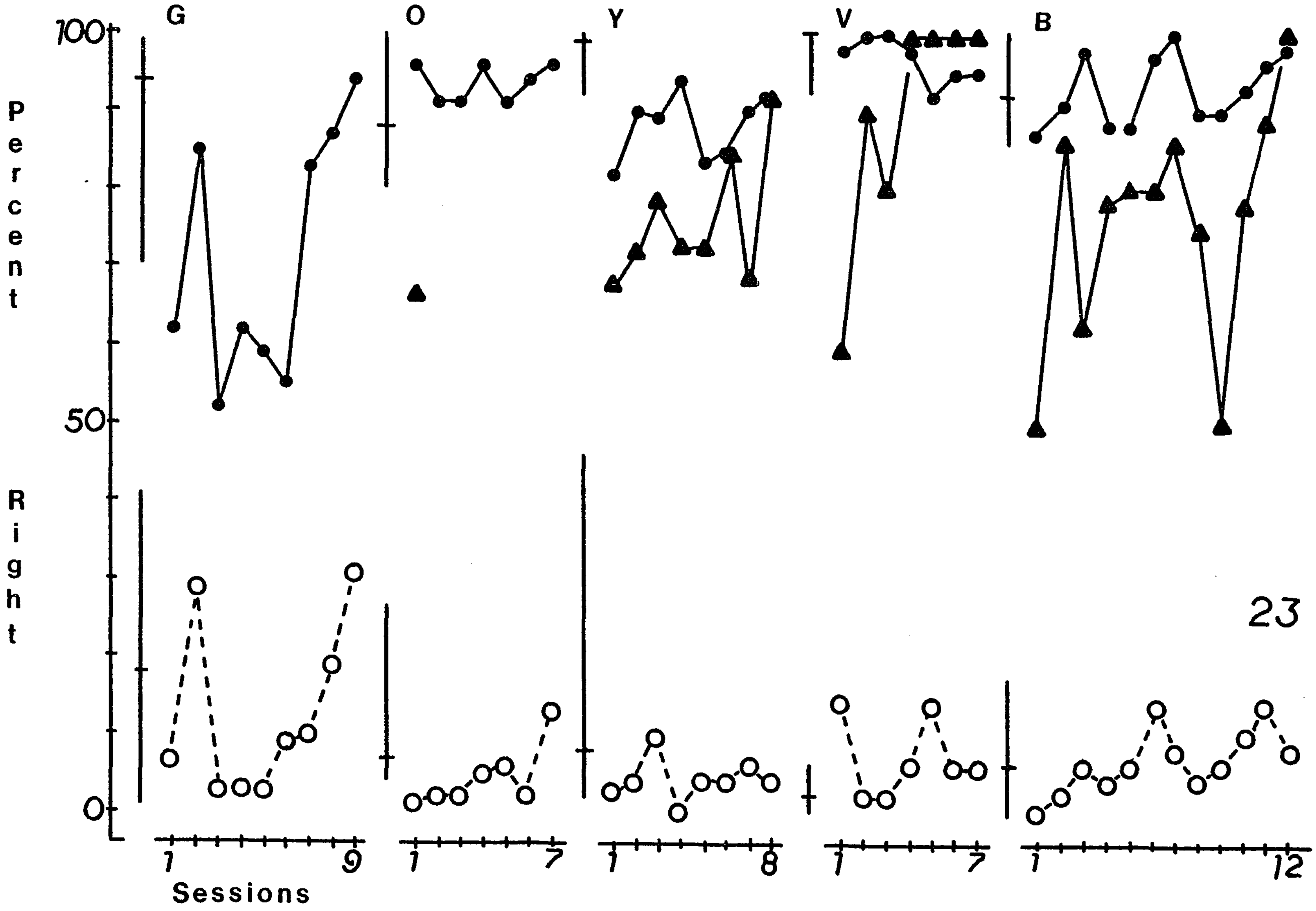
APPENDIX A

ACQUISITION DATA, EXPERIMENT I

Figures A.1 through A.4 include the data of Figures 6.4 through 6.7 which showed behavior on the first day each new color was added to the chromatic set of stimuli. Also included, however, are the data for subsequent sessions. In each case, seven sessions or more (enough so that responding to new and old colors is roughly equivalent) are shown.

Table A.1 expands upon Table 6.3 which showed the number of sessions required to reach 70%, 80% and 90% correct on each new color. Table A.1 shows the number of stimuli presented by the time these criteria were reached, since a session included fewer new stimuli as more new colors were added. No learning-to-learn is evident here, as was the case for the sessions to criterion data.

Figure A.1. Percentage of right responses on the first several sessions that each new color (green, G; red, R; orange, O; yellow, Y; violet, V; blue, B) was added to the chromatic set during Experiment I for bird 23. Filled symbols are for colored slides: circles, old color(s); triangles, new color. Open circles are for achromatic slides. Bars indicate the range and median of the seven days prior to each new color addition for colored (upper bars) and achromatic (lower bars) stimuli. (For birds 23 and 230, the filled circles during G and during O following the first session are for new and old colors combined.)



23

Figure A.2. Percentage of right responses on the first several sessions that each new color was added to the chromatic set during Experiment I for bird 230. See legend of Figure A.1 for details.

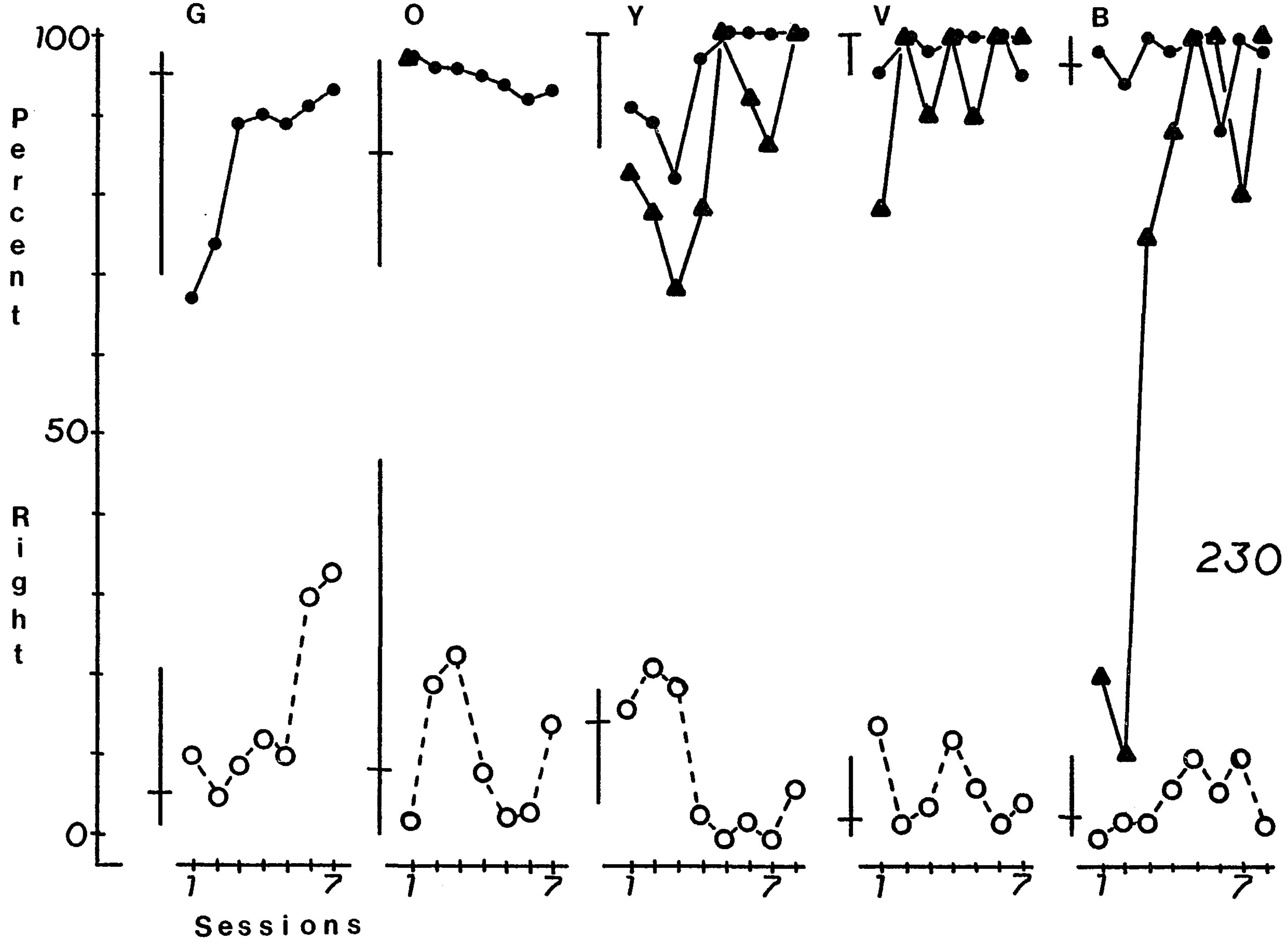
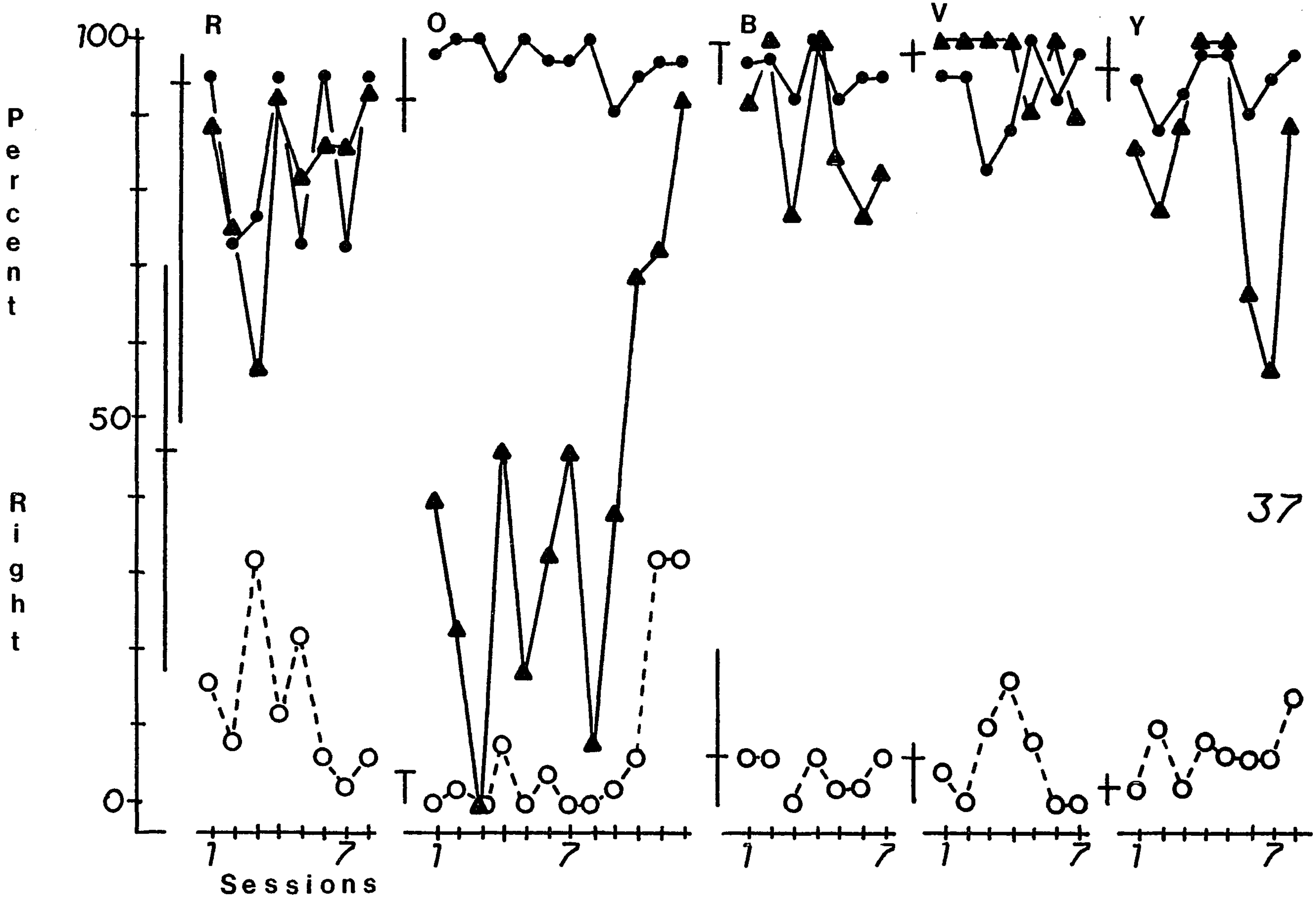
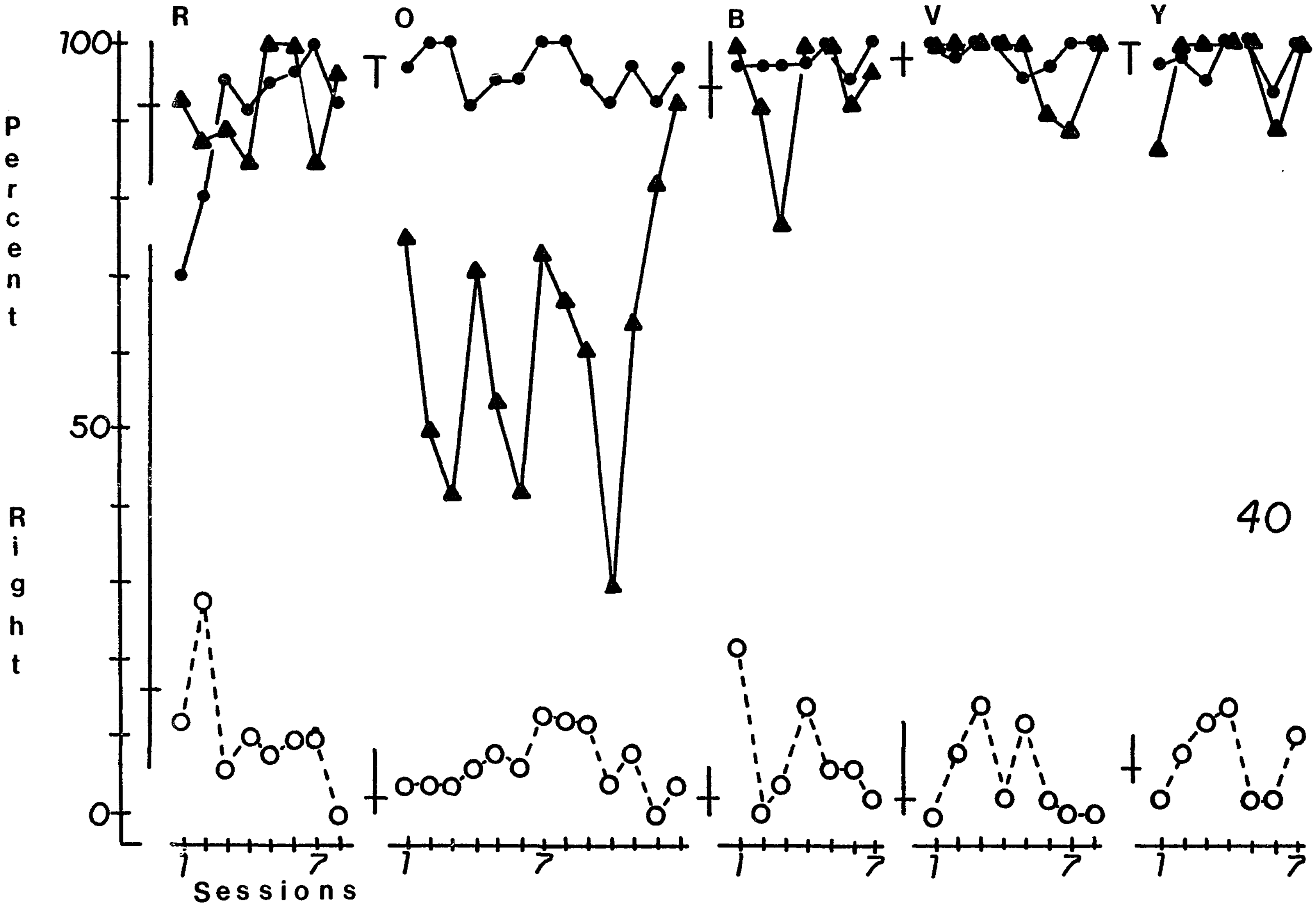

G
O
Y
V
B
100
50
0
Percent Right
1
7
Sessions
230

Figure A.3. Percentage of right responses on the first several sessions that each new color was added to the chromatic set during Experiment I for bird 37. See legend of Figure A.1 for details.



37

Figure A.4. Percentage of right responses on the first several sessions that each new color was added to the chromatic set during Experiment I for bird 40. See legend of Figure A.1 for details.



40

Table A.1

Number of Exposures to New Colored

Stimuli by the End of the Sessions

Reaching Various Criteria During Experiment I.

Bird	New Color	No. Exposures to Criterion 70%	80%	90%
23	G	a	a	a
	O	48	48	48
	Y	24	72	96
	V	20	20	20
	B	16	16	96
230	G	a	a	a
	O	24	24	24
	Y	12	12	60
	V	10	20	20
	B	24	32	40
37	R	25	25	125
	O	288	312	312
	B	12	12	12
	V	10	10	10
	Y	8	8	32
40	R	25	25	25
	O	24	288	312
	B	12	12	12
	V	10	10	10
	Y	8	8	16

[a] Information not available.

APPENDIX B

THE TIME-COURSE OF AFTERIMAGE DECAY IN PIGEONS

In experiment III, evidence was presented that chromatic adaptation changes the pigeon's experience of color. Another simple AE which is closely related to chromatic adaptation is the afterimage. The afterimage occurs following exposure to a light which is more restricted spatially and/or temporally than that producing chromatic adaptation. For example, after observing a brief intense light (called the primary stimulus), human subjects report an afterimage which has the same shape as the primary stimulus, is restricted to the retinal locus of stimulation (so that it appears to move as the eye is moved), and may be of the same or opposite brightness relations and of the same or complementary hue as the primary stimulus. The afterimage may persist for up to eight min or more (Alpern & Barr, 1962), and may change in hue, brightness relations and intensity over time. The specific characteristics of the afterimage depend upon the intensity, duration, and hue of the primary stimulus, the intensity and hue of the background field upon which the afterimage is projected, and various conditions of the subject (see Brown, 1965, for a review). Given that birds are subject to chromatic adaptation, it seems likely that they should also experience afterimages. Indeed, Swindle (1916) concluded that owls and cockatoos do, by noting that they missed or fell off their perch after being exposed first to a brief intense light and then to darkness. The suggestion was that the birds were aiming toward the afterimage of their perch, which would move with head or eye movements, rather than toward the perch itself.

In this study an attempt was made to demonstrate afterimages in pigeons, again using the apparatus, subjects and general procedure of Experiments I-III. A photographic strobe flash was employed as the primary stimulus, which for the human produces a pink afterimage lasting two or three min. If this were also the case for pigeons, reports of color (right key pecks) should occur with achromatic slides for as long as the afterimage persisted. It was hoped that the time-course of afterimage decay could be tracked more easily than was the case for chromatic adaptation since its duration was expected to be considerably longer.

Methods

Subjects

The same four pigeons were employed as served in Experiments I, II, and III.

Apparatus

The same experimental chamber as used in the previous experiments was employed. In addition, a 15 by 13.5 by 6.5 cm frame was affixed to the outside of the viewing sleeve. Within this frame was placed a 5 by 11 by 6.5 cm box containing a Honeywell Auto/Strobonar 110 flash, which could be moved manually to a position either directly behind or above the back projection screen. A trapezoidal-shaped mask was placed over the face of the flash. A green 10 W bulb was also mounted 10 cm from the screen and out of the path of the slide projector beam.

Stimuli

Two sets of slides were selected from the pool employed in Experiments I-III, one for baseline and one for test sessions. The chromatic slides included fairly desaturated colors including slides with pink areas resembling the afterimage produced by the flash for the expeimenter.

Procedure

Baseline sessions were as in the preceding experiments. The probability of reinforcement for a correct response was between .1 and .4, being increased if discrimination behavior deteriorated.

During test sessons, two types of six-min components occurred in alternation. In one type (flash components), the first entry of the head into the viewing sleeve produced the flash, while in the other type (green components) it produced approximately .5 sec exposure to the dim green light. At all other times, the procedure and reinforcement contingencies were the same as during baseline sessions, with the probability of reinforcement for correct responses being .1 or .2. The time, relative to the occurrence of the flash or dim green light, at which key pecks were emitted was recorded. This was done for each of the four types of responses: right or left pecks following colored or achromatic slides. Four test sessions were carried out with at least three baseline sessions intervening.

Results

Figures B.1 through B.4 show the combined data from all test sessions for birds 23, 230, 37 and 40, respectively. The percentage of right key pecks following colored and achromatic slides are plotted for successive 30-sec intervals of the flash and green components. The following were expected: (a) a higher proportion of right key pecks following achromatic slides during the flash than during the green components; (b) a gradual decline in the proportion of right key pecks following achromatic slides during the flash intervals. Clearly, neither of these results obtained. It should be noted, however, that Figures B.1 through B.4 are based upon a fairly small number of responses; this is especially true during the flash components. Figures B.5 and B.6 show the total number of responses emitted during successive 30-sec intervals of the components, again for all test sessions combined, for each bird. The finding to be noted is that many fewer responses were emitted at the beginning of flash components than at other times. Bird 230, for example, made no responses at all during any of the first 30-sec flash intervals. This reduced level of

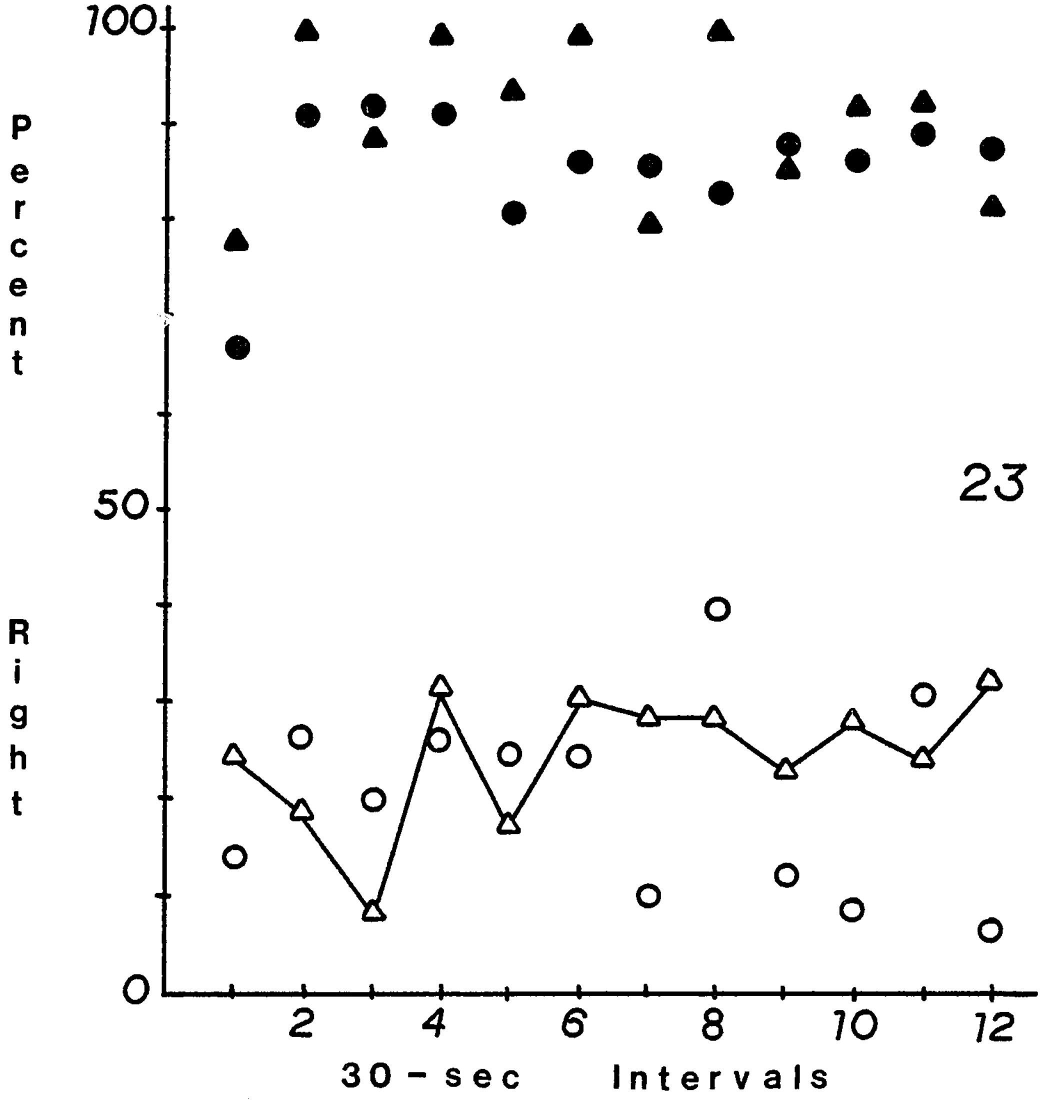


Figure B.1. Percentage of right responses during successive 30-sec intervals of components beginning with a flash (triangles) or a dim green light (circles) during four test sessions combined for bird 23. Filled symbols are for colored stimuli, open symbols for achromatic stimuli.

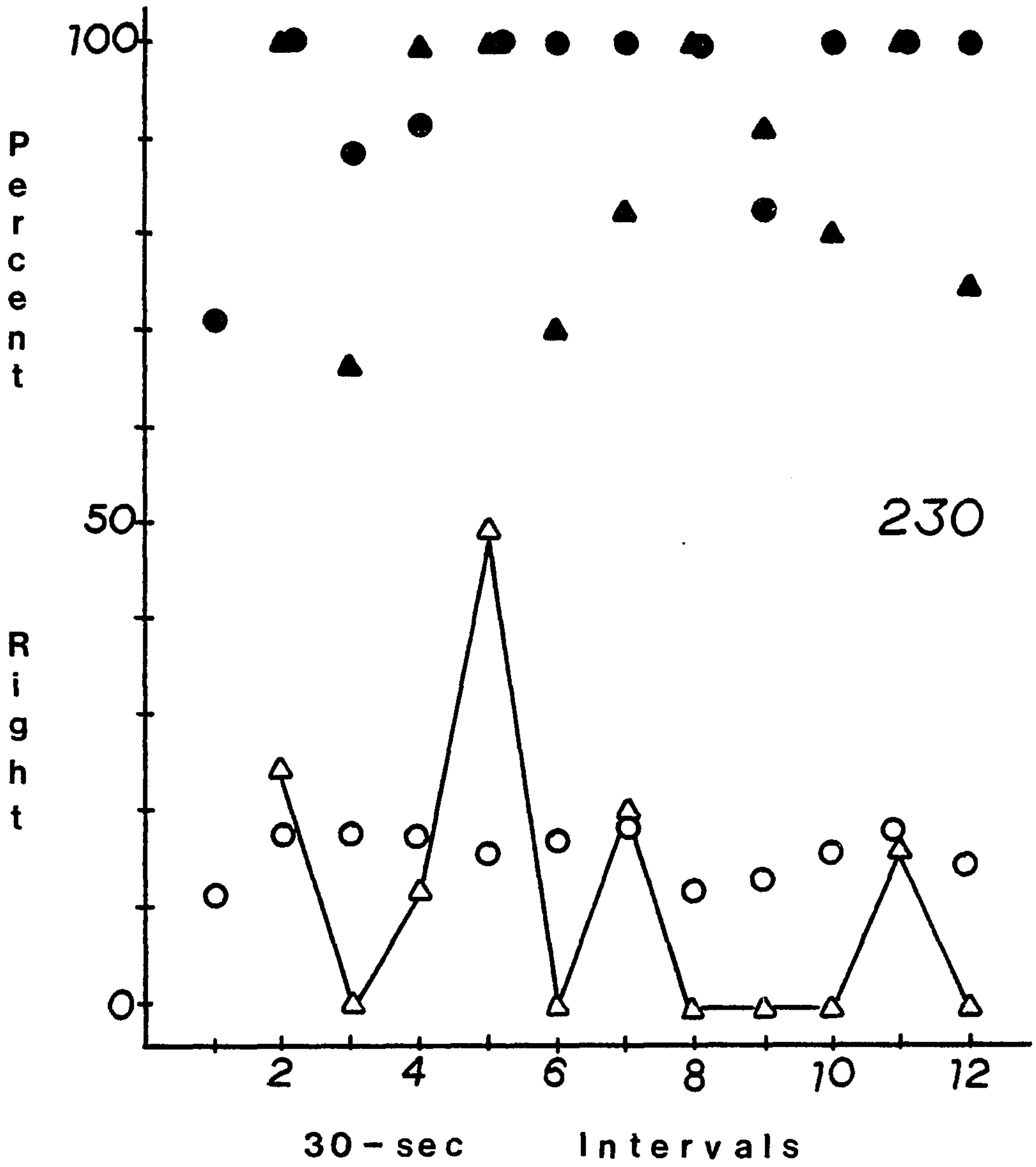


Figure B.2. Percentage of right responses during successive 30-sec intervals of components beginning with a flash or a dim green light for bird 230. See legend of Figure B.1 for details.

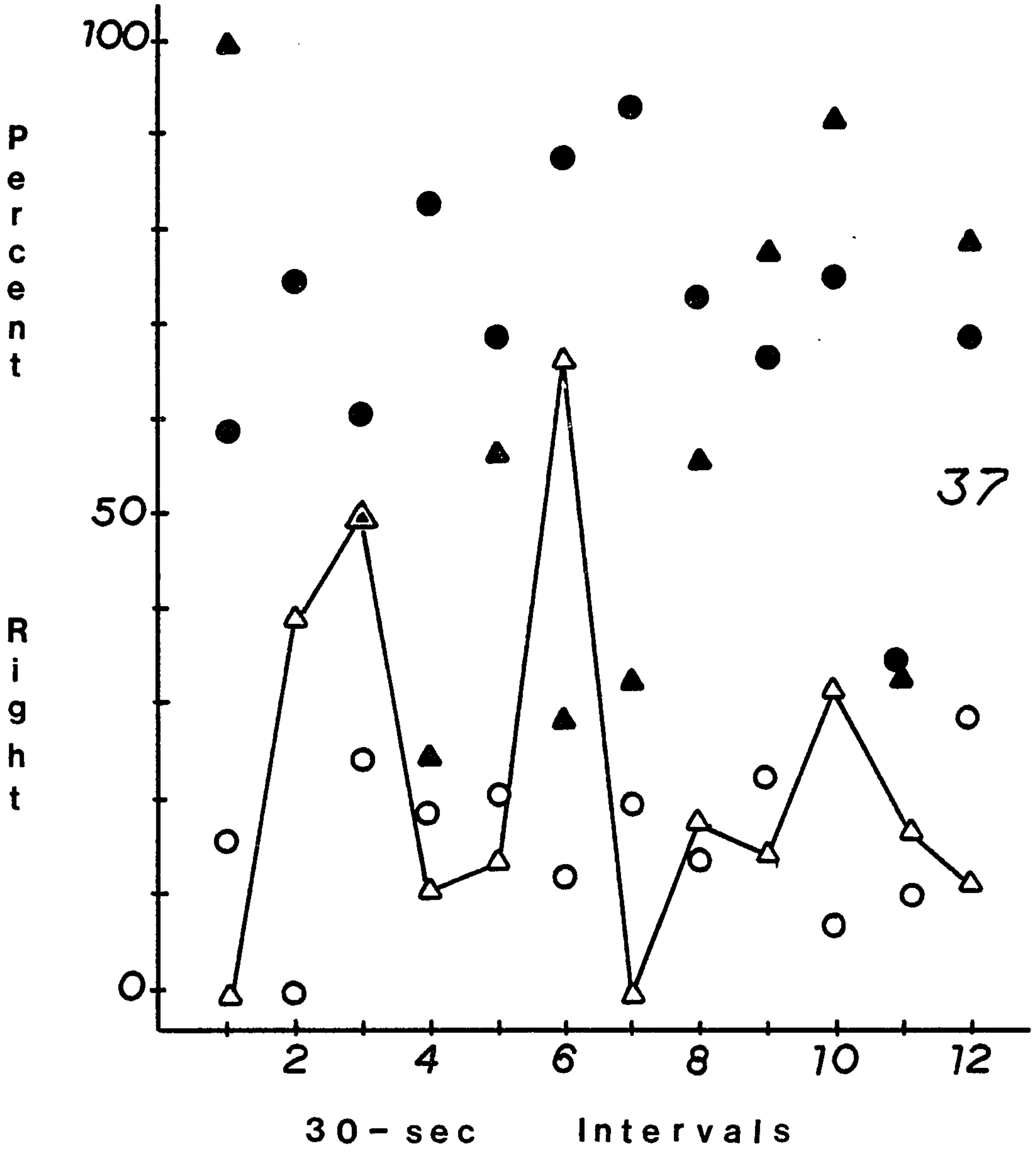


Figure B.3. Percentage of right responses during successive 30-sec intervals of components beginning with a flash or a dim green light for bird 37. See legend of Figure B.1 for details.

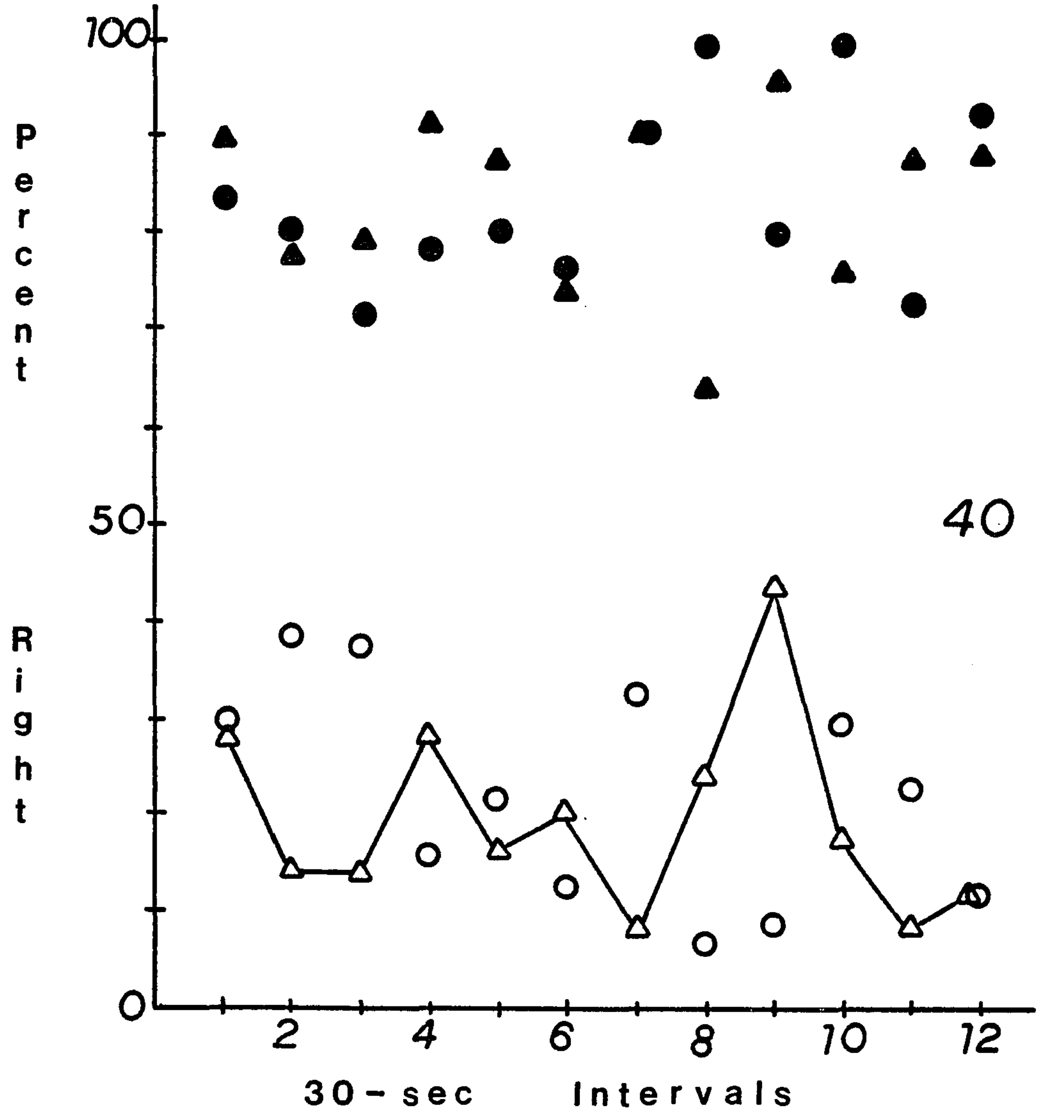


Figure B.4. Percentage of right responses during successive 30-sec intervals of components beginning with a flash or a dim green light for bird 40. See legend of Figure B.1 for details.

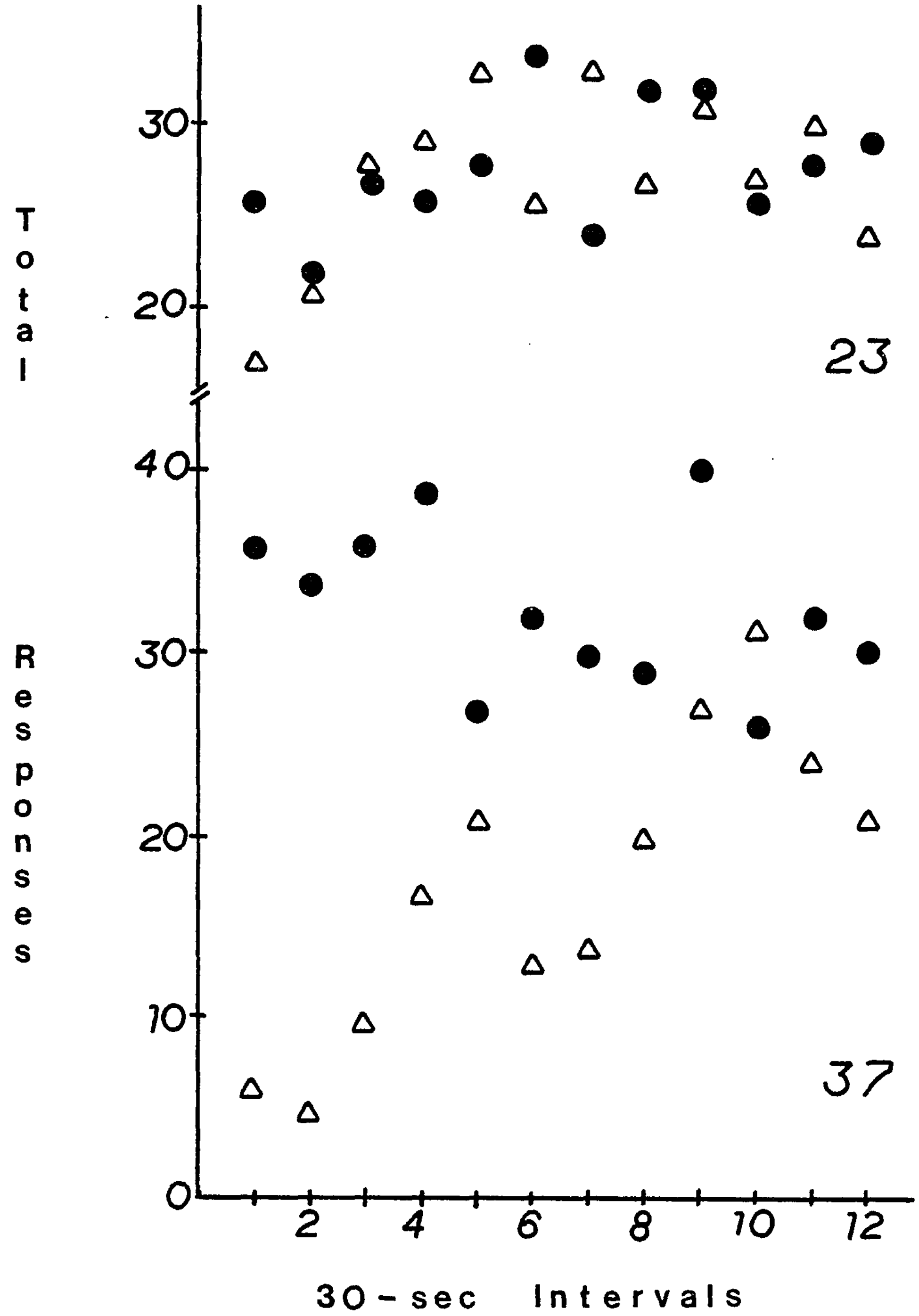


Figure B.5. Total number of responses emitted during successive 30-sec intervals beginning with a flash (open triangles) or a dim green light (filled circles) for four test sessions combined. The upper portion is for bird 23, the lower portion for bird 37.

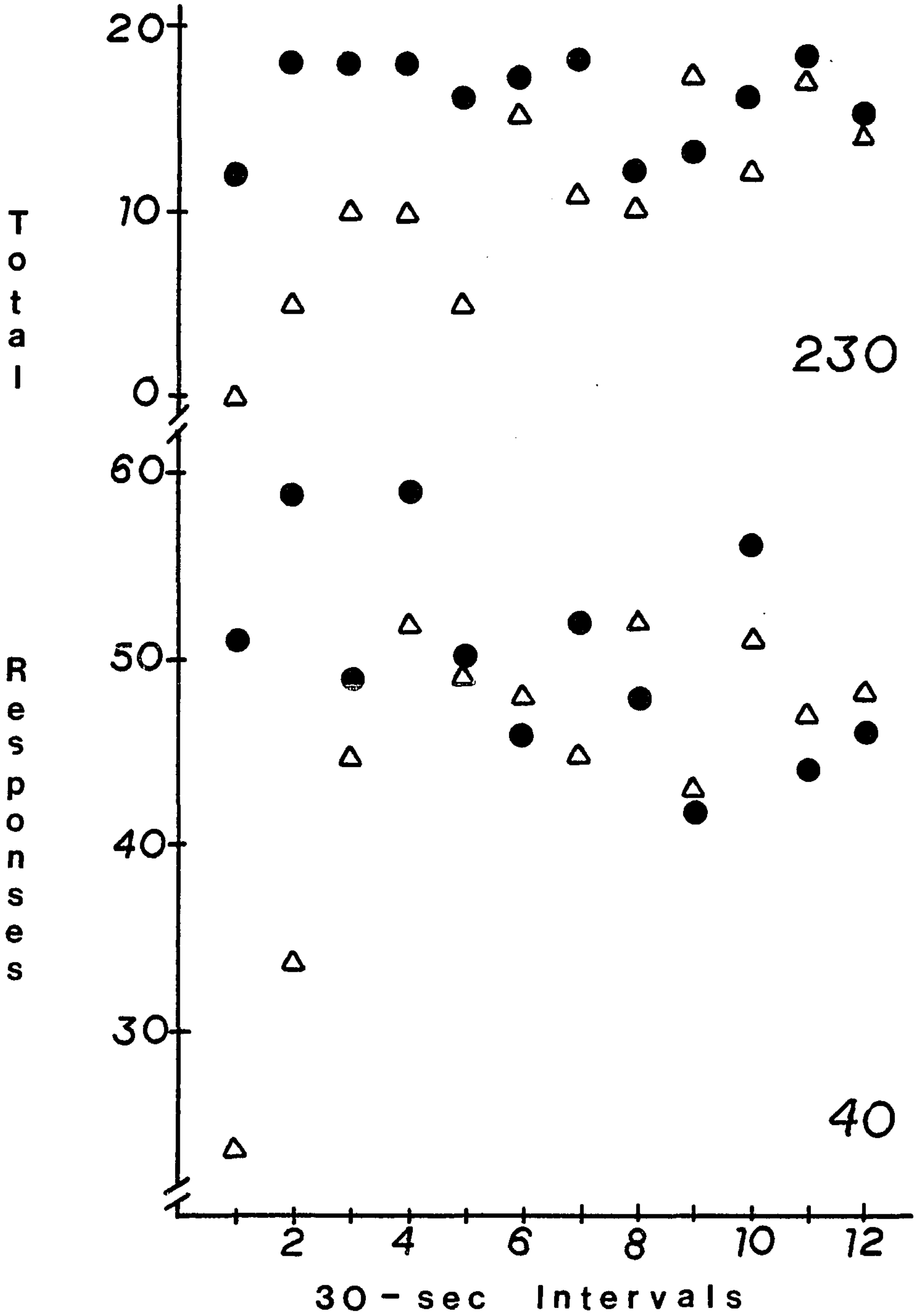


Figure B.6. Total number of responses emitted during successive 30-sec intervals beginning with a flash or a dim green light for birds 230 (upper portion) and 40 (lower portion). See legend of Figure B.5 for details.

responding occurred for all birds and lasted for from one to four min.

Discussion

Evidence of afterimages in pigeons was not found in this study. It seems likely, however, that the procedure employed was inadequate, so that it should not necessarily be concluded that pigeons do not experience afterimages. First of all, the primary stimulus used suppressed behavior exactly during the period when the afterimages were expected to occur. It is even possible that the birds stopped responding until the afterimage faded. On the other hand, birds 23 and 37 made a relatively large number of responses during the critical period and yet showed no evidence of afterimages. It may be that the birds experienced afterimages, but that the afterimages did not appear colored. Even in humans, the afterimage of a stimulus such as that employed here is sometimes reported to be whitish rather than pink (Brown, 1966).

A more adequate procedure for demonstrating afterimages in the pigeon might include using a colored primary stimulus, which would be more likely to produce a colored afterimage.[1] Also, rather than using a discrete trial

---

[1] This was originally planned for the present experiment. However, it was found that the back-projection screen substantially reduced the intensity of the flash and adding a colored filter cut it down further to the point that a "good" afterimage did not occur for the experimenter.

procedure as was done here, it might be better to employ a response which could occur at a relatively high rate while the subject observed stimuli; for example, if response keys were placed below or in front of the screen. This would allow more data to be collected during a given test session. Finally, the stimulus being observed could involve a colored area which waxed and waned as an afterimage might.

APPENDIX C

SPECTRAL ANALYSIS OF TEST SLIDES FOR FILTERS TEST 2

Two types of test slides were employed in Filters Test 2 of Experiment IV. Kodachrome test slides employed Kodachrome film sandwiched with one of four Wratten color-correcting magenta filters, in an attempt to mimick the chromatic appearance of Panatomic-X film. Similarly, Panatomic-X test slides employed Panatomic-X film sandwiched with one of four Wratten color-correcting green filters, this time in an attempt to mimick the chromatic appearance of Kodachrome film. Figures C.1 and C.2 show spectral analyses of examples of each type of test slide. Analyses of the Kodachrome test slides are shown along with an analysis of a Panatomic-X slide, and those of the Panatomic-X test slides are shown along with an analysis of a Kodachrome slide. It is evident that none of the absorptance curves of the test slides is similar to the curve of the to-be-mimicked slide. (Of course this is not required of two metamers.) At any rate, these anlayses unfortunately cannot aid in interpreting the results of Filters Test 2.

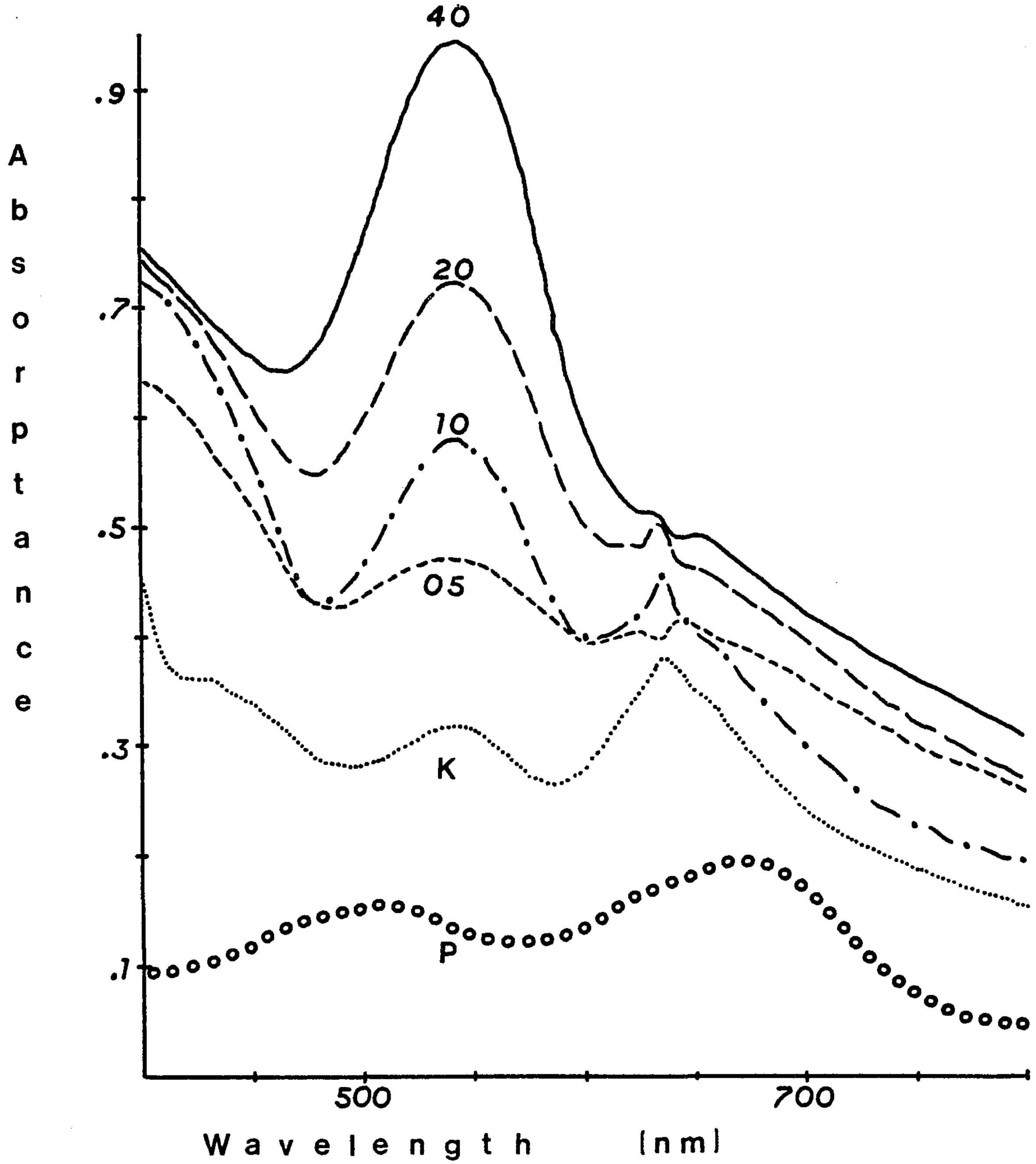


Figure C.1. Spectral analyses of selected Kodachrome test stimuli used in Filters Test 2 of Experiment IV. Curves are labeled according to which Wratten filter was used (CC40M, 40; CC20M, 20; CC10M, 10; CC05M, 05; or no filter, K). The curve labeled "P" (open circles) is the spectral analysis of a Panatomic-X control slide, shown for comparison.

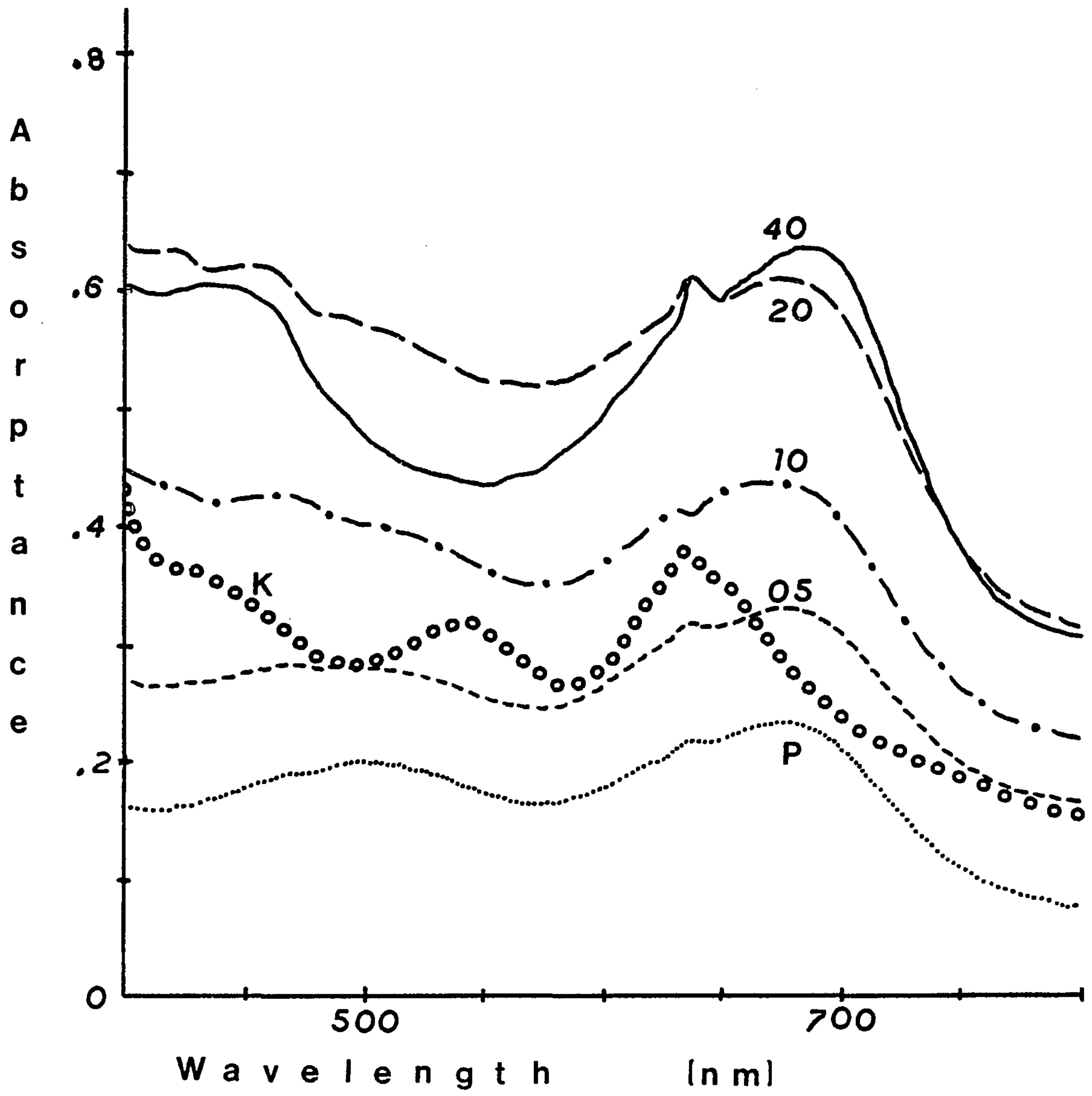


Figure C.2. Spectral analyses of selected Panatomic-X test stimuli used in Filters Test 2 of Experiment IV. Curves are labeled according to which Wratten filter was used (CC40G, 40; CC20G, 20; CC10G, 10; CC05G, 05; or no filter: control slide, P). The curve labeled "K" (open circles) is the spectral analysis of a Kodachrome test slide (no filter), shown for comparison.