THE EFFECT OF ELECTROCONVULSIVE SHOCK ON MEMORY

by

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INTRODUCTION

This review of the literature on the effects of electroconvulsive shock (ECS) on memory will first attend briefly to three originally distinct lines of development which occasionally overlap, and eventually converge in the first publication (Cerletti and Bini, 1938) concerning the use of ECS with human subjects. It will then go on to deal with the literature on ECS and will pay special attention to the effect of ECS on memory when it is interpolated between learning and a retention test.

Use of ECS for the study of memory and retention seems to be the result of three quite separate lines of thinking. Two of these are somewhat less important now: the idea, which has lasted for several centuries, that shock or stress of any kind is useful in treatment of mental illness; and a long-standing biological interest in the effects of electricity on the animal body. The third line, much more recent in origin and also more germane to our present concerns, involves the fusion of ideas about retrograde amnesia and retroactive inhibition in the theory of the consolidation period in learning.

First, historically speaking, is the use of stress, of assorted types, in the treatment of mental disorders. This goes back at least to medieval times when "water treatments" and "gentle torture" were reported to be of therapeutic value (Stainbrook, 1946). One of the first to stress his patients by inducing convulsions was Sakel who wrote of the use of insulin convulsions for therapeutic purposes in 1928.

The second line of development, studies of the effects of electricity on organisms, began shortly after discovery of the Leyden jar. Lovett, in 1756, observed that electricity was of some value in treating mental disorders. Lovett did not report that convulsions occurred and presumably the therapeutic value of electricity was in the stress category discussed above. In 1900 Leduc produced what he called "electric sleep" by passing current through the body of a dog. Robinovitch, in 1906, observed epileptiform convulsions in a dog resulting from direct electrical stimulation of the brain. Weiss (1911) confirmed Robinovitch's findings, and Vaile (1929) was able to produce convulsions in dogs having one electrode in the mouth and one in the anus. Cerletti and Bini (1938) published the first observations of the controlled use of electrically induced convulsions in man.

The third general line of development involves the "consolidation hypothesis" that has been proposed to account for the memory trace. It has two aspects which are united by their involvement with an idea of long standing concerning the importance of neural activity, following an experience, for the memory of that experience. One aspect is found in the theory of retroactive inhibition, the other in the phenomenon of post-traumatic amnesia.

The two phases were related in 1901 by McDougall who discussed evidence indicating that certain events could interfere with memory of previous experiences. He connected a report by Ribot (1892), on amnesia due to head injury, with the suggestion by Müller and Pilzecker (1900) that neural activity must continue for some period of time in order for memory of an event to be established firmly (this is the perseveration or consolidation hypothesis). To account for the fact that new learning could reduce retention of old learning they suggested that the new learning was interrupting the perseveration necessary for retention of the old learning and thereby producing retroactive inhibition. Müller and Pilzecker's findings led McDougall to say that "this demonstration of the 'rückwerkende Hemmung' (retroactive inhibition) throws light upon, we might also say explains, certain recorded cases in which a severe blow on the head has wiped out completely the memory of immediately preceding events" (McDougall, 1901, p. 392-393).

In 1904 Burnham published a detailed discussion of the same problem, based on his account of two cases of retrograde amnesia, Ribot's report, and the hypothesis of Müller and Pilzecker. Burnham proposed that perseverative activity is essential to produce a permanent impression on the nerve cells as well as to bring about association and organization of the new information with old impressions. He concluded that the degree of retrograde amnesia varies with the length of the period between learning and the interruption of the perseverating activity; that the time required for fixation of memory would vary from individual to individual, and vary with the conditions in which it occurred; and that retrograde amnesia could be produced by factors such as intense emotion, narcotics, fatigue, and unconsciousness.

In 1915 DeCamp used Sherrington's (1906) work on after-discharge in spinal reflexes as the physiological basis for elaboration of the perseveration hypothesis. DeCamp suggested that the blockage of after-discharge by subsequent stimulation could be the neural mechanism of retroactive inhibition and retrograde amnesia.

The advent in 1938 of electroconvulsive shock therapy made available a new kind of experimental evidence pertinent to these problems. Since then the two original sources of data, retrograde amnesia resulting from head injury, and retroactive inhibition, have been much less important in discussions of the perseveration hypothesis.

One of the results of application of ECS after completion of learning is some loss of retention, the greatest loss being obtained when ECS follows immediately on the completion of learning. The extent and causes of this loss of retention have been the subject of extensive research and vigorous debate.

Zubin and Barrera (1941) were the first to attempt to quantify the effects of ECS on retention. Their subjects were patients suffering from depression, etc., who were to be treated with electro-convulsive therapy (ECT, a synonym for ECS). They taught the patients paired-associates lists composed of names of commodities paired with nonsense "brand" names. The learning was followed by ECS. Savings and recall methods showed a nearly complete loss of retention, while the recognition method showed much less loss than would be expected with respect to the other measures. Zubin (1942) felt that the discrepancy between the results with the relearning and recall methods and the recognition method might be a key to the dynamics of the effects of ECS on retention.

Subsequent work (Zubin, 1942; Kehlet and Lunn, 1951a, b; Galineck, 1956) has corroborated the finding that recognition measures show better retention than the recall and relearning scores would indicate. Thus it seems, with respect to ECS, that memory of simple stimulus objects or situations may be of a somewhat different nature, or level, than memory of stimulus relations or contingencies. (The difference is hard to define since psychological theorizing has produced no explanation of perception of familiarity, as distinguished from recall or reproduction in absence of the pertinent stimulus event, which can adequately deal with the results of this type of study.)

Other workers have reported loss of retention in man resulting from ECS (Williams, 1950; Lowenbach and Stainbrook, 1942; Zubin, 1942), and some (Carson, 1957; Russell, 1949; Zubin, 1941; Thompson, 1958) have noticed that simple motor, or verbal-motor, habits are not disrupted to the extent of more complex habits, even when the learning-ECS interval is very short. This result also gives support to the idea that there may be different levels or types of memories with respect to ECS effects. It also provides good reason for noting the type of learning situation involved in each of the studies being discussed.

Duncan (1945), using rats as subjects, introduced a control group which received through the hind legs the same current that was passed from ear to ear (producing grand mal convulsions) in the experimental group. There is an interesting difference, after the first shock experience, in the behavior of hind-leg and ear-to-ear or ECS groups when they are being prepared for subsequent shocks. Coons and Miller (1960), and others, report that ECS animals cringe, urinate, defecate and are "fearfully passive"; hind-leg or peripherally-shocked animals, on the other hand, are very active in their attempts to resist or escape. It can be said that in both groups there is some retention of the effects of previous shock experiences and that the quality of the effects retained may be quite different.

In Duncan's experiments the animals that were shocked through the hind legs, and hence were not convulsed, still retained less than unshocked control animals, though the difference was not significant. However, subsequent work (Duncan, 1949), with varying intervals between learning and shock, has shown that with the shortest intervals there is significant loss of retention in the peripherally-shocked group. The shocks were apparently administered outside the learning apparatus, but the very short intervals may produce complications from an interaction of the memory of the experimental apparatus with memory of the shock situation. The close association of the experimental apparatus with the unpleasant shock may give rise to behavior which decreases the accuracy of performance on a retention test.

The problems of the effects of ECS on memory raised by this body of work can be summarized under three general headings. First, there is a larger difference than would be expected between savings and recognition scores. Second, there is a difference in the detrimental effects on habits of different types. Finally, there is a difference in anticipatory behavior with respect to ECS as opposed to non-convulsive shocks of the same intensity. In light of these results recent studies by Adams and Lewis (1962a, b), Miller and Coons (1955) and Coons and Miller (1960) can be compared with a study by Thompson and Dean (1955).

It was noted above that animals show unmistakable signs (urinating, defecating, crouching, etc.) of remembering and being afraid of ECS and here we have a kind of situational recognition similar to Zubin's. In the experiments of Adams and Lewis rats were given ECS in a simple avoidance-response apparatus, and in the experiments of Miller and Coons rats were given ECS in the goal area of a runway. In both experiments the animals may have remembered the situation and that ECS was administered there. Support for this notion comes from Hayes (1948), who reports that rats given ECS in the goal box of a maze were emotional in the maze and avoided the goal box. Subjects may therefore be frozen by the fear of the situation and performance suffers. These observations would explain the superior retention or performance of the avoidance response by a control group which received ECS in a place other than the avoidance apparatus, as was shown by Adams and Lewis.

In the study by Thompson and Dean, rats learned a pattern-discrimination habit in an electrified Y maze. ECS was administered outside of the apparatus at varying intervals after attainment of criterion in a massed-trial session. The result was that the shorter the learning-ECS interval the greater the loss of retention (using the savings method), with the intervals varying from 15 sec. to one hour. Here, with use of a relearning measure, where recognition of the ECS situation does not contribute as immediately to behavior in the apparatus as such, we have a result analogous to the low relearning and recall scores made by human subjects (Zubin).

Attempts have been made (Adams and Lewis, 1962a, b) to attribute all retention loss resulting from ECS to the fear of ECS. However, as we shall see, the weight of evidence is against such an interpretation. In any event, there is still much confusion involving the level of complexity of habits and the place, relative to the learning apparatus, at which ECS is administered.

Duncan's experiment (1949), involving systematic variation of the learning-ECS interval, was an important step in studying effects of ECS on retention. Duncan used an electrified shuttle-box situation with one learning trial per day and with ECS following each trial at intervals varying from 20 sec. to 14 hours. It has already been said that Thompson and Dean (1955) taught rats a pattern discrimination with massed trials and administered one ECS at varying intervals following attainment of criterion. These two experiments provided quantitative data to establish the fact, previously guessed at by other workers, that the loss of retention is a negatively accelerated function of the interval between learning and ECS. The shortest interval at which there was no significant loss seemed to be somewhere between 45 min. and 90 min. However, Adams and Lewis (1962a, b) used procedures which maximized the effects of memory of the situation and demonstrated that ECS may produce loss of retention or decrement in performance after much greater intervals.

PHYSICAL EFFECTS OF ECS

Attempts to understand the effects of ECS on memory are complicated by the physical changes which are brought about by this treatment. Some of these physical changes have not been considered in discussions of the effects of ECS on memory, and it is possible that some of the memory changes are caused by them.

This becomes an important point when one attempts to relate experiments using a single ECS to ones using a series of ECSs. Worchel and Gentry (1950) demonstrated that a series of six ECS treatments had greater detrimental effect on retention than a series of three. Other workers have noted physical changes which increase during the first few treatments and level off or decrease with later treatments (Callaway, 1950; Braun and Patton, 1950). Some effects occur in opposite directions with different species; for example, body weight increases with human subjects (Stainbrook, 1946) and decreases with rats (Braun and Patton, 1950).

Rosvold (1949) reported that ECS produces histological changes in the pituitary gland of pregnant rats. Such changes may be involved in the emotional effects mentioned by many workers (Williams, 1961) and it is also reasonable to believe that these changes may have a profound affect on memory.

Madow (1956) discussed the brain changes which result from ECS. The most frequent symptom was hemorrhage and Madow indicated that other changes such as glial and ganglion-cell reactions are secondary to the vascular changes. It was also indicated that there may be reason to regard these changes as reversible.

Alexander and Lowenbach (1944) proposed the notion that vascular changes occur in the path of the current and suggested that brain-stem hemorrhages in animals are only found with low electrode placement. However, Madow (1956) reported brain-stem hemorrhages in human patients with electrodes placed over the lateral aspects of the cerebral hemispheres and said that rather than being due to electrode placement, the brain-stem vascular changes may be due to acute edema resulting in back pressure on the small blood vessels in the brain stem.

Hartellius (1952) performed a carefully controlled study to determine the physical effects of ECS on cats. He reported that it was possible to differentiate slides of nervous tissue taken from brains of treated cats from those of non-treated cats.

It is not difficult to imagine that one of these physical effects may be involved in the memory changes produced by ECS. It is possible that this physical effect may be quite different from the mechanism proposed by some (Glickman, 1961) which involves interruption of a reverberating system necessary for permanently fixing information in memory. It is also possible that the physical changes discussed above are the events which interrupt consolidation, rather than the direct passage of current as such.

The possibility that these changes are reversible may aid in explaining data obtained by Brady (1951) showing that a conditioned emotional response which had been obliterated by ECS would reappear and increase in strength over time.

A study by Thompson, Haravey, Pennington, Smith, Gannon, and Stockwell (1958) examined the relation of retention changes in young and adult rats to some of the physical effects of ECS. The fact that young rats and ones with brain lesions showed greater loss of retention than normal adult rats was interpreted by the authors as support for the proposal that ECS produces greater loss of retention when there are fewer neural units capable of normal adult activity. An extension of this idea may aid in explaining the increasing effect of an ECS series, in that there may be a certain number of neural units temporarily immobilized by each ECS. Each temporary immobilization may tend to reverse or negate the most recent changes initiated in the units involved. The subsequent spontaneous activity of these units might be grossly different now that they are no longer participating in the recording of recently gathered information. The change of activity in these units may change the response, or resistance, of the nervous system to a subsequent ECS so that neural units not previously affected become immobilized.

SIMILAR EFFECTS ON MEMORY PRODUCED BY OTHER PROCEDURES

There are many events, other than ECS and a blow on the head, which will cause memory loss. First, temperature changes.

Refrigeration (causing body temperature to drop below 33.3°C) of human subjects was shown by Fay (1940) to produce loss of memory for the period of refrigeration even though subjects were conversing during this period. Cerf and Otis (1957) did a study, with fish as subjects and using heat narcosis as the interpolated event, which in design and results closely paralleled the work done by Duncan in 1949 using ECS. Thus temperature changes in both directions appear to affect retention in much the same manner as ECS. It is obvious that in drawing a parallel of this type one is talking of behavioral similarities which may be produced by very different physiological conditions. The evidence pertaining to temperature change and retention is not easy to fit together, but at present an electrochemical or metabolic arrest or disruption, due to effects of temperature change on chemical processes, appears to be a reasonable guess as to the basis of the reported loss of retention. Some support for this notion comes from Adrian and Buytendijk (1931) who showed that during heat narcosis in fish there is a reversible blocking of spontaneous electrical activity in the vagal lobe. Such an electrochemical change may also be the basis of the effect of ECS on retention.

Pressure Change and Anoxia

ECS is known to produce a state of cerebral hypoxia, and the contribution of hypoxia produced by ECS to loss of retention has been examined by Thompson, Haravey, Pennington, Smith, Gannon and Stockwell (1958). This study indicates that the loss of retention produced by ECS cannot be attributed to hypoxia as such. However, other studies indicate that anoxia alone can produce loss of retention of the same order of magnitude as that found with ECS (Hayes, 1953; Ransmeier and Gerard, 1954).

Atmospheric pressure changes have also been found to produce loss of retention, but isolating the physiological variables in these studies is quite difficult. Change in one variable is accompanied by complex changes in other variables; for example, pressure changes mechanically alter aspects of cellular states, thus directly influencing metabolic processes; furthermore, pressure changes, without forced oxygen supply, alter the availability of oxygen and therefore influence metabolic processes in another manner. Although the results are interesting, such complications make these experiments difficult to interpret.

Thompson (1957a) found a graded loss of retention which was more severe with a simulated altitude of 30,000 feet than one of 20,000 feet. On the other hand, loss of retention after ECS does not vary with the strength of the current used to induce convulsions; it seems that the significant variable is whether a convulsion has occurred or not. However, Thompson found that when ECS and simulated 30,000 foot altitude were both administered after a learning session the retention loss was the same as that resulting from either event alone. This probably does not cast much light on the question of the effects of the general convulsive state, but seems to indicate that the failure to get graded results with variations in electrical stimulus may be due to some basic differences in the physiological causes of the loss of retention.

Sensory Input

Another interpolated procedure was investigated by Thompson and Bryant (1955) and Thompson (1957b) who have shown that visual stimulation immediately after visual-discrimination learning results in a lowering of retention score. This result can be observed from several points of view: for example, the interpolated visual stimulation may be considered analogous to interpolated learning in the retroactive inhibition paradigm. On the other hand the stimulation could be considered analogous to the ECS stimulus in producing a change in neural activity which interrupts, or disturbs, the consolidation process. However one looks at these results it is important to remember that interpolated visual stimulation creates electrical and chemical changes in areas responsible for receiving and recording the original visual information. Thus the specific locus of the action of the interpolated input may enable it to act through electrochemical disruption, as ECS may act on a more gross or general level.

Intracranial Electrical Stimulation

It appears that intracranial electrical stimulation of specific structures can produce much the same effect on memory as that produced by ECS. Some experimenters have used the disrupting effect of intracranial stimulation as support for the consolidation hypothesis; however, Glickman (1961) showed that alternative explanations are possible for these effects. A study by Goddard (1963), on the other hand, has pinpointed the disrupting effect of electrical stimulation in time, structure and situation to such an extent that a more clear picture emerges. In this study, low-intensity non-rewarding stimulation to the amygdala, after presentation of the unconditioned stimulus in various kinds of avoidance situations, increased the number of trials taken to learn. No such effect was found when stimulation was delivered prior to the unconditioned stimulus. Furthermore, the effect was not found in learning situations other than the avoidance type. These results make the suggestion of differing effects with various loci and types of habit seem still more reasonable. This also suggests that the fact that the loss of memory for most habits caused by ECS may be due to its effect being widespread enough to disrupt activity in the specific structures which are important for the retention of the habit in question.

Chemical Stimulation

The techniques of electrical stimulation are complemented by recently developed methods of delivering chemicals to specific parts of the nervous system. The use of these techniques may permit a much more exact understanding of the dynamics of retention than would have been possible using ECS alone.

Effects of systemic chemical intervention were demonstrated by Leukel (1957) who injected rats with sodium pentothal one minute, or thirty minutes, after completion of each trial in a maze. Results showed impairment of learning when the injection was one minute after completion of the learning trial. There was no difference between the 30-minute group and the control groups.

Experiments involving some localization of chemical activity are based on techniques developed by Leão (1944), Fisher (1956), and Olds and Olds (1958). Bureš and Burešová (1963), using Leão's technique produced cortical spreading depression, in rats, by directly stimulating the cortex with 25 per cent KCl after attainment of criterion in reversal of a left-right discrimination. Results were compared with similar groups treated with ECS instead of KCl and it was found that both methods produce a significant loss of retention, and that the loss produced by ECS was greater. These results were discussed in terms of the possibility that the cortical component of memory is disturbed by spreading depression and that the difference in retention loss between spreading depression and ECS reflects the degree of participation in memory formation of subcortical structures.

Bureš and Burešová also ran a group which was etherized one minute after learning a one-trial avoidance response. No loss of retention was found. This was discussed in relation to contradictory findings by Pearlman, Sharpless and Jarvik (1961) using a different avoidance situation. Bureš and Burešová's suggested explanation was that the consolidation process may take place at different rates with different types of habits.

Bureš (1959) has also reported that the effect of spreading depression in the hippocampus on retention of a simple conditional avoidance response is greater than that produced by cortical spreading depression.

Flexner, Flexner and Stellar (1963), using mice as subjects, reported that intracerebral injections of puromycin would produce a loss of retention for spatial habits, if the habits were 24 hours to 3 days old when bilateral temporal injections were used (hippocampal zone or entorhinal cortex of caudal rhinal fissure area). They reported also that longer-term memory (11 to 43 days) could be disturbed by combined bilateral temporal, ventricular, and frontal injections of puromycin. These results indicate that there may be a change in the locus of neural units involved in memory as a function of increasing time.

THE PRESENT INVESTIGATION

Thus we begin to get a picture of the possibilities for specific analysis of the process of action of ECS on memory. It seems that we may be dealing with an event capable of disturbing activity in widely separated structures, many of which are involved in the process of recording information. These structures may be of differing relative importance with different types of habits, and the vulnerability of the process to disrupting influences may last longer for some habits than for others.

In view of the fact that loss of retention is produced by ECS and other events interpolated between learning and test, it seems that memory is made permanent by a process which continues after the pertinent stimulus event has occurred. There is, at present, no reliable way of predicting the time course of this process or of indicating the structures involved in various kinds of habits. It may be that the best way to proceed would be to use ECS as an indicator of the time course of consolidation in order to determine the similarities and differences among habits in this respect.

Although it is not within the scope of the present study, relating of the magnitude of loss of retention found with ECS to that found with treatments having a more localized effect may indicate the degree of involvement of specific structures in the process of information recording for the particular habit in question. ECS also may be seen as reflecting the span of susceptibility of specific structures to the disrupting influence of the focused electrical or chemical intervention.

Work along the suggested lines should result in groupings of habits which could be related to specific neural structures and consolidation times. If systematization of this type occurs it will be of great help in understanding the neural basis of learning and memory.

The present experiments are an attempt to further the grouping of habits with respect to their susceptibility to disruption by ECS.

Three separate experiments comprise this investigation and show that the effects of ECS on retention are more complicated than previously believed. These experiments examine the effects of ECS on retention of spatial, brightness and pattern discriminations as such, and as influenced by variations in training schedules.

The presentation is organized as follows: The first section is a description of the method common to all of the experiments; the second section is subdivided into descriptions of the methods and results and discussions for each of the three experiments. These discussions are attempts at relating the three experiments to each other and to previous theories and data; the third section is an attempt to describe the problems raised by this work and suggest a course for future work.

GENERAL METHOD

Hooded rats from the Royal Victoria rat colony, weighing between 200 and 225 grams, were used as subjects. The rats were housed individually with a constant supply of food and water. They were handled in four 2-min. sessions, at 24 hour intervals, prior to the start of formal training.

The learning apparatus employed throughout was a two-choice discrimination box utilizing the motive of shock-escape or avoidance. The box used (see Fig. 1) was a modification of that described by Thompson and Bryant (1955). Illumination was provided by a 100-watt bulb over the choice point and a 75-watt bulb above area 1.

The apparatus for administering ECS included a timer permitting accurate control of current duration. ECS of 50 milliamps was administered for a 0.5 sec. duration by means of alligator-type ear clips. ECS was administered outside of the experimental apparatus. Ear clips were applied to animals in the control groups, but no current was passed.

The general training procedure used throughout is as follows: The subject was placed in area 1 (Fig. 1), facing away from the goal, and was given a brief shock if he did not leave area 1 within 5 sec. If the subject had not passed into the goal area within 30 sec. after having been placed in the apparatus, he was given brief shocks at 5-sec. intervals until he reached the goal area. The grid in front of the negative door remained charged for the duration of each trial. There was a 45-sec. inter-trial interval and the interval between the last trial and ECS averaged 30 sec. (with a range from 20 to 50 sec.).

In the discrimination-learning situations the stimulus cards were alternated in a pre-arranged random order. Gellerman series 15 and 30 were the orders used (Gellerman, 1933).

The Mann-Whitney U test was used throughout in the tests of significance. The number of responses correct in the first 10 relearning trials is used as the primary measure of memory and tables are presented expressing the mean and median of this measure and the total number of trials to learn and relearn for each experiment. Other measures of retention were taken and all followed the same pattern as the number correct in the first 10 relearning trials.

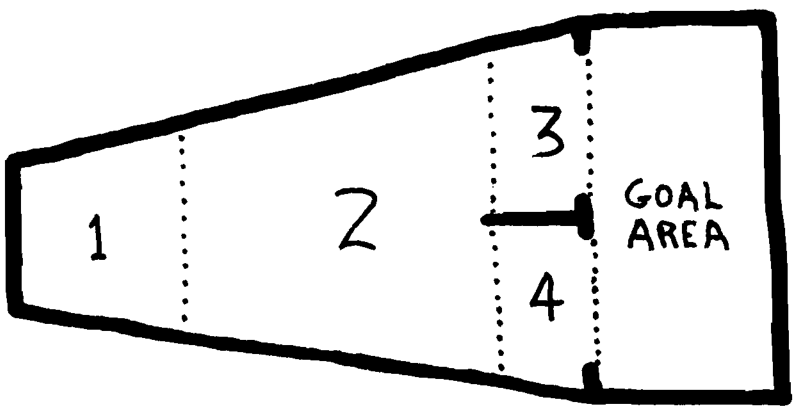

Fig. 1. Floor plan of the apparatus used. The areas shown were separately controlled electrified grids. Area 1 and 2 were electrified at about 1 milliamp, 3 and 4 at about $\frac{1}{2}$ milliamp.

EXPERIMENT I: SPATIAL AND BRIGHTNESS DISCRIMINATION

Experiment I was concerned with the effect of ECS on the retention of a simple spatial discrimination, and a brightness discrimination. Two groups of rats were used, each being trained in a single habit (unlike Experiments II and III, in which the effect of learning more than one habit was studied).

Spatial Discrimination: on day 1, 25 naive subjects were trained to go 9 out of 10 times through the nonpreferred door of the apparatus. This learning, including criterion trials, took from 9 to 14 trials. Thirty seconds after completion of the last trial ECS was administered to the 17 experimental animals. Eight animals were used as controls, not being given ECS. On day 2 the subjects were placed in the apparatus with both doors unlocked; each was given 10 trials.

The results are presented in Tables 1 and 2. For the spatial discrimination, there was no significant difference between the experimental and control groups. Both groups averaged more than 9 out of 10 responses on the first 10 trials to the door which was positive on day 1. Since both doors were unlocked and neither grid was electrified, this measure of preference was seen as indicating retention of the original learning.

Brightness Discrimination: on day 1 (pretraining) 18 naive subjects, 14 experimental and 4 control, were taught to run through either of the doors to the goal area. When they had made three consecutive runs, taking 30 sec. or less per run, a barrier was put in front of the door last chosen and the grid in front of this door was electrified. Pretraining was concluded when a subject made one errorless run to the unblocked door. The maximum number of runs taken for any subject to complete this phase was 11.

On day 2 subjects were taught to run through the door bearing one member of a black and white stimulus pair and to avoid the other. Training was to a criterion of 9 out of 10. This learning, including criterion trials, took from 25 to 89 trials. Thirty seconds after completion of the last trial ECS was administered. The 4 control animals received no ECS.

On day 3 all subjects were retrained on the original discrimination to a criterion of 9 out of 10 correct runs. All subjects were given at least 20 relearning trials. Relearning, including criterion trials, took from 16 to 41 trials for the experimental animals. The control animals showed no loss of retention.

In the brightness discrimination, there was a significant difference ($P = .001$) between experimental and control groups. Rats in the experimental group performed at chance level during the first 10 trials.

<u>Discussion</u>: A comparison of the retention scores of the experimental groups in the two phases of this experiment reveals a significant difference ($P = .001$), indicating that ECS disrupts a recently learned brightness discrimination and does not affect a recently learned spatial discrimination. The difference between the experimental groups in the two phases can be taken as indicating a real difference in the habits involved. The generality of this effect is evidenced by consideration of this experiment in relation to work by Thompson (1958), which involved extensive pretraining and a different criterion of learning, but produced similar results.

The failure of ECS to cause significant loss of retention of the spatial habit seems contradictory to previously published results (for example,

Table 1

Mean and Median Number of Original and Relearning Trials, Including Criterion Trials, For Experiment I

Subgroup	Experimental				Control			
	Original Learning		Relearning		Original Learning		Relearning	
	Mean	Median	Mean	Median	Mean	Median	Mean	Median
Single Spatial Discrimination (Experimental N=17; Control N=8)	10.59	10	9.24	9	9.75	10	9.25	9
Single Brightness Discrimination (Experimental N=14; Control N=4)	50.93	49.5	25.86	25	47.5	42	10.25	10

Table 2

Mean and Median Number Correct on the First Ten Relearning

Trials for Experiment I

Subgroup	Experimental		Control	
	Mean	Median	Mean	Median
Single Spatial Discrimination (Experimental N = 17; Control N = 8)	9.82	10	9.75	10
Single Brightness Discrimination (Experimental N = 14; Control N = 4)	5.78	6	8.75	9

Braun and Patton, 1950), but is really not so. Evidence that ECS produces loss of memory for spatial habits has been obtained only in situations of the following types: (a) when the whole learning situation was concentrated in one day and a series of shocks was used to produce the decremental effects; (b) when one or a few trials was given per day and shock was administered after each session; (c) when the problem being learned was of the "one trial" type; (d) when the reversal situation was employed and the original habit was over-learned relative to the reversal; (e) when the spatial habit is considerably more involved than the T maze habit. There is, consequently, no conflict between results of earlier experiments and those of the present study. In interpreting the fact that ECS failed, in this experiment, to interfere with retention of a spatial habit but did interfere with a brightness discrimination habit, it is important to remember that the learning in these situations was carried out in the same apparatus and to the same criterion, so that the only difference is in the nature of the habits involved. Thus, these results can be seen as reflecting a real difference in the effects of ECS on the habits involved here.

A difference in susceptibility of different habits to the disrupting effects of ECS was demonstrated by Carson (1957) who showed that a wheel-turning response established on the basis of learned fear was not susceptible to the effect of ECS, while the learned-fear response,of running from one compartment to another after the wheel turning had opened the obstructing door,was obliterated by it. This difference in susceptibility may, as previously suggested, indicate a basic difference in neural basis of learning and retention of various habits. It also bears upon the suggestion that there may be a memory for stimulus situations which is resistant to effects of ECS and memory for stimulus relationships or contingencies which is more susceptible to disruption by ECS. In the present experiment learned fear of the grids in the apparatus was obviously retained and demonstrated by most subjects during the first post-ECS relearning trial. The contrary results of Carson's work were obtained when the first ECS of a series of 20 was given 24 hrs. after the last run in the apparatus, while in the present experiment the interval, from the subjects' first chance to become afraid of the grids to ECS, is between 24 and 26 hrs. In other words, the time for consolidation of the fear experience in the present experiment is comparable to that in Carson's experiment, but the fear is retained. However, we are again confronted with the mysteries of the difference between a single ECS and a series of ECSs.

Considering the procedure differences here and the results of experiments with time relationships similar to those of the present work (Miller and Coons, 1955; Adams and Lewis, 1962a, b; Duncan, 1949) the following hypothesis is proposed: memories for spatial learning and for single stimulus objects or situations are more rapidly made immune to the effects of a single ECS than is memory for variations in responses based on stimulus relations or contingencies. This may be related to differences in time taken to learn, neural structures involved, amount of information gathered on each trial, number of possible presolution hypotheses, or to a variety of other variables. This hypothesis, as stated, is supported to a considerable extent, and bears upon the previously discussed results of Adams and Lewis (1962a, b) and Miller and Coons (1955).

EXPERIMENT II: SPATIAL AND BRIGHTNESS DISCRIMINATION REVERSALS

Experiment II was concerned with the effect of ECS on retention of the reversals of spatial and brightness discriminations.

Spatial Discrimination Reversal: on day 1, 10 naive rats were trained to go 9 out of 10 times through one door of the apparatus. The learning, including criterion trials, took from 9 to 11 trials. On day 2 the rats were trained to go 9 out of 10 times through the opposite door; learning, including criterion trials, took from 11 to 14 trials. Thirty seconds after completion of the last trial on day 2 ECS was administered to the 7 animals in the experimental group. Three animals were used as controls. On day 3 both groups were placed in the apparatus with both doors unlocked; each subject was given 10 trials. The results are presented in Tables 3 and 4. There was no significant difference between the experimental and control groups in retention of the spatial reversal.

Brightness Discrimination Reversal: on day 1, 10 naive rats were pretrained in the same manner as the animals learning the brightness discrimination in Experiment I. On day 2 the rats were taught to run through the door bearing one member of a black-and-white stimulus pair and to avoid the other. Training was to a criterion of 9 out of 10. This learning, including criterion trials, took from 30 to 107 trials. On day 3 the rats were taught to run to the opposite member of the pair (i.e., to the card which was on the locked door on day 2). The criterion again was 9 out of 10. This learning, including criterion trials, took from 49 to 115 trials. Thirty seconds after completion of the last trial ECS was administered to the 7 animals in the experimental group. Three animals were used as controls.

On day 4, the rats relearned the day 3 response; each subject was given at least 20 trials. Experimental animals took from 12 to 27 trials to relearn, including criterion trials. The control group met criterion at once, with no evidence of loss of the habit.

There was a significant difference (P = .001) between the experimental and control groups in the retention of the brightness discrimination reversal. The experimental group performed at chance level during the first 10 trials while the control group showed 100 per cent saving of the second, or reversal, habit learned on day 3.

Discussion: Comparison of the experimental groups in the two phases of this experiment reveals a significant difference (P = .001) between brightness and spatial retention. This experiment supports the results of Experiment I in that brightness learning in this situation is susceptible to the effects of ECS while spatial learning is not.

The learning of the reversal of a previously learned spatial discrimination has been shown by other workers to be susceptible to the disrupting effects of ECS (Bureš and Burešová, 1963; Braun and Patton, 1950; Duncan, 1948). However, these earlier results were only obtained when the original habit was over-learned and the reversal was not (Duncan, 1948; Bureš and Burešová, 1963) or when changes were introduced which make the interpolated (or reversal) situation more difficult (Braun and Patton, 1950). Braun and Patton (1950) reported no retention loss, produced by ECS in a swimming maze reversal, when the original and reversal learning were taken to the same criterion and were of equal difficulty.

Table 3

Mean and Median Number of Trials for Original Learning, Reversal Learning, and Relearning of the Reversal, Including Criterion Trials, for Experiment II

Subgroup	Experimental						Control					
	Original Learning		Reversal Learning		Reversal Relearning		Original Learning		Reversal Learning		Reversal Relearning	
	Mean	Median	Mean	Median	Mean	Median	Mean	Median	Mean	Median	Mean	Median
Spatial Discrimination Reversal (Experimental N=7; Control N=3)	9.71	10	12.0	12	9.28	9	10.33	10	13.0	13	9.33	9
Brightness Discrimination Reversal (Experimental N=7; Control N=3)	45.57	33	77.33	78	19.57	21	43.33	44	77.33	70	9.33	9

Table 4

Mean and Median Number Correct on the First Ten Relearning Trials for Experiment II

Subgroup	Experimental		Control	
	Mean	Median	Mean	Median
Spatial Discrimination Reversal (Experimental N = 7; Control N = 3)	9.71	10	9.67	10
Brightness Discrimination Reversal (Experimental N = 7; Control N = 3)	6.43	7	9.67	10

The present comparison of the effects of ECS on spatial and brightness discrimination reversal in the same apparatus, with the same criterion and with the original and reversal situations of equal difficulty is further support for the previously suggested hypothesis, that memories for spatial learning and for single stimulus objects or situations are more rapidly made immune to the effects of a single ECS than is memory for variations in responses based on stimulus relations or contingencies.

EXPERIMENT III: DISCRIMINATION LEARNING FOLLOWING PRETRAINING ON A DIFFERENT DISCRIMINATION

Experiment III was concerned with the effect of ECS on retention of brightness or pattern discrimination when training on one of these two forms of discrimination was preceded by pretraining on the other. In Experiment II ECS produced a loss of retention of a brightness habit when the pretraining was on another brightness habit (i.e., reversal training); now the pretraining was on a different kind of habit. Experiment III also examined the effect of ECS on the retention of a pattern discrimination following pretraining on a brightness discrimination.

Brightness Discrimination Learning Following Spaced Pattern Discrimination Pretraining: on day 1, 11 naive rats (7 experimental, 4 control) were pretrained in the same manner as the animals learning the brightness discrimination in Experiment I.

On days 2, 3, and 4, the rats were given 25 pretraining trials per day on the discrimination of horizontal from vertical stripes. For the first

20 trials on day 1 the positive door was left 1 to 2 inches ajar. Thus at the end of day 4 the rats had a total of 75 trials on the discrimination problem, 55 of them with the doors closed.

On day 5, the rats were trained on a brightness discrimination. Performance was taken to a criterion of 9 out of 10, which took from 21 to 52 trials, including the criterion trials, and the seven experimental subjects received ECS 30 seconds after the last trial. Four animals were used as controls.

On day 6, the rats relearned the day 5 problem. Relearning, including the criterion trials, took the experimental animals from 9 to 12 trials, and the control animals from 9 to 16 trials. The results are presented in Tables 5 and 6. There are no differences in retention between the experimental and control animals.

Pattern Discrimination Learning Following Spaced Brightness Pretraining: The method was the same as above throughout except that on days 2, 3, and 4 the rats were pretrained on a brightness discrimination and on day 5 the rats learned a pattern (horizontal vs. vertical stripes) discrimination. Seven animals were used as experimentals and five were used as controls. The learning, including criterion trials, of the original pattern discrimination took from 14 to 59 trials. Relearning, including the criterion trials, took the experimental animals from 11 to 20 trials and took the control animals from 9 to 11 trials. This difference between experimental and control group in retention scores is of the same order as that found with no brightness discrimination pretraining.

There was a significant difference (P = .001) between experimental and control groups, the control showing 100 per cent savings and the ex-

Table 5

Mean and Median Number of Original and Relearning Trials, Including

Criterion Trials, for Experiment III

Subgroup	Experimental				Control			
	Original Learning		Relearning		Original Learning		Relearning	
	Mean	Median	Mean	Median	Mean	Median	Mean	Median
Brightness Discrimination Preceded By Pattern Pretraining (Experimental N = 7; Control N = 4)	38.0	36	9.86	10	34.75	33.5	12.75	13
Pattern Discrimination Preceded By Brightness Pretraining (Experimental N = 7; Control N = 5)	29.14	22	15.86	15	33.0	36	9.6	9

Table 6

Mean and Median Number Correct on the First 10 Relearning Trials for Experiment III

Subgroup	Experimental		Control	
	Mean	Median	Mean	Median
Brightness Discrimination Preceded By Pattern Pretraining (Experimental N = 7; Control N = 4)	9.28	9	8.5	8.5
Pattern Discrimination Preceded By Brightness Pretraining (Experimental N = 7; Control N = 5)	6.71	6	9.2	9

perimental group performing at chance level in the first 10 trials.

DISCUSSION

The principal significance of the results of the third experiment appears in their relation to the first two experiments, so instead of a separate discussion of Experiment III (as in the presentation of Experiments I and II) these last results are considered together with the earlier ones.

The results of the research can be summarized as follows: a single ECS has no effect on retention of simple spatial learning, or of spatial reversal learning; ECS produces significant loss of retention for a brightness discrimination habit, and for brightness reversal learning; but (Exp. III) does not produce loss in the brightness habit if it is preceded by training in pattern discrimination. Pattern discrimination, however, is lost following ECS, whether it is preceded by training in a brightness habit or not (also Exp. III).

These results give rise to two major types of questions, one involving the possibility of different mechanisms in brightness and pattern discrimination, the other revolving around the different effects of ECS on retention of a brightness discrimination produced by variations in experience occurring 24 or more hours before the learning-ECS session.

Thompson and Rich (1963) have presented evidence indicating that the posterior nucleus of the thalamus in the rat is significantly more important in mediating brightness discrimination than in mediating form discrimination. This may aid in understanding some aspects of the present data. However, this finding, as it stands, is of no aid in understanding why some variations in previous experience are accompanied by invulnerability of the brightness discrimination habit to the effects of ECS. The writer can find in the literature no adequate explanation of this finding, nor any reason to expect such a result.

The question arises as to what aspect of the pattern pretraining causes the brightness discrimination to become immune to the effects of ECS. The possibility that it is due to previous experience with the brightness continuum in this situation can be ruled out due to the results of Experiment II. In Experiment II a reversal of a previous brightness discrimination was shown to be susceptible to the disruptive effects of ECS.

One obvious possibility is that the difference in difficulty during pretraining of the stripes discrimination may have been the factor which made the brightness discrimination immune to the effects of ECS. According to this approach the stripes discrimination remains vulnerable only because the brightness pretraining is relatively easy. An extra experiment, which is not part of those already reported, has been done specifically to examine this possible explanation. The explanation was not supported.

Eleven animals were pretrained on more difficult brightness discriminations and then on day 5 received training on a stripes discrimination. The results (ECS disrupts the stripes discrimination) were the same as those obtained with the relatively easy black-white brightness discrimination.

This work shows that difficulty of a sensory nature (reflected in number of trials taken to learn something) is not the crucial variable. Along these same lines, it seems that the number of trials taken to learn may reflect a number of different influences. For example, comparison of the rates of learning a brightness discrimination of animals in Experiment I with rate of learning a stripes discrimination by animals exposed to identical spatial pretraining is an indication that the stripes discrimination is a more difficult task. However, comparison of the speed of learning on day 5 in Experiment III shows exactly the opposite result. The interpolation of further pretraining is the only difference between the two situations. This indicates that the dynamics of the relationship among neural representations of habits may become more accessible using techniques such as these.

The results of this experiment suggest some changes in the interpretation of the effects of ECS on retention. As was previously mentioned, attempts have been made to attribute all retention loss resulting from ECS to fear of ECS, or to a competition of responses based on fear of ECS (Adams and Lewis, 1962a, b). It can easily be seen from Experiment III that this explanation is not adequate. Groups in both phases of this experiment should have fear of ECS and therefore retention loss would be predicted in both cases. These results and those of Experiments I and II, in which some habits are retained and others disrupted when the fear aspect should be the same, lead to the conclusion that the neural consolidation hypothesis is the more adequate explanation of the retention loss results of these experiments. However, other results (Adams and Lewis, 1962a, b) leave little doubt that retention loss in some situations involving ECS can be explained best with a hypothesis based on fear of ECS. In view of these complications a change in the theoretical orientation is in order. The most reasonable change seems to lead to something of a two-factor explanation of ECS effects on retention -- one involving the consolidation hypothesis and the other involving a modification of the (Adams and Lewis) "competition of response" hypothesis. Specifically with reference to the experiments by Adams and Lewis (1962a, b), it can be said that memory of the place in which the ECS was administered (goal box) acts to reduce the tendency to approach that place again. This is in accord with the previously suggested hypothesis that memory of places and situations is relatively immune to the effects of ECS. Whether this is due to a faster consolidation process, a different neural organization or locus, or to other variables is an open question.

This proposed theoretical modification does not seem to offer any framework in which to fit the results of variations in the susceptibility of brightness discriminations produced by experiences taking place 24 or more hours before the learning session in question.

Another possibility worthy of examination involves the fact that the pretraining in Experiment III was spaced to the extent that it was distributed over 3 days (4 days including spatial pretraining). This gives rise to questions concerning possible differences in influence of a more massed pretraining schedule. Thompson and Pennington (1957) have shown that variations in distribution of original learning produce variations in the susceptibility of the habit to the effects of ECS. Thus, since there is reason to believe that something about the pretraining in the present experiment has an important influence on the vulnerability of subsequent learning to the effects of ECS, another group of animals was tested. Ten naive animals were trained in the same manner as those in part two of Experiment III, except that on day 2 the subjects were trained to the criterion of 9 out of 10 correct responses on the pattern discrimination. In other words, instead of spreading the pattern pretraining over three sessions it was carried to criterion in one session. Seven animals were given ECS 30 seconds after reaching criterion and three animals were used as controls. Experimental and control animals performed equally well in the relearning session. Thus variations in susceptibility of a brightness discrimination habit to the effects of ECS are not influenced by this degree of change along the massed-spaced continuum during pretraining sessions. However, there are some interesting differences between animals in these groups and those in part two of Experiment III. Although there is no difference in original learning speed of the brightness discrimination among these groups, there is a significantly lower level of relearning performance following massed pretraining. This result may be of no immediate help in explaining differences in susceptibility to ECS since ECS seems to have no differential effect with either massed or spaced pretraining in these situations. However, this result may be of great help in understanding the extent of the influence of variations in previous experience on present performance.

SUMMARY AND CONCLUSIONS

A series of experiments was undertaken in an attempt to add to the understanding of the physiological processes underlying learning and retention.

The results give support to the consolidation hypothesis in general, but, due to complications in the results, some changes in interpretation of the effects of ECS on retention were suggested. A two factor explanation was proposed, involving both disruption of consolidation and fear of ECS, and it was suggested that situations can be designed which change the relative importance of these two factors, with respect to post-ECS performance.

The experiments demonstrate differences in susceptibility to the disruptive effects of ECS of spatial discrimination habits as opposed to brightness discrimination habits learned in the same apparatus and under identical conditions.

They also demonstrate differences in the susceptibility (to the disruptive effects of ECS) of brightness discrimination habits which were produced by variations in pretraining experience. These variations occurred 24 or more hours before the brightness discrimination learning session and did not produce significant variations in the speed of subsequent learning.

In order to explain the results of these experiments it may be necessary to postulate a mechanism, possibly specific to brightness discrimination, which rapidly transfers information as to the value of brightness cues to an already consolidated neural organization.

This neural organization would presumably have been established and consolidated during the subject's previous pattern discrimination learning sessions. A logical extension of this notion leads to hypothesizing a hierarchy or continuum of neural organizations underlying different types of habits. Presumably the learning of a habit high on this continuum would permit subsequently learned habits lying lower on the continuum to become more quickly immune to the effects of ECS. A logical step toward testing these suggestions would involve use of stimulus pairs of pattern configurations ranging from simple to complex in the paradigm of varied pretraining.

Considering the fact that in these experiments there are no significant differences (produced by pretraining variations) in speed of subsequent learning, it may be that these phenomena involve a kind of positive transfer of training which is different from the classical variety in that it is not immediately reflected in increased speed of subsequent learning, but in the permanence of subsequent learning. It may also be that this difference in permanence, with different types of pretraining material, could be demonstrated without the use of ECS (as was shown with massed and spaced differences).

These experiments may be of importance to work in areas which at first glance may seem quite foreign to the method and approach employed in this effort, for example, in the study of increase in capacity for intellectual performance.

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