

A PSYCHOPHYSICAL STUDY OF ECHOLOCATION  
IN THE BLINDED RAT

by

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## INTRODUCTION

The phenomenon of echolocation is a relatively recently discovered sensory mode. It has generated much interest because of its unusual nature. In some animals the phenomenon seems to be a primary sensory mode. Animals such as the bat and the porpoise employ echo ranging in their search for food and in the avoidance of obstacles (Griffin, 1950; Kellogg, 1959; Kellogg & Kohler, 1952; Kellogg, Kohler, & Morris, 1953). Also the role of ultrasonic sounds in maternal behavior of mice has been investigated (Noirot, 1964). Other animals have recently been shown to exhibit this sensory ability as a secondary sensory mode. There is evidence that blind human beings are able to detect the presence of obstacles by means of auditory cues (Supa, Cotzin, & Dallenbach, 1944) and Kellogg (1962) and Rice & Feinstein (1965) have provided quantitative evidence concerning this capacity in human subjects. Recently blinded rats have been shown to detect obstacles by means of self produced auditory cues of relatively low frequency (Riley & Rosenzweig, 1957; Rosenzweig, Krech, & Riley, 1955).

The bulk of research on echolocation has centered around the nature of the physical properties of this auditory phenomenon. A comparison of the existing evidence on all species that have been shown to possess the ability to echolocate may provide important clues as to the

essential physical requirements of the echolocation phenomenon as well as the efficiency with which each species can perform this task.

Galambos & Griffin (1942) found that bats emitted short bursts of high frequency sound (30 to 70 kc.) and that these sounds were necessary for the "obstacle sense" of the bat to function properly. When either emittance or reception of these sounds were blocked, the bat became helpless. They also found evidence of relatively low frequency (7 to 15 kc.) sound pulses in the bat which were described as clicks. The band of frequencies in these clicks resembled white noise.

In work with the porpoise, Kellogg, Kohler, & Morris (1953) discovered two distinct types of sounds that are produced by this animal. The first was termed a whistle. It was of .5 sec. duration and contained a melody of increasing pitches. It usually started with frequencies of approximately 7 kc. and ended with frequencies of about 15 kc. The overtones were not usually found to be above 20 kc. The second type of sound found to be emitted by the porpoise was a click. These were emitted at a rapid rate and were by far the most common of the two. The dominant frequencies of these clicks were in the sonic range. These clicks, as in the bat, have a frequency range that resembles white noise. Kellogg & Kohler (1952) have shown that the porpoise is capable of responding to sounds as

high as 80 kc.

The laboratory rat seems to possess some of the same characteristics as the bat and the porpoise. Anderson (1954) has shown that rats produce sounds of 19 kc. and 29 kc. when frightened and produce short snuffing sounds during daily cage activity with overtones as high as 80 kc. Anderson stated that the prolonged duration of these sounds ruled out the possibility that they are merely ultrasonic components of activity, and was able to record the sound when the rat was standing completely still. The rat is most sensitive to frequencies of about 20 kc. and the audible range extends somewhere beyond 40 kc. (Gould & Morgan, 1941).

The ability of blind human beings to echolocate also has been demonstrated (Supa, Cotzin, & Dallenbach, 1944; Cooper, 1940; Kellogg, 1962; and Rice & Feinstein, 1965). However, the auditory mechanism of the human being does not possess any capabilities in the ultrasonic range. The maximum hearing range for the human is 20 kc. This would indicate that ultrasonic capabilities are not necessary for echolocation. Griffin (1953) has shown that the *Steatornis* (bird) apparently also uses low frequency sounds in echolocation.

In view of these considerations, the exact nature of the cues that are utilized by the rat cannot be determined at this time. Work with blind human beings (Cooper, 1950)

has shown that they are able to utilize a variety of cues to detect barriers, with no one individual utilizing a specific cue all the time, or even in the same discrimination situation. The rat also has a variety of self-produced cues available in the discrimination situation, but there is no evidence as to which are utilized.

Relatively recent work with blinded rats has shown, however, that they are able to detect obstacles by means of self-produced auditory cues (Riley & Rosenzweig, 1957). Dashiell (1959) has obtained evidence that blinded rats behave no differently than those with normal vision in a spatial orientation situation. Incidental echolocation evidence was found in this situation when obstacles were introduced into the maze. Neither the sighted nor the blinded animals showed any disorientation when new interrupting walls were placed in the maze.

There are many unanswered questions concerning the echolocation phenomenon. On the basis of existing evidence it can be said that the physical characteristics of the sounds that are utilized do not fall into any one set pattern. The quantitative evidence that exists has not dealt sufficiently with the rat. The present experiments are an attempt to go beyond the existing data for the rat by determining the difference threshold (DL) for the discrimination of distance. Such quantification might eventually provide the basis for interspecies comparisons

in ability to echolocate. Experiment I utilized a modified method of limits for the DL determination. Following this, subjects (S) were studied under a white noise condition designed to mask the cues in the discrimination in order to provide corroborative evidence as to whether or not the discrimination was based on sonic cues. The second study employed a constant stimulus difference threshold procedure for the DL determination. A period of study with black and white barriers followed in order to test the possibility of infra-red heat cues being responsible for the discrimination.

## EXPERIMENT I

### Method

#### Subjects

Subjects (N=4 littermates; 2 males and 2 females) were pigmented rats of the Long-Evans Strain. They were blinded by enucleation at 15 days of age, and were weaned at 25 days of age. A 22 hour food deprivation schedule was begun two weeks prior to training, which was begun at 50 days of age, and was maintained throughout the experiment.

#### Apparatus

The S's were trained and tested on a two choice elevated maze patterned after that used by Riley & Rosenzweig (1957). Runways 5.1 cm wide and 75.5 cm long

formed a square, with the starting and goal box located on opposite corners. The starting box was separated from each runway by a 1.3 cm gap. A wooden barrier 15.2 cm square was suspended independently of the runway over each runway. The distance of the barrier from the choice point could be varied, and each barrier could be raised or lowered, thus allowing S passage along the runway or blocking it.

### Procedure

On each trial S was released from the starting box and allowed to choose one of the runways. Incorrect choices were those in which all four feet were placed on the incorrect runway. Following an incorrect choice, S's were picked up and returned to the start box. Following each correct choice, S was allowed to run to the goal box and to eat for 15 seconds before being picked up and returned to the starting box. The inter-trial interval was 45-60 seconds. Whenever it was necessary to move a barrier, both were moved in order to control for auditory cues. During all phases of experimentation the incorrect runway was blocked by a barrier 21.6 cm from the choice point. Each S received 20 trials per day, with the position (right or left) of the negative barrier being determined by one of three 20-trial Gellerman sequences. The particular sequence employed on any one day was selected at random. The experiment was divided into three phases as follows:

First, the S's were trained to choose the open runway



(i.e., to detect and avoid the barrier). The criterion was an average of 85 percent correct choices for five consecutive days with performance on no one day falling below 80 percent correct choices.

Second, in order to determine the difference thresholds, a barrier was introduced over the positive runway at 75.5 cm from the choice point, and moved 7.6 cm closer each day until performance approached the chance level. After each correct choice the experimenter (E) raised the barrier to allow S to run to the goal box. The DL was defined as that point at which 75 percent of the trials were correct.

Third, following the threshold determination, all S's lived for seven days in a room with continuous white noise, 20 db above ambient level.<sup>1</sup> This was done in order to minimize any disturbing effects of the initial introduction of noise in the test situation. They were then retrained to criterion. Next, a loudspeaker was placed in the center of the maze and white noise was directed at the choice point, with the negative barrier at 21.6 cm from the choice point. The noise was introduced at 5 db above ambient level and increases 5 db each day until performance approached chance level. The S's were then retested with no white noise present.

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<sup>1</sup>The intensities of sounds were measured by a General Radio Company Model 1551-B sound level meter.

## Results

Fig. 1 indicates the mean performance both for individuals and for all S's combined as a function of difference in distance between positive and negative barriers. The average DL was 23.3 cm with individual DL's varying between 15.5 cm and 31.0 cm.

Performance under the white noise condition is indicated in Fig. 2. Noise 20 db above ambient level was sufficient to reduce performance to approximately chance level (performance 70% is nonsignificant for  $\alpha = .05$ ). When retested under ambient noise, however, performance returned to pre-noise levels.

## EXPERIMENT II

The shape of the psychophysical function found in Experiment I is not that customarily found in psychophysical experimentation. The curve does not drop as sharply as the usual ogive curve. Several interesting possibilities for additional research are suggested from the data. The method of quantification employed in Experiment I contained only descending trials of differential distances, and the departure from the expected could have resulted from procedural artifacts due to descending orders. Also the variance of each individual S might have been due to the failure to give adequate discrimination training for each S to reach a stable level

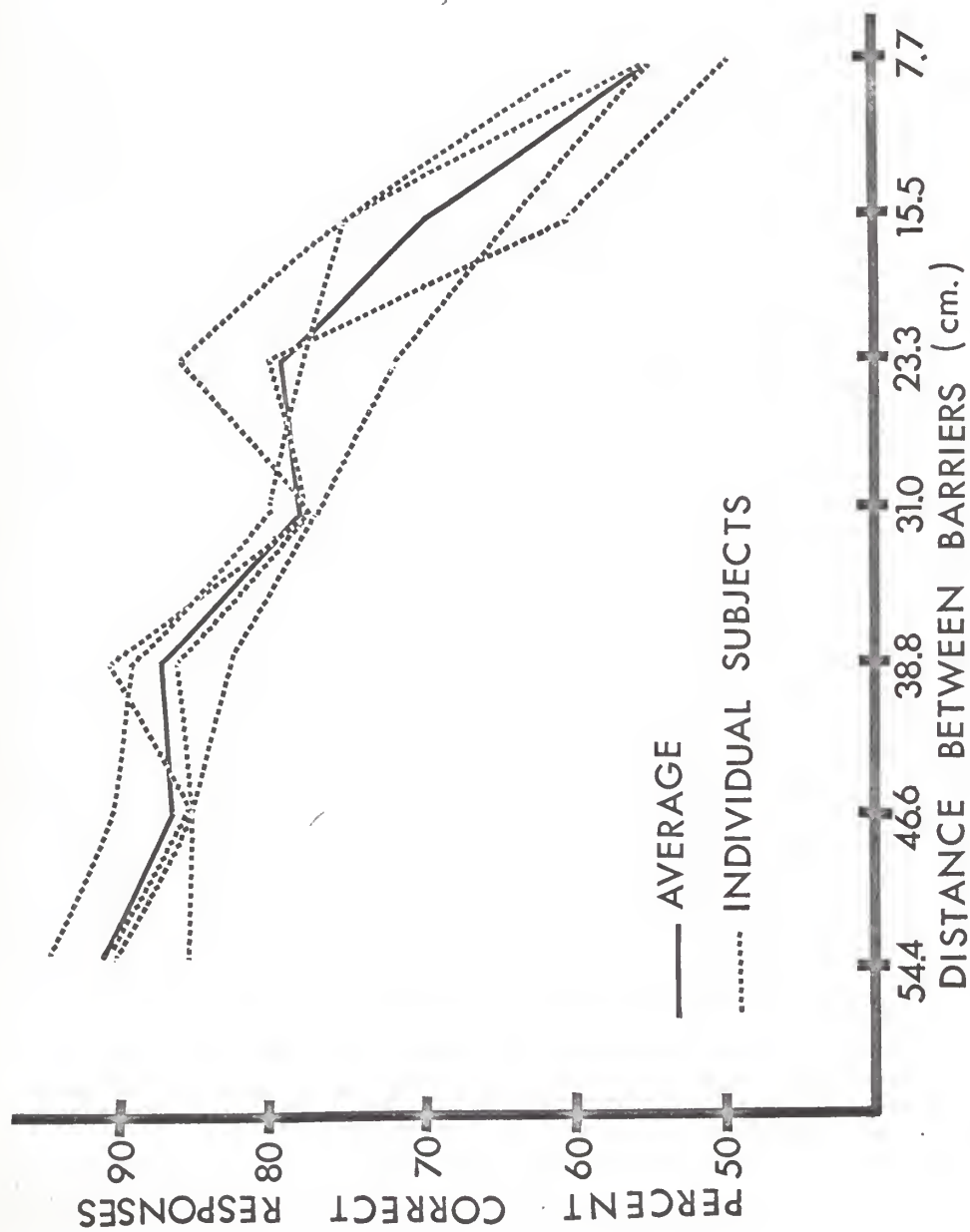


Fig. 1. Mean performance for individuals and for all rats combined as a function of distance between positive and negative barriers in Experiment I.

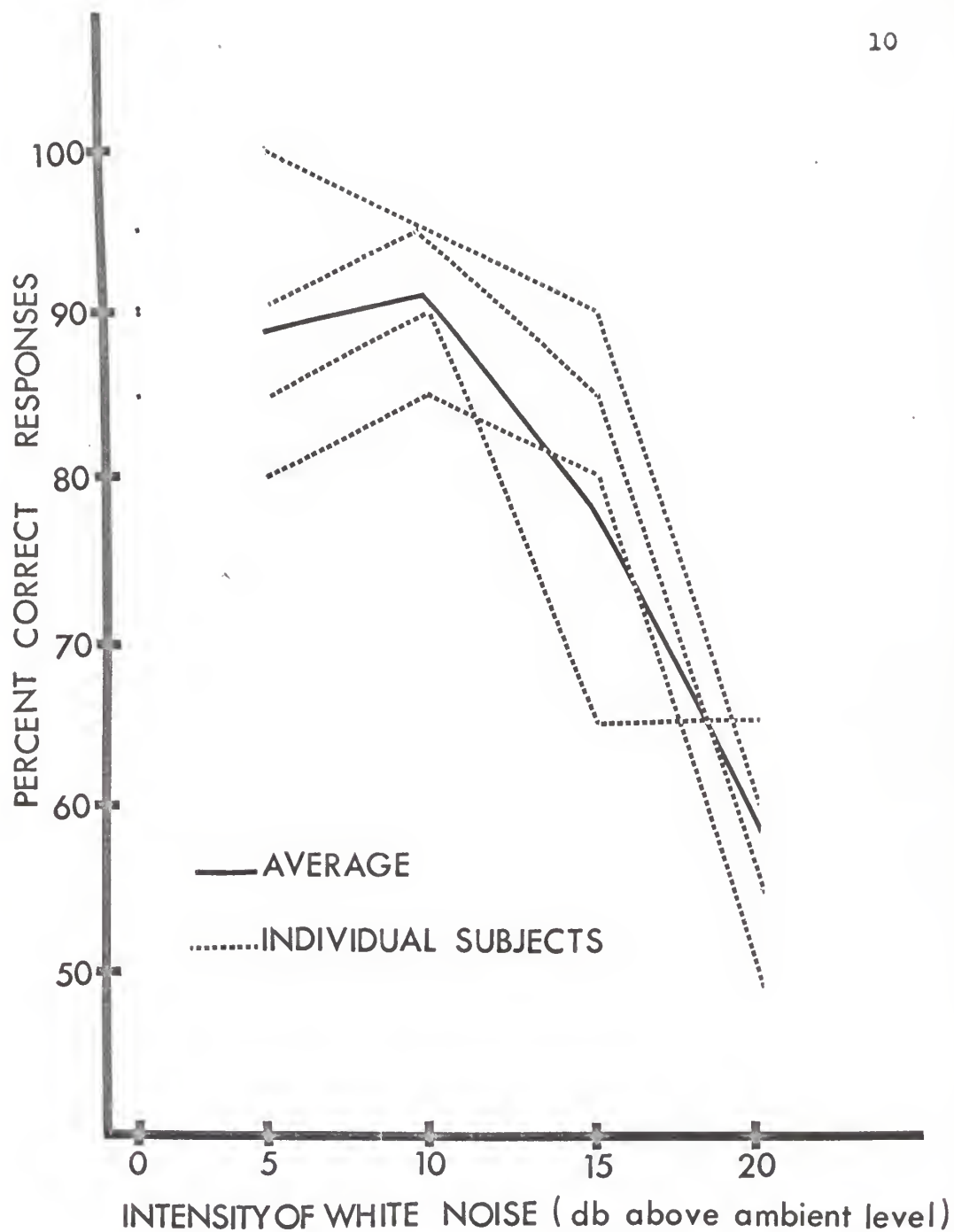


Fig. 2. Mean performance for individuals and for all rats combined as a function of white noise intensity.

in the performance of the tasks. Consequently, further training at the smaller distances could have resulted in improved performance, since the S's may have still been learning a new task. Experiment II was designed to explore these possibilities.

## Method

### Subjects

The seven S's were male albino rats of the Sprague Dawley strain obtained from Dan Rolfsmeyer & Son, Madison, Wisconsin. They were blinded by enucleation at 60 days of age. A 22 hour food deprivation schedule was begun two weeks prior to training, which was begun at 170 days of age, and was maintained throughout the rest of the experiment.

### Apparatus

The S's were trained and tested on a two-choice elevated maze. Runways were 5.1 cm wide and 75.5 cm long with identical goal boxes at each end. The starting platform was separated from each runway by a 1.3 cm gap. The 15.2 cm square barrier was suspended and operated as described in Experiment I. The modifications of goal boxes and starting apparatus were made to allow E to remain in a stationary position during the experimental session and thus reduce the possibility of additional cues. The change from a start box to a platform also was designed

to cause the animals to make more attempts to run the maze early in training.

### Procedure

On each trial S was placed on the starting platform and allowed to move onto one of the runways. A choice was scored as incorrect when both front feet were placed on the incorrect runway. Following each incorrect choice S was removed from the maze. Following each correct choice S was allowed to run to the goal box and to consume three 50 mg Noyes standard Skinner box reward pellets. The animal was then removed from the maze and the barriers were set for the next trial. Whenever it was necessary to move a barrier, both were moved in order to control for auditory cues. Both goal boxes contained equal amounts of food at all times to eliminate olfactory cues. The inter-trial interval was 50-75 seconds. During all phases of the experiment the incorrect runway was blocked by a barrier 21.6 cm from the choice point. The position (right or left) of the negative barrier was determined by one of four 10-trial Gellerman sequences, each of which was presented every fourth day. The experiment was divided into four phases as follows:

First, training to choose the open runway was identical to the first phase of Experiment I.

Second, a second barrier was introduced over the positive runway at 52.0 cm from the choice point and S's

were given five consecutive days of training on this task.

Third, the difference threshold was determined by the method of constant stimuli differences over a twelve day period. The four correct barrier positions of 52.0 cm, 44.5 cm, 36.8 cm, and 29.2 cm were randomly presented five times on each of twelve days for a total of 60 trials per barrier position. After each correct choice E raised the barrier to allow the rat to reach the goal box. The DL was defined as that point at which the rat was correct on 75 percent of the trials.

Finally, following the threshold determination a black and a white barrier 15.2 cm square was placed equidistant from the choice point at 44.5 cm. Each animal received 10 trials per day for two consecutive days to test for the possible utilization of infra-red heat cues in the discrimination.

### Results

The principle results of Experiment II are given in Fig. 3, which shows the mean performance for individuals and for all S's combined as a function of difference in distance between positive and negative barriers. The average DL was 24.3 cm with individual DL's varying from 22.8 cm to 25.1 cm.

Table 1 shows the percentage of responses to the black barrier in the final phase of Experiment II.

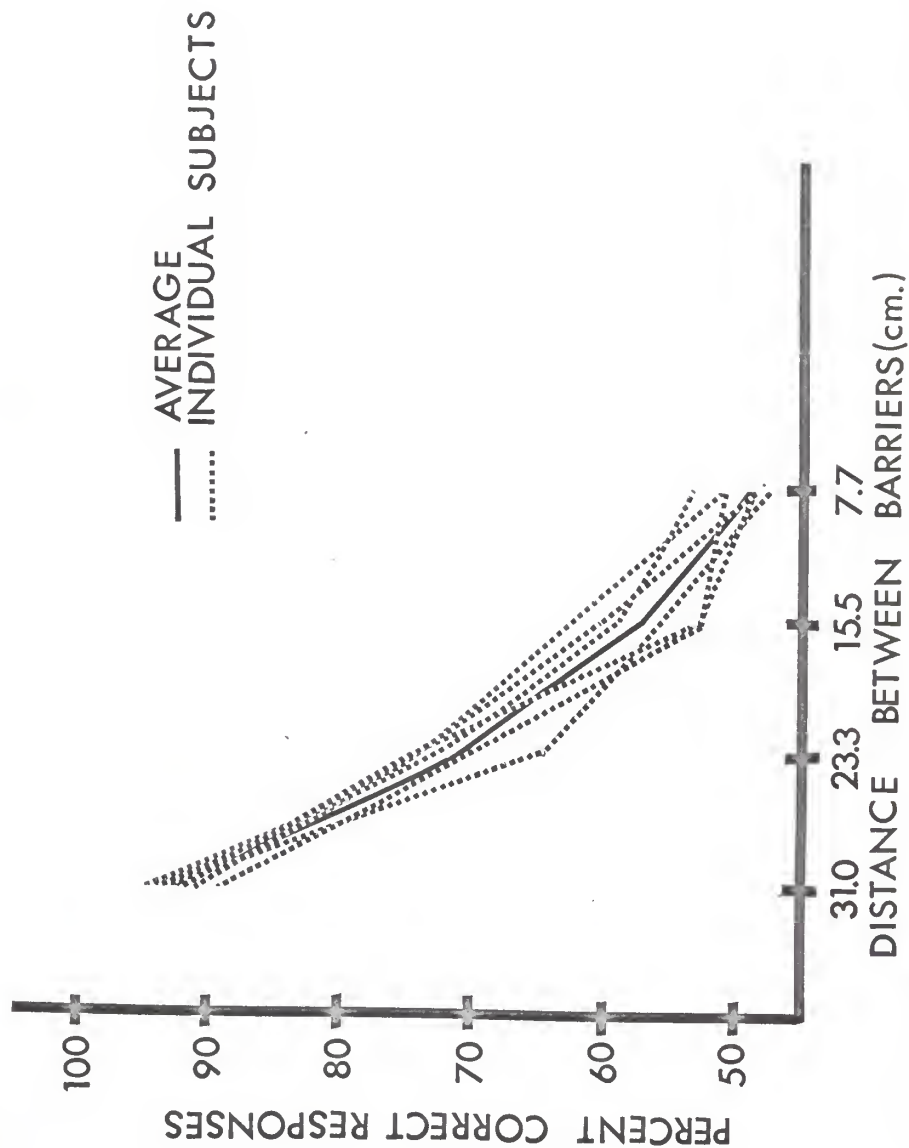


Fig. 3. Mean performance for individuals and for all rats combined as a function of distance between positive and negative barriers in Experiment II.



Table 1  
Number of times the black barrier was  
chosen by individual subjects.

Subject Number	Day 1	Day 2	Average
1	50%	44%	47%
2	45%	50%	47.5%
3	54%	54%	54%
4	55%	50%	52.5%
5	45%	50%	47.5%
6	55%	40%	47.5%
7	54%	60%	57%
Average	52.6%	56.9%	50.1%

The average was found to be 50.1 percent for all animals, thus indicating the possibility that infra-red heat cues as measured in this experiment do not enter into the discrimination.

### DISCUSSION

It now seems rather certain that obstacle discrimination in the blinded rat is based on auditory cues. The evidence of Riley & Rosenzweig (1957) and Dashiell (1959) indicates that this discrimination is auditory and based on self-produced cues. The decrement in performance under the white noise condition of Experiment I also indicates that

the S's were indeed using auditory cues in detecting and discriminating the barriers. However, we have no concrete evidence as to the exact nature of these cues. The S's produced a variety of sounds audible to the E, any of which might have been utilized in the discrimination.

Quantitative evidence on the abilities of various species may provide important clues as to the nature of the physical properties of the auditory cues used in the echolocation phenomenon. Kellogg (1962) has shown that size discrimination is possible in the blind human being and reports a threshold fraction ratio of about  $1/4$ . Rice & Feinstein (1965) report that this ratio of the size of the threshold target to the standard was relatively constant, regardless of the distance.

The present experiments have added quantitative evidence concerning the unusual sensory mode of echolocation in blinded rats. No conclusions or comparisons can be made at the present time on the basis of physical properties of the auditory cues or inter-species efficiency in ability to echolocate. Further systematic research is necessary to accomplish these aims.

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## ABSTRACT

The difference threshold for detection of barriers at different distances using a modified method of limits was found, for 4 blinded rats, to be 23.3 cm when the standard was 21.6 cm distant from the animal. White noise 20 db above ambient level reduced discrimination performance to chance, indicating that auditory cues were involved in the discrimination.

A second determination utilizing the method of constant stimuli confirmed the difference threshold to be 23.3 cm and reduced individual subject variation by further training. Evidence with a black and a white barrier indicated the possibility that infra-red heat cues as measured in this experiment do not enter into the discrimination.