

Activity During Inescapable Shock and Subsequent Escape Avoidance Learning: Female and Male Rats Compared*

Raymond C. Kirk and Neville M. Blampied

Department of Psychology, University of Canterbury, Christchurch

Twelve male and twelve female rats were given 60 1 mA inescapable tail shocks. At first, activity during shock was high immediately after shock onset and decreased during the shock. Over trials this initial burst of activity decreased for both male and female rats. After 50 shocks, males were essentially inactive during shock. Females were generally more active than males, particularly during the first and last block of trials. Equal numbers of control rats remained in their home cages. Twenty-four hours later all rats were trained on an escape/avoidance task with a tone as the warning stimulus and 1 mA scrambled foot-shock as the aversive stimulus. Inescapably-shocked male rats exhibited learned helplessness in that their escape-avoidance responding (two crossings of the mid-line of the shuttle box per trial) was significantly impaired. Inescapably shocked female rats were not impaired in their performance.

In a now classic series of experiments Overmier and Seligman (1967) showed that exposure to inescapable shock produced deficits in subsequent escape and avoidance learning. This interference effect was explained by Seligman as a motivational and associative deficit termed 'learned helplessness' (Maier & Seligman, 1976). Experience of uncontrollable inescapable aversive events causes animals to learn that responses and outcomes are independent, so that in subsequent encounters with aversive events learning is impaired.

Competing-response theory gives an alternative account of the interference effect. Various versions of this theory (Bracewell & Black, 1974; Glazer & Weiss, 1976; Levis, 1976) have in common the notion that during inescapable shock the subject learns to be passive and inactive while being shocked. In subsequent encounters with shock these passive tendencies are reactivated and compete with the active response required for escape and avoidance, thus producing the interference effect.

*This research was supported by Grants C70/20, 70/44 and 72/24 from the N.Z. University Grants Committee and the University of Canterbury. Ray Kirk was supported by a New Zealand Medical Research Council Post-Graduate Scholarship during the preparation of this paper (Grant RG515164). We are very grateful for the help of technical staff of the Psychology Department, and for helpful comments from colleagues, especially Dr R. N. Hughes and Professor K. T. Strongman, and from several anonymous reviewers.

Recent research therefore has measured unconditioned activity in response to shock, both within and across inescapable shock trials. It has found that activity declines rapidly as shock trials continue, and, with one exception (Drugan & Maier, 1982), that activity within each shock trial is not uniform: activity is high at shock onset, and then decreases as shock continues (Anisman, de Catanzaro & Remington, 1978; Nation & Boyagain, 1981). These activity patterns confirm predictions of competing-response theory (Glazer & Weiss, 1976) and are the basis for the postulated conditioning of motor passivity in response to shock, through the adventitious pairing of activity cessation with shock offset.

One neglected variable in all this research has been the sex of the subjects. A review of a decade of interference-effect research (Kirk & Blampied, 1980) showed that of 52 published studies employing dogs, rats or mice as subjects, ten failed to state the sex of their subjects; two used female subjects and three used both male and female subjects, the balance using male subjects only. Of the three studies using both male and female subjects, none used the basic paradigm for demonstrating the interference effect, and only one (Wight & Katzev, 1977) analysed for a sex difference, and failed to find one.

Sex differences in rodent behavior are well established (Archer, 1975) and in particular

female rats have lower thresholds for flinching and jumping in response to shock (Beatty & Beatty, 1970; Satinder & Hill, 1974). This difference may be important in the context of the competing motor response theory, because it suggests different patterns of activity during inescapable shock. Learned helplessness theory, however, is not concerned with activity levels. Female rats also acquire active avoidance responses more rapidly than males (Beatty & Beatty, 1970; Denti & Epstein, 1972; Wilcock & Fuller, 1973). This difference may constrain the generality of the interference effect across different escape tasks (Rush, Mineka, & Suomi, 1982).

Both the parameters of the inescapable shock and the nature of the escape-avoidance task are known to affect the manifestation of learned helplessness. Inescapable shocks which are too few in number, too short in duration and/or too low in intensity may produce no effect, or only a transient interference effect (Glazer & Weiss, 1976). Research has established typical values of inescapable shock sufficient to produce durable learned helplessness as 60 to 80, 1 mA shocks of 5 to 6 s duration (Glazer & Weiss, 1976; Maier, Albin & Testa, 1973; Williams & Maier, 1977). It is also well established (Maier et al., 1973) that the escape-avoidance task used must be relatively difficult (e.g. FR-3 barpress, or an FR-2 shuttle requiring two crossings of the mid line of the shuttle box) if learned helplessness is to be observed. In the present experiment the parameters for the inescapable shock in Phase 1 and the FR-2 shuttle response in Phase 2 were selected in the light of this evidence. Following Maier et al. (1973), and Williams and Maier (1977), five FR-1 shuttle trials were given first as a warm up. In addition, because of the theoretical importance of activity changes during inescapable shock, we measured activity during each second of shock in Phase 1.

Method

The subjects were 48 New Zealand random-bred Wistar rats. The 24 male rats had a mean age of 146 days and a mean weight of 290 g, and the 24 female subjects had a mean age of 148 days and a mean weight of 217 g. They were housed individually, provided with ad lib food and water, and maintained on a reversed day/night cycle. All

testing was conducted during the 12 hr dark phase. White masking noise (74–77 dB) was continuously present in the testing room. In Phase 1, the rat was restrained in a plastic tube, 238 mm in length and 64 mm in diameter, mounted on a Lafayette A501 activity platform, 28×28 cm (L×W). Guillotine doors were placed at each end of the restraining tube. The protruding tail was supported by a steel mesh apron, against which it was held by an elastic strip and was prevented from being pulled into the tube by a washer and ring.

In Phase 1, inescapable shocks were delivered through electrodes attached to the tail, contact being augmented with electrode paste. Gross body movement while the subject was restrained caused the activity platform to move laterally and up and down. This movement was detected as interruptions of a photocell, and each interruption was counted as one activity count. Two channels of an Easterline Angus operations recorder recorded activity counts and shocks.

In Phase 2, two-way active escape/avoidance training was carried out in a Lafayette shuttle box, 61×25×28 cm, divided into two chambers by a partition which contained an opening in its centre flush with the grid floor, 9 cm×9.5 cm (W×H). Two speakers, one at each end of the shuttle box, were used to deliver a 473-Hz, 85 dB tone (warning stimulus) and two 15 W light bulbs immediately above the ceiling permitted each chamber to be illuminated independently.

In Phase 1, 12 male and 12 female rats randomly assigned to receive inescapable shock were placed in the restraining tube, electrodes were attached to their tails, and they were given 60, 1 mA unsignalled shocks, of 5 s duration, scheduled by a variable-time 60-s schedule. Activity levels were recorded throughout the session. The remaining 12 male and 12 female rats remained in their home cages during this Phase.

Phase 2, active escape/avoidance training began 24 hours later for all subjects. Each rat was placed in the shuttlebox for a ten-minute habituation period, followed immediately by 30 escape/avoidance training trials. Each trial began with the onset of the warning stimulus and a change in illumination from darkness to 320 lux¹. After 5 s a 1 mA scrambled shock was presented on the grid floor. For the first five trials, a single crossing of the mid-line terminated the warning stimulus and the shock. The remaining 25 trials required a second crossing of the mid-line to be effective as an escape or avoidance response. Maximum trial duration was 35 s, and if no response occurred

¹Half the subjects were trained with tone onset as the only CS, the lights remaining on all the time. There was no significant difference between the two CS types, so data were collapsed across the variable.

the trial was automatically terminated and a latency of 35 s was recorded. On other trials, the time from warning stimulus onset to offset was recorded as the response latency. The inter-trial interval averaged 60 s (range 10–266 s). The timing of the warning stimulus, the shock and the latency was controlled by Pye Hi-log solid state equipment.

Results

The activity counts were aggregated over blocks of 10 trials, and aggregate scores are presented separately for male and female rats in Figure 1. They were also entered into a 3-way (Sex×Trial Blocks×Seconds of Shock) analysis of variance (ANOVA) (Hartley, 1980; Kirk, 1968).

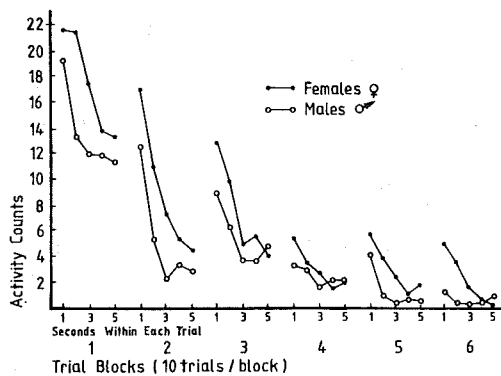


Figure 1. Mean activity counts during each second of shock, averaged over blocks of 10 shock trials.

Figure 1 shows that activity declined over the six blocks of trials ($F(9,90)=35.58$, $p<.001$). Typically, activity also declined from the first to the last second of shock, ($F(4,40)=26.7$, $p<.001$), although there are a few instances where the lowest activity level was recorded during the third or fourth second of shock, and rose slightly during the final second(s). As activity in response to the onset of shock declined in absolute level, so the rate at which it declined over the shock interval also decreased, accounting for the significant Trial Blocks×Seconds of Shock interaction ($F(36,360)=2.67$, $p<.01$). This interaction is especially evident in the data of the male subjects, and in the fourth and sixth trial block in particular their activity changed little during the shocks. During the final block of trials, male subjects were essentially inactive during shock.

In four of the six blocks of trials Figure

1 shows the activity level of the female rats to be consistently higher than that of the male rats. Overall, however, this difference was not significant. The clear and consistent differences between activity levels of female and male rats during the first and the final block of trials shown in Figure 1, were analysed in a separate 3-way ANOVA. Female rates were significantly more active than males during the first and last blocks of trials ($F(1,10)=5.56$, $p<.05$). This analysis also confirmed the finding of a significant reduction in activity from the first to the sixth block of trials, and within each second of shock ($F(1,10)=114.7$, $p<.001$; and $F(4,40)=20.13$, $p<.001$ respectively).

All rats learned to escape during FR-1 trials. Average latency for the 5th trial was 5 sec (response speed of 0.2 s^{-1}). There were no significant differences in response speed between male and female rats, nor between experimental and control groups over the FR-1 trials.

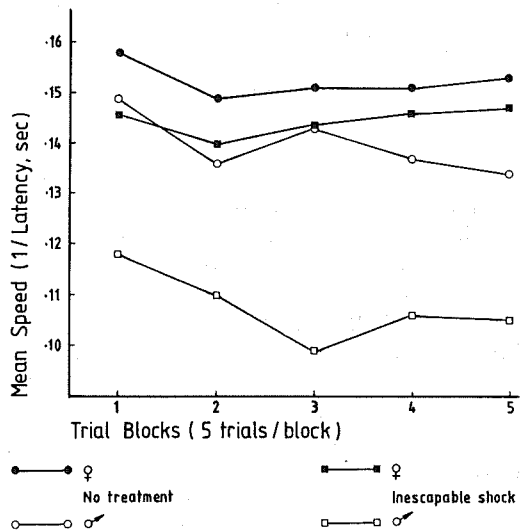


Figure 2. Mean speed of escape responding in the shuttle box during the FR-2 trials.

Performance in the FR-2 trials in the shuttle box is shown in Figure 2. Latency scores were converted to response speed to meet statistical requirements of homogeneity of variance (Kirk, 1968). The female control (no-treatment) rats showed the highest response speeds, which were stable across trials, but never achieved latencies short enough to avoid the shock, so all trials were escape trials. The

male rats in the control group responded less rapidly, and their response speed tended to decrease over trials. Male rats given inescapable shock exhibited the interference effect, with very low response speeds, which also tended to decrease slightly across trials. Although the female subjects given inescapable shock showed mean response speeds that were slightly lower than the female rats in the control group, their mean speeds were not significantly different from the male or female control subjects. Analysis of variance yielded a significant main effect for Sex ($F(1,40)=24, p<.001$), and Treatment ($F(1,40)=16, p<.001$), and a significant Sex \times Treatment interaction ($F(1,40)=6, p<.05$), confirming the above observations.

Discussion

This study demonstrated that activity levels during long duration shock underwent a steep decrement during shock, and over repeated shocks, and that female rats were generally more active during shocks than male rats. It has also shown that inescapable shock exposure sufficient to produce the interference effect (learned helplessness) in male rats did not produce the effect in females.

The activity decrement observed within each episode of inescapable shock is that predicted by Glazer and Weiss (1976) and observed in five experiments by Anisman, de Catanzaro and Remington (1978) and by Nation and Boyagain (1981). Glazer and Weiss (1976) argued that this activity decrement was conditioned superstitiously by the adventitious pairing of activity reduction and shock offset, but Wilson and Butcher (1980) have shown that the aversiveness of shock delivered via a back electrode is inversely proportional to the number of feet grounded during shock. This established a contingency for the positive punishment of jumping and struggling and the negative reinforcement of inactivity. However, this contingency would not have affected our data, since inescapable shocks were delivered through a pair of tail electrodes. None-the-less, we observed the within-shock activity decrement, suggesting that it may be superstitiously conditioned and/or an unconditioned response to long duration shock, perhaps mediated by neurochemical depletion (Weiss, Glazer & Poho-

recky, 1976). Drugan and Maier (1982), however, failed to observe this within-shock decrement in activity, although their rats became less active as the shock session progressed.

Except in the last block of trials, the within-shock and across session changes in activity showed the same pattern for males and females, although females were initially more active than males, as expected (Archer, 1975). At a given age, male rats are on average heavier than females. Might the activity differences be due to differences in weight rather than sex? Within each group there were five females and six males whose weights lay in the range 230–260 g, with a difference in mean weight of 2 g. Mean total activity counts for this subset of females was 773 counts, and 167 for the subset of males, strongly suggesting that in rats of approximately equal weight, female rats were still more active than male rats.

Only in the last block of inescapable shock trials did the pattern of male response to shock differ from the female pattern. After 50 shocks, males were quiescent throughout the shock during the final 10 shocks. Females continued to be initially active although at a much reduced level compared with the first block of trials, with activity declining to zero during the shock. Male rats therefore exhibited the pattern of inactivity in the presence of shock predicted by the competing motor response theory, and should therefore have shown the interference effect in the shuttle box, and did. At shock onset, after 60 shocks female rats still did not show this pattern of inactivity, and might not therefore have been expected to show the interference effect, and did not. However, both groups had been exposed to inescapable, unmodifiable aversive events, and according to learned helplessness theory should have shown the interference effect. Our findings, then, support competing motor response theory.

However, it is likely that had females received more inescapable shock trials they too would have shown the cessation of activity males showed after 60 trials. Female rats may just be more resistant to the interference effect because of their greater and more durable responsivity to shock. Shurman and Katzev (1975) obtained an interference effect in a one-

way jump-up task, using female rats, but only in subjects of the Long-Evans strain, and in groups given more than 225 shocks. These shocks were given in the same apparatus as the escape task, and were signalled by the same warning stimulus as was used in the escape task, so this experiment is not exactly comparable with the standard interference-effect paradigm, but it does support the idea that female rats will show the interference effect if given sufficient shocks. Moran and Lewis-Smith (1979) who observed an interference effect in both male and female rats, used a procedure more like the standard one, except that their inescapable tail shocks were very long (14 sec). Again, it might be predicted that activity levels would be suppressed by such long shock exposures, but no activity data is reported in this experiment.

The present results indicate that the interference effect, whatever its theoretical explanation, is modulated by an interaction between species- and sex-specific reactions (Archer, 1975; Bolles, 1970) and the test task. Male rats tend to freeze in response to shock, and this tendency is enhanced by inescapable shock, while female rats are somewhat less prone to freezing, and remain slightly more active during inescapable shock. It might be predicted, then, that female rats would show an interference effect in passive avoidance tasks, where their reactivity would be a handicap rather than an advantage. There is some evidence that male rats given inescapable shocks are better at passive avoidance than controls, but no comparison of male and female rats on this task has been reported (see Rush, et al., 1982, for a review).

References

- Anisman, H., de Catanzaro, D., & Remington, G. (1978). Escape performance following exposure to inescapable shock: Deficits in motor response maintenance. *Journal of Experimental Psychology: Animal Behavior Processes*, 4, 197-218.
- Archer, J. (1975). Rodent sex differences in emotion and related behavior. *Behavioral Biology*, 14, 451-479.
- Beatty, W. W., & Beatty, P. A. (1970). Hormonal determinants of sex differences in avoidance behavior and reactivity to electric shock in the rat. *Journal of Comparative and Physiological Psychology*, 73, 446-455.
- Bolles, R. C. (1970). Species-specific defense reactions and avoidance learning. *Psychological Review*, 77, 32-48.
- Bracewell, R. J., & Black, A. H. (1974). The effects of restraint and noncontingent pre-shock on subsequent escape learning in the rat. *Learning and Motivation*, 5, 53-69.
- Denti, A., & Epstein, A. (1972). Sex differences in the acquisition of two kinds of avoidance behavior in rats. *Physiology & Behavior*, 8, 611-615.
- Drugan, R. C., & Maier, S. F. (1982). The nature of the activity deficit produced by inescapable shock. *Animal Learning & Behavior*, 10, 401-406.
- Glazer, H. I., & Weiss, J. M. (1976). Long-term interference effect: An alternative to learned helplessness. *Journal of Experimental Psychology: Animal Behavior Processes*, 2, 202-213.
- Hartley, L. (1980). Basic language programs for one-to-three- or four-factor within- and between-subject ANOVAs for Apple II and Commodore PETs. *Behavior Research Methods & Instrumentation*, 12, 567.
- Kirk, R. E. (1968). *Experimental design: Procedures for the behavioral sciences*. Belmont, California: Brooks-Cole.
- Kirk, R. C., & Blampied, N. M. (1980). A bibliography of learned helplessness research. *JSAS Catalog of Selected Documents in Psychology*, 10, 19-20.
- Levis, D. J. (1976). Learned helplessness: A reply and an alternative S-R interpretation. *Journal of Experimental Psychology: General*, 105, 47-65.
- Maier, S. F., Albin, R. W., & Testa, T. J. (1973). Failure to learn to escape in rats previously exposed to inescapable shock depends on the nature of the escape response. *Journal of Comparative and Physiological Psychology*, 85, 581-592.
- Maier, S. F., & Seligman, M. E. P. (1976). Learned helplessness: Theory and evidence. *Journal of Experimental Psychology: General*, 105, 3-46.
- Moran, P. W., & Lewis-Smith, M. (1979). Learned helplessness and response difficulty. *Bulletin of the Psychonomic Society*, 13, 250-252.
- Nation, J.R., & Boyagain, L. G. (1981). Appetitive performance following exposure to inescapable shocks of short and long duration. *American Journal of Psychology*, 94, 605-617.
- Overmier, J. B., & Seligman, M. E. P. (1967). Effects of inescapable shock upon subsequent escape and avoidance learning. *Journal of Comparative and Physiological Psychology*, 63, 28-33.
- Rush, D. K., Mineka, S., & Suomi, S. J. (1982). The effects of control and lack of control on active and passive avoidance in Rhesus monkeys. *Behavior Research & Therapy*, 20, 135-152.
- Satinder K. P., & Hill, K. D. (1974). Effects of genotype and post-natal experience on activity avoidance, shock threshold and open-field behavior of rats. *Journal of Comparative & Physiological Psychology*, 86, 363-374.
- Shurman, A. J., & Katzev, R. P. (1975). Escape avoidance responding in rats depends on strain and number of inescapable pre-shocks. *Journal of Comparative and Physiological Psychology*, 88, 548-553.
- Weiss, J. M., Glazer, H. I., & Pohorecky, L. A. (1976). Coping behavior and neurochemical changes — An alternative explanation for the original "learned helplessness" experiments. In G. Servan & A. King (Eds.), *Animal models of human psychobiology* (pp. 141-173). New York: Plenum Press.

- Wight, M. T., & Katzev, R. D. (1977). Noncontingent positive reinforcers retard later escape/avoidance learning in rats. *Bulletin of the Psychonomic Society*, 9, 319-321.
- Wilcock, J., & Fuller, D. W. (1973). Avoidance learning in rats: Genetic evidence for two distinct behavioral processes in the shuttlebox. *Journal of Comparative and Physiological Psychology*, 82, 247-253.
- Williams, J. L., & Maier, S. F. (1977). Trans situational immunization and therapy of learned helplessness in the rat. *Journal of Experimental Psychology: Animal Behavior Processes*, 3, 240-253.
- Wilson, W. J., & Butcher, L. K. (1980). A potential shock-reducing contingency in the back shock technique: Implications for learned helplessness. *Animal Learning & Behavior*, 8, 435-440.