RESPONSE INITIATION AND DIRECTIONALITY AS FACTORS INFLUENCING AVOIDANCE PERFORMANCE

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Anisman, H., and Wahlsten, D. Response initiation and directionality as factors influencing avoidance performance. Journal of Comparative and Physiological Psychology, 1974, 87, 1119-1128.

Abstract:
In 3 experiments it was found that permitting rats to run in either of 2 directions to avoid shock (any-way training) resulted in performance superior to that of 1-way or 2-way avoidance. Moreover, in the any-way condition subjects often selected a bidirectional mode of responding. Exposure to signaled inescapable shock enhanced avoidance in all avoidance modes. Finally, any-way training enhanced subsequent 2-way avoidance to a greater extent than did 1-way training. Results were interpreted in terms of the need to learn directional responses in avoidance training, role of response initiation in modifying avoidance behavior, and the effectiveness of running responses in determining avoidance performance.

Article:
It has become increasingly apparent that the traditional views of avoidance performance are too encumbering and not sufficiently broad in an ethological sense to account adequately for the various avoidance phenomena. While 2-process models of avoidance performance have been useful in elabborating upon possible factors which influence avoidance behavior, few theorists would maintain that such models in themselves are sufficient to accommodate the behavior of animals in the wild or that of their domesticated counterparts tested in the laboratory. Although the establishment of drive states, defined in terms of motives engendered through Pavlovian processes (Rescorla & Solomon, 1967) or expectancy of shock (cf. Bolles, 1971), and the acquisition of instrumental responses cannot be dismissed, other factors such as preparedness (Seligman, 1970), species-specific defense reactions (Bolles, 1971), establishment of antidrives (Konorski, 1967), feedback stimuli (Bolles, 1970), and the associative and nonassociative effects of shock (Anisman & Waller, 1973; Wahlsten & Sharp, 1969) must be dealt with if a unified explanation of avoidance behavior is to be established. The present study was conducted to elaborate further upon some of the factors that are subsumed in the avoidance process.

EXPERIMENT 1
One of the most replicable phenomena in avoidance research is the fact that 1-way avoidance performance progresses more rapidly than does 2-way avoidance performance (Anisman & Waller, 1972, 1973; Theios, Lynch, & Lowe, 1966; Wahlsten & Sharp, 1969). Presumably, this is a result of the nonassociative freezing responses elicited by shock being readily suppressed in the 1-way task, thus permitting rapid establishment of an effective running response. In the 2-way task, although the response requisite is also one of running, the effectiveness of this response is compromised because the organism must return to a place previously associated with danger. Consequently, the freezing response cannot be suppressed quickly, and avoidance perform - ance progresses relatively slowly (Anisman, 1973; Wahlsten & Sharp, 1969). Just as replicable as the difference between 1-way and 2-way avoidance is the finding that avoidance learning is beset by excessive variability. For example, although some animals perform well on a given task, other animals receiving identical treatment perform quite poorly. This has been found to occur even in the relatively simple 1-way avoidance task, and it is magnified when the avoidance procedure does not involve handling the animal (Anisman, 1973; Anisman & Waller, 1972). Unless a cognitive explanation is invoked, it must be assumed that such differences in avoidance performance result from the preparedness of the organism to adapt to the avoidance requirements. The question,

then, becomes one of determining what specifically leads to these marked differences in avoidance behavior under a single treatment.

Although running in the 1-way task appears to be a species-specific defense behavior, place learning is not (Anisman & Waller, 1972), In an automated avoidance situation it is often noted that animals initiate a running response upon onset of the conditioned stimulus (CS) ; however, the response is directed not toward the hurdle, but to the far end of the compartment. This observation, incidentally, is not so reliable in a nonautomated 1-way avoidance task, possibly because of the intervening handling procedure (H. Anisman, unpublished observations, 1971). It seems then that some animals are more adept at or prepared for running in one direction than in the other, or that animals initially select the direction of the response in a random fashion when specific cues signaling safety are not available. It follows that if animals did not have to learn a specific directional response, but rather were permitted to run in either of 2 possible directions to avoid shock (any-way training), avoidance learning would progress quickly, and variability would be reduced. The first purpose of Experiment 1, then, was to determine to what extent an any-way avoidance procedure would enhance performance relative to 1-way or 2-way avoidance performance. It is noteworthy that in all 3 tasks the response requisites are comparable, in that the subjects must initiate a running response and propel themselves over a hurdle within a set period of time. The tasks differ insofar as successful avoidance in the 1-way situation involves a unidirectional response; the 2-way task involves an ambiguous unidirectional response since the direction requirement changes on successive trials; and the any-way task involves running in either of 2 directions. In effect, the any-way task is not confounded by place learning as are the 1-way and 2-way tasks, and consequently it may be more appropriate in examining response learning. The second purpose of Experiment 1 was to determine the mode of responding that rats would select in the any-way training procedures. Since running toward those cues associated with danger is a maladaptive form of behavior and normally disrupts avoidance behavior (see Anisman, 1973; de Toledo & Black, 1967), rats given a choice should consistently run away from those cues previously associated with danger. Finally, 2 additional purposes of Experiment 1 were to determine, first, whether the locality within the compartment the animal is in will affect avoidance performance. More explicitly, will subjects that sit near the gate be more likely to make an avoidance than either animals that wander about the compartment or animals that rest away from the gate? Second, given that one of the difficulties in learning an avoidance response is the acquisition of the directional component, what is the probability of a response being initiated, but directed in an inappropriate direction, and subsequently resulting in the animal being shocked?

Method

Subjects. Sixty-four experimentally naive male Holtzman rats, approximately 90 days of age, were procured from the Holtzman Co., Madison, Wisconsin. Rats were communally housed, 7 or 8 per colony cage, and were permitted ad-lib fond and water throughout the experiment. Four subjects were dropped from the experiment because of apparatus failure or experimenter error.

Apparatus. The apparatus was the same as that described by Anisman and Waller (1972). It essentially consisted of a circular Plexiglas runway 12.0 cm. wide and 20.5 cm. high, with an outside circumference of 204.1 cm. Slots in the exterior walls of the runway permitted the insertion of sheets of black bristol board. The alley, which was divided equally into 4 compartments by stainless steel gates resting 1.27 cm. above a 5.0-cm. hurdle, had a grid floor made of .25-cm. stainless steel rods spaced 1.75 cm. apart (center to center) at the exterior wall. Each compartment contained 2 6-w. lamps situated 2.5 cm. beneath the Plexiglass roof and 1.0 cm. from each gate.

Five modes of operation were available: (*a*) The illumination of the lamps (CS), introduction of shock, and raising of the gates through a 90° are stepped from one compartment to the next in a counterclockwise manner produced 1-way avoidance without handling. (*b*) Only a single gate was raised, and the CS and unconditioned stimulus (US) switched alternately between 2 adjacent compartments resulting in a 2-way avoidance procedure. (*c*) Gates at either end of the compartment could be raised simultaneously with CS onset; however, responses were permitted only in a 2-way mode by blocking one exit via the insertion of stainless steel walls behind the gates (2-way with gates). (*d*) Gates at either end of the compartment could be raised simultaneously with CS onset, allowing animals to run in either of 2 directions. On the subsequent trial both gates were raised in the compartment the subject occupied, thus permitting the response of returning to the compartment occupied on the previous trial, or running away from that particular compartment. (*e*) The CS and US were presented for preset durations in only a single compartment, and guillotine gates were not activated, producing signaled inescapable-unavoidable shock.

Procedure. Rats were randomly assigned to 4 independent groups (n = 15). Rats in the 1-way group were run from one compartment to the next in a counterclockwise direction; subjects in the 2-way group were run alternately between 2 compartments; the any-way group was permitted to run in either direction, i.e., the gates at both ends of the compartment were raised simultaneously, thus allowing the rat to run back into or away from the compartment it had been in during the preceding trial; and finally, a fourth group (2-way with gates) received standard 2-way training, except that, while both gates in the compartment were raised, the placement of stainless steel barriers immediately behind them at the end of each compartment prevented subjects from adopting a response other then that of shuttling. This group was included to determine what effect raising 2 gates would have on avoidance behavior.

The avoidance training procedure was otherwise the same for each group. Thirty seconds after placement in the avoidance apparatus, the gate(s) was raised, and the CS was presented. If the rat crossed into the adjacent compartment within 7 sec., the gate was lowered and the CS was terminated. If an avoidance response was not made within 7 sec., a 1-ma. shock (constant current, 60-cycle ac) was presented until an escape response was made, after which the CS and US were terminated and the gate(s) was lowered. Each subject received 50 such trials at 30-see. intervals. The dependent measures recorded in addition to the latency of responding were the position subjects maintained in each compartment at CS onset and the occurrence and direction of all running responses initiated during the CS-US interval. In the any-way condition the compartment entered on each trial was also noted.

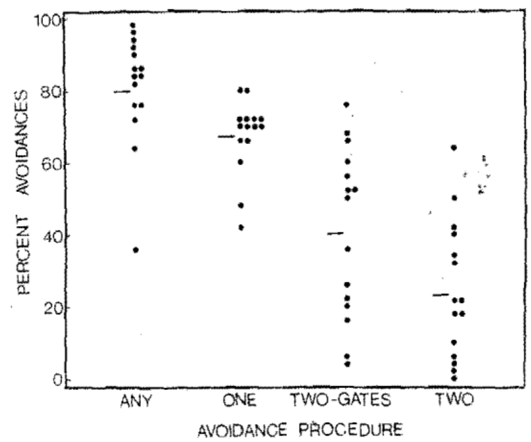

FIGURE 1. Percentage avoidance responses for each animal as a function of the avoidance training procedure. (Arrows indicate group mean scores.)

Results and Discussion

The number of avoidance responses in 50 trials for each subject as a function of the avoidance training procedure is shown in Figure 1. Analysis of variance yielded a significant Training Procedure × Blocks of Trials interaction (F = 3.68, df = 18/336, p < .01). Subsequent multiple comparisons revealed that the groups all differed from each other, with the rank order being anyway, 1-way, 2-way, with gates, and 2-way (see Figure 1). Over blocks of trials the differences between the any-way and 1-way groups decreased, whereas the differences between the 2-way and 2-way with gates groups increased in magnitude.

It is apparent that permitting animals the option of where to go precludes the necessity of animals learning a directional response, and consequently the effectiveness of running as a species-specific defense reaction is magnified. In agreement with such a notion, it was frequently noted that early in training animals in the 1-way group initiated a running response; however, this response was directed toward the far wall rather than toward the hurdle. Indeed, the experimenter's observations of response initiations (see Table 1) revealed that 1- way animals initiated almost as many responses as did any-way animals, but 16.8% of these responses were not appropriately directed and consequently led to the animal's being shocked. Of those responses which were appropriately directed, only .9% resulted in the animal's being shocked. In contrast, among any-way animals only 9.1% of initiated responses subsequently resulted in shock. Apparently, a running response can readily be established, but rats must also learn where to run in a 1-way task. This finding is consistent with the postulation that running per se, rather than running from a dangerous to a safe place, is an innate response. If running to a specific place were an innate response (cf. Seligman, Maier, & Solomon, 1971), then no difference in avoidance performance should have existed between the 1-way and any-way groups.

TABLE 1

MEAN NUMBER OF RUNNING RESPONSES INITIATED DURING CS–US INTERVAL IN 50 TRIALS AS A FUNCTION OF DIRECTION (CORRECT OR INCORRECT) AND SUCCESS (AVOID OR ESCAPE) OF RESPONSE

Training	Correct direction		Incorrect direction		Total initiations	% successful initiations
	Avoid	Escape	Avoid	Escape		
Any-way	—[a]	—[a]	—[a]	—[a]	43.9	90.9
1-way	30.4	.4	2.8	6.8	40.4	82.3
2-way with gates	19.4	6.3	.6	2.6	28.9	68.1
2-way	11.0	4.6	.7	3.1	19.4	50.2

Note. Abbreviations: CS = conditioned stimulus; US = unconditioned stimulus.

[a] All initiated responses can be considered as being in the correct direction.

It is interesting that the performance of the 2-way with gates group was superior to that of the standard 2-way group. It seems that the activation of the gate created a sufficiently large startle response to initiate the running behavior (Fantino, Sharp, & Cole, 1966). One might speculate that the superior avoidance performance of the anyway group relative to that of the 1-way animals might similarly be due to the activation of 2 as opposed to 1 gate. This, however, is an unlikely possibility on 2 counts. First, previous findings employing the same apparatus and strain of rats indicated that factors which aid response initiation have negligible effects on the 1-way procedure where freezing is suppressed quickly (Anisman, 1973; Anisman & Waller, 1972). Second, if the additional gate produced a startle reaction thus initiating the running response, then the avoidance and escape latencies of the any-way group would have been faster than those of the 1-way group. This was not the case, in that the latency of avoiding for the 1-way group was not significantly different from that of the any-way group (mean latencies = 2.65 and 2.70 sec., respectively). In contrast, however, the avoidance latencies displayed by the 2-way with gates group were somewhat faster than those of the 2-way group (mean latencies = 2.70 and 3.34 sec., respectively; $F = 4.16$, $df = 1/28$, $p < .06$). It seems that in the ambiguous 2-way task a startle response may enhance avoidance almost in the same way as a pseudoconditioning response does (Morgan, 1968). This is not the case, however, in the 1-way task where a running response can effectively be established.

Turning to the directional behavior of animals in the any-way group, it was found that on 39.9% of the trials animals ran in a 2-way mode (i.e., returned to the compartment they had occupied on the previous trial). Although a greater number of 1-way responses were made ($\chi^2 = 4.08$, $df = 1$ $p < .05$), it is surprising that so great a proportion of the responses were of the shuttle type. Indeed, over blocks of trials the frequency of 2-way responses increased, such that on the last block of trials 51.1% of the responses were of the shuttle mode with fully one-half of the animals favoring this mode of responding. This finding is even more startling when it is realized that the frequency of correct shuttle responses in the any-way condition was 72.7% compared with 80.1% for correct 1-way responses. Such a finding is seemingly inconsistent with all of the current notions that have attempted to account for the inferior performance exhibited by rats in a 2-way compared with a 1-way avoidance task (cf. Anisman & Waller, 1972; McAllister, McAllister, & Douglas, 1971; Theios et al., 1966;

Wahlsten & Sharp, 1969). Each of these hypotheses has been based on the supposition that animals are either not inclined to return to a compartment just previously associated with shock or are reluctant to make a directional response incompatible with one that previously proved successful. Thus, it follows that, given the opportunity to select the direction of responding, rats would consistently choose a 1-way mode of responding. One possibility for explaining the finding that animals often demonstrate 2-way performance and that such responses are often in the form of avoidances can be expressed in terms of the effectiveness of running responses and the subsequent modification of the animal's defensive behavior. Specifically, in the any-way condition prepotence of the running response in the animal's response repertoire is rapidly established. Accordingly, animals frequently avoid even when a 2-way response is made, and consequently subjects are not so prone to avoid the compartment hey had previously entered. Essentially, then, hypotheses based on response repertoire (cf. Anisman & Waller, 1973) can more readily account for the results of the present experiment than hypotheses based solely on situational cues (cf. Theios et al., 1966) or those based on the relative aversiveness of apparatus cues and of the CS (McAllister et al., 1971) .

Finally, with respect to the position subjects occupied in the compartments prior to escape or avoidance responding, it was found that, in the 1-way condition animals usually (89% of the trials) maintained a position nearest the gate to be opened. In contrast, in the 2-way avoidance tasks subjects tended to position themselves furthest away from the gate to be raised (87% of the trials). This was true in both cases regardless of whether the response on any particular trial or on the previous trial was an avoidance or an escape. Apparently, upon crossing the hurdle subjects tend to run until reaching the farthest wall. One might speculate that this factor may account for the difference in performances in the 1-way and shuttle tasks (i.e., the subject being near the gate in one task, but further from the gate in the other). This supposition, however, is not supported in that the position in the compartment in either task was not found to affect avoidance behavior, Specifically, analyses of the animal's position in the compartment and the probability of an avoidance response occurring revealed that position did not alter the frequency of avoidance responding. Finally, in the anyway condition subjects were found to situate themselves closer to the gate that they subsequently crossed on 64% of the trials. This figure corresponds roughly to the number of 1-way responses made. In any event, position was again not found to be predictive of avoidance responding.

Taken together, the results of Experiment 1 suggest that running can effectively be established in very few trials given the optimum conditions. However, the rate-limiting step in other avoidance procedures might also be the necessity of learning a directional response. When the situation is an unambiguous one (e.g., 1-way avoidance), the rate at which the directional response is acquired progresses quickly, whereas when the situation is an ambiguous one (e.g., 2-way avoidance), the acquisition of the directional response progresses slowly. Indeed, under these conditions, a running response cannot effectively be established, and freezing behavior remains the dominant response in the subject's response repertoire (cf. Anisman, 1973).

EXPERIMENT 2

It is evident that the rate at which an avoidance response is established is modulated, at least in part, by the effectiveness of the running response and whether this response is appropriately directed. Another limiting factor in avoidance situations undoubtedly is the motive for avoidance. It is intuitively obvious that before successful avoidance will progress, a drive state or expectancy of shock must be established, and this, quite independently of the effectiveness, of the running response, also serves to modulate avoidance behavior. Previously, it has been demonstrated that exposure to signaled inescapable-unavoidable shock may, given the appropriate conditions, facilitate avoidance behavior (Anisman & Waller, 1972, 1973). It should similarly follow that if learning a directional response and the expectancy of shock are 2 pertinent but independent factors, then prior exposure to signaled inescapable shock should influence any-way avoidance in the same way as 1-way avoidance: Experiment 2, then, was designed to test just such a prediction. Further purposes of Experiment 2 were to replicate the findings of Experiment 1 and to determine whether position habits and response mode selected by the animals receiving any-way training would be affected by the preshock treatment.

Method

Subjects and apparatus. Eighty experimentally naive male Holtzman rate approximately 90 days of age served as subjects. Rats were communally housed, 7 or 8 per colony cage, and permitted ad-lib access to food and water. The training apparatus was the same as that described in Experiment 1.

Procedure. During pretraining rats were individually placed in one compartment of the avoidance apparatus, 30 sec. after which one-half of the rats received 10 inescapable-unavoidable CS—US presentations. A delay conditioning paradigm was used; the CS was presented for 7 sec., after which the US was presented for 2 sec. Both the CS and US terminated simultaneously. The interval between CS offset and subsequent CS onset was 30 sec. The remaining rats were placed in the apparatus for a period equivalent to that of the preshock group, but neither the CS nor US was presented. Following the pretraining procedure rats were returned to their home cages.

Twenty-four hours after pretraining rats received 50 avoidance training trials. Rats in each of the 2 pretraining groups were subdivided into 4 independent groups which received 1-way, 2-way, any-way, or 2-way with gates training. The procedure was the same as that described in Experiment 1.

Results and Discussion

The number of avoidance responses for each animal as a function of pretraining procedure and avoidance task is shown Figure 2. Analysis of variance of the avoidance scores revealed a significant Pretraining × Task × Blocks interaction ($F = 2.08$, df = 18/432, $p < .05$). Consistent with Experiment 1, the 4 nonpreshocked groups all differed from each other, with the rank order being any-way, 1-way, 2-way with gates, and 2-way avoidance. Moreover, as predicted, the preshock procedure enhanced avoidance performance under each of the training procedures. Over blocks of trials it was found that the differences between the any-way and 1-way groups both with and without preshock were significant only early in training, whereas the converse was true-among the 2-way and 2-way with gates groups. In any event, these findings clearly suggest that the effectiveness of the running response in removing the rat from the aversive situation, the directionality of the running response, and the establishment of a motive for performance are all important factors involved in avoidance behavior, any one of which can serve as a rate-limiting step for successful or efficient learning, depending upon the particular details of the training procedure.

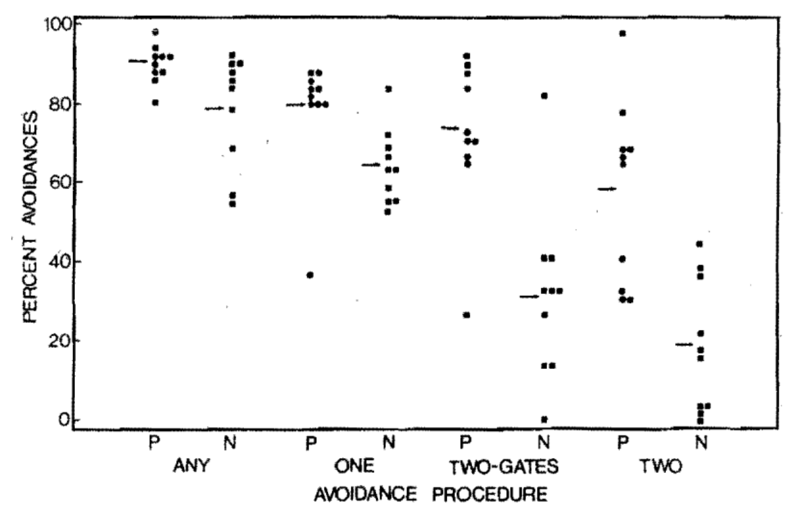

FIGURE 2. Percentage avoidance responses for each animal as a function of preshock treatment and avoidance training procedure. (Dots represent preshocked animals; squares represent nonpreshocked animals. P denotes preshocked groups, N denotes nonpreshocked groups. Arrows indicate group mean scores.)

As in Experiment 1, subjects in the any-way groups showed considerable shuttle responding. In fact, the proportions of such responses were extremely high: 51.8% among nonpreshocked animals and 42.9% among preshocked rats. Moreover, the frequency of correct responses did not differ for shuttle and 1-way responses under any-way training (71.8% and 76.5%, respectively, for nonpreshocked groups; 84.9% and 87.4%, respectively, for preshocked groups). Again, these data might suggest that, given the existence of an effective running response, returning to a compartment subjects occupied on the previous trial does not have the same aversive properties and consequently leads to more efficient learning compared with situations in which a running response is not effectively established early in training.

Finally, it was noted again that in the 1-way and 2-way groups subjects would cross the hurdle and position themselves at the far end of the compartment. The position subjects maintained, however, was not predictive of success in avoiding on the subsequent trial.

EXPERIMENT 3

Experiments 1 and 2 clearly suggest that permitting rats to run in either of 2 directions increases the functional effectiveness of the running response and consequently leads to more efficient avoidance behavior, even if animals select a 2-way mode of responding. It follows, then, that if animals first received any-way training, subsequent 2-way avoidance would progress more rapidly than if prior training consisted of 1-way avoidance training. Similarly, initial 1-way training should lead to 2-way avoidance performance superior to that of animals which initially received 2-way training, even though the directional response is altered somewhat in the group transferred from 1-way to 2-way avoidance. Accordingly, in Experiment 3 rats initially received either 1-way, any-way, or 2-way avoidance training and were subsequently tested on 1 of these 3 tasks. Using this design it could also be determined whether the initial response habits, i.e., training a unidirectional or bidirectional response, would alter the mode of responding exhibited in the anyway situation.

Method

Subjects and apparatus. Ninety experimentally naive male Holtzman rats approximately 90 days of age served as subjects. The apparatus was the same as that of Experiment 1.

Procedure. Subjects initially received 20 avoidance training trials in either the any-way, 1-way,. or 2-way training mode, using the identical procedure described in Experiment 1. Following the twentieth trial subjects in each group were subdivided and tested for 30 trials in 1 of the 3 tasks, Accordingly, the design was a 3 × 3 factorial involving each of the avoidance paradigms. The intertrial interval and the interval during the transition from one mode to another were 30 sec. in duration. Subjects were not handled during the transition phase but rather remained in the avoidance apparatus, No overt cues denoted the transition from one training procedure to another.

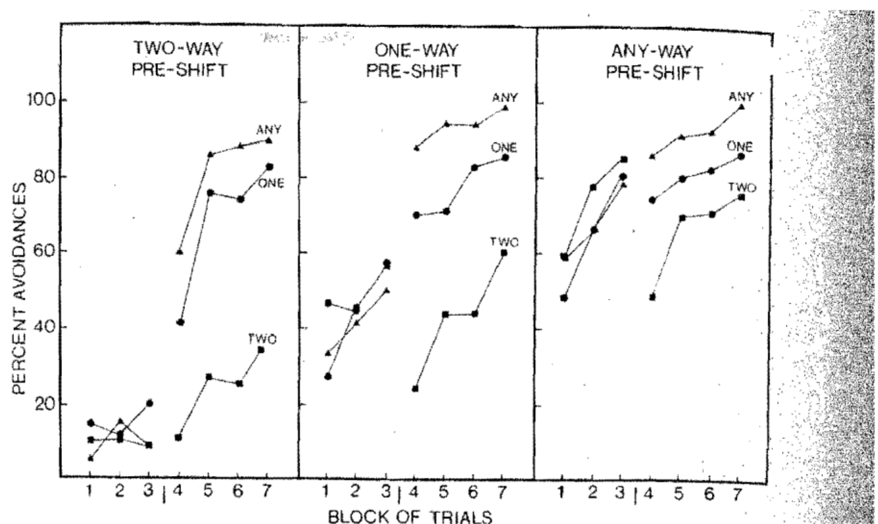

FIGURE 3. Mean percentage avoidance responses over blocks of trials as a function of avoidar training (preshift) and avoidance test (postshift) procedure. (The preshift blocks, 1–3, represent trials each, while postshift blocks, 4–7, represent 7 trials each. The arrow between Blocks 3 and 4 indi-cates the time of shift in the training procedure.)

Results and Discussion

The mean percentages of avoidance responses over blocks of trials during each phase of training are shown in Figure 3. Comparisons between the groups revealed that animals tested in the 2-way task consistently performed more poorly than either the 1-way or any-way groups. However, 2- way avoidance was also found to vary as a function of the initial training procedure (*F* = 2.62, *df* = 4/81, *p* < .05). Specifically,, animals that initially received any-way training were superior to animals that initially received 1-way training, which in turn demonstrated performance superior to that of animals that were originally trained in the 2-way task. When tested in the 1-way task, however, avoidance performance was not differentially affected by animals receiving 1-way or any-way training, although animals initially trained in the 2-way mode performed more poorly than either of the other 2 groups. In contrast, when animals were transferred to the any-way task, the original mode of training did not affect avoidance performance. It appears that the more effective is the running response established during pretraining, then the greater is the transfer to a subsequent training procedure. If the avoidance task in which animals are subsequently tested is one in which an effective running response, can established, then the effects of the initial training procedure are limited. More explicitly, transfer from any-way or 1-way training to a similar avoidance task produces minimal differences in behavior; however, when transfer is made to a task where an effective running response is not readily established (e.g., 2- way avoidance), the effectiveness of the running response established during initial training differentially affects avoidance behavior.

Finally, turning to the mode of responding in the any-way condition, it was found that all 3 groups demonstrated approximately equal levels of shuttle responding ($\bar{X}$ shuttle responses = 53.9, 53.6, and 60.7 for the groups transferred from the anyway, 1-way, and 2-way groups, respectively). It is interesting that initial 1-way training did not decrease the frequency of shuttle responses in the any-way test condition. Again it appears that once an effective running response has been established animals do not differentiate between response modes. When transfer was made from the 2- way task, shuttle responses were not found to be substantially higher than those observed after transfer from 1-way or anyway training. However, the probability of a successful shuttle response occurring in the any-way mode was lower among animals transferred from 2-way training than when the transfer was made from either the any-way or 1-way conditions (percentages of correct shuttle responses were 71.9, 82.3, and 91.5, respectively). When the response mode selected was that of 1-way responding, the initial training procedure did not differentially affect performance (percentages of correct 1-way responses were 90.4, 91.8, and 95.4 for the 2-way, any-way, and 1-way groups, respectively). These data further substantiate the contention that once an effective running response has been established, avoidance performance is enhanced, even when the response mode selected is one that involves conflicting directional components.

In addition to evidence provided by the analysis of total avoidances and rate of learning, detailed examination of behavior exhibited early in training directly confirmed the importance of response directionality. Since considerable variability in performance on the first few trials was apparent, the data of subjects with comparable training in Experiments 1, 2, and 3 were pooled and scrutinized, yielding 35 subjects in each condition. The mean trial of the first successful avoidance occurred earlier under any-way training (3.14 trials) than under 1-way training (4.91 trials; p < .005), which shows that the rats were sensitive to the particular paradigm at a very early phase of training. Unlike the total avoidance score, the trial of first avoidance was significantly less variable under any-way than under 1-way training (*F* = 3.80, *df* = 34/34, *p* < .0001). The reason for this was clear when early anticipatory responses were examined. As mentioned above, the experimenter noted whenever a rat initiated a running response that was not successful. Interestingly enough, the mean trial of the first, running response initiation did not differ for any-way (2.60 trials) and 1-way training (2.89 trials; *F* < 1,0) ; variabilities of this score did not differ significantly either. However, of the first initiations by the 35 rats in any-way training, 26 were successful avoidances, compared to 16 of 35 for 1-way and 8 of 35 for 2-way training. On subsequent trials many subjects under 1-way and 2-way training ran in the wrong direction or darted rapidly back and forth, as though confused about *where* to go (see Table 1). Furthermore, when a subject did poorly under any-way training, response initiation but not directionality appeared to be the problem; the rat that made only 17 avoidances in Experiment 1 (Figure 1) generally did not run at all during the CS—US interval on error trials.

An important aspect of the data discussed above is that anticipatory responses occur very early in the avoidance acquisition process. Only with any-way training are these early responses consistently followed by omission of shock, while they are frequently punished in 1-way and 2-way training; hence any-way training leads to the most rapid acquisition. In the 1-way situation the consistent direction of running is learned relatively quickly. In 2-way training the alternating pattern of direction is especially difficult, running responses are frequently punished, and immobility or freezing frequently becomes the predominant element of the set of species-specific defense reactions (Wahlsten & Sharp, 1969). Two-way acquisition generally does not end at this point, however, because the freezing response itself is consistently punished by shock, and the running response reemerges from time to time and may even be performed consistently by some rats. When these detailed observations on animals in the avoidance situation are included, it is clear than certain of the properties of early avoidance learning may be explained by the combined principles of contiguity (e.g., Sheffield, 1948) and the species-specific defense reaction (Bolles, 1970).

GENERAL DISCUSSION

Following the establishment of a drive state or expectancy of shock, subjects need to learn a locomotor response in order to avoid shock actively. The rate at which this locomotor response is acquired had previously been found to be inversely related to the strength of freezing behavior produced by shock and directly related to the rate at which freezing could be suppressed (Anisman & Waller, 1972, 1973; Blanchard & Blanchard, 1969a, 1969b). The story, quite clearly, does not end here. The functional effectiveness of the running response comes to act as a further limitation on avoidance behavior. In situations where an appropriate running response is established, such as in a 1-way task, avoidance learning progresses relatively quickly ; whereas when the effectiveness of the running response is compromised by the nature of the task, such as in 2-way avoidance, adequate performance progresses slowly. In addition to the occurrences of compromised responses, the effectiveness of the running response may be further limited by directional factors. That is, although running presumably emerges through the suppression or elimination of inappropriate species-specific defense reactions (cf. Anisman & Waller, 1973; Bolles, 1970, 1971), the locale toward which the running response must be directed needs to be learned. This, then, may limit avoidance performance. When a directional response is not a requisite for successful avoidance, the rate at which avoidance responding progresses is greatly enhanced. Moreover, once an effective running response has been established as in the any-way condition, promulgation of running behavior may be transferred to some extent to situations in which running behavior is compromised (i.e., 2-way avoidance), thereby increasing the avoidance response rate.

It is therefore apparent that the acquisition of an avoidance response cannot be considered simply in terms of a 2-process model. Factors such as elimination of inappropriate defense behaviors, establishment of an effective running response, and directionality of these responses all determine avoidance learning rate. Each of these factors taken alone may act as a limitation for avoidance behavior, and the import of each is most noticeable at different phases of the avoidance acquisition process. Once expectancy of shock has been established, animals must be able to initiate an appropriate species-specific defense reaction and be able to direct this response in an appropriate manner. No doubt feedback stimuli, as discussed by Bolles (1970, 1971), serve in the establishment and strengthening of the motoric responses. Moreover, the value of feedback stimuli is also intricately involved with the ambiguity of the avoidance situation. In the any-way situation, extrinsic feedback is less important than it is in the 1-way task, which requires feedback as to directionality. Similarly, the 1-way task requires less feedback than the 2-way task, since in the former case the directional response, once established, results in intrinsic feedback being sufficient for continued success. In the 2-way task, on the other hand, the ambiguous situation may necessitate extrinsic feedback throughout avoidance training.

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