PERFORMANCE OF SPATIAL ALTERNATION UNDER CONDITIONS OF
FOOD APPROACH VS. SHOCK ESCAPE IN THE NORMAL AND ANTERIOR DECORTICATE RAT

by   613-8302

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The impairment commonly associated with certain brain lesions is specific to the motivational condition under which the brain damaged subject is trained. The following is an examination of the possibility that the deficit in alternation learning associated with an anterior cortical lesion in the rat is dependent upon the motivational condition of the subject.

A relatively small but significant amount of evidence exists which suggests that various types of impairment may be motivation specific. An example of this is found in a study by Robbins and Meyer (1971). Their rats were trained on a series of three two-choice pattern discriminations. Each discrimination was learned under one of two motivational conditions, food approach or shock avoidance. The six groups of rats differed with respect to the motivational sequence in which they were trained on the three problems (one group, for example, learned the first task under food approach, the second under shock avoidance, and the third under food approach). Immediately after reaching criterion on the third task the rat was subjected to electroconvulsive shock (ECS). After 24 hours he was tested for retention on either the first or the second task. The authors found that ECS impaired retention of a habit learned under the motivational conditions similar to those existing when ECS was given. It had little effect, however, on habits learned under the motivational conditions which differed from those existing when ECS was given. Retention was a function, not of the task, but of the motivational condition under which training occurred.

Motivational differentiation has also been demonstrated in the deficits associated with lesions or stimulation of certain areas of the brain. Krechevsky (1936) found that, while posterior decorticate rats were inferior to normals in learning a brightness discrimination habit in which

the dark stimulus was the reinforced alternative, the difference was decreased when animals were punished for errors with electric shock. He concluded from this that the brain damaged animal had an impairment in attention level. When shock was delivered as punishment, the attention level was heightened, thus compensating for this deficit and allowing the lesioned animal to perform with efficiency comparable to the normal animal.

Training with different motivational conditions has, in some instances, led to opposite effects on the subject's performance during brain stimulation. Grossman (1966), for example, found that a shuttle box avoidance task was facilitated by stimulation of the midbrain reticular formation, while performance on several appetitive tasks was impaired during stimulation of the same site.

Another hypothesis explaining motivational specificity suggests that certain brain mechanisms capable of mediating the impaired task in place of the damaged area are activated by shock but not food deprivation. Sechser (1963) found that interocular transfer of pattern discrimination in the cat following section of the corpus callosum and optic chiasm occurred if the animal was trained with shock avoidance. It had previously been established that no transfer took place when training was carried out with food approach. Sechser concluded that the extracallosal subcortical pathway mediating the transfer could be activated by shock avoidance but not food approach motivation.

Best and Hamburg (1966) found that a brightness discrimination habit trained under unilateral spreading depression transferred when the contralateral cortex was depressed if an avoidance or escape paradigm was used. Bivens and Ray (1965) had previously shown that transfer did not occur when water reinforcement was used. Best and Hamburg concluded that storage of a brightness habit must occur in brain areas not affected by cortical spreading

depression and that the learning of a task must occur at different levels of the brain depending on the reinforcement conditions.

Together these data suggest that some of the deficits classically associated with damage to some brain structures may be a function of studying the subject under too limited a set of conditions and that, under optimal motivational conditions, the performance of certain brain damaged animals may be made comparable to that of normal animals.

There is evidence which suggests that the impairment associated with anterior cortical lesions in the rat is another example of a deficit which is dependent on the motivational condition under which the subject is tested. The most consistently reported deficit observed in rats with an anterior lesion is a spatial deficit, involving performance on problems requiring alternation of responding. This includes position reversal, single and double alternation, and delayed alternation (Hunter and Hall, 1941; Bourke, 1947; Gross, Chorover and Cohen, 1965; Loucks, 1931; and Carpenter, 1954). In addition, studies by Jeeves (1947), Bourke (1947), and Gross et. al. (1965) demonstrated that the deficit was restricted to tasks involving spatial cues. When visual cues were available, the animal showed no deficit.

Without exception, the above experimenters used food approach as the motivational condition in their studies. When Thompson (1964) used shock avoidance to train anterior rats on a position reversal problem, he observed no deficit. In another study, Thompson (1959) used escape from water as the motivation. He ran blind and nonblind anterior decorticate rats in a water maze having eight culs de sac. For blind rats the task becomes a spatial alternation, yet he again observed no deficit. These studies suggest that the anterior deficit may be dependent on the motivational conditions under which the animal must perform.

A possible explanation for motivation specific impairments, not con-

sidered in the hypotheses discussed previously, is that the nature of the task itself may vary under different motivational conditions. Certain characteristics of the task may be unique to the motivation which is used. An impairment following brain damage might, then, be restricted to those characteristics of a particular task which are unique to only one of the motivational conditions, resulting in a motivation specific impairment. While it is not believed that this hypothesis could explain motivational specificity in all cases, a study by Carpenter (1954) suggests that it may explain the results obtained with anterior decorticate rats. The task used was an example of position alternation, the type of problem which usually reflects the anterior cortical impairment. Run in a four choice-point maze, the subjects were required to go right at the first three choice points and left at the final one (RRRL) in order to obtain a food reward. The results of this study indicated that the normal animal had a tendency to make what Carpenter labelled an anticipatory error, defined as a response in a sequence of responses which, although incorrect when made, would be correct later in the sequence. In Carpenter's problem, the greatest number of errors occurred at the second and third choice points. For rats with anterior cortical lesions, the error trend followed the same pattern as that of the normal rat but many more errors occurred. These data indicate that both normal and anterior rats are predisposed to making the same type of error on the task. This suggests that the anterior deficit on spatial alternation may result from an inability to suppress these errors.

The following experiment was designed, first, to test the hypothesis that the anterior deficit on spatial alternation is restricted to food approach motivation. It was also intended to investigate the possibility that the deficit on this task produced by an anterior cortical lesion is a heightened tendency to make anticipatory errors, and to determine if these

errors are a unique characteristic of a food approach paradigm. The absence of anticipatory errors in a shock escape situation could then explain a relative lack of impairment under these conditions.

The data of Robbins and Meyer (1971) indicate that normal rats learn a task in the four choice-point maze in almost the same number of trials whether the motivation is food approach or shock avoidance. Although subjects may learn in the same number of trials, it is possible that the type of error tendency will differ under food approach vs. shock avoidance.

The evidence suggests that this may not be the case for the anterior decorticate animal. While learning a spatial task is greatly impaired under food approach, it seems to be unimpaired under shock avoidance. This sparing under shock avoidance suggests that differences may occur in the way the anterior animal learns the problem. The difference may be the type of error committed by the animal. It has already been shown that the anterior lesion exaggerates the rat's tendency to commit anticipatory errors. If shock escape differs from food approach in producing some error tendency other than anticipatory errors, it is possible that the anterior animal may have no more difficulty suppressing this error than does the normal rat, thereby explaining the lack of impairment under shock avoidance motivation. The deficit may be due not merely to the spatial characteristics of the task but to the lesioned subject's impaired ability to suppress the errors prepotent in the task as a result of the existing motivational condition.

On the basis of the existing evidence, and in line with the proposed hypothesis, it was expected that the normal animal would learn a spatial task like that used by Carpenter with nearly equal efficiency under both food approach and shock escape motivation. The anterior animal would be comparable to the normal under shock escape but deficient under food approach.

While learning efficiency was expected to be the same for both normal

groups, the type of error committed under shock escape was expected to differ from that found by Carpenter under food approach. The type of error would also differ between anterior groups. However, under food, the number of errors would be much greater than in the normal group, while under shock, the number of errors committed by the anterior decorticate animals was not expected to differ greatly from that of the normal animals.

Method

Subjects

The subjects were 40 male Long-Evans hooded rats approximately 150 days of age and weighing 250-400 grams at the start of testing. Animals trained to run for food reinforcement were deprived to 80% body weight and maintained at this level throughout testing. Animals trained to escape shock were maintained on an ad lib diet of laboratory chow. All animals received water ad lib.

Apparatus

A modified Krechevsky apparatus, similar to that described by Robbins and Meyer (1971) was used. This maze consisted of a start box, 4 two-choice units and a goal box (Figure 1). It was constructed of wood and painted with a semi-gloss black enamel throughout. The apparatus was set on a stainless steel grid which could be covered with a black wooden floor.

Each choice unit was made up of 3 compartments. The first of these (29 cm. long) contained the actual choice point which consisted of two openings (19 cm. high x 14 cm. wide) located in the far wall. The stimuli, consisting of identical black panels with a circular opening (6.3 cm. diameter) centered near the bottom, could be placed into these openings. The next compartment (15 cm. long) was divided so that the rat, having passed through one of the stimulus panels was confined to the alley which he had entered. Each of these alleys opened into the last compartment of the choice unit through an opening (11 cm. wide, 10 cm. high), covered by a black curtain, in the far wall. The final compartment (14.7 cm. long) contained a center opening (10.5 cm. wide x 10 cm. high) in the opposite wall to direct the rat back to center

Figure Caption

Figure 1. A schematic diagram of the modified Krechevsky apparatus designed
after Robbins and Meyer (1971), showing an aerial view of the
structure of the four 2-choice units and a frontal view of the
stimulus panel.

goal box

stimulus panel

choice unit

curtain

stimulus panel

start box
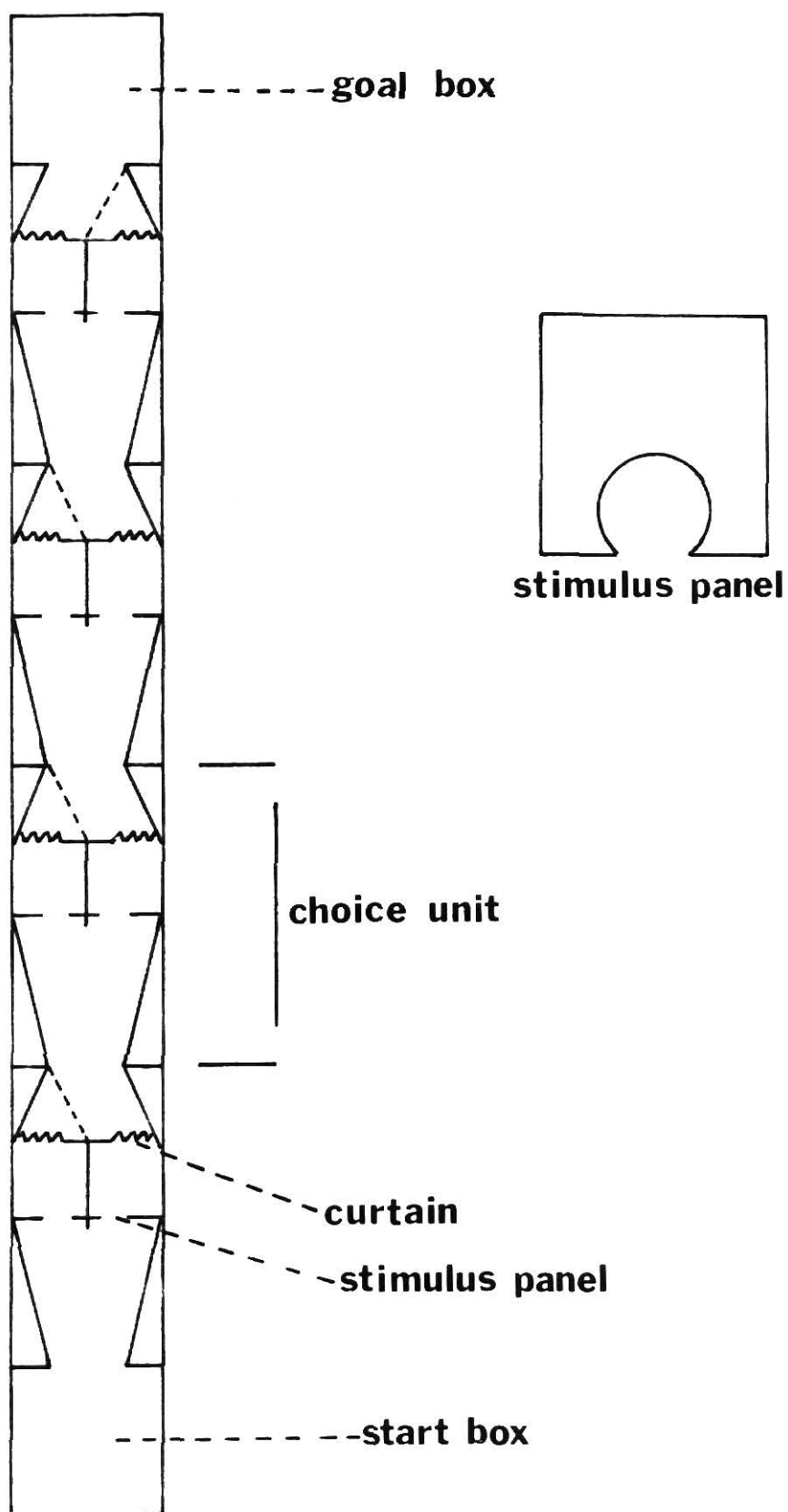
before confronting the choice point in the next choice unit. A black panel placed diagonally across this compartment blocked access to the center opening from the alley which had been designated incorrect. Black curtains were placed over the opening in the far wall of the center compartment to prevent the possibility that the rat would see the unblocked pathway by looking through the opening in the stimulus panel.

Doors separated the 4 choice units and the goal and start boxes. These doors were operated with a pulley system so that they could be raised and lowered by the experimenter from a single point in the room. Illumination was provided by four $7\frac{1}{2}$ watt bulbs placed 1.2 meters above each choice point.

White noise in the room was produced by a Grason-Stadler model 455C white noise generator. A 6-8 ma shock was delivered to the grid by a model E1064GS Grason-Stadler shock generator.

Surgery

All operations were performed under Equithesin anesthesia. Following a longitudinal incision of the scalp and retraction of muscle and connective tissue, the skull was removed anterior to bregma until the olfactory bulbs were visible. The dura was reflected and cortical tissue was removed by aspiration. The extent of the lesion was intended to include the cortical tissue from anterior to the bregma to the frontal pole and from the midline lateral to the rhinal fissure. During the first three postoperative days the rats were fed Gerber's baby cereal since a slight finickiness had been observed in anterior rats immediately following surgery. A two week period was allowed for the rats to regain their preoperative weight.

Following testing, subjects were given an overdose of Equithesin anesthesia and perfused successively with normal saline and 10% formalin.

Brains were removed and examined for extent and depth of the lesions.

Design

Prior to training, half of the 40 subjects received the anterior
cortical lesion. All subjects were then divided into four equal groups. One
normal and one anterior group were trained on the task with shock escape
while one normal and one anterior group were trained with food approach. All
animals trained originally as normals received an anterior cortical lesion
subsequent to testing. After a two week recovery period, these animals were
tested for retention of the task.

Food Pretraining

During all stages of training with food, the grid was covered by a
black wooden floor. On day 1, all doors, curtains and stimulus panels were
removed from the maze and subjects were allowed to explore freely for 15
minutes. Several 45 mg. Noyes pellets were placed in the goal box during
this session. On day 2, subjects were trained to run the entire length of
the maze in the absence of curtains and stimulus panels. The rat was placed
in the goal box several times until he learned to approach the food cup
immediately and eat the pellet placed there. He was next placed in the
final choice unit and trained to run through either alley of this unit into
the goal box for a food pellet. When the subject had learned to run into the
goal box without hesitating, he was placed in the third choice unit and
required to run the length of both choice units to receive the food pellet.
This was repeated for three trials, after which the rat was placed in the
start box and required to run the entire length of the maze. The rat was
reinforced with four Noyes pellets for each complete run through the maze.
Throughout training, as the rat passed from one choice unit to the next, the
door separating the units was closed behind him to prevent retracing.

On day 3, subjects were trained on the correction procedure which would be required during testing. One of the alleys following each choice point was blocked so that, when the subject entered the blocked alley he could progress no further in the maze unless he returned to the choice compartment and entered the other alley. This was repeated for several trials, blocking at random different alleys each time, until animals were correcting wrong choices without hesitation. The curtains were then placed over the openings which led to the final compartment of each choice unit. These were introduced so that the rats could not see which alley was unblocked before entering it. Three additional correction trials were then given so that the subjects could become accustomed to moving through the curtain.

Escape Pretraining

This procedure was essentially the same as for the food subjects, except that the grid was exposed and the rats were trained to run into the goal box to escape shock rather than obtain food, which was never present during the pretraining or discrimination training of shock escape subjects. On day 1, subjects were allowed to explore the maze with all doors, curtains and stimulus panels removed and in the absence of shock. On day 2, subjects were trained to run the length of the maze. Each rat was first placed in the goal box several times so that training would be comparable to that of the food subjects. The rat was then placed in the last choice unit and shocked until he ran into the goal box. This was repeated until the rat ran into the goal box without hesitating. Each subject was moved successively further back from the goal box, in the same manner as the food subjects, until he was running the entire length of the maze to escape the shock. On day 3, subjects were trained on the correction procedure described for the food subjects. Shock was never terminated for these rats until they entered the goal box.

Discrimination Training

On day 4, the stimulus panels were placed in the openings at the choice points and testing was started. Subjects were trained to run to one position at the first three choice points and to the opposite position at the final choice point. Half the subjects in each of the four groups were trained to follow the response sequence RRRL while the rest were trained to follow the sequence LLLR. Subjects were run 10 trials each day to a minimum of 40 trials or until they reached the criterion of 5 successive runs through the maze with no errors. Errors (defined as passing the forefeet through the opening in the stimulus panel of the blocked alley) at each of the choice points were recorded for every trial.

Postoperative Retention

After reaching criterion, all twenty normal subjects were given an anterior cortical lesion, allowed 2 weeks for recovery, and tested for retention of the task. The procedure used in testing for retention was the same as that used during discrimination training. Subjects were tested on the same task and under the same motivational conditions postoperatively as they had experienced preoperatively. No additional pretraining was given prior to relearning.

Results

Diagrams of the anterior cortical lesions for both the learning and retention groups are presented in Figure 2. The extent of the lesion appears to be consistent between groups. The rostro-caudal extent was in compliance with the area intended for removal, but the medial and lateral extent was generally not as great as had been intended.

The mean number of trials required by each group to reach the criterion of 5 successive correct trials is presented in Table 1. An analysis of variance on the number of trials to criterion revealed no reliable differences in the number of learning trials between the food and shock groups ($F=0.002$, $df=1/32$, $p> .05$), the normal and anterior groups ($F=0.044$, $df=1/32$, $p> .05$), or the different sequence groups ($F=0.475$, $df=1/32$, $p> .05$). No reliable interactions were found between these conditions.

Error data were first analyzed by comparing groups with respect to the number of errors made at each choice point within the first block of 40 trials. Square root transformations may be used on scores which consist of frequencies such as number of trials or number of errors (Winer, 1972). An analysis of variance of these scores indicated that a reliable difference occurred between reinforcement conditions ($F=5.13$, $df=1/32$, $p< .05$). Animals run under food approach made more errors than animals run under shock escape. Within the groups, the number of errors differed reliably between choice points ($F=22.53$, $df=3/96$, $p <.001$), and a choice point x reinforcement interaction was found ($F=3.47$, $df=3/96$, $p< .05$). These data are presented in Figure 3a. Newman Keuls' tests indicated that differences between the food approach and shock escape animals occurred at choice point 1 (CP-1) and choice point 4 (CP-4) ($p <.05$). The shock escape subjects made reliably
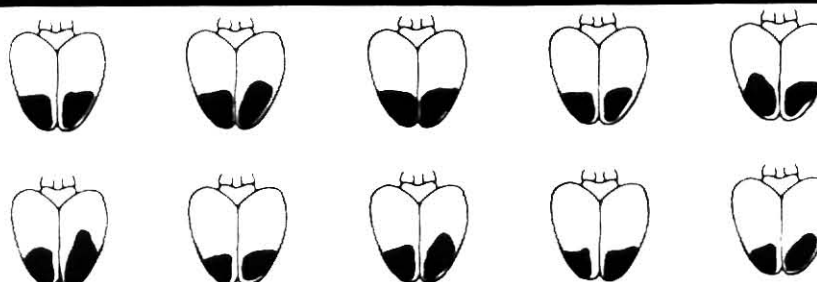
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Figure Caption

Figure 2. Diagrams of the anterior cortical lesions of subjects trained

following surgery (learning) and subjects trained originally as

normals and subsequently retested following surgery (retention).
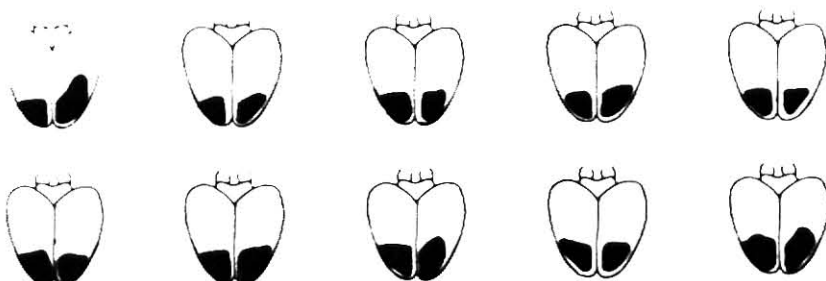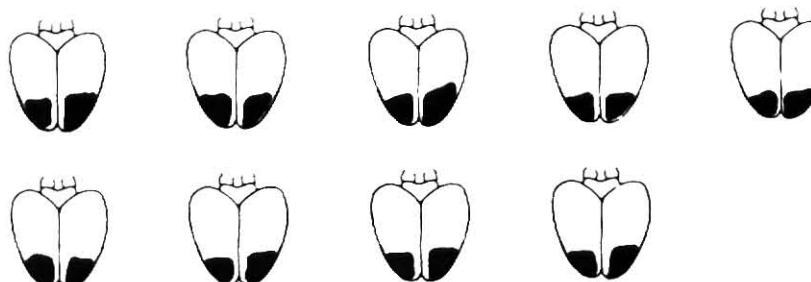
Food Approach Learning
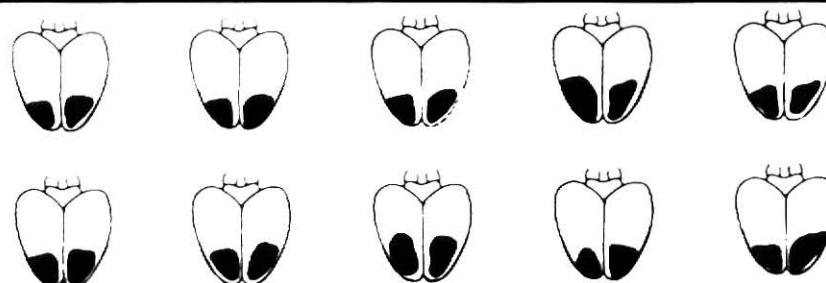
Shock Escape Learning

Shock Escape Retention

Food Approach Retention

Table 1

Trials to Criterion

Groups	Choice Sequence			
	RRRL		LLLR	
	Mean	S.D.	Mean	S.D.
Normal Shock	33.4	14.6	52.2	30.5
Normal Food	48.0	18.6	43.2	20.6
Anterior Shock	36.4	22.7	57.6	37.9
Anterior Food	51.0	19.0	38.8	15.0

Note.- A criterion of 5 successive trials with no errors was required.

fewer errors at CP-1 and CP-4 than did the food approach subjects (Figure 3b).
However, the number of errors did not differ between food and shock at choice
point 2 (CP-2) or choice point 3 (CP-3) (p > .05), accounting for the choice
point x reinforcement interaction.

These results suggest that the error trend across choice points may
be flatter for subjects run under food approach than for subjects run to
escape shock. This is supported by Newman Keuls' tests of the difference
across choice points within groups. In the shock condition, reliably more
errors were made at CP-3 than at any other choice point (p < .05), while the
fewest number of errors were made at CP-1 (p < .05). CP-4 and CP-2 were the
only choice points which did not differ from each other (p > .05). In the food
condition, the fewest number of errors were made at CP-1 (p < .05) but no other
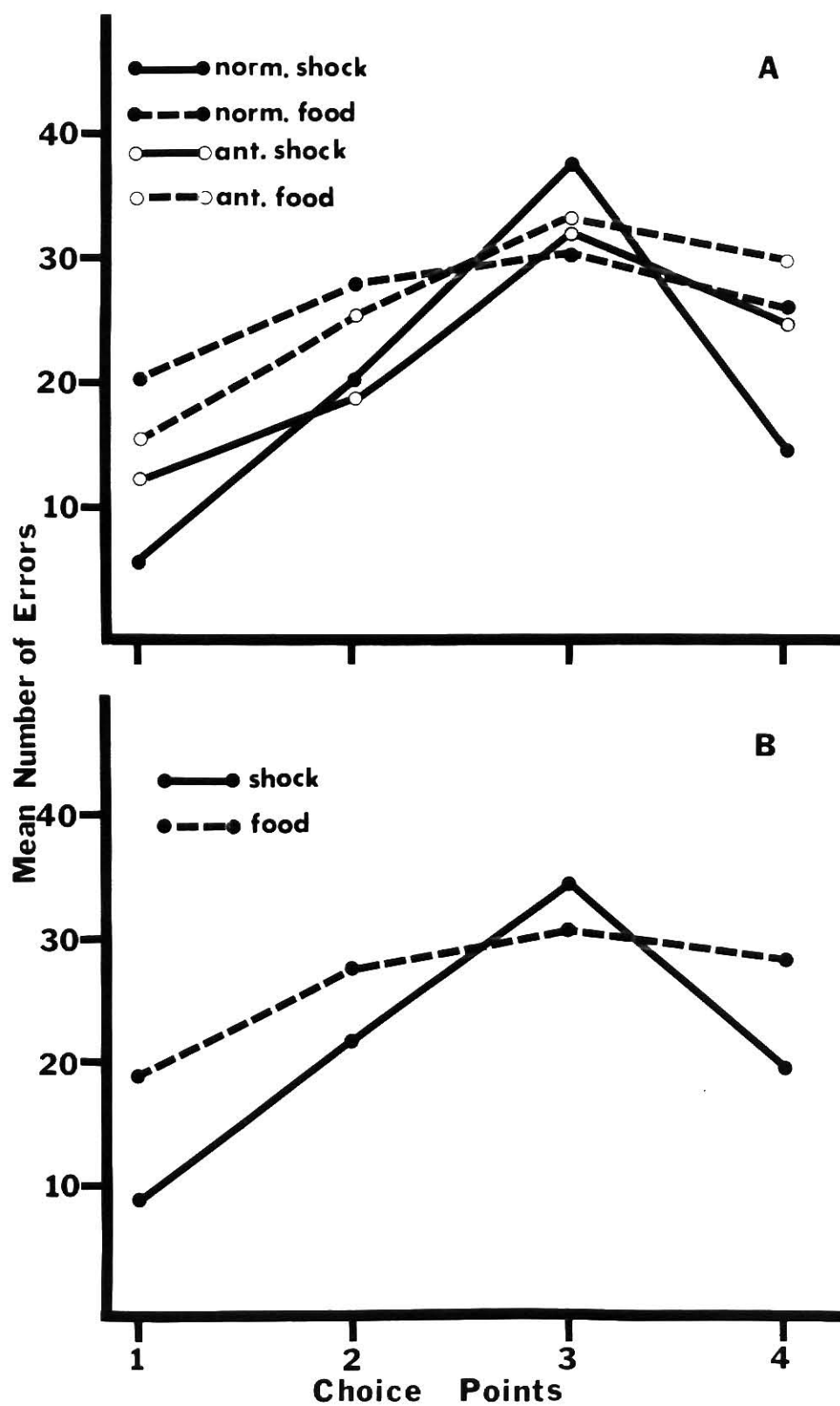differences were found between choice points.

The anterior cortical lesion apparently had no effect on the type or
number of errors made by the subjects. The number of errors made by the
operated subjects did not differ reliably from that of the normal animals
(F=0.31, df=1/32, p > .05). Neither the operation x reinforcement interaction
(F=0.66, df=1/32, p > .05), or the choice point x operation interaction (F=2.02,
df=1/32, p > .05) was reliable.

After subjects had been trained, it was decided that number of errors
within the first 40 trials might not give an appropriate analysis of the
error trend since some subjects took a great deal more than 40 trials to
learn, while others took much fewer trials. For this reason, percentage
error scores were computed. For each subject, the number of errors made at
each choice point was divided by the total number of responses possible. The
number of possible responses was equal to that number of trials required by
the subject to reach criterion. If a subject reached criterion in 40 trials
and made 10 errors at CP-1, his error score for CP-1 would be 25%.

Figure Caption

Figure 3a. The mean number of errors made at each choice point within the

initial 40 trials of discrimination training.

Figure 3b. The mean number of errors at each choice point within the initial

40 trials of discrimination training; scores for normal and

anterior decorticate rats combined to show errors for the shock

escape and food approach groups.

Arcsin transformations were performed on the percentage error scores and the analyses were performed on the transformed scores. Reliable differences were found between the same conditions that had differed reliably in the analysis of the square root transformations of the raw error scores. The percentage error scores differed between choice points (F=24.99, df=3/96, p <.001) and, as in the previous analysis, a choice point x reinforcement interaction was found (F=3.67, df=3/96, p< .05). Newman Keuls' tests revealed that differences between food and shock occurred at CP-1 and CP-4 (p <.05). The percentage error scores for CP-1 and CP-4 were reliably greater for subjects trained under food approach than for those trained to escape shock (Figure 4a and 4b). Again, Newman Keuls' tests indicated that the error trend across choice points was flatter for food subjects than for shock subjects, following the same trend observed in the raw error data.

The percentage error scores made at each choice point did not differ reliably between normal and operated subjects (F=1.647, df=3/96, p >.05).

The relearning data are presented in Table 2. One animal that had been trained under food approach died following surgery so that an unequal n analysis of variance was used to analyze the data. No difference was found between the food approach and shock escape condition in the number of trials required by the subjects to relearn. Newman Keuls' tests indicated that food approach subjects made more errors than shock escape subjects. The distribution of errors across choice points did not differ between groups. As in learning, the greatest number of errors were found to occur at CP-3 (p <.05). More errors occurred at CP-4 than at either CP-1 or CP-2 (p <.05). CP-1 and CP-2 did not differ (p >.05). Percentage error scores gave similar results except that CP-3 and CP-4 did not differ reliably (p >.05).

Figure Caption

Figure 4a. The mean percentage error scores for each choice point (number of

errors at a choice point/number of trials required to reach

criterion).

Figure 4b. The mean percentage error scores for each choice point; scores

for normal and anterior decorticate rats combined to show errors

for the shock escape and food approach groups.
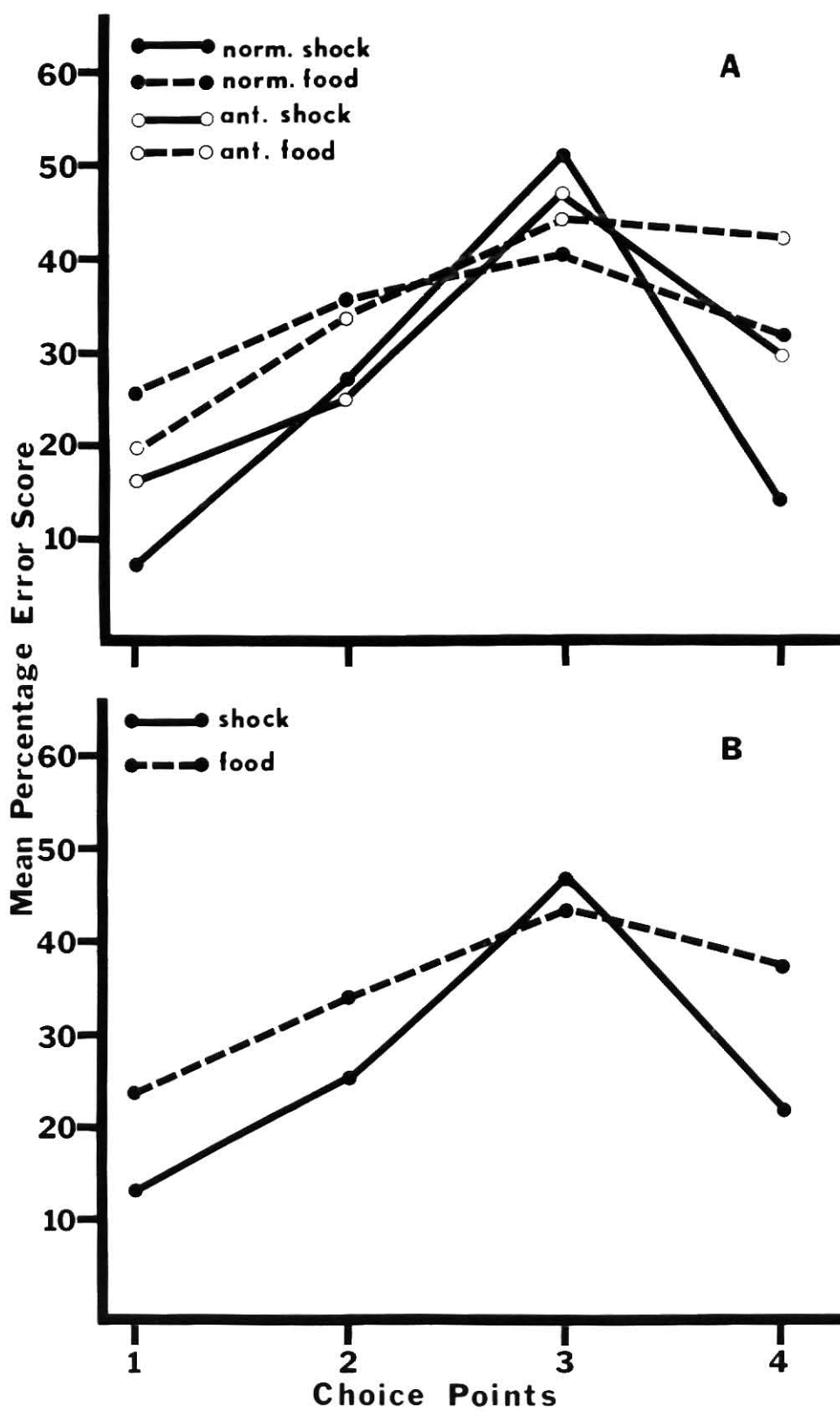
Table 2

Relearning Following an Anterior Cortical Lesion

Groups	Choice Sequence			
	RRRL		LLLR	
	Mean	S.D.	Mean	S.D.
Shock	9.0	8.8	14.6	13.1
Food	29.4	5.2	15.0	12.9

Note.- A criterion of 5 successive trials with no errors on a position alternation task in the Krechevsky apparatus.

Discussion

Contrary to original expectations, subject performance on the task in the present experiment was not impaired by removal of the anterior cortex. The hypothesis that the anterior deficit would be motivation specific was, therefore, impossible to test from these data.

The data do suggest, however, that differences occur in the learning of this task between subjects trained on food approach and those trained to escape shock. Even though learning takes about the same number of trials under both conditions, animals trained under food approach make more errors in reaching criterion, and the distribution across choice points of these errors differs from that of animals trained to escape shock. Food approach subjects show a rather even distribution of errors across choice points, while shock escape subjects show a concentration of errors at CP-3. It should be noted that CP-3 is the final choice point before the subject is required to alternate his response. It is the point at which errors were expected to be most numerous. The food approach and shock escape groups do not differ with respect to the number of errors made at CP-2 and CP-3. Both are committing what Carpenter defined as anticipatory errors. They do differ, however, with respect to the relative dominance of this type of error. For food subjects the number of anticipatory errors is not greater than the number of errors made at CP-4, the goal response. Although they make fewer errors at CP-1 than at the other choice points, the number of errors at CP-1 is still greater than for shock escape subjects. This suggests that the shock escape rats develop a strong tendency to commit anticipatory errors, which must be overcome in order to learn. Food approach rats, on the other hand, develop a more random error pattern which may account for the relatively

higher number of errors which occur during learning.

Perhaps the goal response is more distinctive when it leads to immediate escape from shock rather than immediate presentation of food. Because of this, the shock escape animal may be more sensitive to the goal gradient, making few errors at the choice point most distant from the locus of the goal and few errors on the goal response itself, but having a tendency to anticipate the goal response as its locus becomes closer. The food approach animal, then, would lack the degree of goal gradient sensitivity that is found in the shock escape animal.

The results obtained with food animals are inconsistent with the findings of Carpenter (1954). His subjects, trained under food approach, displayed a stronger tendency to make errors at CP-3 than at any other choice point. The present experiment did not duplicate either Carpenter's procedure or his apparatus precisely. His subjects confronted a locked door when they made an incorrect response. Errors in his apparatus were, therefore, not as costly since the subject did not have to spend time retracing from an incorrect alley. Possibly, animals persisted in making errors since they were so easily corrected. Carpenter trained his rats for 15 trials on the problem, then operated (normal subjects rested during the operation and recovery periods). Following three weeks, subjects were tested for an additional 30 trials. His analysis dealt with the final 30 trials. He may have been ignoring a stage, during the early part of training, in which subjects showed a more random pattern of error distribution. This could possibly explain why his subjects showed a steeper gradient across choice points.

Recently, Seitz (1972) found that nonspecific stimulation in a runway situation could facilitate recovery of a black-white discrimination habit following posterior cortical ablation. When it became apparent that the anterior lesion was not causing an impairment of the present task, it was

thought that the rather extensive pretraining procedure might be contributing to recovery, reducing the differences expected following the operation, and thus preventing the possibility of determining motivational specificity. It was for this reason that the normal subjects in the original design were given the anterior cortical lesion after reaching criterion and subsequently retrained. However, the relearning data indicated that it was erroneous to assume that a lack of impairment might be due to a recovery of function taking place during pretraining. Pre and postoperative scores were not compared statistically although every animal relearned in far fewer trials than he had learned the task. The lesion, therefore, simply did not impair performance on the task. Food and shock did not differentiate the anterior animals' ability to learn the task. This differentiation was not expected, however, in the absence of an impairment.

The question of motivational specificity in the anterior cortical deficit was not answered by this study. In addition, the hypothesis that the number of errors would differ between anterior and normal animals in the food condition but not in the shock condition was not supported. Yet, again, this differentiation was not expected in the absence of an anterior impairment.

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Performance on a spatial alternation task in a four choice point maze in which the subject was required to alternate his response at the final choice point was compared for normal and anterior decorticate rats under conditions of food approach or shock escape. Food approach subjects were found to make more errors than shock escape subjects. The errors were evenly distributed across choice points for food approach subjects while shock escape subjects tended to make more errors at the third choice point than at any other choice point. Differences in number or distribution of errors were not found between anterior decorticate and normal subjects. None of the groups differed in the number of trials required to reach criterion.