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THE EFFECTS OF ENVIRONMENTAL SWITCHOVERS
BETWEEN ENRICHMENT AND IMPOVERISHMENT
ON BRAIN AND BEHAVIOR IN MICE



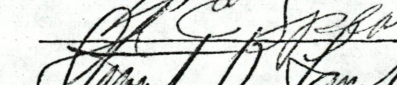
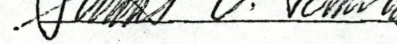
BY

JUDITH K. AHROON

Submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy
in State University of New York
at Binghamton
1976

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INTRODUCTION

Rearing rodents or primates in environments that are comparatively enriched or impoverished results in often impressive physiological and anatomical changes after a certain period of exposure. However, the anatomical and biochemical characteristics that respond to environmental experience (Bennett, Diamond, Krech, & Rosenzweig, 1964; Greenough & Volkmar, 1973; Walsh, Budtz-Olsen, Penny, & Cummins, 1969) have been subjected to a more sophisticated level of analysis than have the less consistent changes in behavioral tendencies. The specific nature of environmentally induced modifications in behavioral tendencies must be better understood, if substantive predictions about brain-behavior relationships can be made. Furthermore, the long-term effects of particular environmental experiences have not been made clear.

This question of permanence would seem to have direct relevance to the current problems in human child development. There are two basic methods of assessing the permanence, or stability, of environmental effects on brain and behavior. The first involves the introduction of a long temporal interval between treatment and testing, which introduces numerous practical and experimental confounds. The second method involves "switching" animals between environmental enrichment and impoverishment, and assessing the degree to which effects of the first environmental exposure are maintained.

This second approach has rarely been applied, and the few reports have been somewhat contradictory. One of the first reported that

rats switched into enrichment (EC) for 48 days, after 33 days in "isolation" (IC), were similar to totally enriched rats in weight of total cortex, but similar to isolated rats in dorsal cortex weight (Rosenzweig, Krech, Bennett, & Zolman, 1962). Additional brain weight measures did not discriminate the groups; however, the switched group retained an intermediate ranking on most measures. Zolman and Morimoto (1962) reported persistent enrichment effects on enzyme activity and brain weights in rats after 30 days in impoverishment. In contrast to these findings, Rosenzweig, Bennett and Diamond (1967) found that cortical weight differences induced by 80 days in EC or IC did not persist through an additional 50 days in the opposite condition. Geller (1971) found a diminution in neurotransmitter level differences between EC and IC after 30 days in standard laboratory conditions. Enzyme activity differences in occipital cortex between EC and standard laboratory reared rats disappeared within three days after the EC rats were placed in standard laboratory housing (Brown, 1971). Finally, Bennett, Rosenzweig, Diamond, Morimoto, and Hebert (1974) manipulated the time rats spent in EC, IC, and after being switched from EC into IC. Cerebral differences persisted up to 21 days after rats were switched into IC; enzyme differences maintained for 47 days. Although persistence, or stability, of enrichment induced cerebral changes is suggested by these findings, the influence of temporal parameters is still unclear. Most importantly, perhaps, the issue of behavioral persistence or stability under these conditions has not been addressed. I think that there are two main questions that frame this issue, one of immediate experimental interest and one of long-term importance to future applications of this knowledge.

First, it is of experimental importance to better understand the relationship, if any, between a level of cerebral persistence and a corresponding stability of a behavioral tendency. Knowledge of probable behavioral stabilities is necessary to establish possible physiological mechanisms mediating persistent changes in behavior. Second, the problem of the stability of environmentally induced modifications of brain and behavior is basic to the proposed utility of particular environmental "therapies" in the ultimate rehabilitation of nonadaptive behavioral tendencies produced by earlier life experiences.

The second question addresses the issue of early experience in a somewhat unique way, i.e. by considering not only the discrete effects of a particular early environment on brain and behavior, but also the general effects on the organism's total developmental tendency, such that its future behavior is biased in a particular, determined direction by these early experiences.

The following experiments are the first attempts to better understand these kinds of problems in applying environmental programs to the modification of physiological and behavioral tendencies.

EXPERIMENT 1

The purpose of this experiment was to investigate the ultimate effects of alternating exposure to environmental enrichment and impoverishment during successive periods of time, on brain weight and behavior. Due to the lack of agreement among previous reports, a large number of behavioral tasks were employed, and two durations of "second state" environmental treatment were used.

METHOD

Subjects

One hundred mice from the genetically heterogenous stock maintained at SUNY Binghamton were used. The use of this stock provided an appropriate baseline for testing the magnitude of impact of these environmental histories on a variable genetic background. This same genotypic heterogeneity also allowed for more substantive generalizations based on the results. All subjects were reared under standard laboratory conditions in litters of eight pups with both parents present. At weaning (21-24 days of age) each subject was randomly chosen, from a population of available litters (usually 4-8), toe clipped, and assigned to one of the 10 treatment conditions. An equal number of male and female weanlings were assigned to each group, and no more than 2-3 pups from the same litter were assigned to the same treatment group. The following designations were used: E = environmental enrichment conditions, I = environmental impoverishment conditions, and S = standard laboratory conditions. Table 1 illustrates the experimental design used in this experiment. The first letter in each group label indicates "first stage" treatment, the second indicates "second stage" treatment, and the number refers to the duration of the second stage treatment, i.e. 14 or 28 days. For example, EI-14 denotes the experimental group which received enrichment, followed by 14 days of impoverishment conditions. There were originally 10 subjects in each group; one male was lost in EE-14 and IE-14. All 10 groups were set up within approximately two weeks of each other, and behavioral testing begun on the day after the end of the second stage treatment period, when the subjects were either

TABLE 1. The Experimental Design for Experiment 1

First Stage (28 days)	Second Stage (14 or 28 days)
E	E
E	I
I	E
I	I
S	S

Note: Each letter represents a period of environmental treatment; E = enrichment, I = impoverishment, S = standard rearing conditions.

63 (21 + 28 + 14) or 77 (21 + 28 + 28) days of age. Following the end of testing, all animals were weighed, sacrificed, and the brains immediately removed, partitioned, and weighed.

Housing and Treatment Apparatus

The following are descriptions of the three basic treatment conditions:

Enrichment. Each clear polycarbonate cage (36.8 x 30.5 x 17.8 cm) covered with a hardware cloth cover was housed in the animal colony under a 12-hour light-dark cycle. Each cage originally contained: one 36.8 x 3.7 cm shelf of 0.6 cm wire mesh, a ping pong ball, two wooden squares, one small and one large mesh triangle, one foam square, one large wood shape, an orange juice can, and a small plastic funnel. Half-way through the first stage of E treatment, the long shelf, orange juice can and funnel were replaced with a 30.5 x 3.7 cm shelf with ladder, a mesh T maze, and 1/2 an egg carton. The same toy changes were also made during second stage of E treatment. The toys chosen were reasonably similar to those used by a majority of researchers, within the bounds of laboratory supplies. The literature clearly indicates that the specific nature of such toys is less critical to subsequent changes than is the variety provided. Five same-sexed animals were housed in each cage, and all cages were in close proximity to one another in the colony room.

Impoverishment. Each translucent plastic cage (29.2 x 17.8 x 14.0 cm) with a clear Plexiglas cover was maintained in a temperature controlled chamber provided with constant white noise and the same 12-hour light-dark cycle as in the colony room. Each subject was housed individually.

Standard. Each clear polycarbonate cage (29.2 x 17.8 x 14.0 cm) with standard metal cover was housed in the colony room, within sound but not sight of the E cages. Each subject was housed individually.

Food and water were replenished, and all cage shavings changed, every 10 days. Shavings were alternated with straw bedding in the E cages. At each cage changing every animal was weighed.

Testing Apparatus and Procedure

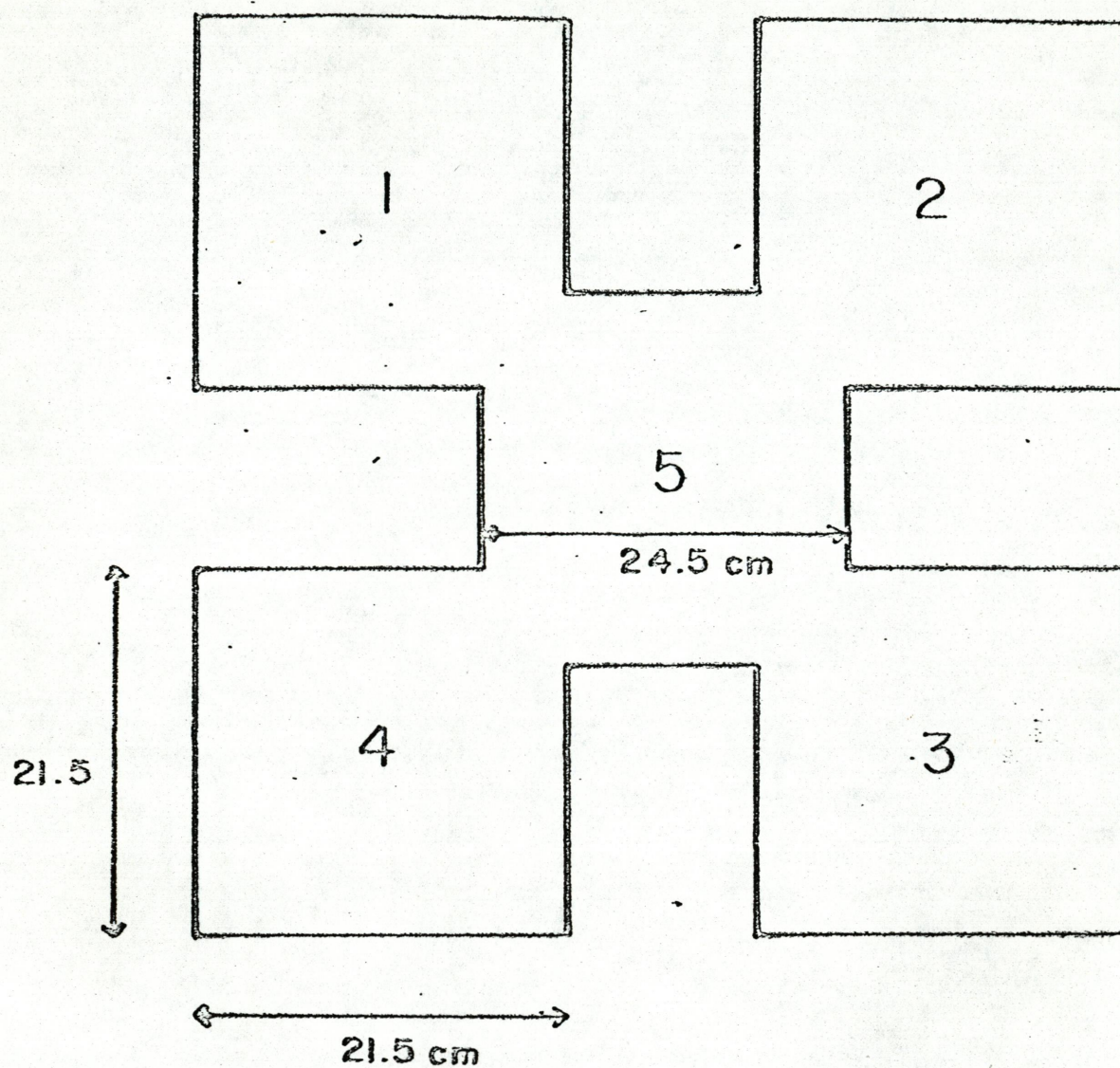
During the periods of environmental enrichment, subjects in each E cage were observed, for 10-s, every 10 min for 60 min, three times weekly. The first weekly observation was made at 10 AM, the second at 3 PM, and the third at 9 PM, on three separate days. The following behaviors were observed: sleeping, grooming, climbing, crawling, contact with mates. The number of animals engaged in a behavior, and their relative positions (grouped or solitary), were recorded.

On the day following the end of the second stage treatment period, each animal began a sequence of behavioral tasks in succession. Due to the nature of some of the tests, and the large number of tests, each animal received the same testing order. This particular sequence of tests was used in order to measure first the behavioral tendencies that can be temporarily disrupted by stimulation extremes (e.g. open field behavior, exploration), and, then, to impose at least a 24-hour interval between exposure to shock stimuli. Hence, all animals were tested first in the open field box and exploration unit, then on tasks involving shock stimuli, and, finally, in the water maze, which required daily training over many days. Subjects were maintained in their respective second stage treatment conditions throughout testing.

Day 1. On the first day of testing, each animal was first placed in a 400 ml beaker, with bedding, for approximately 10 minutes. The beaker with mouse was then placed on its side in a square open field (45.7 x 45.7 x 25.5 cm) under ordinary room illumination. The cover of the beaker was removed, and time to emerge into the field, and number of nose pokes, were recorded. Once the animal moved into the field, a clock was activated and the following behaviors observed: number of re-entries into the beaker, number of 15.2 x 15.2 cm squares entered with all four feet, number of rear-ups (standing on the hind feet), and number of boli excreted, during a 60-s interval. At the end of the interval the beaker was removed and the same measures recorded for another 60-s.

Each subject was then tested for sensitivity to shock in an LVE Model #146-02 shuttle box (24.4 x 9.5 x 12.8 cm). Each subject was placed in the left side of the box, with a stainless steel divider in place and the cover closed. After recording the number of rear-ups made during a 60-s adaptation period, the first shock series was begun at between .02-.06 mA, using an LVE 1531 Constant Current Shocker. A .5-s shock was delivered to the grids every 15-s; each shock increased by .02 mA. The intensity level at which the animal showed a vigorous shuffling of all four feet on the grids (Foot Shuffle) was recorded as the foot shuffle score. The same procedure was used to measure the intensity at which each animal leaped off the grids with all four feet (Jump). Four shock series were run in this order: ascending, descending, ascending, and descending.

Day 2. Each animal was placed in box 5 of the five-unit exploration field illustrated in Figure 1, under low illumination, and observed for the next two minutes. Each entry with all four feet into one of the



FIVE UNIT EXPLORATION FIELD

FIGURE 1. Dimensions of the Five Unit Exploration Field

white, empty boxes was recorded. Number of boli excreted and overall time spent in each box was also recorded.

Following this test, each subject was tested for passive avoidance ability, using the same type of shuttle box previously described. In this task, a bottomless black plexiglas box (10.8 x 8.9 x 12.7 cm) with cover was located on one side of the shuttle box, and the animal placed on a white plexiglas insert (11.4 x 9 cm) covering the grids on the other side. The latency to step through a small hole (2.5 cm) in the black box was recorded. As soon as the animal had entered the box, a door was lowered and, 30-s later, a 1.0 mA shock was administered for 0.5-s. The animal was removed immediately.

Approximately two hours later each subject was tested for color brightness preference in the water maze (Waller, Waller, & Brewster, 1960). This apparatus, having no top or bottom, was placed in water chilled to 20°C, to a level halfway up the 15 cm high walls. The animal was placed in the start alley, and allowed to swim to either the white or black arm (6.5 cm wide). Ladders were provided in both arms, and the arms are curved to prohibit sight of the ladders from the choice point. The distance from the start point to either ladder was 27.5 cm. Eight trials were given, with the position of the black arm varied according to a triple-balanced series (Vandament, Burright, Fessenden, & Barker, 1970). Between trials each animal was placed in a cage lined with paper towels under a 60 W lamp for 20-s. The choices (black, white) of each subject were recorded, and the choice made on four of the last six trials was considered the animal's preference. If the number of choices was equal, black was arbitrarily assigned as the preference.

Day 3. Each animal was returned to the passive avoidance appara-

tus and the procedure repeated, except that shock was not used. Latency to step through the hole into the box was recorded; if the subject had not stepped through within two min a latency of 120-s was recorded.

Discrimination training in the water maze was begun, and each subject was trained to swim to the non-preferred arm, with a ladder provided only in this arm. Eight daily trials were given, with a 20-s ITI. Three kinds of scores were recorded: 1) latency to reach the ladder, if the choice was correct; 2) E, if the subject corrected a mistake and escaped within 30-s; and 3) N, if the animal did not escape within the 30-s maximum. This procedure was repeated daily until 14 of 16 consecutive trials were correct. Two reversals, i.e. the opposite color now being correct, followed acquisition. The same criterion applied to each reversal. Animals which did not achieve either reversal criterion in 14 days were eliminated from statistical analyses of the reversal scores.

Analyses. The data were analyzed in three consecutive stages. First, an overall analysis of variance was performed on each dependent variable (independent analyses for the 14- and 28-day groups were applied) to test for the main effects of environmental experiences (treatment) and sex. Second, the Duncan multiple range test was applied to each treatment effect found significant at the .05 or .01 alpha level, in order to determine which group means were significantly different on a particular dependent variable. In the case of a significant treatment by sex interaction, the test for simple main effects was applied (Keppel, 1973). Third, limited sets of Pearson Product Movement correlation coefficients were obtained, on the following measures: 1) rear-ups and mean foot shuffle/mean jump scores; 2) body weight at testing and mean foot shuffle/mean jump scores; and 3) whole brain weight and body weight

at sacrifice.

RESULTS

The data were grouped into five basic behavioral categories, for the purposes of description.

Figure 2 illustrates the mean performance levels of EE-14, EI-14, IE-14 and II-14 groups on several of the dependent variables. Both percent of animals found sleeping during the first two weeks of morning observations and the percent of animals found crawling about the cage during the first two weeks of evening observations indicate that animals in the IE-14 group tended to actively locomote more frequently during their two week experience in an enriched environment. The mean number of squares entered during open field testing, however, did not differentiate the 14-day groups on this first category -- locomotion behavior.

In terms of the second category, exploration, or contact with objects in the environment, IE-14 subjects tended to make fewer contacts with mates during the first two weeks of evening observations. Both EI-14 and II-14 subjects appeared to make fewer exploration entries during the two min test than EE-14 animals.

For the third category, that of reactivity as measured by the mean number of defecations (boli) in both open field and exploration field testing, it appeared that both EE-14 and IE-14 subjects were most re-active.

The fourth behavioral category was that of pain tolerance, as measured by the mean mA level of shock necessary to elicit the foot shuffle and jump responses, respectively. Figure 2 indicates that for the foot shuffle, IE-14 subjects were significantly more tolerant than

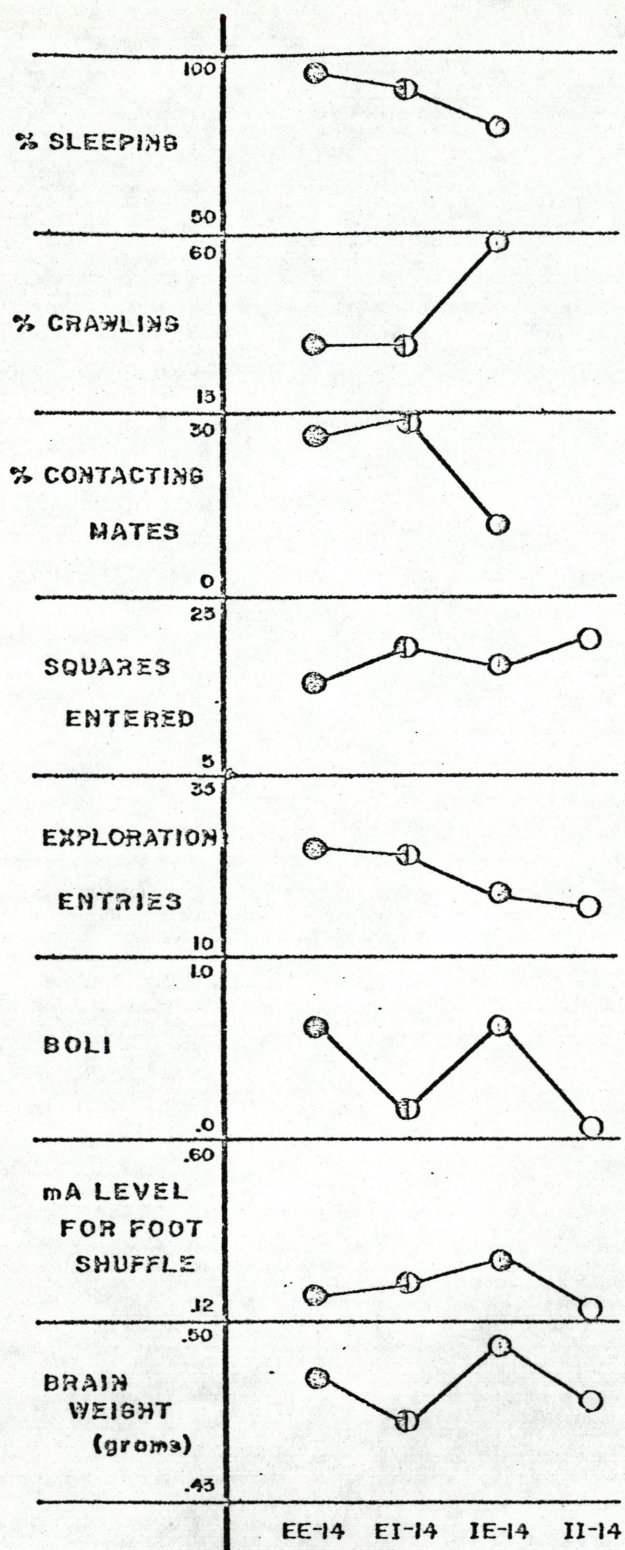


FIGURE 2. Comparison of Mean Brain and Behavioral Scores on Several Variables between the 14 Day Groups

both EE-14 and IE-14 animals ($F = 6.71$, $df = 4/38$, $p < .01$). The same relation was found for the jump response ($F = 4.1$, $df = 4/38$, $p < .01$). Neither initial rear-ups nor body weight was correlated with the foot shuffle or jump scores.

The fifth category, memorial processing, is not indicated in Figure 2. No reliable group differences were found for the passive avoidance response or the discrimination learning in the water maze, although IE-14 subjects ranked poorest on all three tasks.

Mean weights of component brain parts did not differentiate the groups; both EE-14 and IE-14 animals did have somewhat heavier brains, as shown in Figure 2.

All male subjects were significantly heavier than all females in body weight by 31 days of age, and remained so ($F = 33.13$, $df = 1/38$, $p < .01$). Although EE-14 animals were periodically heavier throughout the treatment periods, as indicated in Figure 3, all treatment effects on body weight had disappeared by day 71. Only in the case of IE-14 subjects were brain and body weight found to be correlated ($r = .70$, $df = 8$, $p < .02$).

In general, the functions arbitrarily ordered in Figure 2 describe the animal reared exclusively in environmental enrichment as moderately locomotory, exploratory, reactive, moderately tolerant of painful shock and possessing a large brain and body. Completely impoverished mice, however, locomoted more frequently, and were less exploratory, reactive and tolerant of shock. Animals experiencing both degrees of environmental complexity in different orders differed from each other and from enriched and impoverished animals, particularly subjects in the IE-14 group.

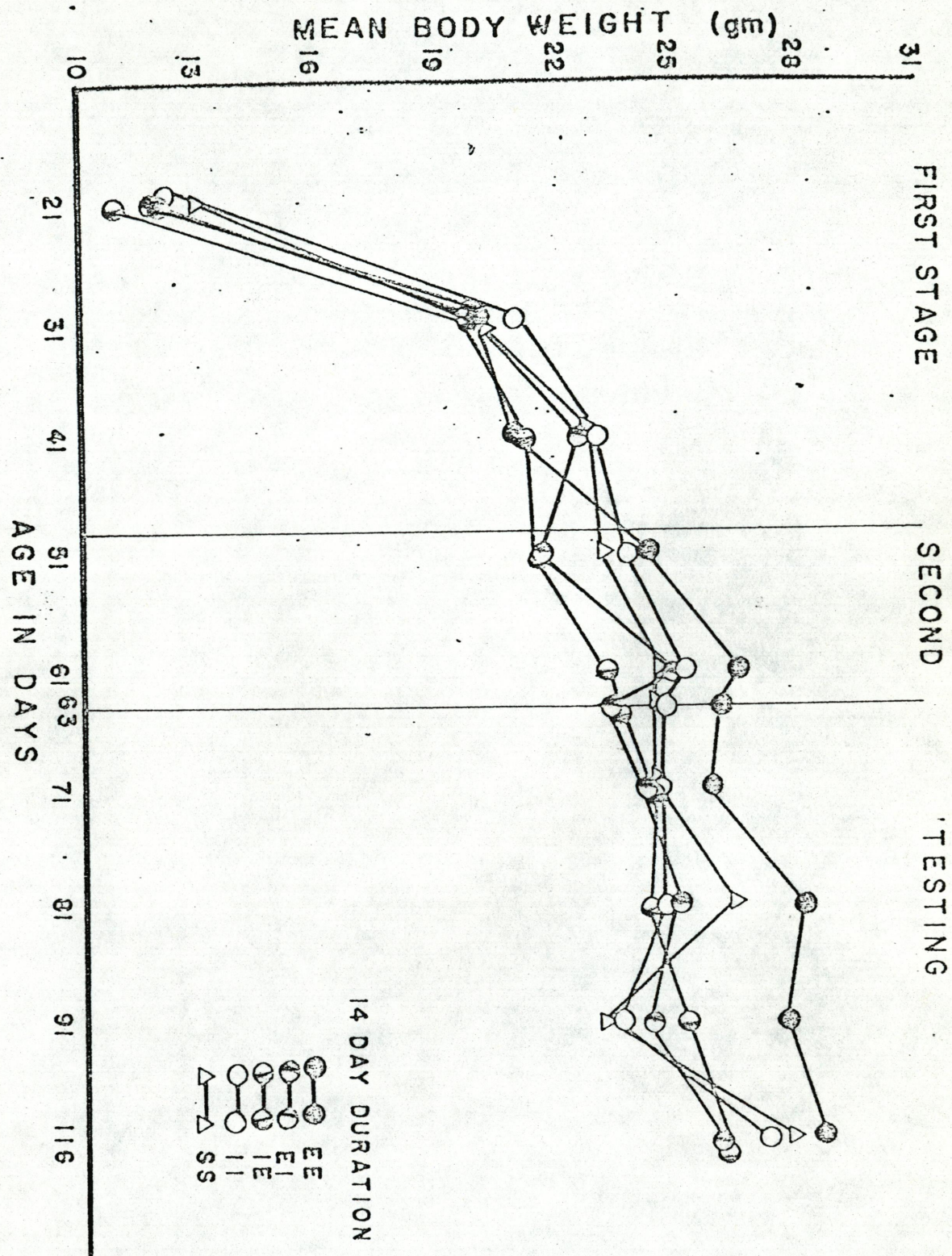


FIGURE 3. Mean Body Weights during Treatment and Testing for 14 Day Groups

In Figure 4, mean performance levels for EE-28, EI-28, IE-28 and II-28 subjects are illustrated, on several dependent variables. As with subjects in IE-14 group, IE-28 subjects tended to sleep less and crawl about more frequently, during enrichment rearing. Both EI-28 and IE-28 groups entered significantly more squares than EE-28 and II-28 animals ($F = 3.51$, $df = 4/40$, $p < .01$). These findings suggest that the IE-28 group, especially, tended to locomote more frequently, both in the home cage and during testing.

Similar to the performance of IE-14 subjects, animals in the IE-28 group tended to make fewer social contacts during enrichment rearing, and made significantly fewer exploration entries than EI-28 subjects ($F = 7.46$, $df = 4/40$, $p < .01$). Subjects in the EE-28 group made more entries than II-28 subjects.

In terms of reactivity, the third behavioral category, animals raised exclusively in enrichment defecated significantly more than all other treatment groups ($F = 6.39$, $df = 4/40$, $p < .01$).

In marked contrast to the 14-day group function, tolerance to painful shock was significantly greatest in II-28 subjects for both the foot shuffle ($F = 6.81$, $df = 4/40$, $p < .01$) and the jump score ($F = 3.63$, $df = 4/40$, $p < .01$). Neither rear-ups nor body weight scores were found correlated with either response, in agreement with the findings in the 14-day groups.

Similar to the results of analyses on memory processing in the 14-day groups, no reliable group differences were found for the passive avoidance response or for discrimination learning in the water maze.

As Figure 4 indicates, EI-28 subjects possessed brains significantly smaller than those of EE-28 animals ($F = 3.13$, $df = 4/40$, $p < .02$),

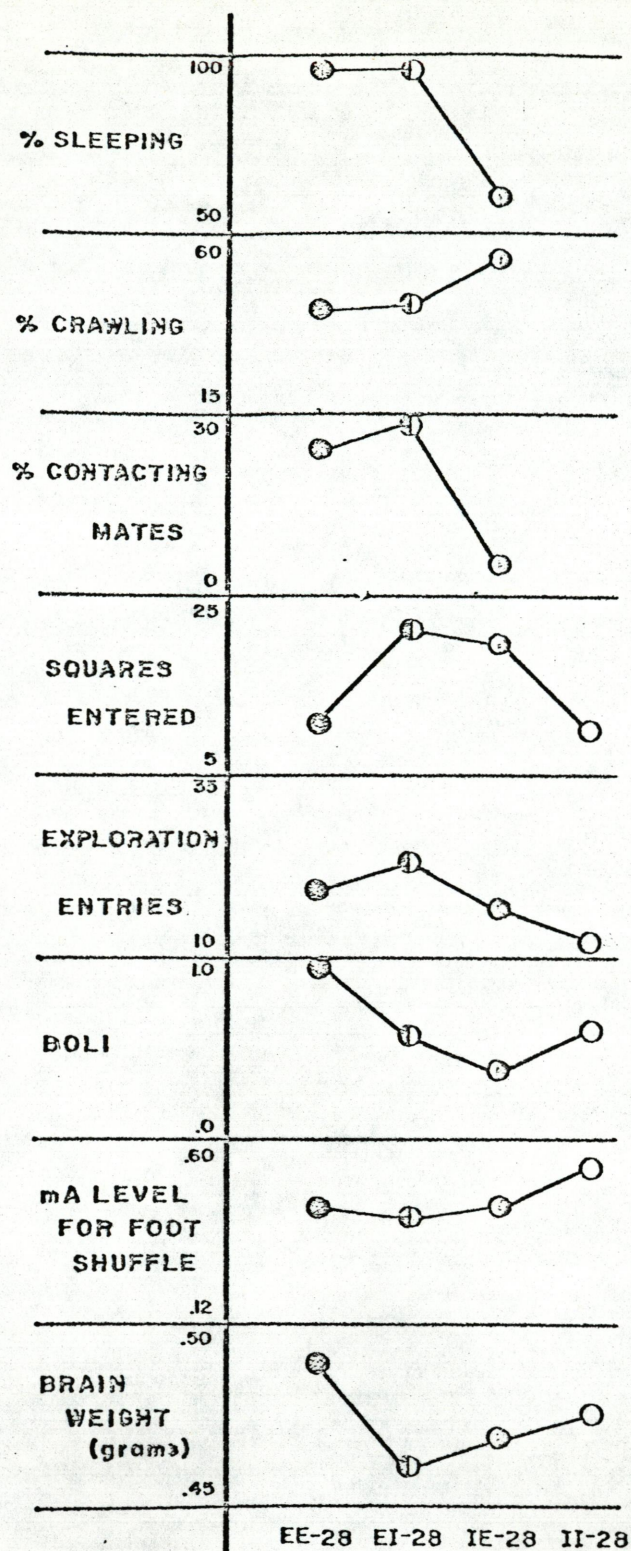


FIGURE 4. Comparison of Mean Brain and Behavioral Scores on Several Variables between the 28 Day Groups

and both switched groups (EI-28 and IE-28) had significantly smaller cerebellums than the other treatment groups ($F = 2.86$, $df = 4/40$, $p < .03$). The mean weights for all brain parts are shown in Table 2.

As in the 14-day groups, males became significantly heavier by 21 days, and continued so ($F = 52.05$, $df = 1/40$, $p < .01$). Figure 5 indicates that the enrichment effect on body weight was less pronounced in the 28-day groups, and that all treatment effects on body weight had disappeared by day 95. Only for EI-28 subjects were whole brain and body weight found correlated ($r = .55$, $df = 8$, $p < .05$).

In general, the descriptions of mice reared exclusively in enrichment or impoverishment discussed previously were confirmed in the 28-day groups. One marked exception was the large increase in tolerance to painful shock evidenced between II-14 and II-28 subjects.

Interestingly, EI-28 subjects exhibited behavioral scores that were similar either to those of EE-28 mice (indicating a stability or primary effect) or to those of II-28 animals (indicating a plasticity of behavior, i.e. a recency effect), but rarely intermediate between these two comparison groups. These relationships are described in Table 3. It is clear from the table that the scores of IE-28 mice, however, frequently ranked intermediate between both these comparison groups.

DISCUSSION

In relating the overall findings to previous reports, it is interesting to note that male and female mice did not often differ in their performance on the behavioral tasks used, although body weights of males and females differed, and remained different, throughout rearing and testing. There were no sex differences in any of the brain weight

TABLE 2. Mean Whole Brain and Component Brain Weights
for each Group (28 Day Duration Groups)

Brain Weights	Groups				
	EE	EI	IE	II	SS
Whole Brain	.4944	.4592	.4699	.4716	.4801
Cerebellum	.0556	.0518	.0501	.0538	.0558
Cerebral Cortex	.1843	.1829	.1757	.1826	.1904
Rest of Brain	.2371	.2051	.2291	.2230	.2181

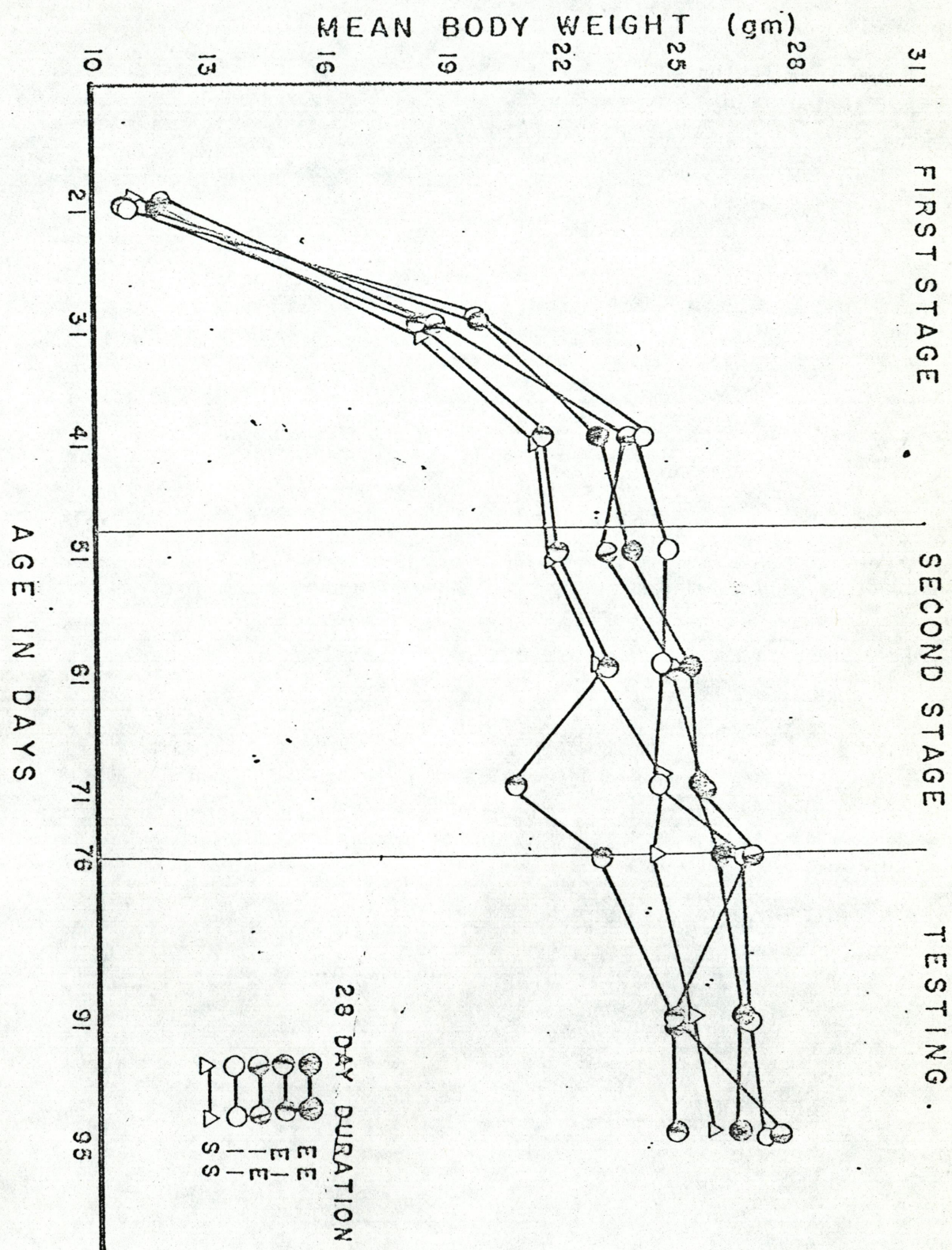


FIGURE 5. Mean Body Weights during Treatment and Testing for 28 Day Groups

TABLE 3. Brain and Behavioral Stability in Switch Groups (Experiment 1, 28 Day Duration Groups)^a

Measures	Switch Groups	
	EI-28	IE-28
Squares, first 60-s interval	X	<u>A</u>
Squares, second 60-s interval	<u>A</u>	=
Rear-ups, second 60-s interval	X	P
Rear-ups, threshold test	A	=
Foot shuffle	X	P
Jump	X	=
Exploration choices	X	=
Boli, exploration test	P	X
Whole brain weight	P	=
Cerebellar weight	P	A

^aScores of each switch group were compared with the non-switch groups EE-28 and II-28.

Note: X indicates stability of effects; P indicates plasticity of effects; A indicates alteration of effects such that the switch group ranked higher (A) or lower (A) than both non-switch groups; = indicates that the switch group's performance was equal to that of both non-switch groups.

measures.

Interestingly, previous reports on mice have suggested that environmentally enriched mice defecate less and are more active in the open field (Manosevitz, 1970; Manosevitz & Joel, 1973); the assumption has been that such measures are indices of a low state of physiological and behavioral arousal. The data presented here, however, suggest that, assuming environmental enrichment experience influences later arousability, high "reactivity" and moderate "locomotion" represent a state of low arousal, one in which the enriched animal demonstrates increased "exploration", or contact with environmental stimuli. This conclusion is supported by the finding that, in this experiment, impoverished mice, which have been assumed to be highly arousable (Walsh & Cummins, 1975), were less "reactive" and "exploratory" than enriched mice.

The fact that switched groups demonstrated both behavioral stability and plasticity suggests that, if arousal systems were altered in these groups, the resultant arousal threshold was other than a simple additive function of periodic exposure to two different levels of environmental complexity. Certainly the sustained diminution in percent of switched mice found sleeping during enrichment rearing, the increase in crawling through the environment, and squares entered during open field testing suggest an alteration in behavioral arousal.

It is not clear whether or not the concept of arousal as a mediator of behavioral changes can explain the dramatic differences in tolerance to painful shock between impoverished mice of the 14- and 28-day groups. The commonly held idea that the impoverished animal is in a state of high arousal would predict that such subjects would be most reactive to painful stimuli. However, earlier work with isolated puppies

(Melzack & Scott, 1957) found that these subjects were remarkably unresponsive to such painful stimuli as a lit match and electrified objects. Further work will be needed in order to discern whether this behavioral change is mediated sensorily or perceptually.

Treatment effects on component brain weights were found for the 28-day groups. Their absence in the 14-day groups can probably be attributed to the fact that the brains were not removed until approximately 25 days after completion of water maze training, and diminutions in gross brain measures during training, and over time in general, have been reported (Ferchmin, Eterovic, & Caputto, 1970; Walsh, Budtz-Olsen, Penny, & Cummins, 1969). The same component brain weights were taken four days after testing ended in the 28-day groups. Both switch groups possessed smaller cerebellums than the other groups. This finding suggests that the weight decrement may reflect a response to some aspect of the switch-over paradigm, rather than to the diminished opportunity for vestibular, motoric experiences. Both groups had smaller cerebellums than impoverished mice, indicating that the lack of extra activity opportunities, as in impoverishment, could not explain this brain weight difference. Here, again, the notion of a sustained alteration in chronic arousal state, leading, in this case, to brain modification is plausible. A diminution in neural characteristics following chronic stimulation has been suggested (Geinismann, Larina, & Mats, 1971).

I think it is clear that the two weeks difference in duration of second stage treatment between 14- and 28-day groups did, indeed, make a difference in several behavioral patterns. The difference in age at testing, between 63 and 77 days, is a confound, but its impact is unclear. Arguments against a real influence of differential testing age include the

fact that these animals were young adults at testing, hence, their potential for rapid developmental change may have been less. Also, characters known to change with increasing age, such as activity and body weight, were not related to performance on certain behavioral measures. The expression of treatment effects was much greater in the 28-day groups, suggesting that the 28-28 day time frame for treatment experiences provides a more useful paradigm for switchover methodologies. With or without the additional influence of different ages at testing, the scores of 14- and 28-day groups indicate that general activity declined, and tolerance to painful stimuli more than doubled.

In summary, the results of this initial experiment suggest that certain behavioral tendencies associated with environmental enrichment "persisted" through subsequent impoverishment experience. Changes in arousal systems may have partially mediated these behavioral stabilities.

EXPERIMENT 2

The results of Experiment 1 suggested that certain of the behavioral tendencies induced by early enrichment experience can persist throughout a period of 28 days in impoverished rearing conditions. Several of the behavioral measures differentiating the treatment groups have been associated with arousal states, such as open field activity, rear-ups, and responsivity to painful stimuli. Recently, Walsh and Cummins (1975) have suggested that enrichment experience effects may be mediated via arousal mechanisms activated by the complexity of stimuli presented in enrichment conditions.

The purpose of the present experiment was to expand the basic switchover paradigm in order to assess the effects of repeated, inter-

mittent switchovers on the potential persistence of enrichment effects on brain and behavior. There were two questions to be asked, the first involving the concept of arousal and its role in the enrichment effect, i.e. the manipulation of general arousal state by means of varying the number of switches a subject received. In Experiment 1, animals faced with an enriched environment following earlier impoverishment (IE-28) were more active and slept less during enrichment exposure; both switch groups (EI-28, IE-28) were more active in the open field. These findings suggest that the interaction between environmental enrichment and impoverishment alters these behavioral manifestations of an internal arousal state. The second question involved an assessment of the therapeutic value of intermittent, short-term, enrichment experience on the potential changes induced by impoverished environmental experience.

METHOD

Subjects

Ninety-three mice from the heterogenous stock maintained at SUNY Binghamton were used. The postnatal rearing conditions, group assignment and identification procedures were identical to those used in Experiment 1. An equal number of female and male weanling mice were assigned to each of the eight groups, as illustrated in Table 4. The letter order for group labeling was the same as in Experiment 1; however, the number following each letter pair indicated the number of "environmental units" delivered to a group of mice. For example, EI4 denoted the group receiving 4 units, over the total 56-day treatment period (28 + 28) in this order: 14 days of enrichment, 14 days of impoverishment, 14 days of enrichment, and 14 days of impoverishment (refer

TABLE 4. The Experimental Design for
Environmental Treatments for Experiment 2

Groups	Weeks							
	1	2	3	4	5	6	7	8
EE	E	E	E	E	E	E	E	E
EI2	<u>E</u>	<u>E</u>	<u>E</u>	<u>E</u>	<u>I</u>	<u>I</u>	<u>I</u>	<u>I</u>
IE2	<u>I</u>	<u>I</u>	<u>I</u>	<u>I</u>	<u>E</u>	<u>E</u>	<u>E</u>	<u>E</u>
EI4	<u>E</u>	<u>E</u>	<u>I</u>	<u>I</u>	<u>E</u>	<u>E</u>	<u>I</u>	<u>I</u>
IE4	<u>I</u>	<u>I</u>	<u>E</u>	<u>E</u>	<u>I</u>	<u>I</u>	<u>E</u>	<u>E</u>
EI8	<u>E</u>	<u>I</u>	<u>E</u>	<u>I</u>	<u>E</u>	<u>I</u>	<u>E</u>	<u>I</u>
IE8	<u>I</u>	<u>E</u>	<u>I</u>	<u>E</u>	<u>I</u>	<u>E</u>	<u>I</u>	<u>E</u>
II	I	I	I	I	I	I	I	I

Note: Each underlined segment indicates an "environmental unit".

to Table 4, p. 26). The use of matched pairs of groups (e.g. EI8, IE8) was to measure the potential "primacy" effects of the first environmental experience. Differences between such pairs of groups would indicate that their earliest experience did effect later performance differentially. Four of these groups (EE, EI2, IE2 and II) were replications of those tested in Experiment 1. There were 12 subjects in each group, except for the loss of one subject in each of these groups: EI2, EI8, and IE8. All eight groups were established within 11 days of each other, and behavioral testing began on the day following the end of the eighth treatment week, when all subjects were 77 days of age (21 + 56 days). Two days after the end of behavioral testing, all animals were weighed, sacrificed, and their brains immediately removed, partitioned, and weighed.

Housing and Treatment Apparatus

Enrichment. The physical dimensions of the E cages were the same as described in Experiment 1. Instead of a set group of toys, as in the first experiment, a series of toy sets (6) were rotated through the enrichment treatments, a different set being substituted in order, on the second, fourth and sixth days of each week of enrichment. The series were as follows: 1) ping pong ball, large wood shape, orange juice can; 2) two paper towels, two wooden squares, mesh T maze; 3) small mesh triangle, foam square, short mesh shelf; 4) plastic funnel, 23 cm long metal chain, 1/2 an egg carton; 5) 12-ounce brown beer bottle, metal food cup, rubber bottle cork and spout; and 6) standard mouse metal cage top, two 3 cm diameter plastic circles, small mesh tunnel. Six same-sexed mice were housed in each cage, and equipped with a mixture of

wood shavings and straw and a long mesh shelf.

Impoverishment. All housing procedures were identical to those described in Experiment 1.

Food and water were replenished, and all cages changed every week. All animals were weighed every two weeks. Every scheduled environmental switch (see Table 4, p. 26) was made in the morning, between 9-10 AM.

Testing Apparatus and Procedure

During the eight week treatment period, behavioral observations were made on animals being reared in enrichment (including all switch groups). Three types of observations were made: 1) at each switch into enrichment, for 10-s every 10 min, for 60 min; 2) baseline observations on days 1 and 5 of each week, during the morning, afternoon, and evening, for 10-s every 10 min, for 60 min at each point; and 3) at each change of toys (days 2, 4, and 6) before, during, 15 min after, and 60 min after each change, for one 10-s observation at each point. The following behaviors were observed: sleeping, resting, functional (eating, drinking, grooming), climbing, moving, contacting objects, contacting cagemates. Observations were made for each cage, indexing the number of animals ($n = 6$, in most cases) engaged in the behavior, and whether as a group or singly.

On the day following the end of the treatment period, each animal began a sequence of behavioral tasks administered in the same testing order. Subjects were maintained in their most recent environmental condition throughout the seven days of testing.

Day 1. The square open field described in Experiment 1 was modi-

fied to include a 70 x 9 cm strip of white plastic mesh draped 6 cm off the floor, a small bottle cap full of nails, and a black plexiglas box (10.8 x 8.9 x 12.7 cm) with one open side. The bottle cap and box were placed in a corner of the field, and the mesh draped across the opposite end of the field. Each mouse was placed in the center square, and latency to move out of the square recorded. Once the subject moved, a clock was activated and the number of squares entered, number of free (unsupported) rear-ups, number of supported rear-ups, number of entries into the box, number of contacts with objects, number of attempts to climb the plastic mesh, and number of boli excreted were recorded. At the end of the first 60-s interval, the clock was re-started and the same seven measures recorded for another 60-s.

The second task employed on Day 1 was the behavioral threshold for response to shock task. All details of the procedure were identical to those described in Experiment 1.

Day 2. Each subject was tested in the five-unit exploration field, as described in Experiment 1.

The procedure used to assess passive avoidance learning was modified in this experiment. Each animal was placed into the clear plexiglas half of a 25.5 x 10 x 16 cm box, divided into a clear and a black half and narrowing to a 3.5 cm base (Jarvik & Kopp, 1967). A 40 W light bulb was placed at the far end of the clear half, and the animal was placed in this half facing the light. The divider, which had covered up the 3 cm hole leading into the black side was removed, and a timer activated. Latency to turn around and face the hole (Time 1), and latency to step through the hole into the black compartment (Time 2) were recorded. Once the animal had stepped through the hole, a .75 mA shock was delivered to

the metal walls and floor of the black chamber for 10-s. The animal was removed and returned to its cage.

Finally, each animal was tested for position preference in the water maze. The dimensions of the apparatus are described in the first experiment; each animal was placed in the start alley of a maze with one horizontal and one vertical striped arm, and allowed to swim to either arm for six trials. Preference for right or left turn was recorded, and the direction chosen on the last four trials was considered the animal's preference. The horizontal-vertical maze was used during this preliminary test to control for brightness preferences.

Day 3. Each animal was returned to the passive avoidance apparatus, and the procedure repeated, except that the shock was not activated. Each animal was assigned an individual latency criterion for retention: the sum of an arbitrary 3 min + the total latency score (Time 1 and 2) on the first day. This procedure has been found useful in similar work with mice (Dudek, 1976). If an animal had not stepped through within the time set by its criterion, that criterion score was recorded and the subject removed.

Following this test, each subject was trained to swim to its non-preferred side in the water maze, for two days of six daily trials, with a 30-s ITI. The correct arm was always black, providing a redundant cue. Latency per trial and the number of daily errors were recorded. This procedure was used to assess potential differences in an animal's ability to attend to the redundant cue, based on the effects of different early environmental experiences. Earlier work (Forgays & Forgays, 1952; Hymovitch, 1952) had suggested that enriched animals might attend to a larger complex of cues in their immediate environment. If this notion

was valid, it seemed logical to predict that different treatment groups would react differentially to the shift of the position cues and the brightness cues. Pilot work with standard reared mice indicated that the task was easily acquired in two days of training.

After the second day of training, subjects in each group were ranked on their mean latency score on the second training day, and randomly assigned to one of two test groups: Position (P) or Color (C). In each P group the correct position was reversed and the new correct arm was black. In each C group the original position response was still correct, but the opposite arm was now black. Latency per trial and the number of daily errors were recorded for two days of six daily trials.

Analyses. The data were analysed in the three consecutive stages described in Experiment 1.

RESULTS

As discussed in the first experiment, the data was grouped, descriptively, into five behavioral categories.

As Figure 6 illustrates, switched groups again tended to sleep less during their first two weeks in enrichment and moved (crawled) more frequently than animals spending all their time in enrichment. These trends for locomotion were clearest in the groups switched every two weeks (EI4, IE4) and every week (EI8, IE8).

On measures of contacts with mates and contacts with objects in the enriched environment, switched groups ranked lower than mice in the EE group. Two other indices of exploratory tendencies, box entries and object contacts, did not differentiate the switched groups as clearly,

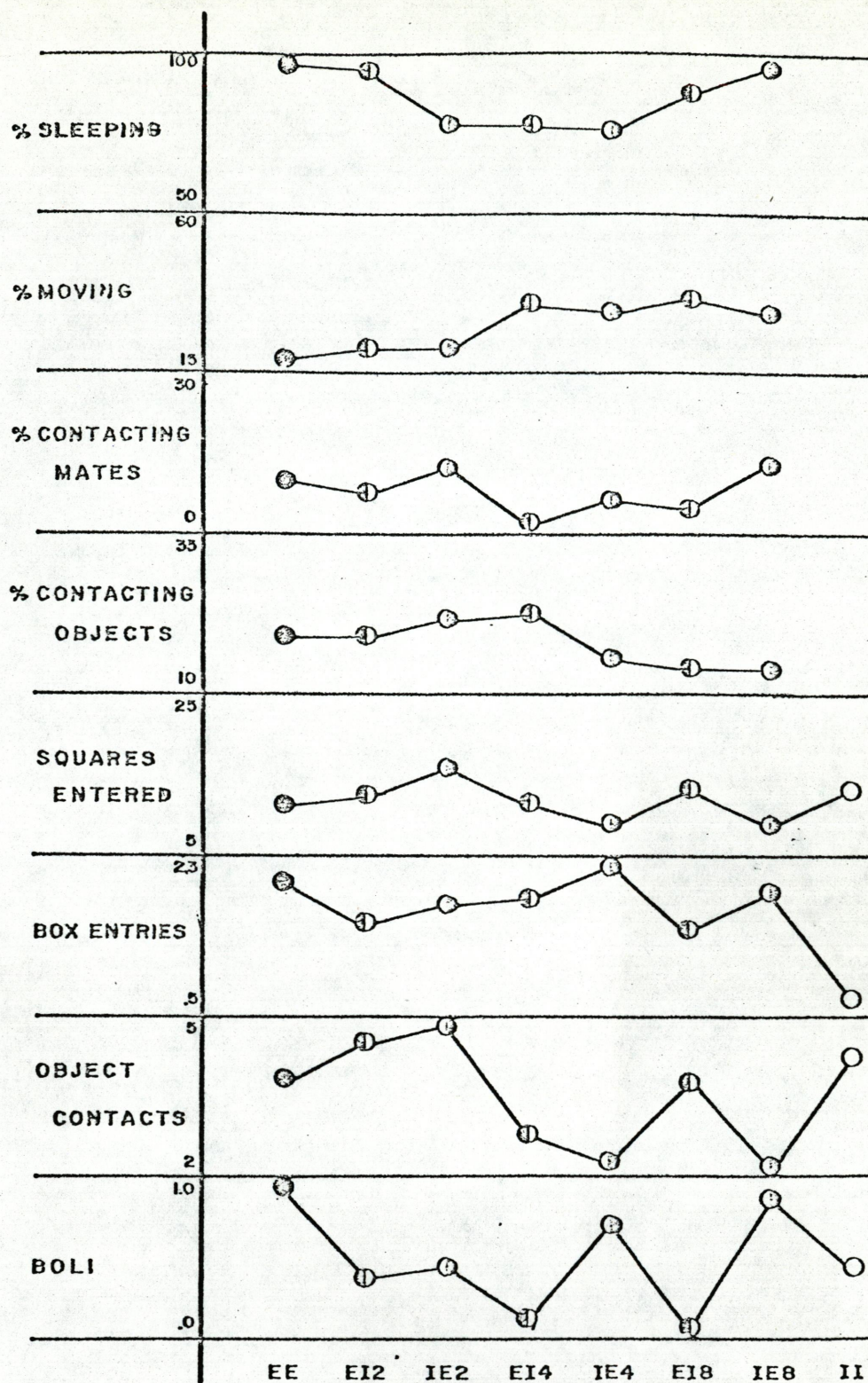


FIGURE 6. Comparison of Mean Behavioral Scores between the Eight Experimental Groups of Experiment 2 (Set 1)

however. EE subjects did enter the box significantly more often than II mice ($F = 2.76$, $df = 7/77$, $p < .04$). In the second panel in Figure 7, mean exploration entries during the two min test are presented. Only the EI4 and IE4 subjects made more entries than EE animals ($F = 9.28$, $df = 7/77$, $p < .01$).

Enriched subjects (EE) appeared to be more reactive than II mice, as indicated by the mean number of boli, as shown in Figure 6; however, several switched groups (IE4, IE8) appeared to be equally reactive.

In confirmation of findings from Experiment 1, II subjects tolerated significantly more intense shock prior to the foot shuffle response ($F = 18.35$, $df = 7/77$, $p < .01$) as shown in Figure 7. The same relationship was found for the jump response ($F = 12.75$, $df = 7/77$, $p < .01$). It is not clear why EI2 subjects were found to tolerate shock levels equal to that of the II group.

Unlike the findings reported in Experiment 1, several correlations between body weight and the foot shuffle and/or jump score were significant in several groups. In EE, the heavier the subject, the higher the score for foot shuffle and jump ($r = .85$, $df = 10$, $p < .05$; $r = .84$, $df = 10$, $p < .05$). The same relationship was found for both response scores in EI2 ($r = .63$, $df = 9$, $p < .05$; $r = .67$, $df = 9$, $p < .05$). In IE2, body weight and foot shuffle score were correlated ($r = .60$, $df = 10$, $p < .05$); however, the correlation between weight and jump score was significant only for the male mice ($r = .76$, $df = 4$, $p < .05$). Finally, weight and jump scores were correlated in II ($r = .62$, $df = 10$, $p < .05$). Although these correlations suggest that body weight differences may explain the treatment effects on tolerance to shock, the overall weight differences between groups on the day of testing are not supportive of

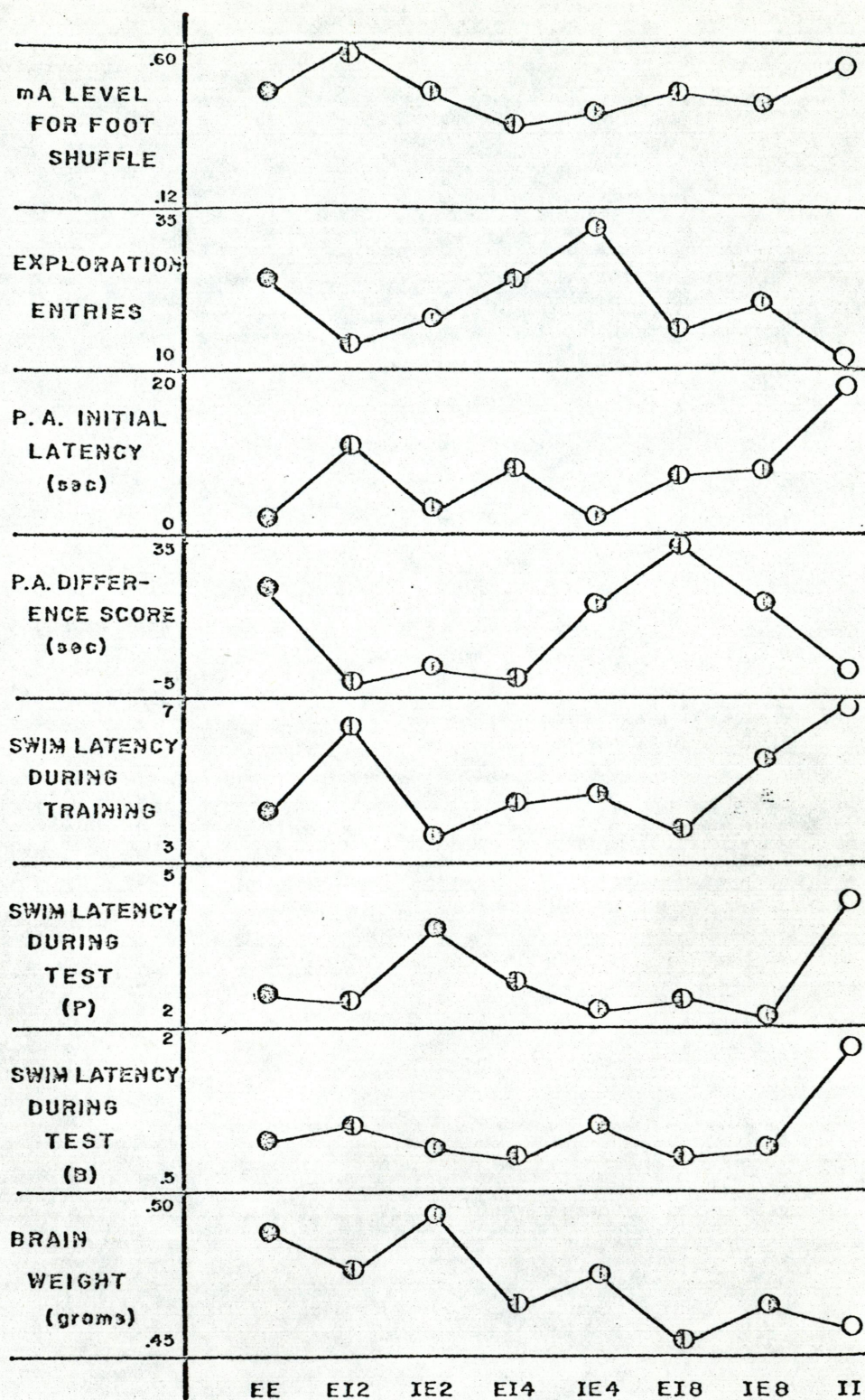


FIGURE 7. Comparison of Mean Brain and Behavioral Scores between the Eight Experimental Groups of Experiment 2 (Set 2)

this suggestion. It was found that IE8 was significantly smaller than EE, IE2, IE4, and II ($F = 5.13$, $df = 7/77$, $p < .001$). Although these latter four groups did not differ in body weight, they are significantly different in their tolerance to shock. Thus, it would not appear that such weight differences are associated with the overall group differences in pain tolerance, although they may be related to the sex differences in shock responsivity within groups.

Correlations between rear-ups and one or both of the tolerance scores also revealed a few significant relationships. The fewer rear-ups made the higher the foot shuffle scores in males of EI2 ($r = .75$, $df = 4$, $p < .05$), and in males of II ($r = .78$, $df = 4$, $p < .05$). The same relationship was found for females in IE2 ($r = -.85$, $df = 4$, $p < .05$). Few rear-ups were correlated with high jump scores in EI8 males ($r = -.71$, $df = 3$, $p < .05$) and II males ($r = -.87$, $df = 4$, $p < .05$). These correlations reflect the general finding that rear-up scores in this apparatus were higher in males; however, the pattern of correlations does not fit exactly with the pattern of group differences in shock tolerance.

Several of the measures dealing with the tests of memory processes are illustrated in Figure 7. Although no group differences due to treatment in passive avoidance responding or redundant cue training in the water maze were found, several patterns emerged. Enriched animals ranked best on the passive avoidance difference measure, i.e. they avoided the longest. The fourth panel in Figure 7 indicates that II subjects ranked very low on this measure, although they were consistently slowest to face the entrance role, on the first ($F = 3.88$, $df = 7/77$, $p < .01$) and second day ($F = 2.21$, $df = 7/77$, $p < .05$). Note that II

subjects also swam slowest during acquisition training with redundant cues in the water maze (fifth panel), and in both test problems. Unfortunately, no clear trends were demonstrated in the switched groups on these measures.

The last panel in Figure 7 indicates that mice of the IE2 group possessed brains heavier than all other groups except EE, and that EE brains were heavier than those of II mice ($F = 4.19$, $df = 7/77$, $p < .01$). However, the cerebellums of EE, EI2, IE2 and II subjects were found to be significantly heavier than the rest of the treatment groups ($F = 11.38$, $df = 7/77$, $p < .01$). Mean group weights for brain parts are shown in Table 5. Brain weight and body weight were not correlated in any of the treatment groups. Similar to Experiment 1, male subjects weighed significantly more from day 35 onwards ($F = 129.82$, $df = 1/77$, $p < .01$), and treatment effects had disappeared by day 86, as shown in Figure 8.

Generally, behavioral and brain measures of EE animals confirms those reported in the first experiment, describing the EE mouse as moderately locomotory, highly exploratory, reactive, and possessing a large body and brain. These data also confirm the II mouse as highly locomotory, less exploratory or reactive, extremely tolerant of painful shock, and possessing a smaller body and brain. Certain of the relative rankings of switched groups on behavioral tests are in the same direction as in Experiment 1, including a tendency towards lower reactivity, tolerance, exploration entries and whole brain weight than EE and II subjects. As Table 6 illustrates, behavioral plasticity (recency effect) and stability (primary effect) were evidenced. Note that the indications of behavioral plasticity were found in switched groups spending their most recent rearing series in enrichment (IE2, IE4 and IE8). Evidence of be-

TABLE 5. Mean Whole Brain
Component Brain Weights for Experiment 2

Brain Weights	Groups							
	EE	EI2	IE2	EI4	IE4	EI8	IE8	II
Whole Brain	.4814	.4753	.4914	.4697	.4748	.4543	.4707	.4666
Cerebellum	.0540	.0559	.0535	.0443	.0439	.0435	.0438	.0526
Cerebral Cortex	.1854	.1799	.1860	.1851	.1817	.1747	.1735	.1789
Rest of Brain	.2257	.2281	.2357	.2208	.2264	.2049	.2278	.2222

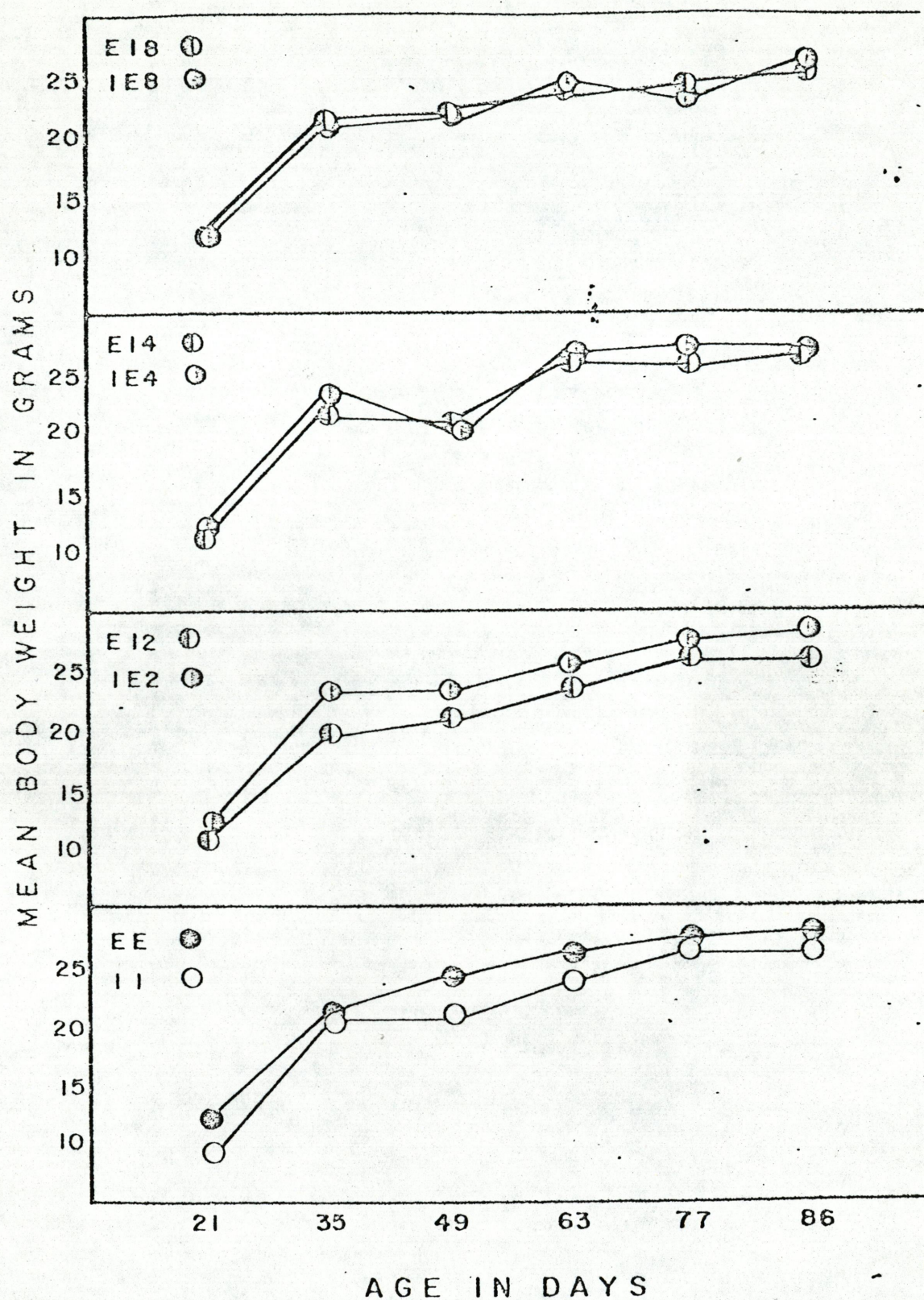


FIGURE 8. Mean Body Weights over Ages for the Treatment Groups of Experiment 2

TABLE 6. Brain and Behavioral Stability
in Switch Groups (Experiment 2)^a

Measures	Switch Groups					
	EE2	IE2	EE4	IE4	EE8	IE8
Latency to move	P	P	P	=	=	X
Box entries, first 60-s	=	=	=	P	=	=
Contacts, first 60-s	=	=	=	=	=	X
Box entries, second 60-s	=	=	=	P	=	=
Foot shuffle	P	P	A	P	X	P
Jump	P	P	X	P	X	P
Exploration choices	P	=	X	P	=	P
Whole brain weight	=	P	=	=	A	=
Cerebellar weight	X	=	A	A	A	A

^aScores of each switch group were compared with the non-switch groups EE and II.

Note: X indicates stability of effects; P indicates plasticity of effects; A indicates alteration of effects such that the switch group ranked lower than both non-switch groups; = indicates that the switch group's performance was equal to that of both non-switch groups.

havioral stability, however, was found in switched groups which had spent their earliest rearing period in enrichment (EI4, EI8). Unfortunately, the switch group EI2 did not replicate the tendencies towards behavioral stability found in Experiment 1.

Observations during Rearing

In addition to those sets of scores illustrated in Figure 6, the other observations of behavior during enrichment rearing demonstrated several trends towards modified general locomotion and interactions with environmental stimuli.

Based on observations made at the time of switchover into enrichment, and 4 hours later, it was found that subjects which had sustained any experience with impoverishment previously remained active as long as 4 hours after the switch. Animals without impoverishment experience were found asleep at this time.

The behavioral observations made before, during, and after the toy changes indicated that EE mice tended to make fewer object contacts, and be less active, 15 min after a change from week 5 on. All EE and EI2 animals were always found asleep or resting 60 min after the change. The IE2 animals appeared to make fewer contacts with the new toys 15 min after the change, but the effect waned after the first toy change. With the other four groups (EI4, IE4, EI8, IE8), no differences in the general pattern were indicated. In all groups with any experience with impoverishment, subjects were actively interacting with toys and mates 15 min after the change and, to some extent, were still active 60 min after changes.

DISCUSSION

Differences in performance between males and females in this experiment were found on eight of the behavioral tasks and in body weight measurements. Overall, females appeared quicker to initially move, reared up more often, and made more box entries during the first 60-s in the open field. Female mice demonstrated lower foot shuffle and jump scores, and a greater number of rear-ups in the adaptation period. In the exploration field, females defecated more frequently than males. Although these differences indicate that female mice were generally more active, and possibly more reactive (boli), the females retained the passive avoidance response significantly better than males, as indicated by the difference score between total latencies 2 and 1. Significant treatment by sex interactions were consistently expressed primarily in switched groups, especially in EI2. Such differences included rear-ups scores, boli scores, squares entered, and contacts, in which females of EI2 exhibited higher scores.

The data confirm the general description of EE mice given in the first experiment, i.e. of a mouse that is highly reactive to novelty, displays moderate locomotion and a consistent tendency to explore its environment. Similarly, these data replicate the description of II mice derived from the results of the first experiment. Unlike an "enriched" animal, an impoverished mouse is less reactive, locomotes more readily and explores environmental stimuli less frequently.

Consistent with the results of the first experiment, switched mice generally demonstrated a sustained increase in locomotion (diminution in sleeping, increase in moving about the environment and squares entered

during open field testing). In combination with a trend towards sustained activity for a long period of time following each switch into enrichment, and a decrease in exploratory tendencies (object and social contacts), these observations suggest that arousal systems mediating these behavioral changes may have been significantly altered.

The role of arousal, if any, in the increased tolerance to painful shock demonstrated by II mice deserves further investigation, especially as the results of this experiment replicate those of Experiment 1 very closely.

With regard to treatment effects on whole brain weights, the extremes of environmental stimulation (EE and II) respectively increased or decreased overall brain size. Most switch groups ranked below both of these groups, with two exceptions. The brains of IE2 subjects were larger than all other groups except EE; and EI8 subjects ranked lower than all other groups on whole brain weight scores. All subjects experiencing enrichment recently (IE2, IE4, IE8) ranked higher in brain weight than animals in impoverished conditions. Interestingly, this pattern is modified for the group cerebellum weights. In this measure, neither long-term enrichment nor impoverishment reduced the size of the cerebellum; the significantly smaller cerebellums of EI4, EI8, and IE8, therefore, must reflect the influences of repeated switching between environments. The two groups experiencing the fewest environmental changes, EI2 and IE2 groups, are most similar to both EE and II animals on this brain measure.

The most consistent trend suggested by the data on the switched groups involves the observation that both behavioral plasticity and stability were in the direction of "enrichment-like" behavioral tend-

encies. In other words, enrichment experience appeared to both modify any behavioral dispositions encouraged by prior impoverishment experiences and to "protect" behavioral tendencies from subsequent impoverishment experiences.

The lack of replication of the standard switched groups tested in Experiment 1 (EI2, IE2) was not anticipated. It is possible that the large increase in introduction of stimuli into the environment, from once every 2 weeks to once every 2 days, may have contributed to this lack of replication. The interactions between enrichment and impoverishment experiences on subsequent behavior and brain measures may have differed, in some way, as a function of this change in procedure.

GENERAL DISCUSSION

Taken as a whole, the results of these two experiments indicate that environmental switchovers between enrichment and impoverishment rearing conditions have effects on the behavioral tendencies of mice. It is also clear that the parameters of treatment and test methods are important to some of the particular trends found in the data. For instance, although sex differences are infrequently studied or reported in this field, a reasonable number of sex differences were found in this study, the nature of which varied between the experiments. The introduction of frequent toy changes, and corresponding additional stimulation, in the second experiments may be associated with the large number of significant treatment by sex interactions found, indicating that treatment effects were expressed differently in females and males. This observation points out the need to better understand the potential role that sex-typical hormones may play in partial mediation of environ-

mental complexity effects. To this point, Greenough and Carter (1975) recently reported that the neural response to early stresses differed between male and female rats. It is interesting to note that the neural responses typically studied in relation to environmental enrichment and impoverishment (weight of whole brain and occipital cortex, enzyme and neurotransmitter concentrations and activity), including the present findings, do not report sex differences in these measures. However, neither the role of early hormonal state nor detailed study of such brain areas as the preoptic have been investigated in the enrichment-impoverishment paradigm.

The present results consistently suggest that mice reared exclusively in an enriched environment are less active, very reactive, and very exploratory compared with impoverished subjects. Previous work with mice has reported that enriched animals were more active, and defecated less, in the open field (Manosevitz, 1970; Manosevitz & Joel, 1973). Historically, reports on rodent behavior in the open field apparatus have been contradictory; in large part, differences in procedure, and apparatus, probably explain a substantial portion of these controversies (Walsh & Cummins, 1976). A clearer understanding of the meaning of locomotor and exploration tendencies in a novel situation may result from more precise analyses of responses to stimuli differing qualitatively, along a novelty dimension. The issue takes on even greater importance when the concept of arousal is introduced as a mediating mechanism. Walsh & Cummins (1975) have suggested that internal arousal state mediates the effects of enrichment experience on brain tissue and chemistry. The fact that enriched and impoverished mice were found to differ behaviorally could be interpreted as evidence for an established difference in arousal

systems, and, indeed, similar results have been interpreted in this manner (Manosevitz, 1970). However, extending Walsh & Cummins' hypothesis to the behavior of switched groups would lead to the prediction that their performance scores should be intermediate between a state of low (enrichment) and high (impoverishment) arousal. In general, this was not found. Certainly, the consistent attenuation of sleeping behavior, increase in movement through the environment, and decrease in exploratory tendencies found in switched groups suggests that some aspect of arousal mediation was involved in these behavioral modifications. It cannot be stated unequivocally, however, that such a modification in arousal systems was unidirectional, especially considering the arguments still raised over interpretation of such behaviors as generalized activity and exploration. To establish at least the consistency, or stability, of such modifications over subsequent exposure, it will be necessary to make observations of ongoing behaviors of switched mice during their experiences in environmental impoverishment. Such data should discriminate between a "peak shift" phenomenon, i.e. altered behavior patterns only in enrichment, and a permanent change in such patterns throughout later enrichment and impoverishment exposures.

Of course, switched animals did not always differ from mice limited to only one of the environmental treatments; indeed, depending on the task, switched animals were found to be similar to either one or the other, or both of these groups. The lack of an apparent pattern towards "stability" or "plasticity" must result from several factors, including measurement reliability and validity. However, especially in Experiment 2, the trend was relatively clear for a greater impact of enrichment experience, whether it occurred early (stability) or recently (plasticity)

in the treatment period.

This conclusion is, of course, an optimistic one, although it must remain tentative at this time. The data clearly indicate that the "personality" of animals exposed to periodic environmental enrichment and impoverishment is the product of interactions between these environmental influences, and is not readily predictable, at this time. The results suggest that certain behavioral effects of early impoverishment can be ameliorated by subsequent enrichment experiences and confirms part of the small literature on brain changes in switched groups (Rosenzweig, et al., 1962; Rosenzweig, et al., 1967).

The future utility of the switchover paradigm in understanding behavioral stabilities and environmental pressures must depend on the worth of the behavioral measures employed, as well as their theoretical application. These data indicate that task specificity of a behavioral tendency, as well as carry-over effects of repeated testing must be considered. Rather than assuming the impact of earlier exposure on a particular behavior, it should be possible to test animals at the end of both the initial and subsequent environmental experiences. This technique would provide a clear estimation of any environmental pressure on a trait, even considering the effect of repeated measurement.

At the theoretical level, arousal mediation can be studied by means of modifications of variables associated with arousal systems. These methods include the use of relevant drugs, natural diurnal rhythms, rodent populations that differ, genetically, in their reactivity, and surgical preparations, such as septal-lesioned animals.

The thoughtful use of these, and other, approaches to the study of long-term environmental complexity effects on brain and behavior will

be critical to the future role of therapeutic environmental programs in potentiating development or inducing recovery from previous environmentally induced incapacities.

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APPENDIX

Behavioral Effects of Environmental Complexity Experience: A Review

Behavioral Effects of Environmental Complexity Experience

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Running head: Behavioral Effects of Environmental Complexity

Abstract

The effects of environmental complexity experience on behavioral organization are discussed from a historical perspective, and in relation to the established changes in neural characteristics reported in the literature. Although knowledge of the brain's responses to enrichment or impoverishment rearing experience has advanced, behavioral analyses have not developed to a comparable level. At present, there is little evidence to suggest that reported brain and behavioral effects of environmental complexity exposure are related; however, an understanding of the mechanisms mediating these effects is dependent on establishing such relationships. Several future approaches to investigations of the brain-behavior interactions induced by environmental complexity experience are discussed.

Behavioral Effects of Environmental Complexity Experience

Evidence that environmental enrichment or impoverishment modifies the central nervous system of animals plays an important part in our understanding of the mechanisms of neural growth and organization. Historically, primary emphasis was placed on the effects of environmental complexity upon behavior, with secondary interest in determining the neural changes mediating the behavioral changes. Although these emphases have been reversed in more recent years the nature of the relationship between observed neural and behavioral alterations is still unclear. The evidence for environmentally induced brain and behavior modifications is reviewed here, and alternative approaches to the problem are discussed.

It is important to be clear on what is meant by the terms environmental enrichment and impoverishment as defined by experimental procedures. By and large, these terms refer to the type of overall environment presented to the organism, and, therefore, differ from specific treatments such as handling, shock, or dietary manipulation. An "enriched" environment traditionally refers to the addition of stimulation beyond the organism's normal environment. "Impoverished" environments refer to the reduction of stimulation below that found in the normal environment. This procedure differs from the study of the effects of specific reduction in certain features of the environment, such as visual, tactile, kinesthetic or haptic deprivation (see Riesen, 1975, for review). With the emphasis on the effects of overall environment, the term "impoverishment" is better suited, reserving "deprivation" for the specific absence of stimuli appropriate to a certain modality. The third commonly used

term, "isolation", is used in reference to restriction of the animal's social environment. It is unfortunate that, in neither the study of environmental deprivation nor impoverishment, has the necessary distinction been made between the total lack of certain stimulation and the loss of that stimulation, at some time following birth. The distinction is critical to understanding the effects of such treatments on the initial differentiation of a system, as opposed to their effects on the continual development of the system (Gottlieb, 1973).

History and Background

Evidence for Behavioral Modification

The history of the study of environmental enrichment and impoverishment effects on development is usually founded on the theoretical insights of Freud. His emphasis on the importance of childhood experiences was an important impetus for the experimental study of the human child. From this early work with children evolved the study of environmental effects on behavioral development of animals. The correspondence between the two fields began to diverge from the time that Hebb (1947, 1949) introduced his notions of the development of perceptual learning and the importance of early experiences with a variety of stimuli. Hebb's studies of home-reared and laboratory-reared rats became the basic model for the study of early environmental influences on the development of learning ability in rats and mice. In the years following Hebb's (1949) presentation of a physiological model of perceptual learning, experimenters studied the behavior of rats reared in what were then called "free" or "restricted" environments. Hymovitch (1952) reported that rats reared with a variety of different objects, whether confined to large or small cage areas,

were superior in the Hebb-Williams maze (Hebb & Williams, 1946) to rats reared without benefit of this experience. This apparatus was constructed so that the organism was forced to deal with an entire environmental complex, rather than to attend to a single relevant cue. This restriction was thought to draw on the organism's ability to organize its perceptions of the environment, and to respond accordingly.

In experiments similar to Hymovitch (1952), rats reared in a large free environment with toys were found superior to restricted rats in the Hebb-Williams maze (Forgays & Forgays, 1952). In contrast to Hymovitch's results, however, these authors reported that rats allowed visual, but not motoric, enrichment, i.e., constrained in small mesh cages surrounded by toys, were inferior to rats allowed both forms of enrichment, although superior to restricted rats. These early attempts to determine the critical contributing variables were followed by a series of studies involving further study of visual and spatial variables (Forgus, 1954, 1955 a & b). Both total-free environment and free-visual (toys could be seen but not touched) groups of rats were superior to totally restricted rats in solving a form discrimination (Forgus, 1954). The author concluded that the restricted rats were more emotional as a consequence of their rearing experience. Forgus (1955a) reported that rats reared in a total-free environment were superior to rats reared in a free-visual environment in solving a spatial problem in an elevated T-maze, when tested in the dark. The opposite was true when the groups were tested in the light. Forgus concluded that the visual-spatial enrichment combination interfered with performance in the lighted condition.

It should be noted that a replication of this study by Walk (1958) reported that the visual-spatial group was superior in the lighted condition, and that no differences were found in the dark condition. Using the same types of groups in an enclosed multi-unit T-maze, Forgas (1955b) found that the visual-spatial enriched group did not differ from the free-visual group in solving a spatial discrimination with redundant cue cards. However, when the cue cards were removed from the apparatus, the visual-spatial group performed significantly better. This result suggests that, contrary to the hypothesis that combination enrichment treatments produce interference in performance in certain situations, (Forgas, 1955a) the more avenues of enrichment that are provided, the greater their influence on later perceptual learning.

A direct attack on the role of spatial factors in enrichment and impoverishment effects was prompted by Zimbardo and Montgomery's (1957) suggestion that the amount of space available to the rat influences later exploratory behavior in tests of perceptual learning. Hoffman (1959) reported no initial differences in exploratory behavior between rats reared in a large enriched environment, and rats reared in the same environment, but restricted in their mobility, and rats restricted to small single cages without toys. However, the free-visual environment group was found poorest in an "Einstellung", or reasoning, test. Hoffman concluded that the experience with space is important for later perceptual learning, but that it is not closely related to changes in exploratory behavior. The notion that differences in exploratory

behavior underlie observed differences in perceptual learning following enrichment and impoverishment treatments was re-examined by Woods, et al. (1960, 1961). Errors and exploration were found to be positively correlated in the Hebb-Williams maze, for rats reared in a free or restricted environment (Woods, et al., 1960). Again in 1961, the same authors found that rats reared in an impoverished environment when subjected to severe food deprivation or shock performed comparably to those reared in a free environment. The authors concluded that the increased drive produced by such procedures served to correct for the increased exploratory drive produced by the impoverished environment, suggesting that environmental restriction results in inferior learning due to an increased exploratory drive (which handicaps test performance), and is not due to a lack of opportunity for learning experiences. No attempts have been made to replicate this finding; however, the earlier work of this period (Hymovitch, 1952; Forgays & Forgays, 1952; Hoffman, 1959) suggests that, while the amount of available space does contribute to later performance, differences in later learning are also closely tied to the earlier experience with a varied environment. The findings of Schweikert and Collins (1966) confirm this conclusion. They reported that rats reared in a free environment were superior in the Hebb-Williams maze to rats reared in equivalent spatial dimensions without toys.

During this early stage of study, some evidence suggested that the impact of environmental enrichment or impoverishment was greatest during the early part of the organism's life. The initial suggestions merely

indicated that, in the rat, exposure to such treatments seemed more influential if administered during the first, rather than the third, month of life (Hymovitch, 1952; Forgas, 1956). Forgas and Read (1962) reported that the period between 22 and 43 days of age was optimal for exposure to a free environment, based on performance in the Hebb-Williams maze. Denenberg, et al. (1968) found that free environmental experience during the first 50 days of life produced the greatest enhancement of learning measures in the Hebb-Williams maze; however, rats placed in a free environment only during the first 21 days of life ranked second in performance in the maze.

At the same time that this group was studying the impact of enrichment and impoverishment on later perceptual learning in the rat, other researchers were exploring the effects of prolonged isolation on the general perceptual integrity of dogs, rhesus monkeys, and chimpanzees. The emphasis was placed on understanding the impact of severe environmental impoverishment on the organism's ability to deal with normal environmental events, including social contacts with other species members. From an initial study of differences between laboratory and home-reared puppies (Clark, et al., 1951), a series of reports emerged concerning the effects of the comparative impoverishment of the laboratory situation. Thompson and Heron (1954a & b) reported an increase in diffuse activity in laboratory reared puppies, and an increase in the frequency of epileptiform seizures was found (Thompson, et al., 1956). These laboratory puppies demonstrated a reduction in their capacity to interact, socially, with other age-mates (Melzack & Thompson, 1956), and a remarkable insensitivity

to painful stimulation (Melzack & Scott, 1957). The authors concluded that these animals were not suffering sensory system deficits, but that their perceptual abilities to respond appropriately to such stimuli were diminished. This body of evidence was taken as support for the Hebbian (1949) theory of the critical importance of an early period of perceptual learning to the organization of the nervous system.

A second program of study on the effects of early isolation on the organization of perceptual capacities in dogs was undertaken at The Jackson Laboratory in the 1960's. Comparisons were made between two basic groups of puppies: those given free run of the laboratory for much of the time, and those subjected to one of several types of isolation conditions, within the laboratory. The bulk of such studies (Fuller, 1964; Fuller, 1966a & b; Fuller & Clark, 1966) are summarized by Fuller (1967). In the latter report, the author points out that there are marked individual differences in the amount of behavioral disruption produced by isolation. In particular, distinct differences in overall behavioral effects were found between beagles and wirehaired terriers. Contrary to the conclusions of the McGill group (Thompson & Heron, 1954), the immediate effects of environmental isolation were interpreted as mediated by the excessive arousal induced in the puppy when meeting a complex environment for the first time (Fuller, 1967). Early support for this hypothesis included work with the tranquilizer, chlorpromazine, administered to isolated puppies prior to their first arena test (Fuller, Waller & Clark, 1960). This pre-treatment permanently attenuated the typical stress syndrome in these puppies, even over subsequent arena tests.

This "emergence-stress" hypothesis is also supported by the finding that puppies receiving gentle handling behaved less bizarrely during their initial exposures to the complex environment following the isolation treatment (Fuller & Clark, 1966). The theoretical distinction made here between the interpretation of isolation effects as a result of necessary perceptual organization early in life (Thompson & Heron, 1954), and the concept of perceptual debilitation as a function of stress on emergence (Fuller, 1967), is somewhat reminiscent of the issues raised concerning the nature of the isolated rat's perceptual deficits (Hoffman, 1959; Woods, et al., 1960, 1961) previously discussed.

Two other complex species were studied during this time, using similar designs. Mason (1960) reported that rhesus monkeys isolated from all social contact during their first two years were far more aggressive, and demonstrated disorganized sexual behavior, in comparison to 2 year old rhesus monkeys born in the wild and maintained in a social laboratory setting. These isolated monkeys showed little tendency to interact socially with age-mates (Mason, 1961a), and were not capable of establishing a stable dominance hierarchy during food competition tests (Mason, 1961b). In addition, isolated monkeys did not develop an attachment, comparable to feral socialized monkeys, to "pet" rats with whom they had been reared (Mason & Green, 1962). The authors concluded that, in the rhesus monkey, early isolation, especially from peers, results in a permanent deficiency in social communication skills. Harlow and Harlow (1962) confirmed and extended these conclusions in their study of social isolation effects on infant rhesus monkeys. While early work suggested

that "surrogate" mothers did much to maintain normal social development (Harlow & Zimmermann, 1959), it was later found that even the presence of the biological mother was not completely sufficient for the normal development of appropriate social behavior (Harlow & Harlow, 1962). These authors further reported that, within a limited period of time, the effects of social isolation were reversible, and that as little as 15-20 min per day of peer contact was sufficient to maintain normal social development. Harlow and Harlow (1966) defined a consistent pattern of behavior, called the "isolation syndrome", which appeared composed primarily of self-directed behaviors (Mason & Green, 1962).

Another species under study at this time was the chimpanzee; however, the focus of such study differed from that involving the rhesus monkey. Menzel, et al. (1961) reported that chimpanzees isolated for the first two years of life showed no differences in their initial reactions to socially reared chimpanzees. However, such isolated chimpanzees were less responsive to both familiar and novel objects, as compared with the feral animals (Menzel, et al., 1963).

At this point in the history of early enrichment and impoverishment effects certain major points had been made and certain theoretical issues were still unresolved. Investigations of perceptual learning in the rat suggested that the degree of environmental experiences plays an important role in later learning ability, perhaps as a function of its impact on perceptual organization (Hebb, 1949). Some data suggested that treatment early in life is particularly influential (Hymovitch, 1952; Forgas & Read, 1962). The attention paid to the effects of early isolation in

puppies, while confirming the critical role of environmental experience, did not resolve the issue of whether that early lack results in a permanent perceptual deficit as a function of non-organization, or in a heightened emotional reaction that over-rides perceptual abilities (Fuller, 1967). The same question can be asked of the work with the infant rhesus, i.e., is the observed lack of communication skills (Mason & Green, 1962) the product of a lack of critical early practice alone, or is it also the result of an overwhelming emotional response? That the social incompetence of the isolated rhesus monkey can be eliminated, in certain circumstances, raises additional questions about the long term effects of early isolation (Harlow & Harlow, 1962) which will require additional research.

The initial thrust of these early studies was primarily behavioral, with one exception. Melzack and Burns (1965) reported finding abnormal EEG patterns in their isolated dogs. In summary, the data indicated that early environmental treatments were effective in altering behavior, but, the lack of supporting physiological evidence prevented either confirmation or disconfirmation of the Hebbian concept that organized "cell assemblies" were the basis for behavioral alteration (Hebb, 1949).

The Physiological Evidence

The first programmatic attempt to establish physiological correlates for the behavioral changes induced by early environmental experiences was initiated by several researchers at Berkeley. Krech, Rosenzweig and Bennett (1960) reported that the level of the cholinesterase was higher in rats exposed to enrichment (EC) compared with rats reared in their

"isolation" (IC) conditions. Based on findings that cholinesterase level differed between two lines of rats selected for good or poor maze learning, Krech, Rosenzweig, Bennett and Krueckal (1954) hypothesized that different environmental conditions might change cholinesterase levels, producing similar behavioral differences. Bennett, Diamond, Krech and Rosenzweig (1964) have summarized the next few years of research, during which it was found that the ratio of cortical to sub-cortical cholinesterase activity was higher in rats exposed to enrichment (Krech, Rosenzweig & Bennett, 1962), and that EC groups demonstrated an increase in cortical depth of the striate cortex (Diamond, Krech & Rosenzweig, 1964). These differences were not due to handling, locomotor activity or stress factors (Bennett, et al., 1964). The following years introduced refinements of the general findings. The visual cortex was confirmed as that brain area most susceptible to EC effects (Diamond, 1967), and the standard EC--IC differences were found to diminish, but not disappear, 30 days after the end of treatment (Rosenzweig, Bennett & Diamond, 1967). The notion that the effects of such environmental treatments depends on the animal's active converse with the environment was supported by the finding that, while methamphetamine potentiated EC effects, phenobarbital attenuated them (Rosenzweig & Bennett, 1968). Comparative studies of gerbils, mice, and rats indicated that the effects of EC were to some degree species-specific (Rosenzweig & Bennett, 1969). The list of such changes was expanded to include increases and decreases in the number and size of synapses in the striate cortex (Rosenzweig, Mollgaard, Diamond & Bennett, 1972) and an increase in the number of basal dendritic spines on pyramidal

neurons in the striate cortex (Globus, et al., 1973). Greenough and Volkmar (1973) reported an increased dendritic branching of basal dendrites of pyramidal cells in the striate cortex of rats.

Recently, the importance of active interaction with the environment for the manifestation of the standard physiological changes has been reconfirmed (Ferchmin, Bennett & Rosenzweig, 1975). While the wealth of information generated by the above reports has done much to establish the existence of physiological changes following early environmental treatments, the data has not been as clearly confirmatory of a definite brain change-behavior change correlation. Rosenzweig, Bennett and Diamond (1972) conclude that their data do not support a close correspondence between the physiological effects of environmental treatments and measures of learning ability, and that the enrichment effects cannot clearly be labeled as either the result of cumulative specific memorial processes, or the result of a generalized "tuning" of the organisms' behavioral capacity.

During the period 1968-1976, numerous other researchers began to investigate the impact of early environmental experiences, in some cases combining both physiological and behavioral measurements. In studying the very young rat, Altman, et al. (1968) reported that early enrichment resulted in an extension of the period of active cerebrum growth, i.e., greater cerebrum length. Edwards, et al. (1969) found that early enrichment hastened the development of visual evoked potentials, and enhanced discrimination learning in the rat. Significantly increased depth of occipital cortex and hippocampus was found in rats exposed to enrichment

(Walsh, et al., 1969). A somewhat different type of enrichment, in which infant rats were subjected daily to handling and stress, was found to produce significant increases in spine growth on pyramidal neurons in the striate cortex at 8 days of age (Schapiro & Vukovich, 1970). Not all enrichment treatments have proven successful, however. Greenough, et al. (1970) found no physiological EC--IC differences in DBA/2J mice, although differences in learning ability were demonstrated in the Lashley III maze and a step-through task. More recently, several researchers have added to the list of brain characteristics affected by enrichment. Ferchmin, et al. (1970) described a temporal pattern of EC changes in brain measures. The most marked EC--IC differences were found within the first week and between 30 and 60 days after treatment commenced. In another experiment with rats, Walsh, et al. (1971) significant differences in brain weight following 80 days of enrichment treatment, but not after 30 days. Geller (1971) has re-introduced the notion of stress related IC changes by reporting that both adrenal weight and norepinephrine level are increased in the rat following isolation. An increase in synaptic density in striate cortex was found in rats exposed to enrichment (West & Greenough, 1972). The subtle nature of certain potential EC--IC differences was demonstrated by the finding that mice of these 2 groups did not differ in learning ability on a black-white discrimination or the Lashley III maze when trials were spaced, but did differ, the EC group being significantly superior, when trials were massed (Greenough, et al., 1972). Levitan et al. (1972) reported a greater incorporation of ^3H -leucine, an amino acid, into the hippocampal

and cortical subcellular fractions of EC rats. Tagney (1973), noting that EC rats, or rats from an IC treatment transferred to an EC condition, demonstrated a greater amount of slow wave sleep, suggested that an increased rate of protein synthesis is part of the enrichment effect. Presumably, the greater amount of slow wave sleep is the result of an increased protein synthesis requirement in the EC animals. Some information comes from the report of Uphouse and Bonner (1975) who found an increase in the amount of specific RNA found in the brains of rats exposed to enrichment.

The bulk of evidence for physiological changes following early environmental experiences is highly supportive of the idea that such treatments alter the organisms' physiology. Furthermore, the reports of more recent years suggest that such physiological alterations are expressed at the levels of fine structure and molecular organization, as well as in more global changes in weight and depth of larger brain structures. Unfortunately, the behavioral analyses of early environmental experience effects have not yielded similar refinements, and recent research has not been substantially more successful than of earlier years in establishing a close correspondence between brain and behavior changes.

Characteristics of the Environment and the Organism

One area of investigation, however, has yielded information concerning early enrichment and impoverishment effects on behavior, and that is the studies of relationships between particular environmental components and later behavioral alterations. With a few marked exceptions, the majority of studies on the effects of early environmental treatments did not involve

analyses of particular components of the experiential environment. Hymovitch (1952), Forgays and Forgays (1952), Hoffman (1959), and Schweikert and Collins (1966) concluded that the amount of space available, while influential, was not critical to behavioral alteration following early enrichment or impoverishment. Woods, et al. (1960, 1961), on the other hand, argued that spatial restrictions influenced emotionality, which served to confound later behavioral measurement. The issue has not been resolved.

A number of variables other than space have been investigated, including properties of the organism, as well as the environment. Hymovitch (1952) reported that blinded rats given enrichment treatment were superior to blinded control rats in the Hebb-Williams maze. Rosenzweig, et al. (1969) reported that enrichment produced similar effects upon brain structure and chemistry in sighted and blinded rats, and in sighted rats reared in darkness. In fact, reliable differences were found even between individually enriched and isolated rats, if the enrichment was provided during total darkness (Rosenzweig & Bennett, 1972). Social rearing as compared with isolate rearing does not have much effect on brain measures (Quay, et al., 1969). Rats reared in groups of 4, under standard laboratory conditions, showed only slight changes in brain measures, compared with isolates. Rosenzweig (1971) found that group rearing in groups of 3 or 12 in an empty cage was not markedly influential in altering their brain compared with IC animals.

The level of arousal during environmental treatments is, apparently, critical to later brain alterations. Rosenzweig and Bennett (1968)

reported that amphetamine potentiated the effects of enrichment, and that certain depressants served to attenuate these effects. It was concluded that such drugs modulate treatment effects via the level of arousal (Bennett, et al., 1973). However, not all changes in level of environmental stimulation appear to be sufficient to alter general arousal states, at least as judged by persistent brain effects. Rosenzweig and Bennett (1972) reported that alterations in the ambient environment, i.e., in the laboratory room, did not elevate brain changes above those correlated with the typical enrichment condition. Supportive of this conclusion was the fact that rearing IC rats in the same room with EC rats did not alleviate the effects of isolation. In line with these findings, Ferchmin, et al. (1975) reported that the opportunity to view, but not come in contact with, an enriched environment was not sufficient to produce the changes in the brain found after living in the environment. Active interaction with some features of the environment appears necessary to the demonstration of alterations in brain measures.

The variety of stimulation provided during treatment may also be critical to later alterations in physiological or behavioral measures. In a modified type of enrichment procedure rats were exposed to a variety of visual stimuli, tactual stimuli or the combination of the two types for 16 days. Nine days later, animals so treated showed a preference for complex situations in comparison to control animals (Gorry, et al., 1971). No differences in activity level were observed. Brown and King (1971) presented rats with a variety of abstract shaped cut-outs, hung in their cages, for 80 days. The number of shapes presented and the

amount of formal training were also varied, over different groups. The variety, but not the number, of objects was found critical for variation in performance on the Lashley jump stand, and changes in brain levels of acetylcholine and acetylcholinesterase. Formal training was not influential. Chang and Hsu (1974) reported that rats given 2 hrs of daily enrichment exposure spent more time interacting with the objects if they were changed from day to day.

As mentioned previously, the earliest investigations of critical environmental components involved the amount of space provided during treatment, and one conclusion of these studies was that space alone, is not sufficient to alter later behavioral measures (Hoffman, 1959; Schweikert & Collins, 1966). Equivalent space dimensions and social grouping, without the presence of a variety of objects, were not sufficient conditions for inducing EC--IC differences in brain measures (Quay, et al., 1969; Rosenzweig, 1971). However, Bernstein (1973) reported that the absence of such objects was irrelevant to later behavioral enhancement of performance in the Lashley III maze, for rats. This finding is in direct contradiction to the above studies. It is not clear, at present, how to interpret this contradiction because the bulk of evidence suggesting that "active interaction" (Ferchmin, et al., 1975) with a variety of objects is critical to the enrichment phenomenon is based on differences in physiological measures, while Bernstein's (1973) report is based on behavioral measures. This issue points out, once again, the need for further investigations of the enrichment phenomenon involving both kinds of behaviors. The extent to which the organism's genetic history, contributes to variability

in environmentally induced changes in brain and behavior, while demonstrated, has not been adequately incorporated into the framework of early environment study. Cooper and Zubeck (1958) were among the first to suggest that the genetic characteristics of subject populations may determine the final outcome of enrichment or isolation experience in rats. They found that rats of both the McGill "bright" and McGill "dull" strains had high error scores after rearing in an impoverished environment; improving the environment to standard laboratory conditions reduced errors in brights but not in dulls; after enriched rearing both strains made fewer errors. The threshold of stimulation necessary to produce development of learning ability is influenced by genotype though the directional effects of enrichment are the same in both. Fuller (1964) reported that terriers and beagles differed in their rates of recovery following long term isolation, the terriers recovering more quickly. The specific pattern of physiological changes induced by enrichment or isolation experience were found to differ among gerbils, rats, and mice (LaTorre, 1968; Rosenzweig & Bennett, 1969). Experience with environmental enrichment or impoverishment was found to modify the behavioral performance of lines of mice selected for high and low brain weight, but did not eliminate certain behavioral differences between the two populations (Collins, 1970). In a series of studies dealing with inbred and hybrid populations of mice, Henderson (1970, 1972) reported that inbred strains of mice were less responsive to the influences of environmental enrichment than hybrid mice derived from these strains. In two experiments, Freeman and Ray (1972) compared two strains (Charles River and F344 inbred) of

male and female rats reared in either enrichment or impoverishment in the open field, Lashley III maze, active and passive avoidance training. Environmental enrichment enhanced maze learning and attenuated passive avoidance responding differentially, depending on the sex and strain of the subject. The issue of sex differences, and their potential impact on environmentally induced brain and behavior changes, has never been emphasized. The contributions of genotype and gender to the outcomes of environmental experience remain to be fully explored; their role in any generalizations about the effects of environmental enrichment and impoverishment on physiological and behavioral organization is clear.

In summary, the literature indicates that experience in enriched or impoverished environments supports modifications of central nervous system organization, and that certain combinations of environmental components are critical to such modification. The work of the Berkeley group, in particular, has served to emphasize the importance of the organism's "active interaction" with such environmental components in resultant brain changes. The recent review by Walsh and Cummins (1975) has suggested that the arousal level of the organism may mediate the demonstrated physiological effects of a particular level of environmental stimulation.

Issues in the Study of Environmental Influences on Brain and Behavior

There are two issues clearly involved in understanding the role of environmental complexity and impoverishment in brain and behavior modification. The first is the problem of developmental stages, i.e., the extent to which the effects of a particular type of rearing condition (enrichment or impoverishment) are determined by the ongoing developmental

process of the organism. Since the 1930's, emphasis has been placed on the susceptible nature of the young child's response to environmental elements, and, historically, animal studies have supported this emphasis. Work with rats has suggested that "early" environmental enrichment (usually within the second 3-4 weeks of life) provided greater enhancement of learning abilities than the same experience at a later age (Forgays & Read, 1962; Forgus, 1956; Hymovitch, 1952). On the other hand, the fact that aged animals have been reported to demonstrate brain and behavioral changes equivalent to those of younger animals indicates that the period of most rapid organization and maturation is not singularly optimal for the manifestation of environmental impact upon the brain (Doty, 1972; Cummins, et al., 1973; Riege, 1971). Whether the specific nature or the permanence of such induced changes is also similar throughout the life span remains to be determined.

The second, and more elusive, issue involves the determination of relationships between environmental modifications in physiological and behavioral characteristics. Given evidences of associated structural, chemical, and behavioral modification resulting from particular environmental experience, what are the mediating processes between brain modification and behavioral alteration? The question has been framed in terms of two notions: 1) that the level of environmental complexity results in a general "tuning" of brain and behavior function, or 2) that the overall effects of environmental complexity are dependent upon the accumulations of many specific learning experiences, and their memorial representation (Greenough, 1975). Whereas Greenough's analysis of

alternative approaches to the effects of environmental complexity is based on a body of recent work involving sophisticated studies of neural modification, the early researchers in this field expressed similar viewpoints with little supporting data. Largely based on Hebb's (1947, 1949) theoretical models of perceptual development, Hymovitch (1952) concluded that the discrepancy between treated (enrichment) and control subjects on his test (Hebb-Williams apparatus) was too great to be explained adequately as a specific transfer of learned habits to the test situation. He pointed out that if enriched subjects had learned only specific habits, such as learning not to enter blind alleys, that then transferred to the test situation, these subjects would have been expected to demonstrate superior performance in a spatial habit learning task. That was not found. Hymovitch pointed out that rats permitted only visual experience with the enriched environment performed in a similar fashion to non-restrained enriched rats in the Hebb-Williams maze. He concluded, therefore, that enrichment experience is not simply the accumulation of specific S-R habits; rather, it represents a general potentiation of perceptual skills resulting from contact with visual or visual and kinesthetic stimuli. A recent attempt to confirm this finding (Ferchmin, et al., 1975) reported that rats permitted only visual enrichment were not equivalent to non-restricted enriched rats on a number of cerebral measures; however, no indices of learning ability were assessed. Schweikert and Collins (1966) reported that rats given visual and motoric experience traversing mazes in their cages, were found inferior to subjects reared in the standard enrichment treatment in solving problems in the Hebb-Williams

maze. They concluded that the specific experiences of the maze-reared group were not comparable to the more global enrichment experience of the group reared in an enriched environment. Hoffman (1959) found that rats reared in an enriched environment were superior to subjects reared in cages of comparable size, or in small cages, in solving a "reasoning test", a test situation which was quite unlike anything experienced by the enriched rats during their treatment.

Another hypothesis, that animals reared in an enriched environment demonstrate superior learning performance as a function of their greater opportunity for acquiring associations between stimuli and responses has also been investigated. In a series of studies, Forgas attempted to demonstrate that the ability of rats to solve a form or spatial discrimination is dependent on the specific associations between stimuli and responses learned during environmental enrichment. He reported that under certain conditions rats given only visual enrichment were superior on a form discrimination to rats given free environment experience. For the physically restricted animals the visual aspects of the environment acquired "prominence", and were thus more effective as discriminanda (Forgus, 1954). In subsequent studies Forgas (1955a) reported that visually enriched rats were superior to free enriched rats in solving a spatial problem. When a redundant visual stimulus was superimposed on the spatial problem, superiority was maintained; however, it was lost when the visual cues were removed (Forgus, 1955b). Forgas (1955a, 1955b) concluded that the greater accumulation of associations between stimuli and response possible in the free enrichment treatment as compared with

visual-only enrichment served to handicap the free enriched subjects faced with a number of familiar cues in the test situation. This interesting interpretation of enrichment-produced modifications in learning ability has not been amply continued in more recent years.

A few studies of what might be called formal training, as opposed to the informal nature of enrichment experience, have attempted to compare the neural changes following these two types of treatment (Rosenzweig, et al., 1969; Greenough, 1975). While certain modifications of neural structure have been reported, these studies face the problem of separating those changes produced by formal learning experience from those produced by such non-learning related variables as stress, arousal state, and exposure to the experimental situation (Greenough & Maier, 1972). More molecular approaches to the notion that enrichment experience represents the accumulation of many specific learning experiences include the investigation of genome transcription in enriched animals, using the DNA/RNA hybridization technique (Uphouse & Bonner, 1975).

There is a sense in which the dichotomy drawn between generalized and specific transfer effects of environmental complexity rearing may be overly simplistic as an explanation of the impact of enrichment experience on the brain and behavior. It is clear that experience with a complex environment increases neural connectivity, in terms of dendritic arborization, number of dendritic spines, and synaptic morphology, and that these kinds of neural responses, while region specific, are not modality specific. Some of the recent work involving the relationship of RNA synthesis to the biochemical basis of learning and memory may be relevant to the issue

of general versus specific effects. Rosenzweig, et al. (1972) have stated that a great deal of transfer of capacities among different kinds of behaviors should not be expected, considering the diverse nature of the behavioral changes reported. It is too early to evaluate the usefulness of the issue of "general tuning" versus "specific memories" to the study of environmentally induced modifications. Nevertheless, it is clear that a more complete understanding of the environmental complexity phenomenon depends on current and future investigations of the mechanisms and processes that mediate neural and behavioral modifications produced by interactions with a particular environment. This task must be complemented by concurrent investigation of the permanence of these environmentally induced alterations. The importance of this problem is founded, not only in the longevity of the initial neural or behavioral modifications, but also in the duration of modifications in brain and behavior that bias the acquisition of new patterns in the future.

Relevance to Human Development

It would appear that the issues and problems discussed above would be of great potential importance to the investigation of human development, especially in relation to the impact of the environment on developmental processes. Historically, animal work in this area has been viewed as admirably suited to investigations of the variables critical to adequate behavioral development, possessing the advantages of strict control of environmental components, specific knowledge of the subjects genetic and experiential history and the use of quantifiable measurement techniques. The repeated demonstration of physiological alterations resulting from environmental complexity or isolation rearing suggests

that behavioral modifications ensuing from these treatments are not artifacts of some uncontrolled variables in the treatment procedure. Many of the behaviors potentiated by complexity rearing in animals find a counterpart in certain of the reports on early educational "enrichment" in young children (Blank & Solomon, 1968; Bereiter & Engelman, 1974). Certain of the variables found critical to environmental modification in animals, such as stimulus variety, cue combination, and organization of stimuli, suggest that a cognitive element is important. However, the apparent lack of physiological alterations (Greenough, et al., 1970), or their waxing and waning (Bennett, et al., 1974) might be interpreted as indicating that benefits accrued from environmental complexity experience are short-lived. The oft-repeated observation that physiological and behavioral alterations do not appear correlated in any direct manner can also serve to reduce the potential applicability of animal work to human developmental problems. The demonstrated relationship between important environmental and organismic variables and particular neural and behavioral modification might appear to preclude simple generalization, both across animal species and from other animal species to man. As a final comment, it might be pointed out that the evidence from animal studies of environmental complexity rearing does not support the notion that the early stages of most active neurological development, i.e., the neonate or human infant, are "critical" stages in terms of environmental impact of the type discussed here. Perhaps the clearest potential relevance to human development lies in the demonstrated amelioration of certain behavioral disfunctions following enrichment experience

(Tanabe, 1972; Wells, et al., 1972; Levitsky & Barnes, 1972; Davenport, et al., 1976; Hughes, 1965; Schwartz, 1964). In each of these reports, exposure to an enriched environment prior to or subsequent to one of several types of experimental insults (surgical lesion, malnutrition) enhanced the recovery of behavioral functioning as compared with non-enriched control groups. To the extent that we are concerned with better understanding the ways in which experience in a particular environment modifies brain and behavior, future researches may lessen the gap between animal and human approaches to these problems.

Future Approaches

The study of environmental complexity effects of brain and behavior has suffered from a situation uncommon to certain other fields of psychology, i.e., a lack of theory. This lack is not equally manifest at both the neural and behavioral level of study; the nature and meaning of neural modifications resulting from environmental experience have been subjected to a level of analysis far more sophisticated than that applied to behavioral modifications. It has been suggested that alterations in the fine structure of the brain may well reflect memorial representations of experience (Rosenzweig, et al., 1972; Ferchmin, et al., 1975), a suggestion which is well in line with current thinking about the anatomical and biochemical bases of learning and memory. These characteristics of the "enriched" brain need to be approached with the techniques already found useful in investigating the potential physiological properties of learning and memory. A second approach, again shared with those interested in the physiological bases of memory, is that of comparisons between

animals exposed to environmental complexity and animals exposed to a large variety of learning experiences. Recent work has indicated that anatomical alterations are, indeed, manifest, although their nature appears different from those changes found in the brains of animals exposed to environmental complexity (Greenough, 1975; Rosenzweig, et al., 1969). A refinement of the problems of appropriate controls (Greenough & Maier, 1972) may serve to clarify the degree to which multiple learning experiences and environmental complexity experience result in similar modifications of neural structure and biochemistry.

The establishment of mechanisms that mediate between the impact of environmental components and consequent anatomical alterations may contribute to our knowledge of how these changes develop and their possible correlation with particular environmental components. Walsh and Cummins (1975) have taken a great step forward in their detailed review of possible mediating mechanisms. They hypothesize that the arousal reaction may serve a vital role in the establishment of brain changes, and suggest several tests of the hypothesis, including drug manipulation of habituation rate, genetic preparations that differ in their baseline level of arousal, and surgical procedures which may modify arousal level. The greatest value of this review may lie in its delineation of opportunities for experimental tests of ideas which have been floated without much data support.

At the level of behavioral analysis of environmentally induced modifications, the overall research results are without synthesis of theories or predictions. Certainly the earliest researchers had clear

ideas of expected behavioral changes and explained their results in view of current thinking about perceptual learning and developmental changes (Hebb, 1949; Hymovitch, 1952; Forgays & Forgays, 1952; Forgas, 1954, 1955, 1956). However, in more recent years, it would appear that the study of behavioral modification, including learning capacity, has been less concerned with experimental tests of hypotheses than with the demonstration of significant differences in behavior between animals reared in enrichment or isolation on a particular task. Greenough, et al. (1972b, 1973) have recently reversed this trend. These researchers have suggested that the experience of environmental complexity may alter the ability of animals to remember relevant information, dependent on the amount of time allowed for such processing. Early work (Hymovitch, 1952; Forgays & Forgays, 1952; Forgas, 1954, 1955, 1956) suggested that enriched animals may be more capable of attending to stimuli in and around the test situation. These authors found that alteration or removal of a stimulus which had previously been a redundant cue in the situation, disrupted performance more in enriched than in impoverished animals. These two suggestions, i.e., of differential memorial processing and differential attentional tendencies, are worthy of further investigation and empirical test. The elegant procedures of Alpern and Marriott (1972) for testing short term memory function in different strains of mice may be appropriate for the investigation of memorial processing in animals reared in different levels of environmental complexity. The enormous body of work on discrimination and attention functions in animals (Mackintosh, 1975) should provide ample guidelines for further

study of such differences as related to mode of rearing. Parsons and Spear (1972) reported an interesting variation of the environmental complexity experiment, in which rats trained to avoid shock were housed in an enriched environment during the retention interval. These animals were reported to demonstrate less retention of the previously learned response than animals housed in standard laboratory cages during the retention interval. This kind of paradigm may be useful in investigating the nature of environmental complexity experience in interaction with previously learned behavior. The study of interactions between environmental complexity and certain organismic variables as they relate to both learned and unlearned behavior may be of great importance in describing the manner in which environmental complexity acts on the organism. Strain differences in response to environmental enrichment have been reported (Henderson, 1972; Manosevitz, et al., 1968), and we have been long aware that animals of different genotypes differ in their response to such environmental treatments (Cooper & Zubeck, 1958). To expand our information about the role of the genotype in the effects of environmental complexity, however, strains that are known to differ along some behavioral dimension, such as arousal level or avoidance conditioning, need to be studied. This kind of work could, again, serve to delineate the specific manner in which environmental enrichment acts on an organism's behavioral capacities. Experimental models of brain disfunction and learning deficits may also serve to elaborate the effects of enrichment rearing. Schwartz (1964) reported that post-operative environmental enrichment treatment attenuated the learning deficits in adult rats with

neonatal cortical lesions; Hughes (1965) found that pre-operative enrichment reduced error scores in the Hebb-Williams maze of rats with antero-dorsal hippocampal lesions. More recently, Donovick, et al. (1973) reported that environmental complexity rearing altered the behavior of septal rats during tests of fluid consumption, exploration, and spatial alternation ability. In a subsequent study (Donovick, et al., 1975) septal mice of two strains were found to behave differently on tests of fluid consumption, rotorod performance, and avoidance conditioning depending on whether they had spent previous time in an enriched environment. Enrichment treatment has been reported to reduce deficits in the learning ability (Tanabe, 1972; Wells, Geist & Zimmerman, 1972) and emotional behavior (Livitsky & Barnes, 1972) of previously malnourished rats. Very recently Davenport, Gonzalez, Carey, Bishop and Hagquist (1976) reported a similar effect of enrichment in hypothyroid rats. It is interesting to note that, across the several types of brain disfunction, the data generally suggest that animals sustaining these types of experimental insults are more behaviorally susceptible to the influences of environmental impoverishment than nontreated controls.

One additional approach to the problem of environmental complexity effects, which can encompass both brain and behavioral analysis, is that of the "switchover" procedure (Greenough, 1975), in which environmental conditions (enrichment or isolation) are switched after a certain period of time, so that the animal has experience with both levels of complexity. Previous work (Rosenzweig, et al., 1962) suggested that the neural effects of impoverishment rearing could be partially reversed by a subsequent

period of enrichment; on the other hand, enriched animals shifted into isolation for 30 days maintained enrichment-induced brain changes (Zolman & Morimoto, 1962). Subsequent work (Rosenzweig, et al., 1967; Geller, 1971; Brown, 1971; Bennett, et al., 1974) has yielded contradictory results. A more thorough approach to the problem, including manipulation of amount of time spent in the two environments, may contribute to our understanding of neural lability in response to environmental stimuli and provide a more sophisticated analysis of consequent behavioral lability or persistence. A recent report on the behavioral effects of alternating exposure to environmental enrichment and impoverishment found evidence of both behavioral persistence and lability, related to the testing task. Overall, however, the direction of these characteristics was towards "enrichment-like" behavioral functions, suggesting that enrichment experience can both modify behaviors influenced by earlier impoverished rearing and maintain behavioral tendencies throughout subsequent impoverishment experience (Ahroon, 1976). This paradigm seems particularly suited to investigations of the stability and/or lability of brain and behavioral responses to environmental complexity, and the extent to which brain and behavioral modifications covary.

Application of these kinds of theoretical and procedural approaches may serve to encourage a more eclectic orientation towards the problem of environmental modification of brain and behavior and contribute to the elaboration of specific principles to explain the interactive nature of organismic response to environmental events.

Footnotes

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