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Conditions that potentiate the effects of electroconvulsive shock administered 24 hours after avoidance training

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Three experiments assessed the conditions that potentiate effects of an electroconvulsive shock (ECS) administered 24 h after avoidance training. Stimuli present immediately prior to the ECS were systematically varied. In Experiment 1, which employed a passive avoidance task, the primary determinant of whether the ECS disrupted retention was whether the situational cues present at the time of ECS delivery were those associated with the initial training experience: ECS disrupted performance only when it was administered in the original training apparatus, regardless of whether or not a footshock was presented immediately prior to ECS. In Experiment 2, which employed an active, shuttlebox avoidance task, both the situational cues from the training apparatus and a footshock were necessary to potentiate the disruptive effects of the ECS. Experiment 3 revealed that ECS effects on performance of the active avoidance task can also be potentiated by a combination of apparatus cues and the warning signal used in initial training. These results are interpreted as indicating that informational functions of stimuli present when an ECS is administered are important determinants of the effects of the ECS.

The disruptive effects of amnestic agents such as electroconvulsive shock (ECS) on retention are usually most apparent when the amnestic treatment is administered with a minimal time lag following the initial learning experience. This time dependency has served as the empirical cornerstone of most theoretical edifices (e.g., Glickman, 1961; McGaugh, 1966) constructed to explain the effects of amnestic agents. This time dependency, however, differs considerably from experiment to experiment, and there are a variety of conditions under which amnestic treatments are effective even when they are administered hours or days after the initial training (Davis, 1968; Davis & Klinger, 1969; DeVietti & Holliday, 1972; DeVietti, Holliday, & Larson, 1973; DeVietti & Kirkpatrick, 1976; DeVietti & Larson, 1971; DeVietti & Zwanziger, 1975; Lewis & Bregman, 1973; Lewis, Bregman, & Mahan, 1972; Misanin, Miller & Lewis, 1968; Potts, 1971; Robbins & Meyer, 1970; Schneider & Sherman, 1968).

Most experiments in which an amnestic treatment has proved effective despite a substantial delay between initial training and the treatment have indicated that the stimulus features and/or motivational states present in the moments just prior to the treatment are important determinants of whether or not performance in a subsequent retention test is disrupted. Lewis and his colleagues (1976; Misanin, Miller, & Lewis, 1968) have argued that those memories disrupted by ECS are those that are "active" when the ECS occurs: cues associated with the initial learning experience serve to reactivate memories, making them susceptible to disruption. Such an account emphasizes the informational, cuing functions of the stimuli present when ECS is delivered. Theories that view ECS effects as representing retrieval failure (Lewis, 1969, 1976; Miller & Springer, 1973; Spear, 1973) similarly emphasize the function of stimuli as reminders or retrieval cues. Other accounts (Howard, Glendenning, & Meyer, 1974; Howard & Meyer, 1971; Robbins & Meyer, 1970; Schneider & Sherman, 1968) emphasize the importance of motivational conditions immediately

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preceding ECS administration, arguing that "arousal" or incentive conditions are determinants of the effectiveness of amnestic treatments.

What conditions potentiate an amnestic treatment administered some time after initial training? The question can be addressed in several ways. DeVietti and Zwanziger (1975), Lewis and Bregman (1973), and Lewis et al. (1972) have shown that the potentiating effects of presenting stimuli associated with an appetitive maze task are not observed when the stimuli are extinguished prior to administering them and the ECS. It thus appears that potentiating stimuli must have some task-relevant signaling function. DeVietti and Zwanziger showed that a footshock presented immediately prior to ECS is not sufficient to potentiate disruption of performance in an appetitive maze task, suggesting that if arousal potentiates amnestic treatments, then the form that the arousal takes must be related to the type of motivation used in initially training the task.

In the experiments reported here, the type of stimuli presented just prior to ECS was systematically varied. Rats were first trained in an avoidance task (passive avoidance in Experiment 1, active avoidance in Experiments 2 and 3). A day later, the animals were given an ECS under varied stimulus conditions. The results indicated that stimuli associated with avoidance training can indeed potentiate ECS effects, but that not all cues related to avoidance training are effective potentiators.

EXPERIMENT 1

In this experiment, animals were given passive avoidance training. A day later they were given an ECS, with variations in the stimulus conditions at the time of ECS administration. Some animals received a footshock prior to ECS, some received situational cues from the training apparatus, and others were given both footshock and situational cues.

Method

Subjects. Sixty male, Sprague-Dawley rats, 90-120 days old and weighing between 300 and 400 g, were employed in this experiment. They were maintained in individual cages where they were given free access to food and water. One animal died during the course of the experiment.

Apparatus. The avoidance training chamber was a wooden box with interior sides painted flat black. Dimensions of the chamber were 37.8 × 37.8 × 35.3 cm high. The floor of the box consisted of stainless steel grids, .6 cm in diameter and spaced 3.5 cm apart. A black Plexiglas platform with a top surface of 12.6 cm × 12.6 cm and a height of 7.6 cm was installed in the middle of the floor of the training chamber. A transparent Plexiglas enclosure with interior dimensions just slightly larger than the platform and with walls 30.5 cm high slid over the platform and was used to restrain the animal on the platform. This enclosure could be lifted and removed to give an animal access to the rest of the chamber.

Some animals received ECS in a second, different chamber. This second box was designed to differ in size, texture, and appearance from the training chamber. It was constructed with clear Plexiglas sides, 22.9 cm high, with all four sides 20.3 cm in width. The floor consisted of stainless steel grids .3 cm in diameter and spaced 1.3 cm apart.

Footshock could be delivered through the grid floors of each of these two boxes. The shock source provided scrambled shock of 225 V through a 220-kΩ resistance.

The ECS treatment was 1,500 V delivered through a 20-kΩ resistance, .5 sec in duration.

Procedure. On 3 consecutive days, all animals received pretraining trials in the training apparatus. Each animal was placed on the center platform with the transparent restraining enclosure present to prevent the animal from leaving the platform. Five seconds later, the restraining enclosure was removed, allowing the rat to step down from the platform. After a rat had stepped to the grid floor (all four legs), it was allowed to explore the box for 10 seconds. One such pretraining trial was administered on each of 3 days.

On the 4th day of the experiment, each animal received one training trial. This trial was identical to the pretraining trials, except that as soon as the animal had stepped down to the grid floor it was administered a footshock and then was immediately removed from the box. All pretraining and training trials were administered in the large black box in a dimly lit room.

The animals were then divided into eight groups, each of which was administered one of four different treatments in one of two different locations. Treatments were administered 24 h after the training trial.

Half of the animals received their treatments in the training chamber. The center platform was removed, and each rat was placed on the floor of the chamber, under the same lighting conditions used in pretraining and training. Treatment followed after 8 sec. The other animals received their treatments under very different conditions. They were placed on the floor of the small, transparent chamber in a well-lit room, with treatment following after 8 sec.

Some animals (the FS-only groups, both ns = 8) received only the 1-sec footshock. They were then removed and returned to their home cages. Other subjects (the two ECS-only groups, both ns = 8) received only the ECS, followed by return to the home cages. The third type of treatment consisted of delivery of the footshock, followed .5 sec later by the ECS (the FS-ECS Groups; n = 7 for the group administered this treatment in the same apparatus as that used in training, n = 8 for the group treated in the different box). Finally, two groups (the SHAM groups, both ns = 6) were placed in the chambers and treated just like the other groups, but they received neither the footshock nor the ECS.

The ECS was administered through small washers, nuts, and bolts that were attached to each rat's ears after the third pretraining trial. A small hole was punched in the ear, and a small stainless steel bolt was placed through this hole and secured with a nut, with a stainless steel washer on each side of the ear. Each rat wore this earring arrangement for the duration of the experiment. Before the treatment session, wires were attached to these earrings. All subjects wore this arrangement during treatment, whether or not they received ECS.

This earring arrangement was used to eliminate confounding effects of the procedure used to prepare an animal for ECS. The alligator clips which are frequently used in experiments with ECS cannot be left on the animal between sessions. If motivational and/or situational cues are indeed an important determinant of the effects of ECS, the pain or discomfort caused by the placing of alligator clips may affect final results. Our rats appeared to adapt readily to their earrings.

On the day following treatment, the animals were tested for retention of passive avoidance. Each rat was again placed on the platform in the large black box (the one used in initial training). The restraining enclosure was then removed, giving the animal access to the rest of the box. The amount of time the rat remained on the platform before stepping down to the floor of the box was recorded. If a rat had not stepped off the platform after 180 sec, he was removed from the chamber.

Results

The ECS treatment was effective in disrupting performance of the passive avoidance task in this experiment even though it was not administered until 24 h after the initial training experience. However, the delayed ECS was not effective in all groups. Figure 1 shows the percentage of animals in each group that remained on the platform for the entire 180-sec test. The major determinant of the effectiveness of the delayed ECS was the situation in which the ECS was administered. Most of those animals which received ECS in the same apparatus used in initial training failed to remain on the platform during the retention test. Those animals that did not receive an ECS and those animals that received their ECS in a situation different from the training apparatus showed good retention of the passive avoidance behavior, remaining on the platform for the entire 3-min test. Placement in the training apparatus by itself, without an ECS, was not sufficient to change avoidance behavior. A series of individual Chi-square tests indicated that each of the two groups given ECS in the training apparatus differed from all the other groups (all $ps < .05$), excepting each other. No other individual group comparisons were significant. Thus, an ECS delayed 24 h after initial training disrupted passive avoidance, but only when it was administered in the same apparatus in which initial training occurred. Presentation of a footshock immediately prior to ECS did not appear to affect the degree of disruption produced by the ECS.

Conclusions

This experiment confirms that the situational cues present when an ECS is administered are important determinants of subsequently assessed disruption of performance of a passive avoidance response. However, despite the clear role played by situational cues in this experiment, a footshock delivered just before the ECS was not sufficient to potentiate the effectiveness of the ECS. Why did placement of the animals in the initial training apparatus prior to administering the ECS produce this effect?

Several features of the situational cue manipulation are shared by the footshock, which was not sufficient to potentiate the ECS effect, so it is unlikely that these shared features are responsible for the effect. For example, the general arousal produced by placing the animals in the presence of situational cues that had previously been associated with footshock was probably less than, and almost certainly no more than, that produced in animals administered an actual footshock prior to ECS. If a general arousal effect determines the effectiveness of the ECS, then the footshock manipulation should have been more effective than the situational cue manipulation.

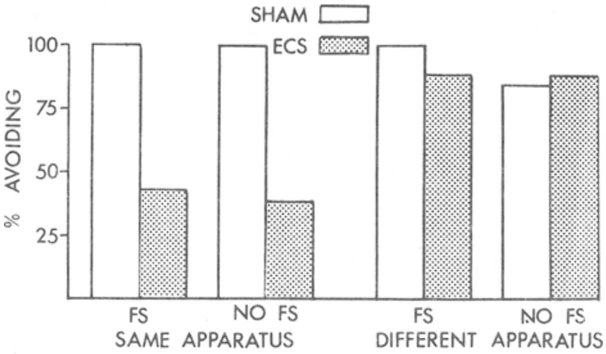

Figure 1. Percentage of animals avoiding in the retention test in Experiment 1.

Both the situational cues and the footshock were features of the initial training experience. Clearly not every feature of the training experience, not even a very salient one such as a footshock, is capable of potentiating the effects of an ECS. One might argue that the situational cues were more effective in "activating" memories of the earlier training trial than was the footshock; however, it is not obvious why one type of stimulus should be a much better "reminder" than the other.

EXPERIMENT 2

A passive avoidance task was used in the preceding study. In order to assess the generality of the results obtained with that task, we performed a second experiment using a two-way, signaled, shuttle avoidance. The two-way, active avoidance task differs from the passive avoidance paradigm in a number of important ways. It requires a series of training trials, rather than just a single trial, before it is acquired. It requires performance of a particular response, moving from one side of the chamber to the other, rather than simply remaining still. Also, the situational cues of the active avoidance chamber can carry information about both danger and safety, depending upon circumstances.

Method

Subjects. Fifty-eight male rats of the Fischer 344 strain were used in this experiment. They were 100-120 days old and weighed 200-250 g at the start of the experiment. They were housed in individual cages where they were given free access to food and water.

Apparatus. A two-way shuttle box, 41.9 × 14.0 × 18.4 cm high, was used for avoidance training. One side and the two ends of the box were aluminum. The ceiling and other side were clear Plexiglas. The floor of the shuttlebox consisted of stainless steel grids, .6 cm in diameter and spaced 1.6 cm apart. The grid was divided into two halves, each of which pivoted independently of the other from a point at the middle of the box. When a rat entered one side of the box, its weight slightly lowered the floor on that side, activating a microswitch. Each time the rat moved from one side of the box to the other, a response was registered. Scrambled shock could be delivered through the grid floor. The shock source provided 700 V through a 700-kΩ resistance. Two 6-W bulbs were mounted over the shuttlebox and were used as warning stimuli. In addition, a tone stimulus was employed, delivered through a speaker mounted in the center of the shuttlebox ceiling. The tone was 1,400 Hz and raised the sound level about 15 dB above ambient level.

Procedure. On the 1st day of the experiment, all animals were administered signaled avoidance training in the shuttlebox. Trials occurred at variable intervals, with a mean interval of 1 min. The signal consisted of a light-tone compound. If the rat did not move from one side of the box to the other within 5 sec following onset of the signal, shock was delivered through the grid floor. The shock continued until the animal moved to to the other side of the box, at which time both shock and signal terminated. If the rat made a shuttle response before 5 sec had elapsed following signal onset, the signal terminated and no shock was delivered on that trial. All rats were trained to a criterion of 11 out of 12 successful avoidances. After the avoidance training session, each rat was equipped with "earrings" of the sort described in Experiment 1.

Twenty-four hours later, the rats were divided into eight groups and given treatments which varied among groups. Half the animals were treated in the same shuttlebox used in avoidance training (the SAME groups), and half were treated in the different, smaller chamber (the DIF groups). In addition, some groups received a footshock (FS) while others did not ($\overline{\text{FS}}$). Finally some groups received an ECS (the ECS groups), while others did not (the SHAM groups). All groups consisted of eight subjects, except the SAME-$\overline{\text{FS}}$-SHAM and the DIF-$\overline{\text{FS}}$-SHAM groups, each of which had an n of 5.

In all cases, the rats were removed from their home cages and leads were attached to their earrings. They were then placed in the treatment chamber (the shuttlebox for the SAME groups, the other chamber for the DIF groups). Three seconds later, a 1-sec footshock was delivered to the FS groups, though not to the $\overline{\text{FS}}$ groups. One second later, the ECS was administered to the ECS groups. All animals were then returned to their home cages.

Twenty-four hours later, the animals were given reacquisition training in the shuttlebox. The training procedure was exactly the same as that used initially. The animals were trained to the same 11 out of 12 criterion, and the number of trials required to reach that criterion was recorded.

Results

All animals acquired the avoidance response. In the initial training session, the mean number of trials required to reach criterion was 62.8.

Table 1 shows the mean number of trials required by each group in this experiment to reach criterion in the reacquisition test. The ECS treatment affected only one group, that which received the ECS in the avoidance apparatus following a footshock. Neither the footshock nor placement in the apparatus was sufficient by itself to render the ECS treatment effective, and neither of these manipulations, alone or in combination, affected avoidance reacquisition in the SHAM groups. It thus appears that both situational and footshock reminders are necessary for producing a disruption in shuttlebox avoidance behavior by a delayed ECS treatment.

Table 1
Mean Trials to Criterion in Retention Test of Experiment 2

	Same Apparatus		Different Apparatus	
	Shock	No Shock	Shock	No Shock
ECS	20.4	13.0	14.0	14.1
Sham	14.5	13.6	13.8	13.8

A 2 by 2 by 2 unweighted means analysis of variance (SAME vs. DIF) by (FS vs. $\overline{\text{FS}}$) by (ECS vs. SHAM) indicated that all main effects and interactions were significant (all ps < .03). Individual comparisons of group means with Scheffé tests indicated that the SAME-FS-ECS group differed significantly from all the other groups (all ps < .02), while none of the other groups differed significantly from each other.

This experiment, like the preceding one, demonstrates that situational cues are important determinants of the effectiveness of a delayed ECS treatment in disrupting learned avoidance behavior. However, situational cues were not sufficient by themselves to potentiate this effect, unlike in the first experiment. A footshock immediately prior to the ECS was also necessary for disruption of the avoidance behavior to occur.

These results contrast sharply with those of the previous experiment, where situational cues by themselves were sufficient to potentiate ECS effects. What accounts for this difference? One possibility is that the difference depends upon the different kinds of experience with the situational cues associated with the two tasks. The passive avoidance animals experienced a single trial in which situational cues were paired with shock. The active avoidance animals, however, underwent many trials with an explicit warning stimulus that was a better predictor of impending shock than were the situational cues. The different results in Experiments 1 and 2 may, in part, reflect this possible difference in signaling functions of the situational cues.

EXPERIMENT 3

If the differences between the results of the first two experiments have something to do with differences in the signaling functions of the situational cues in the two tasks, then an experiment that

Table 2
Mean Trials to Criterion in Retention Test of Experiment 3

	Same Apparatus		Different Apparatus	
	WS	No WS	WS	No WS
ECS	23.0	15.5	14.2	13.6
Sham	15.0	14.4	14.0	13.8

manipulates different types of signaling cues should help illuminate what conditions potentiate amnestic treatments. This experiment is similar to the previous one, except that the warning stimulus (a tone-light compound) is manipulated in place of footshock.

Method

Subjects. Sixty male rats of the Fischer 344 strain were used in this experiment. Two of these were eliminated when they failed to acquire the avoidance response.

Apparatus and Procedure. A shuttlebox identical to that described in Experiment 2 was used, along with the Plexiglas box used in the previous experiments. The design of the experiment was almost identical to that of Experiment 2, except that the warning stimulus (WS) from the avoidance training phase replaced the footshock in the manipulations of stimuli when ECS was delivered. The rats were initially trained exactly as in Experiment 2. The next day, half the animals received ECS and half did not (SHAM), with the stimulus conditions at the time of treatment systematically varied. Half the animals were treated in the avoidance apparatus (SAME), half in the different box (DIF). Half were given the WS prior to ECS, half were not ($\overline{\text{WS}}$). All ns were 8, except the SAME-$\overline{\text{WS}}$-SHAM and DIF-$\overline{\text{WS}}$-SHAM groups, which had 5 rats each. The following day, all rats were administered a retention test, exactly as had been done in Experiment 2.

Results

Two animals failed to acquire the avoidance response in 300 trials and were replaced. For the remaining animals, the mean number of trials to reach criterion in the initial avoidance training was 68.0.

Mean trials to criterion in the retention test are shown in Table 2. The warning signal was effective in potentiating the ECS effects, but it was effective only when the situational cues associated with avoidance training were also present at the time of ECS. All main effects and interactions were significant (all ps $< .05$).

Conclusions and Discussion

This experiment yielded results virtually identical to those of the previous experiment. Only the combination of situational cues and warning signal sufficed to potentiate amnestic effects.

These three experiments, taken together, suggest several conclusions about what conditions potentiate the effects of an ECS delivered 24 h after avoidance training. In neither of the experiments in which footshock was manipulated prior to ECS was the footshock alone sufficient to potentiate ECS effects. This makes it unlikely that arousal, per se, is the determinant of whether an ECS affects retention; situational cues by themselves (Experiment 1) and in conjunction with a warning signal (Experiment 3) potentiated ECS effects, and it is implausible that such cues produced more arousal than a footshock.

Although situational cues were sufficient by themselves to potentiate ECS effects in the first experiment, this was not the case in the second and third experiments. This finding poses a problem for theories that argue that the cues that potentiate amnestic treatments are those that are the better "reminders" of the initial training experience. Animals in the two experiments that used active avoidance tasks underwent many more trials and spent more time in the training apparatus than did animals in the experiment that used a passive avoidance task. Because the two tasks involved different amounts of experience with the situational cues associated with their respective training situations, one would expect situational cues from the active avoidance training apparatus to be better reminders than those from the passive avoidance training apparatus. Yet situational cues by themselves did not potentiate ECS effects with the active avoidance task.

What functional roles must stimuli play if they are to potentiate an amnestic treatment administered a day after initial training? It may be necessary to present, just prior to ECS, cues that signal danger. In Experiment 1, the floor of the training apparatus was a dangerous part of the situation; the safe platform was absent prior to ECS. In the shuttlebox, however, the floor of the chamber was dangerous only when the warning signal was present. Presenting situational cues in conjuncton with either the warning signal (which signals danger) or with shock (which *is* danger) potentiated the amnestic treatment. The failure of either the shock by itself or the warning signal by itself to potentiate ECS effects suggests that informational functions of the situational cues, over and above fear-arousing functions, play a role.

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