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CONTROL OF RESPONDING BY LOCATION OF AUDITORY STIMULI: RAPID ACQUISITION IN MONKEY AND RAT[1]

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Monkeys require a considerably larger number of trials to bring responding under the control of the location of an auditory stimulus than cats, rats, and bats with the same experimental procedures. The present experiment sought to determine the conditions necessary for rapid acquisition of control of responding by location of noise and tone bursts in the monkey. Monkeys were run in an enclosure that contained four loudspeakers and four manipulanda. Two conditions were used in training. In the adjacent condition, a stimulus (noise or tone burst) was presented through one or other of two speakers and a response on the manipulandum adjacent to the speaker was reinforced with food. In the nonadjacent condition, a stimulus was presented through one of two speakers and a response on a manipulandum remote from the speaker was reinforced with food. Acquisition of control was measured by change in the percentage of reinforced responses during training. In the adjacent condition, responding came under control of location within zero to three sessions. In nonadjacent conditions, the animals required 14 to 20 sessions to come under control of location. These latter numbers are comparable to those reported in the literature for localization discrimination in monkeys.

Lever responding in rats can readily be brought under the control of the location of a sound source (tone bursts) provided the rise-decay time of the stimuli is less than 0.5 msec (Harrison and Beecher, 1969). Lever responses in squirrel monkeys, however, failed to come rapidly under the control of the location of a sound source, the animals requiring 15 to 20 sessions to reach a stable level of correct responses (Beecher, 1970).

Wegener (1964) has been concerned with such differences in the acquisition of auditory discriminations between monkeys and other mammalian species and has found that rhesus monkeys required between 492 and 1401 trials to acquire a discrimination based on the location of a buzzer. This is approximately the same number of trials required by Beecher's squirrel monkeys. Cats, working in a comparable localization experiment, required between 130 and 260 trials to reach a 90% correct response level (Neff, Fisher, Diamond, and Yela, 1956).

The major purpose of the present experiment was to investigate possible reasons for the differences in rate of acquisition in rats and monkeys. The conditions under which Beecher ran his experiments were selected without regard to species-specific aspects of hearing in the species concerned. Comparative anatomical investigation of the auditory system (superior olivary complex) in rat and squirrel monkey have indicated differences between the two species (Harrison and Irving, 1966; Irving and Harrison, 1967; Feldman and Harrison, 1970). In the squirrel monkey, the medial superior olive is large compared with the same structure in the rat (2570 and 690 nerve cells, respectively). The lateral superior olive is approximately the same size in both species (1480 in rat and 1300 in squirrel monkey). The size of the medial superior olive has been found to be correlated with the diameter of the eye and the size of the nucleus of the sixth cranial nerve. This correlation has suggested that the auditory pathway that ascends through the medial superior olive may be related to vision, specifically that it may be concerned with the orientation of head and eyes in the direction of a source of sound (Harrison and Irving, 1966).

These anatomical observations suggest that one dimension of hearing that may differ in rat and monkey is the degree to which sounds

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orient the animal's head and eyes in the direction of the stimulus in these two species. The present experiments were designed to investigate this dimension of hearing in the two species by manipulating the relation between the location of the sound sources and the manipulanda.

In designing this, and other experiments of this series, we have been concerned with determining the auditory capabilities of the animal in what might be considered a natural acoustic environment. Thus, the behavior of monkey and many other mammalian species is under the control of the location of sounds in complex acoustic environments under conditions in which they are free to move relative to the sources of sound. In such situations all cues upon which the behavior may be based are present, and one or more may be operative in producing appropriate behavior in the animal. The behavior may be based on monaural or binaural cues, head movements, intensity maximizing (by approaching a sound source), and by ear movements (in appropriate species). In our experiments, the animals are free to move with respect to the sound sources and the acoustic field produced by the sound sources is complex (as against a free field).

This is in contrast to an analytical approach in which the primary concern is with the investigation of the processes upon which localization depends (time or intensity differences at the two ears, for example). In these experiments, relationships between the animal's head and ears and the stimuli are necessarily restricted. Since we are not interested, at this stage, in the analysis of localization we have deliberately allowed the free interaction between the animal and its acoustic environment.

METHOD

Subjects

Four adult naive squirrel monkeys (*Saimiri sciurisis*), one naive adult male owl monkey (*Aotus trivirgatus*), and six naive adult male albino rats (Sprague-Dawley strain) were used.

Apparatus

For the monkeys, a wire mesh enclosure 20 in. (51 cm) on each dimension (see Fig. 1), contained four Gerbrands monkey keys, 3.25 in. (8 cm) diameter, two on the front wall and one each on the two side walls of the enclosure. A 2.5 in. (6 cm) diameter hole was made in each key and fine wire mesh covered the hole so that the key could still be pressed by the animal. Each key was illuminated by a small bulb attached to the center of the fine wire mesh. Behind the hole of each key a loudspeaker (University Sphericon T202) was placed. A Gerbrands liquid food dispenser was mounted on the front wall between the two keys. The houselight consisted of a 100-w bulb run at 40 v and placed on the top of the wire mesh enclosure. The wire mesh enclosure was placed in a room in which no particular precautions were taken to make it sound absorbing. Sound fields produced by the loud speakers in the room were thus complex.

The rat apparatus was similar to that used

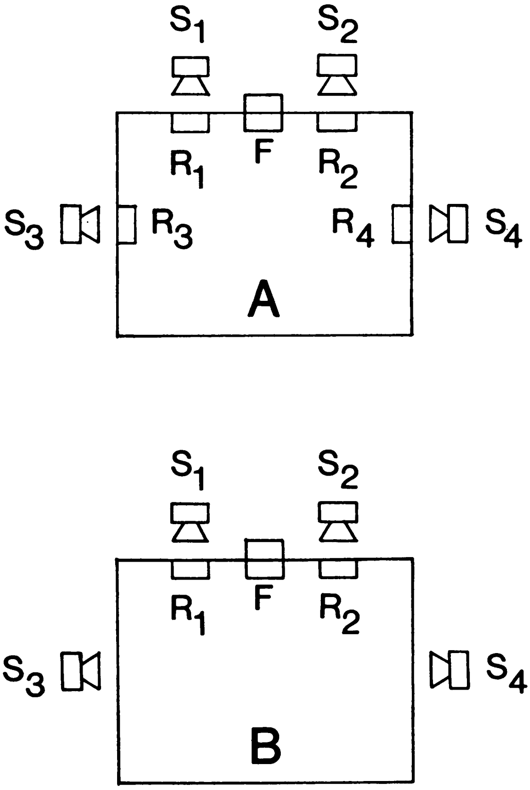

Fig. 1. A. Schematic drawing of the apparatus used with the monkeys. R1, R2, R3, and R4 were Gerbrands monkey keys with a 6-cm diameter hole cut in the center of the plastic key. Loudspeakers S1, S2, S3, and S4 were placed behind the appropriate keys so that the sound entered the enclosure via the hole in the key. B. The apparatus used with rats. R1 and R2 were Gerbrands standard rat levers. Speakers S1 and S2 were mounted as close to the two levers as possible. Speakers S3 and S4 were mounted on the side walls of the cage. F, liquid food dispenser.

for the monkeys (see Fig. 1). The wire mesh enclosure was 18 by 18 by 15 in. high (46 by 46 by 38 cm). Two Gerbrands rat levers were mounted in the front wall and a Gerbrands liquid food dispenser was mounted between them. Two speakers were mounted adjacent to the two levers and two more speakers were mounted one on each side wall. The houselight consisted of a 5-w night-light bulb. This apparatus was also placed in a room in which no precautions were taken to eliminate echos or reflections from the walls.

The stimuli consisted of either noise bursts or tone bursts of 0.2 sec duration (0.2 msec rise-decay time) repeated at a rate of two bursts per second. The signals were derived from a noise (or tone) generator, were switched by an electronic switch (Grason Stadler, type 8290), and fed to the speakers via a Krohn-Hite amplifier (type DCA-10) and matching transformer (type MT-56). The nominal intensity of the signals was measured by a General Radio sound-level meter (type 1551C) with the microphone placed in a standard position in the animal's enclosure. The intensity of the tone and noise bursts measured under these conditions was 67 db (relative to 20 $\gamma N/m^2$). A background sound level of 56 db was produced by a noise generator and University tweeter speaker (Type 4401).

Relay equipment was used to control the experiment and relevant data were recorded on counters. Also, all responses on each lever were recorded on separate cumulative recorders. The motors of the recorders ran throughout the session.

Procedure

The animals were trained on a trial-by-trial basis to respond to one of two manipulanda depending upon which of two loud speakers was used to present the sound. Different animals were trained with different combinations of manipulanda and loudspeakers. The combinations in which the speakers and manipulanda used were adjacent (that is, the speakers and manipulanda mounted on the front wall, or the speakers and manipulanda mounted on the side walls; see Fig. 1) was one general arrangement. The combinations in which the manipulanda and speakers used were not adjacent (that is, manipulanda on the front wall and speakers on the side wall and *vice versa;* see Fig. 1) was a second general condition. This was termed the nonadjacent condition. Details of manipulanda and speakers used with each animal during the experiment are given in Table 1, as is the type of stimulus (noise or tone burst).

The discrimination schedule was the same for all the adjacent and nonadjacent conditions, so only one condition is described here in detail (the adjacent condition using S1, S2, R1, and R2). A trial was started by presenting the stimulus through either S1 or S2. If, say, the stimulus was presented through S1, then one response on R1 (correct response) produced food and turned off the stimulus, or one response on R2 (incorrect response) turned off the stimulus and produced a 7.5-sec blackout. If no response was made, then the stimulus was terminated after a limited hold of 7.5 sec. The stimuli were presented in the following order: S1 S2 S1 S1 S2 S2 S1 S2 S2 S1, the sequence being repeated until the end of the session. The intertrial interval was 30 sec and responses on either R1 or R2 between trials prevented the occurrence of a trial for 5 sec. The houselight and manipulandum lights were on at all times except during blackouts. The reinforcer for the monkeys was 0.1 cc of standard monkey diet (SKF) (Nutritional Biochemicals Corp.) in water (two parts diet, one part water) presented for 7.5 sec. A 33% solution of condensed milk in water was used as the reinforcer for the rats; 0.1 cc was presented for 5 sec.

Training was carried out as follows. The animals were reduced to approximately 80% of their free-feeding body weights and fed the liquid reinforcer in their home cages. When the animals readily took the reinforcer, they were magazine trained and then responses to the levers were shaped. When the animal was responding on one lever, reinforcement was withheld on that lever and the response to the second lever was shaped. All responses on both levers were then reinforced for the remainder of the session. For the next one or two sessions, responses on either lever were reinforced on a fixed-interval 15-sec schedule. During this phase, the animals responded on both levers, although a position preference was usually present, the rate on one lever being higher than the rate on the other. Following this procedure, the animals were exposed to the full trial-by-trial procedure except that the stimuli were not presented (the amplifier was turned

Table 1

Positions of the Manipulanda and Speakers and the Type of Stimulus Used During Training

Subject	*Condition*	*Speakers*	*Manipulanda*	*Stimulus*
Sq. monk. A	Adjacent	S1, S2	R1, R2	noise bursts
Sq. monk. 12	Adjacent	S3, S4	R3, R4	10 kHz tone bursts
Owl monk. 5	Adjacent	S1, S2	R1, R2	noise bursts
Sq. monk. B	Nonadjacent	S3, S4	R1, R2	noise bursts
Sq. monk. 11	Nonadjacent	S1, S2	R3, R4	noise bursts
Rat R100	Adjacent	S1, S2	R1, R2	noise bursts
Rat R62	Adjacent	S1, S2	R1, R2	noise bursts
Rat R91	Adjacent	S1, S2	R1, R2	noise bursts
Rat R63	Nonadjacent	S3, S4	R1, R2	noise bursts
Rat R92	Nonadjacent	S3, S4	R1, R2	noise bursts
Rat R93	Nonadjacent	S3, S4	R1, R2	noisc bursts

off; thus, every 30 sec a trial occurred during which one lever was arbitrarily "correct" and one "incorrect", although no stimuli were correlated with these contingencies). This was continued for one or two sessions and typical behavior at this phase is shown in Fig. 4A. The rates on the two levers typically differed as shown in the figure. On the subsequent session, the stimuli were added by turning on the amplifier. The animals were exposed to this condition until the percentage of correct responses appeared to be stable. Each daily session consisted of 50 reinforcements. A non-correction procedure was used.

RESULTS

The results are presented as the percentage of correct responses made in each session. This number was calculated by summing all correct responses on both levers and dividing this number by the total number of correct and incorrect responses.

Nonadjacent Condition: Monkeys

The acquisition of the discrimination by SM.B and SM.11 is shown in Fig. 2. These animals were run under nonadjacent arrangements of the speakers and manipulanda. The figure shows that the percentage of correct responses continued to increase for both monkeys for 20 sessions, with the 90% correct response level reached after 17 sessions. The behavior of these two animals is similar to that reported by Beecher for his monkeys, which also were trained under a nonadjacent condition.

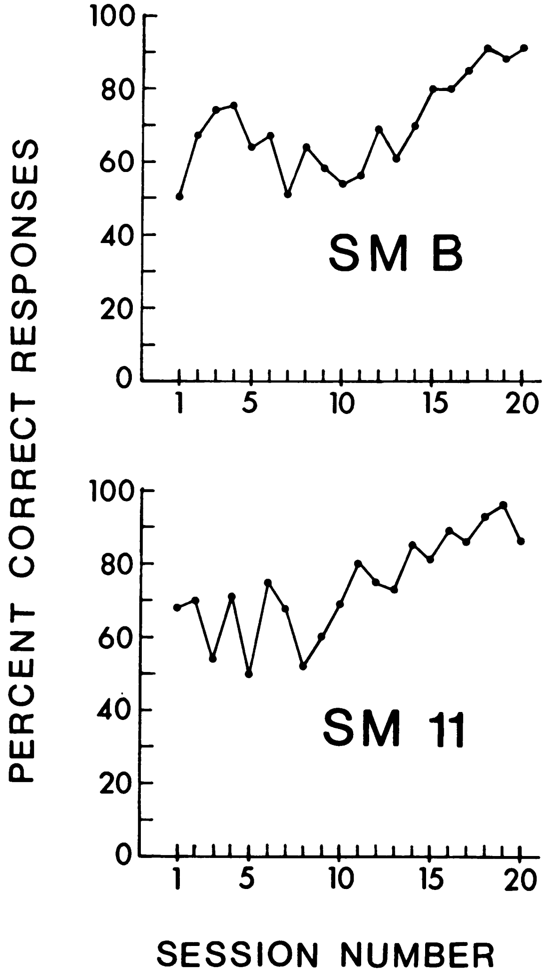

Fig. 2. Acquisition data of the two monkeys, SM.B and SM.11 run under nonadjacent conditions. The sound was first introduced in Session 1. Preliminary shaping and training sessions (no sound) are not included.

Adjacent Condition: Monkeys

The acquisition of the discrimination by Monkeys OM.5, SM.A, and SM.12 is shown in Fig. 3. These animals were run under adjacent arrangements of the manipulanda and speakers (Table 1). The figure shows that all these animals reached a 90% or higher correct response level within one or two sessions. The comparison of the data presented in Fig. 2 and 3 immediately shows the difference in the rate of acquisition of the discrimination under nonadjacent arrangements of the levers and speakers.

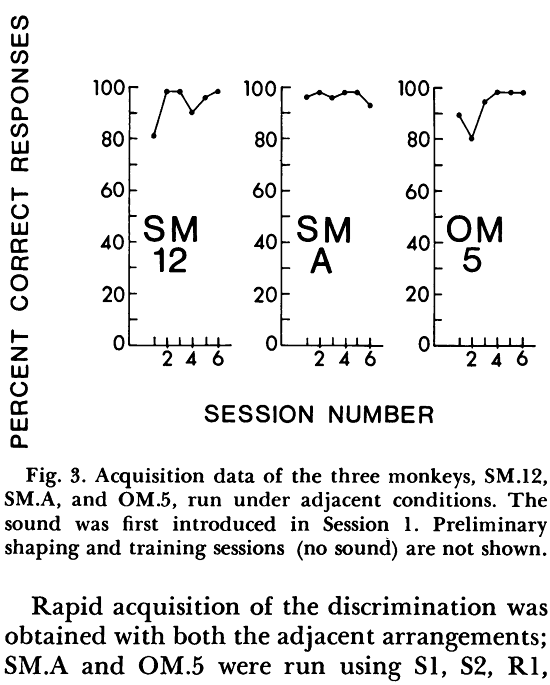

Fig. 3. Acquisition data of the three monkeys, SM.12, SM.A, and OM.5, run under adjacent conditions. The sound was first introduced in Session 1. Preliminary shaping and training sessions (no sound) are not shown.

Rapid acquisition of the discrimination was obtained with both the adjacent arrangements; SM.A and OM.5 were run using S1, S2, R1, and R2 and SM.12 was run using S3, S4, R3, and R4. Thus, the absolute positions of the speakers and the manipulanda were not the relevant variables that produced the rapid acquisition. Rapid acquisition was also obtained with tone and noise bursts and also with both squirrel and owl monkeys.

Cumulative records of responding of SM.A during the last session without sound and three sessions with sound (the first, third, and thirtieth) are shown in Fig. 4. From the comparison of the last session without sound and the first session with sound it can be seen that the introduction of the sound immediately reduced the number of blackouts to a low value (from a total of 43 to six blackouts; incorrect responses). In subsequent sessions, the number of incorrect responses remained low.

The distribution of intertrial responses shown in Fig. 4 is quite typical. The rate on one lever is usually greater than on the other, R1 having the higher rate in some monkeys and R2 having the higher rate in others. The introduction of the acoustic stimuli (Fig. 4B) decreased the occurrence of incorrect responses (or blackouts in the session shown in Fig. 4A) within the first session, but had only a small effect upon the rates of intertrial responses on the two levers. The intertrial response rates fell only gradually over 30 sessions. Rates continued to remain different on the two levers over these sessions. Since an intertrial response could not occur less than 5 sec before a trial there was no immediate reinforcement of these responses by the onset of an acoustic stimulus.

Rats

The acquisition of the discrimination by the rats under adjacent conditions is shown in Fig. 5 and under nonadjacent conditions in Fig. 6. The two figures show that the discrimination was more rapidly acquired than by the monkey under nonadjacent conditions, confirming the findings of Beecher (1970). It can also be seen that in the rats, acquisition in the nonadjacent condition was slightly slower than in the adjacent condition.

Comparison of Fig. 3 and 4 indicates that monkeys under adjacent conditions (SM.A) may acquire the discrimination as rapidly as rats do under either condition.

DISCUSSION

The results support the thesis presented in the introduction, that one dimension of hearing in which rats differ from squirrel monkeys and owl monkeys is the degree to which relative location of stimulus and manipulandum affect behavior. The data, taken together with the findings of Beecher (1970), also support the behavioral implications of the comparative anatomy of the system suggested in the introduction. The data, together with Beecher's data, also confirm the generally held view that hearing in the monkey differs from that in rat, cat, and bat (Dewsen, *et al.,* 1968; Wegener, 1964).

The rapid acquisition of control of responding in the monkey cannot be attributed to

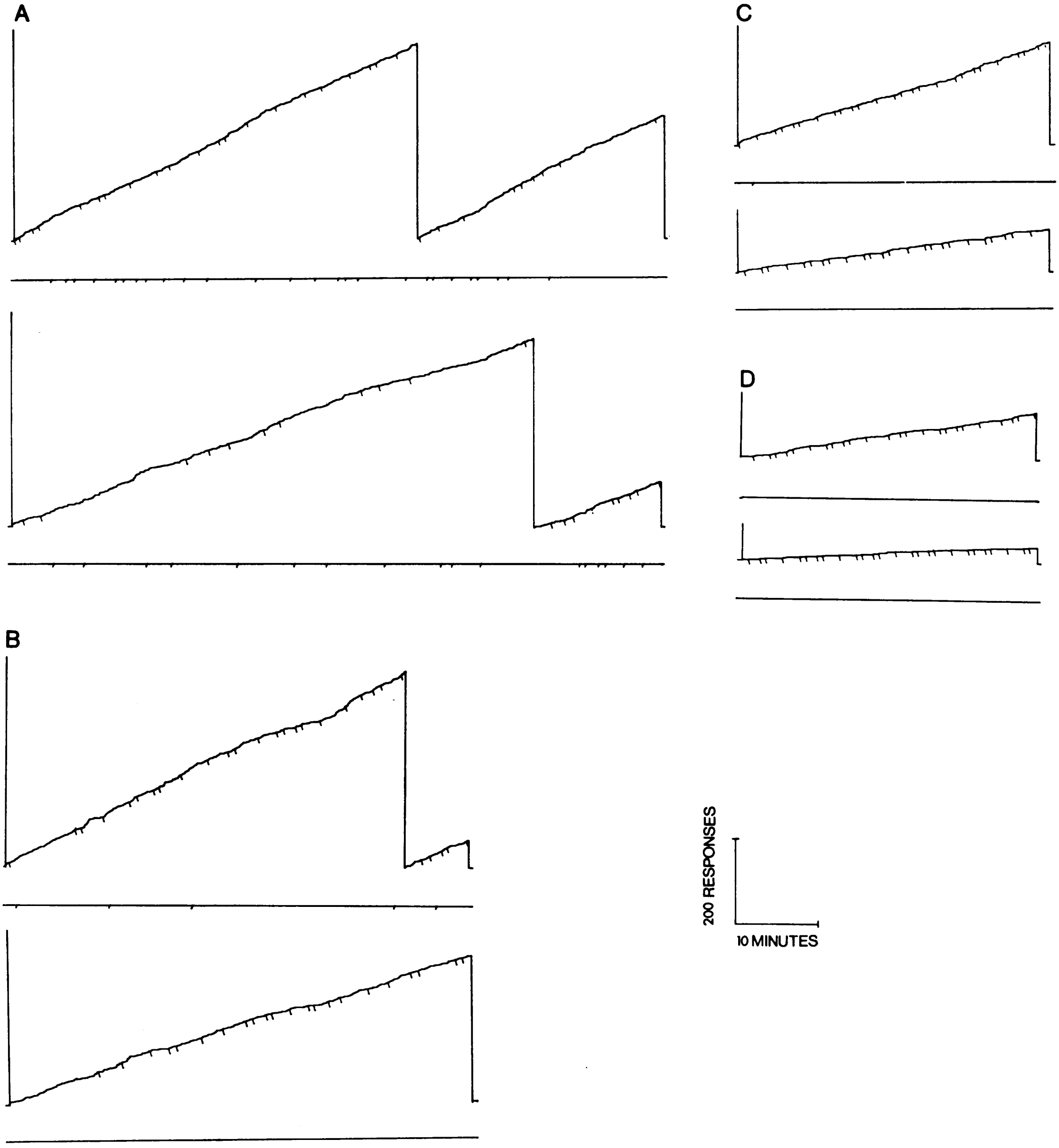

Fig. 4. Cumulative records of Monkey SM.A, run under adjacent conditions. All responses on R1 stepped the pen on one recorder (upper recorder in each session) and all responses on R2 stepped the pen on the other. Hash marks on the records indicate reinforcements (*i.e.*, correct responses) and hash marks on the baselines indicate blackouts (*i.e.*, incorrect responses). A. Responding on R1 (top) and R2 (bottom) during the last session before the sound was introduced. B. Responding on the two levers during the first sessions (Session 1 in Fig. 3) that the sound was introduced. Note the large reduction in the number of blackouts (*i.e.*, incorrect responses when the stimulus was presented). C and D. Third and thirtieth sessions with sound. Note virtual absence of incorrect responses and the reduction in the number of intertrial responses.

certain features of the experiment. The angle between either the front speakers (S1 and S2) or the side speakers (S3 and S4) is not a critical feature of the experiment because rapid acquisition was obtained using either S1 and S2 (Monkeys SM.A and OM.5) or S3 and S4 (SM.12). Nor was the rapid acquisition dependent upon the positions of the manipulanda, because the same results were obtained using either R1 and R2 (SM.A and OM.5) or R3 and R4 (SM.12). Rapid acquisition was also not dependent upon a particular sound, because the same results were obtained using noise bursts and tone bursts.

For rapid acquisition in the monkey, it was necessary that the loudspeaker be adjacent to the correct manipulandum. There are three basic features of such adjacency, one or all of which may be the basis for the rapid acquisition.

Orientation of Head and Eyes to the Sound Source

We have observed that the occurrence of the sound orients the animal's head and eyes to the loudspeaker. When the speaker and manipulandum are adjacent, this results in the animal looking at the manipulandum. This biases the animal towards responding on that manipulandum (that is, the correct manipulandum).

The reason that the acquisition is slow under nonadjacent conditions can also be understood in terms of this mechanism. The onset of the sound orients the animal's head and eyes in the direction of the speaker. This results in the animal looking at neither manipulandum. This does not predispose the animal to make either response. The acquisition of the discrimination in the nonadjacent condition depends upon the formation of a response chain between the orientation to the speaker and an orientation of the head and eyes appropriate for the animal to make the correct response. It is the acquisition of this chain that produces the slow acquisition of the discrimination. As an example of such a chain, one monkey was observed frequently to orient to the nonadjacent speaker as it approached and finally pressed the correct manipulandum.

The monkey orients, or localizes, the sound correctly under both adjacent and nonadjacent conditions, but the latter condition requires that the monkey acquire the correct behavior (chain) in order to take it to the correct manipulandum.

In contrast to the monkey, rats were not observed to orient to the speaker. Thus, there was no difference in visual orientation in the adjacent and nonadjacent conditions and there was also a minimum difference in the rate of acquisition under the two conditions.

Position of Response Relative to Sound Source

According to this hypothesis, the essential condition in the monkey for the rapid acquisition of the discrimination is that the response the animal makes be at the sound source. Translated into behavior in the animal's normal environment, this hypothesis is stating that discriminations with respect to manipulated sound sources are most rapidly acquired. As the distance between the sound source and the reinforced response is increased (a condition that seldom holds in nature) the effect of reinforcement upon the formation of the discrimination weakens and a large number of trials is required to reach a particular percentage of correct responses above the chance level.

Acoustic Intensity Differences and Intensity Gradients

When an animal is run under an adjacent condition, its head is of necessity near the loudspeaker through which the stimulus is presented at the time the correct response is made. Conversely, in a nonadjacent condition the animal's head is remote from the speaker when the correct response is made. Thus, at the time of making the correct response, the intensity of the stimulus at the animal's head is greater under adjacent than under nonadjacent conditions.

The animal may be in any position in the enclosure at the time a trial starts (the stimulus is presented). Under adjacent conditions, the animal must of necessity move up the intensity gradient of the sound when approaching the correct manipulandum (since the speaker is adjacent to this). In the nonadjacent condition, the animal may move in any direction (except up) the intensity gradient from the speaker when approaching the correct manipulandum (since the speaker is remote from the manipulandum).

The acoustic intensity differences and movements in the intensity gradients may be relevant variables upon which the control of responding in part depends.

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