Shock-elicited defensive behavior and passive avoidance performance

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In laboratory rats, low levels of shock elicit freezing, while high levels of shock elicit flight. Both behaviors have been termed species-specific defense reactions (SSDRs). If the punished response is relatively weak to begin with, low to medium levels of shock will be effective in suppressing this response via the SSDR of freezing. Changes in the strength of SSDRs will be reflected by changes in passive avoidance performance.

The postshock effects of a single footshock have been studied by a number of investigators (Adams & Calhoun, 1970; Barcik & Ellis, 1971). Specific responses developed in situations where footshock is presented include escape or activity, on the one hand, and immobility or freezing, on the other (Blanchard & Blanchard, 1968a, b). In general, as the severity of footshock is increased, active behaviors decline, while passive behaviors increase in strength (Atrons, 1967). Inactivity has been shown to augment passive avoidance acquisition (Adams & Calhoun, 1970), and where footshock is repeatedly administered, inactivity retards shuttle avoidance acquisition (Moyer & Korn, 1964).

Bolles (1970) has suggested that avoidance behavior that is acquired rapidly is the result of the interaction of various species-specific defense reactions (SSDRs), which include freezing, fleeing, and fighting with the appropriate avoidance response. Indeed, Adams & Calhoun (1970) have reported an inverse relationship between activity and passive avoidance performance. However, Barcik & Collins (1971) and Barcik & Ellis (1971) have found that, as severity of footshock is increased beyond that reported earlier, passive avoidance performance declines and activity increases. Also, Ulm & Cicala (1971) have reported greater postshock activity for a 3-sec vs a .5-sec footshock. Thus, which SSDR develops depends upon how intense footshock is and for how long it is presented. At higher levels of footshock, flight responses gain in strength, with the result that passive avoidance performance is lowered. The responses of freezing and fleeing may be responsible for the increase and decrease in passive avoidance, respectively, by effecting decreases or increases in postshock activity. In order to clarify further the relationship between activity and intensity of footshock, as well as the relationship between activity and passive avoidance, postshock activity

was measured in Experiment 1, where footshock was not contingent upon a response, and in Experiment 2, where activity was measured during passive avoidance.

EXPERIMENT 1

Subjects

A total of 40 Charles River CD rats, 150-180 days old at the start of the experiment, were used as Ss. All Ss were allowed ad lib access to food and water.

Apparatus

The apparatus consisted of a wood compartment, 42.6 cm square, with walls 35 cm high and a grid floor composed of brass rods, 3 mm in diam, placed 1 cm apart. The floor was mounted on springs placed at each corner, and microswitches were mounted under each of the four sides such that, when S moved, the floor would tilt slightly and a given microswitch would close. The weight of a 150-g animal was sufficient to activate the microswitches. A relay controlled the counting circuit such that during the 3-sec footshock, one counter circuit was operative, whereas a separate counter circuit was operative during postshock activity measurement. Footshock was delivered and timed by a Grason-Stadler E1064GS shock generator and scrambler.

Procedure

The Ss were divided randomly into five groups of eight Ss each. Each group received a 3-sec footshock as follows: 0.0, 0.5, 1.0, 2.5, and 4.0 mA. Each S was dropped from approximately 2 in. above the center of the floor. The weight of S activated a switching circuit which started the timed footshock. One counter recorded activity during the footshock and a second counter recorded postshock activity. For the nonshocked controls, activity was recorded for the initial 3 sec, as well as for all "postshock" intervals. The number of switch closures per 1-min interval was recorded for 3 min starting at the termination of the footshock. Twenty-four hours after

footshock, each S was returned to the apparatus and retested without footshock for three 1-min intervals.

Results

An analysis of variance (excluding controls) of activity during the 3-sec footshock indicated that activity during this interval was a function of the intensity of the footshock ($F = 7.325$, $df = 3/28$, $p < .001$). A two-way analysis of variance of shock day postshock activity (excluding controls) indicated that activity was a function of both intensity of footshock and of postshock interval ($F = 8.183$, $df = 3/28$, $p < .001$, and $F = 9.953$, $df = 2/56$, $p < .001$, respectively), but not of the interaction ($p > .05$). An analysis of variance of the retest day activity (excluding controls) also indicated that activity was a function of footshock intensity and postshock interval ($F = 3.453$, $df = 3/28$, $p < .05$, and $F = 9.136$, $df = 2/56$, $p < .001$, respectively), but not of the interaction ($p > .05$).

Figure 1 summarizes the mean postshock activity on both shock and nonshock days for all intensity conditions. An analysis of variance of the total postshock activity (excluding controls) indicated that activity was a function of shock intensity ($F = 6.825$, $df = 3/28$, $p < .01$), but not of days ($p > .05$). However, the Days by Intensity interaction was statistically significant ($F = 5.348$, $df = 3/28$, $p < .01$). Since the interaction was significant, simple main effects were analyzed. The intensity variable produced activity differences only on the shock day ($F = 10.600$, $df = 3/42$, $p < .001$), and the 0.5-mA group was the only one which changed over test days ($F = 20.529$, $df = 1/28$, $p < .001$). A t test, summing over days

Fig. 1. Mean postshock activity on both shock and nonshock days (Days 1 and 2, respectively) for all intensity conditions.

Fig. 2. Median activity ratios (postshock/preshock + postshock) for both postshock days for all intensity conditions.

and comparing the 2.5- and the 4.0-mA groups, indicated that the postshock activity for these two groups was statistically different ($t = 2.286$, $df = 14$, $p < .05$).

The greatest amount of activity suppression at 2.5 mA was consistent with the results of Barcik & Collins (1971) and Barcik & Ellis (1971) in that the highest percentage of Ss avoiding also occurred at 2.5 mA. In addition, the increase in activity from 2.5 to 4.0 mA was consistent with the earlier work in that the lowered percentage of Ss avoiding also occurred at 4.0 mA.

Thus, it is possible that passive avoidance performance may be partially explained by greater or lesser activity suppression. Therefore, Experiment 2 was designed to measure activity during passive avoidance.

EXPERIMENT 2

Subjects

A total of 32 female Charles River CD rats between 150 and 180 days old served as Ss. All Ss were allowed ad lib access to food and water.

Apparatus

The chamber, shocking system, and activity measurement were the same as in Experiment 1. One wall of the chamber was modified such that an

apparent escape route consisting of an opening 4.5 x 7 cm was placed 4.5 cm above the grids and 7.6 cm from a corner formed by two of the walls. A photoelectric cell with red filter was mounted 2.5 cm out from the opening on the outside of the wall. The photocell was completely enclosed in a cul-de-sac attached to the outside of the chamber wall. When a S explored the opening with his head, the photobeam was interrupted. Latency to wall-opening exploration was measured by a Lafayette Instruments multichoice reaction timer in .01 sec.

Procedure

The Ss were divided randomly into four groups of eight Ss each. Each group, except the nonshocked control group, received a 3-sec footshock of 0.5, 2.5, or 4.0 mA.

Each S was placed in the center of the grid floor, and the latency timer was simultaneously activated. The activity of S was measured until the opening was explored. When the photobeam was interrupted, both the latency timer and the activity counter circuits were opened and the timed footshock was delivered. S was removed from the compartment approximately 20 sec after termination of the footshock. The

footshock was presented on Day 1 only.

On the shock day, all Ss explored the opening within 3 min. On Days 2 and 3, the same latency-activity measurement procedure was used. If S had not interrupted the photobeam within 6 min, the latency was scored as 360 sec and the trial was terminated.

The activity rate per second per day was determined for each of the 3 days. The preshock rate on Day 1 served as the base, and the rates for Days 2 and 3 were expressed as activity ratios as follows: Day 2/Day 1 + Day 2 and Day 3/Day 1 + Day 3.

Results

The expression of activity was such that on the postshock days, if no activity reduction occurred, the ratio was .50; if activity was reduced by half, the ratio was .33, and as activity approached zero, so did the ratio. Figure 2 summarizes the median activity ratios for both postshock days for all intensity conditions. A two-way analysis of variance of activity ratios indicated that activity was a function of footshock intensity and of the Days by Intensity interaction ($F = 10.078$, $df = 3/28$, $p < .001$, and $F = 5.808$, $df = 3/28$, $p < .01$, respectively) but not of the days main effect alone ($p > .05$). Since the interaction was significant, simple main effects were analyzed. The shock intensity manipulation produced significant activity differences on both test days ($F = 46.116$, $df = 3/48$, $p < .001$, and $F = 6.974$, $df = 3/48$, $p < .001$, respectively). The reduction in activity over days for the control group was statistically significant ($F = 10.952$, $df = 1/28$, $p < .01$) and the increase in activity over days for the 4.0-mA group was also statistically significant ($F = 6.178$, $df = 1/28$, $p < .05$), whereas the other shock groups did not change statistically ($p > .05$). The increase in activity for the 4.0-mA group was further tested with a matched sample t test, which indicated that the shift was statistically significant ($t = 3.799$, $df = 7$, $p < .01$).

Figure 3 summarizes the percentage of Ss avoiding (exploration latency of 6 min) for each of the test days. On Day 2, almost all Ss avoided. On Day 3, however, while the 0.5- and 2.5-mA groups continued to avoid, the 4.0-mA group tended to explore the opening within the 6-min testing period such that avoidance performance declined to 62.5%.

The increase in activity on the second postshock day for the 4.0-mA group is consistent with the postshock activity of the 4.0-mA group in Experiment 1. In both experiments, the 4.0-mA condition produced more activity than the 2.5-mA condition.

These results are consistent with the activity and freezing data of Barcik & Ellis (1971). Furthermore, the lowered percent avoidance performance on the second test day for the 4.0-mA group is consistent with the percentage avoidance for the 4.0-mA condition reported by Barcik & Collins (1971).

DISCUSSION

Experiment 1 demonstrated that the defensive reactions of freezing or of fleeing may be produced with different levels of stress (footshock). Freezing, or immobility, developed with lower levels of stress than did flight or increased activity. This supports earlier work with passive avoidance (Barcik & Collins, 1971) and suggests that defensive behavior elicited by footshock may be more or less compatible with a predetermined avoidance response.

Experiment 2 demonstrated that this type of passive avoidance was not initially affected by footshock intensity, but that as extinction of activity suppression developed, passive avoidance performance declined. The higher shock intensity led to higher levels of activity and lowered passive avoidance on the second test trial, which supports earlier work (Adams & Calhoun, 1970; Barcik & Ellis, 1971), as well as the results of Experiment 1. These results also support the suggestion by Bolles (1970) that rapidly acquired avoidance behavior is the result of innate defensive behavior.

An interpretation of passive avoidance performance similar to the SSDR notion has been suggested by Spevack & Suboski (1969). According to Spevack and Suboski, passive avoidance is primarily the result of conditioned emotional response (CER) rather than of a specific response-punishment contingency. This immobility behavior is classically conditioned to apparatus cues, such that S avoids punishment by freezing rather than by learning to inhibit a specific response. However, passive avoidance may not be the simple result of classically conditioned immobility. For example, Barcik (1972) has recently shown that step-down passive avoidance involves both CER and specific response inhibition and that the response-punishment component was the more important.

Whether or not passive avoidance performance is produced by freezing depends on the strength of the punished response itself. The mean pre-shock wall-exploration latency in Experiment 2 was 75.8 sec, whereas the mean pre-shock step-down latency in earlier work (Barcik & Collins, 1971) was 0.86 sec. Furthermore, the 0.5-mA shock was quite effective in Experiment 2, whereas this same intensity did not produce avoidance in

Fig. 3. Percentage of Ss avoiding (exploration latency of 6 min) for each test day.

the step-down task. Thus, the wall exploration response was less prepotent than the step-down response. The exploration response was suppressed by freezing because it was relatively weak to begin with. Thus, the extinction of activity suppression in Experiment 2 led to lowered passive avoidance performance because this performance was the result of CER.¹ This may also explain why noncontingent shock reported by Spevack & Suboski (1967) was as effective as response-contingent shock in that barpress situation, i.e., the punished response was relatively weak to begin with. However, in the more highly prepotent step-down response situation, the passive avoidance performance was a result of a specific response inhibition where freezing was compatible with, rather than the cause of, this avoidance performance.

When higher shock intensities elicit flight, the heightened activity is not compatible with step-down passive avoidance and performance declines. Unpublished data re extinction of step-down passive avoidance with the 4.0-mA Ss of Barcik & Collins (1971) indicate that as massed extinction trials proceeded, avoidance performance increased as a result of weakening of the flight responses. These Ss were quite active on the platform, however, while meeting the avoidance criterion. This observation led to the research reported by Barcik & Ellis (1971), which demonstrated that this passive avoidance performance was the result of specific response inhibition, but that when

shock intensity was high, the resulting heightened activity masked this learning. The data reported by Barcik & Ellis (1971) involved Wistar rats and, as a result, demonstrated that the SSDRs of freezing and flight were elicited by the same shock intensities for both strains. Strain differences in susceptibility to CER or passive avoidance training may simply reflect different SSDR hierarchies.

Both CERs and SSDRs are important to passive avoidance performance. When passive avoidance is the result of CER (the SSDR of freezing), manipulations which affect CER will be important. However, when passive avoidance is the result of specific response inhibition, shock-elicited SSDRs become important in terms of their compatibility with the specific avoidance response.

To summarize, different shock levels produced different SSDRs. Low to medium shock produced freezing, whereas high levels of shock produced flight. The SSDRs produced by shock may be the causal factor in passive avoidance, i.e., CER, or may be compatible with a specific avoidance response. Furthermore, the strength of SSDRs may be changed, for example in extinction, such that avoidance may decline (Experiment 2) as a result of weakening of freezing or increase as a result of weakening of flight.

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NOTE

1. Response-contingent and noncontingent footshock for the 2.5- and 4.0-mA conditions were subsequently run. Passive avoidance performance was not statistically different for the contingent vs

noncontingent comparisons for either the 2.5- or the 4.0-mA conditions on either test day (Mann-Whitney U, $p > .05$). These results support the conclusion that passive avoidance performance in Experiment 2 was the result of CER.