CONTROL OF RESPONDING BY SOUNDS OF DIFFERENT QUALITY: AN EVOLUTIONARY ANALYSIS

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Two experiments investigated the acquisition of discriminations between two acoustic stimuli of different quality (noise bursts vs. a 2-kHz pulsed signal) when features of the everyday environment were incorporated into the experiments. In Experiment 1, rats were trained, using food, to press a lever. Throughout all sessions, 5-s trials of noise bursts (the random stimulus) were presented, after variable intertrial intervals, through a remote speaker mounted outside the experimental enclosure. The noise bursts occurred randomly with respect to reinforcement of lever pressing and had no programmed relationship to the animal's behavior. When lever pressing was established, the 2-kHz signal was presented through a speaker adjacent to the response lever according to a different set of variable intertrial intervals. A response in the presence of the 2-kHz signal terminated the trial and was reinforced. The 2-kHz signal acquired control of responding within the first few trials, whereas the random stimulus exerted no control of responding. In Experiment 2, rats were trained to press the lever in the presence of the 2-kHz signal presented through the adjacent speaker on a variable intertrial interval. After 14 sessions, 5-s trials of noise bursts (random stimulus) were presented through the remote speaker on the second variable intertrial interval. The random stimulus initially elicited exploratory behavior, which then rapidly declined. Subsequently, the random stimulus exerted no or weak control of responding. The introduction of the random stimulus had no effect on responding in the presence of the adjacent stimulus.

In Experiments 3 and 4 the random stimulus was presented through the adjacent speaker, and the stimulus correlated with reinforcement was presented through the remote speaker. In both experiments, there was persistent control of responding by the random stimulus and slow development of control by the stimulus correlated with reinforcement. In Experiment 5, both stimuli were presented through the adjacent speaker. There was persistent control of responding by the random stimulus.

Key words: sounds of different quality, evolutionary analysis, everyday environmental features, auditory discrimination, sound-quality discrimination, rats

That behavior can come under the control of auditory stimuli is one form of behavioral adjustment to the everyday environment. This capacity has evolved in the species and developed in the individual in environments in which many features have been constant over indefinitely long time periods. It is therefore to be expected that this behavioral capacity will fit the environment in which the capacity is normally exercised.

A two-step method has been used to study auditory discrimination within an evolutionary context (Harrison, 1982, 1984a, 1984b). The first step consists of studying the performance of an animal in an auditory discrimination task in which the apparatus and procedure incorporate a number of environmental

features (naturalistic features) that are present when the organism interacts with sound-producing objects and events under everyday conditions. The major assumption underlying this step is that if, at least, the essential naturalistic features are incorporated into the experiment, the discrimination will be very rapidly acquired, possibly within a single trial. Thus, rhesus and squirrel monkeys (Downey & Harrison, 1972, 1975; Harrison, Iversen, & Pratt, 1977), rats (Beecher & Harrison, 1971; Harrison, 1979; Kelly, 1980), cats (Beecher, 1970; Frysz & Stepień, 1983), bats (Beecher, 1970), and dogs (Konorski, 1967; Lawicka & Szczechara, 1979) acquired a sound-source position discrimination in one trial, with no evidence of an acquisition curve, when naturalistic features were incorporated into the experiments.

The second step consists in determining the role, if any, of each naturalistic feature incorporated into the experiment. In this step the acquisition of the discrimination is studied af-

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ter each feature has been modified or eliminated. Thus, it was found that one-trial acquisition of the sound-source position discrimination depended on stimulus novelty at the start of discrimination training, adjacency of sound sources and manipulanda, and the use of stimuli other than pure tones (Downey & Harrison, 1972; Harrison, 1981, 1983, 1984a; Harrison & Beecher, 1969; Harrison, Downey, Segal, & Howe, 1971; Harrison et al., 1977). It was also found that the effect of reinforcing a response in the presence of a novel auditory stimulus was to strengthen the response of orienting to and approaching the sound source (Beecher & Harrison, 1971; Buzsáki, 1982; Buzsáki, Grastyán, Molnár, Tveritskaya, & Haubenreiser, 1979; Buzsáki, Grastyán, Winiczai, & Mod, 1979; Grastyán, 1961; Harrison, 1979; Kelly, 1980; Kupalov, 1969, 1978; Lawicka, 1979; Pavlov, 1934).

The purpose of the present series of experiments was to apply the two-step method to the investigation of the control of responding by two auditory stimuli differing in spectral content and temporal pattern.

EXPERIMENT 1

The purpose of the first experiment was to investigate the development and maintenance of differential control of responding by two sounds differing in spectral content and temporal patterning when a number of naturalistic features were incorporated into the apparatus and procedure. These features, based upon the following considerations, were incorporated into the experiment.

General properties of acoustic environments. Auditory discriminations, which have a number of enduring acoustic properties, are acquired in everyday environments. Many of the sound sources in everyday environments occur randomly with respect to each other; thus some will, by chance, happen at the same time. Some of the sources will be correlated with reinforcing events, whereas other sources, not themselves correlated with reinforcement, will fortuitously overlap the sources correlated with reinforcement. The two stimuli used in this experiment satisfied these requirements. The stimuli occurred randomly with respect to each other; one stimulus (S+) was correlated with reinforcement, whereas the other (the random stimulus) was not correlated with reinforcement

and fortuitously overlapped the S+ from time to time. To make the experimental environment further resemble the everyday acoustic environment, normal laboratory noises were not excluded.

The sound-producing objects of everyday environments usually occupy different locations. These environments also contain many sound-reflecting objects, and reflections from these may give rise to secondary or apparent positions of each sound-producing object. In the experiments, the two programmed stimuli were presented through separate speakers, and no effort was made to eliminate room or apparatus echoes. It has been shown that the actual position of a sound source can control responding in the rat in the presence of artificial echoes (Hoeffding & Harrison, 1979; Kelly, 1974a, 1974b).

Organisms occupy a given area of the environment for an extended period and are thus exposed repeatedly to the recurring sound-producing objects of that area. Discriminative adjustment is required when a new sound-producing object is introduced into the area. In the present experiment, a new programmed stimulus was introduced only after the animal had previously worked in the experimental environment.

Pure tones rarely occur in the field. They are poorly localized and relatively ineffective as discriminative stimuli (Harrison & Beecher, 1969; Harrison & Briggs, 1977; Heffner, 1981; Heffner & Heffner, 1982; Marler, 1955, 1967; Segal & Harrison, 1978; Terhune, 1974). Direct measurement of interaural intensity differences produced by tones of different frequency at different azimuths in rats and squirrel monkeys also indicated that tones are likely to be poorly localized at more than a few degrees either side of zero azimuth (Harrison & Downey, 1970). The sound source must be localizable for the species under study. In general, stimuli of complex spectral content with rapid onset times are most readily localized (Brown, Beecher, Moody, & Stebbins, 1978, 1980; Brown, Schessler, Moody, & Stebbins, 1982; Harrison & Beecher, 1969; Kelly, 1981). Masterton, Thompson, Bechtold, and RoBards (1975) have investigated localization in a variety of species. The stimuli used in the present experiments have been shown to be localizable by rats in previous experiments (Harrison, 1984a; Neill & Harrison, 1987).

Behavioral interactions with the acoustic environment. Natural environments impose certain kinds of behavioral interactions with sounding objects to the exclusion of others. The following are the behavioral features that have been included in the experiments.

The stimuli at the ears in everyday environments are not the same each time a given source sounds because the animal is free to move, and thus occupies different places with respect to the source. The animals were free to move in the present experiments.

An animal approaches and manipulates sounding objects with which it is interacting. Thus, the site of the object, its auditory location, and the terminal responses are all spatially contiguous. This spatial contiguity was preserved in this experiment for the stimulus correlated with reinforcement.

Auditory stimuli above about 85 dB (SPL) are aversive (Barry & Harrison, 1957; Harrison & Abelson, 1959). Because animals approach and interact with the sound source, the intensity present even right at the source must be below the aversive threshold. The stimuli used in the present experiments were below the aversive threshold in all parts of the apparatus. The lowest intensity that can be used is set by the requirement that the stimulus be above the absolute intensity threshold in all parts of the apparatus (see Gourevitch & Hack, 1966; Harrison & Turnock, 1975; Kelly & Masterton, 1977, for measurements of the rat audiogram).

A new low-intensity sound introduced into a familiar environment elicits exploratory behavior, the source being oriented to, approached, and manipulated (Alvarado-P. & Santibañez-H., 1971; Buzsáki et al., 1979; Clements & Kelly, 1978a, 1978b; Czehak, 1977; Harrison, 1979, 1983; Kelly, 1981, 1982; Kupalov, 1969, pp. 740-741; Pavlov, 1927, pp. 29, 43, 1934; Petrinovich, 1973; Potash & Kelly, 1980; Rogozea, Ungher, & Florea-Ciociu, 1970; Santibañez-H., 1976; Sokolov, 1963, 1966; Thompson & Welker, 1963; West & Harrison, 1973). If the sound source is biologically significant (an S+) the approach and exploratory responses will be reinforced, constituting a natural discrimination training trial. These considerations suggest that stimuli correlated with reinforcement should be novel at the start of discrimination training. The directional aspects of the elicited orientation and approach to the source are dependent upon

binaural cues in the rat (Burlile, Feldman, Craig, & Harrison, 1985; Potash & Kelly, 1980), dog (Engelmann, 1928), and guinea pig (Clements & Kelly, 1978a).

Behavioral adjustment to the introduction of a new sound, correlated with reinforcement (S+), into an experimental environment which contained a second stimulus (random stimulus) and all the naturalistic features enumerated above was studied in this experiment. The S+ was introduced through a speaker adjacent to a response lever, and the second stimulus, not correlated with reinforcement, was presented through a speaker mounted outside the animal enclosure and remote from the lever.

METHOD

Subjects

The subjects were four experimentally naive male Sprague-Dawley rats, 100 to 120 days old at the start of the experiment. The animals were housed one to a cage with ad-libitum water. Body weight was reduced to 90% of that under free-feeding conditions. Four animals were used in each experiment.

Apparatus

The apparatus consisted of a wire cloth cage (30 cm deep, 35 cm wide, and 30 cm high) with a single response lever mounted on one wall, 5 cm from the corner and 10 cm above the floor. A funnel was fixed to the front of a speaker (Radio Shack 40-170), and the speaker (adjacent speaker) was mounted so that the opening of the funnel was immediately above the lever. Another funnel was fixed to the front of a second speaker (remote speaker), which was mounted 25 cm above and 35 cm to the side of the animal enclosure. A 7.5-W house-light was mounted on the roof of the enclosure. The apparatus was housed in a room separate from the programming equipment. The performance of the animal could be observed and videotaped through a transparent panel in the door of the room.

Two stimuli were used. One consisted of bursts (125 ms on and off) of wide-band noise, which had a continuous spectrum from 4 kHz to 50 kHz. The acoustic spectrum of this and the second stimulus has been published elsewhere (Neill & Harrison, 1987). The second stimulus consisted of bursts (50 ms on and off) of a 2-kHz rectangular pulse. This stimulus produced a picket-fence acoustic spectrum

Table 1
Intervals (s) in the two variable-interval timers.

Random stimulus	S+
34	44
19	27
72	46
54	15
48	32
35	55
50	22
10	41
79	8
20	25
69	52
Mean 44.55	35
	46
	41
	Mean 34.93

(spaced at 2 kHz) to 50 kHz. Because the two stimuli have been shown to be equally effective behaviorally, not all combinations of stimuli and modes of presentation were used.

The intensities of the stimuli were set using a 0.6-cm Bruel and Kjaer microphone (4135), calibrated with a Bruel and Kjaer pistonphone (model 4220). The microphone was placed 0.5 cm in front of the funnel opening of the adjacent speaker, and the intensity of the noise was set to 75 dB, SPL. The intensity at the center of the cage produced by this signal was 46 dB, SPL. The intensity of the noise when presented through the remote speaker was adjusted to 46 dB, SPL, at the center of the cage. The intensity of the 2-kHz signal when presented through the adjacent speaker was set to the same peak-to-peak value as produced by the noise at that speaker. The stimuli were continuously monitored by two on-line digital multimeters (Tektronix DM 502A).

Previous work has shown the two stimuli to be behaviorally equivalent in the following context. Both elicited the same exploratory behavior when novel, equally rapid acquisition of a go-left/go-right sound source position discrimination was obtained with both stimuli, and the noise and the 2-kHz signal were the same as an S+ in go/no-go sound source position discriminations (Harrison, 1983; Neill, 1986; Neill & Harrison, 1987). Because of the behavioral equivalence of the stimuli it was

decided to keep the sound field created by each stimulus the same across experiments rather than change the sound fields by presenting the stimuli through different speakers in different experiments.

To reduce the background noise of the power amplifiers to below the animal's auditory threshold, the speakers were connected to the amplifiers via -20 dB attenuators. This prevented the background noise from serving as a discriminative stimulus. Random spikes coming in on the AC supply were reduced to the random noise level of the amplifiers by using a constant voltage transformer (Sola, type CVS 2), a line filter (Corcom, 10VR1), and multioxide varistors across common and differential modes on the AC supply. Cross talk between the two signals was reduced to the background noise level by using independent signal paths joined and grounded at only one place.

The noise and rectangular pulses were generated by Coulbourn Instruments modules (S81-02 and S25-05, respectively). The stimuli were gated using Coulbourn Instruments electronic switches (S84-04), set to the minimum rise-decay time. The experiments were programmed by a Sym-1 computer in conjunction with Coulbourn Instruments solid-state equipment.

Procedure

Preliminary training. During preliminary training, 5-s trials of noise bursts (the random stimulus) were presented through the remote speaker on a 45-s variable intertrial interval (see Table 1 for the intervals). The random stimulus was programmed from the first time the animal was placed in the apparatus on the first day of habituation through all the sessions until the end of the experiment. Responding in the presence of the stimulus had no programmed consequence. The adjacent speaker was unplugged during preliminary training.

Lever pressing was shaped using sweetened condensed milk (one part milk to three parts water) as the reinforcer. Responding was then reinforced on a 35-s variable-interval schedule (see Table 1 for the intervals). This schedule was operated by a different timer and used different intervals than the schedule used to program the random stimulus. The tapes on the two timers were of different lengths so that

the relative positions of the tapes in the two timers were constantly changing. Because the two timers were independent of each other, the random stimulus occurred randomly with respect to a reinforced response and was present, from time to time, when a response was reinforced. Preliminary training continued until the animals were responding at least 200 times per hour (usually after two to three sessions). At this stage discrimination was started.

Discrimination training. Discrimination training started in the session following the last preliminary training session with the presentation of the 2-kHz signal (S+) through the adjacent speaker. The adjacent speaker was plugged in. The S+ came on when the 35-s reinforcement timer timed out and remained on until a response, which was reinforced, was made. Thus, S+ trials occurred independently of random-stimulus trials, and the two stimuli overlapped from time to time. A response that occurred during the overlap of the two stimuli was reinforced. That is, reinforcement was delivered, from time to time, in the presence of the random stimulus.

The animals received at least 10 sessions of discrimination training. The remote speaker was then unplugged (thus removing the random stimulus), but all response measures remained unaltered, and the animals were studied for at least an additional five sessions.

Sessions, which were 46 S+ trials (i.e., 46 reinforcements) long, were conducted daily, 7 days a week. Animals received 37 random-stimulus trials per session. The houselight remained on during the session.

Response measurements. Control of responding by the random stimulus was measured by comparing the number of trials per session in which one or more responses were made in the presence of the random stimulus with the number of times per session one or more responses were made in the 5 s preceding the random-stimulus trial (pseudotrial). Equality of responses in trials and pseudotrials indicated no control by the random stimulus. If the number of responses in the random-stimulus trials was larger or smaller than the number of responses emitted in the pseudotrials, then the random stimulus was considered to be exerting some control of responding.

Control of responding in S+ was measured in a similar way, by comparing the number of

trials in which a response was made within 5 s of the onset of the S+ with the number of responses made in the 5 s preceding the random stimulus (pseudotrial).

The average latency of S+ responding per session was measured by dividing the total time the S+ was on by the number of S+ trials (46). The S+ remained on until a response was made. The number of responses occurring during the overlap of the S+ and the random stimulus was also recorded.

RESULTS

The percentage of trials per session in which one or more responses occurred in less than 5 s in S+, the random stimulus, and the pseudotrials for each animal is shown in Figure 1.

Performance in the random stimulus. The percentage of random-stimulus trials in which a response was made and the percentage of pseudotrials in which a response was made are shown in the two bottom lines in each panel. There was no difference between pseudotrial and random-stimulus trial responding; that is, there was no control of responding by the random stimulus. The two points before Session 1 in Figure 1 show the percentage of random-stimulus trials and pseudotrials in which a response was made in the last session before the S+ was introduced. There is no indication that the introduction of the S+ modified the lack of control by the random stimulus. After at least 14 sessions, the remote speaker (through which the random stimulus was presented) was unplugged, thus making random-stimulus trials indistinguishable from pseudotrials. There was no change in performance.

Performance in S+. The percentage of S+ trials in which a response was made within 5 s is shown for each animal in the upper curve in each graph in Figure 1. The measure is equivalent to that used for recording performance during the random stimulus and can be compared with responding during the pseudotrials. Responding during S+ exceeded the level of responding in the pseudotrials in all sessions and for all animals. That is, S+ controlled responding to between the 90% and 100% levels from the first session on. There was a large difference between the percentage level of responding in the random stimulus and S+. In other words, there was differential con-

Fig. 1. Percentage of S+ (adjacent speaker) trials in which response latency was less than 5 s is shown in the upper line of each panel. The percentage of random-stimulus (remote speaker) trials (filled circles, solid lines) and pseudotrials (open circles, solid lines) in which a response was made is shown in the lower two lines in each panel. The random stimulus was discontinued at the vertical line (no RS), the animals now receiving pairs of pseudotrials. The filled (random stimulus) and open (pseudotrials) circles unconnected to the remainder of the points show responding in the last session before discrimination training was started (no S+).

trol of responding by the two stimuli from the start of discrimination training.

The percentage of trials per session, for a typical animal, in which the S+ and the random stimulus overlapped and a response was reinforced is shown in Figure 2. These data show the percentage of trials in which responding was reinforced in the presence of the random stimulus.

The first discrimination session was videotaped. Inspection of the tapes showed that all animals gave the typical exploratory response when the S+ was first introduced (Harrison, 1979, 1983). R446, for example, showed an immediate change in the stream of behavior at the onset of the first S+ trial. The animal ran over to, reared up on its hind legs, and bobbed

around in front of and occasionally sniffed the funnel opening. This animal gave a similar response on the second trial.

DISCUSSION

The animals' behavior fit the experimental environment well. The S+ immediately gained control of responding, whereas responses continued to be uncontrolled by the random stimulus. There was no control of lever pressing by the random stimulus. The role of adjacency in the control of responding by random stimuli is not known, but the work on adjacency cited above suggests that the remoteness of the speaker from the lever was a factor in the lack of control.

The positive stimulus (S+) immediately

gained control of responding. This can be attributed to three factors. First, the sound source was adjacent to the response lever. Prior work has shown that adjacency is a critical variable in the acquisition of sound-source position and quality-difference discriminations (Downey & Harrison, 1972; Harrison, 1981; Harrison et al., 1971, 1977; Neill, 1986; Neill & Harrison, 1987; Segal & Harrison, 1978). Other work has shown that animals' behavior has evolved so that the effect of reinforcing a response in the presence of a remote sound source is to strengthen the response of approaching the sound source.

Second, the S+ was novel when first presented, and it elicited approach to and exploration of the source, thus bringing the animal to the lever (Downey & Harrison, 1972; Harrison, 1979, 1983).

Third, for the first few S+ trials, while the stimulus was novel, responding in the S+ was reinforced. Prior work has shown that rapid acquisition (one or two trials) of auditory discriminations was obtained only when the stimulus was novel at the start of training (Harrison, 1979, 1981; Neill & Harrison, 1987). Animals required many sessions to acquire the discriminations when they were preexposed to the stimulus (Harrison, 1979, 1983, 1984a). The retarding effect of stimulus preexposure of the acquisition of discriminations has been studied by Lubow (1973) under the name of latent inhibition. In experiments in which rats were exposed to an auditory stimulus paired with shock, preexposure reduced its effectiveness as a conditioned stimulus (Carlton & Vogel, 1967; Crowell & Anderson, 1972; Hall & Pearce, 1979; Lubow, Schnur, & Rifkin, 1976; Rescorla, 1971). Equivalent effects in food reinforcement experiments have been reported by Harrison (1979), Halgren (1974), and Mellgren and Ost (1971).

EXPERIMENT 2

In the first experiment the new event introduced into the familiar environment (which contained the random stimulus) was the S+. Under everyday conditions, novel stimuli, uncorrelated with reinforcement, are introduced into familiar environments. It can be expected that such stimuli would initially elicit exploratory behavior of the source, followed by a transient control of responding until sufficient occurrences of the stimulus had occurred to

Fig. 2. The percentage of random-stimulus trials that overlapped a reinforced response in S+ for a typical animal; that is, the percentage of trials in which responding in the presence of the random stimulus was reinforced.

establish its random relationship to reinforcement. In the present experiment, the new event introduced into the familiar environment (which contained the S+) was the random stimulus. The experiment incorporated the same naturalistic features as the first experiment. This experiment was made symmetrical with the first experiment in that the random stimulus was added at Sessions 15 or 16.

METHOD

Subjects and apparatus. The subjects were four experimentally naive male Sprague-Dawley albino rats, 100 to 120 days old at the start of the experiment. The animals were housed and fed as described in Experiment 1, and the apparatus was the same as that used in the first experiment.

Procedure. Animals were trained in a quality-difference discrimination task in which a stimulus, randomly related to reinforcement, was introduced into a familiar experimental environment in which an S+ already controlled responding. (Both speakers were unplugged during preliminary training; otherwise preliminary training was the same as that used in Experiment 1.) When the response rate reached at least 200 responses per hour, the adjacent speaker was plugged in and the S+ introduced as in Experiment 1. The animals worked for 14 or 15 sessions under this condition (the remote speaker was still unplugged).

The timer that controlled the random stim-

Fig. 3. The percentage of S+ (adjacent speaker) trials in which response latency was less than 5 s is shown in the upper line in each panel. The percentage of each of the pairs of pseudotrials in which a response was made (up to Session 16) is shown in the lower two plots of each panel. At the vertical line the novel random stimulus (RS) was introduced by plugging in the remote speaker. Responding in the random-stimulus trials is shown by the filled-circle, solid-line plots, and responding in the pseudotrials by the open-circle, solid-line plots. There was transient weak control by the random stimulus in R275, R281, and R443, and no control in R278. The filled and open circles unconnected to the remainder of the points for R443 show responding in the pairs of pseudotrials in the last session before the start of discrimination training (no S+).

ulus operated throughout the 14 or 15 sessions, but, because the remote speaker was unplugged, the timer was simply setting up pairs of pseudotrials. In Sessions 15 or 16 the random stimulus was introduced as follows. The session was started with the remote speaker unplugged for the first 10 trials. The remote speaker was then plugged in, and the first trial of the random stimulus was programmed to occur 1 s before the next (11th) S+ trial. All subsequent random-stimulus trials were programmed by the random-stimulus variable-interval timer. The random stimulus consisted of the noise presented for 5-s trials through the remote speaker. The animals worked for at least six sessions under this condition.

Response measurements were the same as those used in the first experiment.

RESULTS

The percentage of trials per session (for the first 14 or 15 sessions) in which one or more responses occurred in less than 5 s in S+ and in the pairs of pseudotrials is shown in Figure 3. Responding in the pairs of pseudotrials in the last session before the introduction of S+ was recorded for R443.

Responses in the random stimulus. Responses in the pairs of pseudotrials are presented in Figure 3. The filled-circle, solid-line plots indicate performance in what would have been random-stimulus trials had the remote speaker

Table 2
Response latency (s).

Trial	R275	R278	R281	R443	Condition
1	2.8	1.1	0.75	1.2	No RS
2	1.15	0.6	1.5	2.15	No RS
3	0.85	0.5	0.5	2.2	No RS
4	0.6	1.2	1.3	1.95	No RS
5	1.7	1.7	1.4	1.4	No RS
6	3.2	1.5	0.4	2.4	No RS
7	1.5	0.35	1.65	1.7	No RS
8	2.9	1.5	2.7	1.3	No RS
9	2.4	1.9	0.8	0.5	No RS
10	4.6	0.4	1.65	0.9	No RS
11	9.35	8.3	2.1	3.1	Novel RS
12	1.2	2.2	1.7	1.3	RS (no S+ overlap)
13	1.75	0.85	2.7	1.35	RS (no S+ overlap)
14	1.15	0.8	1.2	0.7	RS (no S+ overlap)

Note: No RS, no random stimulus. RS, random stimulus present.

been plugged in. Pseudotrials are indicated by the open-circle, solid-line plots. It can be seen that there was no difference in responding in the two pseudotrials (remote speaker was unplugged). These data show that no other events correlated with turning on the random-stimulus circuits differentially controlled responding.

In Sessions 15 or 16 the novel random stimulus was introduced for the first time in Trial 11. The effect of the first presentation of the random stimulus can be seen from the latency data presented in Table 2. The latency on Trial 11 was longer for R275, R278, and R443 than any of the latencies of the preceding 10 trials when the stimulus was absent. For R281, one latency (2.7 s) was longer than the latency (2.1 s) of Trial 11. The latencies returned to normal by Trial 12, as can be seen in Table 2. The increased latency was due to the exploratory behavior elicited by the first presentation of the random stimulus. R275, R278, and R443 ran over to the corner of the cage closest to the remote speaker and oriented to the speaker when the stimulus was presented. They then returned to the lever and sounding adjacent speaker and pressed the lever. R281 simply oriented in the direction of the remote speaker from a position near the lever. Inspection of the data suggests that weak control of responding by the random stimulus developed, then faded out, in R281 and R443. There was possible weak control in Session 20 for R275. Control was absent in R278.

Responding in S+. This is shown in the upper curves of Figure 3. R278 and R281

emitted between 90% and 100% of responses in S+ with latencies less than 5 s, this behavior remaining stable from the first session. The level of pseudotrial responding was much lower; that is, there was strong control of responding by S+ from the time it was first introduced. The percentage of S+ trials shorter than 5 s was also higher than the level of pseudotrial responding for R275 and R443 from the first session, showing control by S+, but the level improved over the first one to four sessions. The reason for this was not clear.

The only behavioral effect on responding in S+ produced by the introduction of the random stimulus was in Trial 11 as described in Table 2. There was strong differential control of responding by the two stimuli essentially from the introduction of the random stimulus.

DISCUSSION

Responding in S+ was similar to that in the first experiment, and the points concerning S+ raised in the discussion of the first experiment apply here. The introduction of the random stimulus had no effect on S+ responding, except for the increase in S+ response latency in Trial 11 (Table 2).

The random stimulus acquired weak control of responding at Session 18 in R281 and possible weak control at Session 20 in R275. In both animals there was no control by the random stimulus in subsequent sessions. There was some suggestion of transient control in R443. The random stimulus did not gain control of responding in R278. Because the random stimulus was presented through the re-

mote speaker it was expected that any control of responding that did develop would be weak. The transient control that did develop was, presumably, a manifestation of the fact that the animal must be exposed to some number of overlapping and nonoverlapping of the random stimulus with S+ for the stimulus to cease controlling the animal's behavior. A single occurrence of the random stimulus could not establish its relationship to reinforcement.

The first two experiments included many naturalistic features, one or more of which was probably responsible for the performance of the animals in the two tasks. The significance or lack of significance of each feature can be determined only by the experimental manipulation of that feature. In the following three experiments, the features of adjacency and separate position of two different sound sources were varied.

EXPERIMENT 3

It was suggested in the discussion of the first experiment that, on the basis of previous work, adjacency was probably a significant determinant of the high percentage level performance in S+. The role of the remoteness of the speaker on performance in the presence of the random stimulus is not known. The purpose of the third experiment was to investigate the role of adjacency on performance in the presence of the two stimuli. This was done by presenting the random stimulus through the adjacent speaker and the S+ through the remote speaker. The intent was to change adjacency while keeping all other acoustic features of the experiment identical to those of the first two experiments. Only the behavioral relationship of the organism to the stimuli was changed. The two stimuli appear to be behaviorally similar as described in the method section of the first experiment.

METHOD

Subjects. Four experimentally naive male Sprague-Dawley albino rats, 100 to 120 days old, served as subjects. The animals were housed and fed as described in Experiment 1.

Apparatus. The apparatus was the same as that used in the first two experiments. The random stimulus was the 2-kHz signal presented through the adjacent speaker, and S+ was the noise presented through the remote speaker.

Procedure. The remote speaker was unplugged, and 5-s trials of the random stimulus were presented through the adjacent speaker; otherwise preliminary training was the same as that used in Experiment 1. When response rate reached at least 200 per hour, discrimination training was started and was similar to that of Experiment 1, except that S+ was presented through the remote speaker. After at least 10 discrimination-training sessions, the adjacent speaker (random stimulus) was unplugged. The animals were studied for two to five sessions under this condition.

RESULTS

Preliminary training. During lever-response shaping in the first two experiments, the presentation of the remote random stimulus did not seem to affect the animal's behavior. In contrast, it was found in the present experiment that if the adjacent random stimulus happened to come on when an approximation to a lever press was reinforced, subsequent occurrences of the random stimulus resulted in the animal running over to the vicinity of the lever. This behavior declined if there were no pairings over the next few reinforcements, only to reappear on later overlaps of the random stimulus with reinforcement. The details of the coming and going of the control by the random stimulus were difficult to follow, but they were clearly different from the behavior during shaping in the first two experiments.

Performance during the random stimulus. Performance in the random-stimulus trials and pseudotrials is shown in Figure 4. For 3 animals, the percentage of random-stimulus trials in which at least one response was made was higher than the percentage level in the pseudotrials. That is, there was control of responding by the random stimulus. This control persisted for the duration of training for R458 and for all but the first session for R457. For R459 there was only weak evidence of control of responding by the random stimulus from the second to the sixth session. The performance in the random-stimulus trials and pseudotrials in the last session before the introduction of S+ is shown by the two isolated points before Session 1 for R457, R458, and R459.

At the end of discrimination training, the adjacent speaker was unplugged (no RS), and the animals were then exposed to pairs of pseu-

Fig. 4. Percentage of S+ (remote speaker) trials in which response latency was less than 5 s is shown in the upper line in each panel. Note the slow increase in percentage of response latencies of less than 5 s in R297, R458, and R459 and the low asymptotic level in R457. The percentage of random-stimulus (adjacent speaker) trials (filled circles, solid lines) and pseudotrials (open circles, solid lines) in which a response was made is shown in the lower two lines of each panel. There was a persistently larger percentage of random-stimulus responses than pseudotrial responses for 7 to 14 sessions. The adjacent speaker (random stimulus) was unplugged at the vertical line (no RS); there was no difference in responding between the pairs of pseudotrials beyond the vertical line.

dotrials. There was no difference between performance in the two sets of pseudotrials.

Performance in S+. The first presentation of S+ in the first session at the start of discrimination training elicited typical exploratory behavior. There was an immediate change in the stream of behavior. The animals oriented to and ran over to the corner of the cage nearest the remote speaker. They then climbed the wall to a position close to the speaker.

Performance in S+ is shown in the upper curves of Figure 4. All animals showed a slow increase in the percentage of S+ responses per session emitted within 5 s of the onset of S+. This was most marked in R297. All animals showed a pattern of S+ responding charac-

terized by a few long latencies scattered among sequences of short latencies. The level of responding in S+ was above the pseudotrial level in all animals for all sessions, indicating control of responding by S+.

The difference in level of responding between the S+ and the random stimulus shows that there was differential control of responding by the two stimuli.

DISCUSSION

The switching of S+ to the remote speaker and the random stimulus to the adjacent speaker in this experiment resulted in the appearance of responding in the random stimulus and a worsened control of responding by the S+. That is, the animal's behavioral charac-

teristics were better suited to the naturalistic arrangements of adjacency and remoteness in the first two experiments.

The source speaker of the random stimulus was adjacent to the reinforced response site, and the random stimulus gained control of responding in all animals. The random stimulus did not gain control of responding when it was presented through the speaker remote from the site of reinforced responding (as in Experiment 1). Thus, remoteness was a significant factor in preventing the random stimulus from gaining control of responding.

The relatively poor control of responding by S+ is another example of the importance of adjacency in S+ responding. Grastyán and Vereczkei (1974) and Grastyán and Buzsáki (1979) have shown that when rats and cats were trained in an auditory discrimination using a runway, the effect of reinforcement was to strengthen the behavior of running to the speaker rather than to the food source. This behavior required 10 to 20 sessions to be reduced or eliminated. Similar findings have been reported by Harrison (1979). In other words, the relatively poor performance in S+ in the present experiment was due to the competing behavior of going to the vicinity of the remote speaker when S+ was presented. This behavior weakened only slowly over sessions.

EXPERIMENT 4

The third experiment studied the effect of the reversed adjacencies on the introduction of an S+ into a familiar environment that contained a random stimulus presented through an adjacent source. It was the purpose of Experiment 4 to study the effect of the reversed adjacencies on the introduction of a novel random stimulus through an adjacent source. This experiment was made symmetrical with the third experiment by introducing the novel random stimulus after Session 14.

METHOD

Subjects and apparatus. The subjects were three experimentally naive male albino rats, Sprague-Dawley strain, 100 to 120 days old at the start of the experiment. The animals were housed and fed as described in Experiment 1, and the apparatus was identical to that in the preceding experiments.

Procedure. Both speakers were unplugged,

but otherwise preliminary training was the same as that used in Experiment 1. When the response rate reached at least 200 per hour, discrimination training was started and was similar to that used in Experiment 1, except that S+ was presented through the remote speaker. After at least 10 sessions, the adjacent speaker (random stimulus) was plugged in. The animals were studied for five to 10 sessions under this condition.

RESULTS

Performance in S+. The percentage of S+ trials with latencies less than 5 s (top lines in Figure 5) increased over sessions in R295 and R460. There was no change in the level of responding for R296, who remained between 55% and 60%. Except for Session 3 for R460, the percentage level of S+ responding was above the pseudotrial level. That is, there was control of responding by S+ in all animals.

Performance in the pairs of pseudotrials. Prior to the introduction of the random stimulus, the animals were, in effect, receiving pairs of pseudotrials (the adjacent speaker was unplugged). There was no systematic difference in the level of responding in the two pseudotrials.

Performance in the random stimulus. The first presentation of the random stimulus (RS) through the adjacent speaker in Sessions 15 or 16 elicited the exploratory response in all animals (Figure 5). The random stimulus gained control of responding for the remaining 5 to 10 sessions of the experiment, as shown by the fact that the level of responding during the random stimulus was higher than the pseudotrial level.

DISCUSSION

This experiment was the counterpart of the second experiment, but with the adjacencies reversed. Comparison of the data of this experiment (Figure 5) with that of the second experiment (Figure 3) shows that switching the adjacencies resulted in persistent control of responding by the random stimulus. Similar persistent control of responding by the random stimulus was found in the previous experiment (Figure 4).

In both experiments in which the adjacencies were switched, the percentage of trials per session in which a response was made within 5 s during S+ was low for the first 5 to 15 sessions. This relatively poor performance in

S+ cannot be attributed to the presentation of the random stimulus through the adjacent speaker, because that stimulus was absent for the first 14 or 15 sessions in this experiment (Figure 5).

EXPERIMENT 5

In everyday environments, various different sound sources of different quality occupy different positions. It was the purpose of this experiment to examine the effect of removing the position difference between S+ and the random stimulus, while leaving the quality difference untouched. Position difference cannot be manipulated independently of adjacency. In this experiment, position difference was eliminated by presenting both stimuli through the adjacent speaker. This necessarily made the random stimulus adjacent to the manipulum. Corresponding changes in adjacency would have occurred had both stimuli been presented through the remote speaker. Thus, two naturalistic features were modified, separateness of position and elimination of remote presentation of the random stimulus. If separate position is a significant variable, then responding during the random stimulus should be larger than that found in the third and fourth experiments in which only adjacencies were changed.

METHOD

Subjects and apparatus. The subjects were four experimentally naive male albino rats, Sprague-Dawley strain, 100 to 120 days old at the start of the experiment. The animals were housed and fed as described in Experiment 1, and the apparatus was identical to that used in the previous experiments.

Procedure. Both speakers were unplugged, but otherwise preliminary training was the same as that used in Experiment 1. The first discrimination-training session started with 10 trials during which the speakers remained unplugged. The adjacent speaker was then plugged in and the stimuli were presented separately for the first time so that elicited exploratory behavior could be observed. The S+ (2-kHz signal) was presented first, followed 15 s later by the random stimulus (noise). All subsequent presentations of the stimuli were controlled by the two independent variable-intertrial-interval timers. The animals re-

Fig. 5. The percentage of S+ (remote speaker) trials in which response latency was less than 5 s is shown in the upper line in each panel. Note the slow development of the percentage of trials with latencies less than 5 s in R295 and R480 and the low asymptotic level in R296. The percentage of each of the pairs of pseudotrials in which a response was made is shown in the lower two plots of each panel. The novel random stimulus (RS, the vertical line) was introduced, at Sessions 15 or 16, by plugging in the adjacent speaker. The level of responding in the random stimulus (filled circles, solid lines) was systematically higher than the pseudotrial level (open circles, solid lines).

Fig. 6. Both the S+ and the random stimulus were presented through the same adjacent speaker. The upper line in each panel shows the percentage of S+ trials in which the response latency was less than 5 s. The percentage of random-stimulus trials (filled circles, solid lines) in which a response was made is shown in the middle line in each panel, and the percentage of pseudotrials (open circles, solid lines) in which a response was made is shown in the lower line in each panel. Note the large difference in level of responding in random-stimulus trials and pseudotrials.

ceived at least 18 sessions of discrimination training; each session was 46 reinforcements long.

RESULTS

The first presentation of both the S+ and the random stimulus elicited exploratory behavior as already described. The number of responses per session within 5 s during S+, in the random stimulus, and in the pseudotrials is shown in Figure 6 for all animals.

Performance in S+. All animals performed at the asymptotic level from the first session on. The level of responding in S+ was above the level of responding in the pseudotrials in all sessions (i.e., there was control of responding by S+).

Performance in the random stimulus. Performance in the random stimulus is also shown in Figure 6. There was a difference between

the level of responding in the random stimulus and in pseudotrials in virtually all sessions and for all animals. That is, the random stimulus controlled responding for the duration of the experiment. The difference in performance between that in random-stimulus trials and pseudotrials, however, diminished across sessions.

DISCUSSION

There was persistent control of responding by the random stimulus in the present experiment. This control may be due to the fortuitous reinforcement during the random stimulus or to some other (unknown) factors. Neill and Harrison (1987) used an S- (stimulus explicitly not paired with reinforcement) in place of the random stimulus, whereas other aspects of their experiment were the same as those of the present experiment. They reported

a low response level in S- (their Figure 6). In two of their animals there was essentially no control of responding by S- after Session 7, and in the third animal, control was extremely weak throughout discrimination training. Comparison of these data with those from the present experiment suggests that the fortuitous reinforcement in the present experiment was responsible for the high level of responding in the random stimulus. Fortuitous reinforcement of responding in the presence of the random stimulus fails to lead to control of responding by the stimulus only when the stimulus is presented through a remote and separate source; otherwise control will develop.

Responding in S+ was at a high level throughout discrimination training. This would be expected because S+ was presented through the adjacent speaker. Similar results were also reported by Neill and Harrison (1987) in a similar experiment in which an S- rather than a random stimulus was used. Two of their animals (their Figure 6) were essentially at the asymptotic level throughout discrimination training, and the third animal was slightly below the asymptotic level in the first session.

D'Amato and Salmon (1984) studied rats in an acoustic quality discrimination task in which both stimuli were presented through a single speaker mounted below the manipulandum. The data were presented as the group discrimination ratio per session. This ratio steadily increased from about 0.5 to 0.9 over 12 sessions. This rate of acquisition appears to be slow compared with the performance of animals in the adjacent quality discrimination studied by Neill and Harrison (1987, their Figure 6).

GENERAL DISCUSSION

Implications for Understanding Adjustment to Environmental Change

The present experiments, together with those of Harrison (1984a, 1984b), Neill (1986), and Neill and Harrison (1987), suggest the following interactions between the animal's behavioral characteristics and the features commonly found in everyday environments.

The environment. Organisms normally occupy and behave in a particular environment. It is this environment which defines an event

as new (or novel), and it is the introduction of a new event which elicits the behavior that starts the sequence of events terminating in adjustment to the change.

The new event. New events are significant in three ways. First, organisms orient to and approach new low-intensity sound sources. This behavior ensures contact with a possibly significant event. Second, the response-strengthening effect of reinforcement in the presence of novel sounds is much greater than its effect in the presence of a familiar sound source in the presence of which behavior was not previously reinforced. Thus, if the novel event is correlated with reinforcement, the event is highly likely to be approached on subsequent occurrences. Third, if the new source is randomly related to reinforcement, responding in its presence declines to near zero in a few subsequent occurrences of the stimulus.

Adjacency. The effect of reinforcement of responding in the presence of a new sound source is to cause the animal to approach the source on subsequent soundings. Because of this, rapid control of responding develops only when the reinforced behavior occurs at or near the sound source. Behavior that is not reinforced and that occurs adjacent to a new source (exploratory behavior, for example), which is only randomly related to reinforcement, rapidly declines.

Separateness of position. Rapid adjustment to sound sources of different quality appears to require either the development of control of responding if the source is an S+ or the decline of elicited responding if it is related to reinforcement only randomly. The two modes of adjustment require differences in each case with respect to the adjacency of the behavior to its respective source. In particular, it is necessary that a source randomly related to reinforcement be remote from the site of the reinforced behavior. That is, the kinds of modes of adjustment can occur rapidly only when the sources occupy separate positions.

Responding in S+

The results of the present experiments confirmed that adjacency is sufficient for the rapid development of control of responding by S+. Neill and Harrison (1987) and Neill (1986) reported the same finding in their experiments in which an S- was used instead of a random stimulus.

The introduction of S+ in the first experiment had no effect on responding during the random stimulus as indicated by the behavior in the random stimulus and pseudotrials prior to the introduction of S+. The removal of the random stimulus in Session 16 also had no effect on S+ responding. Likewise, the introduction of the random stimulus in the second experiment had no effect on S+ responding. Neill (1986) and Neill and Harrison (1987) also found no interaction between S+ and their S- in a similar series of experiments.

Responding in the Random Stimulus

It seems that the naturalistic features described below were important in preventing responding in the presence of the random stimulus.

Role of adjacency. Adjacency was manipulated in the third and fourth experiments by presenting the random stimulus through the adjacent speaker and the S+ through the remote speaker. Seven rats were studied in the two experiments, and all showed control of responding by the random stimulus (Figures 4 and 5).

There are no comparable experiments in which an S- replaced the random stimulus, so whether this control of responding was due to fortuitous reinforcement cannot be directly determined. However, responding in the random stimulus might have been due simply to its adjacency, and similar control might be found if an S- replaced the random stimulus. It might be necessary only that the reinforced behavior not be adjacent to the random stimulus.

Separateness of sound sources. Sound sources are often distinct entities in everyday environments, and when two or more are present they must necessarily occupy separate positions. The separateness of sound sources cannot be manipulated independently of adjacency. Separateness was removed in the fifth experiment by presenting both stimuli through the adjacent speaker. However, this necessarily meant that two naturalistic features were modified; the random stimulus was both adjacent to and not in a separate place from the S+.

There was relatively strong control of responding by the random stimulus when it and the S+ were presented through the same adjacent speaker (Experiment 5, Figure 6). These

data can be directly compared with those of the first experiment (Figure 2), in which the two stimuli were presented through separate speakers. The control by the random stimulus when both remoteness and separateness were removed (Figure 6) was stronger than when only remoteness of the stimulus to reinforced responding was removed (Figure 4). Thus, it appears that separateness was a relevant feature in preventing responding in the presence of the random stimulus.

Neill and Harrison (1987) carried out two experiments in which the S+ and an S- were presented through a single speaker. They reported weaker and less persistent control of responding by S- (their Figures 6 and 7) than was found in the present experiment, in which both stimuli were presented through a single speaker (Figure 6). This also indicates that the fortuitous association of reinforcement and the random stimulus contributed to the level of responding in the random stimulus shown in Figure 6.

Constraints on Learning

Performance in all experimental and natural discrimination tasks is constrained by (depends on) the evolved characteristics of the animal under observation. Thus, results obtained in traditional studies of discrimination are as dependent on (constrained by) evolution as the unexpected results that have been obtained in some nontraditional studies (e.g., Konorski, 1967). To single out only the latter results as due to evolutionary constraints is to suggest that results in traditional studies are somehow not dependent on evolved behavior.

Performance in all the present experiments was dependent on the evolved behavior of the animals (as well as on the history of each individual). However, it was only by manipulating experimentally the naturalistic features that a picture emerged of the way the behavior fit the demands of everyday acoustic environments.

Ecologically Valid Experiments

The present Experiments 1 and 2 fell into the general class of "ecologically valid" experiments (Kamil & Yoerg, 1982). The subsequent experiments used "artificial," "arbitrary," or "contrived and simplified" conditions in the sense that one or more of the ecologically

valid conditions was removed (Vaughan & Herrnstein, 1987). One reason for conducting ecologically valid experiments is that they have shown that some general laws of behavior derived from artificial experiments may hold only in a narrow set of artificial conditions (e.g., Bolles, 1970; Breland & Breland, 1961). Furthermore, our series of experiments (Harrison, 1984a, 1984b; Neill & Harrison, 1987) has shown that discriminative behavior cannot be understood wholly in terms of statements about stimuli (as a general class) and their relationship to reinforcers, schedules, or other events. Whereas ecologically valid experiments may cast doubt on the applicability to the field of laws derived from artificial experiments, artificial experiments may call into question the applicability of laws derived from ecologically valid experiments to the experimental environment. The former set of questions seems to be more useful than the latter.

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