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EFFECTS OF ESCAPE PRETRAINING ON ACTIVE AVOIDANCE ACQUISITION DURING FUNCTIONAL DECORTICATION

by

Michael John Pianka

A Dissertation Submitted to the Faculty of the

DEPARTMENT OF PSYCHOLOGY

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I hereby recommend that this dissertation prepared under my direction by Michael John Pianka

entitled EFFECTS OF ESCAPE PRETRAINING ON ACTIVE AVOIDANCE ACQUISITION DURING FUNCTIONAL DECORTICATION

be accepted as fulfilling the dissertation requirement of the degree of Doctor of Philosophy

Sigmund Glicas — Dissertation Director — April 12, 1972 — Date

After inspection of the final copy of the dissertation, the following members of the Final Examination Committee concur in its approval and recommend its acceptance:*

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ABSTRACT

Transfer between learning with the cortex normal (N) and with the cortex under bilateral spreading depression (D) was investigated in three phases (1) escape pretraining (EPT), (2) original learning (OL), (3) relearning (RL). Twenty-eight male hooded rats were randomly assigned to the following conditions: (a) normal EPT, normal OL, depressed RL (NND); (b) normal EPT, depressed OL, depressed RL (NDD); (c) depressed EPT, depressed OL, normal RL (DDN); (d) depressed EPT, normal OL, normal RL (DNN); (e) no EPT, depressed OL, depressed RL (XDD); (f) no EPT, normal OL, normal RL (XNN). The results indicated that (1) D-EPT facilitated D-OL but not N-OL, (2) N-EPT had no effect on D-OL or N-OL, (3) there was no appreciable transfer from D-OL to N-RL although N-OL and D-OL transferred readily to D-RL, (4) no negative transfer was found from either EPT to OL or from OL to RL. The data were interpreted to support state dependent learning theory presenting a case of asymmetrical dissociation. A cortical inhibition model was applied to explain the results. The results suggest that either subcortical and/or extracortical structures are sufficient for the forming, retaining and retrieving of a complex response pattern.

INTRODUCTION

Functional decortication produced by bilateral spreading depression (BSD) has been used in an attempt to investigate the cortical mechanisms subserving the learning process. The temporary depression is induced through a dural application of potassium chloride (KCl) to both hemispheric surfaces. The research in this area has generally involved the transfer of a learned response from the depressed cortical state to the normal state or vice versa. Tapp (1962) found no positive transfer of a conditioned avoidance response previously learned with the cortex normal when retesting occurred with the cortex bilaterally depressed. Tapp suggested that his results were due to motor impairment caused by cortical depression. Since then, a number of researchers using various learning tasks have shown that positive transfer of a response learned while the cortex is normal does occur when the subject is retested in a BSD state (Kukleta, 1968; Russell, Kleinman, Plotkin and Ross, 1969; Thompson, 1964; Winocur, 1965). Winocur (1965) has suggested that due to the difficulty of the balance requirements of Tapp's (1962) task, his results were due to task complexity rather than motor impairment since a more complex task would have less positive transfer from a normal to BSD

state. Indeed, several investigators have shown that by varying task and/or response complexities it was possible to alter performance during relearning by BSD subjects from a slight impairment to a point where the performance was effectively abolished (Kukleta, 1968; Thompson and Hjelle, 1965; Winocur, 1965). The performance decrements are presumed to be due to the differing complexities of the learning tasks since Russell, Plotkin and Kleinman (1968) showed that BSD subjects suffered no motor impairment in running.

Retention of a response learned under a BSD condition when the subject has been bilaterally re-depressed has been shown by Thompson (1964). However, both Travis and Sparks (1963) and Russell et al. (1969) reported no retention under similar conditions. Thompson used an active avoidance task whereas Travis and Sparks used a simple avoidance task and Russell et al. (1969) used a passive avoidance task. Thompson also used a much higher grid shock (1.4mA) as compared to Travis and Sparks (.8mA) and Russell et al. (1969) (.65mA). Thompson's results were possible due to the higher shock intensities since recent research has indicated that BSD subjects fail to actively respond to shock intensities much below 1.2mA (Pianka, 1971).

With the exception of Thompson (1964) and Thompson and Hjelle (1965), previous research has utilized either stepdown platforms, two compartments or simple runway alleys for their avoidance tasks. Thompson (1964) and Thompson and

Hjelle (1965) used a shuttle avoidance task but failed to find acquisition of a free operant avoidance response by the BSD subjects. Pianka (1971) was the first to demonstrate acquisition of an active avoidance response (AAR) during functional decortication in a free operant shuttle avoidance task. This researcher noted that the acquisition deficits displayed by the BSD subjects appeared to result from a failure to acquire the escape response which usually occurs prior to acquisition of an AAR.

Travis and Sparks (1963) failed to find positive transfer of an escape response learned under BSD conditions to the normal state; rather, the pretraining interferred with relearning in a normal state. More recent research concerned with active, passive and simple avoidance have supported Travis and Sparks' (1963) results (Kukleta, 1968; Russell et al., 1969; Thompson, 1964). However, Kukleta (1966, 1967) has shown that a simple avoidance response learned under BSD conditions transfers positively to a unilateral spreading depression state where only one hemisphere is depressed and from that, to a condition where the opposite hemisphere is depressed. Kukleta interpreted these data as evidence for the existence of a subcortical learning process taking place in the normal hemisphere. However, it would seem at least as parsimonious to consider these data as indicating positive transfer to the depressed hemisphere and not to the normal one. Schneider (1966) found

that subjects trained under unilateral spreading depression relearned a task more readily under BSD than those subjects trained with a normal cortex. Schneider and Kay (1968) provide more evidence for the latter interpretation by demonstrating that a subject can learn to use a unilateral spreading depression state as a discriminative stimulus for lever pressing. Another interpretation can be offered in terms of state dependent learning. The stimulus-control theory of Schneider (1967, 1968) is a special case of state dependent learning since Schneider bases his theory solely on kinesthetic feedback differences caused by BSD. A dissociation theory involves a more general internal cue state to which the subject responds (Overton, 1964).

In order to assess the dissociation properties of BSD, the present research was concerned with the transfer relationships from BSD to normal, normal to BSD, BSD to BSD and normal to normal in two different learning situations. The first was one of simple escape learning, the second an AAR. The effects of escape pretraining on the later acquisition of the AAR and its subsequent transfer to a relearning of the AAR was also investigated.

METHOD

Subjects

Twenty-eight experimentally naive male hooded rats of the Long-Evans strain were used. Subjects were housed in community cages (8-10 per cage) until surgical preparation at which time they were housed in individual cages. All subjects were maintained on Purina laboratory rat chow and water ad libitum throughout the experiment.

Apparatus

The apparatus was an automated shuttle box, 31.75 cm. high, 60.95 cm. long and 25.4 cm. wide. The grid floor was elevated 8.27 cm. from the bottom and consisted of two hinged sections separated by a 1.3 cm. high wood obstacle. The grid floor consisted of stainless steel rods, 0.65 cm. in diameter and spaced 1.3 cm. apart center to center. The top had a 12.7 cm. by 50.8 cm. opening which was covered with 0.65 cm. wire mush. The front was a 60.95 cm. x 22.9 cm. x 0.65 cm. thick section of plexiglass. With the exception of the plexiglass, wire mesh, CS and stainless steel rods, the entire apparatus was painted flat black. Inside, symmetrically mounted on each wall 15.3 cm. above the grid floor, were two Edwards #115 6V buzzers turned to the soft position and mounted on rubber grommets. In addition, a

24V 6A diffuse white lamp (house light) was placed at each end 10.8 cm. above the floor and centered. The shock to the two grid sections was delivered by a model E1100DA 28V Grason-Stadler power supply delivering up to 2.5A. A model A-615A Lafayette shock supply regulated the shock intensity and a Ralph Gerbrands Company scrambler was used to alternate the shock between the rods. A model 111-C Hunter timer was used to regulate the intertrial interval and a model 100-B Hunter timer was used to control the CS duration. A model S-1 115V 60hz. Standard Electric Time Corporation timer was used to record response latencies. The apparatus was wired to make the subject respond away from the CS and the current remained on one side or the other throughout the intertrial interval to discourage the subject's return. The CS was stopped via spring loaded microswitches as soon as the subject crossed over the obstacle and was reinstituted if the subject returned to the electrified side during the intertrial interval.

Surgical and Spreading Depression Techniques

The subjects were prepared in a stereotaxic instrument under sodium pentobarbital (35 mg/kg based on a 50 mg/cc concentration) and chloral hydrate (160mg/kg based on a 300 mg/cc concentration) anaesthesia. The jawbone was used to clamp the animal in the stereotaxic instrument in lieu of the ear canals to prevent rupture of the tympanic membrane. A mid-line incision was made in the scalp and a

5 mm diameter trephine opening effected over each hemisphere immediately posterior to the coronal suture and approximately 2mm off mid-line. Subjects with cut dura determined by visual inspection were discarded. Chronic preparations were made by affixing a small cup and plunger device over the trephine openings using jeweler screws and dental cement. The device was made from #15085-25D Tomac disposable lcc tuberculine syringes. Cotton balls soaked in isotonic saline were inserted in the cups after surgery and held in via the plungers. Bilateral SD was elicited by removal of the cotton balls under light ether anaesthesia and replacement of them with cotton balls soaked with 10 percent KCL. Subjects with visually determined evidence of infections were discarded. Hypesthesia (diminished sensibility) onset begins within 30 seconds regardless of KCL strength (Carew, Crow and Petrinovich, 1970). The present chronic preparation provides a relatively constant supply of potassium and chlorine ions for as long as the cotton balls were in contact with the exposed dural surface. Pretraining, training or re-learning began 10 minutes after the application of KCL only if a bilateral abolition of the placing reflex was noted (Bureš, Burešová and Zahorová, 1958). All subjects received the surgical operation. However, the control or normal groups were treated with fresh saline soaked cotton balls. After testing, the KCL soaked cotton balls were removed under light ether anaesthesia, the cups revised with

isotonic saline, saline soaked cotton balls placed in the cups, and the plunger replaced.

Experimental Procedure

Twenty-eight subjects were randomly assigned to six groups. Ten subjects received EPT while experiencing bilateral spreading depression (D), ten subjects received EPT with normal cortices (N) and eight subjects did not receive EPT (X).

On the first day, during EPT, 20 animals received 20 escape trials each in the apparatus without the CS being present. Twenty-four hours later, original learning (OL) was begun as shown in Table 1. Groups NN, XN and DN received OL with normal cortices while groups DD, XD, and ND received OL with depressed cortices. There were five subjects in each OL group that had EPT and four subjects in each OL group that did not have EPT. All subjects were given massed trials until meeting a criterion of nine out of ten successful avoidance responses.

One day after reaching the criterion, relearning (RL) was begun. Groups NND, NDD and XDD underwent RL with depressed cortices while groups DDN, DNN and XNN received RL with normal cortices. The same training procedures used in OL applied to RL. These RL conditions provided a baseline reference from which EPT effects could be assessed.

TABLE 1

CORTICAL STATES AND TRAINING CONDITIONS FOR THE SIX EXPERIMENTAL GROUPS

Group	N	Escape Pretraining (EPT)	Original Learning (OL)	Relearning (RL)
NND	5	Normal (N)	Normal (N)	Depressed (D)
NDD	5	Normal (N)	Depressed (D)	Depressed (D)
DDN	5	Depressed (D)	Depressed (D)	Normal (N)
DNN	5	Depressed (D)	Normal (N)	Normal (N)
XDD	4	No EPT	Depressed (D)	Depressed (D)
XNN	4	No EPT	Normal (N)	Normal (N)

All subjects were trained with a constant grid shock set at 1.4mA and a CS-UCS interval of 5 seconds. The CS duration was terminated by the response. The intertrial interval was randomly varied from 15-25 seconds. All subjects underwent testing approximately 24 hours post surgery whether or not the testing was EPT or OL without previous EPT. A sound CS was used with the two house lights constantly on during OL and RL.

Every subject that was treated with KCl received a single one hour period of drug habituation in their home cage 18-24 hours prior to that phase of the training which was to be performed under a depressed state, e.g., if a

subject had N-EPT and D-OL, drug habituation preceded D-OL or, if a subject had D-EPT and D-OL the home cage drug habituation preceded D-EPT.

In addition to the period of drug habituation, the subjects received two one hour periods of apparatus habituation. If a subject was to perform under a depressed state, an apparatus habituation period was given while the subject was depressed; otherwise, it was given while the cortices were normal. Thus, all groups (except XDD and XNN) received two periods of apparatus habituation, one while depressed prior to that phase of training which was to be performed under depression and the second with normal cortices prior to that phase of training which was to be performed with normal cortices. Thus, if a subject had N-EPT followed by D-OL, the first apparatus habituation with normal cortices preceded N-EPT and the second apparatus habituation with depressed cortices preceded D-OL. Because groups XDD and XNN did not shift in cortical conditions, they received only one period of apparatus habituation under the appropriate cortical state.

Training began immediately following the one hour periods of apparatus habituation. During that phase of training which was not preceded by a one hour period of apparatus habituation, each subject received an additional 10 minute apparatus habituation while experiencing whatever cortical state the following training required, e.g., if a

subject had N-EPT, N-OL and D-RL, N-OL was preceded by a 10 minute period of apparatus habituation with normal cortices whereas if a subject had D-EPT, D-OL and N-RL, D-OL was preceded by a 10 minute period of apparatus habituation with depressed cortices.

Several response measures were taken. They were the number of trials to criterion, number of ARs to criterion and response latencies (either escape or avoidance). These measures (when applicable) were taken for each testing session.

Throughout testing, subjects were checked after drug and apparatus habituation, prior to training, after 100 trials (if training lasted that long) and at the end of each session for the abolition of the placing reflex to assess the continued presence of cortical spreading depression. Each day, prior to KCl application, all experimental subjects were checked for the presence of the placing reflex to assess the resumption of normal cortical functioning from the preceding day. Those subjects performing a phase of the experiment requiring normal cortices were also examined to determine the resumption of normal cortical functioning if the training of the preceding day was carried out under depressed conditions.

RESULTS

Escape Pre-Training

The mean escape pre-training (EPT) latencies for the 20 escape trials given preceding original learning (OL) did not differ significantly between the cortically depressed condition and the normal condition. The mean for D condition was 3.653 seconds and the mean for N condition was 2.753 seconds ($F = .807$).

Original Learning

The effects of EPT were determined by comparing the OL performance of those groups having EPT (groups N<u>N</u>D, N<u>D</u>D, D<u>D</u>N and D<u>N</u>N) to the OL performance of those groups without EPT (groups X<u>N</u>N and X<u>D</u>D). All subjects in all groups reached criterion during OL. Mean and median values for the number of avoidance responses and trials to criterion for all groups are presented in Table 2 and the mean and median values for the latency of the response (LR), percent avoidance responding (%AR) and the total number of non-avoidance responding (non-AR) are given in Table 3. Comparisons between independent groups were made using two-tailed Mann-Whitney <u>U</u> tests. Subjects previously receiving D-EPT were significantly superior to those with N-EPT regardless of whether OL was given with normal or depressed cortices

TABLE 2

MEAN AND MEDIAN (IN PARENTHESES)
NUMBER OF AVOIDANCE RESPONSES AND TRIALS TO CRITERION
DURING ORIGINAL LEARNING (OL) AND RE-LEARNING (RL)
FOR ALL CONDITIONS

	NND		NDD		DDN	
	OL	RL	OL	RL	OL	RL
Avoidance Responses	22.0 (21.0)	11.2 (12.0)	26.6 (26.0)	14.8 (15.0)	16.4 (17.25)	14.8 (13.0)
Trials to* Criterion	47.0 (45.0)	15.4 (14.0)	61.4 (57.0)	20.0 (21.0)	24.2 (25.0)	21.8 (17.25)

	DNN		XNN		XDD	
	OL	RL	OL	RL	OL	RL
Avoidance Responses	19.2 (19.0)	19.2 (19.25)	24.75 (25.0)	18.5 (18.0)	43.25 (43.0)	24.25 (25.0)
Trials to* Criterion	43.6 (38.0)	38.8 (38.0)	64.75 (57.0)	33.5 (35.0)	153.0 (140.0)	42.75 (46.0)

*Includes ten criterion trials.

TABLE 3

MEAN AND MEDIAN (IN PARENTHESES) VALUES OF RESPONSE LATENCY, PERCENT AVOIDANCE RESPONDING AND NUMBER OF NON-AVOIDANCE RESPONSES FOR ALL CONDITIONS DURING ORIGINAL LEARNING (OL) AND RE-LEARNING (RL)

	Response Latency (Sec.)		Percent AR		Non-AR	
	OL	RL	OL	RL	OL	RL
NND	4.44 (4.78)	3.17 (2.50)	46.9 (45.5)	78.8 (81.9)	25.0 (21)	4.2 (2)
DDN	3.81 (3.56)	3.26 (3.20)	68.0 (68.0)	69.5 (72.0)	7.8 (8)	6.8 (6)
DNN	4.11 (4.35)	4.28 (3.96)	51.5 (50.0)	56.6 (49.9)	24.4 (19)	19.6 (19)
NDD	4.68 (5.02)	3.47 (3.46)	44.9 (46.1)	75.9 (71.3)	34.8 (31)	5.2 (6)
XNN	4.67 (4.69)	3.82 (3.80)	39.6 (36.0)	56.3 (56.1)	40.0 (40)	14.7 (17)
XDD	5.52 (5.17)	3.91 (3.69)	40.0 (40.6)	60.9 (62.6)	110.75 (92)	18.5 (19)

when both N and D-EPT and no EPT conditions were compared on (a) percent AR ($p < .02$), (b) non-AR ($p < .02$) and (c) LR ($p < .05$) indicating that N-EPT had less effect on both D-OL and N-OL. These data are reflected in a two-way analysis of variance using percent AR which showed EPT to have an effect on OL with D-EPT having the greater effect ($F = 7.385$), ($p < .05$) (Appendix A, Table A-1, for the summary table of the analysis of variance). A one-way analysis of variance comparing mean percent AR of groups D$\underline{N}$N, X$\underline{N}$N and N$\underline{N}$D during OL showed no significant differences ($F = .760$) whereas a similar comparison of groups D$\underline{D}$N, X$\underline{D}$D and N$\underline{D}$D revealed a significant difference ($F = 6.235$), ($p < .025$) (Appendix A, Table A-2 for the summary table of the analysis of variance) indicating that the OL of group D$\underline{D}$N was significantly superior to that of groups N$\underline{D}$D and X$\underline{D}$D.

Comparisons using the latency performance measure during OL failed to yield any significant differences between any groups.

Comparisons using percent AR showed group D$\underline{D}$N to make proportionately more ARs during OL than group X$\underline{N}$N ($p < .02$), group N$\underline{N}$D ($p < .02$), group N$\underline{D}$D ($p < .02$) and group X$\underline{D}$D ($p < .02$) but no difference was noted between groups D$\underline{D}$N and D$\underline{N}$N ($p > .122$).

Comparisons using non-AR during OL showed that group D$\underline{D}$N executed fewer non-ARs than group X$\underline{N}$N ($p < .02$), group N$\underline{D}$D ($p < .05$), group X$\underline{D}$D ($p < .02$) and group N$\underline{N}$D

($p < .02$) but no difference was noted between group DDN and group DNN ($p > .150$).

Comparisons of groups XDD and XNN, NND and NDD, NND and DNN, NND and XDD, DNN and DDN, DNN and XDD, NND and XDD, NDD and DNN, and NDD and XNN showed no significant differences on any response measure.

Relearning

The conditions under which OL takes place significantly effect relearning showing that D-OL had a greater effect than N-OL ($F = 6.118$) ($p < .05$) (Appendix A, Table A-3 for the summary table of the analysis of variance). Further analyses comparing mean percent AR during RL failed to yield significant differences among groups DNN, XNN and DDN ($F = 2.07$) or groups NND, NDD and XDD ($F = 2.00$).

Comparisons of RL latency scores failed to disclose any differences between any group.

Comparisons of percent AR during RL showed group NND to make proportionately more ARs than group DNN ($p < .04$). Group NDD was found to have a higher percent AR than group XNN ($p < .02$).

Comparisons of RL non-AR scores yielded only one significant difference. Group XNN made more non-ARs than group NND.

All other comparisons showed none of the groups to differ on any response measure. Group XDD was not different from group XNN.

Transfer scores based on percent savings are presented in Table 4. Using the number of trials to criterion, group XDD showed the greatest savings (72.06%) whereas, using mean percent AR places group XDD third (52.25%). It can be seen from Table 4 that groups NDD and NND exhibited the most positive transfer. Both groups XNN and XDD also show positive transfer whereas groups DDN and DNN show very little transfer. The percent savings scores show no negative transfer.

TABLE 4

PERCENT SAVINGS SCORES
FOR ALL CONDITIONS CALCULATED
FROM TRIALS TO CRITERION AND
FROM THE PERCENT OF AVOIDANCE RESPONDING

	NND	NDD	DDN	DNN	XNN	XDD
Trials to Criterion	67.23	67.42	9.92	11.01	48.26	72.06
Percent AR	68.02	69.04	2.21	9.90	42.17	52.25

DISCUSSION

An important feature of this research is that the original learning phase is consistent with Pianka's data (1971). Pianka showed that cortically depressed subjects could acquire a two-way active avoidance response provided the UCS was of sufficient intensity (> 1.2mA). The fact that all subjects reached criterion is significant since research prior to Pianka (1971) has failed to demonstrate two-way active avoidance learning under bilateral spreading depression.

Since D-EPT and N-EPT escape latencies did not differ significantly, it is tempting to suggest that these two conditions were equated due to UCS strength. Such a suggestion seems to be erroneous since these present data further indicate that even though escape latencies for depressed and normal rats did not differ during EPT, rats previously depressed differ in OL from rats not previously depressed. On the other hand, N-EPT was shown not to significantly influence either N-OL or D-OL which suggests that N-EPT has no effect on the acquisition of an AAR. It is also significant to note that D-EPT failed to influence N-OL. The lack of equality suggested by these data may be due in part to the lack of a sensitive response measure at the EPT stage

of training. The response latency measure was a poor predictor of avoidance learning.

Pianka (1971) postulated an escape learning deficit in cortically depressed subjects since, with an increased UCS intensity, he was able to demonstrate AAR acquisition in depressed subjects which varied from control subjects only on the number of trials until the first avoidance response. The present research supports Pianka's interpretation in that, aside from D-OL preceded by D-EPT, the OL performance for the rest of the groups was not significantly different from each other. These data indicate that once escape responding has been established under either N or D conditions, OL performance is the same for all groups except group DDN. Group D-OL preceded by D-EPT was superior to the OL of all the other groups.

Thompson (1964) reported positive D to D transfer for subjects in a one-way AAR. However, Russell et al. (1969) reported no D to D transfer in a passive AR task. besides the obvious differences between the two tasks, these studies differed in UCS strength, number of trials given, and criterion levels and methods used for assessing transfer. The present data represent another difference, that of different tasks for the same subjects. During EPT, a subject learns to escape the UCS without the aid of a CS whereas during OL, the subject was required to successfully avoid shock, utilizing an auditory CS. Since N-EPT did not have a

significant effect on later training, it is not necessary that the N-EPT to N-OL group be comparable to the D-EPT to D-OL group in order to evoke a state dependent learning hypothesis. Normally, to demonstrate state dependent learning which is also called dissociation, a 2 x 2 experimental design is required in reporting results showing groups N to N and D to D displaying good performance with groups N to D and D to N exhibiting poorer performance (Miller, 1957). In the present case, the transfer from EPT to OL can be regarded as a case of dissociation since D-OL was facilitated by D-EPT but not effected by N-EPT. These results further imply that drug dissociation learning can and does exhibit some type of generalization between two similar learning tasks which fail to generalize outside of the drug state.

Since D-RL displays a considerable amount of savings from an N-OL state, the lack of negative transfer from OL to RL as measured by the savings method noted in the present research indicates that AAR learning occurs subcortically and/or extracortically in addition to the presumed cortical involvement. This N to D transfer has been reported for passive AR tasks (Russell et al., 1969), simple AR tasks (Kukleta, 1968; Winocur, 1965) and one-way AAR tasks (Thompson, 1964).

The poor savings score noted for D-OL to N-RL is also in accord with the results of other researchers

(Kukleta, 1968; Bureš and Burešová, 1963; Russell et al., 1969; Thompson, 1964; Travis and Sparks, 1963).

Combining these two results with the performance of group NDD which showed good savings from D-OL to D-RL suggests that this present research can be regarded as a case of asymmetrical dissociation. Asymmetrical dissociation can be seen when there is good savings from D-OL to D-RL as well as N-OL to D-RL with little or no savings noted from D-OL to N-RL (Barnhart and Abbott, 1967; Overton, 1971). Thus, two-way active avoidance responding can generalize from a normal to depressed state but not from a depressed to normal condition. This agrees with the EPT to OL results and implies that there is sub or extracortical learning present during N-OL which transfers to D-RL. The lack of facilitation from N-EPT to D-OL is not important since N-EPT was shown not to effect OL in either the N or D condition. It should also be pointed out that the EPT to OL data refers to two similar tasks whereas the OL to RL data refers to the same task making comparisons between the two phases awkward.

Group DNN presents a problem for this interpretation since the N-OL of group DNN was not different from the N-OL of group XNN, yet the N-RL of group DNN was poorer than the N-RL of group XNN as evidenced by the small amount of savings. Such results suggest that D-EPT had an adverse effect on N-RL. These data need to be replicated before further interpretation can be offered.

Dismissing group DNN, the rest of the data can be explained using a modified version of a cortical inhibition theory postulated by Girden (1940). Girden observed dissociation of conditioned responses in dogs which he attributed to the functional decortication induced by the drug erythroidine. He suggested that learning normally involves cortical structures but that without such structures functioning, the subcortex was capable of acquiring and retaining a learned response. He further postulated that the subcortex could be inhibited by the neocortex thereby dissociating responses learned under the two differing cortical states. When the subject is in a drug state, the original response learned under the drug state appears since the cortical inhibition is absent. If the subject's cortical activity is allowed to resume, the inhibiting functions present in the normal cortex suppress the subcortical structures, thereby stopping the occurrence of the subcortically learned response. Girden's model does not allow for subcortical learning to take place while the subject is in a normal cortical state. The present data suggest that in order for N-OL to transfer to D-RL with savings equal to that of D-OL to D-RL, some sort of sub or extracortical learning must have taken place during learning in the undrugged state. Girden's model would predict a loss of cortical inhibition in D-RL and the good savings noted could only be present if the subject had learned the AAR both

cortically and sub or extracortically during N-OL. Otherwise, D-RL should have resembled the D-OL of group NDD.

The fact that N-EPT failed to transfer to D-OL contradicts this notion of sub or extracortical learning by suggesting that the portion of the EPT experience that is stored sub or extracortically by group DDN fails to become established when EPT is given to a subject with a normal cortex. However, since N-EPT was not shown to be effective for either N-OL or D-OL, there seems to be some doubt as to whether or not N-EPT is generalized to the OL situation. The fact that D-EPT did not transfer to N-OL is readily explained by Girden's model since it would predict that the resumption of normal cortical functioning would allow for cortical inhibition of the sub or extracortical learning that took place during D-EPT.

This interpretation is consistent with the majority of the reported results found in the literature. Kukleta (1966) showed that there was positive transfer in a simple AR task from a bilaterally depressed state to a unilaterally depressed one. These data can be readily explained by considering the transfer to take place from the bilaterally depressed state to the unilaterally depressed hemisphere which is not liable to the cortical inhibition experienced by the normal hemisphere. These data predict that further research should find a progressive increase in the amount of savings from a bilaterally depressed state to a unilaterally

depressed state to a normal state. Since the literature has not shown any transfer from a D to N condition, it would be interesting to discover if the preceding prediction is tenable.

The response measures recorded in the present research point to an interesting problem, that of sensitivity. Analyses performed using trials to criterion and response latencies were not significant. It was found that the most sensitive measure proved to be the percent avoidance responding. Failures to discover the transfer relationships reported in the present research by other researchers may be due to insufficiencies in their response measures.

Explaining these results in terms of asymmetrical dissociation theory based on cortical inhibition does not, however, address itself to the question as to how an animal with a presumably disfunctional cortex can learn a complex task such as a two-way active avoidance response. The implication of these data is that there are subcortical or extracortical capabilities which can retain complex responses and from which, these responses can be retrieved up to 24 hours later. Considering the fact that species other than mammals (e.g., pigeons) with very little neocortical development can learn complex responses, it would seem plausible to suggest that the cortex serves as an evolutionary 'insurance policy' for mammals because of their greater need for plasticity in exploiting their ecological niche.

Forced to rely solely on structures sans cortex requires a reorientation on the part of mammals that takes time.

This present research and that of Pianka (1971) which first demonstrated two-way active avoidance learning differs from all previous spreading depression research on one major point--that of the BSD habituation. It is possible that this feature is the major source for the presence of learning a complex task under BSD conditions.

APPENDIX A

ANALYSIS OF VARIANCE SUMMARY TABLES

TABLE A-1. Summary of the Analysis of Variance for the Escape Pretraining Effects on the Percent Avoidance Responding During Original Learning

Source	df	SS	NS	F	
EPT	1	.056	.096	7.385	$p < .05$
OL	1	.026	.026	2.000	NS
Int.	1	.043	.043	3.308	NS
W/in.	16	.214	.013		

TABLE A-2. Summary of the Analysis of Variance for the Mean Percent Avoidance Responding Differences Between those Groups having Depressed Original Learning Regardless of their EPT Conditions

Source	df	SS	MS	F	
Between	2	.211	.106	6.235	$p < .025$
W/in.	11	.191	.017		

TABLE A-3. Summary of the Analysis of Variance for the Original Learning Effects on the Percent Avoidance Responding During Relearning

Source	df	SS	MS	F	
RL	1	.013	.013	.765	NS
OL	1	.104	.104	6.118	$p < .05$
Int.	1	.033	.033	1.941	NS
W/in.	16	.277	.017		

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