Response Suppression and Recovery in the Mongolian Gerbil as a Function of Shock Duration

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MDC

Abstract

The effects of punishment on a 2-minute variable interval food-reinforced bar press response were investigated in 16 Mongolian gerbils. Punishment consisted of electric shock in 0.3, 0.6, 1.2 and 2.4 second durations, with 4 subjects assigned to each shock duration. Punishment was administered for each response until all subjects ceased responding. After 7 days, subjects were retested on 3 successive days on the 2-minute variable interval schedule, but with no punishment for responding. Results showed that differences in the number of punishments to cessation amomg shock durations were not significant. Recovery of responding was seen to increase as a function of increased retest sessions, while over retest sessions there were differential rates of recovery as a function of shock duration. Support was found for the use of the gerbil in comparative punishment investigations with the laboratory rat.

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Introduction

Background literature

At the beginning of the second half of this century, Beach (1950) issued his warning concerning the then current emphasis given the domesticated rat as the organism on which to construct a science of psychology. Specifically he pointed to the fact that much of the research conducted under the heading of comparative psychology did not concern itself with comparisons between species but rather with rat behavior. More recently Lockard (1968), in his criticism of the albino rat as the sine qua non in comparative psychology, also reiterated the great need for the investigation of other animals' behaviors. At the time of his article, less than 1% of all species had a single behavioral paper devoted to them.

While these papers have spurred a recent growth of interest in the behaviors of more diverse organisms, a truly comparative psychology is still found wanting. Much of the current research in comparative psychology appears to be based on comparisons between animals selected for rather arbitrary reasons. Two important assumptions of the comparative method are that similarities between related forms are the result of phyletic closeness, and that differences between related forms are the result of specialized adaptations to their differing modes of existence. Hodos and Campbell (1969) have convincingly argued for the

death of the ancient "scala naturae" concept, which proposed that all animals could be ranked on a singular dimension such as complexity or perfection. In such a scheme man was seen as the inevitable goal of evolutionary development, with other organisms judged by their position on the scale in reference to man. This belief in a smooth continuity between living organisms did not take into account the divergence of evolutionary lines nor the possible extinction of some intermediate forms. Only by the comparison of species of a common evolutionary lineage can the relationship between evolution of structure and behavior become perceptible. A laboratory comparison, therefore, of two animal species unrelated by descent or ecological conditions may be seriously questioned as to its scientific utility (Lockard, 1968).

Attempts have been made during the past decade to compare more directly related species using the appropriate phyletic tree model (Hodos & Campbell, 1969). One notable example has involved the introduction of the Mongolian gerbil into psychological research by Schwenker (Robinson, 1967). The gerbil is not only in a better comparative position to the rat than many previous species examined, but also has great suitability for the environment of the psychological laboratory (Schwenker, 1968). Both the Mongolian gerbil and the laboratory rat (evolved from Rattus norvegicus) are of the order Rodentia and sub-order Myomorpha. The phyletic closeness of the rat and gerbil,

in addition to the great wealth of literature accumulated on the rat, strongly suggests that comparative research involving these two species would be profitable.

The recent limited comparative literature on rats and gerbils reflects a variety of areas of investigation, including maze-learning (Wise & Parker, 1968), exploratory behavior (Nauman, 1968; Thompson & Lippman, 1972), and avoidance learning (Pearl, 1963). With respect to this latter area, Ashe and McCain (1972) conducted an investigation comparing the avoidance probabilities of gerbils and rats in a one-way and shuttle box task. Their findings indicated that gerbils had higher avoidance probabilities than rats in the shuttle task, but not in the one-way task. The authors concluded that, in the area of avoidance behavior, one could not infer the behavior of the gerbil from that of the laboratory rat. It was pointed out by the authors that few, if any, of the studies reviewed in their article were methodologically comparable. Powell (1971), however, using a free operant (Sidman) avoidance procedure with gerbils and rats found support for comparisons between the two rodent species. While gerbils generally exhibited superior acquisition of free operant avoidance, both species learned to avoid more quickly when the shock-shock interval was of a shorter duration than the response shock interval. This result suggested that perhaps similar learning principles were operating for both species.

The seemingly conflicting findings of the above studies suggest that the areas of punishment and avoidance may lend themselves to further valid comparative investigations of gerbils and rats. Early studies on the punishment of rats were conducted by Skinner (1938) and Estes (1944) using bar slaps and shocks as punishing stimuli. Their results were interpreted to mean that punishment has only a temporary effect upon behavior. Later research, however, particularly in the punishment of consummatory behavior in monkeys (Masserman & Pechtal, 1953), has indicated that dramatic and irreversible response suppression is possible. The degree of response suppression in rats has been demonstrated to be a result of several variables, including the duration of the punishing stimulus (Boe, 1966; Church, Raymond & Beauchamp, 1967). In the pioneer studies by Skinner and Estes, the duration of the punishing stimulus was not precisely specified. Estes (1944) stated only that his shocks lasted "a fraction of a second."

Most studies of recovery following punishment of instrumental responses in rats have been concerned with recovery from partial suppression, and have frequently obtained a "punishment contrast" effect (Azrin & Holz, 1966). As the duration of the punishing stimulus is increased, one encounters, at first, partial suppression and complete recovery, followed by partial suppression and partial recovery at longer durations.

Systematic data concerning recovery from complete suppression of instrumental responses is scarce, although two studies have reported results of no recovery when using severe shock (Azrin, 1960) and prolonged trials (Appel, 1961). Storms, Boroczi and Broen (1963, 1964, 1965) conducted a series of studies investigating, among other variables, the degree of response suppression and recovery as a function of the duration of an electric shock. Domesticated rats were used as subjects in these studies. In the first of these experiments, subjects were trained to bar-press for food reinforcement on a 4-minute fixed-interval (FI) schedule. After eight 1-hour daily sessions on this schedule, punishment contingent upon each bar-press was introduced in the form of a 1-milliampere electric shock, varied for three groups of 0.1, 0.5, and 1.0 seconds shock duration. Punishment was continued until no bar-pressing occurred during a full 1/2-hour daily session. The subjects were then returned to their home cages for a period of seven days. Following this period, the subjects were returned to the test situation for 1-hour with the FI 4-min. schedule in effect, with no punishment for bar-pressing. The subjects were tested again on each of the next two days. The results of the study indicated that the longer the duration of the shock, the fewer punishments needed to cessation of responding. In addition, the different durations of shock did not have parallel effects on recovery from punishment; the 0.5 sec.

shock duration was most effective in that the subjects in this group recovered less than the other two. The relationship between duration of shock and recovery of responding was seen to be non-monotonic. Finally, recovery from the effects of shock appeared to occur on a "all-or-none" basis. Either there were no bar-presses, or the subjects began pressing at a rate indistinguishable from the pre-punishment rate.

A similar procedure was employed in the second study of this series (1964), with the exception that shock intensity and duration were varied factorially. In this second study, no relationship was found between shock duration and recovery, recovery again being defined as a "all-or-nothing" process. In this study it was reported that a slight trend toward less recovery under the two middle values of shock was observed, although the findings were not statistically significant.

The 1965 study by Storms, et al., investigated the relationship between duration of shock and recovery from punishment using an extended range of shock duration. Punishment contingent upon a response in the form of a 0.8-ma shock was divided into durations of 0.1, 0.2, 0.4, 0.8, 1.6, and 3.2 seconds, and was continued until no bar-pressing occurred during a full 1-hour daily session. Similar procedures for retesting as in the previous two studies were carried out and the recovery data analyzed. The results indicated that longer durations of shock were

associated with less recovery. In this particular study, the authors also compared 2-minute FI and VI schedules, finding that more subjects recovered in the FI group than in the VI group. In addition, the 0.4 sec. intermediate shock duration group on the VI schedule displayed the most suppression, in that no subjects recovered from punishment.

From the results of this series of studies by Storms, Boroczi and Broen, it appears that with an extended range of shock duration there is a definite relationship between shock duration and recovery, the longer the duration of shock the less the recovery. However, a significant middle duration effect was found in both the 1963 and 1965 studies, where the intermediate shock duration led to the most suppression and least recovery. A slight, though not significant, trend was noticed in the 1964 study regarding this phenomenon. The experimenters stated that recovery appeared to be "all-or-none" in all three studies, without evidence of the "punishment contrast" effect found in studies dealing with partial suppression of responding. Recent literature reviews have failed to disclose any published research utilizing the gerbil in a punishment problem. Noting the positive implications from previous comparative avoidance studies with rats and gerbils, this author felt that a comparative investigation into the area of punishment would prove worthwhile.

Purpose

The present investigation was an attempt to examine the effects of an extended range of shock duration upon recovery of a punished instrumental response maintained on a variable interval schedule. The study endeavored to ascertain whether the middle duration effect and all-or-none phenomenon reported by Storms, et al, in the domestic rat would be found in a different, phyletically related species, the Mongolian gerbil.

Method

Subjects

The subjects were 8 male and 8 female Mongolian gerbils (Meriones unguiculatus), experimentally naive and between 120-150 days old at the start of the experiment. The animals were obtained from Tumblebrook Farm, Brant Lake, New York. Housing was both individual and in heterosexual pairs. The subjects were maintained on a Grape Nuts, Purina dog chow and sunflower seed mixture. Water was available continuously in the home cages throughout the experiment.

Apparatus

The apparatus consisted of a BRS/LVE model MSP-3004 programming system, including a M-2901 programmer, M-143-03 small rodent test chamber, and M-PDC pellet dispenser. The chamber measured 11 x 7 x 8 in. and incorporated a bar-press lever and food tray on the front wall. A locally-constructed grid floor composed of 1/8-in. stainless steel bars spaced 1/4 in. apart in a plywood frame was installed

1/2 in. above the manufacturer's grid. An auxiliary programming system, interfaced with the MSP-3004 unit, controlled the operation of the pellet dispenser and shock durations. A tape timer unit in the auxiliary programming system was used for programming variable interval schedules utilizing punched 16mm film leader. Activation of the food magazine delivered a 20mg spherical pellet of Noyes Formula A rodent chow according to selected reinforcement schedules. Electric shock was delivered through the locally-constructed grid and consisted of a .833ma constant current produced by a circuit having 132 K-ohms in series with 110 volts and the subject. Shock duration was controlled by an electronic timing relay and was calibrated using an Industrial Timer Clock accurate to 0.01 sec. Bar-press responses and reinforcements were recorded on two separate 4-digit counters incorporated in the M-2901 programmer unit. Timing of successive minutes was accomplished by means of a standard wristwatch with a sweep second hand.

Procedure

Pre-experimental treatment. Prior to the beginning of the experiment the subjects were handled daily and maintained on a 1/2-hour daily feeding schedule for a period of three days. This feeding schedule allowed the subjects to be fed as much food as they could consume in the 1/2 hour. The subjects remained on this deprivation schedule throughout the experiment.

Initial training. Subjects were then magazine trained in the test chamber and conditioned to approach the food magazine for reinforcement at the sound of the operation of the pellet dispenser. Subjects were then trained to press the bar to obtain pellets and were maintained on continuous reinforcement (CRF) for the remainder of the 1/2-hour session during which the training took place. Three 1/2-hour daily sessions were conducted, during which the reinforcement schedule was gradually lengthened from CRF to a 2-minute variable interval schedule (VI 2 min.). On different days, four additional 1/2-hour sessions on a VI 2 min. schedule were then given. In the VI 2 min. schedule, four different randomly-ordered reinforcement intervals were used (60, 120, 180, 240 sec.). Responses per minute for each subject were obtained by recording the figure on the response counters when the watch sweep hand completed a sixty second cycle. After each session the subjects were fed in their cages as much food as they could consume in 1/2 hour.

Punishment and recovery test. Following the four 1/2-hour sessions on the VI 2 min. schedule, punishment contingent upon each bar-press was introduced in the form of a .833-ma electric shock, with the VI 2 min. schedule still in effect. Each punishment session lasted 1/2 hour. The subjects were randomly assigned to one of four punishment durations, 0.3, 0.6, 1.2, or 2.4 sec. Punishment was continued until no bar-pressing occurred during a full 1/2-hour session. Upon reaching this criterion of cessation,

the subjects were returned to their cages for a period of seven days, during which the deprivation schedules continued. Following this period the subjects were retested in 1/2-hour sessions on three successive days with the VI 2 min. schedule effective, but with no punishment for responding. The latency (minutes) to the first response was recorded, as were responses per minute when the subjects had resumed responding.

Design. Two replications of this entire procedure were conducted, containing 7 and 9 subjects respectively. The death of one animal in the 2.4 sec. duration group in the first replication required the addition of an extra subject in the second replication. Thus, a total of four subjects were treated under each of the four shock duration conditions.

Results

The total number of responses in the last pre-punishment session was recorded for each subject. Means and standard deviations for this measure are shown in Table 1. A one-way analysis of variance was performed in order to ascertain whether there were any initial differences in rates of responding among subjects assigned to the four shock duration groups. Results were not significant ($F = .17$, $df = 3,12$).

In the punishment sessions, all subjects ceased responding, with the number of punishments required to cessation ranging from 17-169. As indicated in Table 1, there was a sharp decline in the mean number of punished responses to

cessation between the 0.6 and 1.2 sec. shock duration groups. Subjects in the shorter shock duration groups (0.3, 0.6 sec.) exhibited a greater range of punishments needed to cessation than the longer (1.2, 2.4 sec.) groups. The differences in the number of punishments to cessation among the four shock duration groups were not significant ($F=1.32$, $df=3,12$).

The average number of punishment sessions to complete cessation for each shock duration group was calculated and is shown in Table 1. An analysis of variance revealed significant differences between shock duration groups, in that the longer the shock duration, the fewer the number of sessions to cessation ($F=5.58$; $df=3,12$; $p<.01$).

The number of minutes to the subject's first response in the retest session was recorded, and means for the differing shock duration groups are found in Table 1. One subject (8-A) failed to respond during the three retest sessions, and thus was assigned a score of 90 minutes to the first response. This fact accounts for the large mean shown in Table 1 for the 2.4 sec. shock duration group. The differences between means were not significant ($F=1.53$, $df=3,12$).

A mean percentage of response recovery for each subject was obtained by dividing the subject's total responses for each retest session by its last pre-punishment session response total. The mean percentage of response recovery for the four shock duration groups over the three retest sessions is presented in Figure 1. The means for retest

session 3 show a monotonic trend, in that the mean percentage of response recovery is less when associated with longer shock durations. A groups-by-sessions interaction is evident as illustrated in Figure 1. An analysis of variance was performed for a two-factor mixed design having repeated measures on one factor. This method was used to permit comparison between subjects in different groups, and to determine within-subject effects over several trials. Results of this analysis are shown in Table 2. Different shock durations were shown to have no significant main effect on the overall recovery of responding ($F=1.47$, $df=3.12$). However, subjects' response recovery was seen to be a function of the number of retest sessions, with recovery improving as the number of retests increased ($F=17.23$; $df=2,24$; $p<.01$). The results of the analysis for a groups-by-sessions interaction proved significant at the .05 level ($F=2.55$, $df=6,24$).

Resumption of bar-pressing during the retest sessions was gradual, with no subjects equaling their pre-punishment response totals during the first retest session. Figure 2 presents cumulative response records for the last prepunishment session (top curve) and first retest session (bottom curve) for six representative subjects who responded during the first minute in the first retest session. Of the sixteen subjects in the experiment, only two (4-b, 7-B) equaled their pre-punishment response rate by the conclusion of the study.

Table 1.

Summary of Results of Experiment

shock duration (in sec.)	No. bar presses in session before punishment		Punished responses to cessation		Mean sessions to cessation	Mean minutes to first recovery response
	M	SD	M	Range		
0.3	131.0	37.7	96.0	61-167	4.5	2.0
0.6	177.5	142.3	92.5	17-169	4.5	.75
1.2	147.0	54.5	43.5	26-83	3.5	1.0
2.4	171.0	87.3	45.0	16-71	3.3	27.75

Table 2.

Two-factor mixed design analysis of recovery during retest sessions.

Source	SS	df	ms	F
Total	47,828.31	47	-	-
Between subjects	24,410.98	15	-	-
Conditions	6,899.72	3	2299.91	1.47
Error	17,511.26	12	1459.27	-
Within subjects	23,417.33	32	-	-
Sessions	10,362.12	2	5181.06	17.23**
Sessions x conditions	4,598.22	6	766.37	2.55*
Error	8,456.99	24	352.37	-

* p .05
** p .01

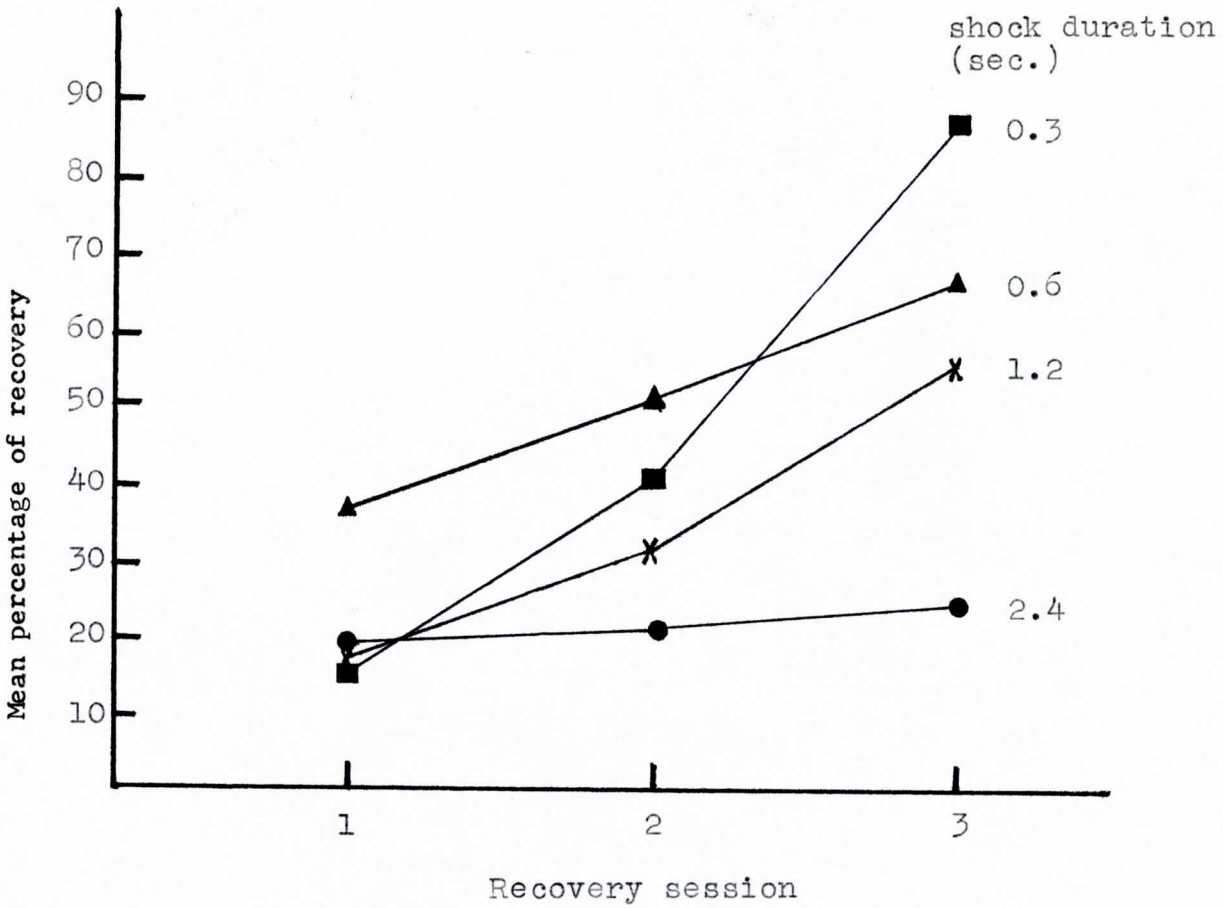

Figure 1. Response rates during three recovery test sessions as a function of punishment duration. Response rate during recovery is expressed as a percentage of the prepunishment rate.

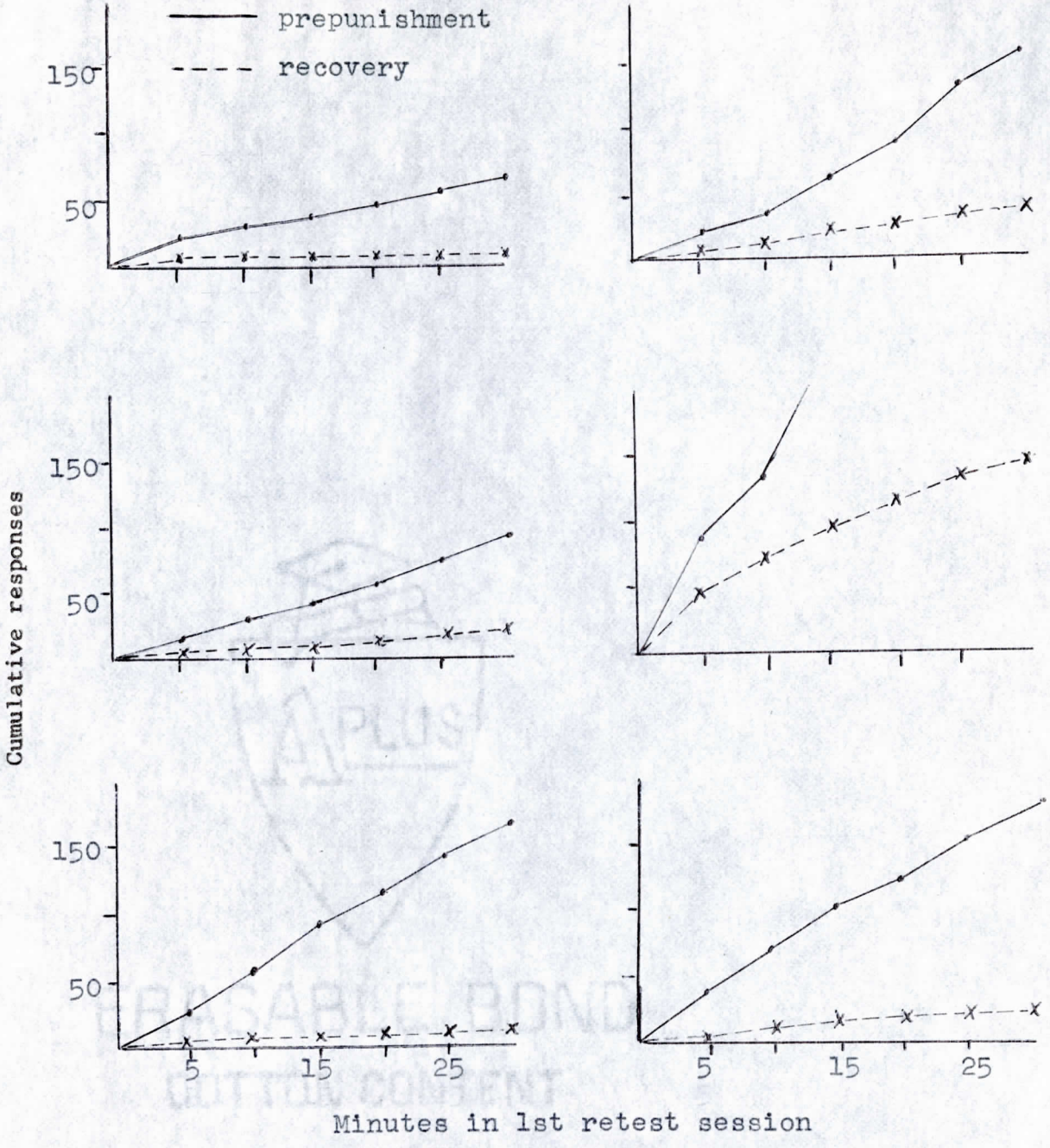

Figure 2. Cumulative response records for the last pre-punishment session and 1st retest session for selected subjects.

Several subjects in the 1.2 and 2.4 sec. shock duration groups learned to escape punishment. Typically their responses after pressing the bar consisted of standing upright in the chamber, placing one rear foot on the grid and one rear foot on the plywood grid frame, and leaning with both front paws on the plexiglas side panel. Once accomplished, this posture was maintained for several seconds, and was observed only following presentation of shock. In the 0.3 and 0.6 sec. shock groups, onset of the shock resulted in jumping behavior to escape the grid shock.

In the longer duration groups, subjects were observed to assume a rigid, freezing posture when emitting the first bar-presses in retest sessions. This freezing posture consisted of the rigid extension of all limbs accompanied by arching of the back and closing of the eyes. This response disappeared within 5 reinforced responses in all subjects.

Discussion

The determination of the effects of shock duration upon recovery of responding was the main concern of this study. A significant interaction was discovered in the present study for groups-by-sessions, a result not found in previous studies with rats. Figure 1, however, illustrates clearly that three group means for percentage of response recovery during the first retest session are similar. The 0.6 sec. shock duration mean for the first retest session included one subject whose recovery was 89%, much higher than that of the next closest subject's 49% recovery. The groups-by-

sessions interaction indicates that in the first retest session there were no significant differences in bar-pressing, with the already noted 0.6 sec. group excepted. Over the next two retest sessions, however, there were differential rates of recovery as a function of shock duration. An explanation of this finding can be approached from several directions. If one assumes that the forgetting of the bar-press response was all that was involved, one would expect all groups to recover in a similar manner, with only a sessions effect. This was not the case. A second approach would be to assume that during the punishment sessions fear was conditioned to apparatus and response-produced cues (Mowrer, 1960), and that during the period between punishment and retest, differential forgetting of fear occurred. Therefore, in retest session 1, initial differences in response rate would occur. Figure 1 again illustrates that this did not happen. A third explanation of this effect may involve the differential conditioning of "fear" in the punishment sessions, combined with the differential extinction of fear. Let us assume that the longer (and thereby more aversive) the shock duration, the greater the "fear" associated with the operant response and test situation. Therefore, during retesting, one would assume that the longer, more fearful shock duration groups would be more resistant to recovery. Extinction of the fear associated with the operants would be quicker for the shorter shock duration groups. This explanation appears plausible in light of the differential rates of recovery shown in Figure 1.

It has been previously reported (Storms, et al., 1963, 1964, 1965) that the longer the duration of shock, the less the recovery, with main effects significant. The present study does not agree with the main effects significance found by Storms, et al. However, the support given in the present study to the findings of increases in recovery over sessions for days of retest is consistent with the interpretations and results of Estes (1944) and Azrin and Holz (1961), who argued that habits are not removed by punishment.

A monotonic relationship between the number of shocks to cessation and duration of shock was reported by Storms, et al.(1964). No exceptions to this finding were reported in any of their studies. In the present experiment no significant differences were found among the means for number of shocks to cessation. Means for the 0.3 and 0.6 sec. shock duration groups were nearly identical, as were the means for the 1.2 and 2.4 sec. durations. This finding that the 2.4 sec. group had a mean similar to the 1.2 sec. group is in agreement with the findings of Storms, et al., who found that the longest durations had little added effect on the number of punishments needed to cessation. Yet there was a marked decrease in the number of shocks needed to cessation between the 0.6 and 1.2 sec. duration groups. In addition, the relationship between groups was not linear, with the 2.4 sec. duration group requiring more shocks to cessation. It is possible that these conflicting results may be due to the limited number of subjects

in each group. Also, successful escape responses as outlined above may have minimized the differential effects of similar shock durations, resulting in the nearly identical means for punished responses to cessation noted above.

The gerbils in the present study responded at a lower rate on the VI 2 min. schedule than the rats in the Storms, et al. experiments. In addition, observations made prior to the start of this experiment indicated that gerbils typically became satiated after consuming 20 food pellets, even though the pellets were the smallest commercially available. This necessitated the use of the 1/2-hour sessions with the gerbils as contrasted with the 1-hour sessions using rats in the Storms, et al. studies. Comparison of total responses per session between the two species is therefore complicated. The lower rate of responding exhibited by the gerbil, however, may be attributed to a high level of exploratory behavior which may compete with operant bar-pressing.

"All-or-none" recovery of responding was not observed in gerbils. Recovery did not show an abrupt resumption of bar-pressing to a previous training rate as reported by the earlier studies mentioned using rats as subjects. All of the 15 gerbils which resumed bar-pressing during the retest sessions exhibited a gradual resumption of responding. In the 1964 study by Storms, et al., the authors stated that in reference to this "all-or-none" effect "either there were virtually no bar-presses, or S's began pressing at a rate indistinguishable from the prepunishment rate." As evidence

for this effect the authors presented a series of cumulative pen recordings for visual comparison. No quantitative method was given for defining "virtually no bar-presses" or "at a rate indistinguishable." In the present investigation, a method was employed to clarify the relationship between the pre-punishment rate and recovery rates. While acknowledging the methodological differences regarding comparisons between the studies, it is nevertheless evident from Figure 2 that recovery during retest was gradual.

No evidence was found in the present study to suggest a "middle duration effect." By examining the 0.6 and 1.2 sec. shock duration groups' recovery in Figure 1, it was clear that at no time during the retest sessions did these two groups exhibit the least percentage of recovery among the total of four groups. This suggests that the effect cited by Storms, et al., in rats may be a species-related phenomenon, which would require further investigation with more varied shock durations.

In this exploratory study it was demonstrated that certain effects of punishment are found in both rats and gerbils, including the increased suppressive effects of longer shock durations on number of responses to cessation, and the recovery of responding across trials in retest sessions. Other results have indicated that a continued investigation with larger sample sizes and more varied shock durations might yield closer agreement with the results of previous studies.

Such results include the non-linear trend in the number of shocks to cessation, and the "middle duration effect." Distinct differences between gerbils and rats were found in the areas of all-or-none recovery and the main effects of shock duration upon number of shocks to cessation.

The data presented in this experiment thus indicates that the gerbil may be successfully chosen as a subject in the comparative investigation of punishment. By making relatively minor mechanical adjustments in the apparatus designed for larger rodents, the gerbil can be used in similar paradigms. For example, in the course of the present study it was necessary to construct a grid with closer spaced grid bars than usually found in a manufactured grid for rats. This was needed to prevent the smaller gerbil from continually falling down between the bars. The gerbils employed in the present study provided every indication that they acquired operant bar-press and escape responses as quickly as domesticated rats. While the front paws of the gerbil are very sensitive, the cutaneous claws in the rear feet are highly resistant to shock conduction. It is therefore suggested that in future studies of this type implanted electrodes be investigated as a better means of delivering shock.

Keeping the importance of either phyletic or ecological relatedness for comparative study in perspective, the gerbil offers many additional advantages as a laboratory animal. It is very easy to handle, rarely bites, and has a gentle disposition. Its small size, cleanliness and hardiness allow

for its economical use in large numbers. In the present investigation food deprivation was used. As a native desert rodent, the gerbil has evolved a unique water metabolism which allows it to survive on a minimum intake of water. Therefore, water deprivation of this animal in the laboratory for a study of this type would not prove feasible. After various unsuccessful attempts at arriving at a method of deprivation, it was found that the animals readily adjusted to the 1/2-hr. daily feeding schedule employed in the present study. No ill effects due to this schedule were observed. Observations of gerbils prior to the start of the experiment led the author to conclude that gerbils are more active and appear healthier when housed in pairs rather than individually. Also, gerbils in the present study learned the necessary operant responses quickly.

The question regarding the extent to which one can extrapolate the behavior of the gerbil from that of the rat requires further investigation. Evidence was presented in this study that, in the area of punishment, certain similarities exist between the species. Yet the results of this study also indicate that there are significant differences between species in the effects of punishment upon response suppression and recovery. That there does not appear to be any serious methodological obstacles to further comparative research between rats and gerbils in the area of punishment is encouraging. From a comparative perspective, it is imperative that researchers understand

the relationships between related organisms before attempting to extrapolate the behavior of man from that of the laboratory rat.

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