

TRANSFER OF TRAINING OF AN
AVOIDANCE RESPONSE BETWEEN NORMAL
AND FUNCTIONALLY DECORTICATE STATES

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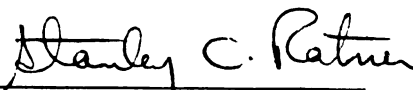
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ABSTRACT

TRANSFER OF TRAINING OF AN AVOIDANCE RESPONSE BETWEEN NORMAL AND FUNCTIONALLY DECORTICATE STATES

by Richard W. Thompson

Two experiments investigated the transfer of an avoidance response from the cortical to the decorticate state and from the decorticate to the cortical state. Ninety rats (50 in the first experiment and 40 in a replication) were trained to avoid shock by running from a shock compartment to a safe compartment at the onset of a buzzer and the opening of the guillotine door which divided the Mowrer-Miller shuttlebox into two compartments. In Experiment I the shock compartment was black with a grid floor and the safe compartment was white with a solid wood floor. In the replication both compartments were black with grid floors. The Ss were trained, then $4\frac{1}{2}$ hours later retrained to a criterion of nine avoidances in ten trials plus ten over-training trials.

In Experiment I ten Ss were trained with no surgical or cortical treatment and were the normal control group for both experiments. In both Experiment I and II a group of ten Ss were trained and retrained under each of the following conditions. Group S-S was an operated control group. Group S-K was trained after application of saline to the hemispheres and retrained under functional decortication achieved by placing 25% KCl on the exposed dura of both hemispheres. (Twenty-five percent KCl causes a spreading depression (SD) of cortical activity which lasts three to five hours and is fully reversible.) Group K-K, the

decorticate control group, was trained and retrained under functional decortication. Group K-S was trained under functional decortication and retrained with the cortex functional.

The two experiments demonstrated that functionally decorticate Ss required almost eight times as many learning trials as Ss with the cortex functional. Surgery alone did not interfere with learning or relearning. All groups showed positive transfer in the second training session, except Group S-K which required more trials to relearn under SD than to learn originally.

Results indicated that subcortical learning accompanies cortical learning. Animals pretrained with a functional cortex required fewer trials to relearn under SD than Ss trained under SD with no such pre-training.

The hypothesis that redominance of the untrained cortex interferes with a subcortically mediated response was supported by the data of the two experiments. Animals pretrained under SD required as many trials to relearn the response with the cortex functional as Ss required to learn it originally with the cortex functional. Several alternatives were offered to explain this result.

Animals trained under SD exhibited a stereotyped response that interfered with the efficient avoidance response. Impairment of the perceptual and motor responses of the functionally decorticate Ss was suggested as the mechanism for stereotyping.

Approved: _____

Alley C. Ratner

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By

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TABLE OF CONTENTS

	Page
INTRODUCTION	1
PROBLEM	11
METHOD	13
RESULTS AND DISCUSSION	17
EXPERIMENT II	30
METHOD	31
RESULTS	33
DISCUSSION OF THE COMBINED EXPERIMENTS	50
SUMMARY	59
REFERENCES	61
APPENDIX	64

LIST OF TABLES

TABLE	Page
1. Design: Cortical treatment for each training session .	13
2. Results of Mann-Whitney <u>U</u> tests comparing groups in Session 1 on trials to criterion	20
3. Results of Wilcoxon Matched-Pairs Signed-Ranks test on trials to criterion comparing groups between the two sessions.	20
4. Results of Mann-Whitney <u>U</u> tests between groups in Session 1 and Session 2 on percentage of TA trials . .	26
5. Results of Wilcoxon Matched-Pairs Signed-Ranks tests for each group between sessions on percentage of TA trials	26
6. Design of Experiment II: Cortical treatment for each training session	31
7. Results of Mann-Whitney <u>U</u> tests comparing groups in Session 1 on trials to criterion in Experiment II. . . .	35
8. Results of Wilcoxon Matched-Pairs Signed-Ranks tests comparing groups between sessions on trials to criterion in Experiment II	35
9. Results of Mann-Whitney <u>U</u> test between groups in Session 1 and Session 2 on percentage of TA trials in Experiment II	39
10. Results of Wilcoxon Matched-Pairs Signed-Ranks tests for each group between sessions in Experiment II on percentage of TA trials	39
11. Median trials to criterion for the two experiments in both sessions	41

LIST OF TABLES - Continued

TABLE	Page
12. Results of Mann-Whitney <u>U</u> tests comparing corresponding groups of Experiment I and II on trials to criterion	41
13. Results of Mann-Whitney <u>U</u> tests comparing corresponding groups of Experiment I and II on the percentage of TA trials	42
14. X^2 tests between corresponding groups in Experiments I and II on the number of Ss showing at least one TA response in all learning trials and in the first ten learning trials	42
15. Results of <u>U</u> tests comparing groups in Session 1 on trials to criterion for the combined experiments	46
16. Results of Wilcoxon Matched-Pairs Signed-Ranks tests comparing each group between sessions for the combined experiments	46
17. Results of Mann-Whitney <u>U</u> tests comparing groups in Session 1 and Session 2 on percentage of TA trials for the combined experiments	49
18. Results of Wilcoxon Matched-Pairs Signed-Ranks tests for each group between sessions for the combined experiments	49
19. Raw data for trials to criterion and TA responses for Experiment I.	65
20. Raw data for trials to criterion and TA responses for Experiment II.	67

LIST OF FIGURES

FIGURE	Page
1. Median trials to criterion Experiment I	18
2. Median percentage of TA trials for each group in . . . Experiment I	25
3. Median trials to criterion Experiment II.	34
4. Median percentage of TA trials for each group in Experiment II	38
5. Median trials to criterion for the combined experi- ments	44
6. Median percentage of TA trials for each group in the combined experiments	48

The search for the engram¹ or memory trace has been diligently pursued since Descartes suggested, over 300 years ago, that the learning or memory mechanism was somewhere in the brain. Typically this search has employed surgical ablation of the structure suspected of being involved. The results with this method have not always been clear. Lashley (1950), reviewing much of the work done using the ablation method, is almost forced to conclude ". . . that learning is just not possible." (Page 478.) But of course, learning and remembering do occur, neurophysiological evidence to the contrary.

Lateralization of the Engram by Means of Homolateral Stimulation

Recently a new surgical technique has been developed which promises to be very helpful in cornering the ever elusive engram. This technique involves splitting the cortical masses so they can not communicate. The brain is a bilaterally symmetrical organ; structures found on the right are mirrored by similar structures on the left. The cerebrum is two hemispheres which are joined by fiber tracts. These fibers join corresponding points in the two hemispheres (Walsh, 1957). The largest of these tracts is the corpus callosum. Sectioning this tract almost completely eliminates communication between the two hemispheres. Further reduction of interhemispheric communication can be achieved by sectioning the hippocampal and anterior commissures. Animals so treated have most of the somesthetic stimulation received from one side of the body restricted to one hemisphere. If the crossing fibers of the optic

¹In the present paper the terms engram or memory trace are used in a generic sense and imply only that the memory mechanism is some physiological process of the nervous system.

chiasma are also sectioned, visual input is also restricted to the homolateral hemisphere. The right hemisphere receives information only from the right eye, the left hemisphere receives information only from the left eye.

Myers (1956) and Sperry, Stamm, and Miner (1956) have made use of this surgical preparation in an attempt to isolate the engram. These investigators trained split-brain cats (this is the term used to describe Ss with the major commissures sectioned) in visual pattern discriminations in an apparatus which restricted visual input to one eye and thus to one hemisphere. When the discrimination had been well learned, the animal was tested with the untrained eye. The results indicated that the engram had been localized in the hemisphere homolateral to the trained eye, the untrained eye and hemisphere took about as long to learn the discrimination as the original eye and hemisphere. There were no consistent positive or negative transfer effects from one hemisphere to the other. Myers and Sperry (1953) and Myers (1955) have shown that sectioning of just the corpus callosum or just the crossing fibers of the optic chiasma had no such restricting effect on the memory trace. The Ss trained with one eye showed good transfer when tested with the other.

Meikle and Sechzer (1960) have shown that above threshold brightness discriminations in split-brain cats transfer from the trained to the untrained hemisphere although pattern discriminations do not. Trevarthen (1962) has also shown the transfer of a brightness discrimination in split-brain monkeys. Pattern discriminations failed to transfer from the trained to the untrained hemisphere. Meikle (1960) found that threshold brightness discriminations did not transfer from trained to untrained hemisphere in the split-brain cat. The data of Meikle and Sechzer and Trevarthen would indicate that the brightness discrimination had been learned subcortically or that it was transferred by a mechanism

other than the corpus callosum. This mechanism could not, however, transfer pattern discriminations nor could the subcortex learn pattern discriminations.

In some ways this is inconsistent with the data of Lashley for the rat (1929). Lashley found that a brightness discrimination trained before ablation of the striate cortex was lost following ablation, but could be relearned in the same number of trials as in original learning. He says, "The available evidence indicates that the rate of learning of a simple brightness habit is independent of any part of the cerebral cortex, although the habit, when formed by normal animals shows a definite cortical localization. I should anticipate quite different results in studies of pattern vision." (Page 60, Lashley, 1929.) Later, Lashley (1950), in reviewing data concerned with the possibility that there is subcortical learning with the cortex present, says, "These few experiments are, of course, by no means conclusive. They constitute, however, the only direct evidence available, and they definitely point to the conclusion that, if the cerebral cortex is intact, the associative connexion of simple conditioned reflexes are not formed in the subcortical structures of the brain." (Page 467.) Lashley's data and that of Meikle and Sechzer and Trevarthen are thus in opposition. Perhaps there is a species difference. The question still remains: Is there learning in subcortical structures with the cortex intact? The early two factor learning theory of Mowrer (1960) suggested that learning occurred at more than one level of the nervous system simultaneously.

Myers (1956) has shown that not only is there no transfer of visual discriminations in the split-brain cat, but that opposing responses can be trained in the two hemispheres without interference between the two. Sperry (1958) found similar results using split-brain monkeys. Trevarthen (1960, 1962), using split-brain monkeys and polarized light which enabled him to present the opposite discrimination problems to

the two eyes and hemispheres simultaneously, found that in some cases the dominant hemisphere learned and the other did not, but that in some animals both discriminations were learned, the two hemispheres learning simultaneously.

Split-brain cats also show cortical lateralization of somesthetic discriminations. Stamm and Sperry (1957) trained split-brained cats to discriminate between two pedals using only one paw. The discrimination was made on the basis of softness, roughness, or shape. When Ss were transferred to the opposite paw no negative or positive transfer effects were detected. Glickstein and Sperry (1959, 1960) have shown that in split-brain rhesus monkeys the specific somesthetic discrimination does not transfer from trained hand to untrained hand, but a generalized test response does. This generalized test response may be due to stimulation which is not restricted to one hemisphere, i.e., postural, visual, or auditory stimuli, or to the homolateral somesthetic projection system.

Myers and Henson (1960) trained five chimpanzees, two with the corpus callosum and anterior commissures sectioned, to solve three latch-box problems of increasing difficulty. The Ss were restricted in their solution to the use of one hand. After mastering each problem S was shifted to the untrained hand. Normal Ss used similar movements to solve the problem with each hand and showed almost perfect positive transfer. The split-brain Ss showed no transfer effects and learned to solve the problems using different movements with each hand. Myers and Henson found no generalized test response which transferred to the untrained hand. They pointed out that in the Glickstein and Sperry experiment, Ss had both visual and tactual experience at the beginning of learning and this permitted the possibility of cross-modality generalization.

Sperry (1961) has reviewed the considerable literature that has been amassed using this technique. He summarizes the data showing

that it is possible to isolate the engram for a particular discrimination in one of the two hemispheres without the other hemisphere showing the effects of the training. It is not clear whether the cases of positive transfer effects are due to subcortical learning, sensory input that is not restricted to one hemisphere, or to some extra callosal communication system which permits the engram to be localized in both hemispheres.

Lateralization of the Engram by Means of Functional Hemidecortication

Another recently developed technique has also shown that the engram can be localized in one hemisphere. Whereas the split-brain technique requires surgical restriction of the sensory input to one hemisphere, a technique first discovered by Leao (1944) provides a way of "un-plugging" either one or both hemispheres for a limited length of time, the "un-plugged" hemispheres becoming gradually "plugged" back in again.

Leao (1944) discovered that stimulation of the exposed cortex causes a spreading depression (SD) of cortical activity from the site of stimulation. Marshall (1959) has reviewed the extensive literature resulting from Leao's original findings. Basically, SD can be evoked by strong mechanical, electrical, or chemical stimulation of the cerebral cortex. This stimulation causes a decrease in the amplitude of the local EEG which spreads very slowly across the cortex at the rate of 3 to 6 mm. per minute. The depression lasts for several minutes in all cortical areas. A single wave of depression may take as many as 20 minutes for complete recovery. If chemical stimuli such as KCl are used, repeated waves of depression spread across the cortex with no recovery of the spontaneous EEG response between waves. Depending upon the concentration of the KCl, the cortex can be depressed for as long as 3 to 5 hours.

"In addition to depression of spontaneous EEG activity, primary direct cortical responses, and strychnine spikes are also abolished in the cerebral cortex and the electrical threshold in the cortical motor areas is considerably increased. All this indicates that spreading depression is connected with deep inhibition of cortical function." (Bures, 1959, page 208.)

Posture of the animal is not much impaired. The cortical postural reflexes, e.g., placing and hopping reactions, are as completely abolished as they are following surgical decortication, but the animal is capable of running and jumping.

Bures, Buresova, and Zahorova (1958), and Bures (1959) have shown that it is possible to functionally decorticate rats by applying KCl to each hemisphere and that this decortication is fully reversible. They found that neither approach responses nor avoidance responses trained before functional decortication were available during the decorticate state but they reappeared as the cortex recovered. They monitored the spontaneous EEG activity of control rats that were also functionally decorticated and found that the recovery of the learned response in the experimental Ss coincided with the EEG recovery in the controls.

Tapp (1962) found that the duration of the depression of a well learned shuttlebox avoidance response during spreading cortical depression (SD) was directly related to the concentration of the KCl applied. The greater the concentration, the longer the depression. Similar results were reported by Bures and Bures et al.

Russell and Ochs (1960 and 1961) have used this functional decortication technique to restrict a learned response to one hemisphere. After depressing one hemisphere they trained rats to make a bar-press response for a food reinforcement, the engram being localized in the normal hemisphere. The next day the trained hemisphere was depressed and the untrained hemisphere was tested in extinction for the bar-press

response. The subjects showed only an operant level of responding. This procedure of depressing opposite hemispheres on alternate days showed that the depressed hemisphere did not benefit from the engram localized in the opposite hemisphere despite the fact that both hemispheres were normal for some 20 hours between sessions. One reinforced trial with both hemispheres normal was enough to transfer the engram from the previously trained hemisphere to the untrained hemisphere. The Ss, when tested with the previously trained hemisphere depressed and the untrained hemisphere normal, showed better than an operant level of responding even though in extinction.

Bures and Buresova (1960) have also shown lateralization of a response using SD. Using a two compartment box they trained three groups of rats to make an avoidance response. The CS were being placed in the apparatus. Five seconds later the grid was charged and S could escape by running to the safe compartment. The S could avoid by running during the five second CS-US interval. On day one Group 1 was trained with both hemispheres normal and Groups 2 and 3 were trained with the left hemisphere depressed. On day two all three groups relearned the same problem. Group 1 was retrained normal, Group 2 with SD in the left hemisphere, and Group 3 with SD in the right (previously trained) hemisphere. Both Groups 1 and 2 showed significant positive transfer, but Group 3 showed only a little (not significant) negative transfer. The avoidance response for Group 3 was localized in the right hemisphere which was not functional during relearning.

In the second half of the experiment, Bures and Buresova trained naive rats to choose the right or left of two alleys to escape or avoid shock. On day one three groups were trained to choose the left alley with both hemispheres normal. All three groups performed about the same. After an hour rest all groups were retrained, this time to go to the right alley. For this retraining Group 1 was normal, Group 2 and 3

had SD in the left hemisphere. This would protect the left alley response from counter training. The two SD groups took slightly fewer trials to learn this reversal than did the normal control group.

On day two all groups were given three free choice trials. Group 1 was tested normal and chose the right alley on all three trials. Group 2 again had SD in the left hemisphere and chose the right alley on all three trials. This is the result expected if SD blocks the left alley response. Group 3 had the right hemisphere depressed and chose the right alley only 17% of the trials. This is the result expected if SD prevents the response localized in the right hemisphere from affecting the response localized in the left hemisphere. All groups were then retrained to take the left alley to avoid shock. Groups 1 and 2 took almost three times as many trials to relearn this left alley response as did Group 3. Again these are the results expected, since for Groups 1 and 2 the functional hemisphere had last learned the right alley response, while the functional hemisphere for Group 3 had last learned the left alley response.

These results indicate that the right or left alley response could be localized in either hemisphere by the proper combinations of SD and training procedures. As in the split-brain studies there was no positive or negative transfer effects of the engram in one hemisphere on the engram in the other hemisphere.

Bures and Buresova said,

In spite of the symmetry and redundancy of input information, inactivation of the neocortex on one side during conditioning caused complete lateralization of the memory trace. This finding is contrary to the hypothesis that CRs are formed in the sub-cortex, especially in the reticular substance. . . . Were this idea correct, the learning would be bilateral at the subcortical level, and its existence could be demonstrated by more rapid elaboration of the same reflex during contralateral spreading depression. The lack of savings indicates, on the contrary that the neocortex or structures immediately associated with neocortex (thalamus) play an essential role in the formation of temporary connections. (Page 561.)

This view is consistent with the view of Lashley described above.

To summarize briefly, the engram can be localized in either hemisphere. Under proper conditions opposing responses can be trained in the two hemispheres with no apparent interference of one response with the other.

Subcortical Learning

Other attempts at isolating the mechanism necessary for learning have used surgical techniques to reduce the nervous system to the minimum structures that will still mediate learning. Culler and Mettler (1934) have tried to train a decorticate dog to make an adaptive leg flexion to avoid shock. This specific response was not learned but a generalized emotional response was conditioned to the bell CS. This same generalized emotional response appears during the early trials in the instrumental conditioning of normal dogs. Most, but not all, of the cortical tissue was removed in the decorticate dog and there was some damage to subcortical structures.

Girden, Mettler, Finch, and Culler (1936) using a decorticate dog have shown the conditioning of the generalized emotional response to acoustic, thermal, and tactile stimuli. Like the earlier study they were trying to train an instrumental avoidance response but failed. Again not all of the cortex was removed and there was some damage to subcortical structures.

More recently Bromiley (1948) successfully trained a decorticate dog to make a leg withdrawal to avoid shock. He carefully avoided giving training trials during the sham rage reactions which decorticate dogs show. Culler and Mettler and Girden, et al. took no such precautions and this may explain their failure to obtain instrumental learning. Bromiley first trained the leg flexion to a whistle. The same response was then trained to a light, and finally, the dog was trained to respond

to the light and not to the whistle. Once again not all of the cortex was removed and there was some damage to subcortical tissue.

Bures (1959) reported that functionally decorticate rats can learn a simple avoidance response but only with difficulty. After application of KCl to depress the cortex, he trained rats to run from a shock grid to a safe place. Being placed in the apparatus was the CS. Five seconds later S was shocked if he had not run to the safe side. The S was always placed on the same side of the box. Bures did not report whether the safe and shock sides were discriminably different. Only 30% of his Ss were capable of learning this response and the introduction of a wall with a door dividing the box into two separate compartments prevented any of the SD Ss from learning. It is possible that the Ss that learned the avoidance response did so because the SD was not effective.

To summarize, it has been shown that dogs and rats deprived of the cortex are capable of learning an avoidance response, the learning apparently being mediated subcortically. This evidence is not unequivocal. It is possible that in the dog studies the remaining cortical tissue may have mediated the learning. In the rat study, the SD may not have been effective so that the cortex was still functional.

PROBLEM

Two main points from all of the above seem to lead to a paradox.

1. It is possible to train one hemisphere on a response and then to train the other hemisphere on the same or opposite response without any evidence of negative or positive transfer effects from the training given to the first hemisphere (Meikle and Sechzer, 1960; Trevarthen, 1962, are exceptions to this). 2. It has been demonstrated that animals deprived of both hemispheres can learn a simple avoidance response, the learning being mediated by subcortical structures. Since both hemispheres have the subcortical structures in common, why is there failure of transfer through subcortical learning in the interhemispheric transfer studies?

The following three hypotheses can be tested by using the functional decortication technique of Leao:

1. Learning without the cortex is not possible. In the studies cited above in which dogs and rats were decorticated and then trained, there was always the possibility that the learning was actually cortical. In the dog studies, the ablation technique always left some cortical tissue. In the rat study using SD, it is possible that the KCl was not effective in the animals that learned. If no learning can occur at subcortical levels, then the failure of transfer in the interhemispheric transfer studies due to subcortical learning is not paradoxical. To test this hypothesis two groups of Ss were trained on a simple avoidance response. One group was an operated control, the other was trained under SD in both hemispheres. If no subcortical learning can occur, then the Ss trained under SD should not reach criterion.

2. Subcortical learning can take place only in the complete absence of the cortex. This is Lashley's position. If this hypothesis were true no subcortical learning would have occurred in the interhemispheric transfer studies since one hemisphere was always functional. To test this hypothesis two groups under SD were trained to make a simple avoidance response. One group was given pretraining with the cortex functional. If subcortical learning could occur only in the complete absence of cortical tissue, then the two groups would be equal when trained under SD. If the group pretrained with a functional cortex required fewer trials to learn under SD than the control group, then the hypothesis would be rejected, this being evidence for subcortical learning concurrent with cortical learning.

3. Cortical redominance. Subcortical structures can mediate a learned response in the presence or absence of the cortex, but the cortex is the dominant nervous structure controlling behavior and can override or in some way obscure the subcortically mediated response. Even if subcortical learning had occurred in the interhemispheric transfer studies, the test for transfer always occurred with the untrained hemisphere in a position to override or in some way obscure that learning. This hypothesis was tested by training two groups to make a simple avoidance response. One group was pretrained under SD to make the same response. If both groups were equivalent when they were tested with a functional cortex, then the hypothesis of cortical redominance would be accepted. If the group pretrained under SD showed positive transfer on relearning, then the cortical redominance hypothesis would be rejected.

METHOD

Design

Fifty rats were randomly assigned to five groups with ten in each group. The Ss had two training sessions separated by $4\frac{1}{2}$ hours.

Table 1 shows the design of the experiment.

Table 1. Cortical Treatment for Each Training Session

Group	Session 1	Session 2
N-N	Normal	Normal
S-S	Saline	Saline
S-K	Saline	KCl (SD)
K-K	KCl (SD)	KCl (SD)
K-S	KCl (SD)	Saline

Group N-N was not treated surgically in any way and served as a normal control. Group S-S was the operated control and was trained and retrained after application of saline to the cortex. Group S-K tested Hypothesis 2 and had pretraining after saline application and retraining under SD. Group K-K was the decorticate control group and was trained and retrained under SD. Group K-S tested hypothesis 3 and had original training under SD and retraining after application of saline.

Subjects

The Ss were 50 naive, male, albino rats 90 to 150 days of age selected from the colony maintained by the Department of Psychology of

Michigan State University. The Ss were individually caged with food and water always available.

Apparatus

Pilot research indicated that although Ss trained under SD failed to learn the shuttling response in a modified Mowrer-Miller shuttlebox, they could learn to avoid shock if the box was modified so that (1) a guillotine door divided the box into two compartments which were discriminably different, and (2) S always ran in one direction.

The 36 x 14 x 4 $\frac{1}{2}$ inch shuttlebox was divided in half by a guillotine door 3 inches wide which could be raised completely out of the box. The front of the box was clear plexiglas. The left half of the box was painted flat black and had a grid floor of brass rods 5/8 inch apart. The right half was painted flat white and its solid floor was 1/8 inch higher than the grid floor. A 90 db buzzer was mounted 2 inches from the top of the outside of the left end wall. The grid could be charged with 1.4 ma current from a C. J. Applegate stimulator (Model 228). Buzzer, shock, and guillotine door were hand operated. The intertrial interval and latencies were timed with stop watches.

Procedure

Surgery

Initial surgery: After S was anesthetized with ether and the hair on top of the skull clipped, the bone overlying the parietal lobes was exposed by a midline incision from just posterior of the eyes to just anterior to the ears. The tissue covering the skull was scraped and clipped away. Holes 5 mm in diameter were trephined bilaterally through the skull. The bone was carefully removed to avoid damage to the dura. The skin was closed with 5 to 8 cotton thread sutures. The S was

returned to his home cage for approximately 24 hours to permit recovery from the surgery.

Pretraining surgery: On the training day S was again anesthetized with ether and the incision was reopened and the holes revised and washed with mammalian Ringer's solution (0.85% NaCl, 0.01% KCl, and 0.02% CaCl₂). A 4 mm circle of filter paper, soaked in Ringer's solution for saline Ss or 25% KCl solution for KCl Ss, was placed on the dura in the bottom of each of the two holes. The incision was re-closed with 4-6 cotton thread sutures. Training procedures began 30 minutes after the application of the filter papers. The S was anesthetized for approximately 15 minutes.

Retraining surgery: Before retraining, the above procedure was repeated so that the filter papers soaked in the appropriate solution were placed in the trephined holes four hours after the last training trial of the first session. The S was returned to the home cage for a 30 minute recovery period.

Training and Retraining

Thirty minutes after application of the appropriate filter papers training was begun. The training was identical for all Ss. The S was placed in the black half of the apparatus with the guillotine door closed for five minutes of habituation. The S was then trained to a criterion of nine avoidances in ten consecutive trials plus ten over-training trials. Each trial began with the onset of the CS (buzzer on, guillotine door opened exposing the white compartment). At the fifth second of the CS, the US (1.4 ma shock) came on charging the grid floor. The CS and US stayed on until S crossed into the white compartment, CS and US terminating together. The S could avoid the US and terminate the CS by crossing into the white compartment during the CS-US interval.

The S remained in the white compartment for 90 seconds and then was picked up and placed in the center of the black compartment facing the guillotine door. Twenty-five seconds later the CS came on again. The CS-offset to CS-onset interval was 115 seconds. Description of the response and latency were recorded for each trial.

Four and one-half hours later S was retrained following the same procedures as in training.

RESULTS AND DISCUSSION

Trials to Criterion

Because the data for trials to criterion were truncated, i.e., some Ss failed to reach the criterion, medians are reported and non-parametric statistics (Mann-Whitney U tests for independent comparisons and Wilcoxon Matched-Pairs Signed-Ranks tests for repeated measures) are used for tests of significance. (Siegel, 1956).

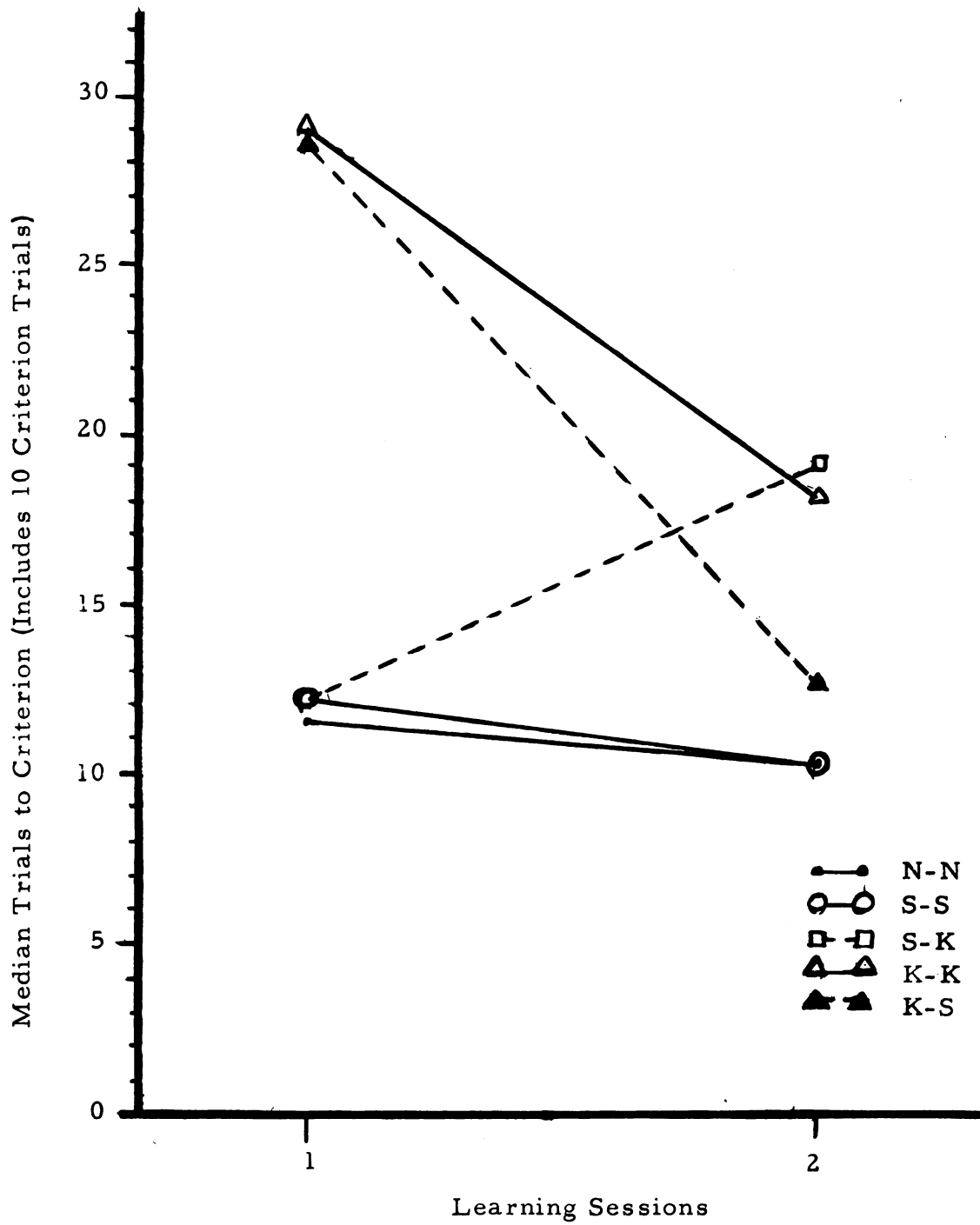
In Fig. 1 are plotted the median trials to criterion (including the 10 criterion trials) for all groups in both training sessions.

Hypothesis 1

Ninety-five percent of the Ss trained under SD met the criterion. This permits rejection of the hypothesis that the subcortex can not mediate learning.

Table 2 lists the comparisons between groups on trials to criterion in Session 1. There were no significant differences among the three control groups on original learning. Surgery alone did not slow the learning rate of the saline Ss. The two groups trained under SD were not significantly different from each other and were matched on trials to criterion. The large difference between the combined control groups and the combined SD groups was significant. As can be seen in Fig. 1, the SD Ss required more than twice as many trials to reach criterion as did Ss trained with the cortex functional. This slower rate of learning by SD Ss is in agreement with the results of others (Lashley, 1929; and Bromiley, 1948) showing that cortically damaged Ss require more trials to learn a response than normal Ss.

Figure 1
Median Trials to Criterion
Experiment I



There was no difference between normal (N-N) and operated (S-S) control groups on relearning ($\underline{U} = 49.0$, $N_1 = N_2 = 10$, $\underline{p} > .10$) which indicated again that the surgery alone did not affect the learning rate of these Ss. There was no significant difference between Group K-K and S-K on relearning in Session 2 ($\underline{U} = 46.0$, $N_1 = N_2 = 10$, $\underline{p} > .10$). The degree of transfer to the second session from the first was the same whether the original training was cortical or subcortical. Groups K-K and S-K combined took significantly more trials to reach criterion than did Group K-S in Session 2 ($\underline{U} = 40.5$, $N_1 = 20$, $N_2 = 10$, $\underline{p} < .02$). Group K-S took significantly more trials to reach criterion than the two control groups (N-N and S-S) in the second session ($\underline{U} = 10.5$, $N_1 = 20$, $N_2 = 10$, $\underline{p} < .002$).

Comparisons between learning sessions for each group appear in Table 3. Except for Group S-K, all groups showed significant positive transfer from Session 1 to Session 2. Group S-K showed significant negative transfer, taking more trials to relearn under SD than to learn originally with a functional cortex.

Hypothesis 2

The hypothesis that subcortical learning can not occur during training with a functional cortex was tested by comparing Groups S-K on relearning with Groups K-K and K-S on original learning. Group S-K benefited from the training with the cortex functional and took significantly fewer trials to relearn under SD than Ss trained originally under SD ($\underline{U} = 27.5$, $N_1 = 20$, $N_2 = 10$, $\underline{p} < .002$). Hypothesis 2 was rejected; the failures of interhemispheric transfer reported in the literature could not be explained using this hypothesis. That all learning was not subcortical was evidenced by the superior performance of Ss trained and retrained with functional cortices.

Table 2. Results of Mann-Whitney $\underline{U}$ Tests Comparing Groups in Session 1 On Trials to Criterion

Groups Compared	$\underline{U}$	N_1	N_2	$\underline{p}$
S-S vs N-N	44.5	10	10	> .10
S-K vs N-N	41.5	10	10	> .10
S-S vs S-K	50.0	10	10	> .10
K-K vs K-S	45.0	10	10	> .10
N-N, S-S, & S-K vs K-K & K-S	-5.90*	20	20	< .00006

*z scored computed from $\underline{U}$.

Table 3. Table of Wilcoxon Matched-Pairs Signed-Ranks Tests on Trials to Criterion Comparing Groups Between the Two Sessions

Group	T	N	$\underline{p}$
N-N & S-S	3	17	< .01
S-K	2	9	< .01*
K-K	7	10	< .01
K-S	0	10	< .01

*All groups showed positive transfer except Group S-K which showed negative transfer.

Rejection of Hypothesis 2 is contrary to Lashley's data which indicated no subcortical learning with the cortex functional. This will be discussed in detail later.

Hypothesis 3

Group K-S in Session 2 was compared with Groups N-N, S-S, and S-K combined in Session 1 to test Hypothesis 3. These groups did not differ significantly ($z = 0.52$, $p > .60$). Group K-S took as many trials to relearn after pre-training under SD as naive Ss with functional cortices required to learn originally. The reported failures to find interhemispheric transfer are explainable by this hypothesis, since in all cases the Ss were tested with the untrained hemisphere functional and thus capable of over-riding the subcortically mediated response.

Although the evidence clearly supports the third hypothesis, certain factors militate against unqualified acceptance. Acceptance of the hypothesis is based on the acceptance of no differences between groups. Aside from the fact that the null hypothesis can never be proved, normal Ss learn the avoidance response so rapidly that there were only a few trials in which to show savings. Group N-N and S-S showed significant savings from Session 1 to Session 2 only because 16 of the 20 Ss relearned in 10 trials, that is, perfect transfer. Anything that interfered with the avoidance response on the first three trials could have prevented significant positive transfer. Group K-S might not have shown savings due to the retention of the subcortically learned response because there were not enough trials (high enough ceiling) in which to demonstrate savings.

Group K-S showed no decrease between sessions in the percentage of trials on which a stereotyped turn around response (to be discussed below) occurred. The Turn Around (TA) response increased the response time and may have caused some Ss to escape rather than avoid shock. In the first three trials of Session 2, six of the ten Ss in Group K-S showed

one or more TA responses which were also escape trials. Retention of the TA response is itself some evidence for retention of the earlier learned response after cortical redominance.

A second possibility is that only part of the response learned subcortically was retained when the cortex was functional again. If S retained the fear response associated with the CS during cortical redominance, then this fear response could have led to freezing, increased latencies, and failure to avoid. Objectively, the freezing response is cessation of on-going activity or continuation of inactivity. The Ss in Group K-S were generally inactive while in the shock side of the apparatus and this made it difficult to tell whether S was freezing or just inactive. Individual protocols of the Ss' behavior did not reveal any responses which were classified as freezing, although freezing may have occurred and not been detected by E.

A third possibility is that the subcortically mediated response may have been forgotten during the $4\frac{1}{2}$ hours between the two learning sessions. Group K-K also showed what might be interpreted as forgetting since it did not show perfect transfer from Session 1 to Session 2 even though training was under the same neural condition in both sessions. The normal and operated control groups did show almost perfect retention. This would suggest that the subcortical engram is weaker than the cortical engram.

Which of the three possible explanations is the most valid can not be determined from the present experiment. A replication of the present study with a more difficult learning task to slow down the learning of control Ss might permit Group K-S to show any transfer effects that could occur. Such a replication would also permit re-evaluation of Hypotheses 1 and 2 as well as afford a second measure of the amount of transfer from Session 1 to Session 2 for Groups K-K and S-S. The difference in degree of transfer of these two groups bears on the hypothesis concerning the relative strengths of the cortical and subcortical engram.

Latency Data

The extreme range of trials to criterion (10 to 62) in this experiment makes it difficult to use the latencies on training trials as a second measure of learning. However, all groups had the ten criterion trials in common and although these criterion trial latency measures were not typical and were heavily weighted by performance, they were analyzed statistically. The results of the comparisons were in general agreement with the trials to criterion data. These results will not be reported here to keep the discussion unencumbered.

Behavioral Data

The typical escape or avoidance response in this experiment was a smooth run from the black box through the door to the safe compartment. On early trials this response occurred after US-onset. As learning progressed it occurred after CS-onset but before US-onset. During the experiment E observed a striking stereotyped behavior pattern different from the typical escape or avoidance response. The Ss trained under SD showed the response more frequently than did Ss trained normal. The Turn Around (TA) response consisted of variations of the following pattern. At some time after CS-onset S would run to the door--not crossing into the white safe compartment--turn 180°, run to the back wall, sometimes stopping there facing the back wall of the shock compartment, at other times turning 180° again, approaching the door to the white compartment. Sometimes S stopped before entering the white compartment; at other times he entered. At times the TA behavior occurred before CS-onset, at other times after US-onset. Sometimes S would turn around at CS-onset and again at US-onset. The TA response increased latencies.

The Ss varied widely in the frequency with which they showed TA responses. Some Ss did not show any, others as often as 90% of the trials. Only one TA was recorded for any trial regardless of the number of TAs actually made. Fig. 2 shows the median percentage of TA trials for each group for both sessions. As can be seen in the figure the SD groups had a higher percentage of TA trials than either the normal or operated control groups.

Table 4 lists the results of Mann-Whitney U tests for differences between groups for both sessions. In Session 1 the combined SD groups (which did not differ significantly from each other) showed a significantly higher percentage of TA trials than the three combined control groups (which did not differ significantly among themselves). The two control groups (N-N and S-S) did not differ significantly in Session 2 on percentage of TA behavior, but they showed a significantly smaller percentage of TA trials than Group K-K in Session 2.

Table 5 lists the comparisons between sessions for each group on percentage of TA trials. Group S-K showed a significant increase in TA trials from Session 1 to Session 2. The other groups showed no significant change between sessions.

The observation of a higher percentage of stereotyped TA responses by rats trained under SD than rats trained with normal cortices indirectly supports the assumption of functional decortication under SD. Lashley (1935) has also reported stereotyped responses in severely brain damaged rats. His Ss were trained to solve a latch-box problem. For both normal and brain damaged Ss, the first solution came accidentally. With continued practice the normal rats refined their responses to just those movements necessary for solution. Brain damaged Ss repeated the same sequence of movements which led to the first solution even though these movements delayed the solution and in some cases actually interfered with the solution of the problems. Much the same description

Figure 2
Median Percentage of TA Trials
For Each Group in Experiment I

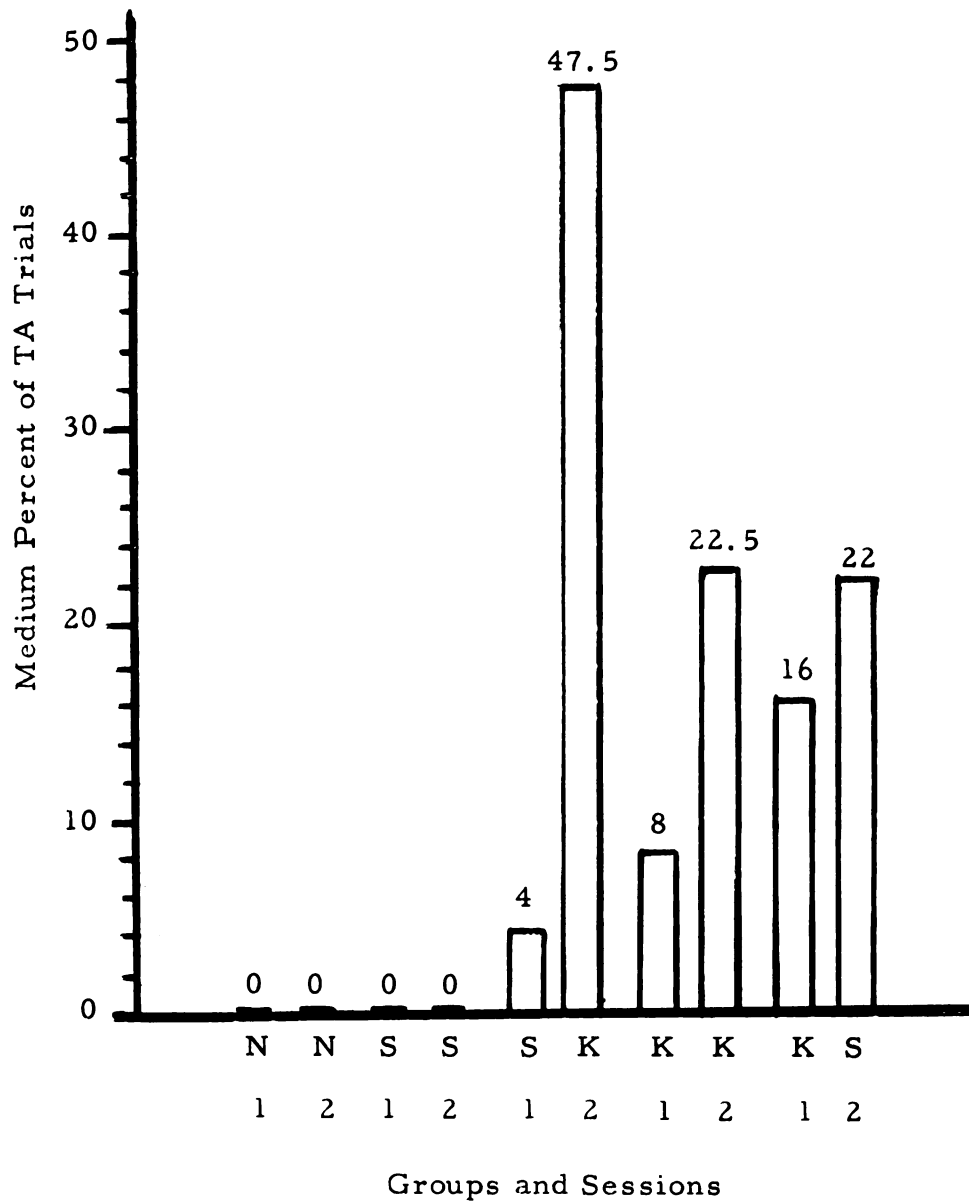


Table 4. Results of Mann-Whitney U Tests Between Groups in Session 1 and Session 2 on Percentage of TA Trials

Groups Compared	<u>U</u>	N ₁	N ₂	<u>p</u>
Session 1				
N-N vs S-S	42.5	10	10	> .10
S-S vs S-K	40.5	10	10	> .10
N-N vs S-K	48.5	10	10	> .10
N-N, S-S, & S-K vs K-K & K-S	-2.06*	20	20	< .039
K-K vs K-S	40.5	10	10	> .10
Session 2				
N-N vs S-S	40.0	10	10	> .10
N-N & S-S vs K-K	44.0	20	10	< .002

*
z computed from U.

Table 5. Results of Wilcoxon Matched-Pairs Signed-Ranks Tests For Each Group Between Sessions on Percentage of TA Trials

Group	T	N	<u>p</u>
N-N	3	5	Not tabled*
S-S	0	4	Not tabled*
S-K	1.5	10	< .01
K-K	24.0	10	> .05
K-S	28.5	10	> .05

*
N too small.

fits the TA response observed in this experiment. Normal Ss showed some stereotyped TA responses which were probably a kind of "superstitious" behavior. These responses soon dropped out to be replaced by the smooth rapid avoidance response. The SD Ss persisted in making the TA response even though it actually interfered, in some cases, with the successful avoidance response.

Not only did SD Ss show a significantly higher percentage of trials on which TA responses occurred, but a greater percentage of SD Ss exhibited the behavior at least once in the first training session than did the operated control Ss. Nine of the twenty Ss (45%) in the operated control groups showed one or more TA responses whereas seventeen of twenty Ss (85%) trained under SD showed at least one TA response. A χ^2 computed comparing the frequencies of TAs for these groups was significant ($\chi^2 = 6.18$, $df = 1$, $p < .01$). Since it might be argued that SD Ss required more trials to reach criterion than did control Ss and this gave them more opportunities to show TA behavior, a second χ^2 was computed using just the first ten trials. Again more SD Ss showed TA responses than control Ss ($\chi^2 = 4.24$, $df = 1$, $p < .05$). Seven of twenty control Ss (35%) and fourteen of twenty SD Ss (70%) showed one or more TA responses in the first ten trials in Session 1.

Observation of stereotyped behavior in functionally decorticate rats is not unexpected considering Lashley's data, but a second question remains: Why did a higher percentage of SD Ss show the response than did normal Ss?

Sensitivity Hypothesis

Not only was the TA response stereotyped, but it could be interpreted as a tendency to avoid the white, safe compartment. It is generally assumed that rats seek the dark and avoid the light when given a free choice. Both sides of the apparatus were lighted equally which made

the white compartment the brighter of the two. Functional decortication may have sensitized the SD Ss to the brightness differential of the two compartments and increased their tendency to avoid entering the white compartment. Since the Ss always ran from black to white this may have resulted in an increase in the percentage of SD Ss making TA responses. If both compartments were the same, black or white, rats should show no differential response to the two on the basis of brightness alone and the frequency of Ss making TA response should be reduced for the SD groups.

Learned Approach Hypothesis

A second explanation of the differential TA behavior between control and SD groups is that the normal Ss learn to approach the white compartment as well as avoid the black compartment. This approach tendency offsets the tendency to avoid the white compartment and reduces the number of TA responses. Several investigators (Barlow, 1952; Denny and Adelman, 1955; Mowrer, 1960; and Beck, 1961) have pointed out that in avoidance learning, S learns to escape from stimuli associated with shock onset and to approach stimuli associated with shock termination. For some reason SD Ss may fail to learn the approach component of the avoidance response. This explanation can be tested in the same way as the sensitivity hypothesis. If the two compartments are not discriminably different, both black or both white, normal Ss can not learn the approach response and will show no reduction in the frequency of TA responses.

The sensitivity hypothesis and the learned approach hypothesis make opposite predictions for an apparatus with both compartments alike. The former predicts a reduction in frequency of TA responses for SD Ss and the latter predicts an increase in frequency of TA responses for normal Ss.

Because of the uncertainty of interpretation of Hypothesis 3 and the equivocal nature of the TA response in this experiment, a second experiment was conducted which was designed to clarify these points.

EXPERIMENT II

Results of Experiment I led to the acceptance of the hypothesis that cortical redominance prevented transfer through subcortical learning in the interhemispheric transfer studies. The acceptance was not unqualified because of the extremely limited number of trials on which transfer effects from pretraining under SD could be effective when Ss were retrained with the cortex functional.

Experiment II replicates Experiment I, but uses what was considered to be a more difficult learning task for slowing down the rate of learning and increasing the range of trials on which to demonstrate transfer. Such a replication also permits re-evaluation of the three hypotheses of Experiment I.

Experiment II also tests the sensitivity hypothesis and the learned approach hypothesis suggested to explain the differential in percentage of control and SD Ss making TA responses.

METHOD

Design

Forty Ss were randomly assigned to four groups with ten Ss in each group. The Ss had two training sessions separated by $4\frac{1}{2}$ hours. Because normal control Ss did not differ significantly from operated control Ss on any of the measures used in Experiment I, no unoperated control Ss were included in this experiment. The other groups were the same as those in Experiment I. Table 6 presents the design for Experiment II and the symbols for each group.

Table 6. Cortical Treatment for Each Training Session

Group	Session 1	Session 2
S-S ₂	Saline	Saline
S-K ₂	Saline	KCl (SD)
K-K ₂	KCl (SD)	KCl (SD)
K-K ₂	KCl (SD)	Saline

Subjects

The Ss were 40 naive, male, albino rats 90 to 150 days of age selected from the colony maintained by the Department of Psychology at Michigan State University. The Ss were individually caged with food and water always available.

Apparatus

The apparatus of Experiment I was modified so that both compartments were flat black and the plexiglas front was covered on the outside with flat black paper except for a strip $1\frac{1}{4}$ inches wide which ran the length of the box and was $2\frac{1}{2}$ inches above the grid floor of the box. Except for a $\frac{3}{4}$ inch wide strip on each side of the right safe compartment, the solid floor was cut away leaving a grid floor. Thus the compartments were alike except for the solid floor border in the right compartment and any external cues detectable through the observation window.

Procedure

The same surgical and training procedures were used in Experiment II as in Experiment I.

RESULTS

Data from Experiment II were analyzed in the same way as those of Experiment I.

Trials to Criterion

The results are summarized graphically in Fig. 3. The median trials to criterion are plotted for each group in each learning session.

Hypothesis 1

Table 7 lists comparisons between groups within Session 1. The two groups trained under saline did not differ significantly nor did the two groups trained under SD. The combined saline groups (S-S₂ and S-K₂) took significantly fewer trials to reach criterion than the combined groups trained under SD (K-K₂ and K-S₂). Ninety percent (18 to 20) of the Ss trained under functional decortication met the criterion. Thus Hypothesis 1, that subcortical learning is not possible, is again rejected.

Group K-K₂ took significantly fewer trials to relearn than Group S-K₂ ($\underline{U} = 23.0$, $N_1 = N_2 = 10$, $\underline{p} < .05$). In Experiment I these two groups did not differ significantly. Group K-S₂ took significantly more trials to relearn than Group S-S₂ ($\underline{U} = 18.0$, $N_1 = N_2 = 10$, $\underline{p} < .05$). Group K-K₂ took significantly more trials to relearn than Group K-S₂ ($\underline{U} = 22.5$, $N_1 = N_2 = 10$, $\underline{p} < .05$). The groups ordered themselves in terms of transfer from Session 1 to Session 2 in this way from least to most: S-K₂, K-K₂, K-S₂, and S-S₂.

Table 8 lists the results of the tests for transfer between sessions for each group. Group S-S₂ showed no significant transfer between

Figure 3
Median Trials to Criterion
Experiment II

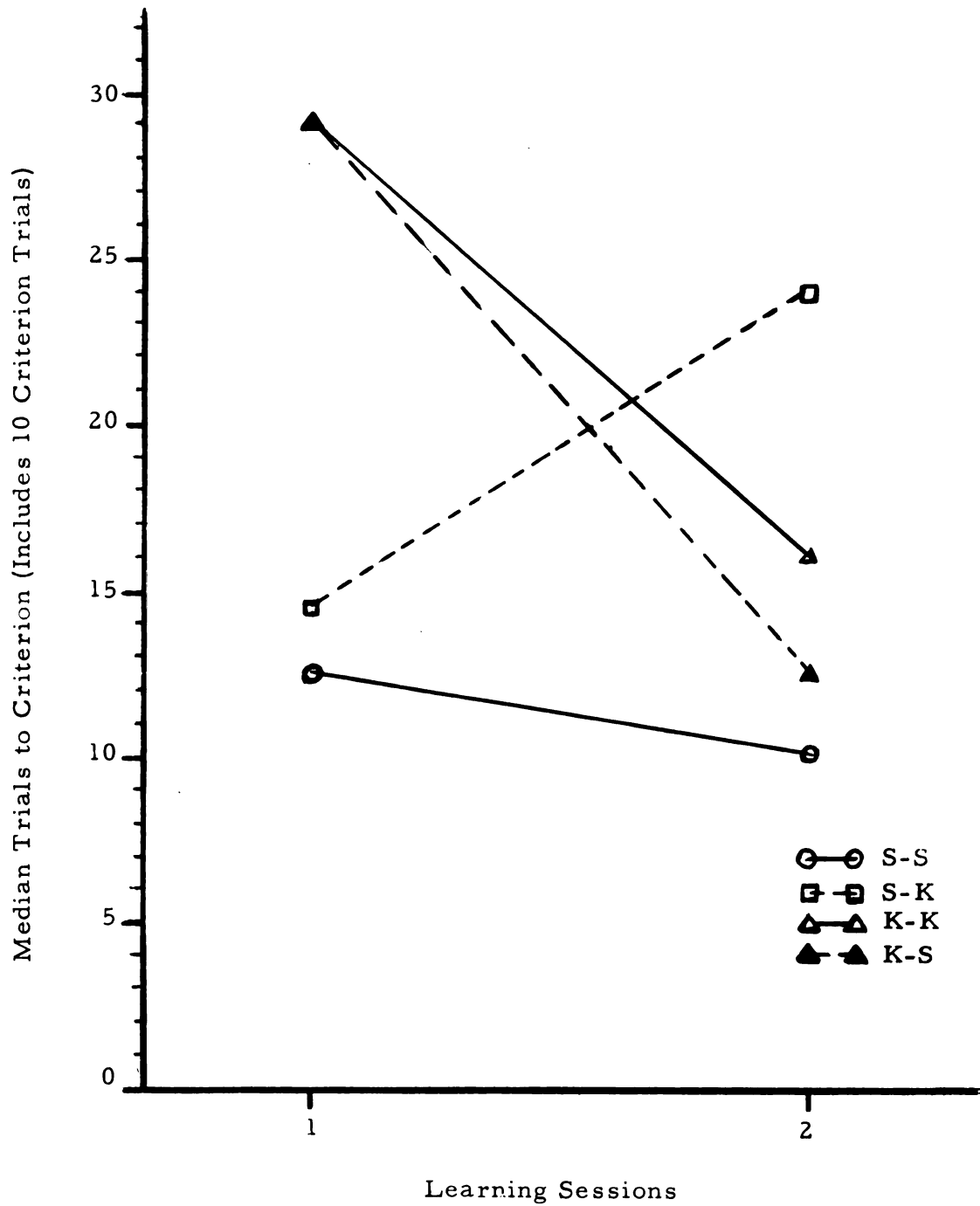


Table 7. Results of Mann-Whitney U Tests Comparing Groups in Session 1 On Trials to Criterion in Experiment II

Groups Compared	<u>U</u>	N ₁	N ₂	<u>p</u>
S-S ₂ vs S-K ₂	28.0	10	10	> .10
K-K ₂ vs K-S ₂	49.0	10	10	> .10
S-S ₂ & S-K ₂ vs K-K ₂ & K-S ₂	-5.15*	20	20	< .00006

* z computed from U

Table 8. Results of Wilcoxon Matched-Pairs Signed-Ranks Tests Comparing Group Between Sessions on Trials to Criterion in Experiment II

Group	T	N	<u>p</u>
S-S ₂	9.5	10	> .05
S-K ₂	4.0	10	< .02*
K-K ₂	1.0	10	< .01
K-S ₂	0.0	10	< .01

* All groups showed positive transfer except Group S-K which showed negative transfer.

sessions as tested by the Wilcoxon test. Only one of the ten Ss showed negative transfer, but the negative difference was as large as the largest positive difference. Group S-S₂ showed significant positive transfer as tested by the sign test ($x = 1$, $N = 10$, $p < .01$). These results were in the same direction as those for Experiment I. Groups K-K₂ and K-S₂ showed significant positive transfer between sessions. Group S-K₂ showed significant negative transfer. These results were the same as those of Experiment I.

Hypothesis 2

Hypothesis 2 was tested by comparing Group S-K₂ on relearning with Groups K-K₂ and K-S₂ on original learning. Although Group S-K₂ took fewer trials to relearn the response than Groups K-K₂ and K-S₂ took to learn it originally, the difference was not statistically significant ($\underline{U}$ to 70.5, $N_1 = 20$, $N_2 = 10$, $p > .10$). This required acceptance of Hypothesis 2, that a functional cortex prevents learning at subcortical levels. This does not agree with Experiment I in which Hypothesis 2 was rejected.

Hypothesis 3

Group K-S₂ required as many trials to relearn in Session 2 as Groups S-S₂ and S-K₂ took in Session 1 ($\underline{U} = 74.5$, $N_1 = 20$, $N_2 = 10$, $p > .10$). The hypothesis that cortical redominance over-rides or in some way obscures the subcortically mediated response was again accepted.

Behavioral Data

The TA behavior described in Experiment I was also observed in this experiment. Fig. 4 shows the median percentage of trials on

which this behavior occurred for all groups for both sessions. The SD Ss showed a higher percentage of TA responses than did control Ss.

Table 9 lists the comparisons between control and SD groups in Session 1 and 2 as tested by Mann-Whitney U tests. There was no difference between the two saline groups nor between the two SD groups in Session 1. The difference between combined control groups and the combined SD groups was significant, the SD group showing a higher percentage of trials with TA responses than control groups. The difference between Groups K-K₂ and S-S₂ in Session 2 was significant. The SD group showed a higher percentage of TA trials.

Table 10 lists the between sessions comparisons with each group. Group S-K₂, which showed a significant increase in TA behavior from Session 1 to Session 2, was the only Group to show a significant change between sessions. These results support the data of Experiment I. Having both compartments black did not change the difference between control and SD Ss on the percentage of trials on which TA responses occurred.

Neither the sensitivity hypothesis nor the learned approach hypothesis was verified by the data of Experiment II. As in Experiment I, significantly fewer Ss with a normal cortex than Ss with the cortex depressed (60% versus 95%) showed a minimum of one TA response over all trials in Session 1 ($X^2 = 5.16$, $df = 1$, $p < .025$). Control and functionally decorticate groups did not differ significantly on the percentage of Ss showing at least one TA response in the first ten trials ($X^2 = 2.60$, $df = 1$, $p > .10$, 45% vs. 75%). In Experiment I 35% and in this experiment 45% of the control Ss showed at least one TA response in the first ten trials. This difference was not significant ($X^2 = 0.104$, $df = 1$, $p > .50$). Seventy percent of the SD Ss in Experiment I and 75% in the present experiment showed at least one TA response in the first ten trials. This difference was not significant ($X^2 = 0.00$, $df = 1$, $p > .95$).

Figure 4
Median Percentage of TA Trials
For Each Group in Experiment II

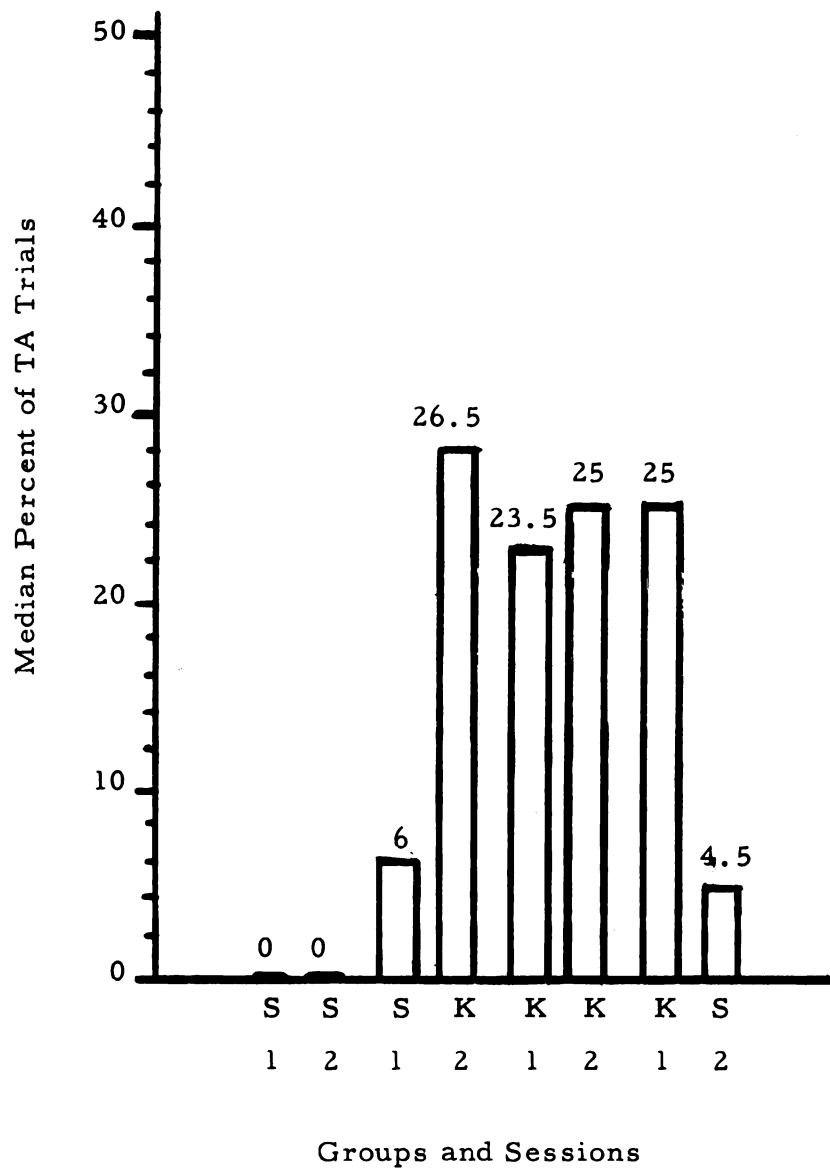


Table 9. Results of Mann-Whitney $\underline{U}$ Tests Between Groups in Session 1 and Session 2 on Percentage of TA Trials in Experiment II

Groups Compared	$\underline{U}$	N_1	N_2	$\underline{p}$
Session 1				
S-S ₂ vs S-K ₂	31.0	10	10	> .10
K-K ₂ vs K-S ₂	40.0	10	10	> .10
S-S ₂ & S-K ₂ vs K-K ₂ & K-S ₂	-3.04*	20	20	< .0024
Session 2				
K-K ₂ vs S-S ₂	22.0	10	10	< .05

* $\underline{z}$ computed from $\underline{U}$

Table 10. Results of Wilcoxon Matched-Pairs Signed-Ranks Tests For Each Group Between Sessions in Experiment II on Percentage of TA Trials

Group	T	N	$\underline{p}$
S-S ₂	3	3	Not tabled*
S-K ₂	4	9	< .05
K-K ₂	13	8	> .05
K-S ₂	9.5	10	> .05

* N too small.

Seventy percent of the SD Ss in Experiment I and 75% in the present experiment showed at least one TA response in the first ten trials. This difference was not significant ($\chi^2 = 0.00$, $df = 1$, $p > .95$). There was no significant difference between the two experiments on the percentage of control Ss showing TA responses over all trials (45% vs. 60%, $\chi^2 = 0.40$, $df = 1$, $p > .50$). There were no significant differences between the two experiments on the percentage of SD Ss showing TA responses over all trials ($\chi^2 = 0.28$, $df = 1$, $p > .50$). There was neither a decrease in the number of SD Ss nor an increase in the number of control Ss showing TA response in Experiment II due to both compartment being black.

Data from Experiment I and Experiment II Compared

Results of Experiment II are in general agreement with those of Experiment I. Examination of Figures 1 and 3 indicates that many of the corresponding groups in each experiment had about the same median trials to criterion. Table 11 lists the median trials to criterion for each group in the two learning sessions for both experiments. Table 12 lists the comparisons between experiments for each group in both learning sessions on trials to criterion. Of the eight comparisons, only Group S-K in Session 1 showed a significant difference between the two experiments. Because the other groups agree so well, the difference for this group was probably due to sampling error rather than to any real differences in the two experiments. Group S-K₂ appears to have a slightly elevated number of trials to criterion in both sessions. From the statistical analysis it can be concluded that the changes in the apparatus did not slow down the learning rate in Experiment II as expected.

Table 13 lists the comparisons between corresponding groups in the two experiments on the percentage of stereotyped TA responses.

Table 11. Median Trials to Criterion for the Two Experiments in Both Sessions

Group	Session 1		Session 2	
	Expt. 1	Expt. 2	Expt. 1	Expt. 2
N-N	11.5	----	10.1	----
S-S	12.1	12.5	10.1	10.2
S-K	12.1	14.5	19.0	24.0
K-K	29.0	29.0	18.0	16.0
K-S	28.5	29.0	12.5	12.5

Table 12. Results of Mann-Whitney U Tests Comparing Corresponding Groups of Experiments I and II on Trials to Criterion

Groups	Session 1				Session 2			
	U	N ₁	N ₂	<u>p</u>	U	N ₁	N ₂	<u>p</u>
S-S vs S-S ₂	44.0	10	10	> .10	45.0	10	10	> .10
S-K vs S-K ₂	17.5	10	10	< .02	31.5	10	10	> .10
K-K vs K-K ₂	55.0	10	10	> .10	39.0	10	10	> .10
K-S vs K-S ₂	50.5	10	10	> .10	53.0	10	10	> .10

Table 13. Results of Mann-Whitney U Tests Comparing Corresponding Groups of Experiments I and II on the Percentage of TA Trials

Groups	U	N ₁	N ₂	<u>p</u>	U	N ₁	N ₂	<u>p</u>
S-S vs S-S ₂	48.0	10	10	> .10	40.0	10	10	> .10
S-K vs S-K ₂	40.0	10	10	> .10	52.5	10	10	> .10
K-K vs K-K ₂	43.0	10	10	> .10	44.0	10	10	> .10
K-S vs K-S ₂	34.5	10	10	> .10	35.0	10	10	> .10

Table 14. X² Tests Between Corresponding Groups of Experiments I and II On the Number of Ss Showing at Least One TA Response In All Learning Trials and in the First Ten Learning Trials

Group	Total Trials						First Ten Trials					
	Expt. 1	Expt. 2					Expt. 1	Expt. 2				
	No. of Ss	No. of Ss	X ²	p			No. of Ss	No. of Ss	X ²	p		
S-S	4	4	0.00	> .95			4	2	0.25	> .50		
S-K	5	8	0.88	> .75			3	7	1.80	> .10		
K-K	8	9	0.00	> .95			6	8	0.24	> .50		
K-S	9	10	0.00	> .95			8	7	0.00	> .95		

There were no significant differences between any of the corresponding groups. The two experiments are equivalent on this behavioral measure.

There were no significant differences between any of the groups in percentage of Ss showing TA responses for all trials or just the first ten trials. Table 14 lists the results of the X^2 tests between groups in the two experiments as well as the number of Ss showing the TA response in the first ten trials or in all trials of Session 1.

Painting the safe compartment black did not significantly change the number of Ss making TA responses in Experiment II. Neither the sensitivity nor the learned approach hypothesis was supported.

In almost all ways the two experiments are equivalent and can be combined for further statistical analysis. The same statistical analysis applied to the two separate experiments was used on the two combined.

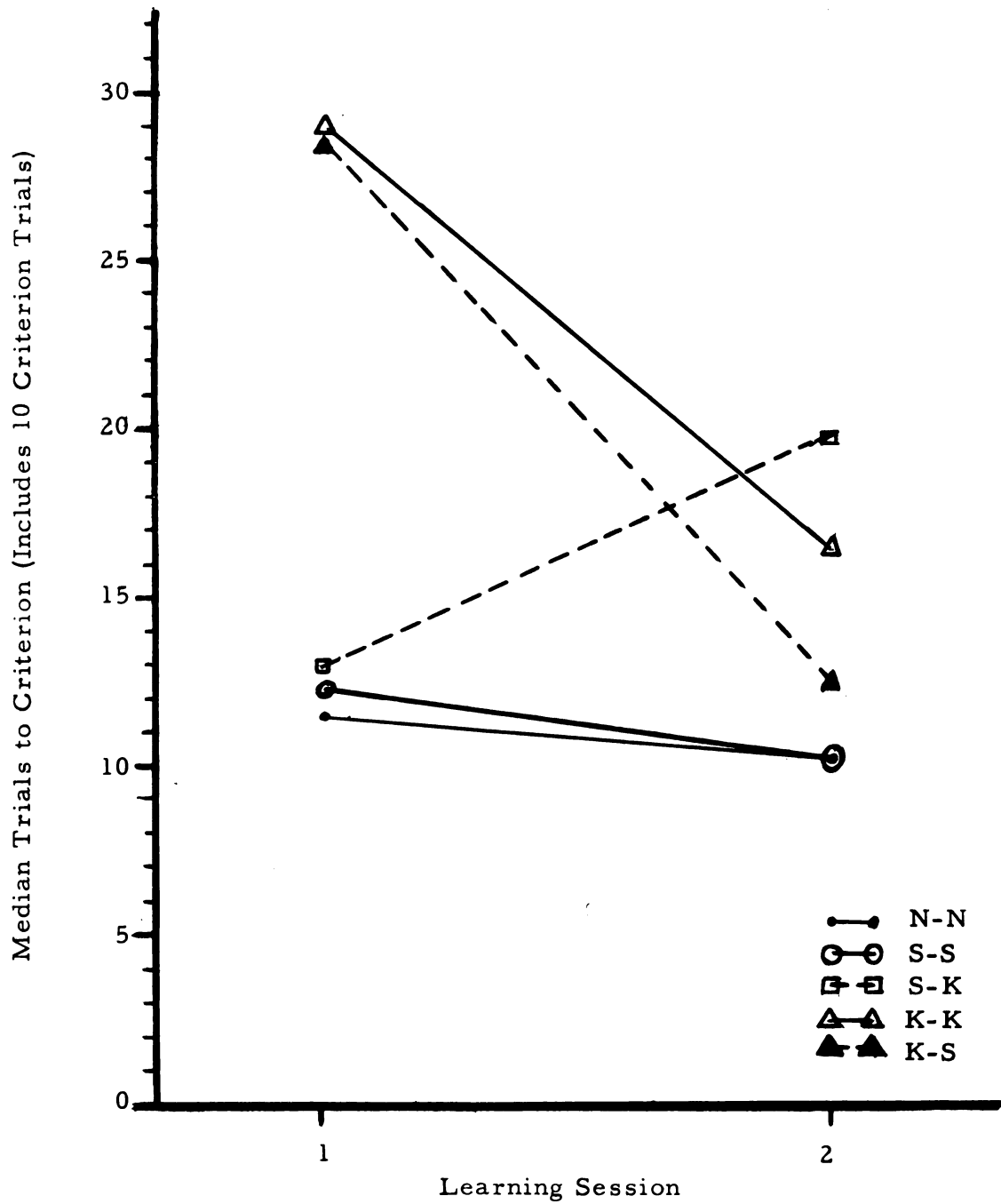
Trials to Criterion

Fig. 5 shows the median trials to criterion for each group in both sessions for the combined experiments.

Hypothesis 1

Table 15 lists the comparisons between groups in Session 1. There were no significant differences between the two saline control groups nor between the two SD groups. The two groups trained under KCl required significantly more trials to reach criterion than did the two saline control groups. Not counting the criterion trials, the groups trained under SD took almost eight times as many trials to reach the criterion series as did the operated controls (18.75 compared to 2.5). Only 7.5% (3 of 40) of the Ss trained under functional decortication failed to learn the avoidance response. Functionally decorticate rats can learn a simple avoidance response. Hypothesis 1 was rejected.

Figure 5
Median Trials to Criterion
of the Combined Experiments



There was no significant difference between Group K-Kc and Group S-Kc on relearning in Session 2 ($\underline{z} = 1.28$, $\underline{p} > .20$) even though one group was trained originally with a functional cortex and the other was trained under SD. Groups K-Kc and S-Kc combined took significantly more trials to reach criterion in Session 2 than Group K-Sc ($\underline{z} = 3.18$, $\underline{p} < .00006$). Group K-Sc took significantly more trials to relearn than Group S-Sc ($\underline{z} = 4.10$, $\underline{p} < .00006$).

Table 16 shows the results of tests for transfer between sessions for each group. Group S-Kc showed a significant increase from Session 1 to Session 2. All other groups showed a significant decrease in trials to criterion in the second session.

Hypothesis 2

The hypothesis that no subcortical learning occurs with the cortex functional was rejected. Group S-Kc took significantly fewer trials to reach criterion under SD in Session 2 than Groups K-Kc and K-Sc combined in Session 1 ($\underline{z} = 3.21$, $\underline{p} < .00006$). Learning occurs at cortical and subcortical levels simultaneously when training is given to a normal S.

Hypothesis 3

Hypothesis 3, subcortical learning is possible but cortical re-dominance over-rides the subcortically mediated response, was accepted. Group K-Sc took as many trials to relearn after pretraining under SD as Groups S-Sc and S-Kc took to learn originally. There was no significant difference between Group K-Sc in Session 2 and Groups S-Sc and S-Kc in Session 1 ($\underline{z} = 0.60$, $\underline{p} > .54$). The Ss in the interhemispheric transfer studies reported in the literature may have failed to show transfer due to subcortical learning because the subcortically mediated responses were obscured by the redominance of the cortex.

Table 15. Results of U Tests Between Groups in Session 1 on Trials to Criterion for the Combined Experiments

Groups Compared	<u>U</u>	<u>z</u>	N ₁	N ₂	<u>p</u>
S-Sc vs S-Kc	154.5	1.23	20	20	> .21
K-Kc vs K-Sc	207.5	0.20	20	20	> .80
S-Sc & S-Kc vs K-Kc & K-Sc	20.5	7.50	40	40	< .00006

Table 16. Results of Wilcoxon Matched-Pairs Signed-Ranks Tests Comparing Each Group Between Sessions for the Combined Experiments

Group	T	N	<u>p</u>
S-Sc	15.5	17	< .01
S-Kc	11.0	19	< .01*
K-Kc	16.0	20	< .01
K-Sc	0.0	20	< .01

* All Groups Showed positive transfer except Group S-K which showed negative transfer.

Behavioral Data

The results of the combined experiments on median percentage of TA behavior is presented in Fig. 6. Except for Group K-Sc in Session 2, the Ss trained under SD showed more TA behavior than Ss trained with the cortex functional.

Table 17 lists the comparisons between groups in both sessions on proportion of TA responses. Neither the two saline groups nor the two SD groups differed significantly on the percentage of TA responses. The combined SD groups showed significantly more TA behavior than the combined control groups in Session 1. Group K-Kc showed significantly more TA behavior than Group S-Sc in Session 2.

Table 18 lists the comparisons between sessions for each group. Group S-Sc and K-Kc showed no significant change from the first to the second session. Group S-Kc showed a significant increase from the normal to the SD condition. Group K-Sc showed a decrease from Session 1 to Session 2, but it was not significant.

As in the two separate experiments, the combined experiments showed that the SD Ss had a higher proportion of TA responses than did normals.

Fifty-two percent of the operated control Ss and 90% of the SD Ss showed at least one TA response over all trials in Session 1 in the combined experiments. This difference was significant ($\chi^2 = 11.96$, $df = 1$, $p < .001$).

Forty percent of the operated control Ss and 72.5% of the SD Ss showed at least one TA response in the first ten trials in Session 1 for the combined experiments. This difference was significant ($\chi^2 = 7.31$, $df = 1$, $p < .01$).

Not only did the SD Ss show a higher proportion of TA trials, but a higher percentage of SD Ss showed the response than did normals. Neither the sensitization nor the learned approach hypothesis was supported.

Figure 6
Median Percentage of TA Trials For Each Group
For the Combined Experiments

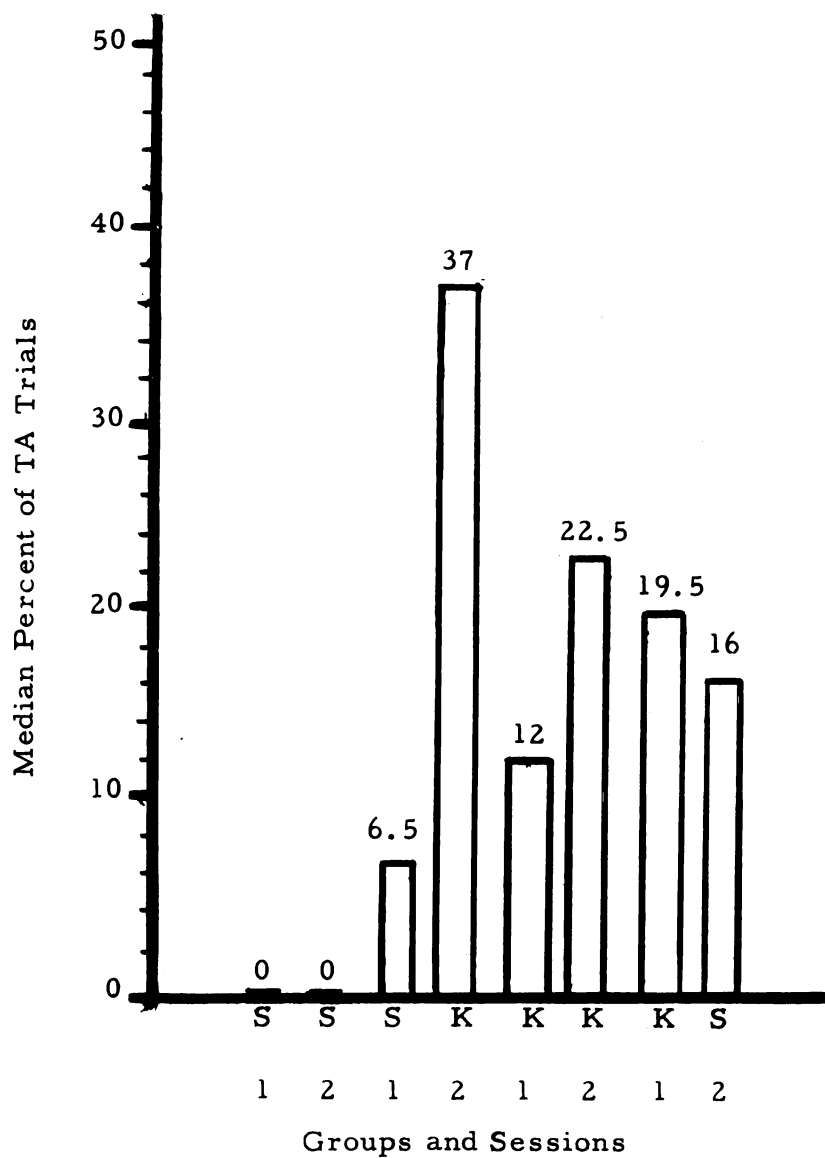


Table 17. Results of Mann-Whitney U Tests Comparing Groups in Session 1 and Session 2 on Percentages of TA Trials for the Combined Experiments

Groups Compared	<u>U</u>	<u>z</u>	N ₁	N ₂	<u>p</u>
Session 1					
S-Sc vs S-Kc	143.5	1.52	20	20	> .12
K-Kc vs K-Sc	164.0	0.97	20	20	> .33
S-Sc & S-Kc vs K-Kc & K-Sc	379.0	4.05	40	40	< .00006
Session 2					
S-Sc vs K-Kc	84.0	3.14	20	20	< .00006

Table 18. Results of Wilcoxon Matched-Pairs Signed-Ranks Tests For Each Group Between Sessions For the Combined Experiments

Group	T	N	<u>p</u>
S-Sc	6	7	> .05
S-Kc	10	19	< .01
K-Kc	69.5	18	> .05
K-Sc	71	20	> .05

DISCUSSION OF THE COMBINED EXPERIMENTS

The combined experiments lead to the rejection of the first hypothesis. All but three of the forty Ss trained under functional decortication learned the avoidance response. These results are in keeping with the data on learning in decorticated dogs and in functionally decorticate rats. Failure of interhemispheric transfer can not be attributed to the inability of the subcortex to mediate a learned response.

That the acquisition of the avoidance response by SD animals was not an artifact of failure to achieve functional decortication is supported by the large difference between SD and control animals in number of trials to criterion.

A second possibility in the present experiment is that the cortex may not have been completely depressed in the SD animals. Thus the learning may have been mediated by still functional cortical areas rather than by the subcortex. Bures (1959) reported that in the rat, SD produced by KCl affects all cortical areas. However, damage to the cortex can block the spread of depression in the area of the injury. In the present experiment care was taken to avoid damaging the dura or the underlying cortex during the surgery. Despite this care, some damage may have occurred. The brains of the SD Ss were not examined for damage after the experiment.

The assumption that the SD was not complete in Session 1 of these experiments raises several questions about the results obtained in Session 2. For Group K-Kc in Session 2, the cortex could have been completely depressed or part of the cortex (either the same part as in Session 1 or a different part) could have remained functional. If all the cortex was depressed in Session 2 for Group K-Kc, why did this

group relearn so fast? If a different cortical area was functional in Session 2 than was functional in Session 1, again, why did Group K-Kc relearn so fast? If the same cortical area remained functional in both sessions, why did Group K-Kc require so many trials to relearn? For Group K-Sc, unless the previously depressed areas of the cortex interfered in Session 2 with the response mediated by the undepressed area of Session 1, why did Group K-Sc fail to show transfer similar to Group S-Sc in Session 2? The incomplete depression hypothesis raises more questions than it answers.

Since trials are confounded with time, a third alternative is that the SD Ss learn only after recovery from functional decortication. Two sources of evidence argue against this interpretation. The first comes from the results of Bures (1959) and Bures et al. (1958). They have repeatedly found that 25% KCl causes SD in the rat which lasts from three to five hours after initiation. Training trials in the present experiment were always terminated within two and one-half hours after initiation of SD. This left a safety factor of one-half hour.

The second source of evidence against the interpretation that learning occurred only after recovery from SD is inherent in the present experiment. If the SD groups had learned only after recovery from the functional decortication it would be expected that Group K-Sc would show transfer similar to that of the control group. They did not. It is concluded that the Ss trained under SD can learn a simple avoidance response, the learning being mediated subcortically.

A higher percentage (92.5) of SD Ss learned in the present experiments than in the experiment by Bures (1959) (30%). In both this and the Bures experiment the learning task was an avoidance response. There were very probably some important differences between the two even though they can not be specified since Bures did not describe his method in detail. The probability of learning in the present experiment

was increased by using a CS with several elements (buzzer and opening of the guillotine door) plus a long safe-side confinement. Weisman (1961) has shown that a long safe-side confinement increases learning rate. Bures reports that in his experiment normal Ss took from 10 to 15 trials to learn the avoidance response. Normal Ss required only 2.5 trials in the present study. Bures also reports that introduction of a wall with a small door which divided his box into two separate compartments completely prevented his decorticate rats from learning. This emphasizes the importance of task difficulty in training decorticate rats.

The results of the combined experiments permitted acceptance of the hypothesis that learning occurs at both cortical and subcortical levels during training with a functional cortex.

These results appear to be at variance with those of Bures et al. (1958), Bures and Buresova (1961), Russell and Ochs (1960 and 1961), and Tapp (1962). These investigators have found no retention or relearning of a response trained with the cortex functional when the S was tested under SD. Bures et al. first trained rats to escape and avoid shock to a buzzer CS by jumping upon one of four balls resting on the grid floor. The safe ball was made of wire mesh, the others were of smooth wood. Actually the task was a visual-tactual discrimination problem and probably of much greater difficulty than the problem used in the present experiment. After Ss met the criterion of 90% avoidances for five days they were tested for the response under SD. Test trials were given every 10 minutes until the response recovered. They found that the response did not recover for from three to five hours or after 25 to 30 trials had been given. Time for recovery and test trials (which were also relearned trials) were confounded in this experiment. From the results of the present experiment it appears that some learning should have occurred during these test trials. No such learning was reported,

although if it had occurred, it may have occurred near the end of the test series and may have been mistaken for recovery of the response rather than relearning by the subcortex. The response may have been too difficult for mastery at the subcortex. Bures et al. reported that some of the SD Ss could not even find the safe ball in order to escape let alone avoid.

Bures and Buresova (1961) failed to find interhemispheric transfer of a simple avoidance response. The response was trained in the right hemisphere with the left hemisphere under SD. When the conditions were reversed, the right hemisphere being depressed and the left hemisphere functional, no savings were detected. Normal Ss in this experiment required an average of 19 trials to reach the criterion of 9 to 10 avoidances. Again the problem may have been too difficult for subcortical learning. Bures and Buresova concluded from their experiment that learning does not take place in the subcortex, a finding which is not substantiated by the present experiment. Their failure to find interhemispheric transfer through subcortical learning may have been due to the complexity of the task used or to cortical redominance, the third hypothesis of the present experiment.

Tapp (1962) in a balanced Latin square design tested the depression effect of five concentrations of KCl on a shuttlebox avoidance response. The response was well learned and relearned before each test session. Each S was trained under all five concentrations and had as few as 20 or as many as 150 trials under each concentration. Training was terminated after the first 20 trials or on any trial thereafter if S met a criterion of 10 consecutive avoidances. This gave a maximum of 750 trials under SD (with recovery of the cortex between sessions) in which S could learn the response subcortically. Tapp reported a CER-like response which occurred under SD but he did not call it subcortical learning. The CER may have been retained from the cortical to the

subcortical conditions or it may have been learned subcortically since test trials were also learning trials. Again subcortical learning may have occurred near the end of a test session and been mistaken for recovery of the cortex. If subcortical learning had occurred, some transfer from session to session should have been detectable. Tapp found no such transfer. Group K-Kc in the present experiment did not show perfect transfer from the first to the second session; some "forgetting" had occurred in the $4\frac{1}{2}$ hour interval. Since Tapp used a more difficult task and a longer intersession interval even more "forgetting" may have occurred than in the present experiment and could account for the failure of transfer. The other interpretation is that no subcortical learning of the shuttlebox response had occurred because the response was too difficult to be mastered subcortically.

Russell and Ochs (1960 and 1961) localized a bar-press response in one hemisphere by training the Ss with the other hemisphere under SD. The Ss when tested in extinction with the trained hemisphere depressed and the untrained hemisphere functional showed that the untrained hemisphere had not benefited from the previous training. The effects of subcortical learning did not appear during these tests. The bar-press response may have been too difficult for subcortical mastery or cortical redominance of the untrained hemisphere may have inhibited the subcortically mediated response.

Russell and Ochs found that one reinforced trial with both hemispheres functional was enough to transfer the engram from the trained to the untrained hemisphere. The Ss when tested in extinction with the trained hemisphere depressed now showed a higher level of responding than would be expected from one reinforced bar-press. This increase in response rate may have been due in part to subcortical learning that had occurred during training of the other hemisphere.

The present experiment indicates that subcortical learning is possible with or without the cortex present. This provides a way for interhemispheric transfer to occur in split-brain animals. Analysis of the data of this and other experiments points out the importance of task difficulty in subcortical learning. The two cases of positive interhemispheric transfer in split-brain Ss (Meikle and Sechzer, 1960; and Trevarthen, 1962) used a simple brightness discrimination. More difficult problems such as threshold brightness or pattern discriminations failed to transfer. The subcortex may not be capable of mastering these responses. The failure of interhemispheric transfer in split-brain Ss may have been due to failure to learn by the subcortex because the problem was too difficult.

Acceptance of the hypothesis that learning occurs at subcortical levels when an S is trained with the cortex functional is in direct contradiction to Lashley's statements that the subcortex does not learn with the cortex present. Lashley's conclusion was based on evidence derived from surgical ablation of cortical structures after training of the response. Since it took as many trials to relearn the response, now by the subcortex, as in the original learning, he concluded that the subcortex had not learned with the cortex present. The explanation of these results may lie in the side effects of surgical ablation. Not only is the cortex removed, but tissue in the subcortex, especially in the thalamus, is also damaged due to retrograde degeneration. Such damage may interfere with the subcortical memory mechanism.

The positive transfer of brightness discriminations in split-brain preparations found by Meikle and Sechzer (1960) and Trevarthen (1962) is also in opposition to Bures et al. (1958), Bures and Buresova (1960), and Lashley (1950). As stated above this interhemispheric transfer could have been due to subcortical learning.

The combined experiments lead to the acceptance of the cortical redominance hypothesis. Although rats can learn an avoidance response with the subcortex, later training with the cortex functional permits the untrained cortex to inhibit the subcortically mediated response.

The negative data of the interhemispheric transfer studies are explainable on the basis of this hypothesis. The positive transfer effects found by Meikle and Sechzer (1960) and Trevarthen (1962) are not. It is possible that in these cases of positive transfer, the transfer was due to transfer of the engram through some extra callosal mechanism rather than through subcortical learning. This mechanism could not however, transfer pattern discriminations nor threshold brightness discriminations. There is no anatomical evidence for such an extra callosal pathway. This evidence of positive transfer of brightness discriminations in split-brain animals is strong evidence against the third hypothesis. Several alternative explanations for the data of the present experiment which led to the acceptance of the cortical redominance hypothesis were suggested in Experiment I.

One alternative explanation of the failure of transfer from the subcortical to cortical condition for Group K-Sc assumes that there is good retention of the CER component of the avoidance response. This CER may have produced freezing responses and inhibition of the avoidance response in the second session. No freezing responses were detected in the second session although they may have occurred and gone unnoticed. Why an S should retain the CER component of the avoidance response and not the motor components from the SD condition is in itself a problem. The early versions of Mowrer's two factor theory assumed the emotional components of the avoidance response was the result of conditioning of the autonomic nervous system. This would explain the retention of the CER but not the loss of the motor response. A second explanation is that the CER had more trials than

the avoidance response in the first session. A differential forgetting hypothesis is more complicated than the weak subcortical engram hypothesis to be discussed below.

A second alternative hypothesis assumes retention of the TA response from Session 1 to Session 2 for Group K-Sc. Retention of this response into the early trials of the second session could have caused longer latencies and failure to avoid. Thus although the third hypothesis was accepted it may not be true. A higher ceiling for learning by normal Ss would provide more opportunity for any transfer effects from subcortical learning to occur on retraining with a functional cortex. The present experiment does not test the third hypothesis adequately.

A final alternative explanation for the data supporting Hypothesis 3 assumes the cortical engram is stronger than the subcortical engram. With the passage of time the subcortical engram fades below the threshold for the response, the cortical engram does not. The Ss trained under SD showed less savings when retrained later on the same response, either under SD or normal, than Ss trained normal and retrained normal. This supports the weak subcortical engram hypothesis. The strength of the engram localized in the subcortex with the cortex present did not differ from the strength of the engram localized in the subcortex with the cortex functionally removed. Both groups required about the same number of trials to relearn with the cortex depressed.

Spontaneous weakening of a memory trace is not generally accepted as an explanation for forgetting. Some interference is usually postulated to account for failure to recall. A source of interfering responses in this pair of experiments could be from the recovered cortex during the period between training sessions. This is really a variation of the cortical redominance hypothesis, the redominance having an effect between sessions rather than just during relearning. This hypothesis would predict greater forgetting with longer delays between training

sessions for Ss trained under SD. Further research using the design of the present experiments but a more difficult learning task to provide a more adequate test for transfer between sessions is needed before the cortical redominance hypothesis can be accepted without qualifications.

The Ss trained under SD showed more stereotyped TA behavior than did normal Ss. This is in complete agreement with Lashley's data for brain damaged rats on the problem box. The first TA response for either normal or SD Ss probably occurred as an accident during the early escape trials. Since this response would eventually end in escape from the shock it would be "chained" in. For normal Ss this "chain" was broken by some change in the internal or external environment and the more adaptive avoidance response took its place. The Ss trained under SD did not break this "chain" as easily. The external and internal environment are probably different for normal and decorticate rats. Stimuli to which normal Ss can respond may not be effective with the impaired Ss. Stereotyping of behavior in SD rats may be a result of this reduction to the perceptual world which ordinarily contributes to changes in behavior.

Neither the sensitivity hypothesis nor the learned approach hypothesis were supported by the data of Experiment II. The greater tendency of decorticate than normal Ss to make TA responses may be due to the general impairment of the SD Ss. This impairment, whether motor or perceptual, may have prevented the rapid escape response on early trials. The longer the S was in the shock compartment, the greater the opportunity for a TA response to occur and become stereotyped. Normal Ss typically showed rapid escapes and thus had less opportunity for the TA response to occur. This explanation does not require the hypothesizing of any avoidance tendency for SD rats nor any approach tendency for normal rats.

SUMMARY

An experiment and a replication investigated the transfer of an avoidance response from the cortical to the decorticate state and from the decorticate to the cortical state. The experiments were designed to test several hypotheses suggested to explain the reported failure to find transfer from the trained to the untrained hemisphere through subcortical learning in the interhemispheric transfer studies. The hypotheses tested were: 1) Transfer does not occur because subcortical learning cannot occur. 2) Transfer does not occur because subcortical learning cannot occur in animals with intact cortices. 3) Transfer does not occur because the untrained hemisphere interferes with the subcortically learned response. Use of spreading cortical depression permitted testing of transfer of an avoidance response between all combinations of cortical and functionally decorticate states.

Ninety rats (50 in the first experiment and 40 in the replication) were trained to avoid shock by running from a shock compartment at the onset of a buzzer and the opening of the guillotine door which divided the Mowrer-Miller shuttlebox into two compartments. In Experiment I the shock compartment was black with a grid floor and the safe compartment was white with a solid wood floor. In the replication both compartments were black with grid floors. The Ss were trained, then $4\frac{1}{2}$ hours later retrained to a criterion of nine avoidances in ten trials plus ten overtraining trials.

In Experiment I ten Ss were trained with no surgical or cortical treatment and were the normal control group for both experiments. In both Experiment I and II a group of ten Ss were trained and retrained under each of the following conditions: Group S-S was an operated

control group. Group S-K was trained after application of saline to the hemispheres and retrained under functional decortication achieved by placing 25% KCl on the exposed dura of both hemispheres. (Twenty-five percent KCl causes a depression of cortical activity which lasts three to five hours and is fully reversible.) Group K-K, the decorticate control group, was trained and retrained under SD. Group K-S was trained under functional decortication and retrained with the cortex functional.

The two experiments demonstrated that functionally decorticate Ss required almost eight times as many trials to learn as Ss trained with the cortex functional. Surgery alone did not interfere with learning or relearning. All groups showed positive transfer in the second session, except Group S-K which required more trials to relearn under SD than to learn originally.

Results indicated that subcortical learning accompanied cortical learning. Animals pretrained with a functional cortex required fewer trials to relearn under SD than Ss trained under SD with no such pre-training.

The hypothesis that redominance of the untrained cortex interferes with a subcortically mediated response was supported by the data of the two experiments. Animals pretrained under SD required as many trials to relearn the response with the cortex functional as Ss required to learn it originally with the cortex functional. Several alternatives were offered to explain this result.

Animals trained under SD exhibited a stereotyped response that interfered with the efficient avoidance response. Impairment of the perceptual or motor responses of the functionally decorticate Ss was suggested as the mechanism for stereotyping.

REFERENCES

- Barlow, J. A. Secondary motivation through classical conditioning: One trial non-motor learning in the rat. Amer. Psychol., 1952, 7, 273 (Abstract).
- Beck, R. C. Secondary reinforcement and shock termination. Psychol. Bull., 1961, 58, 28-45.
- Bromiley, R. B. Conditioning in the dog after removal of the neocortex. J. comp. physiol. Psychol., 1948, 41, 102-110.
- Bures, J. Reversible decortication and behavior in The Central Nervous System and Behavior. Ed. Brazier, M. A. Madison, N. J., Madison Publishing Co., 1959.
- Bures, J. and Buresova, O. The use of Leaõ's spreading depression in the study of interhemispheric transfer of memory traces. J. comp. physiol. Psychol., 1960, 53, 558-563.
- Bures, J., Buresova, O., and Zahorova, A. Conditioned reflexes and Leaõ's spreading cortical depression. J. comp. physiol. Psychol., 1958, 51, 263-268.
- Culler, E. and Mettler, F. A. Conditioned behavior in a decorticate dog. J. comp. Psychol., 1934, 18, 291-303.
- Denny, M. R. and Adelman, H. M. Elicitation theory: II. The formal theory and its application to instrumental escape and avoidance conditioning. Unpublished theoretical paper, Michigan State University, 1956.
- Girden, E., Mettler, F. A., Finch, G., and Culler, E. Conditioned responses in a decorticate dog to acoustic, thermal, and tactile stimulation. J. comp. Psychol., 1936, 21, 367-385.
- Glickstein, M. and Sperry, R. W. Intermanual transfer in split-brain monkeys after somatic cortical ablation. Amer. Psychol., 1960, 15, 485 (Abstract).

- Glickstein, M. and Sperry, R. W. Intermanual somesthetic transfer in split-brain Rhesus monkeys. J. comp. physiol. Psychol., 1960, 53, 322-327.
- Lashley, K. S. Brain Mechanisms and Intelligence. Chicago, Chicago University Press, 1929.
- Lashley, K. S. Studies in cerebral function in learning: XI The behavior of the rat in the latch box situation. XII Nervous structures concerned in acquisition and retention of habits based on reactions to light. Comp. Psychol. Monographs., 1935, 11, No. 2, No. 52.
- Lashley, K. S. In search of the engram in Physiological Mechanisms in Animal Behaviour. Number IV of Symposia of the Society of Experimental Biology, New York, Academic Press Inc., 1950.
- Leaõ, A. Spreading depression of activity in the cerebral cortex. J. Neurophysiology, 1944, 7, 359-390.
- Marshall, W. H. Spreading cortical depression of Leaõ, Physiol. Rev., 1959, 39, 239-279.
- Meikle, T. H. Role of corpus callosum in transfer of visual discriminations in the cat. Science, 1960, 132, 1496.
- Meikle, T. H. and Sechzer, J. A. Intercocular transfer of brightness discriminations in split-brain cats. Science, 1960, 132, 734.
- Mowrer, O. H. Learning Theory and Behavior, New York, Wiley, 1960.
- Myers, R. E. Interocular transfer of pattern discriminations in cats following sectioned of crossed optic fibers. J. comp. physiol. Psychol., 1955, 48, 470-473.
- Myers, R. E. Function of corpus callosum in interocular transfer. Brain, 1956, 79, 358-363.
- Myers, R. E. and Henson, C. O. Role of the corpus callosum in transfer of tactuokinesthetic learning in Chimpanzees. A. M. A. Arch. Neurol., 1960, 3, 404-409.

- Myers, R. E. and Sperry, R. S. Interocular transfer of a visual form discrimination habit after section of the optic chiasma and corpus callosum. Anat. Record, 1953, 115, 351 (Abstract).
- Russell, I. S. and Ochs, S. Localization of behavior control in one cortical hemisphere. The Physiol., 1960, 3, 152 (Abstract).
- Russell, I. S. and Ochs, S. One trial interhemispheric transfer of a learning engram. Science, 1961, 133, 1077-1078.
- Sperry, R. W. Corpus callosum and interhemispheric transfer in the monkey Macacca mulatta. Anat. Record, 1958, 131, 297 (Abstract).
- Sperry, R. W. Cerebral organization and behavior, Science, 1961, 133, 1749-1757.
- Sperry, R. W., Stamm, S., and Miner, N. Relearning tests for interocular transfer following division of the optic chiasma and corpus callosum in cats. J. comp. physiol. Psychol., 1956, 49, 529-533.
- Stamm, J. and Sperry, R. W. Function of the corpus callosum in contralateral transfer of somesthetic discriminations in cats. J. comp. physiol. Psychol., 1957, 50, 138-143.
- Trevarthen, C. B. Simultaneous learning of two conflicting problems by split-brain monkeys. Amer. Psychol., 1960, 15, 485 (Abstract).
- Trevarthen, C. B. Double visual learning in split-brain monkeys. Science, 1962, 136, 258-259.
- Tapp, J. T. Reversible cortical depression and avoidance behavior in the rat. J. comp. physiol. Psychol., 1962, 55, 306-308.
- Walsh, E. G. Physiology of the Nervous System. Longmans, Green and Co., London, 1957.
- Weisman, R. G. The acquisition and extinction of an avoidance response as a function of length of non-shock confinement. Unpublished Master thesis, Michigan State University, 1961.

APPENDIX

Table 19. Raw Data for Trials to Criterion and TA Responses in Experiment I

S#	Trials to Criterion	Session 1		Session 2		
		Number of TA Responses		Number of TA Responses		
		First 10 Trials	Total Trials	Trials to Criterion	First 10 Trials	Total Trials
Group N-N						
1	10	0	0	11	1	1
2	11	2	2	10	3	3
3	11	0	0	10	0	0
4	11	0	0	10	0	0
5	11	0	0	10	0	0
6	12	2	2	10	0	0
7	13	0	0	10	0	0
8	13	6	8	10	0	0
9	14	3	3	10	0	0
10	14	0	0	11	0	0
Group S-S						
1	10	0	0	10	0	0
2	10	0	0	10	0	0
3	12	0	0	10	0	0
4	12	0	0	12	0	0
5	12	0	0	10	0	0
6	12	2	2	10	0	0
7	12	1	1	10	0	0
8	13	1	1	10	0	0
9	18	0	0	10	0	0
10	19	0	0	11	0	0
Group S-K						
1	11	0	0	18	4	5
2	11	0	0	12	8	8
3	12	0	0	12	6	6
4	12	0	0	61	0	8
5	12	0	0	20	0	1
6	12	1	1	16	9	13
7	12	2	2	20	4	9
8	13	0	1	25	3	18
9	14	0	2	11	1	1
10	15	5	5	20	5	15

Continued

Table 19 - Continued

S#	Trials to Criterion	Session 1		Trials to Criterion	Session 2	
		Number of TA Responses			Number of TA Responses	
		First 10 Trials	Total Trials		First 10 Trials	Total Trials
<u>Group K-K</u>						
1	23	5	8	22	1	6
2	23	0	0	39	1	8
3	25	1	3	12	0	0
4	27	1	14	15	8	11
5	28	1	1	13	0	0
6	30	0	1	17	4	4
7	34	6	31	19	3	13
8	35	6	31	21	8	18
9	62	3	23	13	0	0
10	62	0	3	35	0	0
<u>Group K-S</u>						
1	16	6	10	14	5	6
2	21	2	12	11	5	5
3	22	5	12	13	0	0
4	25	1	11	11	5	5
5	28	1	1	12	0	0
6	29	2	5	20	8	14
7	35	2	3	11	2	2
8	41	3	6	13	4	4
9	57	0	3	11	0	0
10	∞	0	0	16	3	3

Table 20. Raw Data for Trials to Criterion and TA Responses in Experiment II

S#	Trials to Criterion	Session 1		Session 2		
		Number of TA Responses		Trials to Criterion	Number of TA Responses	
		First 10 Trials	Total Trials		First 10 Trials	Total Trials
<u>Group S-S₂</u>						
1	11	0	0	10	0	0
2	11	0	0	10	0	0
3	11	0	0	16	0	0
4	12	0	0	10	0	0
5	12	0	0	11	0	0
6	13	0	1	10	0	0
7	13	0	1	10	0	0
8	14	5	6	10	1	1
9	15	0	0	10	0	0
10	21	2	3	18	7	7
<u>Group S-K₂</u>						
1	11	0	0	13	2	2
2	13	1	1	14	4	4
3	13	2	2	0	1	14
4	13	0	0	40	7	36
5	14	7	7	27	5	19
6	15	0	1	17	0	0
7	16	3	3	21	1	1
8	18	4	6	28	9	19
9	20	1	1	31	4	19
10	21	1	1	18	0	0
<u>Group K-K₂</u>						
1	17	0	0	20	0	0
2	18	0	1	16	0	0
3	21	4	10	15	10	15
4	26	3	3	13	3	6
5	26	4	9	13	4	4
6	32	3	3	10	0	0
7	38	3	21	13	2	2
8	40	8	37	16	10	16
9	43	10	31	20	10	15
10	∞	1	1	20	3	4

Continued

Table 20 - Continued

S#	Session 1			Session 2		
	Trials to Criterion	Number of TA Responses		Trials to Criterion	Number of TA Responses	
		First 10 Trials	Total Trials		First 10 Trials	Total Trials
Group K-S ₂						
1	21	4	6	11	0	0
2	23	9	21	11	1	1
3	25	3	3	14	6	6
4	26	2	18	12	7	7
5	27	7	20	13	4	4
6	31	7	28	11	0	0
7	32	2	3	14	2	2
8	34	0	1	14	0	0
9	36	0	8	11	0	0
10	∞	0	9	19	0	0

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