

*CONTROL OF RESPONDING BY THE LOCATION OF AN
AUDITORY STIMULUS: ROLE OF RISE TIME
OF THE STIMULUS¹*

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The control of responding by the location of tone bursts of 0.2- or 50-msec rise time was investigated in three albino rats. The apparatus consisted of an enclosure with two levers, two loudspeakers (in different locations), and a dipper feeder. The animal was exposed to tone bursts from either one or the other of the two speakers, and the speaker through which the tone bursts were delivered on any particular trial alternated in an irregular manner. Responses on one lever were reinforced with food in the presence of tone bursts from one speaker; responses on the second lever were reinforced with food in the presence of tone bursts from the second speaker. Responding came under the control of the location of 4-kHz tone bursts of 0.2-msec rise time within the first session. At this rise time, animals maintained a stable level of correct responding of greater than 95%. When the rise time was increased to 50 msec the percentage of correct responding fell to an average of 80 to 85%. It was concluded that location of an auditory stimulus is a powerful controller of responding in rats and that the degree of control is dependent upon rise time.

The location of a source of sound in the azimuth of an animal can be used to control responding of that animal (Neff, Fisher, Diamond, and Yela, 1965). Control of responding in the case of sounds of short duration depends upon similarities and differences between the sounds reaching the two ears (Neff, 1962). This implies that at one or more sites in the nervous system there are nerve cells innervated by the cochlea of both sides. Several anatomical considerations, summarized below, suggest that the first site at which this occurs is the superior olivary complex.

In mammals, the central end of the acoustic nerve terminates in the cochlear nucleus. Axons arising from nerve cells in the cochlear nucleus terminate (in part) in the three major nuclei of the superior olivary complex (Harrison and Irving, 1964; Harrison and Irving, 1966a; Harrison and Irving, 1966b; Warr, 1966). The lateral superior olivary nucleus (a nucleus of the complex) receives direct connections from the cochlear nucleus of the same side and receives indirect connections from the contralateral cochlear nucleus via the medial

nucleus of the trapezoid body (a second nucleus of the complex) (Harrison and Irving, 1966a; Harrison and Warr, 1962; Warr, 1966). Thus, the lateral superior olivary nucleus is innervated by the cochlea of both sides, one necessary condition for this nucleus to be involved in control of responding by the location of a sound. Recent physiological work has further strengthened the suggestion that this nucleus may be involved in localization of sounds by showing that nerve cells of the nucleus are fired by sound to the ipsilateral ear and inhibited by sound to the contralateral ear (Boudreau and Tsuchitani, 1968).

Comparative anatomical studies of the mammalian superior olivary complex have shown that in echolocating mammals (*Microchiroptera*, Griffin, 1958; *Cetacea*, Turner and Norris, 1966) the lateral superior olivary nucleus is exceedingly large (Harrison and Irving, 1966c; Irving and Harrison, 1967). This finding supports the suggestion that the lateral superior olive may be involved in the control of responding by the location of a sound.

Other characteristics of the structure of the superior olivary complex suggest that control of responding by location of sounds may be a dominant attribute of audition. The lateral superior olive and the medial nucleus of the trapezoid body taken together comprise a substantial portion of the superior olivary complex. Thus, a substantial portion of the

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complex is concerned with the bilateral innervation of the nerve cells of the lateral superior olive. The involvement of so much of the auditory system, at this level, to bilateral innervation suggests that location may be a dominant attribute of hearing.

On the basis of these considerations, preliminary behavioral experiments were carried out to determine whether the location of a sound was a potent discriminative stimulus. The animal's head was not fixed in position relative to the stimuli. The auditory system has evolved in animals that are free to move in their respective environments. This free movement means that all possible relations will exist between the positions of the animal's head and the sounds, and it is under these conditions that a localization mechanism (if it is to be effective) must operate.

Stimuli of short duration were used in these experiments because many auditory stimuli present in the animal's natural environment are of short duration (a snapping twig, for example). The control of responding by the location of such stimuli depends upon the differential stimulation of the two ears as described above. Sustained stimuli, such as a continuous buzzer, for example, can be localized in cats with only a single functioning ear (Neff and Diamond, 1958) and are thus not suitable for experiments investigating binaural hearing.

The preliminary experiments were carried out in a box with a lever mounted on each side of a liquid feeder. A relay was suspended from the ceiling of the room near each lever and was visually shielded from the animal. Responses on one lever were reinforced when the relay adjacent to that lever was activated to give a train of clicks; responses on the other lever were reinforced when its adjacent relay was activated. Under these conditions rats quickly reached a level of 90 to 100% correct responses. However, when tone bursts produced from transistor radio earphones were substituted for the relay clicks, only a 60 to 70% correct response level was reached. These experiments indicated that the location of sounds is a dominant aspect of audition, at least for certain classes of auditory stimuli.

The relay clicks and earphone tone bursts differ in a number of ways. One difference is the kind of transients associated with the two kinds of stimuli. The tone bursts had a rise

time in excess of 50 msec, while the relay produced sounds that had more rapid changes in intensity. This experiment investigated the effect of the rise time of an acoustic stimulus upon the degree to which responding can be brought under the control of the azimuth of the stimulus.

METHOD

Subjects

Three male albino rats, approximately 300 days old, Sprague-Dawley strain, were fed sufficient food, once per day, to reduce body weight to approximately 75% of free-feeding weight. During the experiment, body weight was maintained at this level. Water was available at all times. It has been found that animals with middle ear infection are not suitable subjects.

Apparatus

The experimental chamber was a wire mesh enclosure, 8 in. by 11 in. by 8 in. high. Mounted in the front wall were two Gerbrands rat levers, 4 in. apart and 3 in. above the floor. A Gerbrands liquid food dispenser was mounted between the two levers. A Gerbrands pigeon key was mounted in the middle of the back wall, 3 in. above the floor. The animal enclosure was placed on a table in the middle of a room 7 ft by 8 ft by 9 ft high. The walls, ceiling, and door of the room were covered with acoustic tile. Two loudspeakers (University Sphericon type T 202) were placed on the table on either side of the animal enclosure as shown in Fig. 1. The speakers were 18 in.

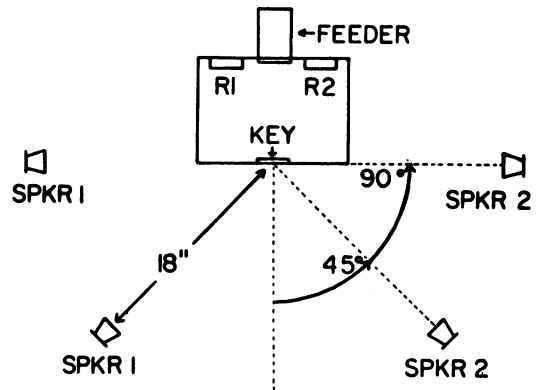


Fig. 1. Schematic diagram of apparatus (from above). Speakers were situated in the 90° position for parts of the experiment and in the 45° position for other parts.

from the midpoint of the key. Speaker position could be varied at any angle relative to the key. The positions marked 90° and 45° in Fig. 1 were used in this experiment. A house-light (10-w bulb), located on top of the wire mesh enclosure, was on continuously except during a blackout.

Standard operant conditioning equipment was used to schedule the experimental procedures. Cumulative records were taken of responding on the two levers.

The stimulus was a tone burst of 0.2 sec occurring at the rate of two bursts per second. The electrical signal that produced the tone bursts was generated by a General Radio oscillator (type 1210C), connected to a Grason-Stadler electronic switch (type 829C) and connected from there to a General Radio amplifier (type 1206B). The output of the amplifier was switched to one or the other of the two loudspeakers by the scheduling equipment. The electronic switch was appropriately operated by the equipment to produce the tone bursts described above.

Acoustic tone bursts in the animal enclosure produced by this equipment were examined with a 0.5-in. condenser microphone (Brüel and Kjaer, type 4133) connected to an oscilloscope via a wide band preamplifier (Tektronix type 122). It was found that acoustic tone bursts having a rise time of from 0.2 to 100 msec and a frequency range of 4 kHz to 40 kHz could be produced in the animal's enclosure. Two 3-msec, 10-kHz tone bursts, with different rise times, are shown in Fig. 2.

In the present experiment tone bursts of 4 kHz and 10 kHz and of various rise times were used. These were set at an intensity of 75 db (reference pressure 0.0002 microbar) using a General Radio sound level meter (type 1551C), with the microphone on an extension lead and placed in the position of the animal's head adjacent to the key.

Procedure

The basic procedure developed a discrimination in which the stimulus was produced by responding on the key. The essentials of the procedure are illustrated in Fig. 3, and details were as follows.

Responding on the key produced tone bursts from either the left or the right speaker on a fixed-interval schedule of 30 sec. The order of selection of either the left (L) or the right (R)

speaker was RLRRLRLLR in all conditions except those noted below. Each presentation of the stimulus consisted of two tone bursts. The first lever response after onset of the stimulus, if the response occurred within 7.5 sec of the onset, was either reinforced (if correct) or followed by a blackout (if incorrect), and started the fixed-interval schedule timer. If a lever response did not occur within 7.5 sec of stimulus onset, the fixed-interval timer started at the end of this interval.

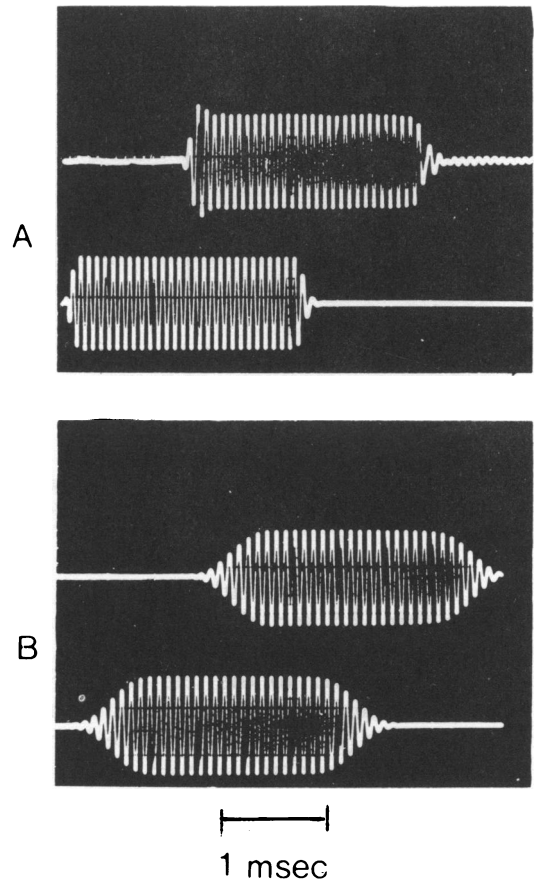


Fig. 2. A. 3-msec, 10-kHz tone burst, rise time approximately 0.2 msec. Lower tracing in A shows electrical signal delivered to loudspeaker; upper tracing shows the resulting acoustic signal as recorded via microphone. The microphone faced the speaker at a distance of 16 in. The time difference between the onsets of the electrical and acoustic signals represents the time taken for the sound to travel from the speaker to the microphone. The reduced waveform observable at the end of the acoustic signal is an echo. B. 3-msec, 10-kHz tone burst, rise time approximately 0.5 msec. Lower tracing: electrical signal. Upper tracing: acoustic signal.

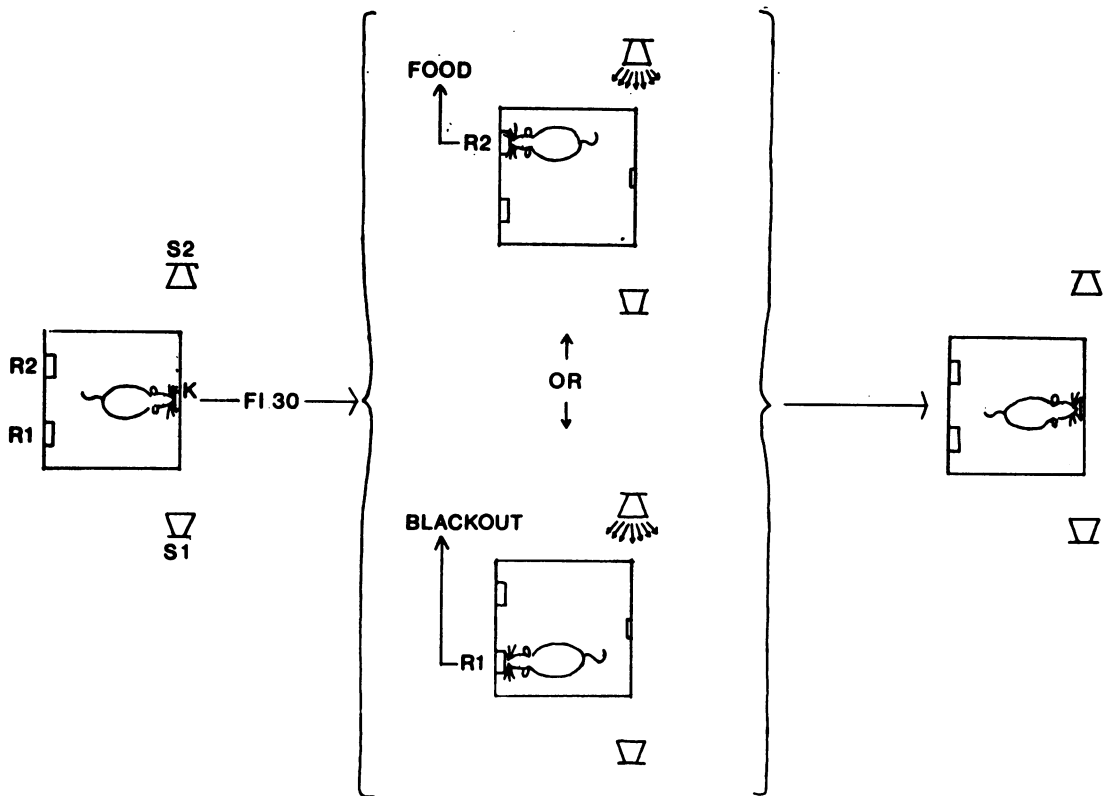


Fig. 3. Simplified diagram of procedure. Key (K) responses, on an FI 30-sec schedule, produced tone bursts from one or the other speaker. The case where tone bursts were produced from speaker S2 is shown. A response on lever R2 produced reinforcement, whereas a response on R1 produced a blackout. Dimensions are not to scale as in Fig. 1.

The first response on either lever that occurred within 7.5 sec of the onset of the tone bursts was reinforced as follows. A response on the lever to the left of the food cup (R1) was reinforced after tone bursts from the loudspeaker (S1) on the same side (correct response). A response on the lever to the right of the food cup (R2) was reinforced after tone bursts from the loudspeaker (S2) on that side. A response on R1 after tone bursts from S2 produced a 5-sec blackout (incorrect response). Similarly, a response on R2 after tone bursts from S1 produced a 5-sec blackout. Responses on either lever in the absence of either stimulus prevented, for 5 sec, the production of a stimulus by responding on the key. Reinforcement was 5-sec presentation of 0.1 cc of a 50% mixture of sweetened condensed milk and water.

After two incorrect responses in a row for tone bursts from the same speaker (unless a response, correct or incorrect, on the other

lever intervened), tone bursts from that speaker occurred on each succeeding presentation until a correct response occurred or until 10 consecutive errors had occurred. After either of these occurrences the speakers were again switched in the predetermined order.

Sessions were 80 min long.

To test whether the behavior was under the control of the tone bursts, rather than electronic or mechanical artifacts, the oscillator gain control was turned down to -60 db and it was noted whether or not a response occurred when the equipment went through the procedure of presenting a stimulus. Responses never occurred during these tests.

RESULTS

The behavior of animal RB 13 is considered in detail; data from the other animals are presented in less detail as supporting evidence. The percentage of correct responses to S1 and

S2 was calculated for all S1s and all S2s for each session, and these numbers are presented in the figures for the three animals. The percentage of correct responses (for each stimulus) was calculated as follows:

$$\% \text{ correct (S1)} = \frac{\text{No. of R1 in presence of S1}}{\text{No. of R1 \& R2 in presence of S1}} \times 100$$

$$\% \text{ correct (S2)} = \frac{\text{No. of R2 in presence of S2}}{\text{No. of R1 \& R2 in presence of S2}} \times 100$$

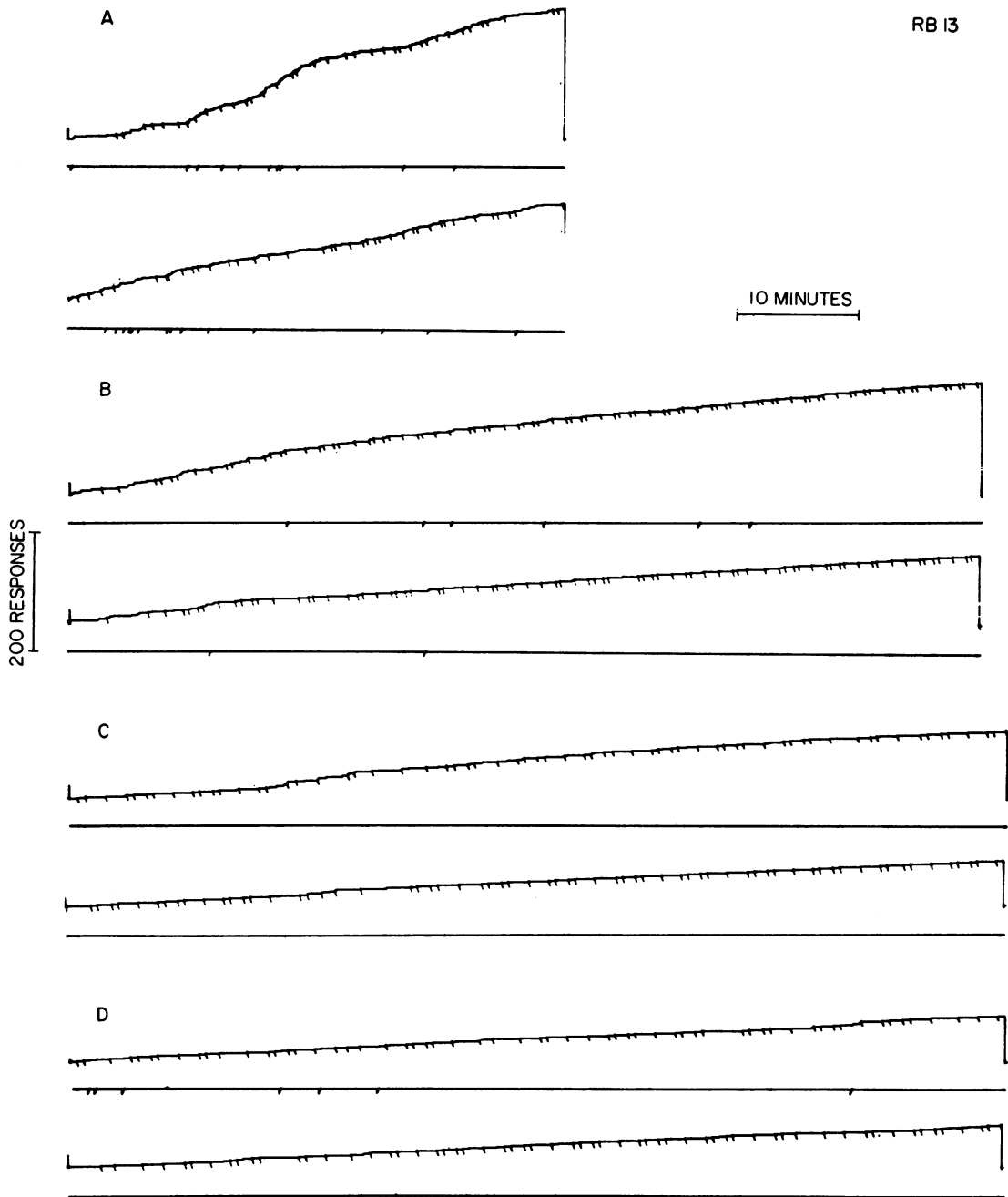


Fig. 4. Cumulative record of responses on right lever, R2 (upper record of pair) and on left lever, R1 (lower record of pair). Deflections of response pen indicate reinforcements (or correct responses), deflections of the event pen indicate blackouts (or errors). A. Session 1. 0.2-msec rise time, 90°, non-chain schedule. B. Session 2. Same conditions. C. Session 21. Same stimulus conditions, chain schedule (record of responses on key is not shown). D. Session 24. 50-msec rise time, 90°, chain schedule.

Development of the Behavior

Presses of RB 13 were shaped on both levers with food. The following day S1 and S2 (without limit to the number of tone bursts per stimulus presentation) were presented in the determined order once every 30 sec and the reinforcement and blackout contingencies were introduced. The loudspeakers were in the 90° position (see Fig. 1) and the tone burst had a frequency of 4 kHz with a rise time of 0.2 msec. By the end of this session the animal

was making only a small number of incorrect responses (Fig. 4, A). The animal continued on these conditions for the next six sessions during which a high level of correct responding was achieved on both levers (see Fig. 4, B, C and 5, Sessions 2 to 7). During Session 8 (see *a*, Fig. 5) key pressing was shaped and stimuli were produced by key responses on the fixed-interval schedule of 30 sec. The stimulus was limited to three bursts in Session 15 and to two bursts in all subsequent sessions. The animal continued to give an essentially errorless per-

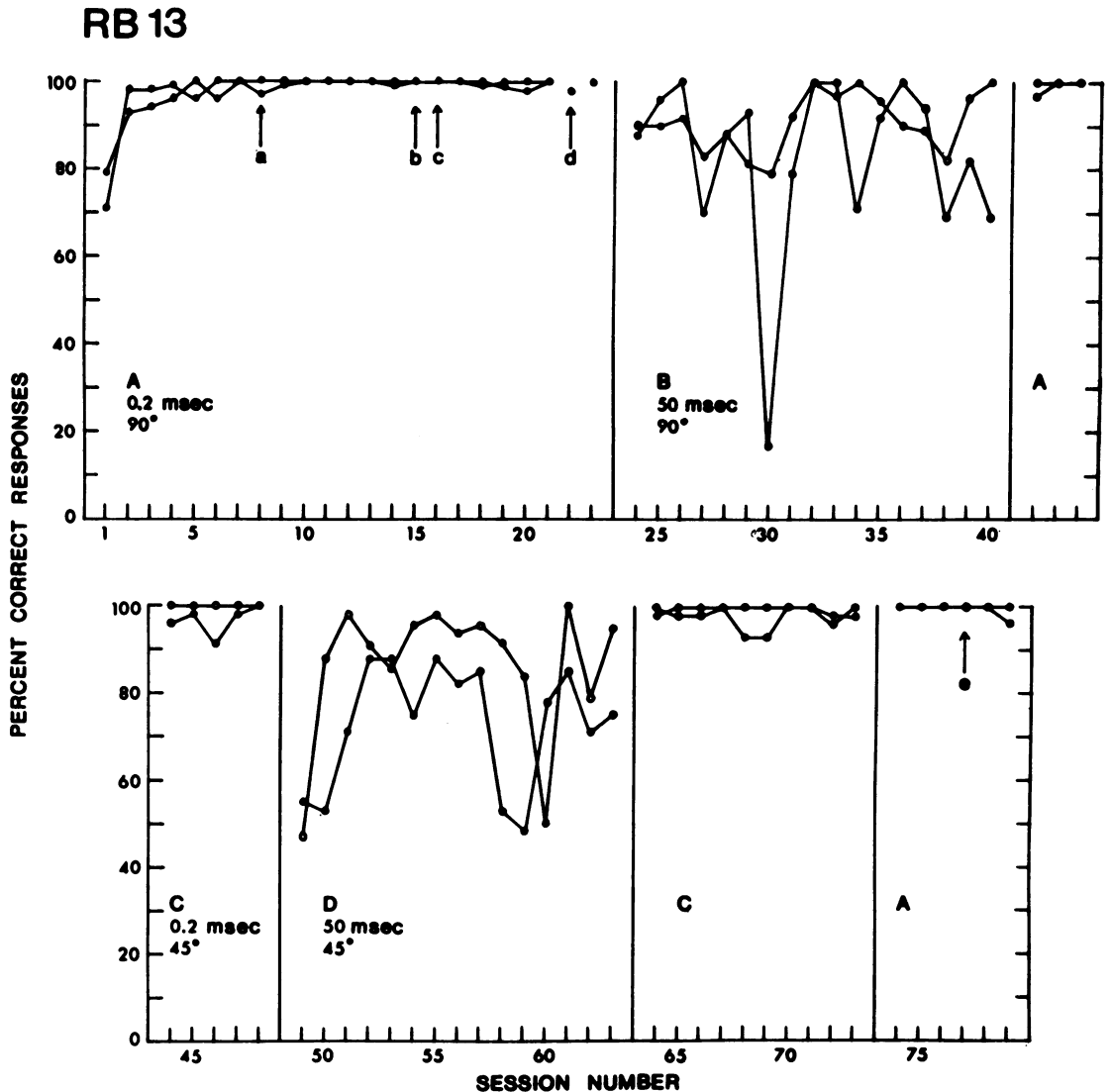


Fig. 5. RB 13. Percentage correct responses under different conditions (indicated by A,B,C, and D) of rise time (0.2 or 50 msec) and speaker angle (90° or 45°). Frequency 4 kHz in all conditions. Filled circles represent per cent correct in S2 (right speaker), open circles per cent correct in S1 (left speaker). Chain schedule begins at *a*. Stimulus limited to three tone bursts at *b*, and to two (final value) at *c*. In session indicated at *d*, only S2 was presented. At *e* speakers were interchanged (S2 still right, S1 still left) and remained so for succeeding sessions.

formance until the end of this part of the experiment. As a control procedure, in Session 22 (see *d*, Fig. 5) only the stimulus from the right speaker (S2) was presented. This was done by disconnecting the sequence stepper that controlled the selection of the speakers. Responding occurred on only the right lever.

From these data it is clear that the location of a 4-kHz tone burst with a rise time of 0.2 msec was an effective controlling stimulus. Stimulus control by location was rapidly obtained and the percentage of correct responses was high.

The development of the behavior in RB 14 is shown in the first segment (A) of Fig. 6. In

Session 22 (see *c* in Fig. 6) the animal was given a test in which all contingencies remained the same except that all tone bursts (whether scheduled as R or L) were channeled through one speaker (S2). Correct responding fell to an average of 53% (both stimuli combined).

The third animal, RB 4, had been run previously in variations of this experiment so the development of the behavior was not studied. Figure 7 (first segment, A) shows the last two days of responding on the initial conditions of this experiment (90° angle of the speakers and 0.2-msec rise time). The animal performed at the same high level of correct responding as did RB 13 and RB 14.

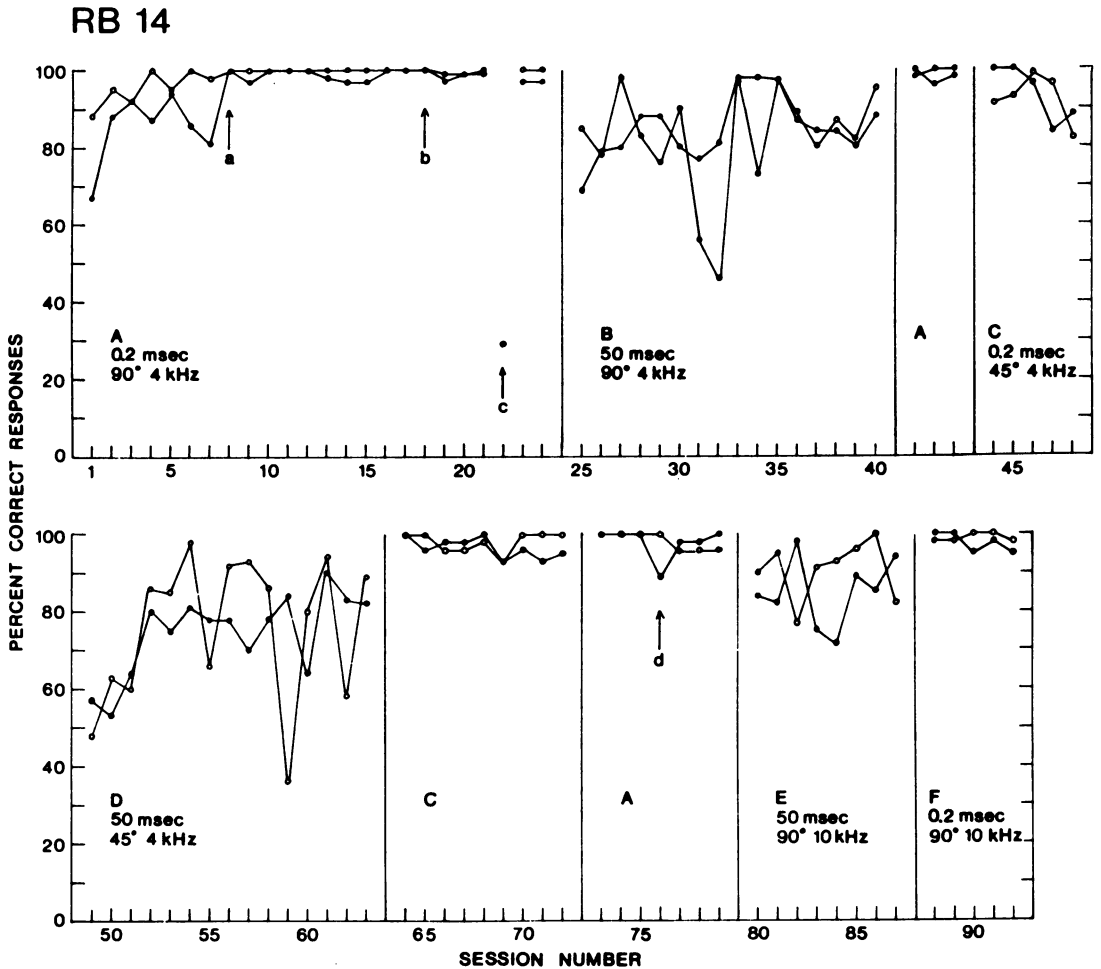


Fig. 6. RB 14. Percentage correct responses under different conditions (indicated by A,B,C, D, E, and F) of rise time (0.2 or 50 msec), speaker angle (90° or 45°) and frequency (4 or 10 kHz). Filled circles represent per cent correct in S2 (right speaker), open circles per cent correct in S1 (left speaker). Chain schedule begins at *a*. Stimulus limited to two tone bursts at *b* and for all following sessions. In session indicated at *c*, all stimuli were channeled through right speaker (normally S2). At *d* speakers were interchanged and remained so for succeeding sessions.

RB 4

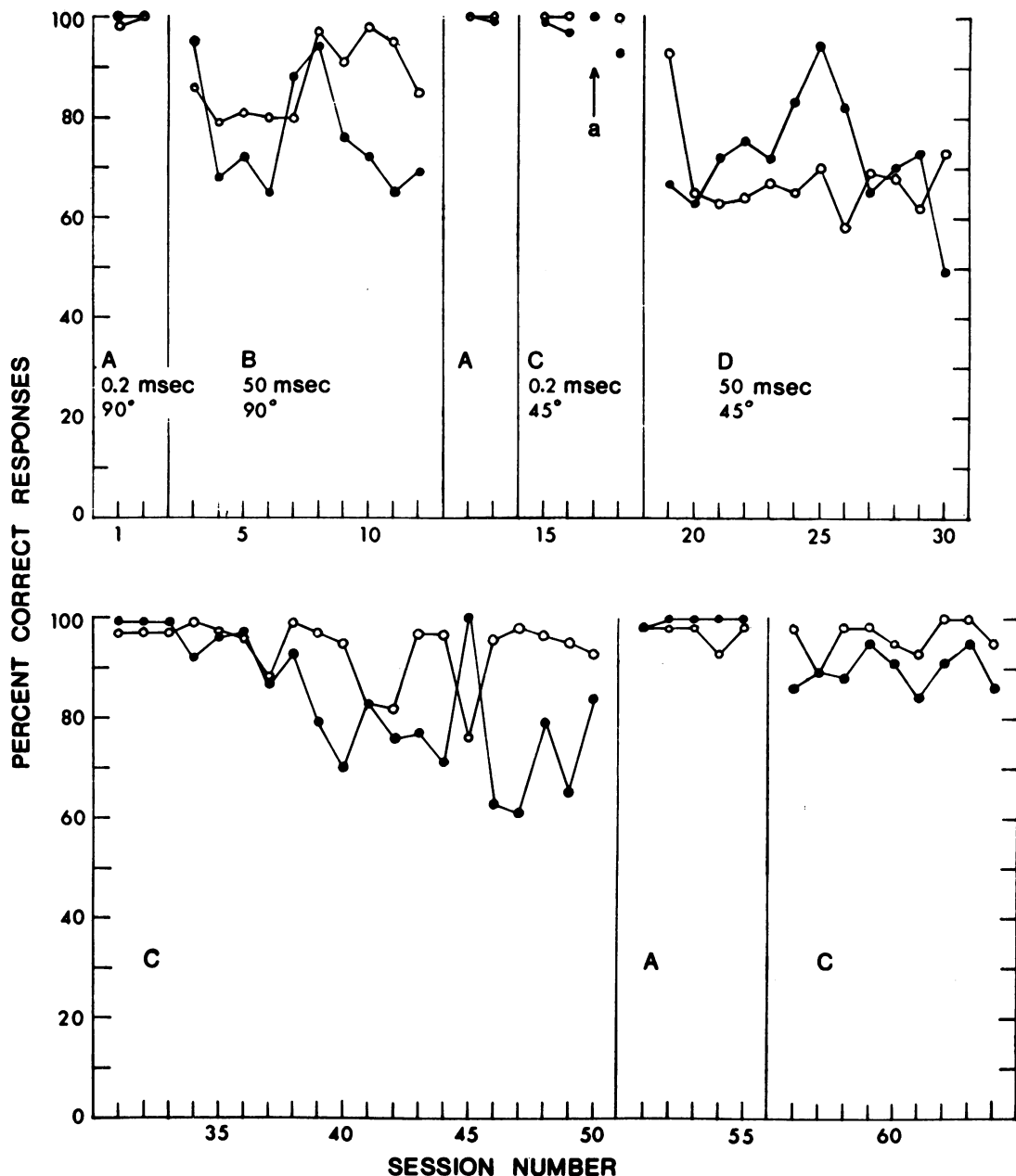


Fig. 7. RB 4. Percentage correct responses under different conditions (indicated by A, B, C, and D) of rise time (0.2 or 50 msec) and speaker angle (90° or 45°). Frequency was 4 kHz in all conditions. Filled circles represent per cent correct in S2 (right speaker), open circles per cent correct in S1 (left speaker). Animal had previous history on variations of this experiment before Session 1. In session indicated at *a*, only S2 was presented.

Effect of Slowing Rise Time to 50 msec

The rise time of the tone bursts for RB 13 was increased to 50 msec for Sessions 24 to 40

(segment B, Fig. 5). The percentage of correct responses immediately fell, showing considerable variability over these sessions. There was no indication of systematic increases in the

percentage of correct responses over these sessions. The cumulative records of the first session under these conditions are shown in Fig. 4 (D). In Session 41 (second A segment, Fig. 5) the rise time of the tone bursts was returned to 0.2 msec and the percentage of correct responses returned to the 100% level by the second session.

In Session 44 (segment C, Fig. 5), the loudspeakers were changed to the 45° position (see Fig. 1). The rise time remained at 0.2 msec for the next five sessions. The animal showed a slight decrease in percentage of correct responses. In Session 49 (segment D, Fig. 5), and for the following 14 sessions, the rise time of the tone bursts was increased to 50 msec. The percentage of correct responses immediately decreased and showed considerable variability over the 15 sessions. The rise time was reduced to 0.2 msec in Session 64 (second C segment, Fig. 5) and the number of correct responses immediately increased to the previous level under this condition. The speakers were returned to the 90° position in Session 74 (final A segment, Fig. 5) and the rise time was maintained at 0.2 msec. The animal made virtually no errors. The speakers were interchanged in Session 77 (see *e*, Fig. 5) to determine if differences between the speakers were supporting the behavior. This had no effect upon the behavior.

It is clear from these data that the decrease in the percentage of correct responses produced by increasing the rise time of the tone bursts was not critically dependent upon whether the speakers were in the 45° or 90° positions. From inspection of Fig. 5 it appears, however, that the degree of control of responding under the 45° position for both fast and slow rise times was less than that for the 90° position.

Animal RB 14 (Fig. 6) was exposed to the same conditions as RB 13. Essentially the same results were obtained as those for RB 13.

In Session 80 (segment E, Fig. 6) for RB 14, the frequency of the tone bursts was raised from 4 kHz to 10 kHz. The speakers were in the 90° position and the rise time was 50 msec. From inspection of Fig. 6 it can be seen that the percentage of correct responses was about the same at 10 kHz as at 4 kHz (segment B). Finally, (segment F, Fig. 6) the rise time of the stimuli was reduced to 0.2 msec and the percentage of correct responses increased to the same level as that obtained at 4 kHz (segment

A). Thus, the effect of slowing the rise time of the stimuli was not critically dependent upon the use of a frequency of 4 kHz.

Animal RB 4 (Fig. 7) was exposed to the same changes of conditions as RB 13 and RB 14. In Session 3 (segment B, Fig. 7), the rise time was increased to 50 msec and percentage of correct responses immediately decreased in the same way as that found for the other animals. When the rise time was returned to 0.2 msec in Session 13 (second A segment, Fig. 7) the percentage of correct responses increased to its previous high value. The animal was then run with the speakers in the 45° position and the rise time at 0.2 msec (first segment C, Fig. 7). The percentage of correct responses decreased slightly. In Session 19 (segment D, Fig. 7), the rise time was increased to 50 msec and the percentage of correct responses immediately decreased. In Session 31 (second C segment, Fig. 7), the rise time was reduced to 0.2 msec. The percentage of correct responses immediately increased. The animal was run for 20 sessions on this condition during which the number of correct responses gradually decreased. In Session 51 (final A segment, Fig. 7), the speakers were returned to the 90° position (0.2 msec rise time). The percentage of correct responses immediately rose to its previous high value. The speakers were returned to the 45° position (0.2-msec rise time) in Session 56 (final C segment, Fig. 7). The number of correct responses decreased but to a level higher than that under the 50-msec rise time condition.

Altering the rise time of the stimulus had the same effect with RB 4 as with the other animals. Under the 45° fast rise-time condition (second segment C, Fig. 7) however, control of responding was not as well maintained as with the other animals. However, the effect of altering the rise time upon responding was still evident in the 45° position.

In summary, these data show that increasing the rise time of tone bursts from 0.2 msec to 50 msec decreases the number of correct responses. This effect was obtained with different positions of the speakers (90° and 45°) and with different stimulus frequencies (4 kHz and 10 kHz).

DISCUSSION

The present results show that responding of unrestrained animals readily comes under the

control of the azimuthal location of certain auditory stimuli. The degree of control was strong, the animals working at high levels of correct responding. This control was obtained in what might be considered a normal acoustic environment for a rat. The experimental room was not anechoic and it contained objects (feeder, levers, key, enclosure, etc.) that were not arranged in any particular way so as to produce a simple (free-field) signal at the ears. A different room, enclosure, and sound producer were used in the preliminary experiments discussed in the introduction; comparable results were obtained. Thus, the effect did not depend in any critical way upon some special feature of the present acoustic environment.

It is reasonable to conclude that the location of appropriate stimuli is a dominant attribute of audition, a conclusion in line with the anatomical analysis presented in the introduction.

The following points must be kept in mind when speculating about the reasons for the effects produced by changing the rise time of the signal.

In the rat, the pinnae stand above the head, so that the head does not lie between the ears as in man and other primates. Thus, intensity differences at the two ears are probably less dependent upon acoustic shadows cast by the head than in the primate. It seems probable, however, that the pinnae will cast shadows as well as having other acoustic effects relevant to location. In the absence of measurements of these effects it is impossible to estimate their role in the behavior observed in the present experiment. However, the magnitude of the effects, at the nominal frequency of the tone burst, is presumably unchanged by changing rise time.

Whatever time relations exist between the stimuli that reach the two ears in the complex acoustic environment of the experiment are unchanged by changing rise time. For stimuli of short rise time any difference in intensity of the stimuli at the two ears due to difference in time of arrival of the stimuli at the two ears will be larger than for stimuli of long rise time. Thus, it appears that differences in intensity due to the difference in rise time may be one variable involved in producing the behavioral effects observed in the present experiment. In the rat, the maximum difference in

time of arrival of the stimuli is approximately 0.1 msec. In the cat, a difference in time of arrival of this magnitude (of clicks delivered one to each of left and right earphones) is sufficient to produce errorless localization (Masterton, Jane, and Diamond, 1967).

Masterton *et al.* (1967) have carried out two lesion experiments, the results of which are relevant to the present results. They found that lesions of the trapezoid body and superior olivary complex abolished the discrimination of pairs of clicks (delivered one to each ear by headphones) separated by an interval of 0.5 msec. In their cat M-329, the superior olivary complex and trapezoid body were destroyed on one side, and in cat M-330 the superior olivary complex and trapezoid body were extensively damaged on both sides. In both these animals discrimination of the click pairs was seriously disrupted. These results are consistent with the view that the superior olivary complex is involved in the discrimination of sound disparities at the two ears. Masterton *et al.* (1968) interpreted these data as indicating that the medial superior olivary nucleus is essential for the discrimination of location of auditory stimuli. The lesions of cats M-329 and M-330, however, interrupt a number of ipsilateral and contralateral pathways other than those to the medial superior olivary nucleus (Harrison and Beecher, 1967). In particular, they interrupt the axons to the lateral superior olivary nuclei or destroy the nuclei. It could well be that this damage, rather than that to the medial superior olivary nucleus, was responsible for the loss of the discrimination in their two cats.

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