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Frontal visual field position and visual discrimination learning in the pigeon (*Columba livia*)

Yamashita, Hiroshi, Ph.D.

City University of New York, 1991

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Frontal visual field position and visual discrimination learning in the pigeon (*Columba livia*)

by

HIROSHI YAMASHITA

A dissertation submitted to the Graduate Faculty in Psychology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1991

This manuscript has been read and accepted for the Graduate Faculty in Psychology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Abstract

Frontal visual field position and visual discrimination learning in the pigeon (*Columba livia*)

by

Hiroshi Yamashita

Adviser : Professor Sheila Chase

The pigeon has a binocular overlap in front within its panoramic visual field supported by its laterally positioned eyes. The purpose of this study was to examine the possible effects of the binocular overlap on shape discrimination learning. In a successive discrimination paradigm, the subjects were trained to discriminate between two stimuli subtending about 2.5° in visual angle. In order to control its position within the frontal visual field, a discriminative stimulus was presented for 50 ms only when the subject pecked at a small fixation point (FP). Nine stimulus positions were located along a horizontal line 2.5 cm (about 20° in visual angle) below the FP with neighboring positions separated by 1.1 cm (about 9°) from each other. The three positions in the center were presumed to be located within the binocular area, and the rest in either of the monocular areas.

Experiment 1 examined the effects of the binocular overlap on visual performance. A discriminative stimulus was presented at one of the 9 positions in each trial. The subjects learned to discriminate between the two stimuli at all positions, and there was little difference in performance among positions. There were no apparent differences in the rate of acquisition.

Experiment 2A and 2B examined the effects on transfer. Seven pigeons were first trained at one of 5 positions which included binocular and monocular positions. Transfer of the discrimination was tested at the 9 positions. Transfer was limited in the vicinity of the training position, and the boundaries between binocular and monocular areas did not appear to limit transfer.

In Experiment 3, the subjects from Experiments 2A and 2B were trained with the same procedure as in Experiment 1. The effect of previous training at a specific position was seen as slower acquisition at positions further away from the training position. After extensive training, however, all subjects learned to discriminate at all positions.

From the results of these experiments, it was suggested that the pigeon's frontal visual field is perceptually homogeneous, and the distinction between binocular and monocular areas does not have much effect on visual discrimination.

Acknowledgements

First of all I would like to thank Dr. Sheila Chase for her support throughout the course of this dissertation project. I would also like to thank Dr. Philip Zeigler and Dr. James Gordon for their valuable suggestions through many meetings and individual conferences. I also feel grateful to my two outside readers, Dr. Eric Heinemann and Dr. Robert Allan, for their careful reading of the manuscript and their helpful comments on it.

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I. INTRODUCTION

With laterally positioned eyes, the pigeon has a panoramic visual field of about 320°. The optical axis is about 80° away from the midline, and points about 5° upward. The area in front of the animal is served by the nasal edge of the visual field of each eye. The extent of binocular overlap has been determined by several researchers (Jahnke, 1984; Martin & Young, 1983; Martinoya, Rey & Bloch, 1981; McFadden & Reymond, 1985). Although there are slight differences among studies, the vertical extent is between 110° and 130° and the horizontal extent at its widest is 30° to 40°. It should be noted that the size of the binocular area is affected by the position of the eyes and also by the distance between the eye and the object (Holden & Low, 1989).

Precisely coordinated pecking behavior of the pigeon (e.g., LaMon & Zeigler, 1984, 1988; Zeigler, Levitt, & Levine, 1980) suggests that binocular vision plays an important role in guiding the behavior. Although the optic nerves of birds cross almost completely at the chiasma, binocular interaction at the neuronal level has been evidenced by the recording of binocular units in the visual Wulst of the pigeon (Perisic et al., 1971) as well as in the owl (Pettigrew & Konishi, 1976), whose binocularity with its more front-facing eyes has recently been well established (Martin, 1984; Porciatt et al., 1990). One of the possible functions of the binocular overlap is in depth perception. Psychophysical studies have shown that the pigeon is capable of judging the distance to an object and between objects (Martinoya, Le Houezec, & Bloch, 1988; McFadden, 1987; McFadden & Wild, 1986). Observations of converging eye movements (Bloch, Rivaud, & Martinoya, 1984) suggest that convergence cues are used in depth perception in the pigeon. The role of binocular disparity is yet to be determined (Martinoya et al., 1988).

The objective of this study is to examine how the pigeon's frontal visual field is organized, and to explore the functions of binocular overlap, besides that of depth perception. The term "frontal visual field" is loosely defined as the representation of the space in front of the pigeon with its coordinates fixed to the pigeon's body. As will be discussed later, this term has been used in the literature in referring to the area in the visual field which is defined by optical and retinal characteristics as being different from the "lateral visual field". Although the terms "frontal visual field" and "binocular visual field" in the pigeon are sometimes used interchangeably, they may not coincide.

In humans, the visual fields of the two eyes mostly overlap, and we rarely notice the difference between binocular and monocular areas. The frontal visual field of the pigeon is very different from ours. "How does the world appear to the pigeon?" is an interesting question, but cannot be scientifically very meaningful. With respect to the frontal view, however, we may ask following questions. In identifying an object in its visual field, how much area is effective? Is there a functional difference between the area covered binocularly and monocularly? If the two types of fields are distinct from each other, does it affect the transfer of learning from one area to the other?

Specifically, two questions were investigated. One question is whether there is better visual performance in the area of binocular overlap, and if there is a facilitative effect in the learning process in that area. A second question is whether a discrimination learned about stimuli in one kind of visual field transfers to the same stimuli presented in the other kind of visual field. In this study these questions were investigated by analyzing processes of shape discrimination. It should be noted that by using a behavioral method (discrimination learning), factors other than simple sensory processes may be introduced. For example, Nye (1973), observing that his pigeons failed to acquire discriminations of luminance or color when the discriminative stimuli were presented at lateral positions, concluded that the pigeon could not associate the information entering the lateral field with the pecking behavior directed to the front. This conclusion, however, was partly refuted by

Bloch and Martinoya (1982). They were able to train pigeons to discriminate between horizontal and vertical gratings, in order to measure visual acuity in the lateral field, using a frontal pecking response. One of the important differences between these studies was in the response requirement for the subject. In Nye's experiment the subject had to choose between two response keys, while in Bloch and Martinoya's experiment only one response key was used and the subject had to peck it only when the positive stimulus was presented (Go-No-go procedure). It is also noted that in Nye's experiment the stimuli were presented above the level of the pigeon's eyes.

D. S. Blough (1979) suggested from the result of his search experiment that the pigeon might "see clearly" over a large portion of its visual field. Reaction time for pecking at a target among non-target stimuli scattered on the display (about 50° in visual angle) was fairly short and was relatively independent of the position of the target within the display. Behavioral experiments have shown that the visual acuity in the frontal field of the pigeon is around 2.5 min of arc in terms of minimum separable angle (Hodos, Bessette, Macko, & Weiss, 1985). The extent of the area of high resolution in the frontal visual field, and the detailed regional differences have not been clarified. It is difficult to position and manipulate visual stimuli small enough to assess the possible regional differences in visual acuity within the frontal field with a conventional experimental setup. Although we may gain some information by mapping the receptive fields by electrophysiological methods, dynamic properties of the system are difficult to study, and behavioral data from non-restricted pigeons are essential for understanding the natural behavior of the pigeon.

Before we consider the possible contributions of the binocular overlap, we have to consider the physiological basis of resolution. Two characteristics of the pigeon's retina have to be considered. One is its relatively homogeneous distribution of cells in general and the other is the specialized area that corresponds to the frontal visual field.

It is a notable characteristic of the pigeon's eye, shared by many species of birds, that the retinal cell density is relatively high in the periphery. The ratio of ganglion cell density from center (foveal region) to periphery (near the edge of the retina) is about 4.5 to 1 in the pigeon, while in human it is about 40 to 1 (Binggeli & Paule, 1969). This suggests that large areas of the pigeon's visual field has high resolution. P. M. Blough's (1973) finding that visual acuity was not significantly impaired by a lesion of the fovea suggests that the fovea does not play as important a role as in humans. Uhrlich, Blough, and Blough (1982), using a behavioral technique, demonstrated that visual acuity for different viewing angles in the lateral visual field was fairly constant. Although their results indicated that visual acuity quickly decreased toward the frontal field, they attributed it to the fact that the stimuli were presented at 70 cm, a large distance considering the myopic nature of the pigeon's frontal vision.

The second characteristic is that the frontal visual field is supported by an area of high cell density of the retina. This area is called "red field" from its appearance, in contrast to the adjacent "yellow field". Galifret (1968) found that the cell density in the inner granular layer of this area of the retina is comparable to that in the foveal region. This area is about 50° wide. This suggests that a fairly large area is highly resolved in the frontal visual field.

Differences between lateral and frontal fields have been well studied since Catania (1964), based on anecdotal evidence, predicted that the pigeon had two separate visual systems that differ in their refractive characteristics, hyperopic in the lateral visual field and myopic in the frontal field. Subsequent studies confirmed his prediction. Marshall, Mellerio and Palmer (1973) constructed a schematic eye for the pigeon. It indicates that the pigeon is hyperopic in the lateral visual field. Differences in refractive characteristics between frontal and lateral fields have been demonstrated by a ray tracing method (Nye, 1973) and also by an electrophysiological method (Millodot & Blough, 1972). Recently, however, Fitzke, Hayes, Hodos, Holden, & Low, (1985), using a new optometric method, reported that the difference in refractive states exists between upper and lower halves of the visual field, rather than between frontal and lateral fields. Behavioral assessments of visual acuity has also provided support for Catania's prediction. P. M. Blough (1971, 1973) found that the visual acuity for a distant target (70 cm) was lower when the pigeon was restricted to the frontal field of view than under free-viewing condition. More extensive data were provided by Bloch and Martinoya (1982). By controlling the position of the test stimuli in the visual field, they demonstrated that frontal acuity decreased with distance, while lateral acuity increased with distance. The lateral and frontal visual systems are known to differ also in spectral sensitivity (Romeskie & Yager, 1976; Yager & Romeskie, 1975) and velocity thresholds (Martinoya, Rivaud, & Bloch, 1983).

Two sources of binocular facilitation have been distinguished (Blake, Sloane, & Fox, 1981). Higher visual performance is expected by simply having two independent channels of input from the binocular field. For example, in the case of a detection task at threshold, the probability of detection will be higher with two eyes than with one eye as expected from probability summation. If there exists some integration of information from the two channels, a higher levels of performance than the simple probability summation can be expected. This type of facilitation is called neural summation. Di Stefano, Kusmic, and Musumeci (1987) investigated the problem of binocular facilitation in pigeons by examining response latencies in discrimination tasks. They found that response latency was shorter under binocular than monocular viewing, but did not find evidence for neural summation between the two eyes.

As for acquisition processes, Watanabe, Hodos, and Bessette (1984) compared binocular and monocular viewing in visual discrimination. They found that acquisition of discrimination of color, luminance, and shape, was quicker with binocular viewing.

The second question is whether the extent of transfer is affected by the binocular overlap. We take it for granted that we can recognize an object in any part of the visual field as long as its image is clear enough. We may expect that what a pigeon learned about stimuli presented at one position in its visual field is easily transferred when the stimuli are presented in different positions. The pigeon's visual field appears to be divided into at least three distinct areas, a binocular and two monocular ones. If the two types of visual fields are distinct from each other, they may provide clear conditional cues for discrimination. There have been few studies that deal with this question directly. In the studies comparing the characteristics of lateral and frontal visual fields mentioned above (Bloch & Martinoya, 1982; Martinoya et al., 1983), Bloch and her colleagues found virtually no transfer at the beginning of the training for the lateral presentation from the preceding training of the same discrimination task in the frontal field. Although their interest was in comparing the frontal and lateral fields, it may be interpreted that the pigeon responded not only to the stimuli manipulated by the experimenter but also to the way the stimuli were viewed, binocularly or monocularly.

The underlying neural structure may influence the nature of transfer. The question of whether the information is shared by the two hemispheres has been studied by looking at interocular transfer in the pigeon. The results of the earlier studies on interocular transfer were not very consistent. Different factors, such as task difficulty and changes in pigeon's viewing position, have been suggested as possible determinants of the success or failure of transfer. Goodale and Graves (1982) concluded, from the results of an extensive series of experiments, that the location of stimulation was a critical factor. They inferred that when the stimulus is presented within the "red area", the corresponding area of the other hemisphere is activated through the bilateral connection, and this process mediates interocular transfer. In order to consider transfer between binocular and monocular fields, further assumptions concerning the way information ("memory trace") is stored and retrieved are necessary.

The design of the experiments which examined these two questions on binocular overlap, binocular facilitation and the effect of binocular overlap on transfer, will be described below. In order to locate a stimulus within a limited area of the visual field of a freely moving pigeon, a method of "behavioral fixation" was developed for the present study. The rationale of this technique will be discussed first.

Method of "behavioral fixation"

In studies on interocular transfer and binocular facilitation, a common method of restricting the pigeon's viewing conditions for the stimulus, is to cover one of its eyes. However, in the present study, in order to locate a stimulus at different positions in the pigeon's visual field within the same session, it was necessary to develop a method that did not require to limit the pigeon's view by blocking the eye.

Bloch and her colleagues developed a method of "behavioral fixation" to compare the characteristics of the central and the lateral visual field of the pigeon (Bloch & Martinoya, 1982; Martinoya et al.,1983). The discriminative stimuli (gratings in horizontal or vertical orientation) were presented for a short duration, namely 300 ms, immediately after the subject pecked on a small "observing" key. A peck on a second key was reinforced when the positive stimulus had been presented. P. M. Blough (1979) used a similar method to compare spectral sensitivity in the pigeon's frontal and lateral visual fields. Better control over stimulus location within the frontal visual field can be attained by further restricting the conditions for stimulus presentation.

It is known that the pigeon's pecking behavior is highly stereotyped. When it continuously pecks at a response key, the interresponse time is fairly constant at about 300 ms (e.g. D. S. Blough, 1963; Yamashita, 1981). Zeigler et al. (1980) observed that, when a pigeon successively pecked at grains, the head position remained relatively stable for about 60 ms after the contact with the grain, prior to the initiation of the next peck. The similarity of the distributions of interpeck intervals in these two situations suggests that the same time relationship holds in a key pecking situation as in pecking grains. If the stimulus is presented only during the period when the head remains stable after a peck, it is expected that the stimulus will fall on a relatively restricted area within the visual field. The location of this area can be further restricted by limiting the size of the area on which a peck will initiate a stimulus presentation. The short duration of stimulus presentation may make the discrimination more difficult than under the more usual condition in which a discriminative stimulus is continuously on the key. Visual acuity reported by Bloch and Martinoya (1982) using their behavioral fixation method, is lower than that determined in other studies that used more conventional methods of stimulus presentation (e.g. Hodos, Leibowitz, & Bonbright, 1976; P. M. Blough, 1971). The short latency of pigeon's responding in D. S. Blough's (1977, 1979) search experiment, however, suggests that the pigeon can discriminate shape stimuli within a very short period of time after their onset.

Since the "fixation" method contrived for the present study depends on the stereotypy of the pigeon's responding, it is necessary to make the subject keep pecking at the target. Thus, in order to assess the discrimination between the stimuli, a variant of a multiple schedule of reinforcement was used. One of the two visual stimuli was presented in positive trials, and the other in negative trials. The stimulus was presented for 50 ms with 100 ms latency, only when a peck was made precisely on a small square which is called the fixation point (FP). The response rates in the two kinds of trials were taken as the basic data.

Limitations. This method has many limitations as a "fixation" method for pigeons. First of all, the actual location of the eyes relative to the stimulus is not directly controlled. The system only limits the location of contact with some variability, and does not have much control over the direction of the pecking movement. Variability in the position of the eyes will give rise to an overestimate of the area in which the stimuli are discriminable, and fixed bias in the direction of pecking movement against the display will appear as a constant error.

Additional sources of variability can be pointed out. Two of them are considered here. First, it may be argued that, when a stimulus is presented, a pigeon may move its head and/or eyes to that stimulus and change the position of stimulus within its visual field. Eye movements of the pigeon have attracted much interest recently. Rapid orienting (saccadic) eye movements as well as fixating vergence movements have been documented (e.g. Bloch, Lemeignan, and Martinoya, 1987). With the duration of the stimulus used in this study, 50 ms, it is possible for a pigeon to shift its eyes toward the stimulus during its presentation. However, it has to be pointed out that a certain amount of time is necessary for fixation in order to recognize a stimulus. Goodale (1983) has shown, using high-speed filming, that pigeons make a couple of fixations, about 100 ms each in duration, during pecking behavior aimed at a grain or a response key. The duration of the stimulus in the present study is much shorter than the duration of fixation, although a smaller amount of time may be required when an overt response toward the stimulus is not involved.

Another possibility is that, since the stimulus can be presented more than once within a trial, the subject may shift its eyes for the second and later stimulus presentation. Some evidence against this possibility will be presented by examining the pattern of responding.

The results based on this technique have to be interpreted with these limitations on variability and bias in mind. On the other hand, if a dependable functional relationship is observed between the stimulus position and discriminative performance, it will give confidence about the technique, and the relationship may be accepted as an indication of some of the characteristics of pigeon's visual system.

Experimental design and hypotheses

Two main experiments and one supplementary experiment were performed in order to examine those questions about the functions of binocular overlap that were discussed above.

In these experiments, the pigeons were trained to discriminate between two kinds of shapes, "x" and "o", which subtended about 2.5° in visual angle and should be clearly distinguishable to the pigeon according to the available data on visual acuity in the frontal field (Hodos et al., 1985; Uhlrich et al., 1982). Since the major concern was the possible difference between the binocular and the monocular visual fields in front, stimulus positions were defined in terms of the location on the tangent screen (computer display) in front of the pigeon. Nine stimulus positions along a horizontal line slightly below the beak and each separated from its neighbors by about 9° in visual angle were used. These stimulus positions were intended to cover the frontal binocular field and the monocular fields on the left and right sides. (Calculation of the visual angles are based on the estimate of the viewing distance of 6.7 cm reported by Macko and Hodos, 1985.)

Experiment 1 compared the rates of acquisition and the levels of asymptotic performance of shape discrimination at different positions in the visual field, by training individual pigeons at different positions in parallel (multiple position training).

The purpose of this experiment was to determine the extent of effective area for visual discrimination. Binocular facilitation may lead to quicker acquisition at positions in the binocular field. If there is a difference in resolution, that would also affect the asymptotic performance. The gradient of the strength of these underlying factors is expected to appear as a gradient in asymptotic performance and/or one in rate of acquisition.

In addition, in order to discuss transfer of discrimination to different positions in the visual field, it is necessary to establish that the discrimination can be acquired equally well at those positions, or to have information about possible differences.

Experiment 2 examined transfer of the shape discrimination learned at one position to different positions in the visual field. The subjects were first trained at one of 5 stimulus positions (single position training), then tested for transfer at the 9 positions. Of 5 training positions, two were located in the monocular area on one side, and the rest were in the binocular area.

Hypothetical outcomes based on different hypotheses are illustrated in Figure 1 in terms of generalization gradients of discriminative performance for original training in binocular or monocular positions. (In the following, the term "discriminative performance" will be used to describe the subjects' responding to the stimuli at each test position. Since no reinforcement contingency was set in test trials, it is not proper and a more neutral term, such as "magnitude of differential responding", is preferable, but the former terminology is used to avoid clumsiness of description.) One possible outcome, if we assume the whole area tested is functionally homogeneous, is complete transfer (Figure 1, 1), that is, the pigeon will respond differentially to the two stimuli at all test positions at similar level as at the position of the preceding training. The other possibility is a partial transfer. Possible different outcomes of partial transfer are considered below.

First, it may be expected that the very change of the stimulus position causes a decrement of discriminative performance, even if the frontal visual field is functionally homogeneous. It may be hypothesized that the position of the stimulus gains control over the subject's responding, along with the shape of the stimulus. Alternatively it may be said that the subject learns to "attend" to a particular position in the visual field as the location of discriminative cues. To dissociate these possible sources of partial transfer is not an objective of this study. In any case, if the stimulus position acquires partial control over responding, it is predicted that the decrement of performance will be a function of distance between the test position and the original one. The gradient of discriminative performance as a function of stimulus positions will then be symmetric around the original stimulus position (Figure 1, 2).

The major issue of this study is the function of binocular overlap. The question in this experiment is whether the division between monocular and binocular areas in the visual field has an effect on the nature of transfer. The "division" may be in appearance. In a similar argument as above, the pigeon may be said to "pay attention" to a particular area (binocular or monocular) where the stimuli are presented. The difference is that a distinct area, rather than position becomes an additional factor controlling the pigeon's discriminative behavior. If it does, the transfer is expected to be limited to the visual field, monocular or binocular, in which the training stimuli were presented (Figure 1, 3a).

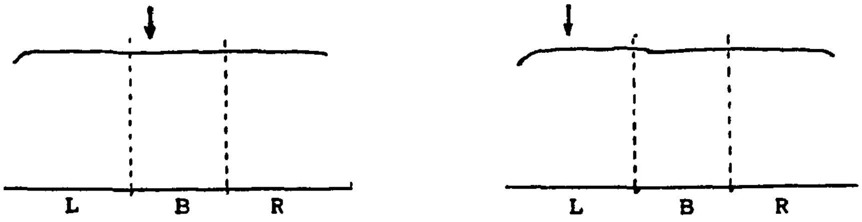
The organization of associated neural structures may affect the nature of transfer. Goodale and Graves (1984) hypothesized that the bilateral connections between binocular areas of the brain mediates interocular transfer in pigeons. A stimulus presented in the binocular visual field activates these areas at the same time even if the visual input comes from one eye. When the visual input from the same stimulus comes from the other eye, the subject will react the same way, thus showing interocular transfer. But if a stimulus has been presented in a monocular area of one eye, since only one side of the brain is activated, the subject will not show an appropriate response when the stimulus is presented to the other eye. From this line of reasoning, it follows that, when the pigeon is trained at a position in a monocular area, it will not show transfer to the stimuli presented in the other monocular area. If the information is not shared within a hemisphere, transfer will be limited within each respective field (the same as Figure 1, 3a). If information is utilized within a hemisphere, transfer from a monocular field is expected within that monocular field and the corresponding binocular field (Figure 1, 3b). In this regard a recent report by Remy and Emmerton (in press) of directionally selective transfer of detection of visual stimuli between the frontal and the lateral fields, is notable. They found that transfer occurred when the stimulus was changed from the lateral to the frontal visual field but not in the other direction (Figure 1, 3c).

In summary, three kinds of hypotheses have been considered. One is complete transfer. Of two hypotheses that predict partial transfer, the first one regards the position of stimulus presentation as an additional controlling factor, and predicts a symmetric generalization gradient around the training position. These two hypotheses assume that the frontal visual field is functionally homogeneous regardless of monocular and binocular differences. The third hypothesis is that the division between monocular and binocular visual fields is a determining factor of the extent of transfer, and predicts an asymmetric gradient.

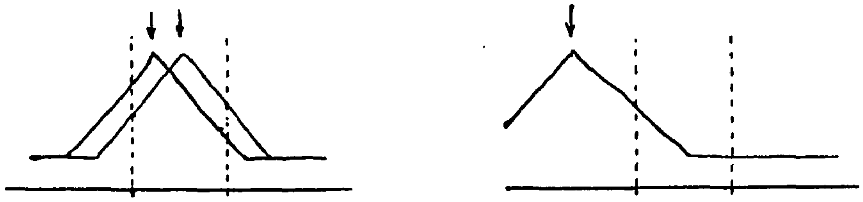
In Experiment 3, those pigeons that had served in Experiment 2 were trained with the same procedure as in Experiment 1. The amount of transfer to other positions from that of original training can also be measured by the rate of acquisition when a reinforcement contingency comes into effect at those positions. Thus a correlation between the results of this experiment with those of Experiment 2 will enhance the validity of the latter. The second purpose of this experiment was to supplement the data of Experiment 1 by training the subjects to asymptotic performance at all 9 stimulus positions.

Figure 1. Hypothetical generalization gradients of discriminative performance under different hypotheses about transfer. The curves depict discriminative performance (ordinate) as a function of stimulus positions (abscissa). An arrow points to the position of the preceding training either in binocular area (left figures) or in monocular area (right figures). Boundaries between different areas are denoted by broken lines.

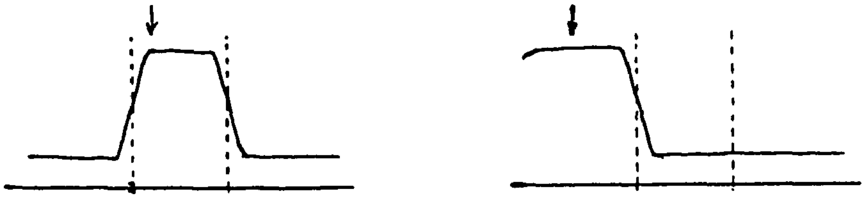
1. Complete transfer



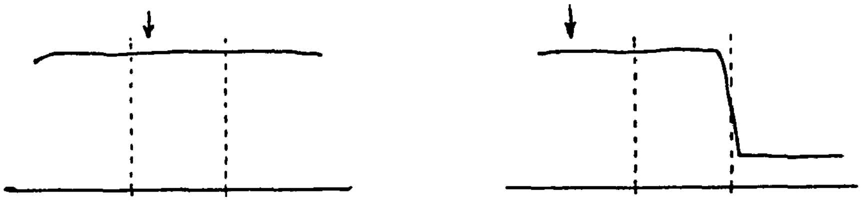
2. Partial transfer - positional control



3. a. Limited transfer within respective visual field



b. Limited transfer within respective hemisphere



c. Directional transfer binocular-- monocular

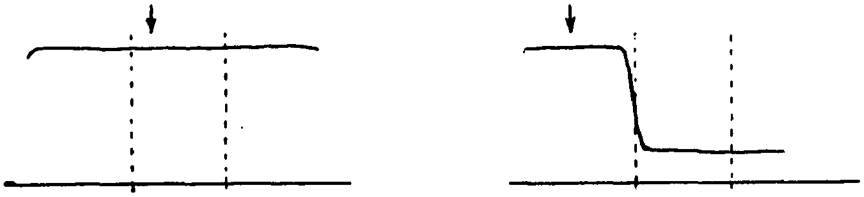


Figure 1

General Method

Subjects

The data from 9 White Carneaux pigeons (*Columba livia*) are reported here. Several other pigeons were trained to various stages, but they did not reach training criteria and were dropped. All the subjects had previous experience in visual discrimination experiments with stimuli presented on a monochrome (black and white) computer monitor in a pigeon chamber equipped with conventional response keys and a grain feeder. They were kept in individual cages and maintained at 80% of their free-feeding weights with supplementary food (mixed grain) given after daily experimental sessions. They had free access to water and grit in their home cages.

Apparatus

A standard experimental chamber for pigeons was modified for this series of experiments. Its internal dimensions were 35 cm x 35 cm x 35 cm. Except for the aluminum working panel, all the walls were painted white. The subject inside the chamber could be observed through a one-way mirror on a side wall.

The working panel had a rectangular opening, 22.6 cm wide and 16.6 cm high, with rounded corners. The lower edge of it was 12.3 cm from the floor, and the bottom 3.3 cm of it was covered by a clear plexiglas sheet to prevent the subject from perching on the edge of the opening. Experimental stimuli were presented on a computer monitor (12-inch green monochrome, Radio Shack, VM-4), which was placed behind the panel. It was positioned so that the fixation point (FP) was located 23.5 cm from the floor and horizontally at the center of the opening.

The display was set at medium resolution mode (320 x 200 pixels). The visual stimuli were composed of illuminated pixels and presented on a dark background. The FP was a 3-mm square. The discriminative stimuli consisted of 8 pixels. One formed the shape of the letter x and the other the shape of the letter o. Both stimuli measured 3 mm horizontally and vertically. The average luminance of the FP and the discriminative stimuli was 21 cd/m^2, and that of the background was 0.44 cd/m^2. (Because of the characteristics of the computer monitor, a visual stimulus on the display does not form a contiguous shape, and the luminance level of it changes with a frequency of 60 Hz. This frequency, however, is above the critical fusion frequency of the pigeon at the luminance level employed here according to the data reported by Powell, 1967.) Assuming a viewing distance of 6.7 cm estimated by Macko and Hodos (1985) these forms subtend about 2.5° of visual angle.

An infrared emitter-detector touch screen (BFANM Corp, Soft-Touch) was placed in front of the display in order to determine the location of a peck. The touch screen with its interface hardware scans the horizontal and the vertical sets of detectors every 8 ms and reports which beams are interrupted. Neighboring elements are separated by 5.3 mm horizontally and 6.2 mm vertically. Averaging of a scan cycle, however, provides slightly higher resolution. A sheet of clear plexiglas, 1.6 mm thick, was mounted behind the touch screen. The distance between the front surface of the panel and that of the plexiglas sheet was 4.5 cm. The distance between the plexiglas surface and the beam of an element of the touch screen was 1.2 cm for the vertical and 2.0 cm for the horizontal elements around the FP. The surface of the display was situated 0.5 cm behind the plexiglas sheet at the point where the FP was presented. Since the display is curved, the distance from the panel to the display increases toward the edges of the display up to a maximum of about 1.0 cm within the area in which the discriminative stimuli were presented. Pecks on the plexiglas were sensed by two small microphones (Radio Shack, Cat. No. 270-090) attached to the left and right edges of the sheet about the height of the FP. Relative positions of the touch screen and the display were checked before each subject was run.

A pellet feeder (Gerbrand, G5110) delivered 45-mg pigeon pellets (Noyes, Formula C1) into a rectangular (8.0 cm x 5.0 cm) metal cup placed at the bottom left corner of the working panel. An electric buzzer (Radio Shack, Cat. No. 273-060A) attached on the ceiling behind the working panel provided auditory feedback, 20 ms in duration, when a peck was made on the FP. An electric fan on the wall facing the working panel ventilated the box and provided masking noise. A house light at the center of the ceiling illuminated the chamber. The ambient luminance was measured at the center of the left side wall around the height of the FP. The luminance was about 2.0 cd/m^2 when the house light was on, and it was reduced by half when the light was dimmed during the intertrial interval.

A microcomputer (Radio Shack, Tandy Model 1000A) with an interface unit (Alpha Product, A-Bus) controlled the experimental events and recorded the data. Duration of the discriminative stimuli was controlled by the number of refresh cycles of the computer display. Timing of other intervals was accomplished by using the internal clock of the computer, the setting of which was adjusted to give a 10-ms time base.

Stimulus positions. The arrangement of the stimulus display is illustrated in Figure 2. The 9 stimulus positions were located along a horizontal line 2.5 cm below the FP, with neighboring positions separated by 1.1 cm. These positions will be referred to by the numbers 1 through 9 from left to right. Position 5 was located directly below the FP, and was expected to fall in the center of the binocular visual field. Assuming that the pigeons viewed all stimuli from a distance of 6.7 cm, Positions 4 through 6 correspond to the binocular field, and other positions to the monocular fields.

Procedure

Preliminary training. Following training to eat pellets from the tray as soon as they were delivered, the subjects were first trained to peck at the FP presented on the display. Pecks made on the FP (effective responses) were followed by the auditory feedback, and only these pecks could be followed by reinforcement. Larger squares, 12 mm and 6 mm in size with a corresponding sensitive areas, in place of the regular FP (3-mm square), were used for initial training. Using variable interval (VI) schedules of reinforcement, the rate of reinforcement for the effective responses was decreased over sessions. At least 10 sessions with VI 20 sec schedule were given before the next step of training was started.

General procedure of discrimination training. A trial started with the presentation of the FP on the display. The first peck on the FP (effective response) started a 5-s sampling interval. The number of pecks that fell within the 3-cm square centered at the FP during the sampling interval was taken as the measure of response strength. No reinforcement was given during the sampling interval. Every effective response was followed by a presentation of the discriminative stimulus, an "x" in a positive trial and an "o" in a negative trial, at one stimulus position, and by auditory feedback, the onset of which was synchronized with that of the stimulus. The stimulus was turned on 100 ms after the contact and lasted about 50 ms (4 refresh cycles of the display). In positive trials, the first effective response after the sampling interval was reinforced, provided that more than one effective response had been made or 5 s had passed since the end of the sampling interval. One pellet was given as reinforcement, and an extra pellet was given with the probability of 0.2 (the value was decreased from 1.0 over the training sessions). A negative trial ended after the sampling interval, provided that no peck had been made during the last 2 s. The trial was continued until the subject ceased pecking for 2 s. Successive trials were separated by an intertrial interval (ITI) of 3 s, during which the display remained blank and the illumination in the chamber was slightly lowered. Timing and contingency of a typical trial is depicted in Figure 3. An equal number of positive and negative trials were presented in a quasi-random order within a block made up of a fixed number of trials for each type of experiment, with the restriction that no more than three of the same type (positive or negative) were presented successively.

Data analysis. The discriminative performance is evaluated by the ρ index, which is defined as

$$\rho = 1 - U / (N_p \times N_n)$$

where U is the Mann-Whitney U statistic, which is computed by ranking the numbers of responses in positive and negative trials. N_p and N_n are the numbers of positive and negative trials, respectively. If the number of responses in any positive trial is greater than that in any negative trial (perfect discrimination), ρ is 1.0. When there is no difference between the numbers of responses in positive and negative trials (no discrimination), ρ is 0.5. Statistical significance of discriminative performance can be evaluated by the corresponding U statistic.

A discrimination ratio, however, was used to define a criterion of acquisition in order to be consistent among different conditions (in case of detection in multiple position training in Experiment 1 described below, it was not feasible to calculate ρ). The discrimination ratio is defined as the proportion of responses made in positive trials to the total number of responses, and was calculated here with the average number of responses of each type of trial in each session.

Figure 2. Schematic illustration of stimulus positions. Estimates of visual angles, which are determined based on the assumption that the viewing distance is 6.7 cm, are shown. Dotted lines indicate the boundaries between the binocular and the monocular areas assumed in this study.

Figure 3. Timing charts of three types of trials, positive, negative, and test. The longer ticks among pecking responses (Pk) depict effective pecks on the FP.

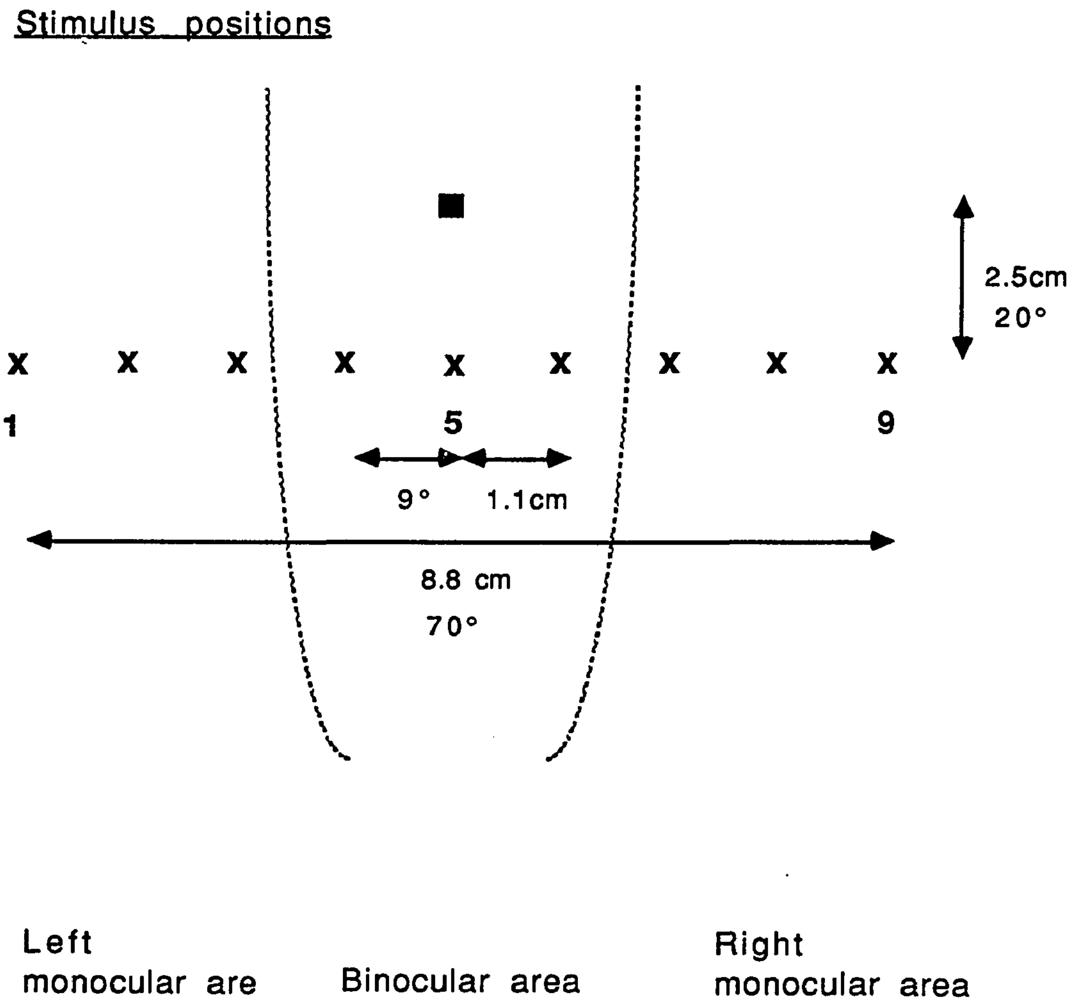
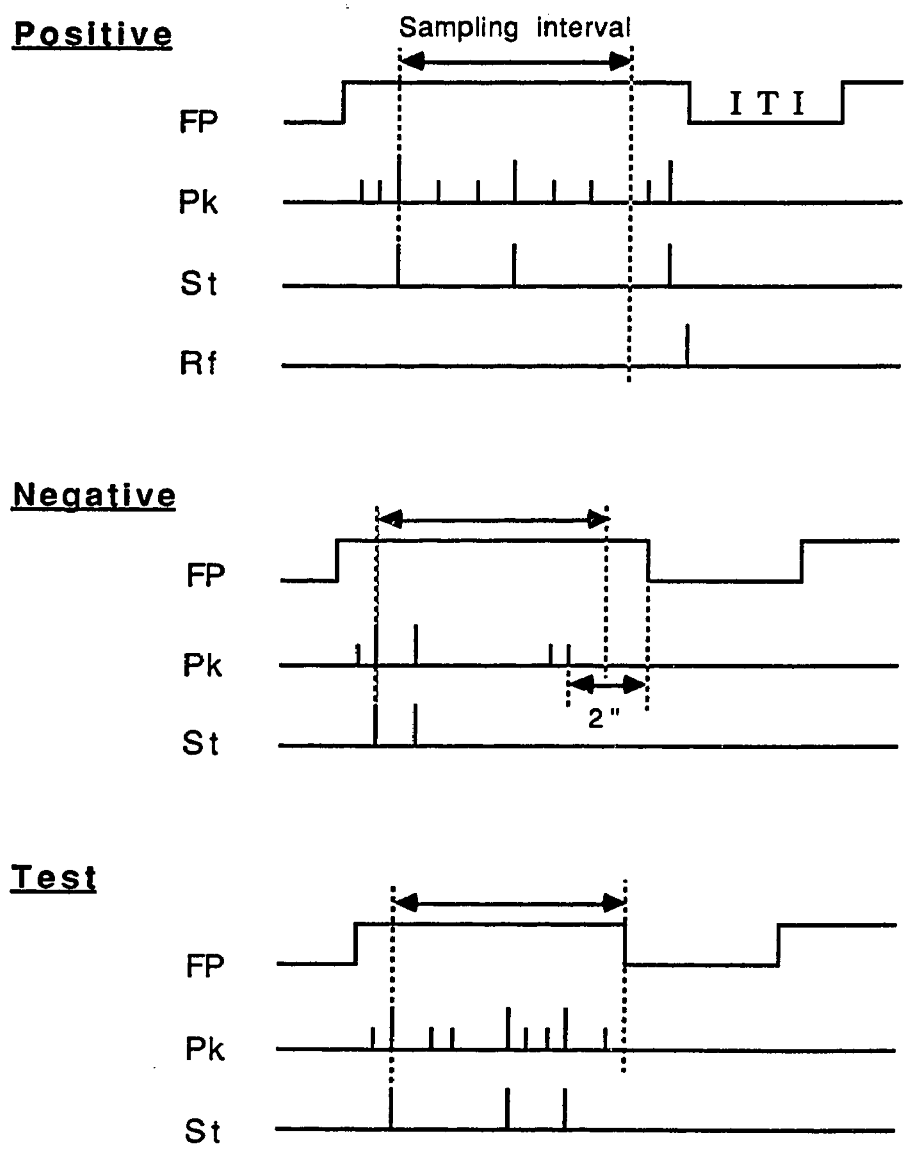

Stimulus positions
2.5cm
20°
x x x x x x x x x
1
5
9
9°
1.1cm
8.8 cm
70°
Left
monocular are
Binocular area
Right
monocular area

Figure 2



FP : Fixation point
St : Discriminative stimulus
ITI : intertrial interval
Pk : Pecking responses
Rf : Reinforcement

Figure 3

Experiment 1

Method

Subjects

Two White Carneaux pigeons served as subjects.

Procedure

The subjects were trained at 9 stimulus positions. The discriminative stimulus was presented at one position in each trial, and the contingency described in the general procedure was in effect.

In a block of 36 trials, each discriminative stimulus was presented in two trials at each position. The order of presentation was randomly permutated in each block, with a restriction that the same type of trials (positive or negative) were not presented in more than three consecutive trials.

Before the discrimination training, the subjects were trained for detection. In detection training, the discriminative stimulus ("x") was presented only in positive trials. An effective response in a positive trial was followed by the stimulus and auditory feedback, but one in a negative trial was followed only by auditory feedback. The same reinforcement contingency as in discrimination training was in effect. Eight positive trials at each position and 72 negative trials were given in a daily session. For each position, detection training was continued until the performance criterion, a discrimination ratio higher than 0.67 (i.e., at least twice as many pecks in positive as in negative trials on the average) in three consecutive sessions, was satisfied. When the criterion was attained at two positions equidistant from the center (Position 5), these positions were dropped, in order to avoid possible effects of overtraining at these positions on subsequent discrimination learning. This was necessary only for pigeon #31. Three additional detection sessions were given with all positions for this subject, after the performance reached the criterion at all the positions.

Five blocks of trials (180 trials) were given in a discrimination training session. Both subjects were run for 60 sessions.

Short stimulus duration. After the regular training sessions were completed, the duration of the stimulus was reduced to 1 refresh cycle of the computer display, and 5 more sessions were given with otherwise the same procedure. (Although the exact specification of the display was not available, the duration of the stimulus in this condition was estimated to be around 1 ms by using a photodiode and an oscilloscope.)

Results and Discussion

Detection training

Filled columns in Figure 4 depict the numbers of trials required for each subject to reach the criterion at the 9 stimulus positions. The number of negative trials, which was half the total number of trials, is not included. Occasionally the subjects did not complete all trials in a session, but these trials are also counted. Pigeon #27 attained the criterion at the same time for all but one position. Pigeon #31 appears to have acquired the discrimination progressively more slowly, the further away the position was from the center.

Discrimination training

The entire course of discrimination training is shown in Figure 5. The performance in terms of ρ index is plotted as a function of positions and sessions. The data points for each position were smoothed by the method of running medians (Tukey, 1977). With 10 pairs of positive and negative trials, ρ greater than 0.72 is significant at 5% level, and ρ greater than 0.80 at 1 % level (one-tailed test).

The performance at all positions increased rapidly around the 5th session. In both pigeons highly significant discrimination was attained, except at extreme positions, by the 10th session. The discriminative ratio kept increasing slowly after that point, mainly reflecting the decrease of the number of responses in the negative trials.

The rate of acquisition is compared in Figure 4. The same criterion is used as in detection training. Discrimination ratio was employed for this purpose because it seems to be more reliable than ρ for the small number of trials, and also to facilitate comparison with detection data. For pigeon #27 there is an orderly relationship between the number of trials and the distance from the central position, although it is not symmetric and there is a reversal. It took more than twice as long at position 9 than the second slowest position. As can be seen in Figure 5, the variability across sessions was very high at this position. For pigeon #31 the contrast between the two sides is marked. In fact, the acquisition took longer at the center position (5) than at any position on the right side.

Since it was very difficult to set a reliable criterion for asymptotic performance, 60 sessions were given to both pigeons. By the end of these sessions, no increasing trend of performance was observable in either pigeon. The representative discriminative performance at the end of training is shown in Figure 6. The average numbers of pecks in the positive and the negative trials (columns) and ρ (line) of the last five sessions are shown as a function of stimulus positions. There was little difference in the discriminative performance at different positions. Response rates are also similar at all positions.

Short stimulus duration. The results of the sessions with the stimuli of short duration are summarized in Figure 7 in the same format as Figure 6. The ρ indices shown in Figure 6 are also plotted with a broken line for comparison. Although a slight decrement in performance was observed, both pigeons maintained a relatively high level of discrimination at all positions. This result clearly stands against the possibility that the subject moved its eyes toward the stimulus after it was presented.

Negative trials without second stimulus presentation. Another possible problem in controlling the stimulus position within the pigeon's visual field was that the pigeon might adjust its viewing position after the first stimulus presentation in a trial. It could have happened that the pigeon noted only the position of the stimulus in the first presentation, and made some adjustment in preparation for the second and later stimulus presentations. In order to check this possibility, the pattern of responding in the negative trials were examined. Table 1 shows the percentages of trials that ended without a peck, and those without a second stimulus presentation. The data were averaged over the last 10 sessions. The standard errors of the means are shown in parentheses. If the pigeon makes the adjustment after the first presentation, it is expected that at least two stimulus presentations are given in one negative trial. If only one stimulus presentation is enough, no peck will be made in a negative trial. Because the pigeon tends to peck in a series consisting of a few pecks, the number of trials without pecks is not very indicative. It was also observed that the subject started pecking after a short pause in a negative trial, and that in some negative trials it made as many pecks as in a typical positive trials. The number of trials without a second stimulus presentation may be more reliable, although it does not necessarily mean the number of pecks in those trials was always very low. The percentages ranged from 35.0 to 59.0 in pigeon #27, and from 49.0 to 69.0 in pigeon #31. Although the figures may not be regarded very high, considering the factors mentioned above, that might have inflated the number of pecks and consequently the number of stimulus presentations, it appears unlikely that the pigeon made an adjustment to obtain information from the second stimulus presentation.

Table 1. Percentages of negative trials without pecks (0pk) and without second stimulus presentation (0sp) at each stimulus position.

Subject	#27		#31	
Position	0pk	0sp	0pk	0sp
1	21.0 (3.48)	38.0 (7.12)	42.0 (5.54)	55.0 (5.63)
2	22.0 (3.59)	35.0 (3.73)	39.0 (6.40)	49.0 (6.57)
3	32.0 (3.89)	57.0 (4.96)	46.0 (6.18)	52.0 (5.33)
4	31.0 (6.40)	49.0 (7.81)	50.0 (4.22)	56.0 (4.00)
5	24.0 (4.00)	50.0 (5.37)	50.0 (3.33)	60.0 (2.58)
6	36.0 (4.27)	59.0 (6.90)	55.0 (5.22)	63.0 (5.17)
7	30.0 (4.47)	50.0 (6.32)	65.0 (3.73)	69.0 (4.33)
8	37.0 (5.39)	55.0 (4.53)	49.0 (3.79)	61.0 (4.07)
9	25.0 (5.43)	48.0 (6.96)	59.0 (7.52)	64.0 (7.18)

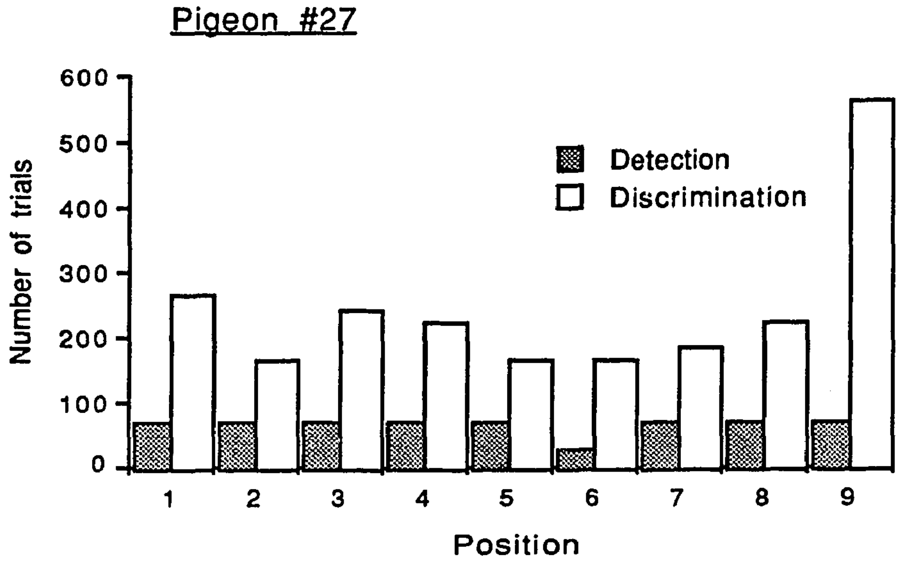
Note: Data were taken from the last 10 sessions. Standard errors of the means are shown in the parentheses.

Figure 4. Number of trials to criterion required to attain the criterion (discrimination ratio greater than 0.67 in three successive sessions) at each stimulus position in detection and discrimination for each subject.

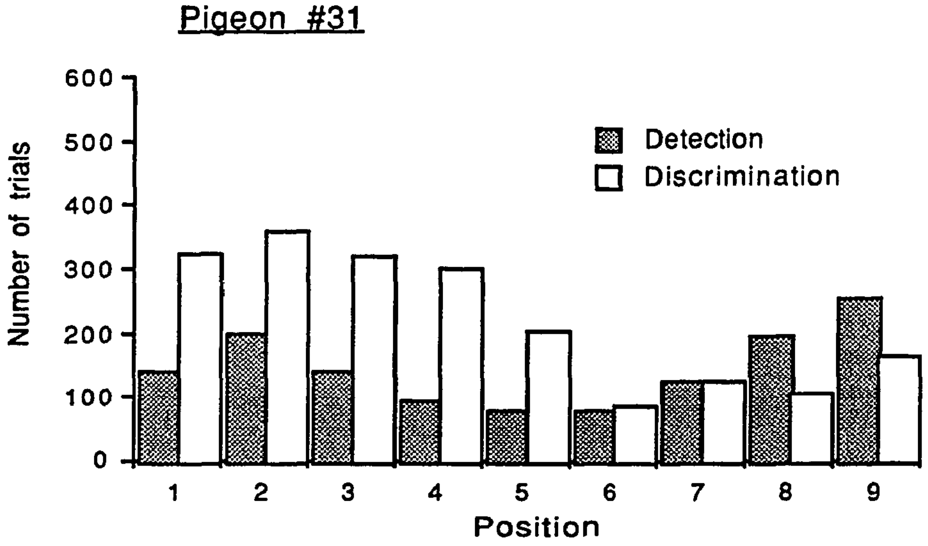
Figure 5-1 & 2. Discriminative performance in terms of ρ index as a function of stimulus positions and sessions for each subject. Data for each stimulus position are smoothed by the method of running medians (Tukey, 1977).

Figure 6. Mean numbers of pecks per 5-s sample interval in positive (empty column) and negative (filled columns) trials and ρ (line) of the last 5 sessions as functions of stimulus positions for each subject.

Figure 7. Mean numbers of pecks per 5-s sample interval in positive (empty column) and negative (filled columns) trials and ρ (line) of the 5 sessions with the short stimulus duration as functions of stimulus positions. Average ρ indices of the last 5 sessions of the preceding training (presented in Figure 5) are also shown by a dotted line for comparison.



Pigeon #27



Pigeon #31

Figure 4

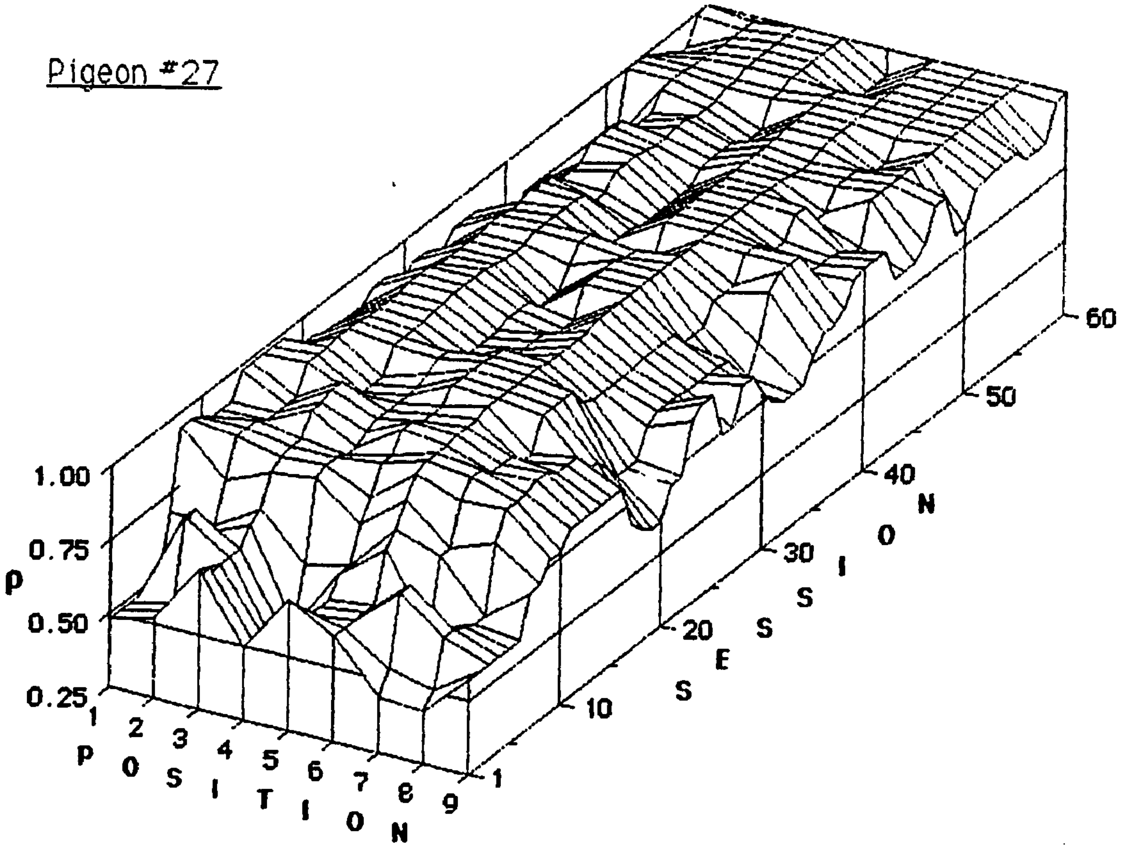

Pigeon #27
p
1.00
0.75
0.50
0.25
1
2
3
4
5
6
7
8
9
POSITION
1
10
20
30
40
50
60
SESSION

Figure 5-1

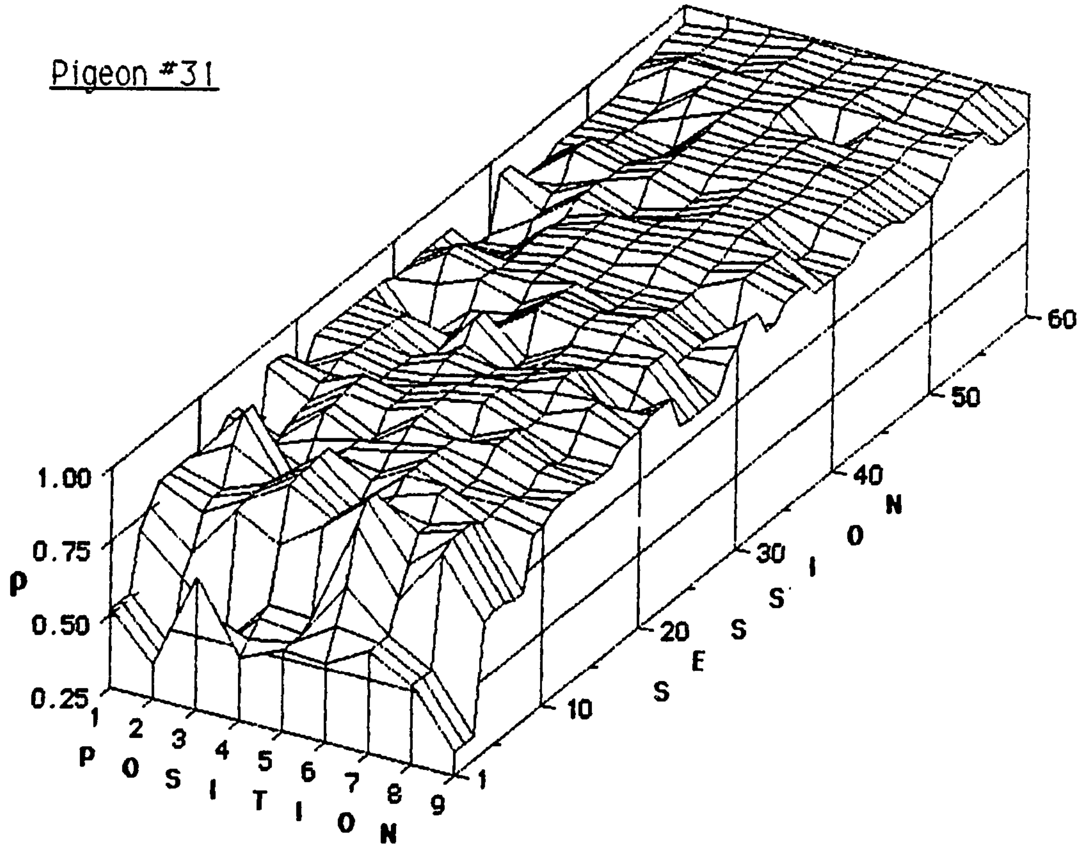

Pigeon #31
1.00
0.75
p
0.50
0.25
1
2
3
4
5
6
7
8
9
P O S I T I O N
1
10
20
30
40
50
60
S E S S I O N

Figure 5 - 2

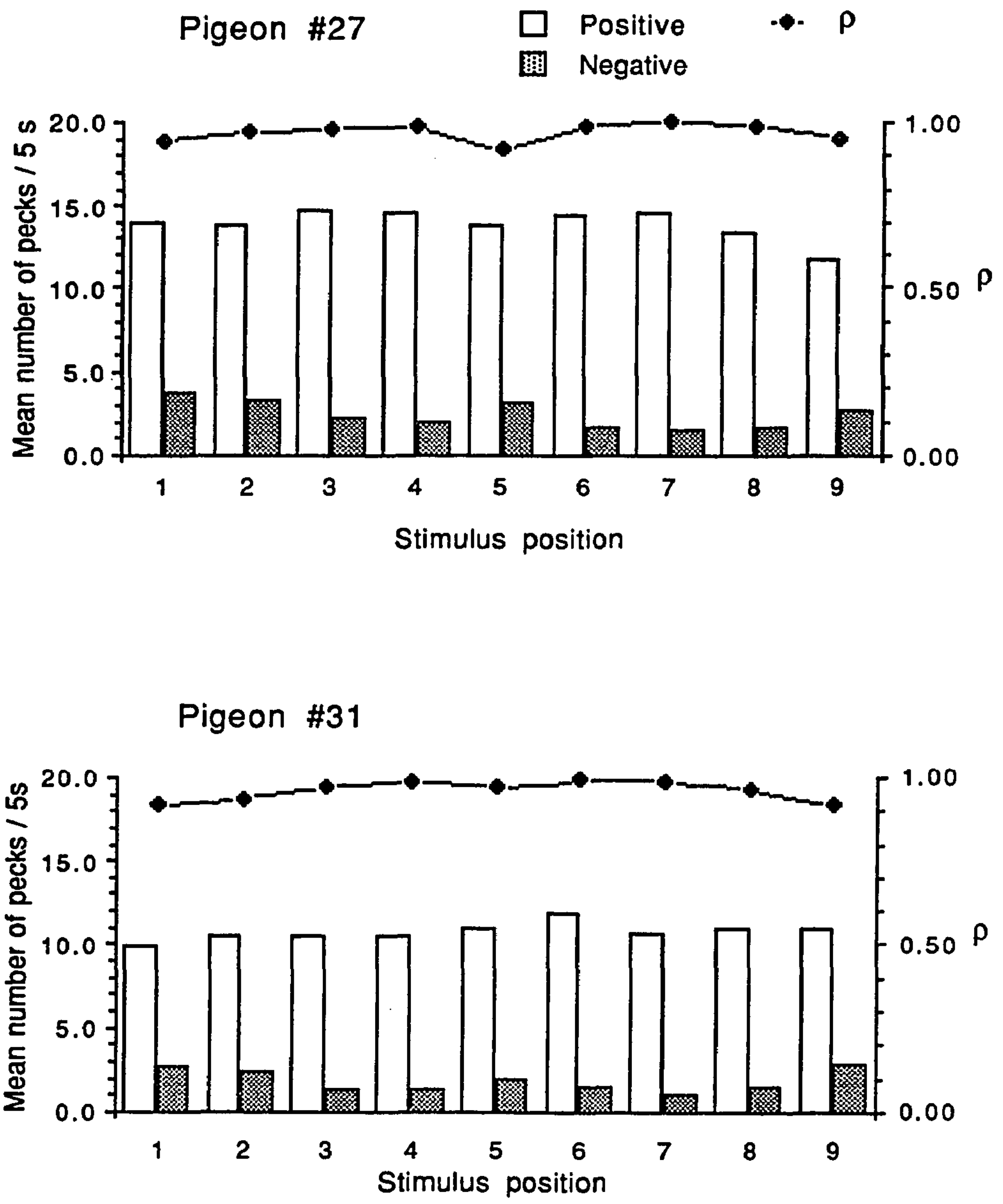

Pigeon #27
□ Positive
▨ Negative
-◆- ρ
Mean number of pecks / 5 s
20.0
15.0
10.0
5.0
0.0
1.00
0.50
0.00
ρ
1
2
3
4
5
6
7
8
9
Stimulus position
Pigeon #31
Mean number of pecks / 5s
20.0
15.0
10.0
5.0
0.0
1.00
0.50
0.00
ρ
1
2
3
4
5
6
7
8
9
Stimulus position

Figure 6

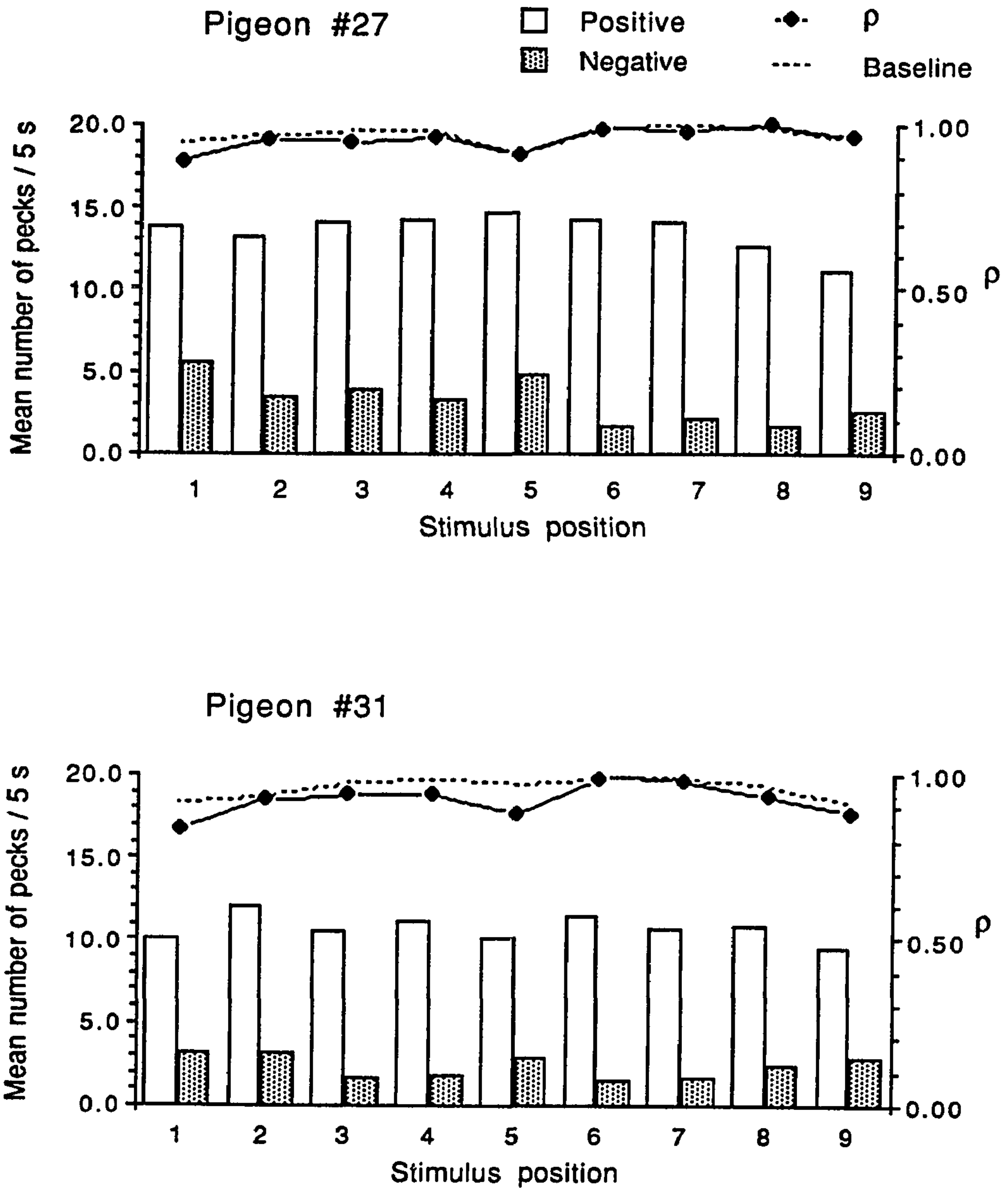

Pigeon #27
☐ Positive
▨ Negative
-◆- ρ
---- Baseline
Mean number of pecks / 5 s
0.0
5.0
10.0
15.0
20.0
ρ
0.00
0.50
1.00
1
2
3
4
5
6
7
8
9
Stimulus position
Pigeon #31
Mean number of pecks / 5 s
0.0
5.0
10.0
15.0
20.0
ρ
0.00
0.50
1.00
1
2
3
4
5
6
7
8
9
Stimulus position

Figure 7

Experiment 2A

In the following two experiments, the subject was trained at one stimulus position, then tested for transfer at 9 stimulus positions including the original position. Two pigeons were first trained at the central position (Position 5), and 5 other pigeons were trained at one of 5 positions which include monocular and binocular positions. Since there were slight differences in the experience of the subjects and in the procedure, these will be described separately as Experiments 2A and 2B.

The two pigeons serving in this experiment had been trained in detection at a single position (Position 5), then tested for transfer, and trained at multiple stimulus positions. They completed this experiment and Experiment 3 before all other subjects started. As a consequence, the procedure employed for them deviated slightly from the one specified in General Method. The transfer test, however, followed the same procedure except for a difference in stimulus duration.

Methods

Subjects

Two White Carneaux pigeons served as subjects. In addition to previous experience similar to that of the other subjects, they had been given extensive training in detection before this experiment.

Procedure

Discrimination training. The discrimination training followed the procedure described in General Method except that the duration of the discriminative stimulus was set at 150 ms which was timed by the internal clock of the computer. For both subjects the discriminative stimuli were presented at Position 5. Positive and negative trials were presented equally often in a quasi-random order in 20-trial blocks.

Since the subjects of this experiment had been trained in detection, in which a discriminative stimulus ("x") was presented only in positive trials, the discrimination was established by introducing the negative stimulus gradually ("fading" method). First only one pixel that was a part of the negative stimulus ("o") was presented in negative trials upon effective responses. Additional elements of the negative stimulus were added over sessions so that the subject's performance might not be disrupted. The number and configuration of the negative stimulus at each step are depicted in Figure 8.

The number of trials per session was increased from 200 to 240 trials during discrimination training. Ten sessions were given before the transfer test.

Transfer test. A session consisted of 208 trials. A block of 10 regular trials was given at the beginning. Then one probe trial was inserted at a random position in every block of 10 trials. In each block an equal number of regular trials was given in a quasi-random order with the same restriction as in discrimination training. In a probe trial, "x" or "o" was presented in a different position on the display, contingent on an effective response on the FP. As in regular trials, the first 5 s after the first effective response was designated as the sampling interval. A trial was terminated at the end of the sampling interval without reinforcement regardless of the subject's behavior. (The contingency of a test trial is depicted in Figure 3) The test stimuli were presented at Positions 1 through 9. Each of the 18 possible types of probe trials (9 positions x 2 stimuli) was presented once in a daily session, in a different order from session to session. Data were collected from 8 test sessions on successive days.

Results and Discussion

Fading and discrimination training

Figure 8 shows the value of ρ calculated in each session for each subject, for the last four sessions of retraining in detection, for fading in of the "o", and for discrimination training. The number of pixels that made up the negative stimuli for the sessions during the fading phase is indicated in the figure. Each increase in the number of pixels was mastered within a few sessions. During discrimination training, further improvement in performance was observed. It should be noted that pigeon #1 performed better on the discrimination task than in detection.

Transfer test

Figure 9 shows the average numbers of responses per trial in test trials with the positive and the negative stimuli and ρ as a function of test positions for each subject. Significant differences between responses in test trials with positive and negative stimuli are indicated by asterisks. ρ greater than .88 is significant at 5% level, and ρ greater than .92 at 1% level (one-tailed test).

It is evident that the transfer was limited to the region around the position of the preceding training. At the remaining positions there was no sign of discrimination. Sharp contrast of discriminative performance between these areas is notable.

Figure 8. Learning curves in terms of ρ index during the three phases of training, retraining in detection, fading, and discrimination, for each subject. The number of pixels that made up the negative stimulus during a fading session is depicted in the figure. The configurations of the stimuli used in the negative trials are also shown schematically.

Figure 9. Mean numbers of pecks per 5-s sample interval in test trials with the positive stimulus (empty column) and the negative stimulus (filled columns), and ρ (line) as functions of stimulus positions for each subject. Statistical significance of ρ is indicated by asteriscs (* $p < 0.05$; ** $p < 0.01$).

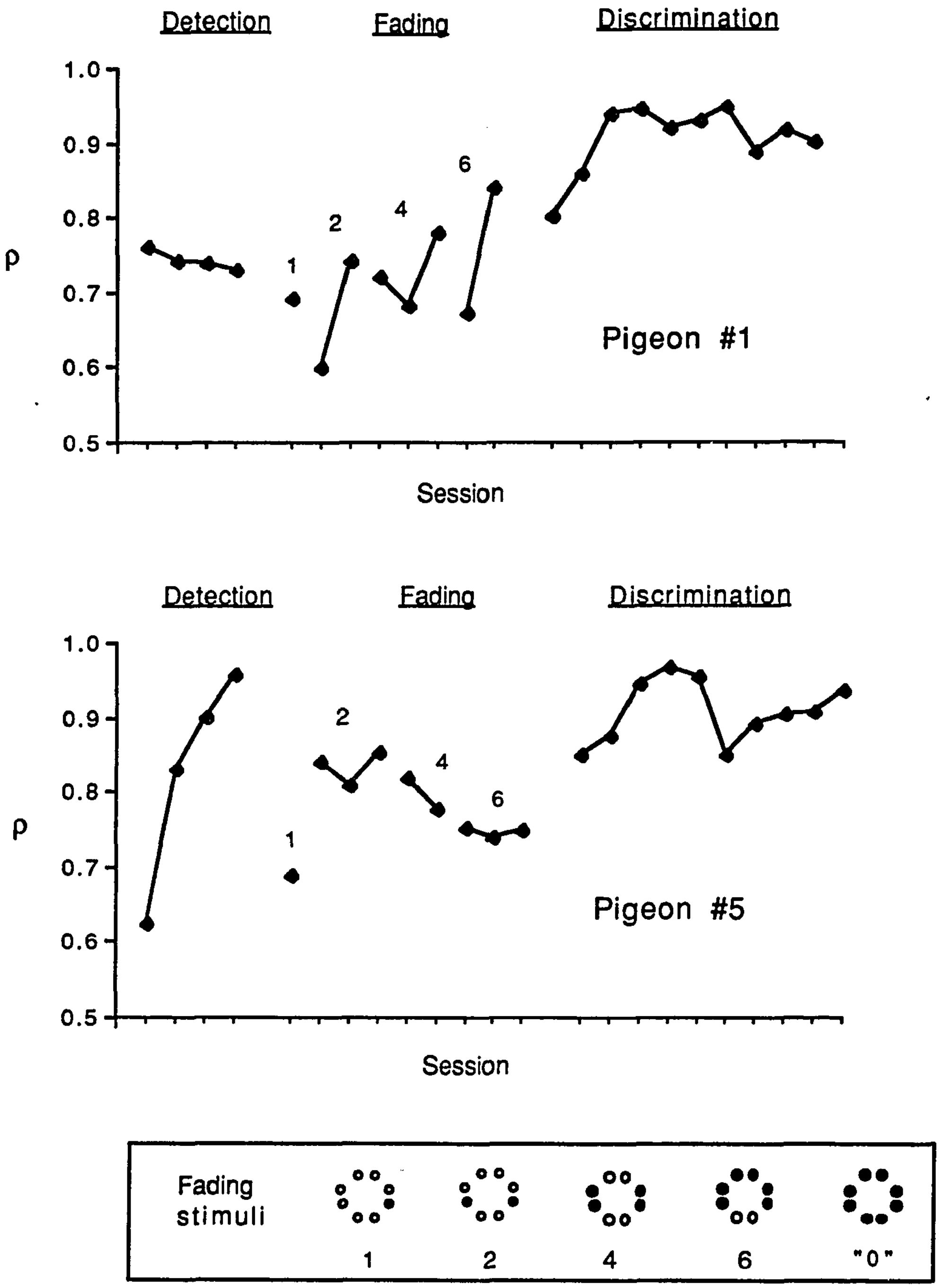

Detection
Fading
Discrimination
1.0
0.9
0.8
0.7
0.6
0.5
p
1
2
4
6
Pigeon #1
Session
Detection
Fading
Discrimination
1.0
0.9
0.8
0.7
0.6
0.5
p
1
2
4
6
Pigeon #5
Session
Fading stimuli
1
2
4
6
"0"

Figure 8

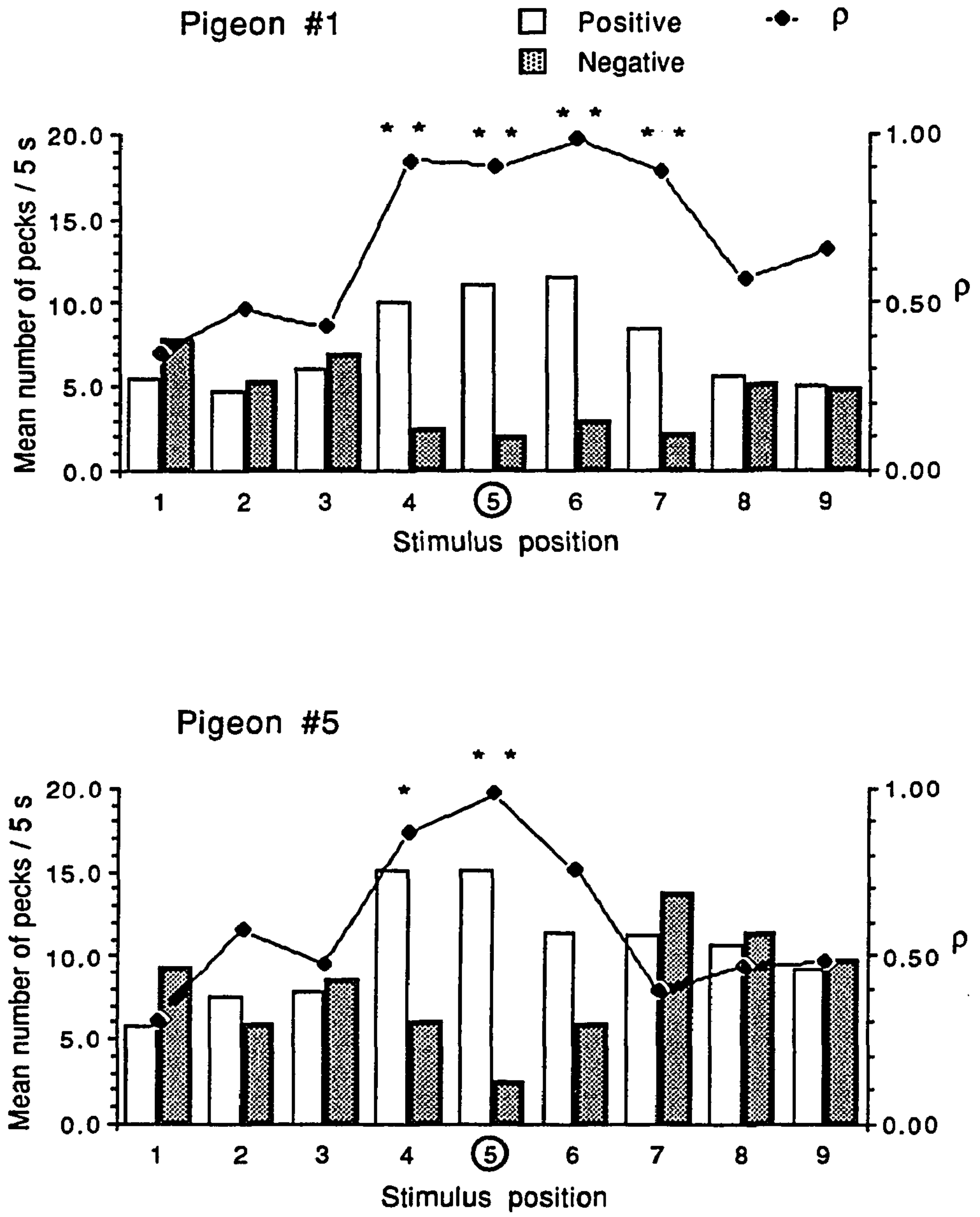

Pigeon #1
☐ Positive
▨ Negative
-◆- ρ
Mean number of pecks / 5 s
20.0
15.0
10.0
5.0
0.0
1.00
0.50
0.00
ρ
* *
* *
* *
* *
1
2
3
4
⑤
6
7
8
9
Stimulus position
Pigeon #5
*
* *
Mean number of pecks / 5 s
20.0
15.0
10.0
5.0
0.0
1.00
0.50
0.00
ρ
1
2
3
4
⑤
6
7
8
9
Stimulus position

Figure 9

Experiment 2B

In this experiment, the subjects were first trained at one position either in the monocular or the binocular area, and then tested for transfer. In order to obtain some information about the difference in acquisition among different training positions, the subjects were trained in detection to the same criterion, and then moved directly to discrimination training without experiencing the "fading" procedure employed in Experiment 2A. Extensive comparison of acquisition among different positions, however, was not intended.

Methods

Subjects

Five White Carneaux pigeons served as subjects.

Procedure

Discrimination training. Each subject was trained at one of five positions, Positions 2, 4, 5, 6, or 8. Positive and negative trials were presented equally often in a quasi-random order in every 20-trial block.

Detection training preceded discrimination training, and was continued until the performance criterion, a discrimination ratio greater than 0.67 in three consecutive sessions, was satisfied. During detection training, the number of trials per session was 120. This number was increased to 180 in discrimination training. After the same criterion for discrimination ratios was attained in discrimination training, 20 additional sessions were given before the transfer test was performed in order to establish a stable baseline.

Transfer test. The same procedure as in Experiment 2A was followed. In this experiment, data were collected from 10 test sessions, and one training session was given after every two test sessions to prevent a possible decline of discriminative performance.

Results and Discussion

Detection training

The course of acquisition in terms of ρ index is shown in Figure 10. All subjects showed a similar pattern of acquisition. After the initial few sessions during which responding was not differentiated in two types of trials, the ρ index decreased below 0.5, that is, more pecks were made in negative than positive trials. During this period it was observed that the subjects paused longer after an effective peck in positive trials, which was followed by stimulus presentation, than in negative trials, and sometimes moved its head toward the location of stimulus presentation. After this period the performance improved very quickly. However, it took more than 10 sessions before the criterion based on the discrimination ratio was attained, and in case of #29, the criterion was not attained after 70 sessions. The results of acquisition in terms of numbers of trials required before attaining the two different criteria, first significant ρ index at 1% level (ρ > .623) and discrimination ratio greater than 2/3 in three consecutive sessions, are summarized in Table 2. The number of trials includes those from all incomplete sessions, but the number of sessions includes only those in which the subject completed more than 80% of the predetermined number of trials.

Inspection of Figure 10 and Table 2 reveals no obvious relation between rate of acquisition and stimulus position.

Discrimination training

The course of acquisition is shown in Figure 11, and it is also summarized in Table 2. Subjects #23 and #33, which were trained at positions 4 and 5, respectively, showed statistically significant discrimination (ρ > .60; p < .01) within a few sessions. Compared to the preceding detection training, the increase of discriminative performance over sessions appeared to be more gradual. Subjects #29 and #30, which were trained at positions presumably in monocular areas, seem to share a pattern of acquisition, that of a relatively long period of no discrimination and a rapid increase after that. During the period of overtraining, after the criterion was reached, little increase of performance was observed.

The effect of the stimulus position on the rate of acquisition and the level of asymptotic performance is not very clear. The small number of subjects and large individual differences preclude a meaningful evaluation of the possible effect of stimulus position.

Transfer test

Figure 12 shows the average numbers of responses per trial in test trials with the positive and the negative stimuli and ρ as a function of test positions for each subject. Significant differences between responses in test trials with positive and negative stimuli are indicated by asterisks. ρ greater than .72 is significant at 1% level, and ρ greater than .80 at 1% level (one-tailed test).

For pigeon #33 which was trained at Position 5, the difference between the two kinds of test trials was significant only at the training position and the value of ρ appears to decrease rather gradually toward the extreme positions. However, since the overall rate of pecking was much lower than other subjects, the data cannot be regarded as very reliable.

Of the two pigeons which were trained at binocular positions, pigeon #23 showed a sharp peak of ρ at the training position (4). On the left side of that position, the performance was intermediate, at around the 5 % significance level. On the right side, however, no sign of discrimination is seen. The sharp decline from Position 4 to Position 5 is notable. In pigeon #25, transfer was observed to Position 5, but there was a sharp decline to Position 4, although significant performance was observed at Position 3.

In pigeon #30 trained at Position 2, equally high levels of discrimination were retained at 3 positions, and there was a sharp decline to Position 4. The performance at the right side of Position 4 did not indicate any sign of discrimination. Pigeon #29 showed a broader transfer toward the center. Although the performance declined at stimulus positions to the left of Position 6, it reached a statistically significant level at Position 2. This secondary peak on the left side, however, will be suggested to be spurious in Experiment 3.

It may be concluded that the transfer is limited to the vicinity of the position in which the stimuli were shown during training.

Table 2

Number of trials and number of sessions required to reach criteria of acquisition for the subject trained at each stimulus position.

Position	2	4	5	6	8
Subject	#30	#23	#33	#25	#29
Detection					
significant ρ*	1174	1474	960	2257	874
	(10)	(12)	(8)	(16)	(7)
Disc. Ratio†	2374	3344	2626	5530	9264+
	(20)	(27)	(22)	(40)	
Discrimination					
significant ρ*	1434	180	480	1292	1800
	(7)	(1)	(3)	(7)	(10)
Disc. Ratio†	3706	3042	4800	5878	3060
	(18)	(16)	(26)	(32)	(17)

Note: The number of sessions is indicated in parenthesis below the number of trials.

*First significant ρ index ($p < 0.01$). †Discrimination ratio $> 2/3$ in three consecutive sessions.

Figure 10. Leaning curves in terms of ρ index for the detection training.

Figure 11. Leaning curves in terms of ρ index for the discrimination training.

Figure 12. Mean numbers of pecks per 5-s sample interval in test trials with the positive stimulus (empty column) and the negative stimulus (filled columns), and ρ (line) as functions of stimulus positions for each subject. Statistical significance of ρ is indicated by asteriscs (* $p < 0.05$; ** $p < 0.01$).

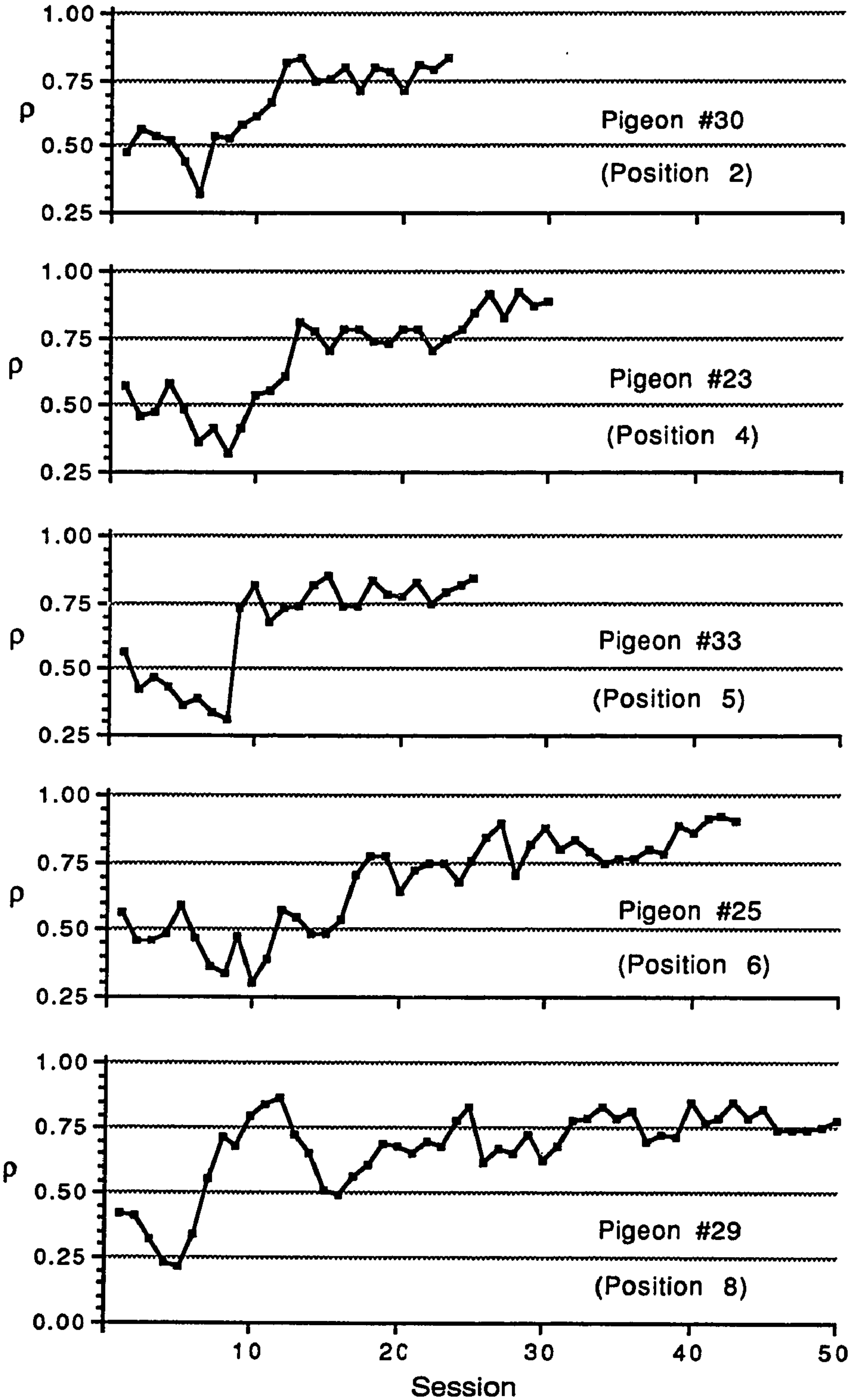

1.00
0.75
0.50
0.25
0.00
ρ
Pigeon #30
(Position 2)
Pigeon #23
(Position 4)
Pigeon #33
(Position 5)
Pigeon #25
(Position 6)
Pigeon #29
(Position 8)
10
20
30
40
50
Session

Figure 10

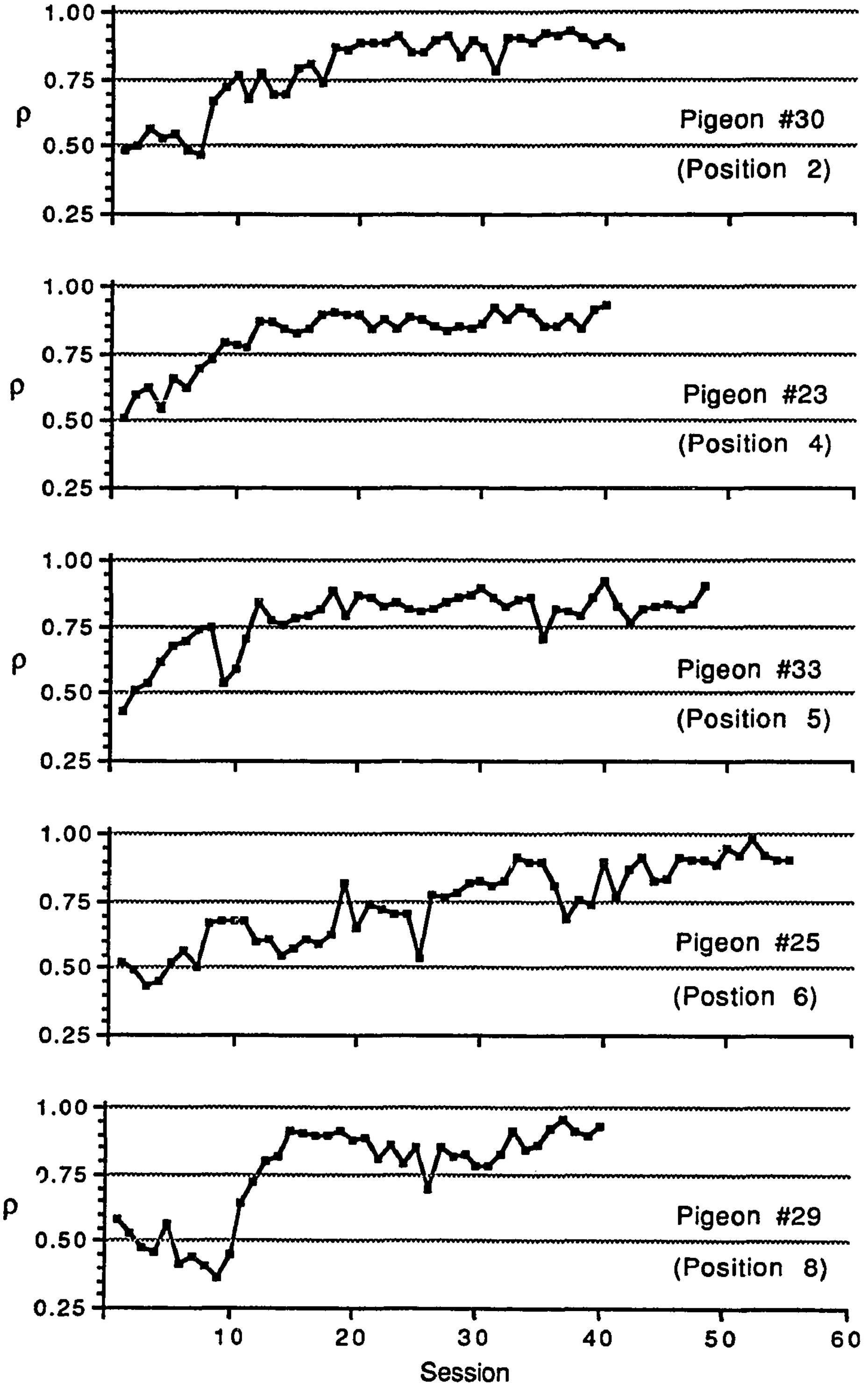

1.00
0.75
0.50
0.25
ρ
Pigeon #30
(Position 2)
1.00
0.75
0.50
0.25
ρ
Pigeon #23
(Position 4)
1.00
0.75
0.50
0.25
ρ
Pigeon #33
(Position 5)
1.00
0.75
0.50
0.25
Pigeon #25
(Postion 6)
1.00
0.75
0.50
0.25
ρ
Pigeon #29
(Position 8)
10
20
30
40
50
60
Session

Figure 11

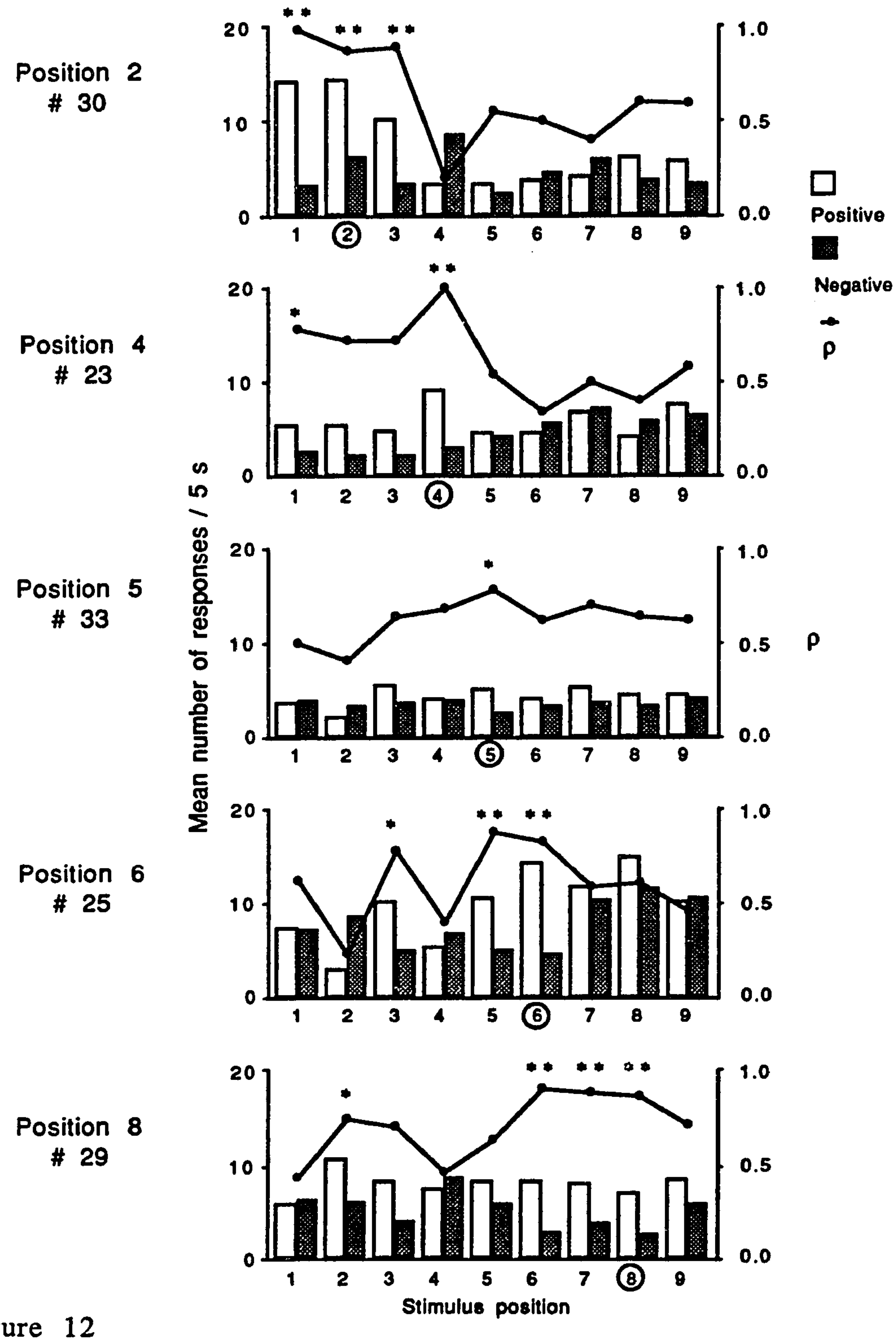

Position 2
30
Position 4
23
Position 5
33
Position 6
25
Position 8
29
Mean number of responses / 5 s
Stimulus position
ρ
Positive
Negative
0
10
20
0.0
0.5
1.0
1
2
3
4
5
6
7
8
9
*
**

Figure 12

Experiment 3

In this experiment, the subjects that served in Experiment 2 were trained in the same task as in Experiment 1. The purpose of this experiment was twofold. One is to examine the transfer of single position training by a different method, and to check the reliability of the results obtained in the transfer test of the previous experiment. The other is to obtain additional data for Experiment 1, and to determine whether aymptotic performance for the 9 positions is dependent on the history of training.

Method

Subject

The two subjects, #1, and #5 trained at the central position (Position 5) in Experiment 2A, and the three subjects from Experiment 2B, #23, #29, #30, which were trained at non-central positions, served as subjects. Subject #25 became ill after the completion of Experiment 2, and could not be tested.

Procedure

Essentially the same procedure as in Experiment 1 was followed. For pigeons #1 and #5, the parameters were slightly different. As in Experiment 2A, the duration of the discriminative stimuli was controlled by the internal clock of the computer and set at 150 ms. A daily session consisted of 216 trials, i.e., 12 of each type of trial at each position. Thirty sessions were given. For the remining subjects, a session consisted of 180 trials, and the training was continued until the criterion that the discrimination ratio was greater than 2/3 on three consecutive sessions was satisfied at all positions. Subject #23, which could not attain the criterion for one position and training was terminated after 60 sessions.

After the criterion was satisfied, an additional 5 sessions were given with the short stimulus duration (1 refresh cycle of the display as in Experiment 1) to the second group of subjects (#23, #29 and #30).

Results and Discussion

The course of training is shown for each bird in Figure 13, in the same format as Figure 5. Three points should be noted. First, after training, the subjects came to discriminate between the two stimuli presented at all 9 positions. The performance in the last 3 sessions of the training is shown in Figure 14. Although there still remains some variation among positions, the value of ρ index is higher than 0.9 at almost all positions. There also is a slight variation in response rates, but no systematic differences among the positions are evident. Secondly, the effect of previous single position training in the early part of this training is evident in Figure 13. The gradient of ρ peaked at the position of the original training, and away from that position it stayed near 0.5 (no discrimination). It should be noted that in pigeon #29, at positions 1 through 4, the discriminative performance stayed very low during the first 5 sessions. This suggests that the secondary peak of the generalization gradient observed in the transfer (Experiment 2) test might be spurious. Thirdly, the effect of previous training had a rather lasting effect. The lower discriminative performance at positions away from the original position was still observable after 20 to 30 sessions.

The results from the sessions with the short stimulus duration are shown in Figure 15. The averages from the last 3 sessions out of 5 were taken, to make them compatible with Figure 14. Although larger disruption of the performance was observed immediately after the short stimulus duration was introduced, the effect was not very severe. The ρ indices shown in Figure 14 are also plotted with a broken line for comparison. Although a slight decrement in performance was observed, all three pigeons maintained a significant level of discrimination at all positions.

The results of this experiment supplement the results of the preceding experiments. With extensive training, the pigeons learned to discriminate between stimuli briefly presented over a fairly large area of their visual field. There is little difference in asymptotic performance among different positions in this area, although the performance is somewhat more variable at extreme positions.

It was also observed that the acquisition of the discrimination at positions different from those in which stimuli were shown in the preceding training was not immediate but influenced by that training. This supports the findings of Experiment 2 that transfer of discrimination acquired at one position is limited to the vicinity of that position.

Figure 13-1 to 13-5. Discriminative performance in terms of ρ index as a function of stimulus positions and sessions for each subject. Data for each stimulus position are smoothed by the method of running medians (Tukey, 1977).

Figure 14-1 & 2. Mean numbers of pecks per 5-s sample interval in positive (empty column) and negative (filled columns) trials and ρ (line) of the last 3 sessions as functions of stimulus positions for each subject.

Figure 15. Mean numbers of pecks per 5-s sample interval in positive (empty column) and negative (filled columns) trials and ρ (line) of the 3 sessions with the short stimulus duration as functions of stimulus positions for each subject. Average ρ indices of the last 3 sessions of the preceding training (presented in Figure 11) are also shown by a dotted line for comparison.

Pigeon #1

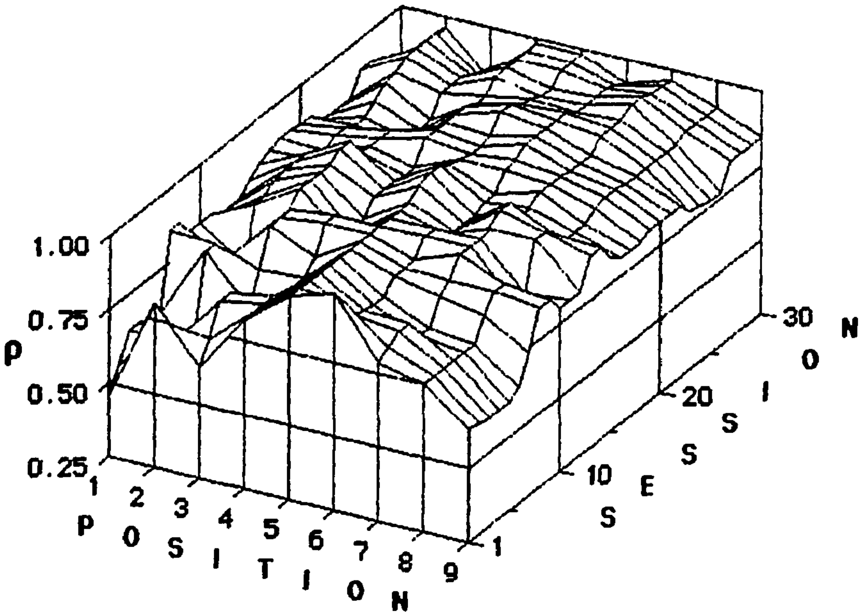


Figure 13 - 1

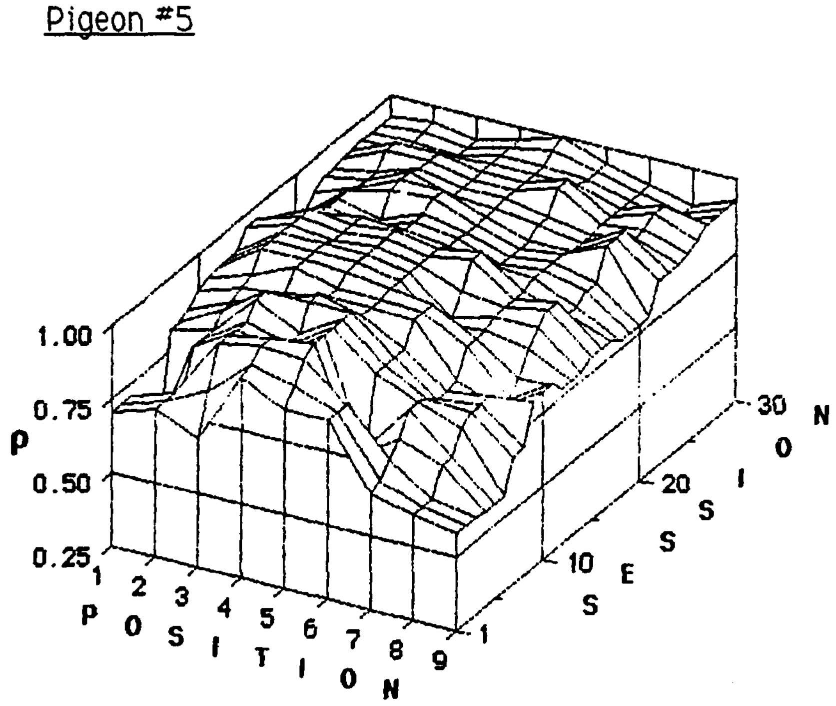

Pigeon #5
1.00
0.75
p
0.50
0.25
1
2
3
4
5
6
7
8
9
POSITION
1
10
20
30
SESSION

Figure 13 - 2

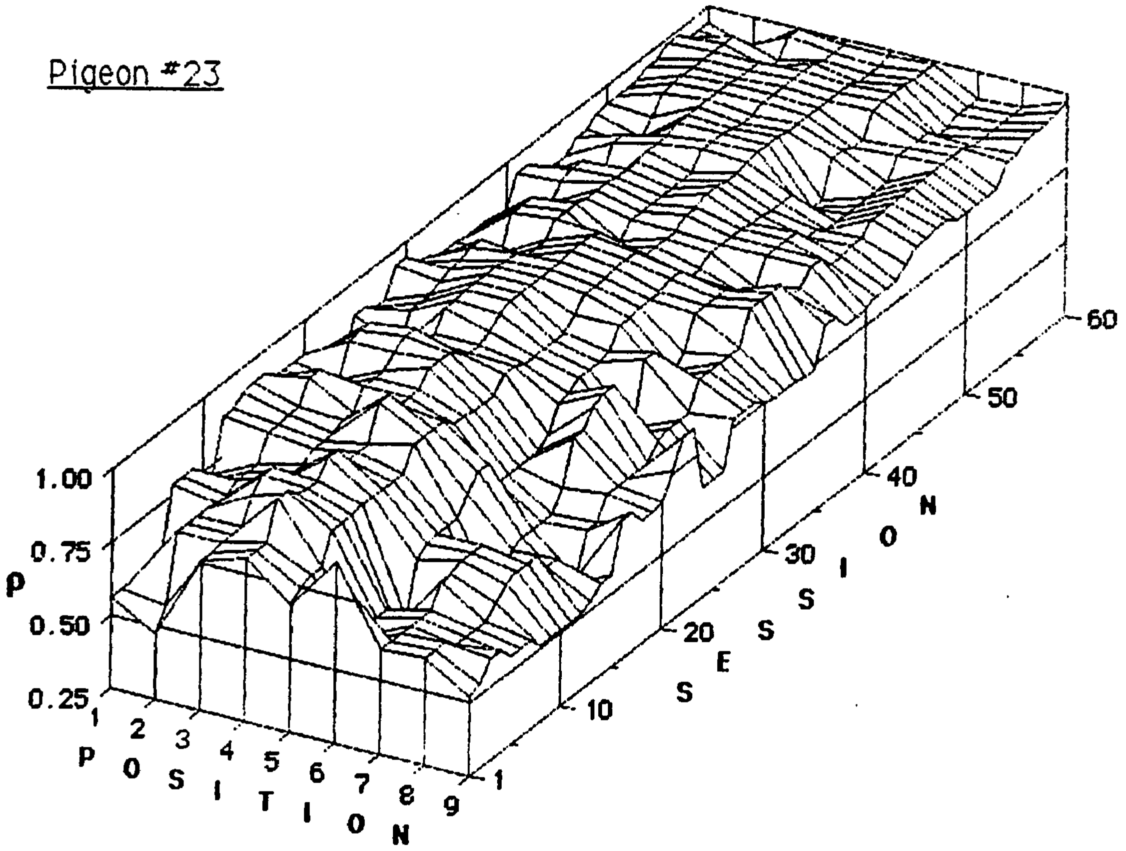

Pigeon #23
1.00
0.75
p
0.50
0.25
1
2
3
4
5
6
7
8
9
P O S I T I O N
1
10
20
30
40
50
60
S E S S I O N

Figure 13 - 3

Pigeon #29

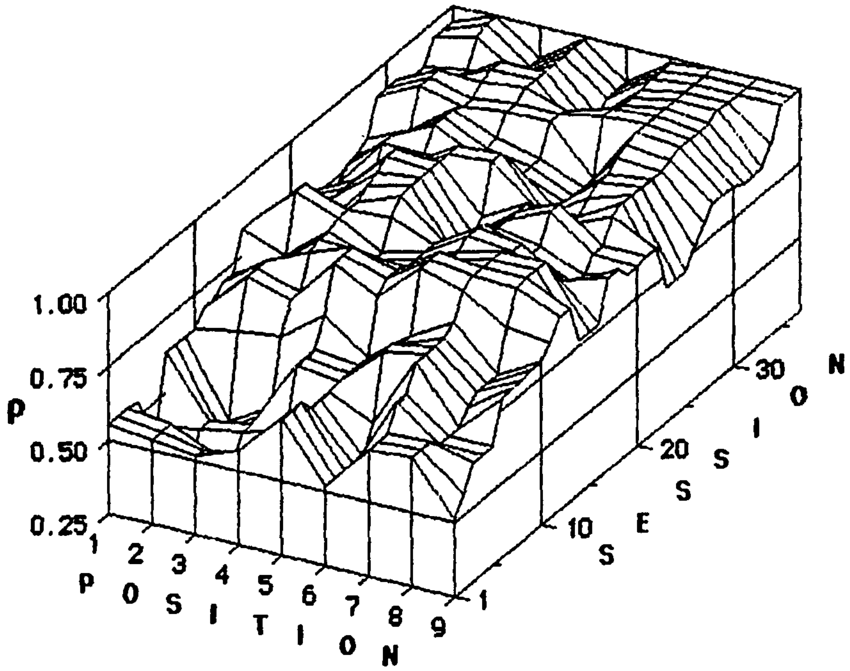


Figure 13 - 4

Pigeon #30

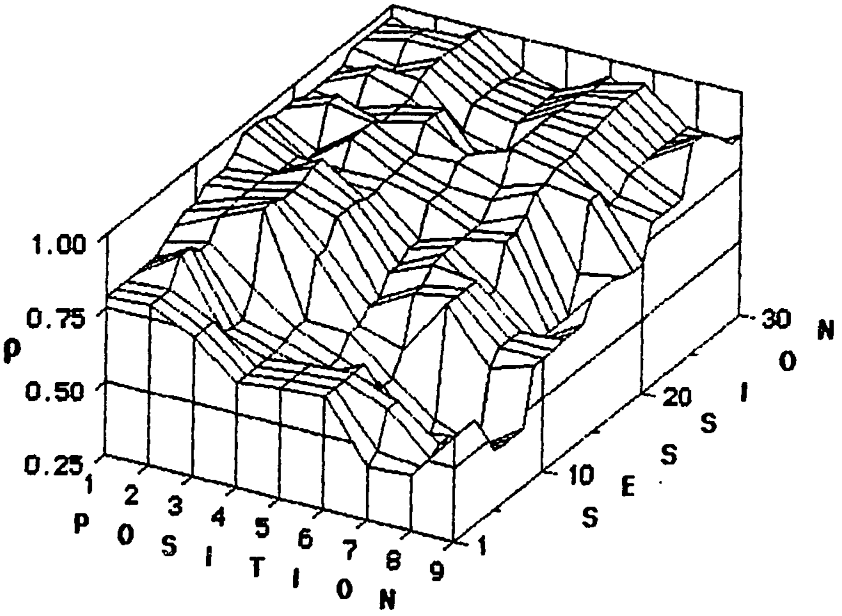


Figure 13 - 5

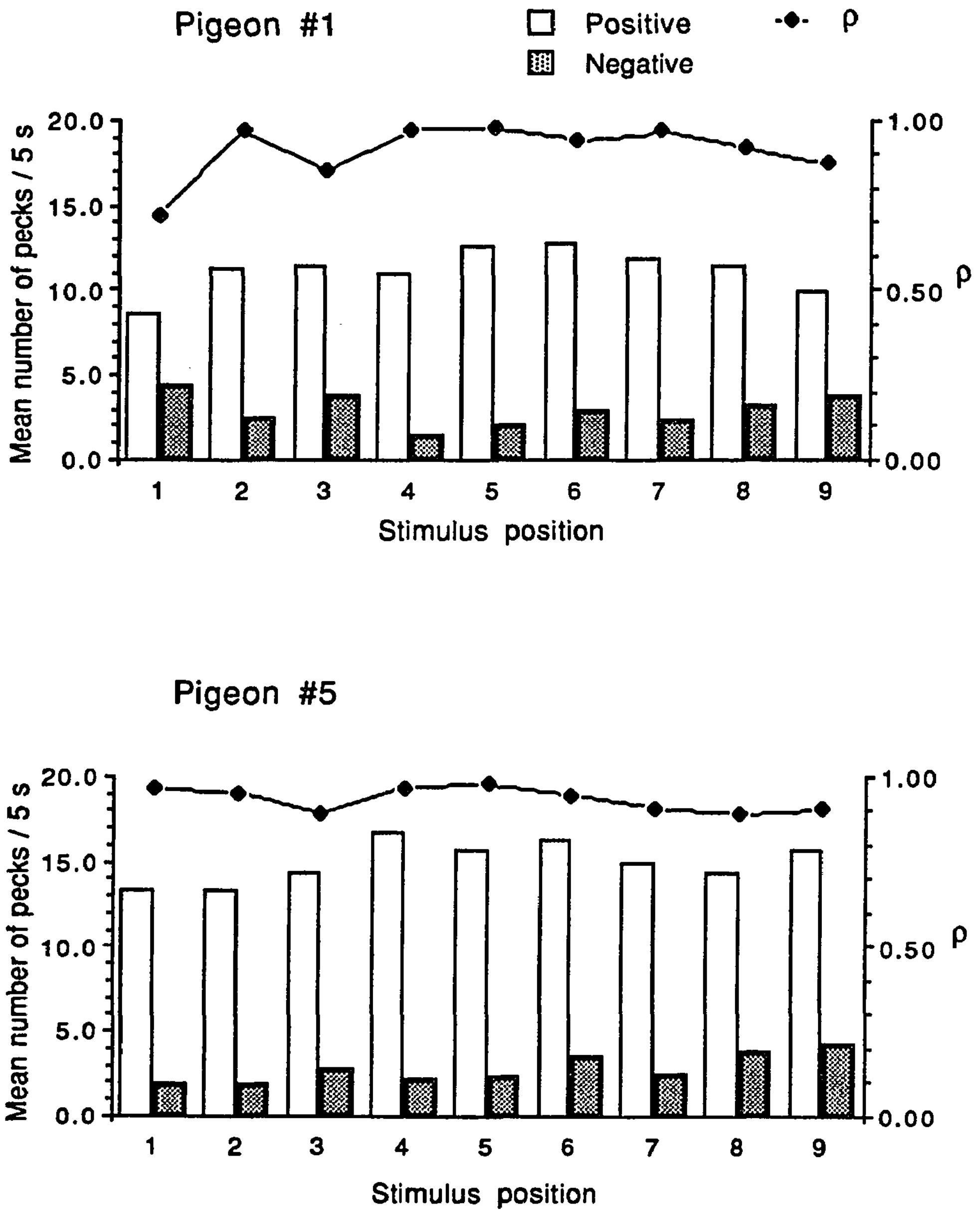

Pigeon #1
Positive
Negative
ρ
Mean number of pecks / 5 s
20.0
15.0
10.0
5.0
0.0
1.00
0.50
0.00
ρ
1
2
3
4
5
6
7
8
9
Stimulus position
Pigeon #5
Mean number of pecks / 5 s
20.0
15.0
10.0
5.0
0.0
1.00
0.50
0.00
ρ
1
2
3
4
5
6
7
8
9
Stimulus position

Figure 14-1

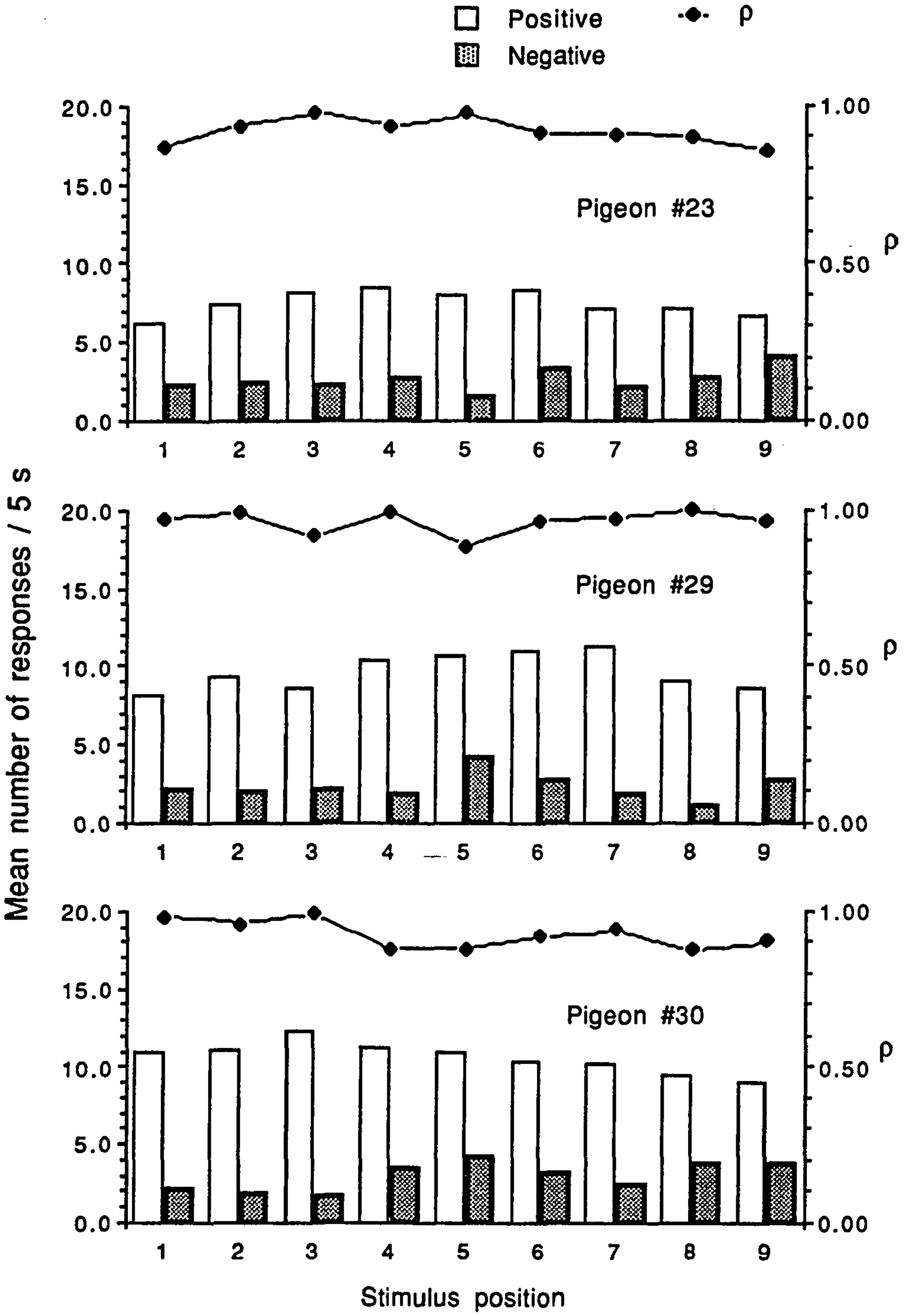

Positive
Negative
ρ
Pigeon #23
Pigeon #29
Pigeon #30
Mean number of responses / 5 s
ρ
20.0
15.0
10.0
5.0
0.0
1.00
0.50
0.00
1
2
3
4
5
6
7
8
9
Stimulus position

Figure 14-2

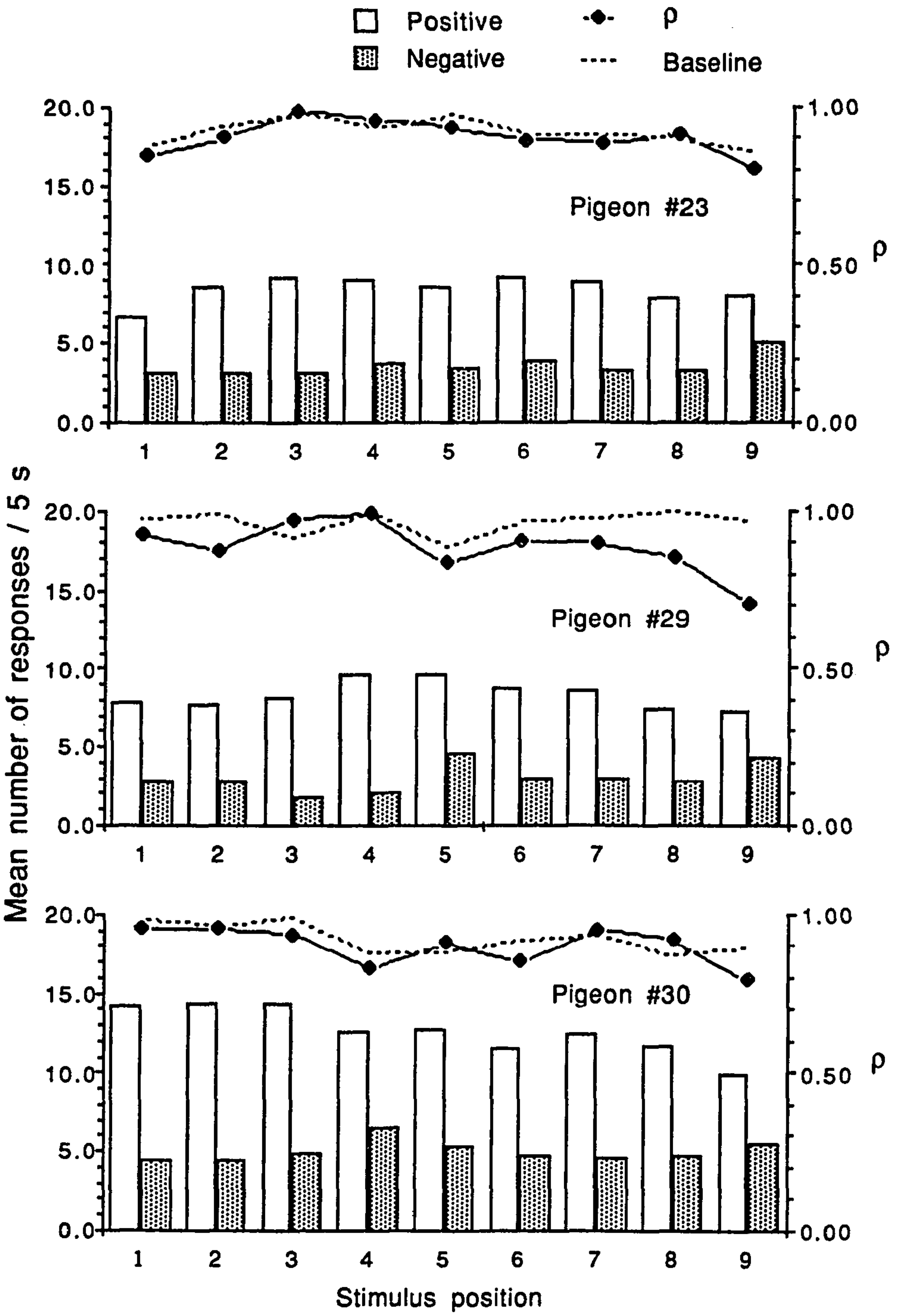

Positive
Negative
ρ
Baseline
Pigeon #23
Pigeon #29
Pigeon #30
Mean number of responses / 5 s
Stimulus position
ρ
20.0
15.0
10.0
5.0
0.0
1.00
0.50
0.00
1
2
3
4
5
6
7
8
9

Figure 15

III. DISCUSSION

In this chapter, before discussing the results of the experiments, the method of "behavioral fixation" used in this study is evaluated with the information obtained from the experiments.

Evaluation of the "behavioral fixation" method

The most important question is whether the stimuli were located in the pigeon's visual field as intended. An exact mapping between the position of stimulus on the display and its position on the retina is not possible. But in interpreting the results for the objective of this study, whether binocular and monocular fields were stimulated separately is very crucial. The extent of the binocular overlap is not known exactly, and verging eye movements change the size of it. With the current state of knowledge, however, the estimates used in this study may be considered reasonable ones.

It may be argued that, especially in single position training, the pigeon could place the stimuli in a better position by pecking at an oblique angle. Since the position of the peck was determined on a two-dimensional space, this was not impossible. In order to do so, however, the pigeon probably has to peck off the target (fixation point). But this appears quite unlikely considering the tendency of the pigeon to peck at a distinctive feature even when no reinforcement contingency exists as demonstrated in the "feature-positive effect" (Jenkins and Sainsbury, 1970; Goodale, 1983).

Variability in angles of pecking would make the differences among stimulus positions more ambiguous. If, because of this kind of variability, the discriminative performance at one stimulus position represents characteristics of different positions within a relatively large area in the visual field, it will indicate their average effect. Thus the change in performance between two neighboring stimulus positions would be more gradual than in the case where correspondence between a stimulus position and visual field position is more well defined. In many cases in transfer test, there were clear differences in discriminative performance between two neighboring positions. This suggests that the variability could not have been very large, but was confined within the range between two neighboring positions.

Next, the possibility of adjustments on the part of pigeon within a trial is considered. One possibility is that upon presentation of a stimulus, the pigeon relocates it within it's visual field by way of head and/or eye movements. In the single position training the pigeon could have learned to move its head after it had made an effective peck and a stimulus was presented. Although the pigeon was observed to orient its head toward the stimulus early in the detection training, and some pigeons actually had to be dropped because this pattern of behavior became persistent, it became less frequent as the learning progressed. In addition, the pigeon was required to keep pecking at the FP to view the stimulus and to obtain reinforcement in positive trials. This must have discouraged the subject from moving its head toward the stimulus during its presentation.

In multiple position training, in addition to the evidence above, the results of the sessions with the short stimulus duration argue against the notion of stimulus relocation during stimulus presentation. Although these results were obtained after extensive training and only in the multiple position training, the possibility of adjustment right after the stimulus presentation can be refuted, at least with regard to discriminative behavior after it is established.

The other possible adjustment is between stimulus presentations. The pigeon may prepare for the second and later stimulus presentations after the first one. This would be a problem in the transfer test and multiple position training. Generally, in many negative trials, the pigeons stopped pecking after only one stimulus presentation. Data to support this observation have been presented in Experiment 1. This observation argues against the possibility of this type of adjustment. In test trials it was also observed that they stopped pecking as soon as the stimulus was presented for the first effective response. Since the sample was small and other factors controlling responding must be considered, no further analysis was attempted.

Summary of results

The major findings of this series of experiments can be summarized as follows.

1. The pigeon can discriminate between stimuli presented in a fairly wide area in the frontal visual field, about 9 cm in actual length, and more than 50 degrees in visual angle horizontally, which apparently includes monocular as well as the binocular areas. After the discrimination is established, there is little difference in responding within this area. This lends support to the conjecture that the pigeon can "see clearly" over a wide area of its visual field (Blough, 1979). The variability and instability of performance at extreme positions may mean that these points were at the edge of this effective area.

Acquisition appears to be slower away from the center of the frontal field. But this is not very clear. Watanabe et al. (1984) suggested differences in task difficulty as a source of contradictory findings in binocular superiority in visual learning. Possible difference in acquisition can be obscured with easily acquired tasks. The task for the pigeons in the current experiments, however, cannot be considered a very easy one. A discriminative stimulus was presented briefly after a selected response, and this is in contrast to more common discrimination tasks in which the pigeon pecks at a discriminative stimulus which is continuously available.

2. Transfer of discrimination is limited around the location of the preceding training.

Although the variability in the transfer test was high, it can be concluded that the transfer does not occur to all positions immediately. The performance of the subjects in the early part of Experiment 3 confirmed this point.

The results of the pigeons trained at different positions and the results of multiple position training in Experiments 1 and 3, preclude the possibility that the failure of transfer was due to inferior visibility of the stimuli at the test positions.

It was also noted that the effect of the preceding training was rather long-lasting.

Effects of binocular overlap

The first question of this study was whether the binocular overlap contributes to better visual performance.

Performance after discrimination learning is established will be considered first. We may consider that it reflects mainly the visibility of the stimulus at different positions in the visual field. As already pointed out, a difference between positions in the monocular and binocular fields was not evident. In addition to the results of Experiment 1, no clear difference was found between subjects trained at binocular and monocular positions in Experiment 2. Although the individual differences are large and no statistical test is possible because of the small number of subjects, it appears that there is no definite difference among conditions.

As to the acquisition of the discrimination: there appeared to be a tendency for slower acquisition at positions further away from the center of the frontal field. The differences in Experiment 1, however, were not very large, and incremental rather than abrupt between neighboring positions. Differences among subjects trained at single positions can be evaluated only by statistical tests based on data from a larger number of subjects.

These conclusions appear to contradict those of Watanabe et al. (1984) about acquisition, and Di Stefano et al. (1987) about visual performance. Although these investigators compared the effects of binocular and monocular viewing, the methods are quite different from those used in the present experiments. In their experiments, one of the pigeon's eyes was covered for monocular viewing.

It may be argued that since the pigeons in Experiment 1 of this study were trained at multiple positions and there must have been some facilitative influence from that arrangement. Although the data are not directly comparable, it appears that single position training took longer than multiple position training. With respect to Experiment 2, it may be argued that the stimulus at the position that was supposed to be in the monocular area was actually viewed binocularly. Although the possibility cannot be completely denied, it has been argued that this was very unlikely. On the other hand, it may be possible that by restricting the pigeon's view, their method had introduced extra factors that affected its performance other than the differences between binocular and monocular viewing.

The conclusion on binocular facilitation, however, must be limited to visual discrimination between stimuli highly distinctive from each other in regard to the pigeon's visual capacity (contrast sensitivity, visual acuity, etc.) We may find facilitative effects of binocular viewing when the pigeons are tested with stimuli of lesser contrast and/or of smaller size.

The second question of this study was whether the extent of transfer was affected by the binocular overlap. The results of the transfer test did not support either of the hypotheses that predicted partial transfer. (The two hypotheses concerning the binocular overlap that predicted a complete transfer after training at a binocular position, do not have to be considered any further.) One hypothesis predicted that the decrement of discriminative performance would be a function of the distance between the test position and the training position. None of the subjects that were trained at non-central positions showed this pattern of transfer. The gradients of these subjects' are all asymmetric. But neither does this result support the other hypothesis, which predicted that the transfer would be limited to the subfield (binocular or monocular) within which the stimuli were presented during training. The gradients of pigeons #1 and #5 in Experiment 2 were almost symmetric (see Figure 9). But this is predicted by both hypotheses. Pigeon #23 did not show any transfer to other binocular positions, but a little transfer to the positions on the same side, which are supposed to be monocularly viewed (see Figure 12). Although the gradient of pigeon #25 was not a mirror image of pigeon #23's, and there was no transfer on the same side, it did not show transfer to all binocularly viewed positions. The transfer in pigeon #30 appears to be restricted within monocular area, but pigeon #29 trained at the opposite position showed significant discriminative performance at a binocular position.

Considering the level of control over the stimulus positions and the large variability inherent in the method of testing, it is difficult to make a definite conclusion. However, the boundary between the binocular and the monocular area may be eliminated as a factor that limits the transfer. It may be argued that, because of the bias in the angle of pecking the correspondence between the stimulus positions on the display and the areas in the visual field was not as intended. Although this possibility cannot be completely refuted, arguments against it have been presented above. Secondly there is a possibility that the whole area where the stimuli were presented was viewed binocularly. It is noted that McFadden (1989) has suggested that the binocular overlap may reach 70°. This value can be attained, if we assume that the values so far reported (about 30°) is the amount of overlap when the eyes are in resting position and that the eyes converge from that position when a peck is made. This suggestion, however, has not been confirmed.

The other hypothesis that predicted a partial transfer, assumed homogeneity of the frontal visual field. Although it predicted a symmetric gradient of discriminative performance, it can be modified to allow for an asymmetric gradient. It was simply hypothesized that the effect of the change in the position was a linear function of the distance from the original position in any direction. But it is not the only possibility. In any case, it is necessary to look into factors that possibly limit the extent of transfer of discrimination. The results of Experiment 3 show that these factors have relatively long-lasting effects (see Figure 13).

A simple explanation, however, may be provided without referring to additional limiting factors. The results of the four pigeons trained at off-center positions may be viewed that the transfer was limited to the one side of the FP (see Figure 12). The results of pigeon #25 do not fit this view, but it should be noted that the response rate to the positive stimulus was high at the three rightmost positions. These results may be interpreted that the pigeons responded to larger configurations on the display, that is, not only to the stimulus that was manipulated but to the stimulus and the FP. Noting that the pigeon can "clearly see" a wide area in its visual field, this seems to be plausible. It should also be noted that this is in accord with the conjecture that the binocular overlap does not affect the nature of transfer.

In conclusion, it appears that the pigeon's visual field is perceptually homogeneous. The difference between binocular and monocular areas does not affect its visual performance, as far as supra-threshold stimuli are concerned. A stimulus presented at any position within this area is recognized equally well. The structural boundaries between the two types of visual fields do not affect the extent of transfer of discrimination learning.

Bibliography

Binggeli, R. L., & Paule, W. J. (1969). The pigeon retina: Quantitative aspects of the optic nerve and ganglion cell layer. *Journal of Comparative Neurology, 137*,1-18.

Blake, R., Sloane, M., & Fox, R. (1981) Further development in binocular summation. *Perception and Psychophysics, 30*, 266-276.

Bloch, S., Lemeignan, M., & Martinoya, C. (1987) Coordinated vergence for frontal fixation, but independent eye movements for lateral viewing, in the pigeon. In J. K. O'Regan & A.Lévy-Schoen (Eds.), *Eye movements: From physiology to cognition* (pp. 47-56), North-Holland: Elsevier Science Publishers B. V.

Bloch, S., & Martinoya, C. (1982). Comparing frontal and lateral viewing in the pigeon. I. Tachistoscopic visual acuity as a function of distance. *Behavioural Brain Research, 5*, 231-244.

Bloch, S., Rivaud, S., & Martinoya, C. (1984) Comparing frontal and lateral viewing in the pigeon. III. Different patterns of eye movements for binocular and monocular fixation. *Behavioural. Brain Research, 13*, 173-182

Blough, D. S. (1963) Interresponse time as a function of continuous variables: A new method and some data. *Journal of the Experimental Analysis of Behavior, 6*, 237-246.

Blough, D. S. (1977) Visual search in the pigeon: Hunt and peck method. *Science, 196*, 1013-1014.

Blough, D. S. (1979) Effects of the number and form of stimuli on visual search in the pigeon. *Journal of Experimental Psychology: Animal Behavior Processes, 5*, 211-223.

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

Blough, P. M. (1973) The visual acuity of the pigeon. II. Effects of target distance and retinal lesions. *Journal of the Experimental Analysis of Behavior, 20*, 333-343.

Blough, P. M. (1979) Functional implications of pigeon's peculiar retinal structure. In A. M. Grand & J. H. Maxwell (Eds.), *Neural mechanisms of behavior in the pigeon* (pp. 71-88), New York: Plenum Press.

Catania, A. C. (1964) On visual acuity of the pigeon. *Journal of the Experimental Analysis of Behavior, 7*, 261-366.

Di Stefano, M., Kusmic, C., & Musumeci, D. (1987) Binocular interactions measured by choice reaction times in pigeons. *Behavioural Brain Research, 25*, 161-165.

Fitzke, F. W., Hayes, B. P., Hodos, W., Holden, A. L., & Low, J. C. (1985) Refractive sectors in the visual field of the pigeon eye. *Journal of Physiology (London), 369*, 33-44.

Galifret, Y. (1968) Les diverse aires fonctionelles de la rétine du pigeon. *Zeitschrift für Zellforschung, 86*, 535-545.

Goodale, M. A. (1983) Visually guided pecking in the pigeon (*Columba livia*). *Brain Behavior and Evolution, 22*, 22-41.

Goodale, M. A., & Graves, J. A. (1982) Retinal locus as a factor in interocular transfer in the pigeon. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 211-240). Cambridge, MA: The MIT Press.

Hodos, W., Bessette, B. B., Macko, K. A., & Weiss, S. R. B. (1985) Normative data for pigeon vision. *Vision Research, 25*, 1525-1527.

Hodos, W., Leibowitz, W., & Bonbright, J. C., Jr. (1976) Near-field visual acuity of pigeons: Effects of head location and stimulus luminance. *Journal of the Experimental Analysis of Behavior, 25*, 129-141.

Holden, A. L., & Low, J. C. (1989) Binocular fields with lateral-eyed vision. *Vision Research, 29*, 361-367.

Jahnke, H. J. (1984) Binocular visual field differences among various breeds of pigeons. *Bird Behviour, 5*, 96-102.

Jenkins, H. M., & Sainsbury, R. S. (1970) Discrimination learning with the distinctive feature on positive or negative trials. In D. J. Mostofsky (Ed.), *Attention: Contemporary theory and analysis* (pp. 239-273). New York: Appleton-Century-Crofts.

LaMon, B. C., & Zeigler, H. P. (1984) Grasping in the pigeon (*Columba livia*): Stimulus control during conditioned and consummatory responses. *Animal Learning and Behavior, 12*, 223-231.

LaMon, B. C., & Zeigler, H. P. (1988) Control of pecking response form in the pigeon: Topography of ingestive behaviors and conditioned keypecks with food and water reinforcers. *Animal Learning and Behavior, 16*, 256-267.

Macko, K. A., & Hodos, W. (1985) Near point of accommodation in pigeons. *Vision Research, 25*, 1529-1530.

Marshall, J., Mellerio, J., & Palmer, D. A. (1973) A schematic eye for the pigeon. *Vision Research, 11*, 1019-1022.

Martin, G. R. (1984) The visual fields of the tawny owl, *Strix aluco L. Vision Research, 24*, 1739-1751

Martin, G. R. , & Young, S. R. (1983) The retinal binocular field of the pigeon (*Columba livia*: English racing Homer). *Vision Research, 23*, 911-915.

Martinoya, C., Le Houezec, J., & Bloch, S. (1988) Depth resolution in the pigeon. *Journal of Comparative Physiology: A, 163*, 33-42.

Martinoya, C., Rey, J., & Bloch, S. (1981) Limits of the pigeon's binocular field and direction for best binocular viewing. *Vision Research, 21*, 1197-1200.

Martinoya, C., Rivaud, S., & Bloch, S. (1983) Comparing frontal and lateral viewing in the pigeon. II. Velocity thresholds for movements discrimination. *Behavioural. Brain Research, 8*, 375-385.

McFadden, S. A. (1987) The binocular depth stereoacuity of the pigeon and its relation to the anatomical resolving power of the eye. *Vision Research, 27*, 1967-1980.

McFadden, S. A. (1989) Eye design for depth and distance perception in the pigeon: An observer orientated perspective. *International Journal of Comparative Psychology, 3*, 101-130.

McFadden, S. A., & Reymond, E.(1985) A further look at the binocular visual field of the pigeon (*Columba livia*). *Vision Research, 25*, 1741-1746.

McFadden, S. A., & Wild, J. M. (1986) Binocular depth perception in the pigeon. *Journal of the Experimental Analysis of Behavior, 45*, 149-160.

Millodot, M., & Blough, P. M. (1972) The refractive condition of the pigeon eye. *Vision Research, 11*, 1019-1022.

Nye, P. W. (1973) On the functional differences between frontal and lateral visual fields of the pigeon. *Vision Research, 13*, 559-574.

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

Pettigrew, J. D., & Konishi, M. (1976) Neurons selective for orientation and binocular disparity in the visual Wulst of the Barn Owl (*Tyto alba*). *Science, 193* 675-677.

Porciatt, V., Fontanesi, G., Raffaelli, A., & Bagnoli, P. (1990) Binocularity in the little owl, *Athene noctua* II. Properties of visually evoked potentials from the Wulst in response to monocular and binocular stimulation with sine wave gratings. *Brain Behavior and Evolution, 35*, 40-48.

Powell, R. W. (1967) The pulse-to-cycle fraction as a determinant of critical flicker fusion in the pigeon. *Psychological Record, 17*, 151-160.

Remy, M., & Emmerton, J. (in press) Directional dependence of intraocular transfer of stimulus detection in pigeons (*Columba livia*). *Behavioral Neurosciences.*

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

Tukey, J. W. (1977) *Exploratory Data Analysis.* Reading, MA: Addison-Wesley.

Uhlrich, D. J., Blough, P. M., & Blough, D. S. (1982) The pigeon's distant visual acuity as a function of viewing angle. *Vision Research, 22*, 429-431.

Watanabe, S., Hodos, W., & Bessette, B. B. (1984) Two eyes are better than one: Superior binocular discrimination learning in pigeons. *Physiology and Behavior, 32*, 847-850.

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

Yamashita, H. (1981) Analysis of pecking duration in DRL schedules in pigeons. [Abstract] (in Japanese) *Annual of Animal Psychology, 31*, 46-47.

Zeigler, H. P., Levitt, P. W., & Levine, R. R. (1980) Eating in the pigeon (*Columba livia*): Movement patterns, stereotypy, and stimulus control. *Journal of Comparative and Physiological Psychology, 94*, 783-794.