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ORIENTATION AND LEVER RESPONDING IN AUDITORY DISCRIMINATIONS IN SQUIRREL MONKEYS[1]

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Head orientation during auditory discriminations was studied in squirrel monkeys using a two-lever trial-by-trial procedure. Animals were studied using auditory discriminations based on the position of the sound and on the spectral content differences between a pure tone and a noise. After the percentage of correct responses reached asymptote, head orientation was measured using videotape recordings. Orientation occurred on virtually every trial and was under the control of the position of the sound under all conditions. Lever responding was controlled by the same parameters of the sound under some conditions, and by different parameters in others. Orientation and lever responding were correlated (a lever response could be predicted from the direction of orientation) when both responses were under the control of the same parameter of the sound. The two responses were uncorrelated when they were controlled by different parameters of the sound. Orientation and lever responding were not functionally related.

Key words: auditory discrimination, orientation, monkeys

It is well known that monkeys are difficult to train in auditory discriminations. Even seemingly simple auditory discriminations require many more trials than simple visual discriminations (see Cowey, 1968 and Wegener, 1964, for reviews of relevant literature). Recent work has revealed some of the reasons for difficulties in training monkeys (Brown, Beecher, Moody, and Stebbins, 1975; Downey and Harrison, 1972, 1975; Harrison, Downey, Segal, and Howe, 1971; Segal, 1976). First, an environmental sound possesses a position in space in addition to other parameters, such as intensity, spectral content, or duration. Second, the position of the sound in space readily controls responding, and this control may be more prepotent than control by other stimulus parameters. Third, auditory discriminations in monkeys rapidly develop only when the spatial relation between the sound source and correct response manipulandum is contiguous, *i.e.,* when responses made on a manipulandum placed very close to the sound source are reinforced.

In the study of auditory discriminations using squirrel monkeys, it was noticed that animals oriented in the direction of the sounding speaker (Downey and Harrison, 1972). It was suggested that orientation might be a stable component of auditory discriminations and that this might account for the rapid acquisition of control of responding by the position of a sound when the response and speaker sites were spatially contiguous. The present experiments investigated orienting responses of monkeys in auditory discriminations to determine the following: (1) The degree to which head orientation to the sound is a stable accompaniment to lever responding in auditory discriminations in monkeys. It is known that some species give unconditioned orienting responses to novel sounds, but these responses cease with continued presentation of the stimulus (Thompson and Welker, 1963; West and Harrison, 1973). It is not known whether orientation ceases in discrimination. (2) The extent to which orientation is controlled by the position of the sound source. (3) Is there a consistent relation between the orientation direction and the subsequent lever response in the discrimination of the position of a sound source? Does the direction of orientation predict the subsequent lever response? (4) In discriminations involving nonpositional parameters of sounds (such as spectral content), is the direction of orientation controlled by

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the position of the sound or its spectral content? (5) If there is a consistent relation between one direction of orientation and subsequent lever responding, does this represent a correlation between the two responses, or are they functionally related in the sense that direction of orientation determines lever responding?

In the experiments reported here, squirrel monkeys were trained in two discriminations based on the position of a sound source and one discrimination based on spectral content differences between the stimuli (tone *versus* noise). In preliminary experiments, it was found that the results obtained were independent of the duration of the stimulus (whether presented once or repeated during a trial), the precise form of the apparatus, the acoustic characteristics of the room in which the experiment was carried out, and the nominal frequency of the stimuli (from 4 kHz to 16 kHz). For this reason, these parameters were deliberately varied in the following experiments to show the generality of the results.

METHOD

Subjects

Six adult male squirrel monkeys, which had been used in prior auditory discrimination experiments, were maintained at approximately 80% of their free-feeding body weights and were fed once a day following the experimental session.

Apparatus

Two of the animals (SM 221 and SM 514) were studied in one apparatus and the remaining animals were studied in a second. Since the two forms of the apparatus were similar, only one is described in detail.

The animal enclosure consisted of a wire-mesh cage, 45 cm by 45 cm by 38 cm high. Mounted on one wall (Figure 1) were two Gerbrands rat levers, 28 cm apart and 7 cm above the floor. Mounted contiguously with each lever was a speaker (Grason-Stadler TDH 39 headphone) through which the stimulus could be delivered to the animal. A small signal light (continuously on during a session) was also mounted contiguously with each lever. A liquid feeder was mounted midway between the two levers, 9 cm above the floor. Illumination suitable for videotape recordings was provided by two 15-W fluorescent lamps mounted over the top of the wire-mesh cage. The lamps were illuminated for the duration of the experiment. A TV camera was placed as shown in Figure 1 so as to obtain a view of the monkey from behind the response levers.

Standard relay equipment was used to program the experiments and data were collected using counters and cumulative recorders. Videotapes were made of two or more sessions at least 10 sessions after the percentage of correct responses was judged to have reached asymptotic levels.

The stimuli consisted of pure-tone bursts (50-msec rise-decay time), tone bursts of complex spectral content (0.2-msec rise-decay time), and noise bursts (2 kHz to 20 kHz bandwidth). The tones were generated by a General Radio signal generator (type 1210-C), and switched using a Grason-Stadler electronic switch (type 829-C). The electronic switch was operated by the relay programming equipment. The signal was then passed to a Krohn-Hite type DCA 10-power amplifier. The output of the power amplifier was switched to one or other of the two speakers by the relay programming equipment. The stimulus generating equipment was examined for electrical artifacts that were correlated with the onset of the stimulus, and when these were found they were electrically suppressed. Care was taken also to determine that the signal lights mounted at the levers did not fluctuate in intensity with the operation of the programming equipment.

The intensity of the stimulus was specified by measurements taken at the center of the wire-mesh enclosure. A Bruel and Kjaer 0.6-

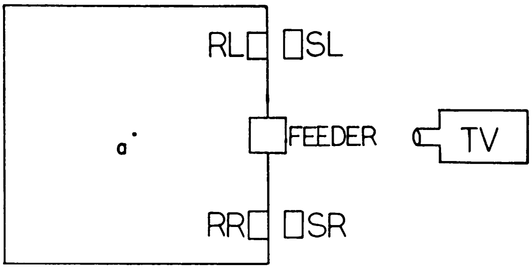


Fig. 1. Top view of the arrangement of the apparatus and TV camera. Stimulus intensity measurements were made at point "a" in the geometrical center of the cage.

cm microphone was suspended in this position and measurements of intensity were taken. The microphone was regularly calibrated using a pistophone (model 4220). The nominal intensity of all stimuli was approximately 70 dB, SPL.

Procedure

Since the animals had a history of auditory discrimination in similar apparatus, little preliminary training was needed to obtain responding on the two levers. Following this, the animals were exposed to the appropriate auditory discrimination for at least 10 sessions beyond the point at which the percentage of correct responses was judged to have reached asymptote. The following features were common to all daily sessions: a session consisted of 50 reinforced responses; the reinforcer was 0.1 ml of ground SKF monkey chow mixed with water; the intertrial interval was variable with an average of 30 sec (range 5 to 55 sec); a response on either lever during the intertrial interval prevented the onset of a trial for at least 2 sec following the response; a correct response operated the feeder and terminated the trial; an incorrect response simply terminated the trial; if no response was made during a trial, the trial terminated after 10 sec; at least 10 sessions after the level of correct responses was judged to have reached a steady level, two or more sessions were videotape recorded to be studied at a later time.

Condition 1—contiguous position discrimination. This was a position discrimination in which responses on the lever contiguous with the sounding speaker were reinforced (correct response). Animals were studied using pure tones (16 kHz, 50-msec rise-decay time for SM 70; 8 kHz, 50-msec rise-decay time for SM 54; and 5 kHz, 25-msec rise-decay time for SM 221 and SM 514) and stimuli of complex spectral content (8 kHz, 0.2-msec rise-decay time for SM 54). On each trial, the same stimulus (16 kHz for SM 70, for example) was presented through one or the other of the two speakers, the order of presentation being L L R R L R R L L R R L R L L R, repeated. For SM 221 and SM 514, the stimuli were presented in 200-msec bursts at the rate of two bursts per second for the duration of the trial. For the remaining animals, the stimuli were presented as either a single 350-msec or 150-msec burst. Reinforcement was available if a response was made on the correct lever within the duration of the trial (10 sec).

Condition 2—noncontiguous position discrimination. This was a sound-position discrimination in which responding on the lever not contiguous with the sounding speaker was reinforced. SM 52 was studied using pure tones (8 kHz, 50-msec rise-decay time) and stimuli of complex spectral content (8 kHz, 0.2-msec rise-decay time). The stimuli were alternated from side to side in the same order used in Condition 1. The stimuli were presented as single 350-msec bursts at the beginning of the trial. Reinforcement was available following a response on the correct lever for the duration of the trial (10 sec).

Condition 3—tone-noise discrimination. The animals were required to respond on the left lever (RL) whether the tone was presented through the left or right speaker, and reinforcement followed responses on the right lever (RR) whether the noise was presented through the right or left speaker. The stimuli thus varied in both spectral content and position, lever responding being reinforced on the basis of spectral content differences. Since the stimuli varied in both spectral content and position, results could be used to determine which parameter controlled the direction of orientation. Animals (SM 221 and SM 514) were studied using pure tones (5 kHz, 25-msec rise-decay time) and the stimuli of complex spectral content (noise bursts, 2 kHz to 20 kHz bandwidth). The stimuli were presented as bursts of 200-msec duration repeated at the rate of two bursts per second for the duration of the trial. Since there were two different stimuli, each of which could be in one of two positions, there were four kinds of trials, as follows:

1. Tone left (TL)—RL reinforced
2. Tone right (TR)—RL reinforced
3. Noise left (NL)—RR reinforced
4. Noise right (NR)—RR reinforced

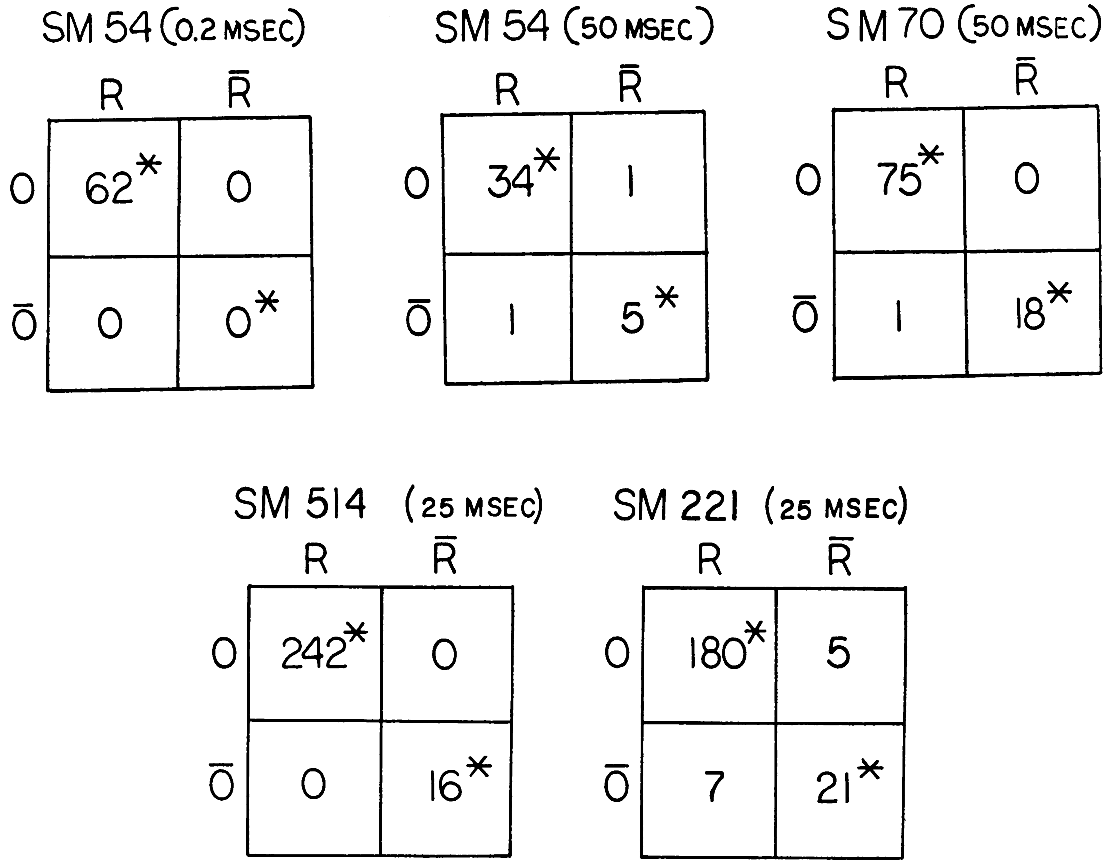
The four trials were presented in the order NL, TL, TR, NR, TL, NR, TR, TL, NL, NR, TR, NL, NR, TL, NL, TR, repeated.

The tapes were studied to determine the direction of orientation of the monkey's head at the onset of each trial. Regular speed, slow motion, and stop action were used as necessary. Trials in which the monkey's head was obscured, or in which the animal happened to be oriented to one or other speaker at the onset of a trial, were not included in the analysis. The latter were excluded because if the monkey's head was already oriented toward either speaker, one could not determine that it oriented when the trial began. The tapes were studied independently by two experimenters and later compared. There was virtually perfect agreement. Since it was possible that the animals were continually orienting to one or other of the two speakers, and that the analysis of the tapes simply represented the chance coincidence of an orientation with a trial onset, two control tapes were prepared. These tapes consisted of the sound part of one session recorded with the video part of the succeeding session (for the same monkey). If the distribution and number of orientations was the same in control as regular videotapes, then the data from the regular tapes could not be interpreted as orientations to the sound.

RESULTS

All animals oriented to one or other of the speakers on virtually every trial. The average percentage of orientations for all animals under all conditions was greater than 99%. The percentage of orientations measured from the control videotapes was 16%. The comparison of these two numbers indicates that orientations to the sound were being observed and counted.

Condition 1—contiguous position discrimination. Orientation and lever responding data are presented in two-by-two tables showing the number of correct (O) and incorrect ($\bar{O}$) orientations associated with correct (R) and incor-



SM 54 (0.2 MSEC)

	R	$\bar{R}$
O	62*	0
$\bar{O}$	0	0*

SM 54 (50 MSEC)

	R	$\bar{R}$
O	34*	1
$\bar{O}$	1	5*

SM 70 (50 MSEC)

	R	$\bar{R}$
O	75*	0
$\bar{O}$	1	18*

SM 514 (25 MSEC)

	R	$\bar{R}$
O	242*	0
$\bar{O}$	0	16*

SM 221 (25 MSEC)

	R	$\bar{R}$
O	180*	5
$\bar{O}$	7	21*

Fig. 2. Relation of orientation (O, correct orientation; $\bar{O}$, incorrect orientation) and lever responding (R, correct response; $\bar{R}$, incorrect response) under the condition where responding on the lever spatially contiguous with the sounding speaker was reinforced. SM 54 was studied using sounds of complex spectral content (top-left table) and pure tones (second table from the top left). All other animals were studied using pure tones. Contiguous orientation-response sequences are marked with an asterisk.

rect ($\overline{R}$) responses (Figure 2). It can be seen that correct orientations were associated with correct responses and incorrect orientations with incorrect responses; that is, the lever response could be predicted from the direction of orientation. If the direction of orientation is regarded as the behavioral definition of the sounding speaker, then the animals were responding on the lever contiguous with the sounding speaker. Cells marked with an asterisk in Figure 2 indicate responses that were contiguous with the direction of orientation. The prediction of the lever response, from the direction of orientation expressed as a percentage of the total number of orientations and responses, is given in the top part of Table 1. Also included in this table are the percentages of correct orientations and responses and the number of trials on which these figures are based. The percentage of correct orientations and responses was higher for stimuli of complex spectral content (8 kHz, 0.2-msec rise-decay time) than for pure tones (8 kHz 50-msec rise-decay time), as demonstrated by the behavior of SM 54, which was studied under both conditions.

Condition 2—noncontiguous position discrimination. These data are presented in two-by-two tables in Figure 3. The percentage of lever responses predicted from the direction of orientation, the percentages of correct orientations and responses, and the number of trials are given in the second part of Table 1. The percentage of correct orientations and responses was higher (92% and 94% respectively) for sounds of complex spectral content (8 kHz, 0.2-msec rise-decay time) than for pure tones (8 kHz, 50-msec rise-decay time) (89% and 92% respectively), as shown by SM 52 which was studied under both conditions. Figure 3 shows that the numbers in the cells O-$\overline{R}$ and $\overline{O}$-R are larger than the numbers in the corresponding cells of Figure 2. These cells in Figure 3 (marked with an asterisk) represent lever responses that were contiguous with the direction of orientation, whereas in Figure 2, the same cells (not marked with an asterisk) represent lever responses that were not contiguous with the direction of orientation. The significance of this point is considered in the Discussion.

Condition 3—tone-noise discrimination. The overall data for the tone-noise discrimination are given in Figure 4 for SM 221 and SM 514. The percentage of correct orientations and responses and the number of trials are given in the third section of Table 1. Because of the difference in the type of discrimination, the percentage of prediction of lever responses from the direction of orientation cannot be obtained from the data of Figure 4. A more detailed analysis of the data is required to reveal the type of stimulus control of orientations and lever responses and the degree of prediction; this is examined in the Discussion. The percentage of correct orientations in this condition did not differ from that found in the other two conditions.

DISCUSSION

The percentage of orientations did not differ over the three experimental conditions, nor did

Table 1

Relation between direction of orientation and responding expressed as a percentage of the total number of trials (percentage prediction). The percentages of correct orientations and responses are also tabulated.

Animal	*% Prediction*	*% Correct Orientation*	*SD**	*% Correct Responses*	*SD**	*Number of Trials*
SM 54 (0.2-msec)	100%	100%	0	100%	0	62
SM 54 (50-msec)	95%	89%	4.2	89%	4.2	56
SM 70 (50-msec)	99%	80%	0	81%	1.4	94
SM 514 (25-msec)	100%	94%	1.9	94%	1.9	258
SM 221 (25-msec)	95%	88%	4.0	89%	2.5	213
SM 52 (0.2-msec)	92%	92%	5.5	94%	3.6	104
SM 52 (50-msec)	93%	89%	3.1	92%	2.5	115
SM 221 (25-msec)	—	86%	7.7	96%	2.5	220
SM 514 (25-msec)	—	91%	3.1	73%	3.4	146

*SD = Standard Deviation

SM 52 (0.2 MSEC)

	R	$\bar{R}$
O	93	3*
$\bar{O}$	5*	3

SM 52 (50 MSEC)

	R	$\bar{R}$
O	100	2*
$\bar{O}$	6*	7

Fig. 3. Relation of orientation (O, correct orientation; $\bar{O}$, incorrect orientation) and lever responding (R, correct responses; $\bar{R}$, incorrect response) when responding on the lever opposite to the sounding speaker was reinforced (the noncontiguous position discrimination). Spatially contiguous orientation-response sequences are marked with an asterisk.

it vary with the type of stimulus presentation (single burst *versus* repeated bursts). These findings suggest that orientation is a stable accompaniment to all auditory discriminations in the squirrel monkey.

Relation of orientation direction to lever responding. It has been shown that squirrel monkeys have a strong tendency to respond on the lever that is contiguous with the sounding speaker in auditory position discriminations (Downey and Harrison, 1972, 1975; Harrison, Downey, Segal, and Howe, 1971). In these experiments, sounds of complex spectral content were used and the percentage of

SM 221

	R	$\bar{R}$
O	210	10
$\bar{O}$	27	1

SM 514

	R	$\bar{R}$
O	94	39
$\bar{O}$	12	1

Fig. 4. Relation between orientation and lever responding during the tone-noise discrimination. O, correct orientations; $\bar{O}$, incorrect orientations; R, correct responses. $\bar{R}$, incorrect responses. Responding on the left lever in the presence of tone was reinforced and responding on the right lever was reinforced in the presence of noise.

correct responses was at or near 100%. SM 54 (8 kHz, 0.2-msec rise-decay time) was studied under identical conditions to those used in these experiments and all responses were made on the lever contiguous with the sounding speaker and all orientations were correct. When pure tones were used, the percentage of correct orientations fell to between 80% and 94%. Inspection of the data presented in Figure 2 shows that incorrect orientations were followed by responses on the lever contiguous with the speaker oriented to ($\overline{\text{O-R}}$) in the vast majority of cases. This finding, together with the finding that correct orientations were followed by responses on the lever contiguous with the sounding speaker, indicate that the prior findings actually represented a strong tendency of squirrel monkeys to respond on the lever contiguous with the speaker oriented to (direction of orientation), rather than to respond on the lever contiguous with the sounding speaker. Cells containing such contiguous responses are marked with an asterisk in Figure 2. Cells O-$\overline{\text{R}}$ and $\overline{\text{O}}$-R represent responses on the lever not contiguous with the direction of orientation, and the numbers in these cells are small compared with the numbers in the other two (contiguous) cells. Squirrel monkeys are unlikely to make such orientation-response sequences.

In noncontiguous as well as contiguous position discriminations, the animal oriented toward the sounding speaker with essentially the same percentage of correct orientations found in Condition 1. Lever responding was under control of the position of the noncontiguous sounding speaker (the reverse of that found in Condition 1). Hence, changing the relation of lever responding to reinforcement from Condition 1 to Condition 2 did not change the control of orientation, but did change the control of lever responding. The prediction of lever responses from the direction of orientation in Condition 2 was slightly lower than the values found in Condition 1 (Table 1). The reason for this can be seen from the distributions in Figures 2 and 3. The cells O-$\overline{\text{R}}$ and $\overline{\text{O}}$-R in Figure 3 represent contiguous orientation-response sequences, whereas the corresponding cells in Figure 2 represent noncontiguous sequences. The numbers in these cells in Figure 3 are larger than those in the corresponding cells in Figure 2. This is interpreted as showing that in spite of the reinforcement of noncontiguous responding in Condition 2, the tendency of the squirrel monkey to give contiguous orientation-response sequences was not completely abolished. Contiguous orientation-response sequences raise the prediction value in Condition 1 and lower it in Condition 2.

In the tone-noise discrimination, orientation was also under the control of the position of the two sounds (compare the percentage of correct orientations of SM 221 and SM 514 in Conditions 1 and 3 in Table 1). The stimulus control of responding was different for the two animals. This can be seen most clearly by analyzing the behavior in the presence of the noise trials in Condition 3 (Figure 5). SM 221 and SM 514 gave 98% and 100%, respectively, correct orientations. In SM 221, lever responding was under control of the spectral content of the noise (95% correct responses). Thus, whether the animal correctly oriented to the left or right speaker, 95% of the responses were RRs. Prediction was at the chance level (52%), *i.e.,* one could not predict lever response choice on the basis of orientation direction. In SM 514, lever responding came under control of the position of the noise, and not its spectral content (48% correct responses), responses being on the lever contiguous with the sounding speaker (see inset tables in Figure 5). Hence, the lever response could be predicted from the direction of orientation in 100% of the trials. In this animal, the tendency to respond on the lever spatially contiguous with the sounding speaker was sufficiently strong to prevent development of control by the spectral content of the noise, although differential reinforcement was correlated with this dimension of the sound.

Stimulus control of responding and orientation. Downey and Harrison (1972) suggested that orienting behavior may determine the rapid acquisition of the control of responding by sound position when the reinforced response is contiguous with the sounding speaker. It was assumed that the monkey oriented to the speaker, and that this orientation brought the correct response lever into the line of sight. The resulting visual stimulus then produced the correct response. This hypothesis implied a functional relation between orientation and lever responding, the orientation

SM 221

	$\overline{RL}$	RR
O	6	129
$\overline{O}$	1	2

SM 514

	$\overline{RL}$	RR
O	38	35
$\overline{O}$	0	0

NOISE RIGHT

	$\overline{RL}$	RR
OR	0	34*
$\overline{OL}$	0*	0

NOISE LEFT

	$\overline{RL}$	RR
OL	38*	1
$\overline{OR}$	0	0*

Fig. 5. Responding of SM 221 and SM 514 in the noise trials of the tone-noise discrimination. RR (response on right lever) was correct and $\overline{RL}$ (response on left lever) was incorrect. O, correct orientation: $\overline{O}$, incorrect orientation. The two small inset tables (SM 514) show the breakdown of the data for noise-right and noise-left trials to demonstrate that responding was under the control of noise position. Contiguous orientation-response sequences are marked with an asterisk.

being a necessary determiner of the response. An alternative hypothesis is that orientation and lever responding are correlated when they are both under the control of the same parameter of the sound, but that they may be under the control of different aspects of the sound.

That is, in certain conditions, they may be uncorrelated.

The present data favor the independent stimulus-control hypothesis. In Conditions 1 and 2, both the orientation and the lever responding were under control of the position of the stimulus, hence the two responses were correlated. In SM 221 (Condition 3) orientation was under control of the position of the sound for the noise trials, and lever responding was under control of the spectral content of the noise. Since these two parameters of the noise were not correlated in terms of control, orientation and lever responding were not correlated.

The results of an experiment by Downey and Harrison (1975) also suggested that orientation and lever responding may be correlated, but that they are not functionally related. Squirrel monkeys were trained in an auditory position discrimination in total darkness. Responding on the lever contiguous with the sounding speaker was reinforced. Acquisition of stimulus control was as rapid in complete darkness as in normal illumination, indicating that the visual stimulus of the lever produced under conditions of normal illumination by the orientation was not essential for the rapid acquisition.

Stimulus parameters and control of responding by the position of a sound. It is well known that in man and other mammals, the control of responding by the position of a pure tone is weaker than control by the position of stimuli of complex spectral content (Beecher and Harrison, 1971; Brown, Beecher, Moody, and Stebbins, 1975; Casseday and Neff, 1973; Gentry, 1967; Harrison and Beecher, 1969; Stevens and Davis, 1938, p. 197; Terhune, 1974). This finding is confirmed and extended to orientation responses in the present experiment. SM 52 and SM 54 were studied using both pure tones and sounds of complex spectral content. Both the percentage of correct orientations and lever responses were lower for pure tones. In the tone-noise discrimination, SM 221 gave 98% and SM 514 gave 100% correct orientations to the noise and only 77% and 82%, respectively, to the tone. West and Harrison (1973) have also shown that unconditioned orientation responses in cats were accurate when sounds of complex spectral content were used.

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