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# Behavioral correlates of visual acuity (minimum separable) in the Northern bluejay (*Cyanocitta cristata*)

Robert James Stone

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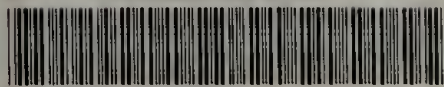
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BEHAVIORAL CORRELATES OF VISUAL  
ACUITY (MINIMUM SEPARABLE) IN THE  
NORTHERN BLUEJAY (CYANOCITTA CRISTATA)

A Thesis Presented

by

Robert James Stone

Submitted to the Graduate School of the  
University of Massachusetts in partial  
fulfillment of the requirements for the degree of

MASTER OF SCIENCE

February, 1975

Major Subject: Psychology


BEHAVIORAL CORRELATES OF VISUAL  
ACUITY (MINIMUM SEPARABLE) IN THE  
NORTHERN BLUEJAY (CYANOCITTA CRISTATA)


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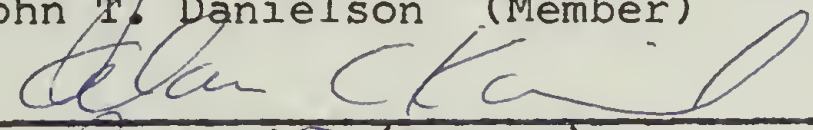
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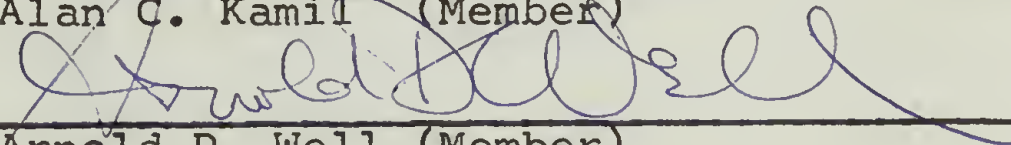
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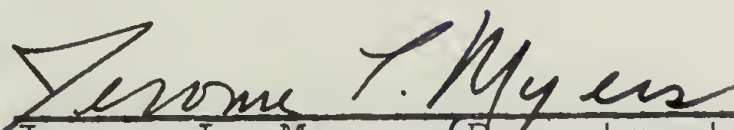
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## ABSTRACT

A psychophysical experiment was performed to determine the behavioral correlates of visual acuity in the Northern bluejay (Cyanocitta cristata). Maximum resolution for this species of jay was 3.4 minutes of arc between 0.0 and 1.0 log millilamberts. Evidence was obtained for two different components of the acuity function thought to be mediated by rods at low luminance levels and cones at higher luminance levels. Results were discussed and compared to other avian species with special reference to the functional significance of both foveal and extra-foveal regions of the retina.

## ACKNOWLEDGEMENTS

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## TABLE OF CONTENTS

Abstract . . . . .	ii
Acknowledgements . . . . .	.iii
List of Figures . . . . .	v
Introduction . . . . .	1
Method . . . . .	15
Results . . . . .	24
Discussion . . . . .	38
Summary . . . . .	54
References . . . . .	56

## LIST OF FIGURES

<u>Figure</u>		<u>Page</u>
1	Illustration of apparatus . . . . .	17
2	Psychometric functions obtained for one subject ( $S_1$ ) with 6 different grating patterns, indicated in terms of angular subtense of a single stripe. Dashed line represents luminance-acuity threshold values at 75 percent correct responses. (0.0 is equivalent to 1.4 log mL.) . . . . .	25
3	Psychometric functions obtained for one subject ( $S_2$ ) with 6 different grating patterns, indicated in terms of angular subtense of a single stripe. Dashed line represents luminance-acuity threshold values at 75 percent correct responses. . . . .	27
4	Psychometric functions obtained for one subject ( $S_3$ ) with six different grating patterns, indicated in terms of angular subtense of a single stripe. Dashed line represents luminance-acuity threshold values at 75 percent correct responses. . . . .	29
5	Luminance-acuity threshold functions obtained for 3 subjects with 7 different stimulus patterns . . . . .	31
6	Averaged luminance-acuity threshold function for 3 subjects with 7 different stimulus patterns . . . . .	33
7	Same data as in Figure 6, replotted in terms of decimal visual acuity (1/angular subtense of a single stripe) as a function of luminance . . . . .	36
8	Same data as in Figure 6, replotted in terms of log minutes of arc to derive maximum acuity value. Dashed line represents hypothesized asymptotic performance. . . . .	41
9	Comparison of luminance-acuity threshold functions between diurnal and nocturnal avian species. Replotted from Fite (1972). . . . .	48
10	Same data as in Figure 9, replotted in terms of decimal visual acuity values (1/angular subtense) as a function of luminance. . . . .	50



Behavioral Correlates of Visual  
Acuity (Minimum Separable) in the  
Northern Bluejay (Cyanocitta cristata)

Robert James Stone

INTRODUCTION

Visual acuity may be thought of as comprised of both a static and dynamic component. Static visual acuity is the spatial resolving capacity of the visual system, i.e., the ability of an organism to discriminate the fine details of objects in its field-of-view. Static acuity refers to four general types of sensitivity depending on the stimulus object used for its determination.

1. Acuity based on the ability to recognize and name or specify the location of certain critical aspects of the test objects such as the Snellen letters and Landolt rings.

2. Vernier acuity is the ability to localize small lateral displacements between two straight lines placed end to end.

3. Minimum-visible acuity is the ability to detect the smallest object (line or point) that can be distinguished from its background.

4. Minimum-separable acuity is the ability to resolve the minimum distance between objects for the discrimination of separateness. Various test objects include two points, two lines, or groups of lines (gratings), with the black

lines and white interspaces being of equal width. Visual acuity in terms of resolution is the reciprocal of the angular separation between two elements of the test pattern when the two images are barely resolved. This angular separation has been termed the minimum angle of resolution or MAR (Graham, 1966). Most animal studies have been limited to a determination of minimum-separable acuity with the animal required to react in some way to a grating pattern thereby allowing for the calculation of the MAR.

Dynamic visual acuity may be thought of as the ability of an organism to discriminate the movement of objects within its field-of-view. However, the problem should be separated into those situations in which the object image moves relative to the retina and those where visual pursuit is possible. When the object image remains stationary on the fovea because the eye is tracking perfectly, there is no decrement in acuity; however, if object speed is so high that tracking cannot take place, acuity suffers. In addition, if the eye is moving, acuity for stationary targets decreases (Westheimer, 1965).

Both static and dynamic visual acuity comprise the total spatial resolving power of the visual system of any organism. Although the present paper is concerned with the more static aspects of visual acuity, namely minimum-separable, the dynamic properties of the visual system should not be overlooked.

The literature contains numerous references to the high resolving power of the avian eye; the results for the most

part have been based upon inferential (cell counts and convergence ratios) and field-ornithological observation (spotting prey from various distances) techniques (Walls, 1942; Rochon-DuVigneaud, 1943; Pumphrey, 1948a; Polyak, 1957; Duke-Elder, 1958). The few studies that have produced quantitative data concerning the spatial resolving power of the avian visual system have been based almost exclusively on the pigeon.

Gundlach (1933) using a two-choice situation (alley maze) and grating patterns reported minimum-separable acuity values for the pigeon on the order of 25 seconds of arc. However, Blough (1971) appears to have been the first to notice the methodological problems inherent in the Gundlach (1933) article, since his values were based on a sequential statistic, i.e., probability of X number of correct alley choices in sequence above chance occurrence, with little or no control over such chance responding. Although acuity values were calculated there seemed to be no apparent relationship between the birds' performance and visual acuity, since all values were based totally on choice of alley rather than a discrimination of the grating pattern with some pigeons unable to discriminate even the widest pattern. Chard (1939), in an attempt to determine the effect of target distance of a striped pattern of visual acuity (minimum-separable) found values that varied with distance but ranged between 3.5 and 5.0 minutes of arc at a 60 cm. distance. He concluded that the near-point

of accommodation was in the region of 40 cm. with poorer acuity being associated for distances below the 40 cm. value and better acuity for distances farther away from this value. However, Chard (1939) made no attempt to distinguish between the various portions of the visual field used by the pigeon in this discrimination and their relationship to an acuity-distance function.

In an attempt to determine the maximum resolving power for other avian species, Donner (1951) using a two-choice situation, determined the acuity values (minimum-separable) for seven species of passerine birds (blackbird, fieldfare, robin, skylark, chaffinch, yellow-hammer, and reed-bunting). He reported values ranging from between 1.3 to 4.5 minutes of arc for the highest luminances used. Donner's (1951) values may be somewhat misleading due to various methodological considerations. The basic two-choice alley maze was again used with no control for either brightness cues or position preferences, since no correction procedure was applied. A similar sequential statistic was used to calculate threshold acuity which provided a rather lax criterion of threshold performance, and again no attempt was made to distinguish between those portions of the visual field used since viewing distance was held at one meter for all trials.

All of the above studies suffered from one or more methodological problems as discussed: however, with the advent

of modern animal psychophysical procedures based on operant techniques many of the problems have been resolved. The two-response, forced-choice method is still the most common paradigm for studying visual acuity with animal subjects. However, the early experimenters may have introduced variability and response biases into their results due to excessive handling of the animals during the experiment. To minimize difficulties of this nature, automatic programming of experimental contingencies are now used in most studies. Response biases, usually position preferences, are now reduced or avoided through the use of a trial-rerun correction procedure which was lacking in the earlier studies (Blough and Yager, 1969). If the animal responds incorrectly, the correction procedure assures that the same stimulus pattern is repeatedly presented in the same position until the animal makes the correct response and is reinforced. This procedure assures that the animal will make equal numbers of correct responses to both sides and will receive equal reinforcement for correct responses. However, the responses on the corrected trials should not be included in the data analysis, since the animal may follow the rule "switch sides if no reinforcement", for the correct response.

A more critical form of response bias involves a tendency of the animal to respond to brightness differences when a mismatch in brightness exists between the two response alternatives. The possible effects of brightness cues and their confounding effects upon acuity measures cannot be excluded

from earlier studies. Hodos and Bonbright (1972) have shown that the pigeon can detect visual intensity differences on the order of 0.40 to 0.10 logarithmic units with an average value of 0.12; however, this problem can be avoided in studies of visual acuity by assuring equal space-averaged luminance of the two response alternatives. Other factors that must be controlled when determining visual acuity include the effect of the surround luminance and retinal position. Westheimer (1965) has found that the most accurate acuity values are achieved when the surround has luminance equal to that of the grating pattern. If the surround is of a higher luminance than the stimulus array, lower than normal acuity values will result. In addition, if the surround is of a somewhat lower luminance than the array, higher acuity values will result.

The retinal location used in viewing the stimulus pattern, given an optimal luminance value of 1.5 log millilamberts, appears to be the major factor responsible for the high acuity values reported for both human and non-human primates. Visual acuity is highest at the fovea and falls off progressively towards the periphery of the retina. Sloan (1968) confirmed the work of earlier investigators who found acuity values on the order of 0.5 to 1.0 minutes of arc when viewed foveally using single Landolt ring targets. For stimuli viewed only  $2^{\circ}$  away from the fovea in the nasal field visual acuity fell to 1.3 minutes of arc. At  $10^{\circ}$  in the nasal field, the acuity value fell to 4.0 minutes of arc, thereby confirming the importance

of the fovea for maximum spatial resolution in humans.

Ordy and Samorajski (1968) working with both diurnal and nocturnal primates found acuity values for the diurnal species to be on the order of 1-2 minutes of arc, while acuity values for the nocturnal species ranged between 3.5 to 8.0 minutes of arc. All subjects except the tree shrew viewed the stimulus pattern either foveally or from within the area centralis. Those diurnal primates that possessed a foveal depression (Squirrel monkey) showed lower acuity thresholds than did those possessing only an area centralis (marmoset and lemur) or undifferentiated retina (tree shrew), again lending support to the functional significance of the fovea for maximum spatial resolution in the higher-order primates. Further evidence has been provided by Yarczower (1966) showing that photocoagulator lesions of the primate fovea have a pronounced effect on acuity, producing marked decrements in visual acuity.

As was stated above, there appears to be little doubt about the role of the fovea and its functional significance in maximum visual acuity for the primates. However, there appears to be a great deal of doubt about the functional significance of the foveal depression and related areas of increased ganglion cell concentrations as they relate to visual acuity in the avian visual system. The retinas of many avian species including the pigeon, owl (Bubo virginianus), and bluejay possess a single fovea which is extremely well-defined in the bluejay

and owl, although more shallow and variable in the pigeon (Chard, 1939; Galifret, 1968; Blough, 1971). These foveas are of the convexiclivate variety described by both Walls (1937, 1940) and Pumphrey (1948b) as compared to the extreme concaviclivate form found in man and primates.

A basic theoretical question exists concerning the function of the convexiclivate fovea as well as the function of the fovea in general as it relates to the avian visual system. Walls (1937, 1940) believed the convexiclivate fovea to be an optical device that served to expand the retinal image as it crossed the clivus, thereby increasing the spatial resolving power of the eye. Walls (1940) calculated that given a refractive index of 1.3475 for the retina and 1.3391 for the vitreous, the computed areal expansion of an image in the center of the fovea would be increased by approximately 30 percent. Pumphrey (1948b), on the other hand, suggested that the convexiclivate fovea found in birds may be a highly specialized structure used for detecting movement and the angular displacement of objects, rather than for the resolution of fine detail as proposed by Walls (1939, 1940). Pumphrey (1948b) allowed for a slight "magnifying effect" due to foveal refraction; however, he believed the main advantage to be gained from a convexiclivate fovea was the accurate detection and fixation of a moving object. As an object approached the fovea, the object image would lag behind the object until the center of the fovea was



reached, at which time the image would immediately lead the actual object. It was thought that the abrupt shift from the lag to lead position of the object image was responsible for the accurate detection of a moving object (Pumphrey, 1948b).

In regard to the avian visual system, Pumphrey (1948a,b) points out that distinct central (monocular or lateral) and temporal (binocular or frontal) foveas occur in the retinas of many birds (usually predators) with a large binocular field. In addition, many birds with a small binocular visual field, appear to scrutinize distant objects monocularly using the central fovea if they have one. Pumphrey (1948a) goes on to state that diurnal birds, (being more fully diurnal than man) could be expected to possess an extra-foveal acuity nearly as good as man's in the fovea, due to the large extra-foveal cone population of their retinas as well as a lower overall convergence ratio of cones to ganglion cells as compared to man, since rods are relatively scarce in the retinas of diurnal birds. Therefore, they would be nearly blind at night and inactive unless disturbed, while during the day their extra-foveal acuity would be almost as good as man's.

As was previously discussed, many of the earlier studies of avian visual acuity suffered from one or more methodological problems. Blough (1971, 1973), with the proper controls, has attempted to separate out the role of the fovea and non-foveal portions of the pigeon retina by a determination of the maximum resolving power for both near and distant targets.

When viewing the stimulus targets binocularly from a distance of 13 cm. (near condition), acuity values were obtained across subjects which ranged from between 5.0 to 8.3 minutes of arc; with monocular viewing from a distance of 73 cm. (far condition), the acuity values ranged from 1.2 to 4.0 minutes of arc.

Blough (1971, 1973) has interpreted the results as indicating that the pigeon visual system is composed of two separate components, one for the frontal visual field (binocular) and one for the lateral visual field (monocular), as previously suggested by Catania (1963).

Anatomical support for an area containing an increased density of retinal cells (mainly bipolar) located in the superior quadrant and subserving the lower portion of the frontal (binocular) field in pigeons has come from Galifret (1968) and Binggeli and Paule (1969). The lateral visual field is subserved by a variable and somewhat shallow central fovea of the convexiclivate type described by Walls (1940). In addition, since eye movements are quite restricted in the pigeon, an area located in the superior temporal quadrant subserving the frontal field of view would seem quite plausible. In an attempt to test Wall's (1937, 1940) foveal theory, Blough (1973) lesioned the central fovea and found that the pigeon fovea was relatively unimportant in mediating visual acuity for the lateral field of view; thereby confirming similar findings reported by Yarczower (1964) on the pigeon fovea. Both Blough (1971,

1973) and Nye (1973) have concluded that the pigeon appears to be somewhat myopic for targets in the frontal field, while for those targets in the lateral field it is hypermetropic as suggested earlier by Catania (1964). Thus the effect of target distance on acuity threshold data can not be overlooked when investigating other avian species.

Although much of the data on the resolving power of the avian visual system comes from the pigeon, Fite (1972), in a quantitative study using operant techniques, appears to have been the first investigator to study a predatory species of bird (Bubo virginianus) in order to determine its visual acuity. The Great Horned Owl, a nocturnal predator, possesses a single well-defined fovea of the convexiclivate type in the temporal retina. Anatomical studies have found that the fovea of this species of bird contains a significant number of cones as well as a high density of rods (Fite, 1972). The fovea of this species of bird subserves the frontal (binocular) visual field of view and appears to be hypermetropic for near targets, since birds were observed during testing withdrawing their heads as if to bring the stimulus pattern (grating) into focus. Maximum resolving power for this species was on the order of 4.0 to 5.0 minutes of arc, which is surprisingly low considering the high degree of foveal differentiation when compared with cats (5.0 minutes of arc) which possess only an area centralis but have similar acuity

values (Fite, 1972). There were also indications that spatial resolution (minimum-separable) for the owl was being mediated by two different processes at low vs. high luminance levels over a range of approximately seven log units of luminance (Figure 7).

The study of the Northern bluejay (Cyanocitta cristata) may be of importance for a wide variety of reasons. Hardy (1961) made a thorough study of the behavior patterns of the Northern bluejay (Cyanocitta cristata) both in captivity and in the wild; however, no attempt was made at that time to determine the degree of spatial resolving power for that species of jay. Hardy (1961) did note, however, that this species of jay exhibited aerial feeding in the early morning hours which might require a high degree of dynamic visual acuity. Brown (1961), observing the Stellers jay (Cyanocitta stelleri) states unequivocally that,

"In animals with a strongly developed visual sense, particular behavior patterns are often associated with specialization in form and color of the structures that serve as visual signals."

Brown (1961), like Hardy, (1961), made no attempt to determine in a quantitative manner the spatial resolving powers of the jay family (Corvidae). Recently, Hunter and Kamil (1971) have used the Northern bluejay in an object-discrimination learning set task and have discussed their results in terms of the comparative significance to other species

in the learning set paradigm. However, no specific test of the spatial resolving power of this species was undertaken, even though a basic assumption which underlies a discrimination task is one of some minimal level of visual acuity.

On anatomical grounds the study of the Northern bluejay may be of further importance. Fite and Rosenfield-Wessells (1974) have shown that the retina of Cyanocitta cristata contains a single, centrally placed fovea which is extremely well-defined and is of the convexiclivate variety as described by both Walls (1937, 1940) and Pumphrey (1948b). Although histological examination of the retina of this species has failed to distinguish between rod and cone nuclei with light microscope techniques, Hardy (1961) has pointed out that the activity cycle for this diurnal "predator of opportunity" begins approximately one-half hour after dawn and ends at around 6:00 P.M., which suggests the presence of two receptor types.

The present study was undertaken to collect behavioral data on the spatial resolving power (visual acuity) of the Northern bluejay (Cyanocitta cristata) with special emphasis on a comparative evaluation of the data with other avian species. It is hoped that the data from the present study may be used in a subsequent experiment in which foveal lesions would be made and a post-operative determination of the visual

resolving power taken. It may then be possible to make a quantitative statement as to the role of the convexiclivate fovea in the avian visual system, if indeed it can be established that the bluejay uses foveal vision for minimum-separable resolution.

## METHOD

Subjects

The subjects were three Northern bluejays (Cyano-citta cristata) captured locally and hand raised in the laboratory. The subjects were maintained on a free-feeding schedule of food and water for 3 months prior to the start of the experiment. All subjects were maintained on a normal light-dark cycle with lights on at 0600 hours and off at 1800 hours. All subjects had been run in prior experiments:

S<sub>1</sub> -- 3 years old, Object reversal, WGTA paradigm

S<sub>2</sub> -- 3 years old, Position reversal, WGTA paradigm

S<sub>3</sub> -- 2 years old, Object alternation, WGTA paradigm

Apparatus

A modified refrigerator chassis housed the experimental chamber. Its door contained a 6 in. X 7 in. one-way mirror which was covered by a black curtain. Inside the chamber, a white masonite panel extended from the ceiling to 6 in. above the floor and was supported vertically on a framework of flex-angle. The panel divided the chamber into two compartments, one 14 in. wide, 16 in. deep, and 23 in. high which housed a wire cage 12 in. wide, 14 in. deep, and 20 in. high that served as the bird chamber. A perch was then placed 3 in. in front of the

masonite panel, and was firmly attached to the sides of the bird chamber. The second compartment was 8 in. wide, 16 in. deep, and 23 in. high. It contained a white noise source, buzzer, stimulus presentation apparatus and two response keys, 30 mm. in diameter placed 3 in. apart, to which had been attached viewing tubes, 2.5 in. long and 1 in. in diameter, to restrict the field of view. The interior of the experimental chamber was illuminated by two 4.32 w bulbs. All interior portions of the apparatus were painted a non-toxic flat white. Figure 1 is a picture of the apparatus.

The stimulus presentation apparatus was a  $45^{\circ}$  pie-shaped wedge of 3 mm. thick translucent plexiglas attached vertically just above its center to the shaft of a 1/25 h.p. reversible clock motor. The front surface of the wedge was located 4 in. behind the rear surface of the masonite panel and could be rotated through an angle of  $22^{\circ}$  either to the right or left of the center position and held in either of the two positions. Three stimulus patterns could then be attached on the lower edge of the wedge. Movement of the wedge to the right placed the left-hand and center patterns immediately behind both the response windows and viewing tubes, while movement of the wedge to the left placed the center and right-hand patterns behind both the response windows and viewing tubes. The position of the wedge was determined in a random sequence on a trial-by-trial



FACE PAGE FOR FIGURE 1

Figure 1. Illustration of apparatus

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basis with a solenoid-operated shutter occluding movement of the wedge when it changed positions. All experimental contingencies were programmed by solid state and electromechanical circuitry.

Stimulus patterns were a series of photographic negatives of square-wave, black and white, 50 percent gratings with constant luminance ratios of approximately 0.98, but which differed in spatial frequency. They were taped to the wedge, two on the right and left edges facing the viewing tubes and response windows, with a third pattern of a different spatial frequency on the reverse side of the wedge in the center during each experimental series. Depending upon the position of the wedge, a grating pattern appeared behind one window and a blank field of the same average luminance appeared behind the other window. Due to the diffusing properties of the plexiglas, the blank field appeared homogeneous. The two fields were equated for equal photometric brightness with the use of a Honeywell Spotmeter both between and during experimental series.

The test fields were illuminated from the rear by a 300-w tungsten projector bulb housed in a 35 mm. slide projector. This was placed 100 cm. away from the rear surface of the wedge and continuously monitored at 2.4 A, a.c. Maximum luminance of the test fields with this source

was 1.4 log millilamberts (mL) as measured with a MacBeth Illuminometer. Although luminance is an inappropriate photometric unit for any species whose photopic sensitivity function is unknown, the luminance measure will be used in the present study, thereby allowing for comparison with data obtained for other species.

Reinforcements were delivered through a 1 in. pipe to a small metal food cup, 1 in. wide, 1 in. high, and 2 in. long, attached between and 1 in. below the response windows. The bottom edge of the pipe was 3 in. above the food cup and extended upward through a hole in the top of the refrigerator. A rotary reinforcement delivery mechanism was attached to the roof of the refrigerator. This device consisted of a 3/4 in. plexiglas dish mounted on a circular steel plate and attached to a stepping relay and gear assembly. The dish was 10 in. in diameter and contained 80 equally spaced holes, each 5/8 in. in diameter along the outside edge of the dish. A slot in the steel plate was lined up with the opening in the top of the refrigerator, allowing the contents of a single hole to fall into the food cup as a pulse to the stepper rotating the dish. Reinforcement was one-half of a mealworm (Tenebrio larvae).

Four Gerbrands counters recorded both correct and incorrect responses from the response keys. A total of

80 trials per day were recorded from each of the three subjects. All subjects were run between 0800 hours and 1500 hours EST.

### Procedure

The experiment was conducted in three stages: habituation to the experimental chamber, shaping of the key pecking response, and visual discrimination training. During habituation each subject was gradually reduced to between 75 and 80 grams regardless of ad lib weight and maintained at that level for the duration of the experiment. At the same time that deprivation began, each subject was given daily sessions in the apparatus with reinforcement in the food cup and white noise present.

The second stage consisted of shaping, by successive approximations, a key pecking operant. All three subjects were trained to peck at a single window 30 mm. in diameter for food reinforcement. This window was occluded on alternate days and a second window (also 30 mm. in diameter) was used. This procedure avoided the initial development of a position preference. The windows and viewing tubes were placed in the center of the white masonite panel and were attached to microswitches mounted on the rear side of the panel. After all three subjects had been reliably key-trained to both windows on alternating days, then the two response windows were presented simultaneously and

discrimination training began.

Visual discrimination training began with a series of grating patterns with individual stripe widths subtending 51.0, 33.0, 22.5, 14.2, 8.2, 4.7, and 3.5 min. of arc, at a viewing distance of 7 in. The 7 in. viewing distance was chosen based upon the observed pre-response head position for this species of jay. The series of patterns were presented in descending order across experimental sessions, beginning with the 51.0 min. of arc pattern. Within each one hour session a modified method of limits was followed on consecutive days, which utilized only a descending series of luminances.

The luminance of the stimulus patterns was controlled with Wratten neutral density filters placed in the focal plane of the projector beam. Each pattern was presented initially at a high luminance level to insure discriminability. The luminance levels were then logarithmically reduced in daily sessions in 0.30 steps. Panel luminance was adjusted by the Experimenter to match stimulus pattern illumination by means of a rheostat connected to the two 4.32 w bulbs which provided the ambient illumination for the experimental chamber. Subjects were dark-adapted for a minimum of 30 minutes prior to experimentation at lower luminance levels. All subjects began responding immediately when placed in the experimental chamber except at the lowest luminance levels.

Subjects responded to the window containing the grating pattern on a trial-by-trial basis. A trial was defined as 7 consecutive key pecks (FR-7) on either key. Correct responses (FR-7, grating present) were rewarded 100 percent of the time, which allowed for both a higher level of stimulus control and a more stable response rate. Each correct response set up a new randomized trial. Incorrect responses (FR-7, blank field) were followed by a 20 second time out during which the response windows were occluded and both keys were electronically inactivated. After an incorrect response, a correction procedure then went into effect. The wedge remained in the same position it occupied prior to the incorrect response and the subject was reinforced only when a correct response occurred. In this way, response position preferences were held to a minimum. Correct and incorrect responses on the right and left response keys were recorded only during the randomized trials and not during the correction procedure.

Psychometric functions were obtained for each subject which related the percentage of correct responses to the luminance level for each grating pattern. Threshold luminance for all patterns used was defined as the luminance value at which the subject responded correctly 75 percent of the time. Psychometric functions were then obtained which related luminance thresholds to angular subtense of

individual stripes across test patterns for each subject.  
All measurements were obtained with tungsten (white)  
illumination.



## Results

Psychometric functions relating percent correct response to luminance of the stimulus field were obtained for each grating pattern on each subject. All psychometric functions were based on a minimum of 160 trials per subject, i.e., for each grating bar width at least 160 responses were required for a determination of percent correct as a function of luminance. Threshold acuity was defined as the luminance value at which each subject responded correctly 75 percent of the time. Figures 2, 3, and 4 represent a plot of the data collected in this manner for each subject.

A second function (Figure 5) was then derived for each subject which related the acuity-luminance threshold (75% correct response) to angular subtense of a single stripe for each grating pattern. Figure 5 demonstrates that inter-subject variability was minimal, with only a slight deviation for  $S_3$  at 51.0 minutes of arc. Due to the low inter-subject variability it was decided to average all three subjects thereby providing a single psychometric function, for each grating bar width based upon a minimum of 480 trials, which related acuity-luminance threshold to angular subtense for all grating patterns. Figure 6 is a plot of that data. Replotting the data of Figure 6 in terms of decimal visual acuity (1/angular subtense of a single stripe) provided the data points of Figure 7.

Figures 7 and 8 indicate that visual acuity in this

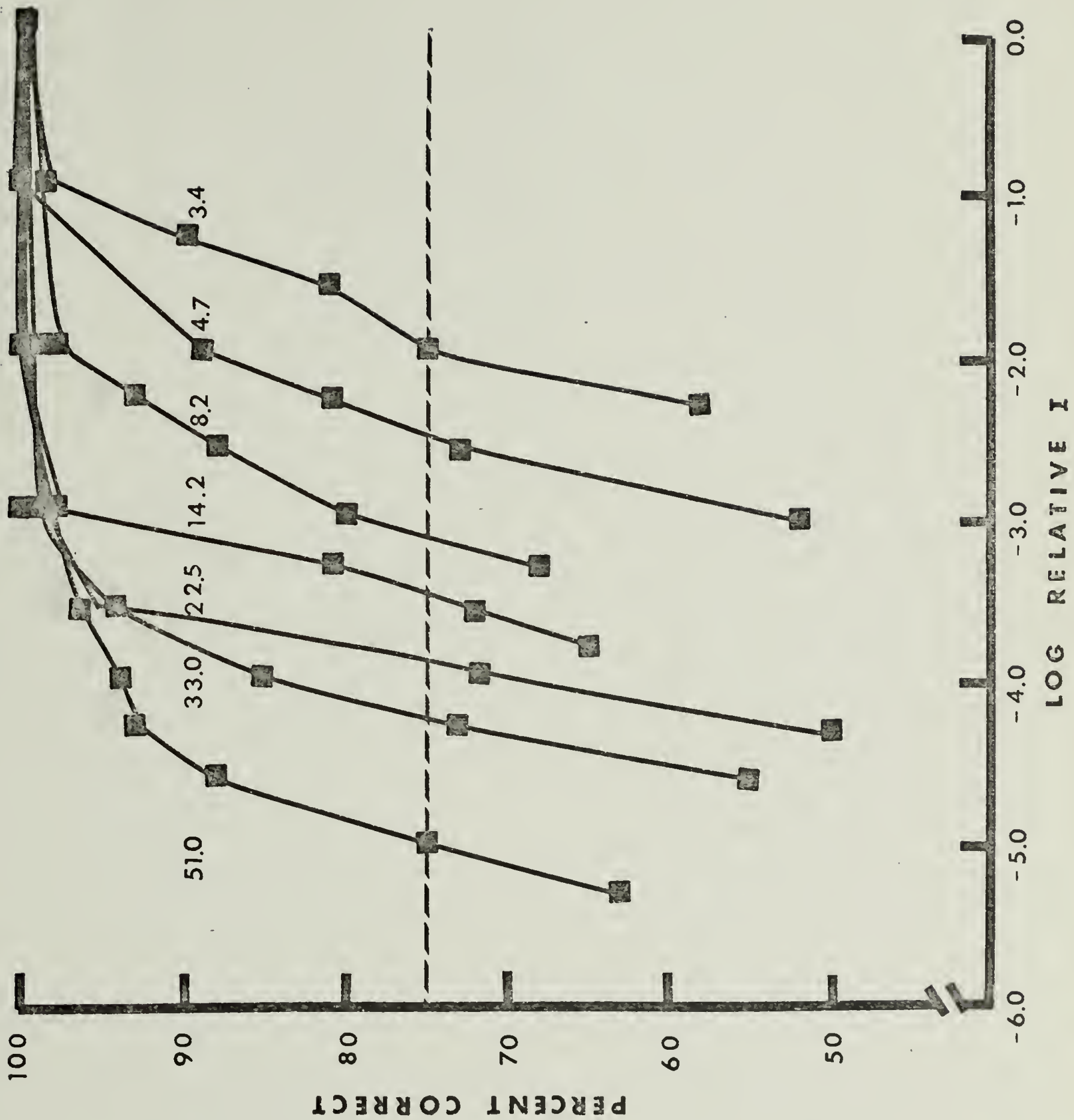
## FACE PAGE FOR FIGURE 2

Figure 2. Psychometric functions obtained for one subject ( $S_1$ ) with 6 different grating patterns, indicated in terms of angular subtense of a single stripe. Dashed line represents luminance-acuity threshold values at 75 percent correct responses. (0.0 is equivalent to  $1.4 \log \text{mL}$ .)



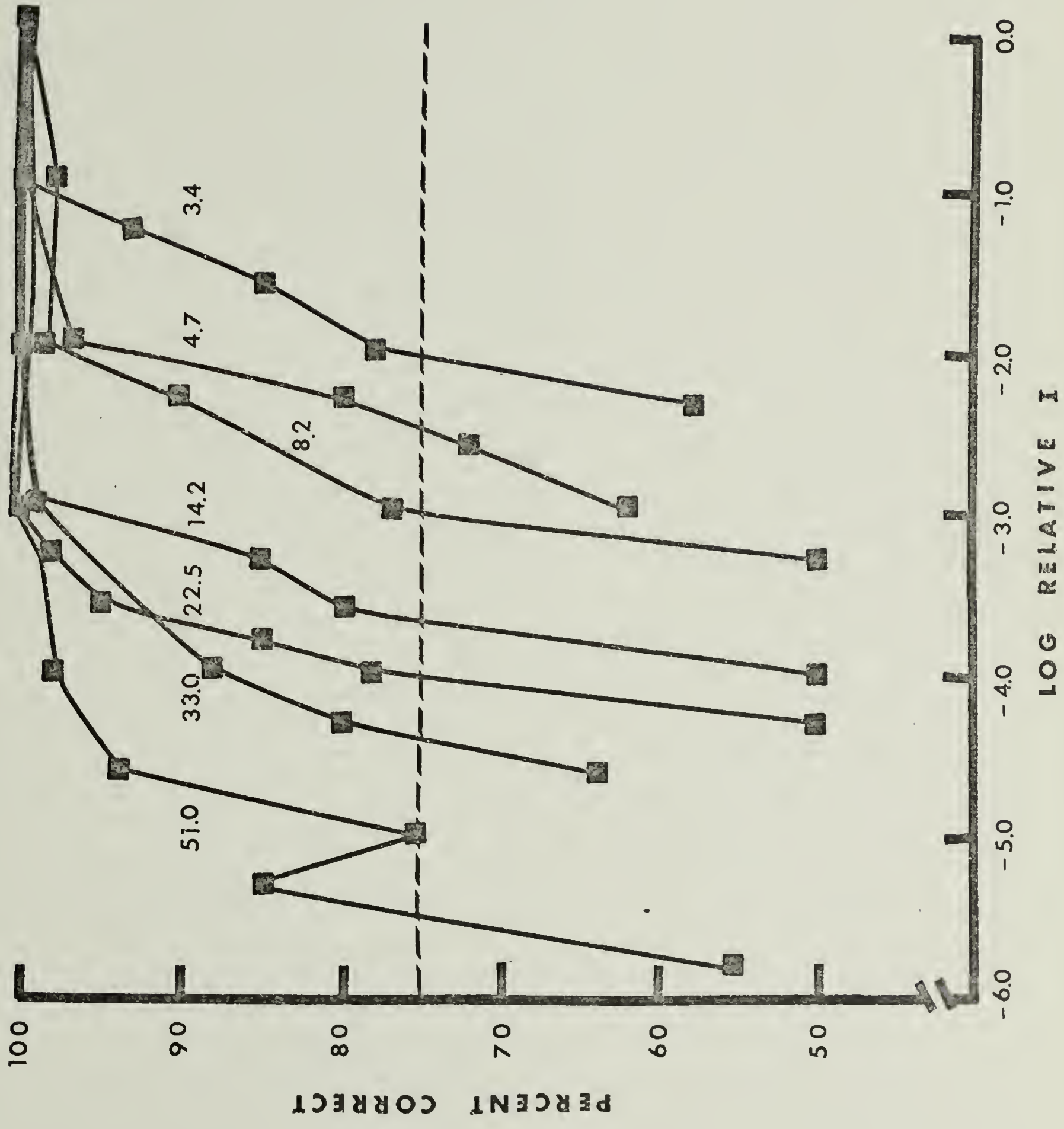
## FACE PAGE FOR FIGURE 3

Figure 3. Psychometric functions obtained for one subject ( $S_2$ ) with 6 different grating patterns, <sup>2</sup> indicated in terms of angular subtense of a single stripe. Dashed line represents luminance-acuity threshold values at 75 percent correct responses.



## FACE PAGE FOR FIGURE 4

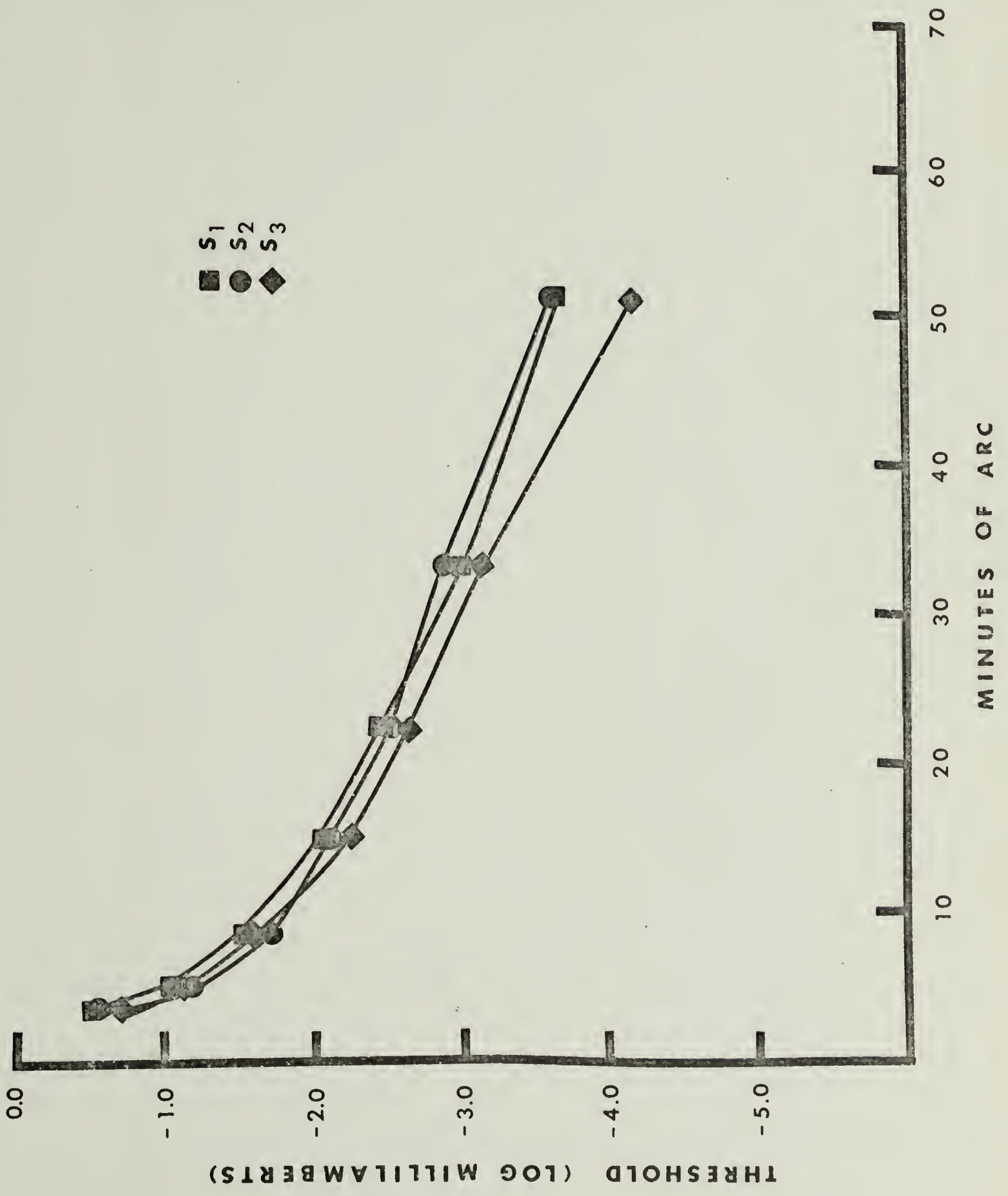
Figure 4. Psychometric functions obtained for one subject ( $S_3$ ) with 6 different grating patterns, indicated in terms of angular subtense of a single stripe. Dashed line represents luminance-acuity threshold values at 75 percent correct responses.



## FACE PAGE FOR FIGURE 5

Figure 5. Luminance-acuity threshold functions obtained for 3 subjects with 7 different stimulus patterns.





## FACE PAGE FOR FIGURE 6

Figure 6. Averaged luminance-acuity threshold function for 3 subjects with 7 different stimulus patterns.

0.0

-1.0

-2.0

-3.0

-4.0

-5.0

THRESHOLD (LOG MILLIAMBERTS)

10

20

30

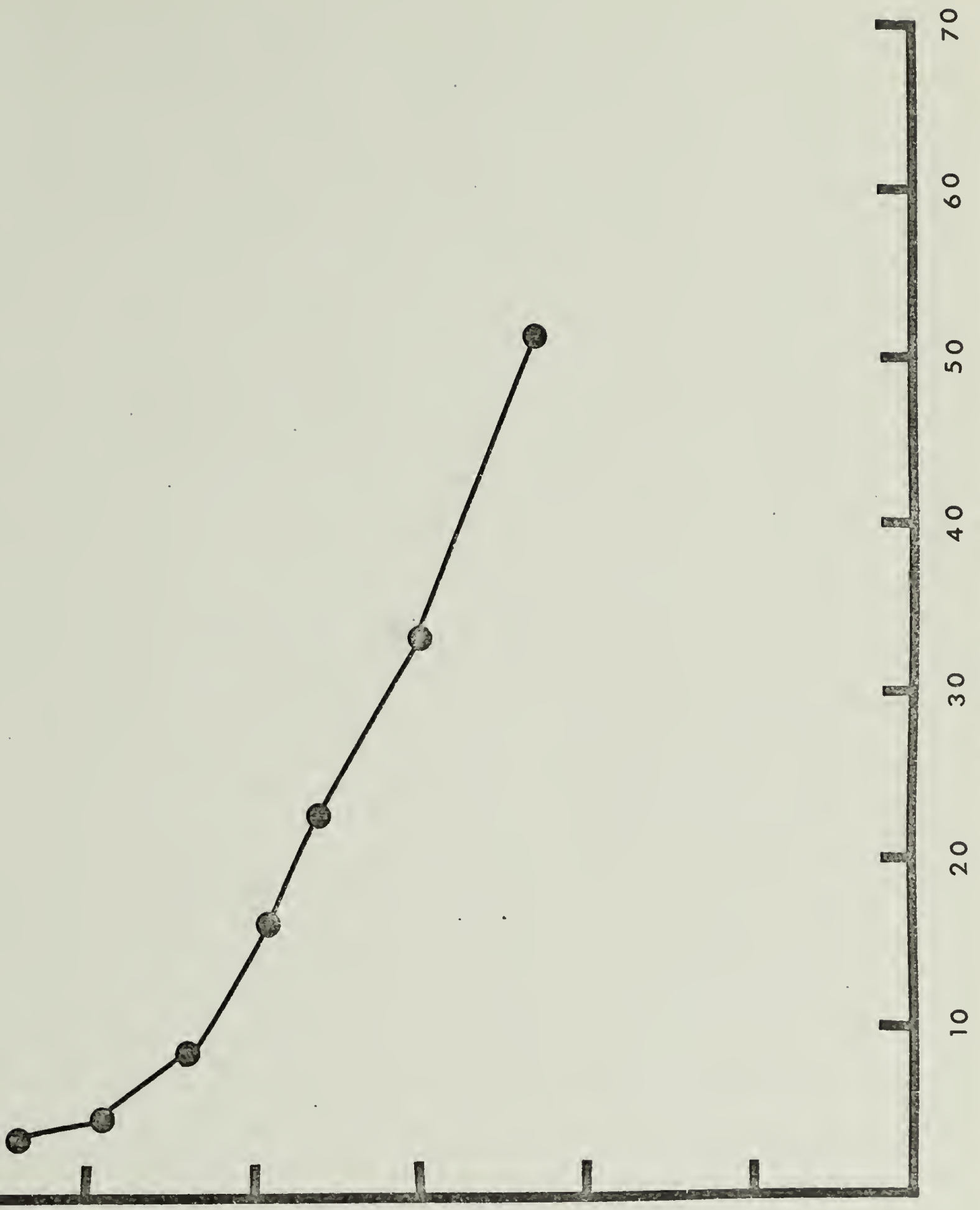
40

50

60

70

MINUTES OF ARC

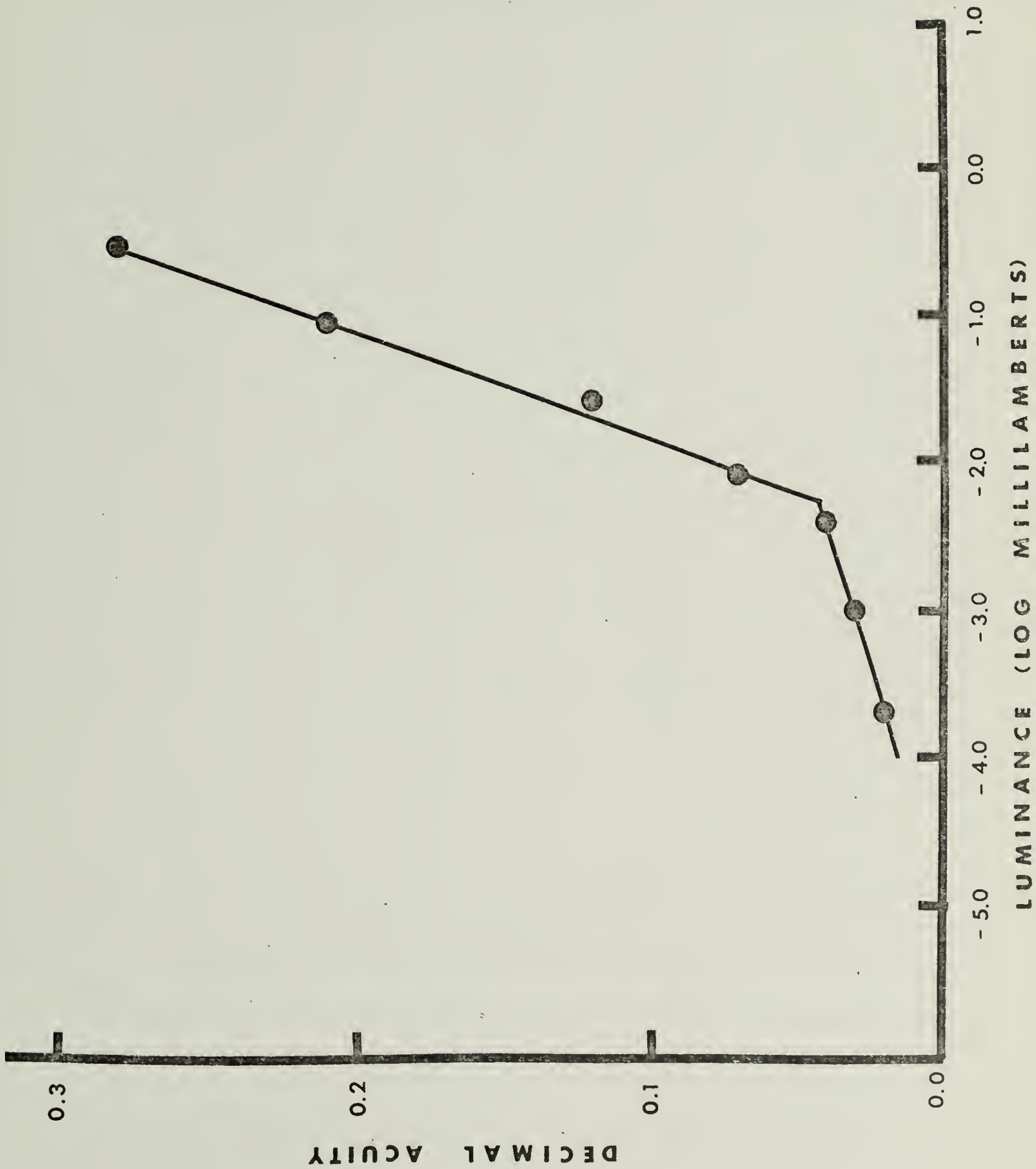


experimental situation would be on the order of 3.5 minutes of arc at  $-0.6$  log millilamberts. In addition, these figures (6 and 7) indicate that visual acuity for this species of jay is clearly dependent upon luminance over a range of at least 4 log units. All subjects refused to peck at the widest strip width (51.0 min. of arc) at luminance levels below  $-4.0$  log millilamberts and were observed to roost in the experimental chamber (Figure 6).

Two regression lines were used to describe the data points of Figure 7. The lowest acuity values obtained at low luminances fell upon a line with slope of 0.015, while acuity values above 2.4 log millilamberts could be described by a line with a slope of 0.140, which may substantiate the existence of two markedly different components.

## FACE PAGE FOR FIGURE 7

Figure 7. Same data as in Figure 6, replotted in terms of decimal visual acuity ( $1/\text{angular subtense of a single stripe}$ ) as a function of luminance.



## Discussion

Visual acuity (minimum-separable) for the Northern bluejay in the present study was not measured beyond 3.4 min. of arc, and therefore does not represent the "best" acuity this species may achieve for finer stimulus patterns. At the time of the study grating patterns subtending less than 3.4 min. of arc could not be used due to limitations in the level of luminance required for their use under the present experimental conditions. However, 3.4 min. of arc is within the same range of acuity values reported for other avian species, i.e., pigeon, 1.2-8.3 min. of arc (Blough, 1971, 1973; Nye, 1968); Passerine birds, 1.3-4.5 min. of arc (Donner, 1951); and owl, 4.0-5.0 min. of arc (Fite, 1972). It should be noted that comparison of the present study to other avian acuity studies (with the exception of the Great Horned Owl study) is somewhat difficult due to differences in procedure, luminance levels, criterion for threshold performance, and viewing conditions, i.e., binocular vs. monocular, foveal vs. non-foveal.

In an attempt to estimate the maximum resolving power for this species of jay, the data of Figure 3 were replotted in terms of log minutes of arc and certain assumptions were then made concerning the correspondences between the avian and human visual systems. It has been shown that a linear

relationship exists between log min. of arc and log luminance over a range from -2.0 to +1.5 log mL. for human observers (Graham, 1966). If it can be assumed that this same relationship holds for this species of jay and, in addition, that bluejay acuity mechanisms function like those of the human, then it appears possible to estimate the maximum resolving power for the bluejay in the present study. Figure 8 indicates that maximum visual acuity would be on the order of 0.190 log min. of arc (1.5 min. of arc) given the above assumptions. If this prediction is upheld, spatial resolution in this species of jay would be lower than expected considering the presence of an extremely well-defined fovea of the convexiclivate variety. However, it is questionable in the present study whether the birds were using foveal vision since observations made during testing indicated that all birds appeared to view the stimulus patterns binocularly. However, the bluejay appears to have more extensive eye movements than does the pigeon, and the centrally placed fovea may have been directed more frontally than is possible in the pigeon. One should consider Blough's (1973) results in relationship to the present study. Blough (1973) reported that pigeon acuity was on the order of 5.0-8.0 min. of arc for near targets when viewed binocularly, which was the case in the present study. When pigeons used their foveal region, acuity values ranged from 1.2-4.0 min.

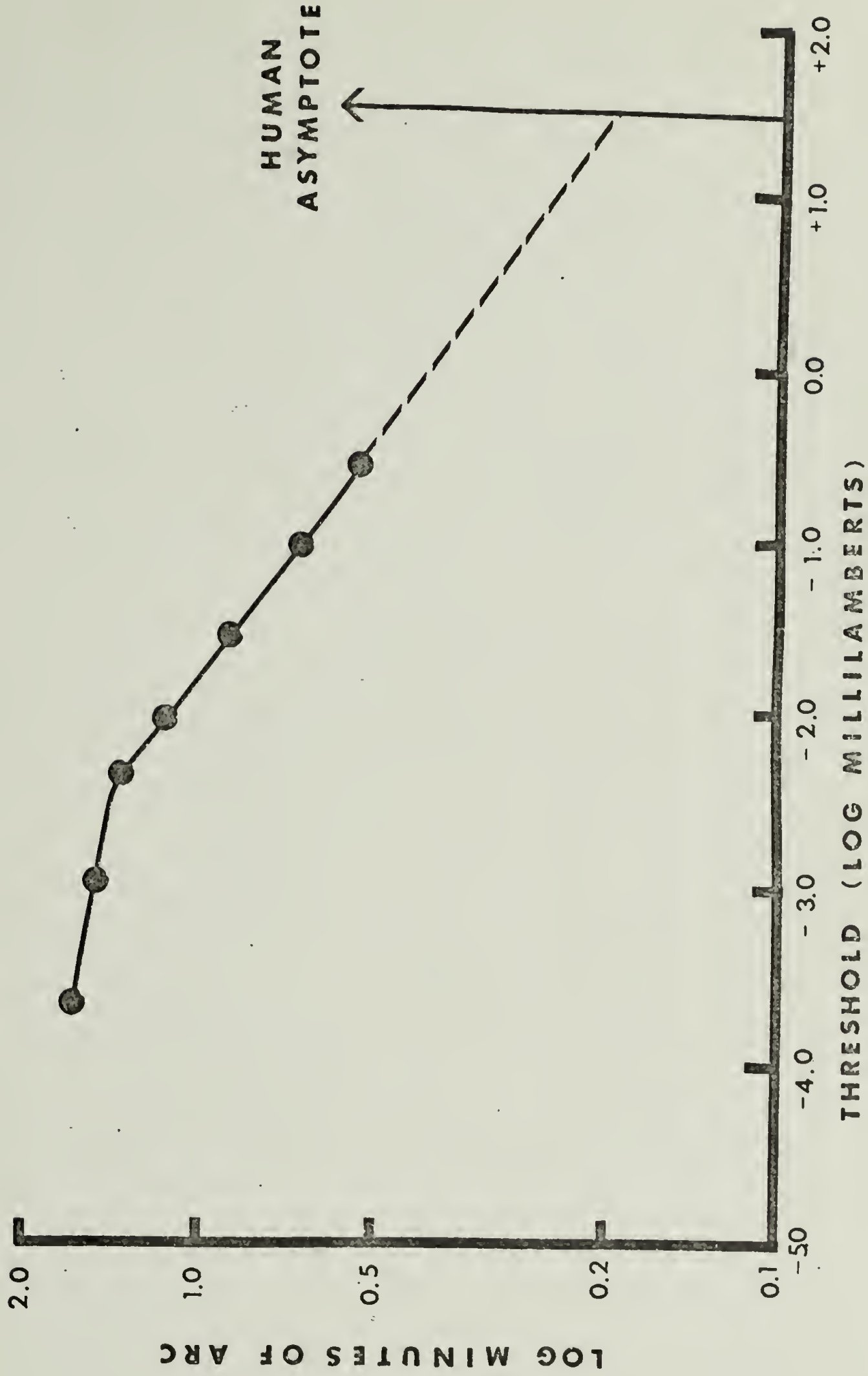


of arc, with an average of 2.6 min. of arc, which coincides with the values predicted in the present study. Furthermore, no area of increased ganglion cell concentration has been found in the superior temporal quadrant of the bluejay (Fite, personal communication), as exists in the pigeon (Galifret, 1968; Binggeli and Paule, 1969). If on the other hand, one accepts Pumphrey's (1948a,b) contention that diurnal avian species should possess acuity values nearly equal to man on the basis of cone density alone, then no area of increased ganglion cell concentration would be necessary to account for the results.

The estimated maximum resolving power for this species of jay, under the conditions of the present study, would be approximately 1.5 min. of arc, which is considerably better than the averaged 2.6 value obtained by Blough (1973), under monocular (foveal) viewing conditions for the pigeon. As was mentioned earlier, due to limitations in acquiring grating patterns subtending visual angles of less than 3.4 min. of arc, more accurate determinations of maximum resolving power could not be obtained. However, it seems quite possible that bluejay acuity (foveal) may exceed those values that have been reported for other avian species, but until a determination has been made for the effects of both target distance and the possibility of separate frontal vs. lateral viewing systems, it is merely conjecture.

## FACE PAGE FOR FIGURE 8

Figure 8. Same data as in Figure 6, replotted in terms of log minutes of arc to derive maximum acuity value. Dashed line represents hypothesized asymptotic performance.



If the estimated acuity threshold (1.5 min. of arc, Figure 8) is accurate given the above assumptions of linearity and functional similarity of visual acuity mechanisms between human and avian species, then Pumphrey's (1948a,b) suggestion of the functional significance of the convexiclivate fovea appears to gain support; i.e., the presence of a fovea of the convexiclivate variety may be involved in other than static spatial resolution. If the fovea is used for the detection and accurate fixation of moving objects as Pumphrey (1948a,b) suggests, then the acuity values reported for foveal viewing (2.6 min. of arc) in the pigeon (Blough, 1971) may be explained on the basis of Pumphrey's assumptions, i.e., one could expect a much higher degree of spatial resolution than has been found in the foveal region if the fovea's only function was to increase spatial resolution. Blough's (1973) lesion study lends further support to Pumphrey's (1948) hypothesis since lesions of the fovea produced no significant loss in acuity. However, it should be kept in mind that the fovea of the pigeon is shallow and somewhat degenerated. It is interesting to note that the maximum resolving power for a nocturnal predatory species of owl possessing a convexiclivate fovea was only on the order of 4-5 min. of arc (Fite, 1972). Such poor spatial resolution given the high degree of foveal differentiation may be explained on the basis of Pumphrey's contention that the fovea is used for the

detection and accurate fixation of a moving object instead of increasing static spatial acuity.

Visual acuity for this species of jay was dependent on luminance over a range of approximately four log units. The lowest luminance-acuity threshold obtained was on the order of 51 min. of arc at  $-4.0$  log millilamberts since the birds refused to work in the apparatus and were observed to roost at luminance levels below  $-4.0$  log millilamberts.

There were indications that two separate processes were contributing to the acuity-luminance function with a sharp discontinuity in the function occurring at  $-2.4$  log millilamberts (Figure 6). The most likely hypothesis concerning the observed discontinuity is that rods, with increased convergence ratios (receptors/ganglion cells) and lower thresholds are contributing to maximal spatial resolution at lower luminances. At luminances above  $-2.4$  log millilamberts, non-foveal cones may become functionally significant due to a lower convergence ratio and higher luminance thresholds.

The avian retina contains both rods and cones, with cones being more numerous in diurnal species. The actual number of rods in diurnal species varies with a tendency for an increase in the size of the receptor outer segment as well as an increased number of rod receptors towards the periphery of the retina. Therefore, it seems quite possible, given the viewing conditions of the present study, that the discontinuity observed in Figure 7 can be explained on the basis of a

rod-cone break. Further support for rod-cone mediation in the avian species comes from Blough's (1956) study on dark adaptation, where it was found that such a break did occur in the retina of the pigeon. In addition, data from human subjects indicate that such a break does occur at approximately  $-2.5 \log \text{ mL}$  (Graham, 1966), which is almost identical to the value reported in the present study,  $-2.4 \log \text{ mL}$ .

One means of verifying the existence of such a break in the present study would involve using lights of different spectral compositions which have been equated for equal scotopic effectiveness when compared to tungsten (white) illumination. On the basis of the differential sensitivity between rods and cones to various regions of the spectrum, i.e., rods being more sensitive in the short region (blue), with cones more sensitive in the long region (red), one would predict that if a rod-cone break were occurring the luminance-acuity threshold for a given grating pattern would vary depending upon both the population of receptors stimulated (rods or cones) and the spectral composition of the stimulating light. Therefore those points falling below  $-2.4 \log \text{ mL}$  in Figure 7 (thought to comprise the rod portion) would show lower luminance thresholds (increased sensitivity) to "blue light" while points above  $-2.4 \log \text{ mL}$  would be relatively less sensitive with illumination from the short wavelength region (blue) of the spectrum. If cones are responsible for the data points in Figure 4 above  $-2.4 \log \text{ mL}$

then one would predict a lower luminance threshold for each point with "red" light, while acuity-luminance thresholds below  $-2.4 \log \text{ mL}$  would be relatively less sensitive with illumination from the long wavelength region (red) of the spectrum. However, until such a determination has been made using lights of different spectral composition the exact location of a rod-cone break must remain inferential.

Comparison of the present study to other diurnal avian acuity studies is somewhat difficult due to methodological differences. However, it is possible to compare the present study dealing with the diurnal Cyanocitta cristata with the nocturnal predator Bubo virginianus. Fite (1972), using the same basic procedure as well as the same luminance levels found acuity-luminance thresholds for the Great Horned Owl. Figures 9 and 10 are a replot of that data in comparison to the results obtained in the present study. The most interesting comparison as regards Figure 9 concerns the one log unit difference in absolute sensitivity between the owl and bluejay, with the owl being much more sensitive at lower luminance levels. At approximately  $-1.6 \log \text{ millilamberts}$  both the owl and bluejay possess equal visual resolving capabilities. Above this value bluejays have superior resolving capabilities relative to luminance required for threshold performance. Below this value owls are superior in terms of luminance-efficiency for spatial resolution.

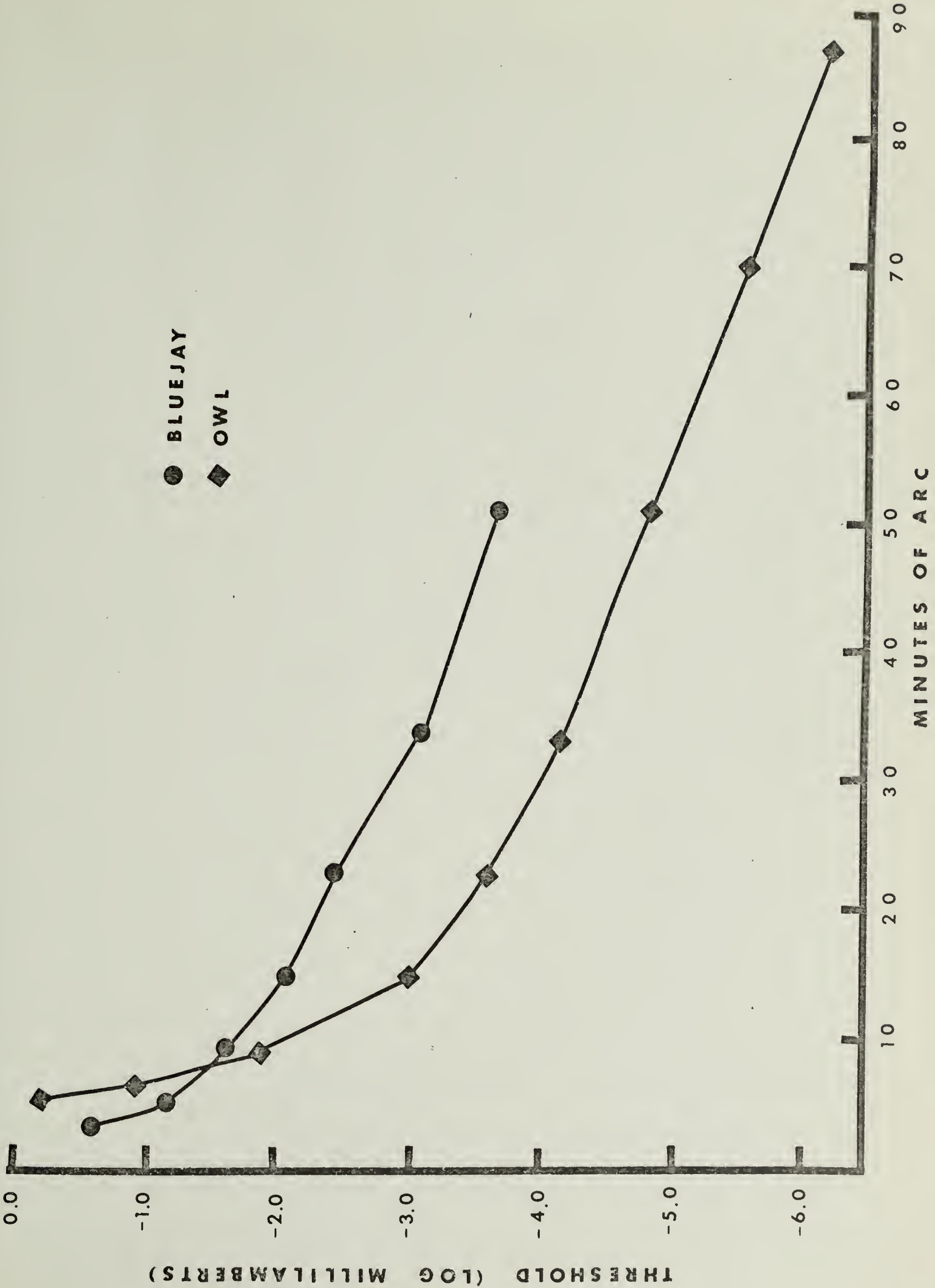
Replotting the data in Figure 9 in terms of decimal visual acuity as a function of threshold luminance provided the data points of Figure 10. These points could be fitted with two regression lines that differed markedly in slope, with acuity values below  $-3.5$  log millilamberts falling on a line with slope of  $0.010$ , while values above  $-3.5$  fell on a line with a slope of  $0.049$  (Fite, 1972). The bluejays had slopes of  $0.015$  and  $0.140$  respectively for the two regression lines, with the break occurring at  $-2.4$  log millilamberts. In comparison to data obtained by Sloan (1968) for human subjects viewing test objects (Landolt rings)  $5^\circ$  in the nasal field, the regression line is almost identical to that obtained for the bluejay at the higher levels of luminance, i.e.,  $0.140$  (bluejay) as compared to  $0.130$  (human). In addition, the ratio between regression line slopes for  $5^\circ$  nasal vs. foveal acuity is almost identical to that obtained in the present study for the lower vs. higher luminances.

The main difference between the two species is the more rapid improvement in visual resolving power with increases in luminance for the bluejay as compared to the owl. This difference between the two species may be based on differences in receptor populations, i.e., rod vs. cones as well as retinal convergence ratios (receptors/ganglion cells). The owl, being a nocturnal predator, has a much higher concentration of rods per unit retinal area, while the diurnal



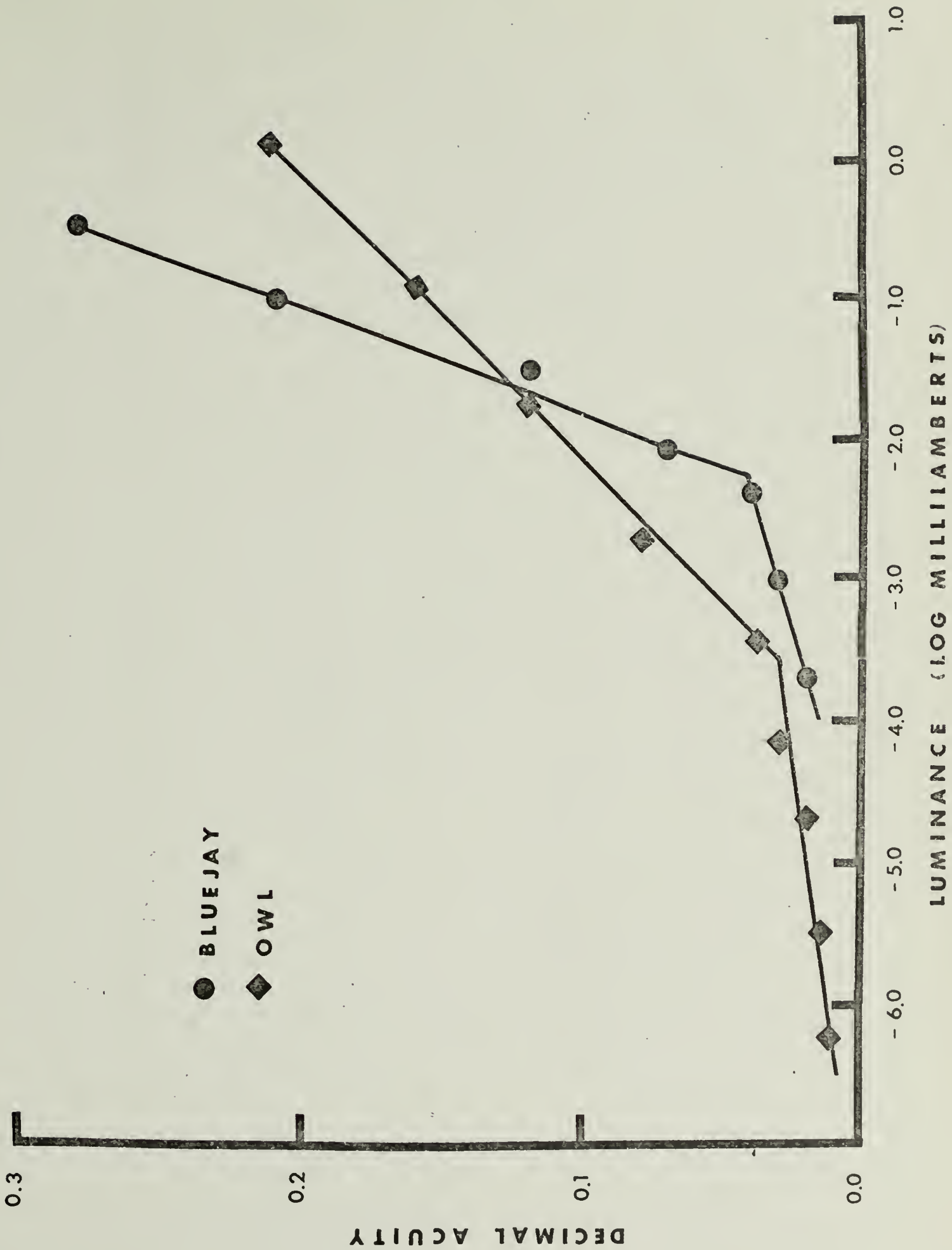
FACE PAGE FOR FIGURE 9

Figure 9. Comparison of luminance-acuity threshold functions between diurnal and nocturnal avian species. Replotted from Fite (1972).



## FACE PAGE FOR FIGURE 10

Figure 10. Same data as in Figure 9, replotted in terms of decimal visual acuity values ( $1/\text{angular subtense}$ ) as a function of luminance.



bluejay should have a much higher cone population per unit retinal area. Therefore, the marked increase in visual acuity with increasing luminance levels for the bluejay seems to be based on characteristics associated with a relatively cone-rich retina. The owl, possessing a more rod-dominated retina, should be expected to benefit less with increasing luminance levels since the overall convergence ratio is much higher in the owl as compared to the jay (Fite and Rosenfield-Wessels, 1974). However, the owl does possess a substantial number of cones, so one would expect an increase in visual acuity with increasing luminance levels once the cone thresholds had been reached. However this increase occurs at a much slower rate of change as compared with the bluejay and may be due to either differences in photopigment; i.e, photochemical characteristics; pigment density, (total amount of pigment per receptor) or both, such that higher levels of luminance are required for further increases in quantum efficiency. In addition, retinal convergence ratios (receptors/ganglion cells) vary between the two species; therefore, spatial resolution would not be expected to be as acute.

It is interesting to note that the discontinuity observed in Figure 10 for the bluejay at  $-2.4 \log \text{ mL}$  corresponds almost exactly to the reported rod-cone break in humans ( $-2.5 \log \text{ mL}$ ). The discontinuity for the owl occurs at  $-3.5 \log \text{ mL}$  which is well below the human rod-cone break.

One possible explanation for the difference between these two avian species as regards the possibility of an avian rod-cone break concerns the possibility that the photopigment associated with the owl cones may be more rod-like in its characteristics as compared to the bluejay (Fite, 1972). The bluejay, being a diurnal species, may possess photopigment whose characteristics are almost identical to those found in humans. The owl, a predominantly nocturnal species, may require a photopigment whose characteristics are similar to rhodopsin for both the rods and cones. Therefore the cone portion could be expected to be somewhat lower than observed for both the bluejay and human since they may be serving a more rod-like function in terms of luminance efficiency for spatial resolution.

Both the bluejay and Great Horned Owl seem well-adapted for their respective environments, one predominantly diurnal and the other predominantly nocturnal. Each can function to a remarkable degree given less than optimal conditions, i.e., radical changes in luminance levels may either call into play different receptor populations or change the balance between those receptor populations whose characteristics provide some degree of spatial vision for the changing conditions. At luminance values below  $-4.0$  log millilamberts, jays either roost or are totally inactive while the owl appears to be in the peak of its activity cycle (Figure 10).

One word of caution about the comparisons made between these two species concerns the viewing conditions under which the acuity-luminance functions were derived. The owl data was obtained under binocular (foveal) conditions based upon observations made during testing as well as anatomical evidence that indicates that the fovea of this species is located in the superior temporal quadrant and subserves the frontal visual field. At no time were the owls observed viewing monocularly (Fite, 1972). The data reported in the present study appeared to have been obtained under binocular conditions based upon observations made during testing although it cannot be said conclusively that the jays were not viewing the stimuli monocularly. Anatomical evidence indicates that the fovea of this species of jay is centrally located but the existence of extensive convergent eye movements may have enabled foveal viewing.

#### SUMMARY

The present experiment was performed to determine the behavioral correlates of visual acuity in the Northern bluejay (Cyanocitta cristata). Resolution for this species of jay was 3.4 min. of arc between .00-1.0 log millilamberts under binocular conditions. Of major importance is the prediction that maximal acuity for this avian species may be less than acuity values reported for humans under binocular (foveal) conditions and comparable conditions of illumination.

Furthermore, Pumphrey's (1948) contention that birds may possess acuity values nearly equal to man on the basis of cell density alone appears to have some experimental support, although the role of foveal vision could not be assessed in the present study. In addition, it was shown that the bluejay possesses superior resolving power as compared to the owl above  $-1.6$  log millilamberts. Before any conclusive statements can be made concerning the role of the avian fovea, a thorough determination of the maximum resolving power for both the foveal and non-foveal portions of the avian visual system should be made. The bluejay appears to be an excellent choice for such behavioral-physiological studies.



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