

# Avoidance, classical, and pseudoconditioning as a function of species-specific defense reactions in high- and low-avoider rat strains

NIGEL W. BOND

*Macquarie University, North Ryde, New South Wales, Australia*

Rats of the Australian High Avoider (AHA) and Australian Low Avoider (ALA) strains and their reciprocal crosses were exposed to 50 trials of one of three shuttlebox procedures. The avoidance group received pairings of a tone and shock. If the animals shuttled during the tone, they avoided the shock. If they waited until the shock came on, they could then escape it. The classical group received pairings of the tone and a brief inescapable shock. If they shuttled during the tone, the tone ceased and they immediately received the shock. If they did not shuttle, they received the brief shock at the termination of the tone. The pseudoconditioning group received the tone and the shock explicitly unpaired. If they shuttled during either the tone or the shock, the stimulus was terminated. There was no acquisition of anticipatory responding under the pseudoconditioning procedure. All groups evidenced an increase in anticipatory responding over trials under the classical procedure. The AHAs acquired the response faster and reached a higher asymptote than did the ALAs. Performance of the two reciprocal crosses fell in between. A similar pattern was observed under the avoidance procedure, albeit at slightly higher response levels. Subsequent studies established that the AHAs acquired a one-way avoidance response quickly, but were impaired on a passive avoidance task, whereas the reverse was the case for the ALAs. The reciprocal crosses were proficient at both tasks. These results suggest that shuttlebox avoidance is largely accounted for by classical conditioning of the predominant defensive response. When that response is compatible with performance on the task, acquisition is rapid (AHAs), and when it is not, acquisition is slow (ALAs).

Avoidance learning presents its students with a continuing paradox. Why are animals able to learn to avoid rapidly in some situations and yet appear to be confused and confounded in others? Why is it that rats can learn to jump out of a box to avoid an electric shock after only one or two experiences of shock in the box, yet fail to learn to press a level to avoid shock after several thousands of trials? The most influential account seeking to resolve this paradox is provided by Bolles's (e.g., 1970, 1972) delineation of the role played by species-specific defense reactions in avoidance learning. Bolles starts with the assumption that animals have innate species-specific defense reactions (SSDRs). In rodents, these include fleeing, freezing, and fighting. (We might now have to add "burying" to this list; see Pinel & Treit, 1978.) Bolles then suggests that avoidance learning will be rapid when the response required is an SSDR. In early formulations, he suggested that the prerequisite SSDR became more probable because all other responses were punished by association with the aver-

sive stimulus and were thus less likely to reoccur (Bolles, 1970, 1972). In more recent formulations, Bolles has noted that, paradoxically, such SSDRs as freezing and fighting appear to be increased in probability by punishment (Bolles, 1975). This latter finding suggests that the behavior of the frightened rat seems to depend upon the stimulus situation. If escape is possible, the rat will flee; if escape is not possible, it will freeze. The animal's behavior, however, is not a direct reflection of associative learning (Bolles, 1978).

The view of avoidance espoused by Bolles is clearly predicated upon the assumption that an animal's defensive behaviors are a product of its evolutionary development and, as such, are heavily influenced by hereditary factors. The notion that avoidance learning is influenced by genotype has been the subject of a large number of studies that have employed a variety of methodologies. Thus, there are a number of demonstrations that rats can be selectively bred for differences in avoidance responding. Bignami (1965) selected for high or low rates of avoidance responding during two sessions of shuttlebox avoidance testing, and also on the basis of high or low retention from each session to the succeeding one. Selection was extremely rapid, and after five generations the Roman High Avoiders (RHA) were making approxi-

This research was supported by a Macquarie University research grant. Thanks are due to Cheryl Hume and Len Glue for their valuable technical assistance. The author's mailing address is: School of Behavioural Sciences, Macquarie University, North Ryde, N.S.W. 2113, Australia.

mately 175 avoidance responses in 250 trials, whereas the Roman Low Avoiders (RLA) were making only 50 avoidance responses. Similar results have been obtained by Brush, Froehlich, and Sakellaris (1979) and Bammer (1978). A number of further studies have demonstrated that extant strains of rats and mice differ in the efficiency with which they acquire avoidance responding (cf. Fuller & Thompson, 1978). Although such studies indicate that an animal's genotype influences avoidance responding, they do not indicate the heritability and genetic architecture underlying this influence. However, several studies have addressed this question. In general, a variety of techniques, including full-sib, half-sib correlations, parent-offspring regression, diallel analyses, and the triple-cross test, have given heritability estimates of approximately 0.5 (Collins, 1964; Hewitt, Fulker, & Broadhurst, 1981; Oliverio, Castellano, & Messeri, 1972; Oliverio, Eleftheriou, & Bailey, 1973; Royce, Yeudall, & Poley, 1973; Wilcock & Fulker, 1973). There is less agreement as to whether there is single-gene or polygenic control of the avoidance response.

A recent review of the area by Fuller and Thompson (1978) has drawn the general conclusion that hereditary influences produce differences in the alternative initial responses to a CS or UCS. As yet, there is no substantial evidence from the avoidance literature that there are genetic differences in associative learning ability (cf. Wahlsten, 1978). It is interesting to compare this conclusion with that of Bolles (1975), working with a different literature.

There have been a number of attempts to draw together an analysis of avoidance learning from both behavioral and genetic perspectives, most notably by Satinder and his colleagues (Satinder, 1976, 1977; Satinder & Hill, 1974; Satinder & Petryshyn, 1974). Employing a variety of selectively bred strains of rats, including the RHA, RLA, RCA, Maudsley Reactives (MR), Maudsley Non-reactives (MNR), Tryon Maze Brights (TMB), and Tryon Maze Dulls (TMD), and differing levels of task complexity, Satinder has demonstrated that differences in avoidance behavior between these lines of rats may be understood as deriving from genetically related differences in sensory responsiveness and levels of arousal. Again, the similarity of this conclusion to those of Bolles and those of Fuller and Thompson is obvious.

Seemingly, the conclusion to be drawn from the work described above is that avoidance responding has little to do with associative learning. If this is so, however, why is it that studies that have degraded the various avoidance contingencies have observed that avoidance responding deteriorates (e.g., Bolles, Stokes, & Younger, 1966; Kamin, 1956)? If associative learning is unimportant, it is difficult to see how such changes could have such profound effects.

The present studies sought to answer this question by employing some of the techniques described above. Specifically, two lines of rats selectively bred for differences in performance on a shuttlebox avoidance task, the Australian High Avoiders (AHA) and Australian Low Avoiders (ALA) and their reciprocal crosses, were exposed to two-way avoidance, a classical conditioning contingency, or a pseudoconditioning contingency. Having established their relative performances on these tasks, I then sought to determine the source of the difference between the AHA and ALA strains by examining the role played by the predominant defensive behaviors, "fleeing" and "freezing," in their respective performances.

## EXPERIMENT 1

The first study was designed to examine the role played by the pairing of the CS and UCS in avoidance conditioning. Specifically, the typical two-way shuttle avoidance paradigm was compared with a classical conditioning contingency in which the rat was presented with the CS followed by a brief UCS regardless of its behavior. (The brief UCS ensured that the rat would be unable to escape the shock once it was presented.) In addition, to determine if it was the pairing of the CS and UCS that was important, a third group of animals were exposed to a pseudoconditioning procedure in which the CS and UCS were presented randomly. Katzev and Mills (1974) employed similar procedures in examining the role of classical contingencies in avoidance conditioning but failed to control for nonassociative effects by including a random control group.

### Method

**Subjects.** Forty-eight AHA, 48 ALA, 36 ALA/AHA, and 36 AHA/ALA rats were employed; half were male. (Following convention, the reciprocal crosses are represented with the dams designated first and the sires second.) The AHA and ALA animals were the 11th generation of two lines of Sprague-Dawley-derived rats developed at Sydney University for differences in two-way avoidance responding (Bammer, 1978). The reciprocal crosses were derived from littermates of the animals used to produce the AHA and ALA animals employed here. Details of husbandry techniques and selection criteria may be found in Bammer (1978). Briefly, the animals were 100 days old at the time of testing and were housed with their same-sex littermates in groups of three to five in plastic wire-topped cages (27 × 38 × 15 cm) with food and water freely available. The cages were kept in a temperature-controlled room on a 12-h light/dark cycle with lights on at 0700 h. All testing took place between 1000 and 1500 h.

**Apparatus.** The shuttlebox consisted of two clear Perspex compartments (13 × 30 × 10 cm each) separated by a black guillotine door. It was fully automated and responses and response latencies were recorded using a Processor Technology "Sol" microcomputer. All equipment was situated in a darkened, temperature-controlled, sound-attenuated cubicle.

**Procedure.** The contingencies for the avoidance group were as follows. The animals were allowed 5 min to explore the apparatus and were then given 50 test trials. Each trial began with the presentation of a 2800-Hz tone. If the rat had not moved to the other side after 5 sec of tone, a 1-mA scrambled shock was delivered to

the floor of the compartment in which the animal was standing. Both the tone and the shock then remained on for 25 sec or until the animal crossed into the other compartment. The intertrial interval was kept constant at 30 sec. An avoidance response was recorded if the animal moved to the other side of the shuttlebox during the 5-sec warning period preceding the shock.

After the 5-min exploration period, the classical conditioning group were presented with 50 trials consisting of the presentation of the 2800-Hz tone and shock. If the rat moved to the other compartment of the shuttlebox within 5 sec, the tone terminated and the animal received a brief, .5-sec, 1-mA scrambled shock in the compartment it had just entered. If the rat did not move to the other compartment within 5 sec, the tone was terminated and the rat received the brief shock in the compartment in which it was standing. This procedure represents a delayed classical conditioning procedure in that the rat received the pairing of the tone and the shock regardless of its behavior. The only effect of shuttling or "anticipatory" responses was to turn off the tone and to cause the immediate presentation of the shock.

Following their 5-min exploratory period, the pseudoconditioning group received 50 presentations of the 2800-Hz tone and 50 presentations of the 1-mA scrambled shock. Each trial consisted of the presentation of the shock for a 25-sec period or until the rat moved to the other compartment, at which time the shock was terminated. Within each trial, the tone was programmed randomly with the restriction that no tone occur within 5 sec prior to or following the shock. This restriction ensured that there was no close forward or backward pairing of the tone and shock. Each trial lasted 30 sec plus the time spent in the presence of the tone and the shock. This procedure made the trials slightly longer than they were under the avoidance and classical procedures, but this was difficult to avoid without yoking. A pseudoconditioned response was scored if the rat moved to the other side of the shuttlebox during the 5-sec presentation of the tone. At the same time, the tone was terminated.

## Results

Two factors are known to be important in influencing an animal's performance on shuttlebox tasks—its weight and its activity (cf. Wahlsten, 1978). Lighter and more active animals tend to make more avoidance responses. All animals were weighed prior to the test session, and intertrial crossings were used as an index of activity. The latter seemed to be the most appropriate measure, since it was obtained under the same stressful conditions as the actual response of interest. In subsequent analyses, both the rat's weight and the number of intertrial crossings it made during the test session were included as covariates. A third factor that may influence the acquisition of avoidance responding is the rat's sensitivity to the shock employed as the UCS (Satinder, 1976; Wahlsten, 1978). To determine whether there were strain differences in the response to shock, an analysis of covariance was carried out on the latency to escape from the shock on the first trial. Weight was employed as a covariate, since the size of the animal is known to influence its sensitivity to shock. This analysis was restricted to the avoidance and pseudoconditioning contingencies, because the shock was too brief to be escaped under the classical conditioning procedure. The analysis revealed only a significant effect of condition; rats exposed to the avoid-

ance contingency escaped from the shock more quickly than did those exposed to the pseudoconditioning procedure [ $F(1,95) = 4.3, p < .05$ ]. As a result of this analysis, it would appear that the strains and their reciprocal crosses do not differ in initial sensitivity to shock, so this factor was ignored in subsequent analyses.

A 4 (strains)  $\times$  2 (sex)  $\times$  3 (condition) analysis of covariance with repeated measures on trials (5 blocks of 10 trials) was carried out on the responding of the various groups of animals during the 2800-Hz tone, with the weight of the rat and its intertrial crossings as covariates. Intertrial crossings proved to be a significant covariate [ $F(1,142) = 48.7, p < .0001$ ]. As a result, all the scores were adjusted for this covariate and the adjusted scores were used in the final analysis. The analysis of responding during the tone yielded a significant effect of strain [ $F(3,142) = 8.3, p < .0001$ ] and a significant effect of task [ $F(2,142) = 170.1, p < .0001$ ]. There was also a strain  $\times$  task interaction [ $F(6,142) = 2.5, p < .05$ ]. The trials effect was significant [ $F(4,576) = 141.6$ ], as was the interaction of trials with strain [ $F(12,576) = 2.2, p < .01$ ] and task [ $F(8,576) = 28.7, p < .0001$ ]. The interaction among strain, task, and trials was also significant [ $F(24,576) = 2.3, p < .001$ ].

To sort out some of these effects, individual analyses were carried out on the various tasks. The analysis on pseudoconditioning did not yield any significant results. The analysis on the classical conditioning task yielded an effect of strain [ $F(3,46) = 2.78, p < .05$ ] and trials [ $F(4,192) = 47.2, p < .0001$ ] and a strain  $\times$  trials interaction [ $F(12,192) = 1.9, p < .05$ ]. Finally, the analysis on the avoidance task yielded a significant effect of strain [ $F(3,46) = 8.3, p < .0001$ ] and trials [ $F(4,192) = 146.4, p < .0001$ ] and a strain  $\times$  trials interaction [ $F(12,192) = 3.3, p < .0001$ ].

The adjusted scores are shown in Figure 1. (The two reciprocal crosses did not differ from each other on any of the above analyses, and as a result they have been combined in Figure 1.) Examination of this figure together with the above analyses indicates that all animals evidenced low levels of pseudoconditioned responding, and there was no change in the likelihood of these responses as the session progressed. In contrast, all four groups evidenced significant levels of anticipatory responding on the classical conditioning task, and the probability of such responding increased markedly across trials. The interaction of strains and trials appears to be due to the fact that the AHA animals acquired anticipatory responding at a faster rate than did the ALA animals and that their rate was still increasing at the end of the session whereas that of the ALAs appeared to have reached asymptote. The performance of the two reciprocal crosses fell between that of the AHAs and ALAs. All four groups acquired the avoidance response to

asymptote. However, they differed in the rate at which they acquired it, the AHAs being the fastest and the ALAs being the slowest.

The task effect in the overall analysis of variance appears to be due to the fact that the order of the levels of anticipatory responding made by the various strains was: avoidance conditioning, classical conditioning, and pseudoconditioning. Inspection of Figure 1 indicates that the addition of the classical contingency to the situation causes a marked increase in the probability of anticipatory responding over that observed in the pseudoconditioning procedure. Indeed, the present results are in accord with those reported previously by Katzev and Mills (1974), in indicating that the addition of such a contingency appears to be more profound in terms of enhancing responding than is the addition of the avoidance contingency.

The data in Figure 1 are presented in terms of number of responses. A second measure employed in studies of avoidance learning is the latency of the anticipatory response. While there is some debate about this (Kimble, 1967; Mackintosh, 1974), it would seem to be the case that as avoidance responding becomes more probable, so the avoidance response occurs more quickly following CS onset (Brush, 1962). To determine whether this was also the case for the classical conditioning contingency, the latencies of anticipatory responding for both the avoidance and classical contingencies were computed for the AHAs. (the examination of latency was restricted to the AHAs because the aim was to compare the changes in latency between avoidance training and classical conditioning, not the various strains. This was best restricted to the AHAs in which acquisition was rapid.) This was done by finding the mean latency of anticipatory responding, that is, the time from the

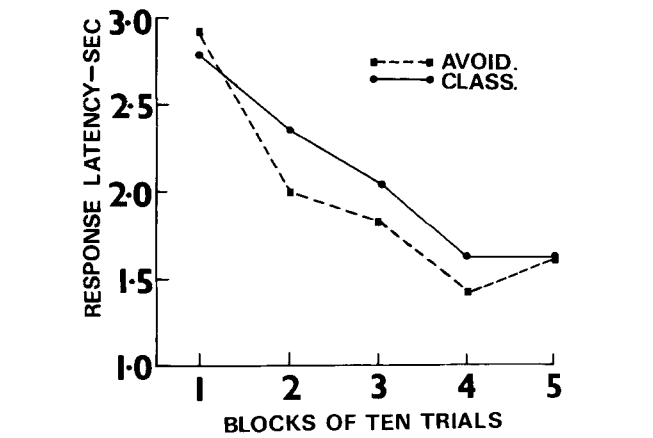


Figure 2. Latency of anticipatory responding, in 10-trial blocks, under both the avoidance (broken line) and classical (unbroken line) procedures, for the Australian High Avoiders.

onset of the CS to when the animals moved to the other side of the shuttlebox, over 10 trial blocks. The data are illustrated in Figure 2. Separate analyses of variance indicated a significant effect of trials for both avoidance responding [ $F(4,36)=14.26, p < .0001$ ] and the classical contingency [ $F(4,36)=21.5, p < .0001$ ]. Clearly, in both cases, as the anticipatory responding became more probable (Figure 1), it also occurred more quickly.

### DISCUSSION

The present results add to our knowledge concerning the fact that rats can be selectively bred for avoidance responding. The AHAs and ALAs represent the 11th generation of a line of rats so selected (Bammer, 1978), and they differ quite clearly in their ability to acquire the avoidance response in the shuttlebox. Note that the conditions employed here, which allowed the animals to cross during the intertrial interval, are conducive to high rates of avoidance responding. Under conditions in which the guillotine door is lowered between trials, the difference between the AHA and ALA strains is much larger (Bond, 1981a). These findings are in accord with those of Bignami (1965) and Brush et al. (1979). As with these other studies, the performance of the reciprocal cross animals derived by mating the AHAs and the ALAs tended to be intermediate between the two parent strains. The fact that the reciprocal crosses did not differ from one another in performance indicates that the difference between the AHAs and ALAs is not due to maternal factors. Of greatest interest, however, is the fact that the strains also differed when exposed to a classical conditioning contingency in which the only outcome of anticipatory responding was the immediate termination of the CS and the delivery of the UCS. Indeed, the ordering of the strains—AHA, RCs, ALA—was

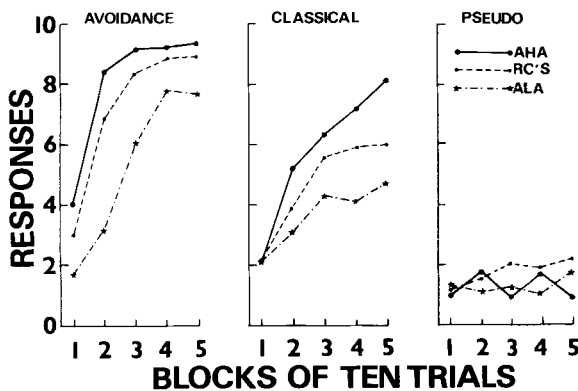


Figure 1. Mean anticipatory responding during the tone, in 10-trial blocks, for each of the avoidance, classical, and pseudoconditioning procedures. The continuous lines indicate the Australian High Avoiders, the dashed lines joining the stars (\*), the Australian Low Avoiders, and the dashed lines joining the dots the reciprocal crosses. (The latter two groups were combined since they did not differ.)

identical under the two conditions. However, once the associative pairing between the CS and the UCS was removed, the differences between the strains disappeared. Thus, there were no differences between them under the pseudoconditioning procedure.

Katzev and Mills (1974) observed that anticipatory responding to the CS accounted for a considerable number of the avoidance responses they observed in a variety of rat strains. As a result, they have suggested that if the avoidance response required is compatible with the anticipatory responses elicited by the classical contingency embedded in the typical avoidance contingency, the acquisition of the avoidance response will be rapid. In contrast, if the avoidance response is incompatible with the anticipatory response, the acquisition will be slow. Certainly, the present data are in accord with such a suggestion. The ordering of the strains under the classical procedure was the same as that under the avoidance procedure, as one would predict. Furthermore, when the association between the CS and the UCS was removed, all differences between the groups were removed.

The classical conditioning procedure necessitated the use of a brief shock. The length of shock under the avoidance procedure was determined by the animal's behavior. Indeed, this difference might account for the superiority of the avoidance procedure in both the present study and that of Katzev and Mills (1974). A yoked control group might have overcome this difficulty. Some might argue that the termination of the CS under the classical procedure introduces a confound. However, in acquisition under a classical procedure, Katzev and Mills (1974) found no differences between a condition in which the CS terminated and one in which it does not. Thus, this factor is unlikely to have influenced the outcome of the present experiment.

As noted previously, as avoidance responding becomes more probable, such responses occur more quickly following CS onset (Bond, 1981b; Brush, 1962). Given the profound influence that anticipatory responding has on avoidance performance, it is instructive to examine whether anticipatory responding under a classical procedure also occurs more quickly after CS onset, as it becomes more probable. As illustrated in Figure 2, anticipatory responding decreased in latency as its probability increased, perhaps accounting for the decrease in the latency of the avoidance response.

If avoidance responding is largely a function of a classically conditioned anticipatory response, the question arises as to why there are strain differences in the acquisition of such behavior? Katzev and Mills (1974) have followed Bolles (1970) in suggesting that these are likely to be SDRs. As noted in the introduction, there appear to be four basic SDRs in the rat. Of these, two are unlikely to be elicited when the animals are tested in isolation in the shuttlebox, that is, fighting and burying. This leaves fleeing and

freezing. A number of authors have pointed out that shuttlebox avoidance may be a function of the interaction between these two behaviors (Wilcock & Fulker, 1973). For example, it is assumed that on early trials rats freeze and are reluctant to return to the side of the shuttlebox that they have just vacated, inasmuch as they have recently received shock there. It is only when they have overcome this reluctance that the avoidance response emerges. In support of this notion, it has been demonstrated that unlike other forms of avoidance, shuttlebox avoidance acquisition is inversely related to shock intensity, presumably because more freezing is elicited by the initial shocks (Reiss & Farrar, 1972). Given this suggestion, one might predict that the differences in avoidance performance between strains are likely to be due to differences in the SDRs elicited by the experimental situation. Thus, one would surmise that the AHAs would display a preference for fleeing whereas the ALAs would be more likely to exhibit freezing.

To examine the above proposition, Experiments 2 and 3 looked at the performance of the AHAs and ALAs and the RCs on passive avoidance and one-way active avoidance. The shuttlebox employed in Experiment 1 was modified to enable these two tasks to be investigated in a situation similar to that of the shuttlebox. Essentially, the AHAs were expected to do well on the active avoidance task and the ALAs to do well on the passive avoidance task.

## EXPERIMENT 2

Experiment 2 examined one-way avoidance to determine whether there were differences between the strains in "fleeing" behavior.

### Method

**Subjects.** Thirty-two AHAs, 32 ALAs, 24 AHA/ALAs, and 24 ALA/AHAs were employed, half of each sex. Details of background and housing conditions were the same as those given for Experiment 1.

**Apparatus.** The shuttlebox and control equipment were as described in Experiment 1 except that the roof and the walls on one side of the shuttlebox were covered with black card and the other side was illuminated with a 10-W bulb situated 10 cm directly above its midpoint.

**Procedure.** Each rat was placed in the darkened half of the shuttlebox facing away from the guillotine door. After 30 sec, the door separating the two compartments was raised and, at the same time, the 2800-Hz tone commenced. If the rat had not moved to the lighted side of the shuttlebox within 5 sec of the onset of the tone, shock was delivered to the grid floor of the darkened compartment. The shock and tone remained on until the rat ran to the lighted side of the box, at which time the tone was terminated and the guillotine door separating the two compartments was lowered. The rat was placed in a holding cage on its own for a 60-sec intertrial interval and then was given another trial as described. Each rat received 10 trials in all.

### Results and Discussion

The mean number of avoidance responses in the 10 trials for each strain is illustrated in Figure 3. A 4 (strain)  $\times$  2 (sex) analysis with body weight as a co-

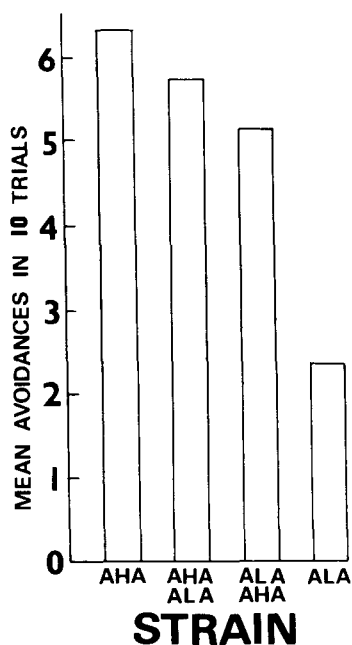


Figure 3. Mean anticipatory responses during the tone out of a total of 10 trials under the one-way avoidance procedure. Australian High Avoiders (AHA), Australian Low Avoiders (ALA), and reciprocal crosses (AHA/ALA and ALA/AHA).

variate yielded a significant effect of strain [ $F(3,47) = 19.1, p < .0001$ ]. Post hoc Bonferroni *t* tests indicated that the ALA strain made significantly fewer avoidance responses than the AHA strain and the two reciprocal crosses ( $t > 4.6$ , in all cases). No other differences were significant. The present results indicate that the ALA strain are deficient at performing an active avoidance response, even under conditions in which the difference between the "dangerous" side and the "safe" side is unequivocal. However, they do not allow us to determine whether the difference is due to the fact that the ALAs freeze when exposed to a stressful situation or whether they are simply deficient in learning to associate the CS with the impending shock. To decide between these two accounts, Experiment 3 examined the performance of the strains and the reciprocal crosses on a passive avoidance task. If the ALAs are more likely to freeze in a stressful situation, then they should be more proficient at this task.

### EXPERIMENT 3

In the third experiment, the strains and their reciprocal crosses were exposed to a passive avoidance task. Again, the same shuttlebox was employed, modified to allow for examination of this behavior.

#### Method

**Subjects.** Thirty-two AHA, 32 ALA, 24 AHA/ALA, and 24 ALA/AHA rats were employed, half of which were male. The husbandry and housing were as described in Experiment 1.

**Apparatus.** The shuttlebox and control equipment were as described in Experiment 1, modified as in Experiment 2.

**Procedure.** Half of the rats in each strain were placed one at a time in the lighted half of the shuttlebox facing away from the guillotine door, which was closed. Thirty seconds later, the door was raised. When the rat had moved to the darkened half of the box, a 1-mA shock was delivered to the grid and remained on until the rat had returned to the lighted compartment, at which time the guillotine door was lowered. The time it took the rat to enter the darkened compartment was noted. The rat was then returned to its home cage. On the following day, it was once again placed in the lighted half of the shuttlebox. The door was raised after 30 sec and interest focused upon how long it took the rat to enter the darkened compartment. A maximum of 300 sec was allowed, and no shock was delivered if or when the rat moved across (Jarvik & Kopp, 1967).

The other rats in each group were exposed to the same procedure except that when they moved to the darkened side on Trial 1, the guillotine door was lowered and they received no shock. Instead, they were immediately removed and returned to the lighted side for a brief period. They were then returned to their home cage. The procedure on Trial 2 was identical to that for the shock groups. These latter groups allowed an indication of the effects of the shock over and above any habituation that might have taken place.

### Results and Discussion

Time scores were not normally distributed, so they were converted to log 10, and a 4 (strain)  $\times$  2 (sex)  $\times$  2 (shock) analysis of covariance was performed on the transformed data. The covariates were the time to enter the darkened side on Trial 1 (an index of activity) and bodyweight. Of the covariates, only the latency to cross on the first trial was significant. It appeared that rats that took longer to cross on the first trial took longer to cross on the second. The analysis of the scores adjusted for the covariates revealed significant effects of shock [ $F(1,94) = 61.5, p < .0001$ ] and strain [ $F(3,94) = 4.3, p < .01$ ]. There was also a significant shock  $\times$  strain interaction [ $F(3,94) = 8.9, p < .0001$ ].

The mean transformed latencies are illustrated in Figure 4 for each group. The figure indicates that the significant interaction arises from the fact that the AHA animals that received shock following their entry into the darkened side on Trial 1 did not differ from their nonshocked controls in latency to cross on Trial 2. In contrast, the shocked animals in all the three other groups were much slower to cross over than were their nonshocked counterparts. The various nonshocked groups did not differ from one another.

It would appear from these results that the AHA strain are deficient in acquiring an avoidance response that requires them to withhold a response, in this case walking to the other side of the shuttlebox. All the other three groups acquired the response rapidly. Indeed, many animals within each of the other three groups did not cross over to the darkened compartment within the allotted time if they had been shocked there on Trial 1. Clearly, the selection that led to the development of the AHA and ALA strains was not for "avoidance" responding per se. If that

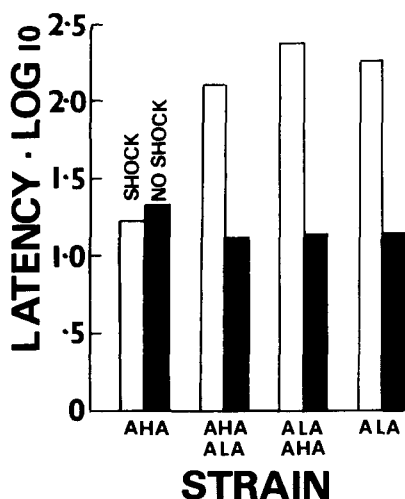


Figure 4. Mean transformed latencies (log 10) to cross from the lighted side to the darkened side on Trial 2 of the passive avoidance procedure. Animals receiving the shock on the training trial are indicated by the open bars, and those not receiving the shock are indicated by the closed bars. Key as in Figure 3.

had been the case, then one would have expected the AHAs to be superior to the ALAs. In fact, the opposite was the case.

## GENERAL DISCUSSION

The results of the three experiments reported here provide a clear indication of what has been selected for during the development of the AHA and ALA strains. Experiments 2 and 3 indicate that when the animals are provided with a simple avoidance task that requires them to run or "flee," then the AHA rats are clearly superior to the ALA rats (Experiment 2). In contrast, when the response required of the animals is that they stay on one side of a box or "freeze," then the ALA rats are superior (Experiment 3). These results suggest that, during the selection process, the "freezing" response has been partially bred out of the AHA rats and, to a certain extent, that the "fleeing" response has been bred out of the ALA rats. In this, they provide support for the view that the major defensive behaviors of the rat are under hereditary control (Bolles, 1970; Fuller & Thompson, 1978). This reversal of performance between strains when exposed to active and passive avoidance has been reported on a number of occasions for inbred lines of mice (cf. Wahlsten, 1978).

Further support for the above propositions can be gleaned from the behavior of the two reciprocal crosses. If the analysis is correct, it suggests that if we cross the two strains, then the crosses should have both "fleeing" and "freezing" in their repertoire. Such would appear to be the case. When the avoidance response required was an active one, the reciprocal

crosses were as efficient at acquiring it as the AHAs. Similarly, when the response required was a passive one, the reciprocal crosses were as efficient as the ALA rats. The present strains thus differ from such strains as the Roman strains, in which, Satinder (1977) has suggested, the differences in avoidance responding between the RLA, RHA, and RCA strains derive from differences in levels of arousal rather than differences in specific behaviors. This difference is reinforced when one considers that the present strains do not differ in their responses to the shock UCS (Experiment 1; Bammer, 1978), whereas the Roman strains do differ quite markedly, with the RLA animals often freezing in the presence of shock. This difference makes the ALA and AHA strains useful additions to extant selected rat strains.

Given the above analysis, how do we account for the ordering of the strains on the shuttlebox task under both the classical and avoidance contingencies? We must remember that there are two requirements in the shuttlebox task: the rat is expected, not only, because of imminent danger, to leave the side in which it is standing, but also to enter a compartment in which it has previously been shocked. These two factors probably elicit quite different responses in that the former will elicit flight and the latter will elicit freezing. Initially, these two factors will conflict with each other. As training proceeds, however, so the flight response becomes more likely, although why this is so is not immediately clear. Crawford and Masterson (1978) have suggested that movement and a change in the spatial location of the rat play a special role in avoidance learning, and it may be this factor that predisposes rats to run even where running has no effect on the occurrence of the UCS. If we now apply this analysis to the present case, we see that the AHA rats should learn the avoidance response quickly, because the probability of their freezing is low and the probability of their running is high. Similarly, the ALA rats will acquire the response slowly, since the probability of their freezing is high and the probability of their running is low. The AHA/ALA and ALA/AHA crosses will acquire the response at an intermediate rate because the probability of their both running and freezing is high. The inclusion of the reciprocal crosses is helpful in determining whether we need two behavioral categories. Clearly, we do in that the crosses are as adept at active avoidance as the AHAs and as adept at passive avoidance as the ALAs and yet fall in between the two parent strains in the shuttlebox task.

The bulk of the data reported here seem to indicate the profound influence played by the classical conditioning contingency in determining avoidance responding. In Experiment 1, the increase in responding following introduction of such a procedure was marked in comparison with the further increase seen when the avoidance contingency was introduced. This point is emphasized when one notes that a de-



crease in response latency was observed during the classical contingency as well as the avoidance contingency (cf. Bond, 1981b). In this respect, they agree with the findings of Katzev and Mills (1974), Schlosberg (1934, 1936), Turner and Solomon (1962), and Woodard and Bitterman (1973). It is true that a number of studies have found more efficient acquisition of responding under an avoidance contingency than under a classical contingency (Bolles et al., 1966; Kamin, 1956, 1957). However, such a result need not be embarrassing to a theory of avoidance based upon classical conditioning. Examination of these studies indicates that the classical procedures employed a lengthy UCS. It may be that under these conditions the CR elicited is freezing rather than running, which would of course be evidenced as poorer avoidance acquisition in a shuttlebox (cf. the ALA strain here). There is some evidence to support the suggestion that a longer shock is more likely to elicit freezing (Fanselow, 1980, 1981; Reiss & Farrar, 1972).

Mackintosh (1974) has suggested that the acquisition of free operant avoidance is a problem for a classically based theory of avoidance learning. However, such avoidance is rather poorly acquired in comparison with the responses reported here, and it is unlikely that any one theory will be able to cover what Seligman (1970) has referred to as "prepared" and "contraprepared" learning. Furthermore, such avoidance creates a problem for every other theory of avoidance, and these other theories have the added disadvantage of being unable to account for avoidance acquisition under classical procedures (see below).

The present data relating to the influence of the classical contingency provide difficulties for most extant theories of avoidance. They indicate that there is a profound influence of the association between the CS and the UCS in determining the occurrence of anticipatory responses and, in doing so, provide difficulties for expectancy theory as developed by Bolles (1978). Bolles has suggested that running is an invariant response that becomes more probable as the rat discriminates that the side it is on is "dangerous" and the other side is "safe." Under the classical procedure employed here, it is not apparent why the rat should make such a discrimination, given that the UCS occurs irrespective of what the rat does. Furthermore, in demonstrating that avoidance responding can occur at high levels where there is no effect of the response on the UCS, they provide difficulties for two-factor theories that rely on the reduction of fear or aversiveness as the basis for avoidance (Rescorla & Solomon, 1967; Schoenfeld, 1950). Note that one cannot argue that the noise itself was aversive and that its termination led to the acquisition of responding, since no such pattern was observed in the behavior of the pseudoconditioned animals.

In summary, the present data indicate that the AHA and ALA strains appear to have been selected for fleeing and freezing, respectively, and that crosses between the two strains have both responses in their repertoire, suggesting that these behaviors are under hereditary control. Furthermore, they are in accord with the data of Katzev and Mills (1974) in indicating a profound influence of the classical contingency in leading to anticipatory responding in a shuttlebox task. They go further in indicating that this influence is associative in nature and not due to pseudoconditioning, and in demonstrating that as the anticipatory response becomes more probable, it also occurs with a shorter latency. In conclusion, they add to our knowledge concerning the profound influence of the stimulus-reinforcer contingency in controlling behavior.

#### REFERENCES

- BAMMER, G. (1978). *Studies on two new strains of rats selectively bred for high or low conditioned avoidance responding*. Paper presented at the Annual Meeting of the Australian Society for the Study of Animal Behavior, Brisbane.
- BIGNAMI, G. (1965). Selection for high rates and low rates of avoidance conditioning in the rat. *Animal Behaviour*, *13*, 221-227.
- BOLLES, R. C. (1970). Species-specific defense reactions and avoidance learning. *Psychological Review*, *77*, 32-48.
- BOLLES, R. C. (1972). Reinforcement, expectancy, and learning. *Psychological Review*, *79*, 394-409.
- BOLLES, R. C. (1975). Learning, motivation and cognition. In W. K. Estes (Ed.), *Handbook of learning and cognitive processes* (Vol. 1). Hillsdale, NJ: Erlbaum.
- BOLLES, R. C. (1978). The role of stimulus learning in defensive behavior. In S. H. Hulse, H. Fowler, & W. K. Honig (Eds.), *Cognitive processes in animal behavior* (pp. 89-107). Hillsdale, NJ: Erlbaum.
- BOLLES, R. C., STOKES, L. W., & YOUNGER, M. S. (1966). Does CS termination reinforce avoidance behavior? *Journal of Comparative and Physiological Psychology*, *62*, 201-207.
- BOND, N. W. (1981a). Effects of prenatal alcohol exposure on avoidance conditioning in high- and low-avoider rat strains. *Psychopharmacology*, *74*, 177-181.
- BOND, N. W. (1981b). A re-examination of response latency in shuttlebox avoidance learning. *Australian Journal of Psychology*, *33*, 253-256.
- BRUSH, F. R. (1962). The effects of intertrial interval on avoidance learning in the rat. *Journal of Comparative and Physiological Psychology*, *55*, 888-892.
- BRUSH, F. R., FROELICH, J. C., & SAKELLARIS, P. C. (1979). Genetic selection for avoidance behavior in the rat. *Behavior Genetics*, *9*, 309-316.
- COLLINS, R. L. (1964). Inheritance of avoidance conditioning in mice: A diallel study. *Science*, *143*, 1188-1190.
- CRAWFORD, M., & MASTERTON, F. A. (1978). Components of the flight response can reinforce bar-press avoidance learning. *Journal of Experimental Psychology: Animal Behavior Processes*, *4*, 144-151.
- FANSELOW, M. S. (1980). Conditioned and unconditioned components of post-shock freezing in rats. *Pavlovian Journal of Biological Sciences*, *15*, 177-182.
- FANSELOW, M. S. (1981). Naloxone and Pavlovian fear conditioning. *Learning and Motivation*, *12*, 398-419.
- FULLER, J. L., & THOMPSON, W. R. (1978). *Foundations of behavior genetics*. St. Louis, MO: Mosby.



- HEWITT, J. K., FULKER, D. W., & BROADHURST, P. L. (1981). Genetics of escape-avoidance conditioning in laboratory and wild populations of rats: A biometrical approach. *Behavior Genetics*, *11*, 533-544.
- JARVIK, M. E., & KOPP, R. (1967). An improved one-trial passive avoidance learning situation. *Psychological Reports*, *23*, 221-224.
- KAMIN, L. J. (1956). The effects of termination of the CS and avoidance of the US on avoidance learning. *Journal of Comparative and Physiological Psychology*, *49*, 420-424.
- KAMIN, L. J. (1957). The effects of termination of the CS and avoidance of the US on avoidance learning: An extension. *Canadian Journal of Psychology*, *11*, 48-56.
- KATZEV, R. D., & MILLS, S. K. (1974). Strain differences in avoidance conditioning as a function of the classical CS-US contingency. *Journal of Comparative and Physiological Psychology*, *87*, 661-671.
- KIMBLE, G. A. (1967). *Foundations of conditioning and learning*. New York: Appleton-Century-Crofts.
- MACKINTOSH, N. (1974). *The psychology of animal learning*. New York: Academic Press.
- OLIVERIO, A., CASTELLANO, C., & MESSERI, P. (1972). A genetic analysis of avoidance, maze and wheel running behaviors in the mouse. *Journal of Comparative and Physiological Psychology*, *79*, 459-473.
- OLIVERIO, A., ELEFTHERIOU, B. E., & BAILEY, D. W. (1973). A gene influencing active avoidance performance in mice. *Physiology & Behavior*, *11*, 497-502.
- PINEL, J. P. J., & TREIT, D. (1978). Burying as a defensive response in rats. *Journal of Comparative and Physiological Psychology*, *92*, 708-712.
- REISS, D., & FARRAR, C. H. (1972). Shock intensity, shock duration, Sidman avoidance acquisition, and the "all or nothing" principle in rats. *Journal of Comparative and Physiological Psychology*, *81*, 347-355.
- RESCORLA, R. A., & SOLOMON, R. L. (1967). Two-process learning theory: Relationships between Pavlovian conditioning and instrumental learning. *Psychological Review*, *75*, 151-181.
- ROYCE, J. R., YEUDALL, L. T., & POLEY, W. (1973). Diallel analysis of avoidance conditioning in inbred strains of mice. *Journal of Comparative and Physiological Psychology*, *76*, 353-358.
- SATINDER, K. P. (1976). Sensory responsiveness and avoidance learning. *Journal of Comparative and Physiological Psychology*, *90*, 946-957.
- SATINDER, K. P. (1977). Arousal explains differences in avoidance learning of genetically selected rat strains. *Journal of Comparative and Physiological Psychology*, *91*, 1326-1336.
- SATINDER, K. P., & HILL, K. D. (1974). Effects of genotype and postnatal experience on activity, avoidance, shock threshold, and open-field behavior in rats. *Journal of Comparative and Physiological Psychology*, *86*, 363-374.
- SATINDER, K. P., & PETRYSHYN, W. R. (1974). Interaction among genotype, unconditioned stimulus, d-amphetamine, and one-way avoidance behavior of rats. *Journal of Comparative and Physiological Psychology*, *86*, 1059-1073.
- SCHLOSBERG, H. (1934). Conditioned responses in the white rat. *Journal of Genetic Psychology*, *45*, 303-305.
- SCHLOSBERG, H. (1936). Conditioned responses in the white rat: II. Conditioned responses based upon shock to the foreleg. *Journal of Genetic Psychology*, *49*, 107-138.
- SCHOENFELD, W. N. (1950). An experimental approach to anxiety, escape and avoidance behavior. In P. H. Hoch & J. Zubin (Eds.), *Anxiety* (pp. 70-99). New York: Grune and Stratton.
- SELIGMAN, M. E. P. (1970). On the generality of the laws of learning. *Psychological Review*, *77*, 406-418.
- TURNER, L. H., & SOLOMON, R. L. (1962). Human traumatic avoidance learning: Theory and experiments on the operant-responder distinction and failure to learn. *Psychological Monographs*, *76*(40, Whole No. 559.)
- WAHLSTEN, D. (1978). Behavioral genetics and animal learning. In H. Anisman & G. Bignami (Eds.), *Psychopharmacology of aversively motivated behavior* (pp. 63-118). New York: Plenum Press.
- WILCOCK, J., & FULKER, D. W. (1973). Avoidance learning in rats: Genetic evidence for two distinct behavioral processes in the shuttle box. *Journal of Comparative and Physiological Psychology*, *82*, 247-253.
- WOODARD, W. T., & BITTERMAN, M. E. (1973). Pavlovian analysis of avoidance conditioning in the goldfish. (*Carassius auratus*). *Journal of Comparative and Physiological Psychology*, *82*, 123-129.

(Manuscript received November 9, 1983;  
revision accepted for publication April 22, 1984.)