1973

A Test of the State-Dependent Hypothesis of Ecs Effects.

Gary Dwayne Fuselier

*Louisiana State University and Agricultural & Mechanical College*

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A TEST OF THE STATE-DEPENDENT HYPOTHESIS
OF ECS EFFECTS

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Psychology

by

Gary Dwayne Fuselier
B.S., Louisiana State University, 1969
M.A., Louisiana State University, 1971
May, 1973
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ABSTRACT

Eighty male albino rats were given a series of treatments in a lever pressing situation in order to test specific predictions of a state-dependent hypothesis of ECS effects. Animals received an initial treatment of either ECSO or FS + ECS followed 24 hrs. later by a second treatment of either FS or FS + ECS. Half of the animals were tested 24 hr. after the second treatment and half 96 hr. after treatment. Two control groups received only lever press training. Results of both latency to the first lever press and number of lever presses in a 15 min. extinction session showed no differential effect of initial treatment. The second treatment main effect was highly significant, indicating that ECS following FS alleviated the suppression of responding due to FS. No interactions were significant and thus indicated that the effect of the second treatment was the same regardless of the initial treatment or time of testing. As the state-dependent hypothesis would predict significant interactions among levels of the three treatments, these results were interpreted as presenting no behavioral evidence in support of the hypothesis and the most parsimonious explanation of ECS effects in this study is in terms of a disruption of a retention and/or retrieval mechanism.
INTRODUCTION

Consolidation theory has occupied a prominent position in psychological theory since Muller and Pilzecker (1900) first used the concept in order to account for retroactive inhibition. They posited the existence of a neural preseverative process, subject to external interference and requisite to the consolidation of the memory trace for recently acquired material. DeCamp (1915) supported this position and clarified the theoretical process by which consolidation of a memory trace occurred. He maintained that immediately after the learning process, an after discharge continues for a short time, tending to "set" associations between just learned syllables. Any mental activities engaged in during this period of after discharge, involving or partially involving the same neurological group, tends to block the after-discharge and give rise to retroactive inhibition.

A logical step was taken by Burnham (1903) in using consolidation theory to explain the retrograde effects of electroconvulsive shock (ECS). Burham postulated that a) the time required for the "fixation" process to be completed may vary with individuals and conditions, b) ECS produces its effects by arresting the fixation process in the nervous tissue, and c) retrograde amnesia (RA) is not all or none, and the extent of the amnesia is relative to the amount of time elapsing before the fixation process is interrupted.

Most researchers agreed with the presumption that the
consolidation process was time bound although no one had yet specified the time relations involved. Duncan (1949) gave empirical support to this theoretical tenet. He trained rats to avoid a grid floor through which foot shock was delivered. They were given one trial a day for 18 days and ECS was given after each trial at either 20 sec., 40 sec., 1 min., 4 min., 15 min., 1 hr., 4 hr., or 14 hr. He also had controls that were given the same amount of shock through the hind legs. He found depression of learning in the first five groups, that is, when ECS was administered within 15 min. after each trial. No depression in learning was found in groups receiving ECS 1 hr., 4 hr. or 14 hr. after learning. Thus, Duncan inferred that the ECS treatments at 15 min. or less after the avoidance trial were disrupting the neural trace before consolidation could occur. Likewise, at 1 hr. or more, the trace had consolidated and thus was not susceptible to the effects of ECS.

The first serious alternative to consolidation theory was put forth by Miller and Coons (1955). They shocked rats for eating in a runway, producing avoidance. ECS treatment following avoidance training procedures produced no attenuation of the avoidance response. In this study and a later study as well (Coons and Miller, 1960), results were interpreted as showing that ECS does not eliminate memory, but merely induces anxiety or conflict and apparently has aversive properties. They argued that the depression in learning found by Duncan (1949) was merely the result of placing a rat in a conflict situation.
This line of thought was the first serious alternative to consolidation theory and it prompted a renewed interest in the area (Lewis, 1969). A number of studies supporting consolidation theory (Thompson and Dean, 1955, Gerard, 1955) appeared at this time.

Gerard (1955) reported a study similar to that of Duncan (1949), in which hamsters were given ECS at varying intervals after the termination of each trial in a maze situation. The results from the study were essentially the same as those of Duncan's, except that the administration of ECS 1 hr. after each trial still had some retarding effect of maze learning. Besides the afore-mentioned difficulty of aversive properties of ECS resulting in negative conditioning, both Duncan (1949) and Gerard (1955) gave their animals multiple ECS treatments, which, according to Thompson and Dean (1955), further complicated the issue. Thompson and Dean (1955), therefore, attempted to investigate the functional relationship between the degree of memory loss and age of the required habit without these complications. Five groups of rats were given training on a horizontal-vertical visual discrimination problem. For four groups, one ECS was administered at 10 sec., 2 min., 1 hr., or 4 hr., respectively, after learning. The fifth group constituted normal controls. Two days later, all groups were required to relearn the discrimination. Results indicated that groups receiving ECS at 1 hr. or less after reaching criterion showed significant deficits in memory of the habit, the amount of deficit being inversely related to the time interval between reaching criterion and receiving ECS. There was no significant difference in retention of
the habit between the control animals and those receiving ECS 4 hr. after learning the problem. Thompson and Dean interpreted their results as consistent with a perseveration theory of memory.

Although Thompson and Dean (1955) greatly reduced the likelihood of passive avoidance conditioning occurring when ECS is presented soon after learning, they did not completely eliminate the possibility. What was needed was an experimental situation in which the proposed amnestic effects and the aversive effects would have opposite behavioral consequences. This situation was provided by Madsen, Millard and McGaugh (1961). They used a stepdown platform, by which a rat was given shock to the feet immediately after stepping down, resulting in one-trial passive avoidance learning. Thus, the point in time of learning could be precisely determined and any aversive or amnestic properties of ECS should have opposite behavioral effects. Rats receiving foot shock (FS) followed by ECS showed significantly shorter step-down latencies than those given FS only. The investigators concluded that they had demonstrated amnestic properties of ECS.

Hudspeth, McGaugh and Thompson (1964) designed an experiment by which both amnestic and aversive properties of ECS could be shown. They used a step-down platform and three experimental groups: FS only, FS+ECS and ECS only. Three consecutive treatments were administered 24 hr. apart. Rats that received FS only showed increased step-down latencies. Those that received FS+ECS showed significantly smaller increases in latencies and the ECS only group showed increases in latencies after three treatments but not after only one. Thus, the
Amnestic effects were observable after one trial while the aversive effects appeared only after three treatments.

A second alternative to consolidation theory was put forth by Adams and Lewis (1962). They posited that ECS acted as an unconditioned stimulus with situational cues functioning as conditioned stimuli. The pairing of ECS with these situational cues resulted in the conditioning of a partial convulsion to these cues. This partial convulsion in turn acts as a competing response interfering with the performance of the previously learned response. They provided further evidence for their theory (Lewis and Adams, 1963) by distinguishing between the competing response conditioning and aversive properties of ECS. Using a one-way active avoidance box, rats were given a daily set of three training trials. Each daily set was followed by ECS either in the start compartment, in the safe compartment or outside the apparatus. Performance was best by the group given ECS outside the apparatus and poorest by the group convulsed in the start compartment, which conformed to the competing response hypothesis.

New support for consolidation theory was put forth by Heriot and Coleman (1962). They trained rats to lever press for food in an operant chamber. After a stable rate of lever pressing had been established, a lever press was followed by two intense foot shocks. The treatment groups received ECS at either 1, 7, 26, 60, or 180 min. after foot shock. Those groups receiving ECS at up to 60 min. after foot shock did not differ significantly from pre-treatment levels. Those animals receiving ECS 180 min. after FS showed a slower rate of
responding. Therefore, the effect of ECS on lever press rates was shown to be a negatively decreasing function of the shock-ECS interval.

Two other alternatives to consolidation theory are those proposed by Chorover and Schiller (1965) and Adams, Peacock and Hamrick (1969). Chorover and Schiller (1965) posited that the effects of ECS given at an interval of 10 sec. or more after learning are on the punishment produced conditioned emotional response (CER), while short term effects (learning-ECS interval of less than 10 sec.) are on memory. That is, ECS administered up to 10 sec. after FS causes RA, while ECS given later than 10 sec. alleviates the suppression of locomotor activity caused by the CER. Adams, Peacock and Hamrick (1967), on the other hand, suggest that the effect of ECS is to cause a disinhibition of the inhibition of responding produced by foot shock.

It is obvious from the material mentioned above that there are now numerous alternatives to consolidation and that this theory cannot account for much of the data. Three more recent lines of evidence provide even more difficulty for consolidation theorists.

The first such evidence is that reported by Adams, Peacock and Hamrick (1967) and Young and his co-workers (Young and Galluscio, 1970a, 1970b, Young and Day, 1970, Young and Galluscio, 1971, Young and Fuselier, 1971) in which data is presented showing that the effects of ECS are related to the schedule of reinforcement under which the animal is trained and therefore the rate of operant responding on the animal. Adams, Peacock and Hamrick (1967) report an absence of
disinhibition following ECS in groups trained on a fixed ratio (FR) schedule of reinforcement. That is, there was no difference between FR groups receiving FS+ECS and those receiving FS only, obviously not conforming to the theory of consolidation. Young and Galluscio (1970b), using a discrete trial procedure, showed that the absence of disinhibition in the FR(FS+ECS) groups was due to the higher response rate generated by the FR schedule and not by the schedule itself. Young and Galluscio (1970b) also reported the loss of the partial reinforcement effect (PRE). Typically, animals receiving partial reinforcement training would emit significantly more responses in extinction than a continuously reinforced (CRF) group, while in this study, the CRF animals made more total responses than did the FR-trained animals. This loss of the PRE was substantiated by Young and Day (1970) using animals trained on a variable ratio (VR) schedule. In an effort to test the permanence of the effects of ECS, Young and Galluscio (1971) delayed testing for 10 days following treatment and found that there was recovery from ECS-induced amnesia but no recovery of the PRE. Thus, although the ECS-induced suppression of a CER may recover over time, the loss of the PRE seems to be permanent.

The second line of evidence which presents difficulty for consolidation is that in which memory return has been reported, either by being induced by a reminder shock or by delaying testing for some period of time, usually 5 or more days.

Lewis, Miller and Misanin (1968) used a step-down procedure, with a FS of 1.6 mA for 5 sec. contingent upon step-down. Subjects
were divided into FS only, FS+ECS, ECS only and no treatment (00) groups. All animals were given treatment after three adaptation trials and when tested 24 hr. later, the ECS was found to have produced amnesia for the FS. Four hours after this test, all animals were placed in a different compartment and given another 5 sec. 1.6 mA foot-shock. Step-down latencies of the four groups showed that the reminder shock had no effect on the FS only, ECS only and 00 groups, while the FS+ECS group showed significantly increased step-down latencies. Lewis et al. concluded that at least part of the memory of the original FS remained but that its retrieval was prevented by ECS. Similar results have been reported by Koppenaal, Jagoda and Cruce (1967) using FS to suppress drinking from a tube, followed by ECS, with a reminder shock given 24 hr. later; by Flexner and Flexner (1968) using injections of puromycin and saline; and by both Galluscio (1971) and Young and Fuselier (1971) who found recovery from ECS-induced amnesia using a reminder shock given in a different experimental chamber 4 hr. after passive avoidance training in a lever pressing situation.

Obviously, consolidation theory cannot account for a return of memory following ECS. Most, though not all (Deutsch and Deutsch, 1966), hold to the position that ECS following learning closely in time results in a disruption of a neural reverberatory trace (Hebb, 1949) causing permanent memory loss. Therefore, once the memory trace has been disrupted by ECS, the memory should be lost, and no reminder of any sort should be able to reinstate that memory.
The third group of studies not supporting consolidation has been those in which ECS has been administered some time after consolidation should have been completed, yet there was evidence of a loss of memory. The first such study is one by Schneider and Sherman (1968). They used a step-down passive avoidance task with training-ECS intervals of either 30 sec. or 6 hr. One group was given FS for stepping off a platform, 30 sec. later given a noncontingent foot shock (NCFS), and then received ECS 6 hr. later. No RA was found for this group when tested 24 hr. later. However, animals given FS followed 6 hr. later by NCFS and immediate ECS did show RA when tested. Thus, a memory which had 6 hr. during which consolidation could take place was apparently disrupted by ECS. In a similar study by Fuselier and Dempsey (1972), animals received FS contingent upon pressing a lever, producing passive avoidance. Four hr. later, these animals were given a NCFS followed immediately by ECS. Upon testing 24 hr. after original treatment, these animals pressed significantly more than groups receiving FS only or FS followed 4 hr. later by ECSO, indicating a relief from the suppression due to FS, presumably due to the retrograde effects of ECS. Misanin, Miller and Lewis (1968) produced RA with an interval of 24 hr. separating learning from ECS. The response used was a cessation of drinking brought about by pairing a CS with foot shock while the animal was drinking. They showed that if the sequence was CS, followed immediately by foot shock, followed immediately by ECS, RA occurred. If, however, 24 hours separated the CS and the foot shock from the ECS, there was no RA. Further, RA could
also be produced 24 hours following foot shock if the CS immediately preceded the ECS. The interpretation given by the authors is that ECS is an inhibitor for those processes which it follows closely in time.

Thus, if an old memory could be rather precisely reactivated and followed immediately by ECS, an amnesia-producing inhibition should result.

These studies that show ECS producing amnesia long after consolidation should have been completed have one factor in common. That is, the fact that the ECS is preceded either by a reminder shock or a CS that has been paired with the original FS. Thus, it seems evident that certain environmental conditions can render a supposedly "fixated" memory trace susceptible to the effects of ECS. Exactly what these "ECS effects" are is obviously not clear at this time.

In addition to the interpretation of Misanin et al. (1968), another fairly recent theory can account for the studies which show ECS effects with a long learning-ECS interval.

Nielson (1968) has postulated a "state-dependent" theory which suggests that ECS does not disrupt memory fixation which is dependent upon a neural reverberation process for consolidation, but that memory retrieval may depend upon brain excitability states. The hypothesis is offered that the neurological aspect of learning may involve changes in levels of brain excitability as reflected in the thresholds of functional neural systems, that retention implies a maintenance or reconstruction of these modifications of brain excitability, and that failure of retention occurs whenever brain excitability is modified away from that established by the training procedure. Nielson (1968)
reported 4 studies that led to the formulation of the state-dependent hypothesis. The first study showed that the attachment of alligator clips to a rat's ear depressed the animal's activity and thereby interfered with the acquisition of an active avoidance response, and these results may have been erroneously interpreted as being produced by RA. Nielson's (1968) second experiment was aimed at exploring the effect of a single ECS upon brain excitability levels. This study stemmed from a suggestion by Doty (1961) that the engram may represent a change in the neural threshold of the system being conditioned. Also, Rutledge (1965) reported that the excitability of a multi-synaptic pathway is increased during the pairing of stimuli as is found in conditioning experiments. To determine changes in brain excitability, Nielson's second experiment measured the change in the intensity of electrical stimulation necessary for the maintenance of Conditioned Responses (CR) elicited by electrical stimulation of various subcortical areas following ECS. Results were as follows: 24 hours after ECS, CR's established to a tone CS were either abolished or elicited so infrequently that they could not be distinguished from indiscriminate flexions. Further, the thresholds at nine loci were sufficiently elevated so that CR's could not be elicited with CS intensities five times their pre-ECS thresholds. These thresholds gradually returned to near normal levels 4-7 days after ECS treatment.

The purpose of the third experiment was to determine whether following ECS, there would be a recovery of a passive avoidance response corresponding to the changes in brain excitability produced by ECS when
the increased activity levels of convulsed animals are suppressed by ear clips. Nielson refers to Routtenburg and Kay (1965) who have shown that convulsed rats have shorter latencies of descent from a platform than do non-convulsed rats. The implication is that the increased activity levels produced by ECS may result in shorter step-down latencies and may be interpreted incorrectly as retrograde amnesia. Nielson (1968) therefore in experiment 3 gave rats FS or FS+ECS contingent upon step-down and tested the animals either 24 hr. or 96 hr. later and either with or without earclips. Results showed that animals tested 24 hr. after treatment showed RA for the foot shock either with or without the earclips. However, when tested 96 hr. after treatment, the convulsed animals tested with ear clips attached showed recovery of the passive avoidance response while the animals tested without ear clips did not show recovery. According to Nielson, the recovery of a passive avoidance response when ear clips are attached, and by inference activity levels are suppressed, raises serious questions about the traditional interpretation of ECS effects upon consolidation. If ECS did impair memory consolidation, there should be no memory to recover.

Nielson's (1968) fourth experiment tested the hypothesis that if amnesia produced by ECS is the result of differences in brain excitabilities existing between the learning state and the recall state, and if, by grid shock and ECS, the threshold for neural firing is raised prior to step-down training, and then ECS is administered immediately after FS contingent upon step-down, there should be no
evidence of retrograde amnesia. Therefore, rats were first trained in a T-maze to give an active avoidance response. Following acquisition of the active avoidance response, each animal was given one of three treatments to induce various brain states: No ECS, ECS immediately after acquisition or ECS 4 hr. after acquisition. Twenty four hours after the brain states were induced, rats were trained in a step-down apparatus for a passive avoidance response. Contingent upon step-down, they received a 1 sec. foot shock followed by no ECS, ECS immediately, or ECS 4 hr. later. The animals were tested for the passive avoidance response either 24 or 96 hr. after stepping off the platform. Results showed that when brain excitability states were the same during both the training and recall sessions, ECS did not produce any retention deficits. However, when learning occurred at one state of brain excitability and the animal was then tested for retention of learning in a different state of brain excitability induced by ECS, the animal failed to show retention of the response. Thus, Nielson (1968) reported temporary amnesia when differences existed between the states of brain excitability during learning and recall, but not when learning and recall sessions were conducted at the same levels of brain excitability.

Nielson has received support from DeVitti and Larson (1971) who report a) recovery from amnesia when animals are tested 96 hrs. after treatment, presumably when brain states have returned to normal and b) a failure of animals to recall an extinction procedure carried out when brain excitability was lowered by ECS.
brain excitability states by ECS administration and to test specific predictions of the Nielson's state-dependent hypothesis.
METHOD

Subjects

The Ss were 80 male albino Wistar rats, 175-200 gm. in weight at the start of the experiment.

Apparatus

The apparatus consisted of two identical LeHigh Valley operant chambers, each enclosed in a sound-insulated, ventilated box. Each operant chamber had a grid floor constructed of 1/8 in. steel rods, set apart 7/16 in. on centers. A liquid dipper, which dispersed .01 ml. of a 40% sucrose solution, was attached to an end wall of the chamber. The dipper was activated by a retractable metal lever which required 15 gm. of force to depress.

A separate box made of 1/4 in. Plexiglas was used to administer the non-contingent foot shock. It had a grid floor constructed of 1/4 in. bronze rods, set apart 5/8 in. on centers. All experimenter controlled events were operated by an electronic programming device.

Procedure

Ss were randomly chosen from the LSU colony, housed in individual cages and placed on a food deprivation schedule consisting of 10 gm. Purina chow every 24 hr. Water was available in cages at all times and Ss were fed immediately after each experimental session.

On days 1-4, Ss were handled in groups of three for
approximately five min. each day. On days 5-9, Ss were given magazine training on a VI-30 sec. schedule, and experimental periods consisted of 20 presentations of the dipper. On day 10, all Ss were trained to lever press and were allowed to make 50 reinforced lever presses. On day 11, Ss began acquisition training on a continuous reinforcement schedule using a discrete trial procedure. After each lever press, the lever retracted fully and was inoperative for 2 sec. Each experimental session consisted of 100 lever presses and acquisition continued for five days. Following completion of acquisition on day 15, each animal was given an initial treatment consisting of either ECS only (ECSO) or non-contingent foot shock plus ECS (FS+ECS) and was returned to its home cage. On day 16, for each animal, the first lever press produced either foot shock (FS) or foot shock plus ECS (FS+ECS), the lever retracted and the animal was returned to its home cage. Half of these animals were tested 24 hr. after the second treatment and half were tested 96 hr. after the second treatment. These treatments were combined factorially to yield eight treatment groups. The nomenclature is as follows: the first term (ECSO or FS+ECS) indicates the initial treatment, the second term (FS or FS+ECS) indicates the second treatment and the third term (24 or 96) indicates the time of testing. The groups: ECSO(FS)-24, FS+ECS(FS)-24, ECSO(FS+ECS)-24, FS+ECS(FS+ECS)-24, ECSO(FS)-96, FS+ECS(FS)-96, ECSO(FS+ECS)-96, FS+ECS(FS+ECS)-96. Two additional groups served as controls and received no FS or ECS treatments and were tested either 48 or 120 hr. after completion of acquisition. They were designated C-24 and C-96.
**Design**

The basic design was a completely randomized design with a 2x2x2 factorial arrangement of treatments and two additional control groups. Animals were run in eight replications with each replication consisting of one animal from each experimental cell.
RESULTS

Two dependent measures were recorded, latency to the first lever press and total number of lever presses in a 15 minute extinction session, and a separate analysis was run on each measure. Considering the latency measure first, these results were subjected to an analysis of variance and results showed that the overall control versus treatment comparison was significant beyond the .001 level, indicating that there was an effect due to treatment on latency to lever press. Results further showed that the main effect of the second treatment (FS only versus FS+ECS) was significant beyond the .001 level and the main effect of time of testing (24 versus 96 hr.) was significant beyond the .05 level (Table 1). These results indicate, respectively, that ECS immediately following the FS contingent upon lever pressing significantly reduces the latency to the first lever press and that delaying extinction testing for 96 hours also significantly reduces latency to the first lever press (Fig. 1). No other main effects or interactions reached significance at the .05 level. Both a square root and a log transformation were performed on the latency data and results of these analyses were identical to that of the raw latency scores. Therefore, all discussion of latency data will be in terms of raw latency scores. The mean latency for each group is presented in Table 2.

Considering the measure of total number of lever presses in
### Table 1

**Analysis of Variance: Latency Data**

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<td>21.92***</td>
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<td>C-24 vs. C-96</td>
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*p<.05<br>***p<.001
Fig. 1 Mean latency to first lever press.
<table>
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<th>Mean Latency</th>
<th>Group</th>
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<td>C-24</td>
<td>2.75</td>
<td>C-96</td>
<td>7.37</td>
</tr>
<tr>
<td>ECSO(FS)-24</td>
<td>618.75</td>
<td>ECSO(FS+ECS)-24</td>
<td>81.25</td>
</tr>
<tr>
<td>FS+ECS(FS)-24</td>
<td>613.75</td>
<td>FS+ECS(FS+ECS)-24</td>
<td>115.38</td>
</tr>
<tr>
<td>ECSO(FS)-96</td>
<td>370.38</td>
<td>ECSO(FS+ECS)-96</td>
<td>50.00</td>
</tr>
<tr>
<td>FS+ECS(FS)-96</td>
<td>405.63</td>
<td>FS+ECS(FS+ECS)-96</td>
<td>57.88</td>
</tr>
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</table>
the 15 minute extinction session, results of the analysis again showed both the control versus treatment comparison and the second treatment main effect to be highly significant (p < .001). However, using this measure, the main effect of time of testing did not reach significance at the .05 level (Table 3). No other main effects or interactions were significant at the .05 level (Fig. 2). The means for these groups are presented in Table 4.

A number of planned comparisons, using t tests with the error term based on the residual mean square in the analysis of variance, were made to test specific predictions of the state-dependent hypothesis. Again considering the latency measure first, Group FS+ECS(FS)-96 had significantly longer latencies than did Group FS+ECS(FS+ECS)-96 and Group ECSO(FS)-96 had significantly longer latencies than did Group ECSO(FS+ECS)-96 (p < .01). Further, Group FS+ECS(FS)-24 had significantly longer latencies than did Group FS+ECS(FS+ECS)-24 and Group ECSO(FS)-24 had significantly longer latencies than did Group ECSO(FS+ECS)-24 (p < .01). Finally, Group FS+ECS(FS)-24 had significantly longer latencies than did Group FS+ECS(FS)-96 and Group ECSO(FS)-24 had significantly longer latencies than did Group ECSO(FS)-96 (p < .01).

In considering the total number of lever presses in the 15 minute extinction session, the following comparisons were made: Group FS+ECS(FS+ECS)-24 made significantly more lever presses than did Group FS+ECS(FS)-24 and Group ECSO(FS+ECS)-24 made significantly more lever presses than did Group ECSO(FS)-24 (p < .01). Group ECSO(FS)-96 pressed
### TABLE 3

**ANALYSIS OF VARIANCE: LEVER PRESS DATA**

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Controls vs. Treatment</td>
<td>1</td>
<td>5080.08</td>
<td>11.79***</td>
</tr>
<tr>
<td>C-24 vs. C-96</td>
<td>1</td>
<td>10.56</td>
<td></td>
</tr>
<tr>
<td>Initial Treatment (A)</td>
<td>1</td>
<td>192.52</td>
<td></td>
</tr>
<tr>
<td>Second Treatment (B)</td>
<td>1</td>
<td>9726.89</td>
<td>22.57***</td>
</tr>
<tr>
<td>Time of Testing (C)</td>
<td>1</td>
<td>21.39</td>
<td></td>
</tr>
<tr>
<td>A X B</td>
<td>1</td>
<td>165.77</td>
<td></td>
</tr>
<tr>
<td>A X C</td>
<td>1</td>
<td>213.89</td>
<td></td>
</tr>
<tr>
<td>B X C</td>
<td>1</td>
<td>546.39</td>
<td></td>
</tr>
<tr>
<td>A X B X C</td>
<td>1</td>
<td>0.77</td>
<td></td>
</tr>
<tr>
<td>Residual</td>
<td>70</td>
<td>431.01</td>
<td></td>
</tr>
</tbody>
</table>

***p < .001
Fig. 2 Mean number of lever presses in extinction.
<table>
<thead>
<tr>
<th>Group</th>
<th>Mean Lever Presses</th>
<th>Group</th>
<th>Mean Lever Presses</th>
</tr>
</thead>
<tbody>
<tr>
<td>C-24</td>
<td>49.12</td>
<td>C-96</td>
<td>47.50</td>
</tr>
<tr>
<td>ECSO(FS)-24</td>
<td>14.63</td>
<td>ECSO(FS+ECS)-24</td>
<td>48.13</td>
</tr>
<tr>
<td>FS+ECS(FS)-24</td>
<td>10.50</td>
<td>FS+ECS(FS+ECS)-24</td>
<td>38.00</td>
</tr>
<tr>
<td>ECSO(FS)-96</td>
<td>17.75</td>
<td>ECSO(FS+ECS)-96</td>
<td>40.00</td>
</tr>
<tr>
<td>FS+ECS(FS)-96</td>
<td>21.38</td>
<td>FS+ECS(FS+ECS)-96</td>
<td>36.75</td>
</tr>
</tbody>
</table>
significantly less than did Group ECS0(FS+ECS)-96. However, Groups FS+ECS(FS)-96 and FS+ECS(FS+ECS)-96 did not significantly differ at the .05 level.
DISCUSSION

Examination of the overall analysis of variance for both dependent measures presents no support for Nielson's hypothesis. The highly significant \((p<.01)\) control versus treatment comparison indicates that, overall, treatment did have an effect. The highly significant \((p<.001)\) effect of the second treatment \((\text{FS vs. FS+ECS})\) indicates that ECS immediately following FS attenuates the fear due to FS regardless of initial treatment or time of testing.

The initial treatment of either ECSO or FS+ECS was used in order to determine whether ECSO is able to initiate changes in brain excitability or whether arousal brought about by FS is necessary for the ECS to initiate these changes. The effect of initial treatment was not significant in the analysis of either latency to the first lever press or number of lever presses in the 15 minute extinction session. Thus, the conclusion that there is no differential effect due to the FS preceding ECS is straightforward. Whether or not the change in brain excitability was brought about by both these treatments is somewhat more involved.

If the brain state had been changed, one would have expected no differences between groups receiving FS only \((\text{FSO})\) versus FS+ECS as a second treatment and tested 24 hours later. According to the state-dependent hypothesis, if ECSO or FS+ECS did change brain excitability, then both the fear conditioning \((\text{due to contingent FS})\)
and subsequent testing would have occurred during a similar brain state. It is implicit in the hypothesis that the second ECS would not further alter the brain excitability and is explicit that the brain state would not return to normal for 72-96 hours, thus the contingent FS should be remembered in both groups. Analysis of the latency data, however, did not support this hypothesis in that Group FS+ECS(FS+ECS)-24 yielded a significantly shorter mean latency than did Group FS+ECS(FS)-24 \( (p < .01) \) and likewise, Group ECSO(FS+ECS)-24 exhibited a significantly shorter mean latency than did Group ECSO(FS)-24 \( (p < .01) \). Thus, the fear due to contingent FS was present after FSO, while ECS following FS did attenuate the fear when tested 24 hours later.

These differences were virtually identical when testing was delayed for 96 hours. Groups FS+ECS(FS+ECS)-96 and ECSO(FS+ECS)-96 yielded significantly shorter mean latencies \( (p < .01) \) than did Groups FS+ECS(FS)-96 and ECSO(FS)-96, respectively. In this case, Nielson's hypothesis would predict that the contingent FS, administered during an altered brain state, would no longer be remembered 96 hours later when the brain state returned to normal. That is, the aforementioned differences between groups receiving FS versus FS+ECS as a second treatment should not have occurred.

Consideration of these same eight treatment groups with respect to number of lever presses in the 15 minute extinction session yielded results very similar to that of the latency data. Groups ECSO(FS)-24 and FS+ECS(FS)-24 pressed, on the average, significantly fewer times
than did Groups ECSO(FS+ECS)-24 and FS+ECS(FS+ECS)-24, respectively and Group ECSO(FS)-96 pressed, on the average, significantly fewer times than did Group ECSO(FS+ECS)-96 (p < .05). However, Group FS+ECS(FS)-96 versus Group FS+ECS(FS+ECS)-96 did not reach significance at the .05 level (X's = 21.38 and 36.75, respectively). The evidence of this latter comparison, viewed alone, would seem to support Nielson's contention that as the brain state returns to normal, a response (in this case, the passive avoidance response of not lever pressing) learned during the altered brain state will become unavailable. Two important factors, however, make this interpretation less feasible. The first is that this interpretation receives no support from any previous group comparisons, and in fact, the mean difference between these two groups is nearing significance (p < .07). A second factor to be considered is that the main effect of time of testing was significant in the analysis of latency data (p < .05), but not in the analysis of the lever press data. This indicates that, while the animals in the 24 hour test group waited significantly longer than those in the 96 hour test group to begin to lever press, by the end of the 15 minute extinction session, they had pressed enough times to eliminate any statistical difference between these groups in terms of total number of lever presses. Thus, the possibility of a type II error in this case should be considered.

An obvious implication here is that in this experimental situation the dependent measure of latency to the first lever press is perhaps a more appropriate measure than total number of lever presses. Once an animal makes the first response and is not punished, the
conditioned fear will begin to diminish and will continue to do so with each succeeding lever press. Thus, it seems logical to assume that, if one is attempting to measure how well an animal remembers a single fear conditioning trial, the latency to the first lever press will give a more valid indication of the strength of the fear than will total number of lever presses.

The fact that groups receiving treatments of either ECSO(FS)-96 or FS+ECS(FS)-96 had significantly (p < .05) shorter latencies than the same respective treatment groups tested 24 hours after treatment could be construed as indicating that the contingent FS was forgotten as brain states returned to normal 96 hours post treatment. This interpretation is rendered unlikely, however, when Groups ECSO(FS)-96 and FS+ECS(FS)-96 are compared to Groups ECSO(FS+ECS)-96 and FS+ECS(FS+ECS)-96 respectively, and, as was shown above, the former groups have significantly longer latencies, indicating a still strong fear response. Thus, the most logical interpretation of the significant time of testing main effect is a simple lessening over time of the fear due to contingent FS.

Overall the hypothesis that ECS administration lowers the level of brain excitability was not confirmed and these data may be interpreted as supporting the view that ECS disrupts a memory consolidation process. It should be mentioned, however, that groups receiving FS+ECS as a second treatment showed much longer, though not significantly different, latencies to the first lever press than did their respective control groups (X's = 98.3 vs. 2.75 for 24 hr. test and
53.94 vs. 7.37 for 96 hr. test, averaged across initial treatments). Thus, it may be that there is some residual memory of the FS present after ECS. This was also mentioned by Luttges and McGaugh (1967) in a study interpreted as supporting consolidation theory. The possibility of some residual memory following ECS presents difficulty for a consolidation viewpoint and strengthens the position of alternative explanations of ECS postulating an interference with a retrieval mechanism rather than a disruption of a memory consolidation process.

In conclusion, the idea that ECS alters brain excitability states and that this temporary change in brain states may account for behavioral evidence of RA, is not supported by these data. Further, the most parsimonious explanation of these results is that ECS disrupts some as yet unknown neural process necessary for the retention and/or retrieval of memory and thus would best fit into a consolidation framework.
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Major Field: PSYCHOLOGY

Title of Thesis: A TEST OF THE STATE-DEPENDENT HYPOTHESIS OF ECS EFFECTS

Approved:

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Major Professor and Chairman

Max Goodrich
Dean of the Graduate School

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Preston J. Schilling

Date of Examination:

APRIL 23, 1973