

INTRODUCTION OF ACOUSTIC STIMULATION DURING ACQUISITION AND RESISTANCE TO EXTINCTION IN THE NORMAL AND HIPPOCAMPALLY DAMAGED RAT¹

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The basic experimental question in each of three experiments was whether exposure to acoustic stimulation in acquisition of an FR chain would increase persistence in the subsequent extinction of that response. Other factors manipulated in the experiments were (a) the manner of introduction of the tone stimulus (gradual increase in intensity or terminal intensity from the outset), (b) locus of introduction of tone in the response chain (at beginning or end), and (c) the interaction of tone-in-acquisition treatment with presence or absence of hippocampal lesions in the subjects. The findings were that introduction of the tone in acquisition increased resistance to extinction (a) more greatly under terminal than under gradual conditions, (b) both when it was introduced at the beginning and at the end of the response chain, and (c) in operated controls but not in rats with lesions of the hippocampus.

Recently, a general principle of persistence has been proposed (Amsel, 1972) which holds that the maintenance of any ongoing behavior (R_0) in the face of a stimulus (S_X) that evokes an orienting-disruptive response (R_X) increases resistance to extinction. According to this view, the mechanism responsible for this increased persistence is a more general form of the counterconditioning mechanism in the frustration theory of the partial reinforcement effect (PRE)—the counterconditioning of S_X to R_0 . The possibility is also raised in this statement that behavioral habituation is an active process involving counterconditioning, and that habituation to a disruptive stimulus may render the animal less susceptible to the effects of anticipatory frustration and so increase resistance to extinction.

The potential usefulness of this more general principle would be in its ability to integrate a variety of experimental findings on resistance to punishment (e.g., Banks, 1967;

Miller, 1960; Terris & Wehkin, 1967) and to broaden the class of transfer-of-persistence experiments (Amsel, Wong, & Scull, 1971; Brown & Wagner, 1964; Terris & Barnes, 1969; Terris, German, & Enzie, 1969; Terris & Rahhal, 1969; Wong, 1971). In all previous experiments of this sort the introduction of S_X in acquisition is in the form of anticipated electric shock, air blast, or nonreinforcement. In the present series of experiments, acoustic stimulation was used as the disruptive event, and in the last one the treatment was applied to subjects with lesions of the hippocampus.

EXPERIMENT 1

A study by Davis and Wagner (1969) was very influential in our thinking about the first experiment. They found that 750 exposures to tones, gradually increased in intensity from 83 to 118 db. in 2.5-db. steps, resulted in greater habituation of a startle response to subsequent 120-db. tones than did 750 exposures to an unchanging 120-db. tone. If habituation to disruptive stimulation makes rats more resistant to extinction, and a gradual procedure is more effective than a terminal one for habituation, then

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habituation to gradually increasing stimulus intensities as opposed to the terminal intensity might be expected to have the greater effect on resistance to extinction.

In the first experiment, a pure tone was presented either in a gradual, incremental fashion (GRA) or at its terminal intensity from the outset (TER) at the end of a chain of 21 bar presses leading to food reward. A hungry rat is typically engaged in approaching and consuming food following such a fixed-response chain. The experiment will determine whether the disruptive effect of the introduction of acoustic stimulation at this stage becomes anticipatory to affect the FR responding and results in increased persistence in bar pressing during extinction. We can also determine whether the GRA procedure is more or less effective than the TER procedure in the development of persistent responding.

Method

Subjects. The subjects were 27 male albino rats, supplied by Hormone-Assay Company of New York, approximately 90–120 days of age at the beginning of experimental training.

Apparatus. One commercially made standard Skinner box was housed in a sound-attenuating wooden cabinet equipped with a ventilation system. The Skinner box had a Plexiglas top and sides with metal end plates. It was 23 cm. long, 21.5 cm. wide, and 20 cm. high, and was equipped with a Lehigh Valley retractable bar on one end panel, 5 cm. from the left side and 5 cm. from the floor. The food cup was 5 cm. to the left of the bar and 3 cm. from the floor.

Programming of stimulus events and recording of responses were done on-line by a SCAT computer system manufactured by Grason-Stadler.

The acoustic stimulation consisted of a 4,000-Hz. 10-sec. tone generated by a Grason-Stadler generator and fed into a 7.63-cm. loudspeaker directly mounted on the center of the Skinner box. Tone intensities varied according to the experimental plan, and were calibrated inside the Skinner box. The intensity levels of both the ambient noise level and the acoustic stimulation inside the box were measured by a General Radio sound survey meter set on the C weighting scale.

Procedure. Subjects were placed on a 12 gm/23 hr food deprivation schedule 3 wk. before experimentation. They were then gradually shaped up to FR 21 responding. To minimize carry-over effects from trial to trial, a discrete-trial procedure was used. When the FR was completed, the lever was retracted and a 300-mg. Noyes pellet was delivered. At the same time, an intertrial interval (ITI) of 2

min. was initiated. Response measures recorded were (a) time to the first bar press from extension of the bar (0–1 time), (b) time from the first response to the eleventh (1–11 time), and (c) time from the eleventh response to the twenty-first (11–21 time). If the subject failed to complete the requirement within 90 sec. for any segment of the response chain, the bar was retracted, the ITI was put into effect, and a score of 90 sec. was recorded for each of the incompleting response segments.

After shaping, all groups were subjected to 18 days of training on FR 21. There were four trials a day during this and all subsequent phases. This was followed by 9 days of training with tone stimulation. Group TER received a 4,000-Hz., 110-db. tone (re .0002 dyne/cm² SPL) upon completion of the FR 21 chain. For Group GRA the initial tone intensity was 85 db., and the intensity was incremented in 5-db. steps each day to the terminal level of 110 db. A control group (CON) experienced no tone stimulation. After the tone phase, all three groups were given 2 days of training at FR 21 without the tone, so that they would all start extinction training following identical acquisition conditions. Since, in extinction, no tone was presented for any group, the no-tone acquisition phase preceding extinction also minimized generalization-decrement effects.

Results and Discussion

Figure 1 presents mean log time (+1.0) for all three measures for the last 2 days of original acquisition at FR 21, for the last 2 days of the tone-stimulation phase, for the 2-day interpolated FR 21 phase, and for the 11-day extinction period. All statistical analyses were performed on the transformed data.

Since there was no differential treatment in original acquisition at FR 21, no differential responding was expected. However, for the 0–1 measure only, Group GRA reached a higher asymptote, producing a groups main effect on the last 2 days of acquisition ($F = 6.81$, $df = 2/24$, $p < .01$). The mean log latency scores for these 2 days for Groups GRA, TER, and CON were 1.22, 1.41, and 1.59, respectively. A Newman-Keuls test showed that the terminal times for GRA were shorter than for TER and CON ($p < .05$), which did not differ from each other. The superior terminal performance of Group GRA for the 1–11 measure can only be attributed to sampling error. It may be worth mentioning that during this phase the subjects developed idiosyncrasies in pressing the bar: nose press-

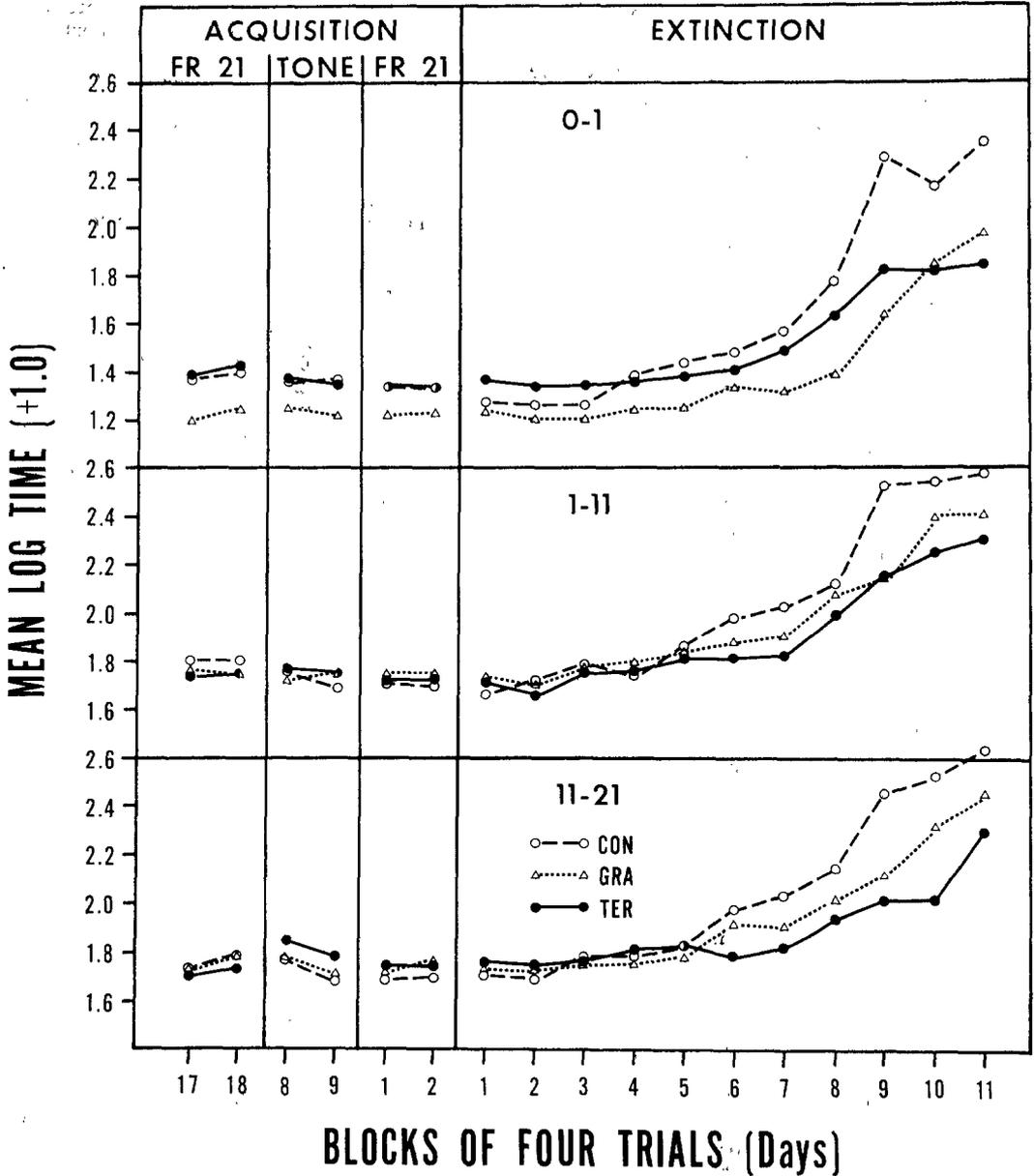


FIG. 1. Time measures for the four phases of Experiment 1 for the gradual, terminal, and control groups. (Data are plotted separately for three segments of the total response chain. The 10-sec. tone was introduced at the completion of FR 21 responding.)

ing, paw pressing, chewing, holding the bar with rotating body movements, and combinations of these behaviors.

In the tone-stimulation phase, 0-1 latency for Group GRA remained lower than for the others, resulting in a significant groups main effect ($F = 7.08, df = 2/24, p$

$< .01$); there were no significant differences in the 1-11 and 11-21 measures. The presentation of a tone contingent upon completion of a chained bar-pressing response had no apparent suppressive effect on any segment of the response chain.

Although acoustic stimulation had no

suppressive effect on bar pressing, it seemed to have some disruptive effect on the consummatory behavior during the first few days of tone phase under the TER condition. Some TER subjects showed hesitancy in approaching the food cup or recoiled after picking up the food pellet while the tone was on. These behaviors were not observed in any of the GRA subjects. While we did not monitor the startle response, the Davis and Wagner (1969) data tell us that sudden introduction of the 4,000-Hz., 110-db. tone should elicit substantially greater startle than the incremental method of tone presentation. Thus, on the basis of both direct observation and extrapolation from Davis and Wagner, we are confident that acoustic stimulation was more disruptive under the TER than under the GRA condition.

In the preextinction session without the tone there was no significant groups effect in any measure, although the graph shows that Group GRA continued to show shorter latencies in the 0-1 measure.

In extinction there was a significant groups main effect in the 0-1 measure ($F = 5.26$, $df = 2/24$, $p < .05$). The Groups \times Days interaction was significant in all three measures (F s = 4.30, 2.91, and 3.40; $df = 20/240$; all $ps < .01$), reflecting differential rates of extinction, the TER group being most persistent. The increased resistance to extinction following acoustic stimulation is of particular theoretical interest. According to the counterconditioning view of persistence, internal stimuli resulting from the anticipation of acoustic stimulation are of the class S_x . Thus the maintenance of bar pressing in the face of these stimuli during acquisition produces increased resistance of bar pressing to extinction. There is evidence that a 110-db. sound produces behavioral effects equivalent to the application of low intensities of electric shock (Campbell & Bloom, 1965); that a 95-db. noise is sufficient to function as a negative reinforcer (Bolles & Seelback, 1964); and that a pure tone (1,500 Hz., 100 db., 3.6-sec. duration) is sufficient to suppress a drinking response (Peeke & Zeiner, 1970). Other investigators (Barnes & Kish, 1957; Harrison & Tracy,

1955) have shown that intense sound can be used to promote escape or avoidance learning. All these findings indicate that an intense sound is functionally similar to electric shock or frustrative nonreward in its aversiveness. In addition to the aversiveness of the acoustic stimulation itself, the blocking of consummatory responses may function like delay of reinforcement, producing primary frustration. Thus, in Experiment 1, the aversive stimuli at the goal may include both the acoustic stimulation and frustration.

Contrary to expectation the GRA condition produced less persistence in extinction than TER. One possible explanation for this reversal is that at lower intensities the tone did not have disruptive effects. The observation that the acoustic stimulus was ineffective in modifying food-approach and consummatory behavior under GRA conditions supports this contention. Group GRA received very few trials with the higher intensities of tone, which may account for the fact that counterconditioning did not progress to the same stage as in Group TER, which received much more training under effective levels of disruptive stimulation. In the Davis and Wagner (1969) study, which showed greater habituation under conditions of gradual introduction of disruptive acoustic stimulation, subjects received 750 exposures to the tone stimulus. The size of the tone-intensity increment and the duration of tone stimulation, as well as the number of exposures, may also be factors in determining the effectiveness of gradual introduction of disruptive stimulation in producing subsequent response persistence.

EXPERIMENT 2

In Experiment 1, we have demonstrated that acoustic stimulation presented with food reward upon the termination of FR 21 responding results in increased resistance to extinction of bar pressing. In this second experiment, we introduced the tone after the first bar press. This new arrangement allows us to assess whether the stimulation suppresses portions of the instrumental response which both precede and follow it, and whether, introduced at this stage, it

still promotes persistence in responding. Another control feature of this experiment, which differs from both Experiments 1 and 3, is that a condition was included in which tones ranging from 85 to 110 db. were presented in random order (RAN). Thus, there were four tone conditions: TER, GRA, RAN, and CON.

Method

Subjects. The subjects, 40 albino rats, were supplied by Holtzman Company, Wisconsin, and were approximately 120 days old at the beginning of experimental training.

Apparatus. Three operant conditioning chambers, each measuring 21 cm. wide, 23 cm. long, and 20 cm. high, were employed in this experiment and in Experiment 3. On one of the metal end plates of each chamber was mounted a Lehigh Valley retractable lever 2.75 cm. above the floor and 2.5 cm. from the right side. Each lever was fenced in by a metal guard so that only a direct press from above could activate the feeder. The guard was intended to render the bar-pressing responses more homogeneous. A recessed food cup measuring 5 cm. high, 5 cm. wide, and 5 cm. deep was mounted 2.75 cm. above the floor and 2.5 cm. to the left of the lever. Plastic tubing connected a Gerbrands feeder to the food cup. A 7.5-cm., high-frequency speaker was mounted on the lid of the chamber. Each box was housed in a separate sound-attenuating enclosure equipped with individual ventilation which also provided a 75-db. SPL masking noise. Programming and recording were done on-line by a SCAT computer system manufactured by Grason-Stadler.

Procedure. The procedure was the same as in Experiment 1 except that, after shaping, all groups received 24 days at FR 21 without tone and 14 days with tone stimulation, four trials a day. During the tone phase for the TER group, a 4,000-Hz., 110-db. tone of 10-sec. duration was introduced immediately upon the first bar press. For the GRA group, the tone intensity was increased from 85 db. in 5-db. steps every other day and remained at 110 db. for the last 4 days. Under the RAN condition the different tone intensities were presented as frequently as under the GRA condition, but they were presented in a quasi-random order.

Results and Discussion

Results for all three measures are presented in Figure 2. Data are for the last 2 days of original acquisition at FR 21, the last 2 days of the tone-stimulation phase, the interpolated phase of FR 21, and extinction.

There was no significant groups main effect, nor any significant interaction involv-

ing groups in the first three phases. In other words, presentation of the tone even in the TER group had no appreciable effect on bar pressing. During extinction the TER group was more persistent than any of the others. This observation was confirmed by a significant groups main effect ($F_s = 3.85, 4.98, 5.76$; $df = 3/36$; $p < .05$ for the first measure, $p < .01$ for the last two measures), and a significant Groups \times Days interaction ($F_s = 2.60, 3.30, 2.88$; $df = 27/324$; $p < .01$ for all three measures).

Since the acoustic stimulation had no appreciable effect on bar pressing, the relative persistence of the TER group cannot be attributed to counterconditioning of bar pressing to anticipatory frustration resulting from delay of reinforcement. Neither can it be attributed to the direct evocation of the ongoing bar-pressing response to the tone, because in extinction the tone was never presented. In our theoretical framework, S_X is present in two forms during the tone-stimulation phase. Both the tone and the internal stimuli resulting from the anticipation of the tone are assumed to evoke disruptive responses. The transfer would, then, appear to be from these effects of the TER treatment in acquisition to frustration-generated stimuli, both unconditioned (S_F) and conditioned (s_F) in extinction. Another possible mechanism for the transfer is some form of fear-frustration commonality: that there is in acquisition an aversive motivational state similar to that produced by frustrative nonreward in extinction (Hoffman & Stitt, 1969; Wagner, 1963, 1966).

The absence of any difference in persistence between Group GRA and the control group was at variance with the results of Experiment 1. Following the argument of the earlier discussion, the GRA condition may provide less opportunity than the TER condition for counterconditioning of the bar-pressing response to S_X .

EXPERIMENT 3

The purpose of the third experiment was twofold: (a) to repeat the essential features of the first experiment, and (b) to assess

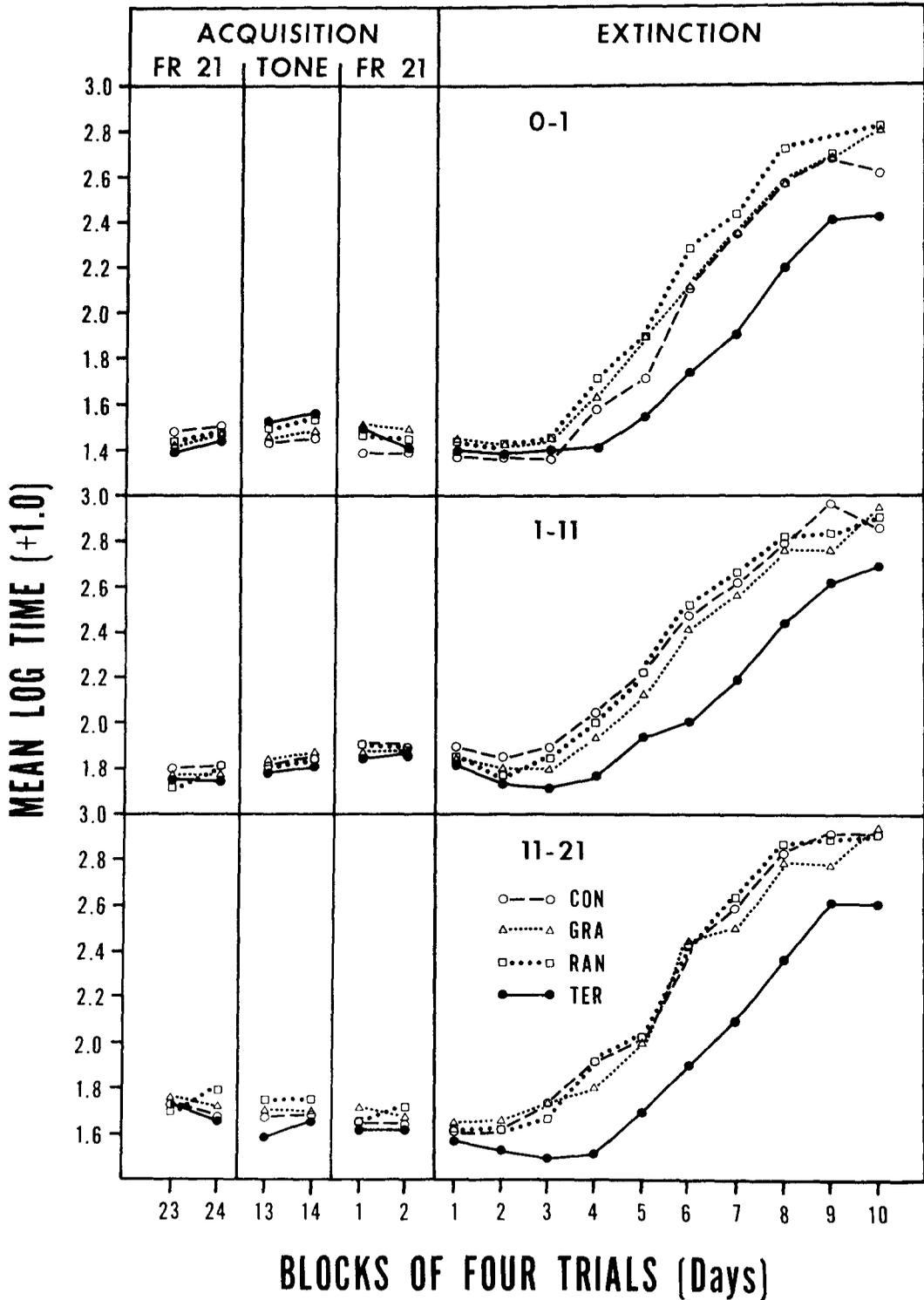


FIG. 2. Time measures for the four phases of Experiment 2 for the gradual, terminal, random, and control groups. (Tone was introduced after the first response of the 21 response chain.)

the effects of this procedure on rats with hippocampal damage.

The new question of interest in this experiment is the degree to which the tone-habituation procedure will affect hippocampally damaged animals. A variety of behavioral deficits relevant to the present experiment have been found following hippocampal lesions. These include greater resistance to extinction following instrumental conditioning (Kimble & Kimble, 1965), a deficit in the capacity to alter responding in line with changed reinforcement contingencies (Ellen & Wilson, 1963), decreased distractibility to novel stimuli (Hendrickson, Kimble, & Kimble, 1969), and slower behavioral habituation (Jarrard & Korn, 1969). On the basis of these last two studies, particularly, the tone in the present experiment would be expected to produce lesser but longer-lasting disruption in subjects with hippocampal lesions than in controls. Subjects with hippocampal lesions should also show more resistance to extinction regardless of whether or not they were subjected to the tone.

Method

Subjects. The subjects were 36 naive male albino rats 90–120 days old at the beginning of training.

Surgery. All surgery was done with the rats under Nembutal anesthesia (35 mg/kg). Atropine sulphate (.05 mg.) was also used prior to surgery to decrease secretions. Duracillin (.05 mg.) was administered intramuscularly before surgery to decrease the chances of infection.

Subjects were assigned randomly to the lesion or operated-control groups. The lesions were produced electrolytically by passing 2.0 ma. for 20 sec. through the uninsulated tip of a stereotactically positioned stainless-steel electrode. The circuit was completed through a rectal cathode. Four lesions were made in the subjects assigned to the hippocampal groups: two in bilateral dorsal hippocampus (from bregma: 3 mm. posterior, 3 mm. lateral, and 3 mm. down from dura), and two in bilateral ventral hippocampus (from bregma: 4.5 mm. posterior, 4.5 mm. lateral, and 6.0 mm. down from dura). For operated controls the electrode was lowered as for the lesion subjects but without the induction of electrolytic current.

Histology. Following the completion of behavior testing, subjects were perfused with isotonic saline followed by 10% Formalin solution. Frozen tissue techniques were used to section the brains at 20 μ and every fourth section was mounted for staining. Sections were stained with Eosin Y and cresyl

violet. Figure 3 shows representative lesion placements for each group. Dorsal lesions showed good intersubject consistency and in all cases portions of the dorsal hippocampus were ablated. The amount of dorsal hippocampus ablated was estimated to vary from 30% to 60%. Other structures involved in the dorsal lesions included fimbria hippocampi and in a couple of cases the truncus corporis callosi and minimal amounts of overlying cortex. The ventral lesions showed greater variability in respect to both amount and location of destruction. Ventral hippocampus destruction was estimated at 25–85%. Other structures showing damage in some subjects included crus cerebri, substantia nigra, subiculum, and the tapetum. In all cases damage to these structures was minimal.

Apparatus. The three conditioning chambers, sound-attenuating enclosures, and the programming and recording equipment were the same as in Experiment 2, except that in the present experiment the lever was not fenced in by a metal guard.

Procedure. Following at least 4 days of post-operative recovery, during which they were fed ad lib, all subjects were put on a 10 gm/23 hr food deprivation schedule and handled for 3–4 min. per day for a period of 10 days. Subjects were divided into four groups of nine each on the basis of a 2 \times 2 factorial design. The first factor was lesion vs. control, and the second factor was tone vs. no tone. The groups were labeled as follows: no-tone-control (NC), tone-control (TC), no-tone-lesion (NL), and tone-lesion (TL). There were three squads of 12 subjects each. Squad 1 included Subjects 1–3 from each group. Squad 2 included Subjects 4–6 from each group, and Squad 3 included Subjects 7–9 from each group. For each squad of 12 subjects, four running orders were devised. These four running orders were randomized over days but held constant over squads within days. Each squad was run in one of the three chambers and the same squad was run in the same chamber each day.

Through all four phases of the experiment a discrete-trial procedure was employed. Following the completion of the FR 21 response a 300-mg. Noyes pellet was delivered and the lever was simultaneously retracted. The ITI was 2 min.

All subjects were shaped to FR 21 responding, starting at FR 1 and incrementing the FR requirement by five responses every other day. There were four trials a day during shaping and throughout the remainder of the experiment, which involved four additional phases: (a) On the first 18 days all subjects were run on the FR 21 schedule. (b) On the next 21 days subjects in Groups TC and TL received a 10-sec. 4,000-Hz., 110-db. SPL tone upon completion of each 21 bar presses. As in Experiment 1 the tone was delivered simultaneously with the lever retraction and food delivery. Subjects in Groups NC and NL continued as in Phase 1. (c) For 8 days the tone was discontinued and all subjects continued on FR 21 as in Phase 1. (d) The last 10 days constituted a 40-trial extinction

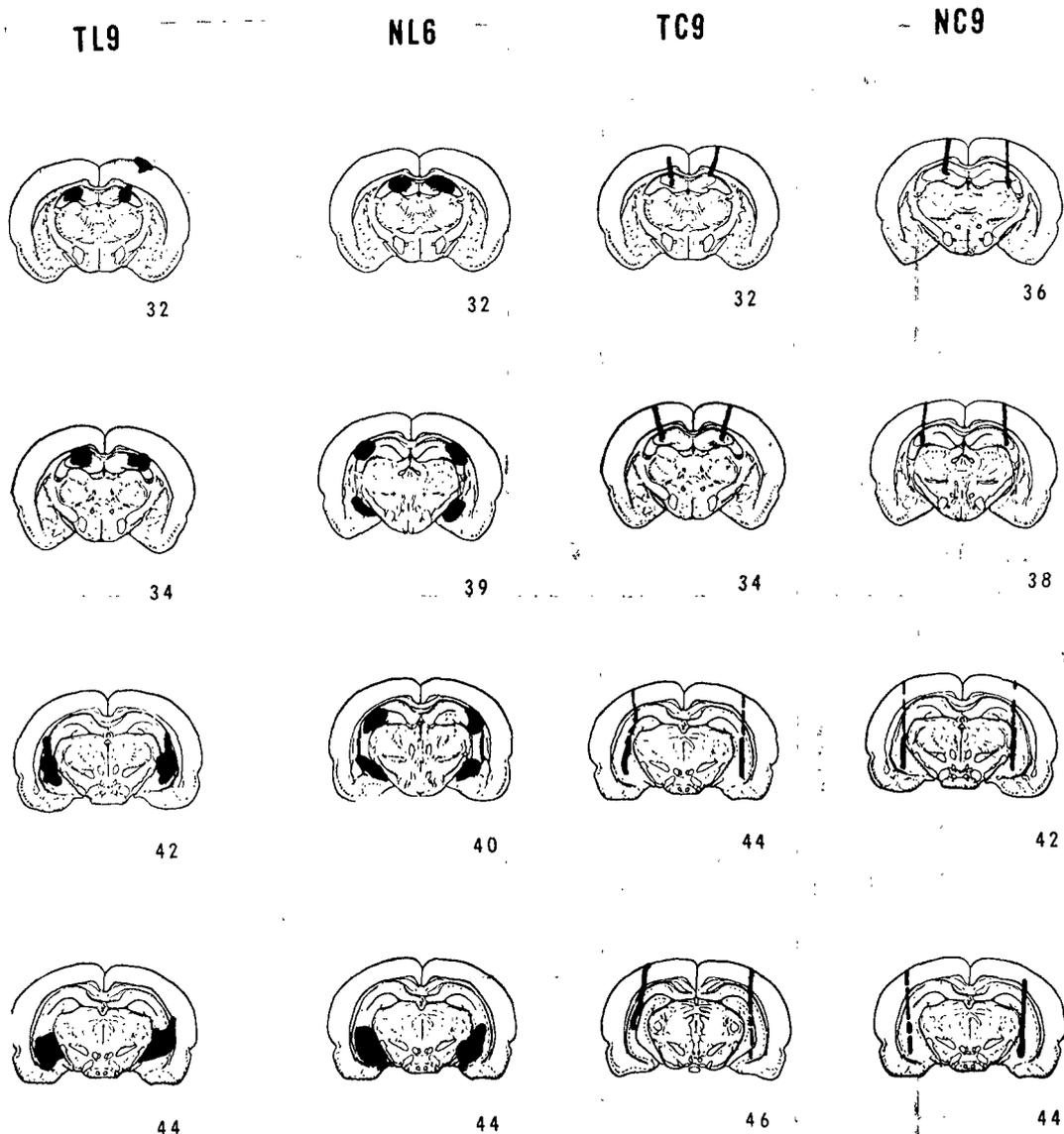


FIG. 3. Schematic representation of lesions and tracts for one subject in each group of Experiment 3. (The plates are from König and Klippel [1963]. The number below each section refers to the plate number in the atlas.)

phase during which the pellet dispenser remained operative but no food was delivered.

Results and Discussion

One subject from each of Groups TC and TL died during the fourth phase. To maintain equal group size, the data from one animal, chosen randomly from each of the remaining two groups, were removed.

Figure 4 presents data over successive

days for each of the three time measures (see Experiment 1) as follows: for the last 2 days of Phase 1, the first 2 and the last 2 days of Phase 2, the last 2 days of Phase 3, and for the entire 10-day extinction phase. An analysis of variance was performed on each measure for each phase.

As expected, time to respond decreased significantly in Phase 1 for all three measures, which reflects strengthening of the

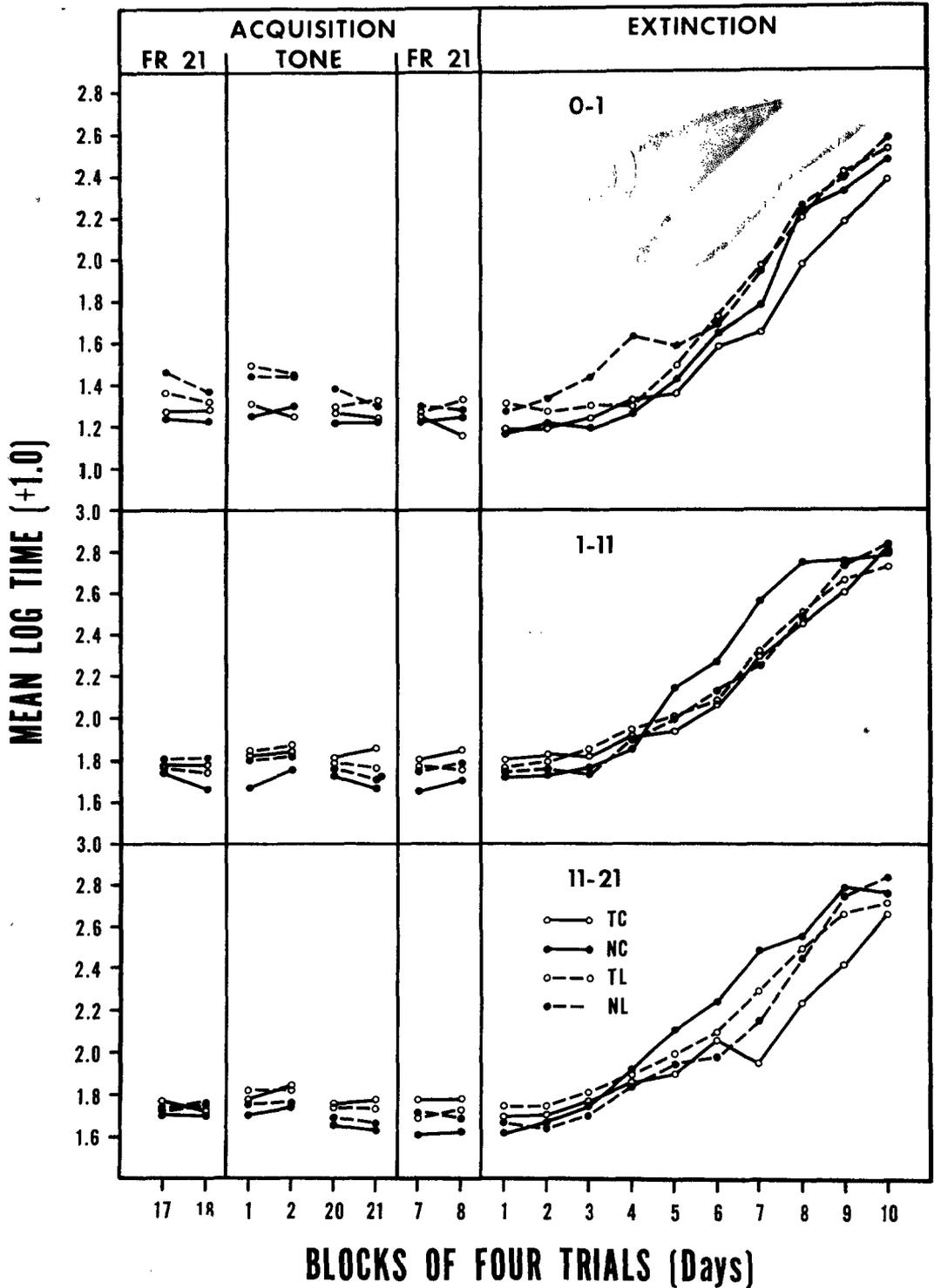


FIG. 4. Time measures for the four phases of Experiment 3 for the four groups combining the tone and lesion factors. (As in Experiment 1, tone was introduced at the completion of FR 21 responding.)

FR 21 response. A significant lesion effect was found in the 0-1 time ($F = 4.84$, $df = 1/28$, $p < .05$), indicating slower initiation of responding in the lesion groups.

On the first 2 days of the tone phase, lesion subjects continued to show longer latencies to the first response ($F = 4.44$, $df = 1/28$, $p < .05$). On the last 2 days there was no such difference, yielding a significant Lesion \times Days interaction in the 0-1 measure ($F = 2.55$, $df = 20/560$, $p < .01$). The significant day effects found in all three measures ($F = 3.63$, $df = 20/560$, $p < .01$; $F = 1.60$, $df = 20/560$, $p < .05$; $F = 3.28$, $df = 20/560$, $p < .01$) resulted from a general decrease in response times during the progress of the tone phase. As in Experiment 1, the introduction of the tone at the completion of the ratio run was ineffective in modifying bar-pressing response times in any of the groups, but had some disruptive effect on food approach and consummatory responses. There appeared to be no difference in tone-elicited disruption, however, between the lesion and nonlesion groups.

The hypotheses concerning the decreased distractibility and slower habituation of hippocampal animals could not be properly evaluated since control subjects, like hippocampally damaged subjects, showed little reaction to the tone. The finding of little reactivity to the tone in hippocampal animals is, however, in line with the results of Hendrickson et al. (1969) showing that thirsty rats with hippocampal lesions did not emit orienting responses to a novel auditory stimulus while they were drinking. The importance of deprivation level in controlling reactivity in animals with hippocampal lesions is also supported by the work of Ford, Bremner, and Richie (1970) relating hippocampal theta rhythm to level of deprivation.

The interpolated continuous reinforcement in Phase 3 produced no significant effects on responding in any of the three measures.

In extinction a significant Tone \times Days interaction for both the second and third measures indicates that Phase 2 tone presentation enhanced response persistence ($F = 5.30$, $df = 9/252$, $p < .01$; and $F = 4.00$, df

$= 9/252$, $p < .01$). The significant Tone \times Lesion \times Day interactions ($F = 6.50$, $df = 9/252$, $p < .01$; and $F = 5.00$, $df = 9/252$, $p < .01$) also found in Measures 2 and 3 suggest, however, that the effectiveness of the tone in retarding extinction was restricted to the control groups. A Newman-Keuls test on 1-11 time showed that the NC group differed significantly from the remaining groups ($p < .01$) which did not differ significantly from each other. The Newman-Keuls test on 11-21 time showed that the NC and TC groups differed significantly from each other and from the remaining two groups ($p < .01$). There was no significant difference between NL and TL groups in any measure. It appears that the tone treatment had a differential effect in control groups, confirming Experiment 1; it had no differential effect in the lesion groups.

Consistent with the results of previous experiments, subjects with hippocampal lesions did show response perseveration in extinction. The absence of an effect of acoustic stimulation on the resistance to extinction of lesion subjects and the greater resistance to extinction for lesion subjects compared to the no-tone control subjects seems best attributable to an emotional deficit. Presumably the absence of expected reward in extinction is less frustration producing in hippocampally damaged animals. This analysis is supported by some recent findings by Gray (1970) showing a correlation between certain bands of electrical activity in the hippocampus and frustration.

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