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THE REVERSIBILITY OF DIFFERENTIAL REARING IN RATS

LeAnn M. Taylor

The Reversibility of Differential Rearing in Rats

by

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Abstract

Two groups of rats were raised in two different environments for 75 days beginning at 25 days of age. One group was raised in an enriched condition (EC), and one group in an impoverished condition (IC). At 91 days of age, all rats were tested on a spatial reversal learning task to determine if their early environments had affected their learning ability (Test 1). After Test 1 was completed, the rats were then placed in the opposite environment for another 75 days, with a second testing (Test 2) beginning at 165 days of age to determine if the new environment affected their ability to relearn the spatial reversal task. There were no significant differences between the two groups at Test 1 and both groups performed better at Test 2 than at Test 1. However, the rats raised in EC performed better at Test 2 than the rats raised in IC, indicating that the rats which received EC early in life were not negatively affected by receiving IC later in life. The research hypothesis was not supported regarding the potential reversibility of differential rearing. Rats raised in IC and later shifted to EC did not perform as well at Test 2 as rats initially raised in EC and later shifted to IC. Discussion centers on possible reasons for these results.

The Reversibility of Differential Rearing in Rats

A substantial amount of research has been done to study the effects of environments on animals raised in an enriched condition (EC) and an impoverished condition (IC) (Renner & Rosenzweig, 1987). An enriched condition is usually characterized by a larger living area, social interaction with other animals, various objects to encourage exploration such as tunnels and domes, and an abundance of toys with which to play, such as balls, running wheels, and simple blocks of plastic or wood. An impoverished condition is characterized by the lack of such objects and social interaction. It is usually a small living area with only water and food dispensers (Renner & Rosenzweig, 1987).

Researchers have used several approaches to determine the extent to which different aspects of behavior and learning are influenced by such environments. Morgan (1973) tested rats on several learning tasks to determine what effect their post-weaning environment had on their learning ability. He found that the rats raised in isolation were slower to enter a large open environment than those in the social group. He also found that the isolates ran faster for their food reward in one phase of the experiment, but they were slower to climb a ladder in another phase. He did not find any difference in the emotionality of the social-reared and isolated rats. Also of interest, Morgan found that when two groups of rats were raised socially but one group was given an enriched environment with objects, there were no significant differences in their learning abilities during the transfer phase of the tasks. However, there was a difference between those raised in an isolated/impoverished environment and those raised in a social/enriched environment. Morgan speculated that rats raised in isolation exhibit reduced behavioral inhibition compared with rats raised in a social environment.

Gill et al. (1966) also found that IC rats are more cautious when investigating an unfamiliar environment, and they spend more time exploring the environment closest to them. These researchers also found non-significant differences in learning between IC and EC groups in a black-white visual discrimination task and in the reversal of the discrimination.

Chapillon et al. (1999) tested the effect of environment on emotional reactivity in two strains of inbred mice known to have different “anxiety” levels. They found that one strain showed less anxiety-like behavior in “state” and “trait” anxiety testing conditions after being reared in an enriched environment. The other strain showed less state anxiety behavior. The authors suggest that EC may have affected structures in the limbic system related to fear and anxiety responses.

Several researchers have examined the effect of a shorter length of time in EC, often called restricted exposure. Widman & Rosellini (1990) placed rats in individual cages at 44 days of age and provided one group with environmental enrichment for 2 hours a day for 30 days while the IC group was handled daily but not exposed to enrichment. They found that the restricted exposure to enrichment was sufficient to demonstrate significant differences in the two groups. When given an object exploration test, EC rats were found to explore objects more than IC rats as measured by the amount of time spent in contact with the objects and the number of bouts with the objects. The researchers also noted that while both groups would explore a given object for about the same amount of time, the EC rats showed more diversity of exploration with the objects.

Several arguments surround the validity of the EC vs. IC studies. One is that researchers may be mistaking exploratory behavior for low intelligence. Woods et al. (1960), for example, concluded that exploratory differences, instead of differences in intelligence, seemed to be a major factor in the typical finding that rats raised in EC are better problem-solvers compared to rats raised in IC. This was because IC rats explored more and this resulted in more errors in maze tasks. They found that there were high correlations between error scores on the Hebb-Williams maze and exploration measures. This was true even when the tests were several months apart. Woods et al. predicted that there would be no differences in learning between EC and IC rats when behavior was not being confounded by the exploration factor, and that "differences in discrimination learning ability *should* show up in a T-maze where the animals' behavior is motivated to a greater extent by an exploratory drive."

In a follow-up study by Woods et al. (1961), they set out to test that hypothesis, finding that IC rats with high-drive (greater food deprivation) "caught up" with the EC high-drive rats and eventually surpassed them in their performance on the Hebb-Williams maze. The food deprivation reduced the exploratory drive of the IC rats because it made them motivated to find the end of the maze to obtain their food reward. Without the high-drive state, the main motivation of the IC rats was to explore the maze, not to find food. Therefore, they did not perform as well on maze tasks where exploratory behavior produces errors. Woods et al. concluded that the inferior maze-solving performance of the IC rats in previous studies is not due to a lack of intelligence or inability to solve mazes, but more likely due to a heightened exploratory drive.

Caston et al. (1999) looked at the effect of an early enriched environment on Lurcher mutant mice, which have massive degeneration of the cerebellar cortex, to see if EC could have any positive effect on their motor and cognitive deficits. They found that enrichment improved motor coordination on several tasks and resulted in a reduction of the number of trials needed to reach criterion in a landmark water maze task, suggesting that early enrichment might alter brain morphology and neurochemistry in animals with cerebellar damage.

Another study looked at the effect of different environments on photic evoked potentials and brightness discrimination in rats (Edwards et al., 1969). It was found that evoked potential latencies were shorter in rats raised in enriched environments compared to those raised in impoverished environments, differences that were noted only after differential rearing and not at weaning. The EC groups also attained superior scores on black-white discrimination tasks when compared to the IC groups. The authors concluded that the results suggest different levels of CNS arousal exist in the two groups as a result of the different rearing environments.

In addition to behavioral changes due to EC, research has shown that anatomical and physiological changes in the brain occur in rats as well. Pham et al. (1999, 2002) found that rats raised in EC had increased nerve growth factor (NGF) gene expression and protein levels in the hippocampus. They believe that this may play a role in environmentally induced neural plasticity. Their rats were either handled or not handled for 21 days after birth, then placed in IC and EC environments for 2 months. Rats that were not handled but raised in enriched environments had the highest hippocampal NGF levels compared to the other groups, possibly suggesting that the nonhandled rats were more responsive to some of the neurochemical effects of the enriched environment. Nonhandled rats raised in isolation had lower NGF levels and learned a spatial task more slowly than those raised in EC. The researchers found that EC benefited both the handled and nonhandled rats, but the uniqueness of EC and behavioral testing caused greater neurochemical effects with the nonhandled animals. Pham et al. imply that their results could demonstrate that stimulation received in early life may protect the neurogenic ability of the brain, and “it is the novelty of complex stimuli...which elicits the environmental effects on adult hippocampal plasticity." Also of interest, they found that rats that were handled early in life but did not receive enrichment performed as poorly on the spatial learning task as rats that were not handled early in life.

Naka et al. (2002) studied the effects of environmental enrichment on noradrenaline, serotonin, and dopamine concentration in mouse brains. They found that when mice are raised in EC for 40 days, the amount of noradrenaline increased significantly in the parieto-temporo-occipital cortex, the cerebellum, and the pons/medulla oblongata. However, there were no changes in the levels of serotonin or dopamine in the same regions. Naka et al. point to the fact that noradrenaline has been shown to promote synaptic plasticity, to regulate ocular dominance plasticity, and to enhance learning and memory.

Paylor et al. (1992) placed rats in either standard laboratory cages or enriched environments at 15 days of age, which is considered the pre-weaning stage, and tested them either 6 or 12 days later on a spatial learning task (Morris water task). Their hippocampal protein kinase C (PKC) activity was also examined, which is thought to be a possible neural substrate that underlies learning and memory processing. Paylor et al. found that rats receiving EC for 12 days, but not 6 days, performed better on the Morris task than those in the control group. Cytosolic PKC activity was also influenced by the 12-day treatment but not the 6-day treatment. The authors suggest that Morris task performance is related to hippocampal PKC activity, which is enhanced by environmental enrichment.

Rosenzweig et al. (1962) measured the effects of a combination of environmental complexity and training on brain chemistry and anatomy in rats. They found that rats which received formal training on several mazes after being raised in EC environments from weaning until 105 days of age had lower specific activity, but higher total activity of cholinesterase (ChE) in the cerebral cortex, higher specific ChE activity in the subcortex, and a lower cortical/subcortical ratio of specific ChE activity. They also showed significantly greater weight of cerebral cortex and significantly greater total ChE activity in the subcortex and in the whole brain. These results further support the idea that enrichment can lead to dramatic changes in the chemistry and anatomy of the rat brain.

Another study compared the effects of altering the total amount of visual stimulation rats received to the effects of altering the diversity of visual stimulation received (Brown & King, 1971). The visual stimuli were solid objects suspended in the rats' cages. The rats had been placed in these two environments for 80 days beginning at 25 days of age. The researchers looked at the effects of these rearing conditions on visual discrimination of similar objects using the Lashley Jumping Stand. They also analyzed the activity and protein concentration of acetylcholinesterase (AChE) and ChE in the visual cortex. They found that changes in diversity of stimulation contributed to significant differences in AChE and ChE activity and to differences in learning performance, whereas the same was not true for changes in the overall amount of visual stimulation. Specifically, EC decreased AChE activity, increased ChE activity, and reduced the number of errors in the visual discrimination task. The authors suggest that this learning effect may be due to the fact that greater novelty in visual stimulation causes rats to be more flexible in performance. This flexibility may generate a quicker transfer of attention to one stimulus after not receiving reinforcement from responding to another.

Krech et al. (1962) looked at the relationship between brain chemistry and problem-solving in rats raised in EC and IC environments for 30 days and found that in the EC group there was a significant correlation between the behavioral score on a series of brightness reversal problems and the cortical-subcortical ratios of specific ChE activity, as well as between the behavioral scores and the cortical-subcortical ratios of brain weight. Specifically, EC rats with higher cortical-subcortical brain weight ratios and lower cortical-subcortical ChE activity made fewer errors on the problems. Krech et al. suggest that the EC rats had an advantage in problem-solving ability early in the experiment. Overall, the EC rats were superior to the IC rats. However, as training proceeded, the brains of the IC rats became more similar to the EC rats, and at the end of the study, there were little or no differences in the brains of the two groups. The authors suggest that intensive training with complex problems like brightness reversals can alter an IC rat's brain and make it more similar to the brain of an EC rat.

Rosenzweig et al. (1968) showed that providing rats with only 2-4.5 hours of enrichment a day for either 30 or 60 days can produce the same cerebral changes as 24-hour a day exposure for the same period. The cerebral changes in activity of AChE, ChE, and weight of the brain samples were similar to changes observed in previous experiments with 24-hour EC. Of particular interest with respect to such limited EC exposure, Ferchmin and Eterovic (1986) showed that after only four daily 10-minute exposures to enrichment, there was a significant increase in RNA content of the occipital cortex.

Nyman (1967) looked at problem solving in rats as a function of environmental enrichment at different ages and found that the total developmental period can be delimited by a ten-day period between 50 and 60 days of age in which enrichment is most effective for spatial discrimination and maze learning. In addition, he found that less experience during the critical period may produce results equal to that of more experience during earlier or later periods.

However, Bennett et al. (1970) found that for a positive effect to occur on brain weight, rats did not have to be placed in EC at weaning. They found that similar effects could be obtained when rats began enrichment at 105 days of age. Similarly, Doty (1972) looked at avoidance responding as a function of environmental influence in very old rats and was particularly interested in whether EC increases the behavioral “flexibility” of older animals. Rats were assigned to EC or the IC control condition at 300 days old. She tested the rats at 660 days of age and found that enrichment increases performance mainly on an avoidance response reversal task and to a lesser extent on a passive avoidance problem. She gives a possible explanation for this phenomenon as “rearing in laboratory cages [IC] impairs the rats’ capacity to shift his behavior in recognition of new reinforcement contingencies.”

Upon realization that the environment in which rats are raised can affect their learning ability, researchers began to examine whether or not this effect was reversible. Bernstein (1971) showed that non-handled rats eventually reached the same performance on a brightness discrimination task as handled rats after a two-month interval, but not after a one-month interval. To determine if this effect was the result of practice on the task or if the IC group had become as “intelligent” as the EC group, he allowed the IC rats to catch up with the EC rats on the brightness task and then tested them in the Lashley III maze, a task on which neither group had been previously tested. His findings indicated that the reversibility of the effects of non-handling may not be limited to the original learning problem since the non-handled rats later performed as well as the handled rats on the Lashley III maze. He concluded that “it appears that the early deprived animals, after they ‘catch up,’ may well be generally as bright as the early enriched animals.”

In a follow-up study, Bernstein (1972) found that rats raised in IC for 45 days and which later received EC for 90 days were not significantly different on a brightness discrimination problem from rats receiving EC for 45 days then IC for 45 days. This confirms the hypothesis that extended experience with EC after early IC reverses the effects of early IC. However, time in an enriched environment equal to previous time in an impoverished environment was not adequate to make up for the effects of the early IC. Bernstein demonstrated this by finding that rats receiving IC for 45 days and then EC for only 45 days were significantly poorer learners than those receiving EC for 45 days and then IC for 45 days.

Much research on IC/EC effects has been done with rats and mice. In addition, research has also shown significant influences of EC environments on cats and primates (Cornwell & Overman, 1981; Gluck et al., 1973; Wilson et al., 1965), indicating that the effect is not limited to rodent species. Bennett et al. (1970) suggest that "it might be found that effects of early restriction of experience are progressively more severe as one goes from rodents to carnivores and from carnivores to infra-human primates." If that hypothesis is true, then the effects of an impoverished environment on a human child might be especially negative. Pham et al. (2002) state that research on the effects of enriched environments is important in furthering understanding about child development, successful aging, and superior recuperation after brain damage in humans.

The purpose of the present research was to further investigate the question of whether or not rats raised in IC and who later receive EC could eventually reach the learning ability of rats initially raised in EC (e.g., Bernstein, 1972). The research hypothesis was that rats receiving EC in young adulthood after having received IC early in life would perform as well on a spatial reversal task as rats receiving EC early in life and moved to IC in young adulthood. The present study examines the potential reversibility of the effects of these different rearing environments.

Method

Subjects

Eight male rats of the DA/OlaHSD inbred strain were acquired at 25 days of age from Harlan/Sprague Dawley. When not being trained or tested, they were fed Lab Diet 5001 (Purina) *ad libitum*. On days prior to training and testing, they were initially deprived of food for 24 hours, but later received an average of 15 grams of food per day during Test 1 and 10-16 grams of food per day during Test 2, which was adequate to maintain normal growth and weight. Water was provided *ad libitum* in their cages at all times.

Because of Morgan's (1973) findings that a social/enriched environment affects learning in rats the same as a social/impoverished environment, social influence was controlled by housing all of the rats in social environments (two per cage) with the environmental enrichment or impairment the rats received being the only independent variable manipulated. All rats were housed in pairs in the animal colony at the Psychology Department at Columbus State University with the room temperature maintained at 21° Celsius. The light/dark cycle was 12/12 with the lights on at 8:00 a.m. and off at 8:00 p.m.

Upon acquisition (25 days-old) the rats were randomly assigned to either Group 1 (an enriched environment) or Group 2 (an impoverished environment) for 75 days. During the course of the study, the only handling the rats received occurred during marking of their tails for identification, cleaning their cages, and weighing them. All subjects were treated according to the ethical standards of the American Psychological Association.

Apparatus/Materials

The enriched environment was a 46 cm wide x 36 cm deep x 58 cm high, four-level cage (Model RT-4, Quality Cage Company). Inside the cage were several objects, including a wire running wheel, colorful plastic blocks, plastic “igloos,” tubes made of vegetable parchment paper, large plastic balls, small wooden logs, etc. The impoverished environment was a 42 cm wide x 34 cm deep x 18 cm high cage with nothing in it except the water bottle-dipper tube. While the specific objects in EC were rotated between cages every day, entirely new objects were never added.

Four identical wooden tables (78 cm high, 61 cm wide, and 273 cm long) were used for testing. There were two 4 mm deep food wells located 15 cm from the side edges of the table, 102 cm from one end of the table, and 31 cm apart. Only one end of each table, the end closest to the food wells, was used as the actual testing arena. Two plain white cards in clear plastic picture frames (9 cm wide x 12 cm high) were used to cover the two food wells and served as the spatial stimuli. Sweetened 45 mg food pellets (Noyes Formula P) were placed in the food wells and served as reinforcers.

Procedure

Training began when the rats were 85 days-old (60 days in first condition). Training consisted of six days of handling and familiarization with the tabletop, the cards, and the food pellets for 30 to 75 minutes daily. During this time, the rats were encouraged to get the food pellets from off the tabletop and out of the food wells. The white cards were placed behind the wells and sometimes partially covered the wells. The rats were trained at approximately the same time each day in the same room on individual tables.

Spatial reversal testing began on day seven when the rats were 91 days-old (66 days in first condition). Testing began by placing a food pellet in the left food well and placing the cards over both wells. The researcher then placed the rat at the end of the table opposite the wells and allowed him to go to the cards. If he pushed the correct (left) card out of the way, it was counted as a correct response. If he pushed the incorrect (right) card even slightly, it was counted as an incorrect response. He was allowed to eat the pellet if he made the correct response. If he made an incorrect response, he was allowed to self-correct and choose the correct card. He was then allowed to eat the pellet. After he self-corrected, the researcher put a new pellet in the left well (out of view of the rat) and placed the rat back down at the end of the table. Subsequent trials were run in the same way.

When the rat made 18 correct responses in a block of 20 trials, the spatial discrimination problem was considered to have been "learned." If he did not get 18 correct in the given 20, a new block of 20 trials began. This continued until he got 18 correct in a single block of 20. When this occurred, the side of the correct response was reversed. Therefore, after the rat got 18 correct in a block of 20 on one side, the pellet was placed under the card on the other side, and testing continued until he learned that spatial discrimination problem. The researcher repeated this spatial reversal procedure for a total of eleven problems (one original problem and ten reversals).

After all eight rats had learned all eleven problems (Test 1), the toys in the EC were cleaned, the IC rats were moved to the EC housing, and the EC rats were moved to the IC housing. This occurred when the rats were 101 days-old. All rats remained in their new environments for 75 days. The same spatial reversal procedure described above was again used to test the rats after they had been exposed to their second environment (Test 2). Test 2 began when the rats were 165 days old (64 days in second condition).

Results

The number of errors each rat made on each of the eleven problems of Test 1 and Test 2 were analyzed with ANOVA for a mixed design using SPSS version 10. The number of errors made by Group 1 (EC-IC; the rats that initially received EC) was compared to the number of errors made by Group 2 (IC-EC; the rats that initially received IC). Separate analyses were performed for Test 1 and Test 2.

For Test 1, there was a significant repeated measures effect, F(10,60) = 2.58, p = 0.011, but there was no significant difference between the groups, F(1,6) = 0.041, p = 0.846. There was also no significant interaction, F(10,60) = 1.92, p = 0.06. The mean number of errors on each problem of Test 1 for each group is shown in Figure 1.

For Test 2, there was no significant repeated measures effect, F(10,60) = 1.67, p = 0.110, but there was a significant difference between the groups, F(1,6) = 9.66, p = 0.021. Group 1 (EC-IC) made fewer errors across all eleven problems than Group 2 (IC-EC). There was no significant interaction, F(10,60) = 1.21, p = 0.30. The mean number of errors on each problem of Test 2 for each group is shown in Figure 2.

The number of trials each rat needed to learn each of the eleven problems of Test 1 and Test 2 was also analyzed with ANOVA for a mixed design. Similar to the analysis for errors, for Test 1 there was a significant repeated measures effect, F(10,60) = 2.11, p = 0.037, but there was no significant difference between the groups, F(1,6) = 0.144, p = 0.717. There was also no significant interaction, F(10,60) = 1.22, p = 0.295. The mean number of trials on each problem of Test 1 for each group is shown in Figure 3.

For Test 2 there was no significant repeated measures effect, F(10,60) =1.61, p = 0.126, and no significant difference between the groups, F(1,6) = 0.692, p = 0.437. There was also no significant interaction, F(10,60) = 1.80, p = 0.08. The mean number of trials on each problem of Test 2 for each group is shown in Figure 4.

Two additional analyses were then performed on the total number of errors and trials for each rat across all eleven problems of each test, giving each rat a single score for errors and trials on both Test 1 and Test 2. When looking at the total number of errors made on Test 1 compared to Test 2, there was a significant repeated measures effect, F(1,6) = 19.61, p = 0.004, but there was no significant difference between the groups, F(1,6) = 1.628, p = 0.249. There was also no significant interaction, F(1,6) = 0.862, p = 0.389. The mean total number of errors on each test for each group is shown in Figure 5.

When looking at the total number of trials required for learning on Test 1 compared to Test 2, there was a significant repeated measures effect, F(1,6) = 28.06, p = 0.002, but again, there was no significant difference between the groups, F(1,6) = 0.40, p = 0.550. There was also no significant interaction, F(1,6) = 0.005, p = 0.945. The mean total number of trials on each test for each group is shown in Figure 6.

Discussion

The present study examined the reversibility of the effects of differential environmental rearing on spatial reversal learning in rats. Contrary to the research hypothesis, at Test 1 the rats that received IC early in life (Group 2, IC-EC) did not perform significantly worse than the rats that received EC early in life (Group 1, EC-IC). Also contrary to the research hypothesis, at Test 2 the rats that received EC later in life (Group 2) performed worse than the rats that received IC later in life (Group 1). The research hypothesis was that Group 2 should have "caught up" with Group 1 at Test 2, which is demonstrated by the hypothesized results shown in Figure 7. The present results are also contrary to some findings from previous research on the reversibility of the effects of environmental rearing (Bernstein, 1971, 1972; Krech et al., 1962; Pham et al., 1999). As expected, both groups of rats did make fewer errors and required fewer learning trials on Test 2 than on Test 1, which is simply a result of practice with the task.

Of notable interest, Group 1 did not perform better than Group 2 at Test 1. Previous research has found that IC and EC rats differ significantly on learning tests after receiving the two different rearing conditions, with EC rats being superior. The present findings may suggest that the spatial reversal task was not hard enough, or that the environments were not different enough to reveal the expected effects. This will be discussed in further detail below.

However, other researchers have found results similar to those of the present experiment (Gill et al., 1966, Morgan, 1973). When Morgan controlled for social influence by providing both IC and EC rats with a social environment (similar to the conditions of the present research), he found that there were no significant differences in learning abilities in the two groups. This supports the idea that something was different about Morgan's testing procedure compared to procedures used by other researchers who obtained significant differences.

Interestingly, the rats initially raised in EC (Group 1) did significantly better at Test 2 than the rats initially raised in IC (Group 2), even though Test 2 was conducted after the environments were reversed. A conclusion that can be drawn from this result is that raising rats in EC and then switching them to IC in adulthood does not cause them to lose the benefit of early environmental enrichment. The early EC may have "protected" them against the negative effects of IC later in life.

The possibility of Group 1 receiving too little time in EC early in life can be ruled out as an explanation for why there were no differences between the groups at Test 1. Seventy-five days of EC should have been sufficient to obtain an effect since substantially less EC exposure has been shown to be effective in previous research (Ferchmin & Eterovic, 1986; Paylor et al., 1992; Rosenzweig et al., 1968; Widman & Rosellini, 1999). Therefore, there must be another explanation for the lack of significant group differences at Test 1. One explanation is that the EC may not have been enriched enough. The EC cages were relatively small compared to those used in previous studies (Renner & Rosenzweig, 1987) and the rats were housed in pairs instead of with several other rats. Additionally, Brown & King (1971) found that diversity of visual stimulation was more important than the total amount of stimulation. While the specific objects in EC in the present study were rotated every day, entirely new objects were never provided. The rotation of the same objects may not have been adequate to provide optimal enrichment.

Another possible explanation for the lack of significant group differences at Test 1 is that the spatial reversal task may not have been hard enough to identify differences in learning between the groups. However, this possibility is not supported by the fact that the rats in Group 1 (EC-IC) performed better than the rats in Group 2 (IC-EC) at Test 2. If the enrichment condition had not been sufficient to cause a difference in learning ability, then this difference in performance at Test 2 is difficult to explain.

Additionally, Group 2 may not have “caught up” with Group 1 at Test 2 because Group 2 did not receive enrichment during a proposed critical period of development, a 10-day period between 50 and 60 days of age (Nyman, 1967). Therefore, the developmental period of enrichment may not have been optimal. Nyman suggests that less enrichment during the critical period may produce results similar to more enrichment during other periods. Because Group 1 and Group 2 received equal amounts of enrichment but at different points in development, the enrichment cannot be assumed to be equivalent. Future research should use two additional groups, which receive each condition throughout the entire experiment. This would double the amount of time in IC and EC and allow for an examination of the effects of leaving the conditions constant.

However, receiving EC later in life has been found to have some positive effects on learning (Bennett et al., 1970), but considering the need for enrichment during the critical period, maybe Group 2 required more than 75 days of EC to catch up with Group 1. Bernstein (1972) found that doubling the amount of time that rats initially raised in IC spent in EC later in life caused the rats to be superior in performance to rats that received an equal number of days of IC and EC.

Another factor that may have affected the results of the present study is the influence of exploratory drive (Woods et al., 1961), for which there may not have been adequate experiment control. Although the researcher tried to eliminate excessive complexity of the task and testing arena, no measure was made of exploratory behavior of the two groups. Therefore, one cannot determine whether or not this may have been a factor in the present study. Again, however, it is interesting to note that the rats did not differ on Test 1 but did differ on Test 2. It is unclear how the influence of exploratory drive could have produced the difference at Test 2 since Group 2 was then experiencing the enriched environment which is associated with less exploratory behavior in Woods et al.'s studies. However, other studies have found EC rats to exhibit more exploratory behavior compared with IC rats (e.g., Gill et al., 1966) so the potential confound of exploratory drive remains a possibility.

An additional possible explanation for Group 2 not catching up with Group 1 at Test 2 is that potential detrimental effects to the brain resulting from early IC were irreversible, or at least not repairable with the amount of EC received later. Doty (1972) explains the effect of IC as impairing the rats' ability to transfer his behavior in recognition of new stimuli. In addition, rats raised in EC have anatomical and chemical benefits to the brain that are believed to play a role in neural plasticity (Pham et al., 2002). The rats raised in EC may have received this early benefit and been resistant to the effects of the IC, while the rats raised in IC suffered brain effects from the IC that could not be reversed by EC in adulthood.

Although the effects of rearing environments in animals has been carefully researched over the past several decades, there is still a great deal more that can be learned, especially concerning the reversibility of the effects of IC and EC. Future research can use better and more thorough controls for each condition. Further investigation should be made into the length of time in EC required to reverse the effects of IC, in particular to determine if there is a critical period when EC is most effective. Better, more agreed-upon definitions should be established of IC, EC, and "novelty" of stimuli. Studies similar to the present one could be done that control specifically for the potential confound of exploration and exploratory drive. Decades of study on the topic of rearing environment have still not answered all the questions that can be asked about it.

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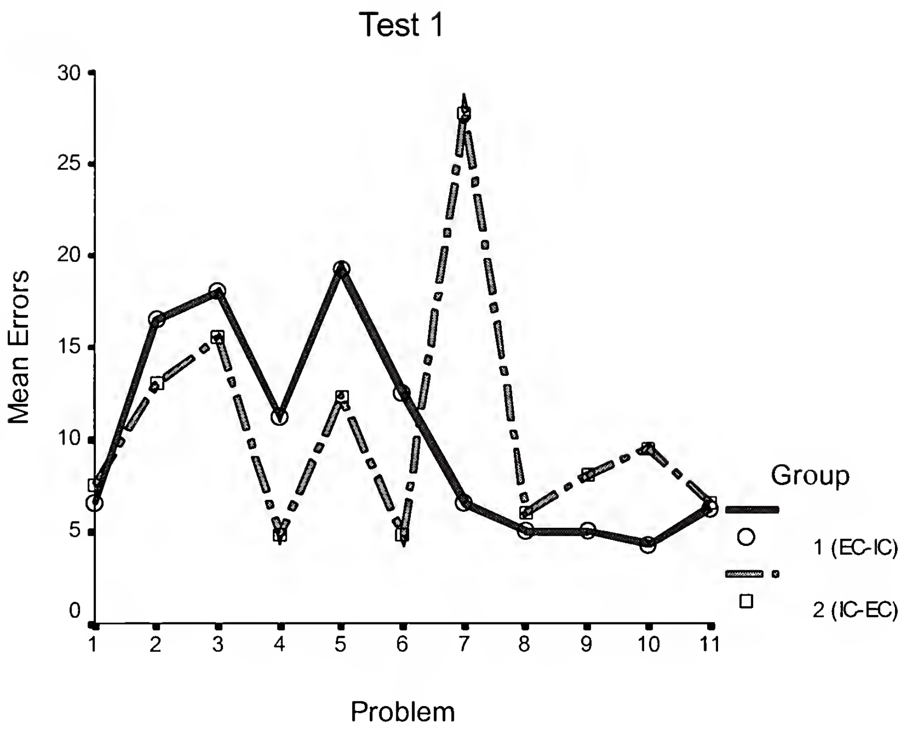

Figure 1. Mean number of errors on each problem of Test 1 for each group

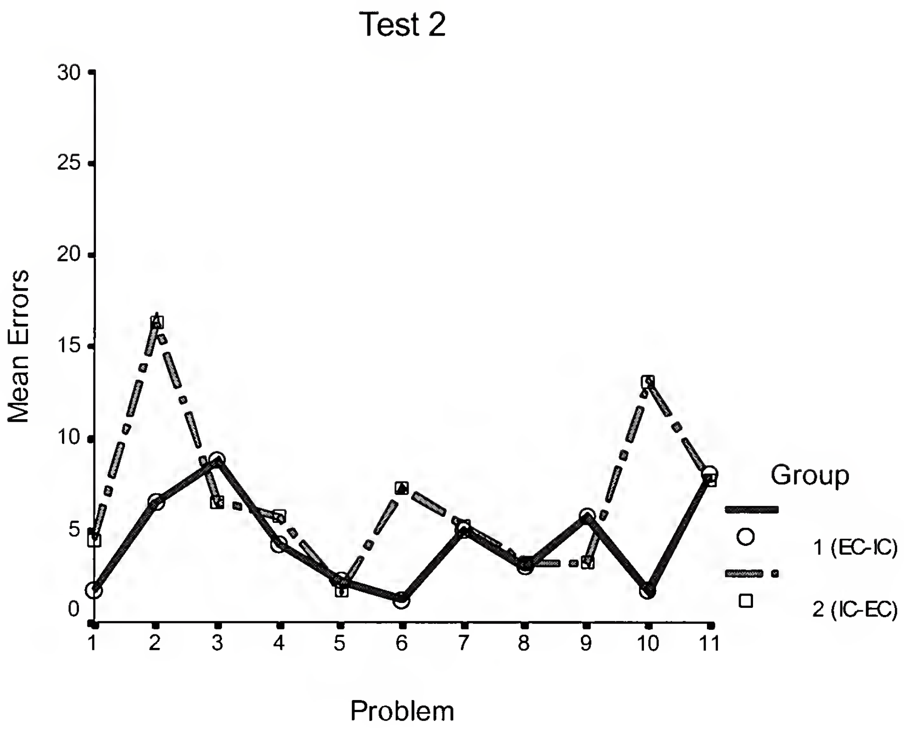

Figure 2. Mean number of errors on each problem of Test 2 for each group

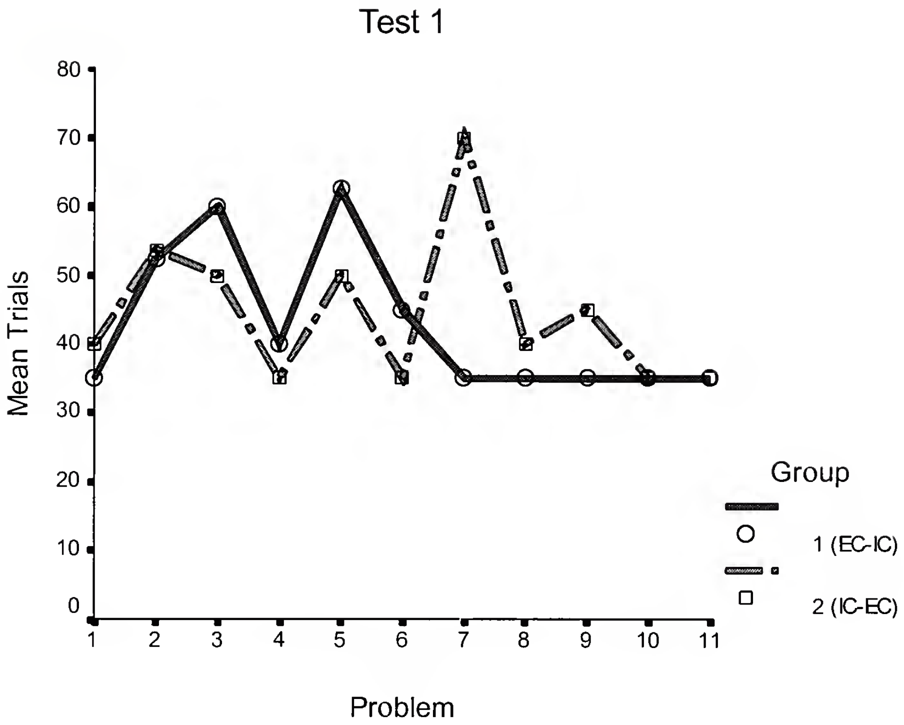

Figure 3. Mean number of trials on each problem of Test 1 for each group

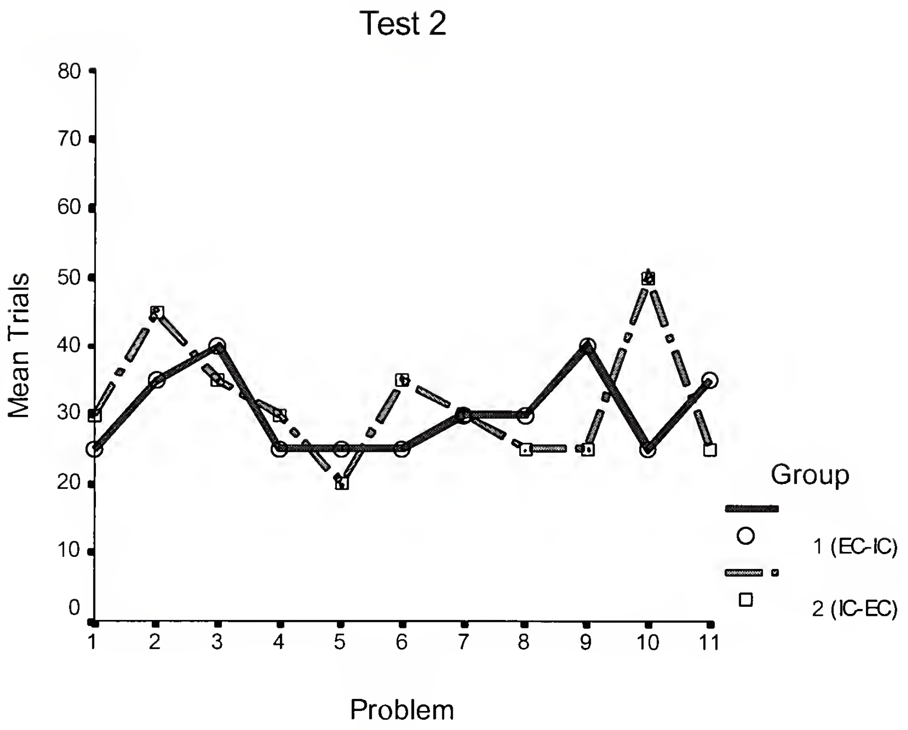

Figure 4. Mean number of trials on each problem of Test 2 for each group

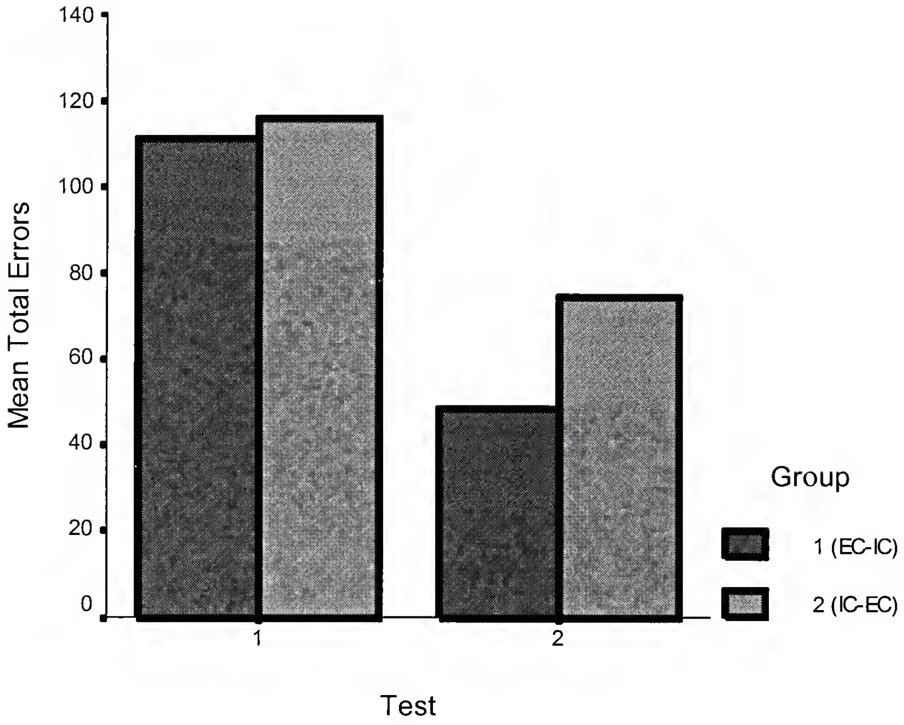

Figure 5. Mean number of total errors on each test for each group

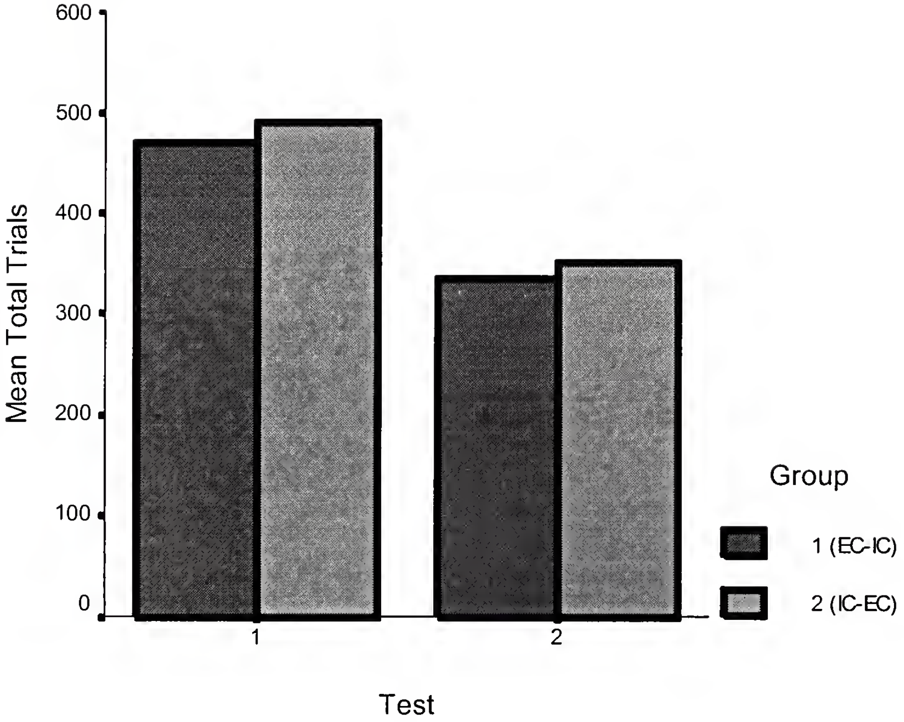

Figure 6. Mean number of total trials on each test for each group

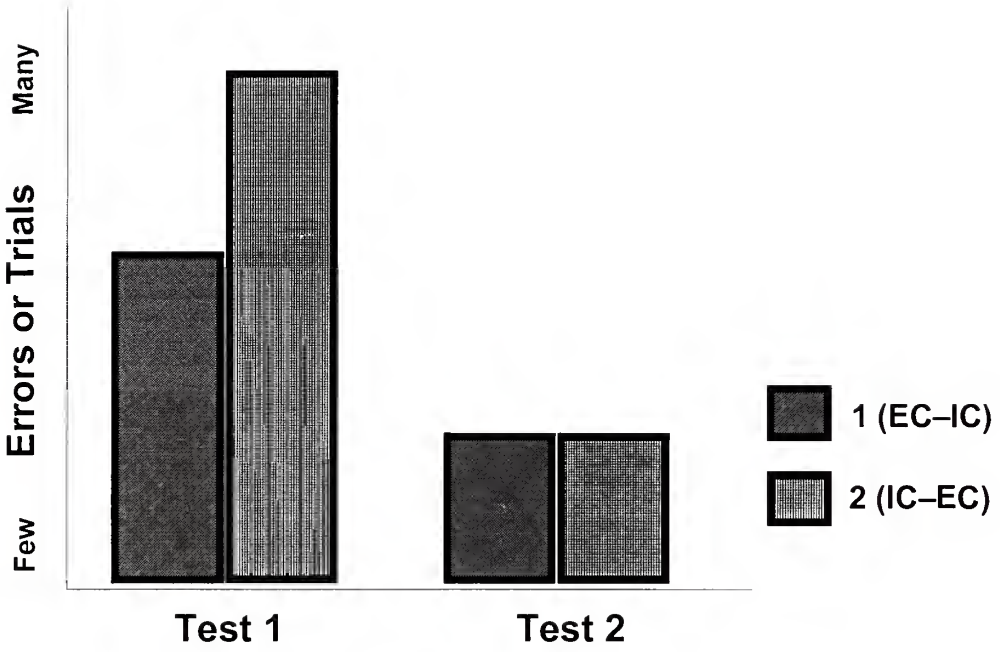

Figure 7. Hypothesized results for each group on Test 1 and Test 2