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The Elevated Plus-Maze Is Not Sensitive to the Effect of Stressor Controllability in Rats

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GRAHN, R. E., B. A. KALMAN, F. X. BRENNAN, L. R. WATKINS AND S. F. MAIER. *The elevated plus-maze is not sensitive to the effect of stressor controllability in rats.* PHARMACOL BIOCHEM BEHAV **52**(3) 565–570, 1995.— The present experiments examined the sensitivity of the elevated plus-maze to the effects of stressor controllability. Previous work had established that inescapable but not an equal amount of escapable electric tail shock reduced social interaction. The present experiments demonstrate that prior exposure to shock alters elevated plus-maze behavior, but that this effect is not sensitive to the escapability of the shock. These experiments include a replication of the usual pharmacologic effects of benzodiazepine ligands (2 mg/kg diazepam; 0.4 mg/kg methyl 6,7-dimethoxy-4-ethyl-β-carboline-3-carboxylate) to demonstrate the sensitivity of the elevated plus-maze procedures used. The results provide additional support for the idea that the social interaction and elevated plus-maze measures of "anxiety" are sensitive to different processes.

Inescapable shock Learned helplessness Stress Anxiety Rat Social interaction Elevated plus-maze Animal models Diazepam DMCM

EXPOSURE to a variety of stressors has been shown to result in subsequent anxiogenic behavior in a number of putative tests of anxiety in animals. For example, social defeat (10,25), inescapable electric foot-shocks (29), immersion in water (4), and exposure to a cat odor (34) result in decreased entries into, and time on, the open arm of a plus-maze when testing is administered 30 min to 24 h later. Both inescapable shock (27) and exposure to cat odor (34) also result in reductions in social interaction measured 24–72 h and 1 h later, respectively.

Many of the behavioral and physiologic consequences of stressors are modulated by the behavioral controllability of the stressor [see (2,26,14)]. For example, inescapable electric shocks result in escape learning deficits (26), as well as reductions in movement in reaction to aversive events (1), swimming when placed in water (30), shock-elicited aggression (15), prod burying (32), aggressiveness (31), competition for food (24), brain self-stimulation (18,33), and so forth. With regard to anxiogenic behavior, Short and Maier (27) reported that rats administered inescapable electric shocks 24–72 h before testing displayed attenuated levels of social interaction but did not show altered levels of locomotion in a novel arena. Exposure to identical amounts and intensities of escapable shock had no impact on subsequent social interaction (27). Similarly, inescapably shocked rats later showed exaggerated fear to contextual cues paired with shock (13,19), but escapably shocked rats did not. Enhancement of fear conditioning beyond normal may also reflect anxiety (14).

Potential interactions between stressor controllability and the generation of anxiety are interesting (14). Indeed, it has been argued that uncontrollability of stressors may be of special importance in the production of anxiety by stressors (14). However, different models of anxiety present different behavioral (6), pharmacologic (5,9), and neural profiles (7), and have been argued to reflect different types of anxiety (6). Indeed, the social interaction and plus-maze models can respond differently to the identical stressor (34). Thus, the fact that shock controllability determines the effect of shock on social interaction (27) makes it interesting to assess whether controllability also modulates the effect of shock on plus-maze behavior. It should be noted in this context that shock controllability does not modulate all of the behavioral (20) and physiologic (16) outcomes of shock. Thus, it is not implausible a priori that controllability might fail to be an important factor.

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EXPERIMENT 1

The first study was conducted to demonstrate anxiolytic and anxiogenic effects of benzodiazepine (BZ) ligands on the elevated plus-maze under our laboratory conditions. The purpose was to demonstrate sensitivity of our testing procedures so that any subsequent absence of effect would be unlikely to be attributable to the testing conditions. A benzodiazepine agonist, diazepam, and a β-carboline inverse agonist, methyl 6,7-dimethoxy-4-ethyl-β-carboline-3-carboxylate (DMCM), were tested.

Methods

Subjects. We used 13 male Holtzman Sprague–Dawley rats (300–450 g, 70–85 days old) in Experiment 1a and 14 in Experiment 1b. Subjects were housed individually under a 12 L : 12 D cycle with free access to standard rat chow and water. Subjects were allowed to acclimate to colony conditions for at least 1 week and then were handled two to three times. Experiments were performed during the early half of the light cycle. All experiments were conducted in accordance with protocols approved by the University of Colorado Institutional Animal Care and Use Committee.

Apparatus. Elevated plus-maze testing was conducted in an isolated room illuminated with red lamps in an effort to create baseline maze performance maximally sensitive to both anxiogenic and anxiolytic manipulations. A videocamera was mounted in the ceiling above the testing area to allow observation. The elevated plus-maze was a black wooden platform consisting of four arms in a plus-sign arrangement raised 50 cm above the floor. Each arm was 10 × 38 cm long. Two opposing arms were enclosed with walls (38 × 31 cm), whereas the other opposing arms were open with a 1-cm wooden lip forming an edge around the arm.

Procedure.

Drugs. In Experiment 1a, 2 mg/kg diazepam (LyphoMed, Rosemont, IL, injectable) was administered intraperitoneally (IP) once daily for 5 days. On the 5th day, rats were tested on the elevated plus-maze 10 min following drug administration. This chronic administration of diazepam was employed to allow tolerance to the sedative and motor effects of the drug to develop. Experiment 1b assessed the effects of the inverse agonist DMCM (RBI, Natick, MA). DMCM was dissolved in acidic saline made from a solution of one part Dulbecco's phosphate-buffered saline and one part injectable-grade saline with two to three drops of 4 M hydrochloric acid added to obtain a pH of 3.1. A dose of 0.4 mg/kg of the inverse agonist was administered once IP 10 min before testing on the elevated plus-maze. The 10-min interval was adopted based on pilot work indicating that other behavioral manifestations of drug action observed at higher doses were evident during this time interval. Control subjects were given the appropriate vehicle.

Elevated plus-maze. Subjects were removed from the colony room and brought in separate cages to the elevated plus-maze testing room, which was isolated in a quiet area of the laboratory. Drug injections began approximately 15 min after transport. The level of anxiety on the elevated plus-maze was measured by placing a rat in the center of the maze facing an open arm. The experimenter observed a 5-min taped session and scored the duration the subject spent on both arm types and the number of entries into each type of arm. An entry was defined as an occasion during which all paws crossed a line at the beginning of the arm. Once an entry was complete, the duration on the appropriate arm was measured. The plus-maze was wiped with a sponge soaked with 70% isopropyl alcohol before each session.

Results

As shown in Fig. 1, the duration of open-arm activity and the percentage of open arm entries on the elevated plus-maze were increased in animals given the BZ agonist diazepam. A one-way analysis of variance (ANOVA) revealed a significant difference in open arm duration [$F(1, 11) = 32.30$, $p < 0.05$]. There was also a significant difference between subjects given diazepam and those given vehicle on the percentage of open-arm entries [$F(1, 11) = 14.72$, $p < 0.05$].

The duration of open-arm activity and percentage of open-arm entries were reduced by DMCM. A significant effect of group was demonstrated for the duration of open-arm activity [$F(1, 13) = 11.76$, $p < 0.05$], and there was a trend toward a reduction in the percentage of open-arm entries [$F(1, 13) = 4.056$, $p < 0.1$].

EXPERIMENTS 2–4

The results of Experiment 1 indicated that our plus-maze procedure revealed the typical effects of BZ agonists and inverse agonists (22). Experiments 2–4 were conducted to assess the effects of shock controllability on elevated plus-maze behavior. A triadic design was employed in each experiment. In an escape shock condition, rats learned a wheel-turn response to terminate each shock that they and their yoked partner received. The rat in the yoked condition (inescapable shock) had no control over shock termination. Each shock simply terminated when the escape subject responded. The third rat in each triad was restrained in the apparatus and did not receive a shock. The experiments differed with respect to the interval of time between shock treatment and plus-maze testing and the intensity of shock.

Methods

Subjects. The 135 subjects used in Experiments 2–4 had the same characteristics as those described for Experiment 1.

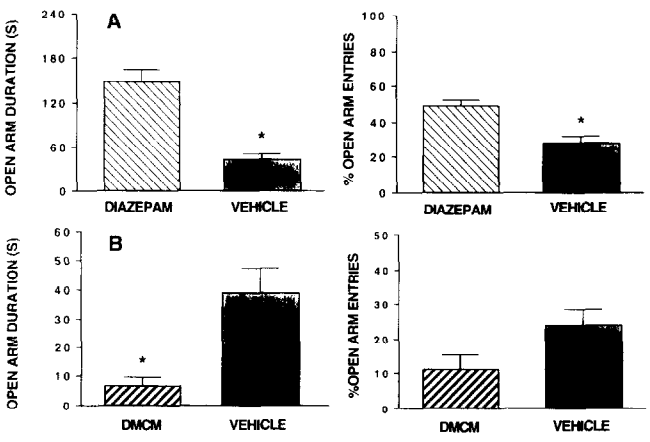

FIG. 1. The effects of BZ ligands on the percentage of open-arm entries and duration of open-arm activity show anxiolytic and anxiogenic profiles on plus-maze behavior. Diazepam (2 mg/kg, IP) had an anxiolytic profile, as shown in (A), whereas the effect of DMCM (0.4 mg/kg, IP), shown in (B), was anxiogenic. *Statistically significant difference from control.

Apparatus. Shock was delivered to the distal portion of the rat's tail through two electrodes placed 3 cm apart, augmented with electrode paste, and secured with tape. The shock source was modeled after a Grason-Stadler model 700 shock generator (Quincy, MA). Subjects were administered shock in wheel-turn boxes that measured 14 × 11 × 17 cm with the wheel situated in one wall. The wheel consisted of two 14-cm-diameter disks connected by 9-cm metal rods. Animals in the escape condition were provided with wheels that turned easily; the subjects in the yoked and restraint conditions were placed in boxes in which the wheel was immobilized.

Procedure. Subjects in the shock conditions received 100 1.0 mA tail shocks that occurred 30–90 s apart (average intertrial interval = 60 s). Shock duration on any given trial depended on the latency at which the escape subject responded by turning the wheel. The shock was terminated after 30 s if the escape subject did not respond. At the beginning of the shock session, a quarter turn of the wheel was required to terminate the shock. When three consecutive trials were completed in < 5 s, the response requirement increased by a quarter turn on the next trial. Subsequent trials under 5 s duration were followed by a 50% increase in the response requirement until the maximum response requirement of 16 quarter turns was achieved. If the subject failed to respond in < 5 s following any of these initial trials, the response requirement for the next trial decreased by a quarter turn. Response latencies of 30 s, indicating failure to respond, reset the requirement to the initial quarter turn. This contingency is identical to that used by Short and Maier (27) in assessing the effects of controllability on social interaction.

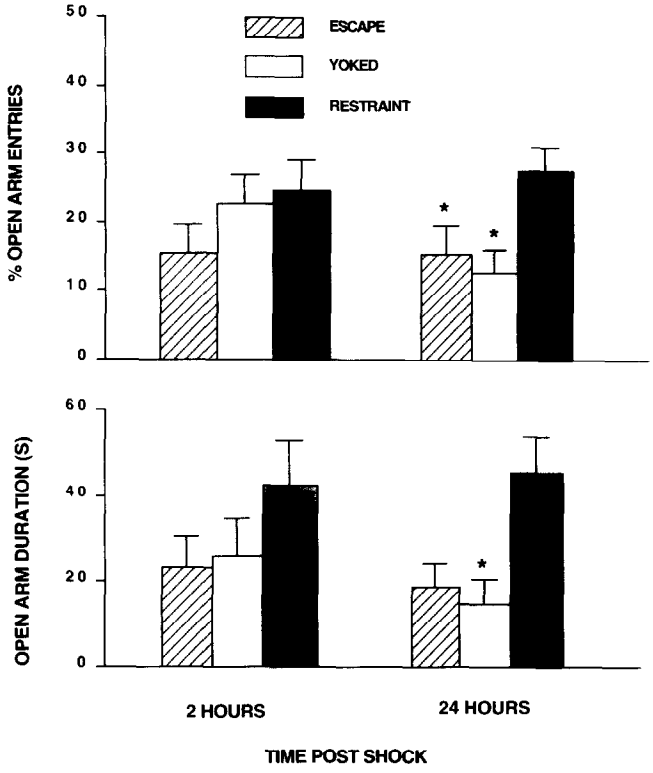

FIG. 2. The percentage of open-arm entries and duration of open-arm activity measured 2 and 24 h after escapable shock (ESCAPE), inescapable shock (YOKED), and restraint (RESTRAINT). Shock intensity was 1.0 mA. *Statistically significant difference from restraint.

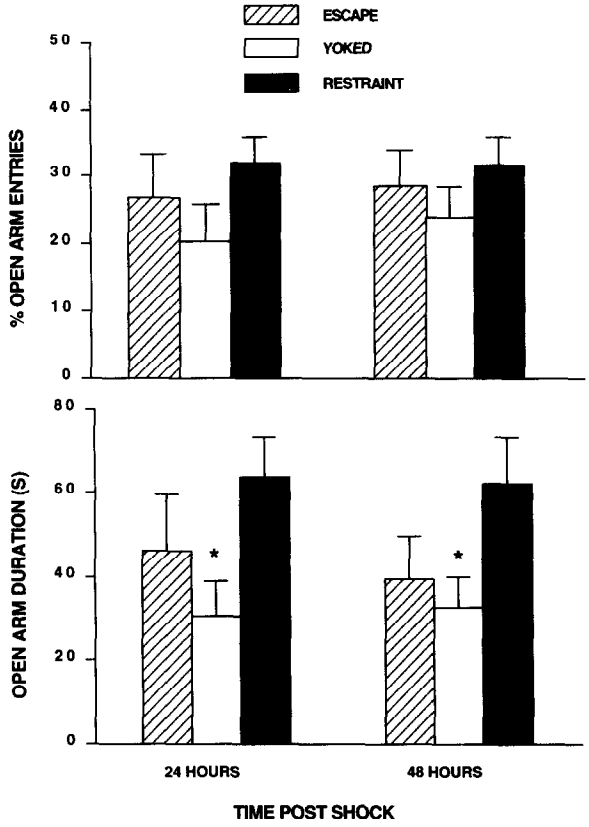

FIG. 3. The percentage of open-arm entries and duration of open-arm activity measured 24 and 48 h after escapable shock (ESCAPE), inescapable shock (YOKED), and restraint (RESTRAINT). Shock intensity was 1.0 mA. *Statistically significant difference from restraint.

Elevated plus-maze testing was conducted 2 and 24 h after shock in Experiment 2 in separate groups, 24 and 48 h after shock in Experiment 3 in separate groups, and 24 h after shock in Experiment 4. The shock intensity was 1.0 mA in Experiments 2 and 3, and 1.6 mA in Experiment 4. The testing procedure was the same as described for Experiment 1. Separate groups were employed for each time point to exclude prior exposure to the plus-maze as a confounding factor. The percentage of open-arm entries and the duration of open-arm activity were assessed for each time point.

Results

The duration of open-arm activity and percentage of open-arm entries in Experiment 2 are shown in Fig. 2. Neither escapable nor inescapable shock affected the duration of open-arm activity [$F(2, 27) = 1.574$; $p > 0.05$] or the percentage of open-arm entries [$F(2, 27) = 1.266$; $p > 0.05$] when testing occurred 2 h later. There was a significant group effect on the duration of open-arm activity measured 24 h after shock [$F(2, 30) = 5.757$, $p < 0.05$]. Posthoc analysis using Fisher PLSD [$p < 0.05$] revealed a significant difference between the yoked and restraint groups for the duration of open-arm activity. There was no difference between the escape and yoked groups. The percentage of open-arm entries measured 24 h after shock also exhibited a group effect [$F(2, 30) = 4.464$, $p < 0.05$], with significant differences between the escape and restraint and yoked and restraint groups (Fisher

PLSD, $p < 0.05$). There were no differences between the escape and yoked conditions, indicating that the controllability of the shock did not affect plus-maze behavior.

The purpose of Experiment 3 was to determine whether a longer interval between shock and testing might reveal the effect of controllability on plus-maze behavior. The duration of open-arm activity and the percentage of open-arm entries are shown in Fig. 3. There was no significant difference among the three groups for the duration of open-arm activity [$F(2, 33) = 2.489$; $p > 0.05$] or for the percentage of open-arm entries [$F(2, 33) = 1.206$; $p > 0.05$] when testing occurred 24 h after shock. However, open-arm duration was significantly different between the yoked and restraint groups 24 h after shock according to Fisher PLSD posthoc analysis. Likewise, the duration of open-arm activity and percentage of open-arm entries were not significantly different among the three groups [$F(2, 30) = 2.528$; $p > 0.05$, and $F(2, 30) = 0.708$; $p > 0.05$, respectively] when testing occurred 48 h after shock. Again, however, posthoc Fisher PLSD analysis revealed a significant difference of open-arm duration measured 48 h after shock between the yoked and restraint groups, indicating an effect of inescapable shock but not of escapable shock. A post-hoc analysis was conducted without an overall group effect, because there was a theoretical basis to expect that IS would reduce plus-maze activity exclusively. In no case were there significant differences between the escape and yoked groups.

The purpose of Experiment 4 was to determine whether more intense shocks might produce differences among the three groups. The plus-maze performance measured 24 h after shock can be seen in Fig. 4. Neither shock condition had an effect on the duration of open-arm activity [$F(2, 19) = 0.409$, $p > 0.05$] or on the percentage of open-arm entries [$F(2, 19) = 0.17$, $p > 0.05$].

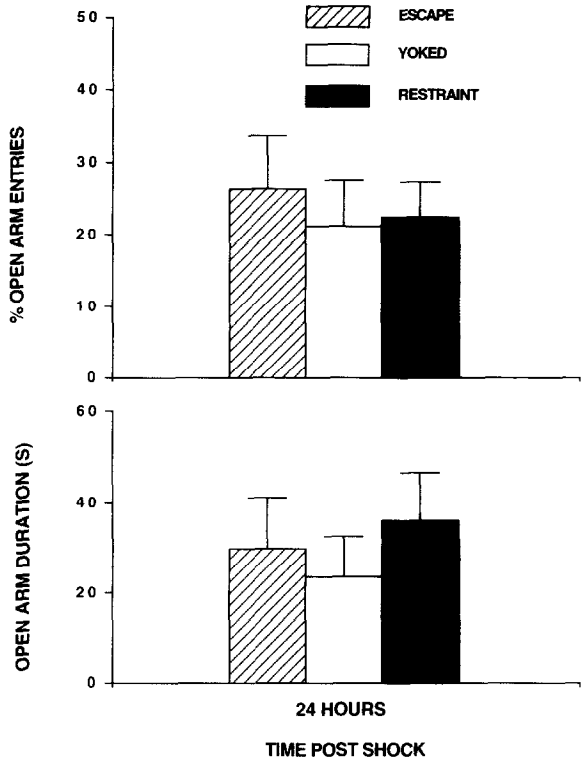

FIG. 4. The percentage of open-arm entries and duration of open-arm activity measured 24 h after escapable shock (ESCAPE), inescapable shock (YOKED), and restraint (RESTRAINT). Shock intensity was 1.6 mA. *Statistically significant difference from restraint.

DISCUSSION

In the present experiments the elevated plus-maze was not consistently sensitive to the effects of escapable or inescapable tail shock. These experiments were conducted in the same laboratory using the same shock parameters and equipment as in experiments in which the social interaction test of anxiety was shown to be sensitive to differences between escapable and inescapable shock (27). In both Short and Maier (27) and subsequent work, the social interaction test has been consistently sensitive to inescapable shock. One possible procedural change that might result in more reliable effects of IS on plus-maze behavior would be to use a home cage control group instead of a restraint control group. However, a comparison of plus-maze behavior between two such groups revealed no significant differences, although the home cage control group produced an increased mean percent of open-arm activity [home cage = 21%, restraint = 14%; $F(1, 14) = 1.341$; $p > 0.05$] and a greater duration of open-arm activity [home cage = 33.75 s, restraint = 20.38 s; $F(1, 14) = 0.997$; $p > 0.05$]. Although using a home cage control group may lead to more consistent effects of IS on plus-maze behavior, the use of this control group would not change the lack of stressor controllability effect on the plus-maze. That is, the possible "floor effect" of low baseline activity would not prevent the ES group from exhibiting plus-maze behavior that was comparable to that of the control group, be it a home cage or restraint treatment. Moreover, the elevated plus-maze behavior measured here was sensitive to BZ ligands in the usual manner, thereby providing some assurance concerning the adequacy of the procedures.

One issue related to the interpretation of the present results is the behavioral specificity of the elevated plus-maze as a measure of anxiety. A true anxiogenic effect would consist of decreases in both the percentage of open-arm entries and duration of open-arm activity without, or independent of, decreases in general activity as measured by total arm entries (23). This issue is especially germane to the present experiments, because IS has been shown to reduce activity levels (1). However, total arm entries were not significantly different in any of the present experiments examining the effects of IS and ES.

One possible interpretation of these results is that the elevated plus-maze measures a type of anxiety that is not produced by IS. Indeed, inconsistent effects of IS have been reported in other studies of IS and plus-maze behavior. In a study conducted by Steenbergen and colleagues (29), male rats exhibited a significantly lower number of open-arm entries 20 h following IS than did nonshocked controls; in a later study (28), however, male rats exposed to the identical stressor did not show significant reductions in open-arm activity. Overall, the effect of IS on elevated plus-maze activity in the Steenbergen studies was weak and mirrored the pattern of effects of IS on plus-maze behavior reported here.

Different types of stressors, such as exposure to cat odor (34), social defeat (10,25), and swimming (4) have revealed anxiogenic effects on plus-maze activity. The results of these studies indicate that the elevated plus-maze is indeed sensitive to the effects of some stressors. Perhaps the stress reaction produced by exposure to inescapable shock is different from

that produced by social defeat or cat odor such that the elevated plus-maze can detect one stress effect but not another. Indeed, there is abundant evidence that different stressors produce different neurochemical and neuroendocrine profiles (2,11,12,21).

The present results can be added to those of Zangrossi and File (34), demonstrating that the identical stressor conditions can have quite different effects on plus-maze and social interaction measures. These data further support the contention that the two tests measure different "types" of anxiety (6). Indeed, a factor analysis of plus-maze and social interaction performance revealed different and independent "anxiety" factors for each test, directly supporting the idea that the two tests are sensitive to different processes. File suggested that the plus-maze, or elevation in general, may induce a state similar to panic, whereas the social interaction test is sensitive to something more like generalized anxiety. This distinction has been made by Graeff and colleagues as well (8). If this characterization of these tests is correct, the present results in combination with those of Short and Maier (27) argue that IS produces a mild panic anxiety-like state but a potent and long-lasting generalized anxiety-like state. The pattern of results further suggests that the panic is not regulated by the controllability of the stressor, but that generalized anxiety is highly responsive to the controllability dimension. Characterization of the elevated plus-maze and social interaction models of anxiety as models for different types of clinical anxiety is tempting, but perhaps premature at this time.

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