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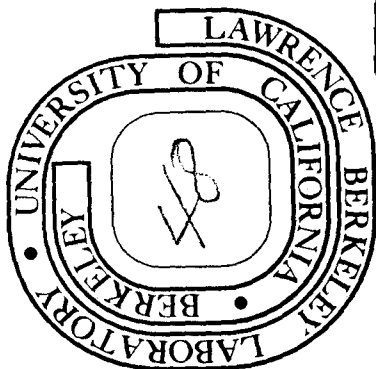
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ENRICHED ENVIRONMENTS: FACTS, FACTORS, AND FANTASIES

(Manuscript for Chapter in Krech Festschrift)

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Enriched Environments: Facts, Factors, and Fantasies

ABSTRACT

Rats and other rodents maintained in enriched (EC) or impoverished (IC) environments have been shown to differ in a number of behavioral, anatomical, and biochemical measures. We would prefer to attribute these effects to experience--that is, learning and memory. However, other factors such as stress or accelerated maturation have frequently been suggested as possible causes. This Chapter reviews research which provides information concerning alternative explanations for the causative factors leading to cerebral and behavioral differences between rodents raised in EC and IC environments.

Among the suggested explanations that we feel can be eliminated are differential locomotion and/or handling, greater stress of the IC (or EC) group, hormonal mediation, maturation, and differences in water content of the brain. The extracage environment, at least within a wide range of stimulation, also seems to be unimportant for producing cerebral differences in rats. The relative roles of enrichment and impoverishment from the standard colony baseline of 3 to a cage is more complex to evaluate, since the relative effectiveness depends both on the measure considered and the starting age. The respective roles of size of the social group and inanimate stimuli have also been considered in a few experiments. Both factors have been shown to be effective separately, but we believe that both inanimate and social stimulation are essential for full enrichment effects.

Finally, the role of learning in producing EC effects is discussed. While learning and memory have not yet been shown conclusively to be a major factor producing the observed changes in brain measures, a number of other causes have been eliminated, and reasons are given to support the hypothesis that learning and memory are a major causative factor. This problem remains an important and fertile field for further research on possible mechanisms of memory. Eventually, the understanding gained from extensions of such studies should be useful in evaluating the importance of social environments for man.

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Enriched Environments: Facts, Factors, and Fantasies

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INTRODUCTION

As we prepared to write this article and reviewed the varied and sometimes contradictory reactions of some investigators to our reports on effects of environment on brain and behavior, an old story came to mind: A villager was accused of returning a borrowed teapot in poor condition. Vehemently he replied, "In the first place, I never borrowed it; in the second place, I returned it in perfect condition; in the third place, the teapot was already dented when I got it!" Thus, the initial criticism of our work was that our results were unlikely or probably unreproducible; that is, the effects didn't exist in the first place. This charge we believe, has been abundantly answered by replications of the findings, in other laboratories as well as our own. Cragg (1972) has stated, "Initial incredulity that such differences in social and psychological conditions could give rise to significant differences in brain weight, cortical thickness, and glial cell numbers seems to have been overcome by the continued series of papers from Berkeley reporting consistent results. Some independent confirmation by workers elsewhere has also been obtained" (p. 42). A second criticism was the opposite of the first--that the brain is known to be so plastic that almost any experience can produce measurable effects in it. And a third criticism

has been that although the effects exist they should not properly be attributed to experience--that is, to learning and memory--but are really due to other factors such as stress or accelerated maturation. It is these latter two criticisms that we plan to take up in this chapter. A brief review of the cerebral effects caused by differential environments and of the history of their discovery will help to set the stage for the rest of this report.

As we pointed out in our first discussion of this question at the 1959 Pittsburgh symposium (Rosenzweig, Krech & Bennett, 1961), we began research with the enriched and impoverished conditions after obtaining unexpected results indicating that formal training produced changes in brain chemistry. To enhance the opportunities for differential learning and thus "to maximize the possibility of obtaining relatively sizeable effects," we then designed a program involving varied informal experience. Specifically, we set up three experimental conditions: (a) The baseline condition was originally called Social Control and was later called Standard Colony (abbreviated SC in either case). In this condition, 3 rats of the same sex were assigned to a usual colony cage (32 x 20 x 20 cm) with no special stimulation. (b) The enriched environmental condition was first called Play and Training, then Environmental Complexity and Training (ECT), and eventually Enriched Condition (EC). In this condition, 10 to 12 rats of the same sex were assigned to a large cage (70 x 70 x 46 cm) equipped with varied stimulus objects (ladders, blocks of wood, etc.). In our first experiments (Krech, Rosenzweig & Bennett, 1960), the ECT cage contained a small wooden maze and two wooden objects selected each day from a set of seven. Later we increased the variety by placing about six objects in the cage each day from a set of about

25 objects of varied forms and materials (chains, plastic tubes, light bulbs, etc., as described and illustrated in Rosenzweig & Bennett, 1969). The rats were also placed for 30 minutes daily in a 75 x 75 cm open field with patterns of barriers that were changed daily. Until 1966, the rats were also given a few trials a day of maze training, but this formal training was later dropped from the schedule, so ECT became EC. (c) The isolated or impoverished condition (IC) has single rats living in cages about the size of colony cages. Originally these cages were kept in dimly lighted sound-deadened rooms, and the cages had solid side walls to prevent the rats from seeing each other. Later, as will be described, we found that it was the lack of cage mates that seemed to be the essential feature of the IC treatment; animals housed alone in colony cages in a brightly lit and active laboratory room developed brain measures indistinguishable from those of rats in the original IC condition.

These environmental conditions were originally found to produce differences in cholinesterases, AChE-ChE (Krech, Rosenzweig & Bennett, 1960), then in weights of brain sections (Rosenzweig, Krech, Bennett & Diamond, 1962), then in thickness of cerebral cortex (Diamond, Krech & Rosenzweig, 1964), and eventually in a large variety of brain measures (Rosenzweig, Bennett & Diamond, 1972a). For readers who wish additional information about the variety of brain changes induced by differential experience, here are references to some recent articles and reviews: Bennett (1975), Geller (1971), Greenough (1975), Rosenzweig, Bennett & Diamond (1972a & c).

In the 1959 report we wrote of focusing down on the crucial aspects of the environmental situation, and we attempted experimentally to rule out several tied variables--differential activity, differential handling, and diet. In collaboration with David Krech during the period 1958-66

and with Marian C. Diamond during 1960-74, we pushed a two-pronged attack on the problem, on the one hand studying effects of formal training on brain measures and, on the other, examining the roles of various factors in the informal environmental situations. The present paper will be restricted to the latter aspect, and among the factors to be considered are the following: locomotion, handling, stress, endocrine mediation of the effects, fluid content of brain, differential rates of maturation, social grouping, and active vs. passive experience. Other evidence will also be considered concerning the hypothesis that differential memory formation plays a role in producing the cerebral effects. This account will extend from our initial research on these questions up to the present (1974) and will draw upon the work of other laboratories as well as our own.

ARE THE EC-IC BRAIN DIFFERENCES DUE TO VARIABLES
OTHER THAN DIFFERENTIAL OPPORTUNITY TO LEARN?

Effects of Handling and of Locomotion

Two of the most obvious ways in which the ECT and IC conditions differed from each other was that rats in ECT were handled more often and they showed more locomotor activity than their littermates in IC. Furthermore, many studies have shown effects of at least early handling on behavior and on physiology of rodents. Of course, the amount of handling received by ECT rats was not great--simply being picked up to be placed in the open field and removed from it, and brief handling when stimulus objects were changed or when the rats were moved from one cage to another. The IC rats were picked up every week or two for weighing. Even though differences in handling did not seem to be marked, we nevertheless wanted to control for this factor.

In our initial publications on the ECT-IC effects, we therefore reported further experiments run to determine whether differential handling and locomotion might account for the effects (Krech et al., 1960; Rosenzweig et al., 1961). In the two experiments on handling, some rats were handled two minutes each day, for either 30 or 60 days, while littermates were never handled. In the experiment on possible effects of greater locomotor activity, the active group had access to individual running wheels at all times. We concluded "that handling alone probably contributes very little to the observed ECT effect, and that sheer locomotor activity plays no role at all" (Krech et al., 1960, p. 518). More work on this was considered necessary, however, since neither of the experiments on handling lasted as long as the ECT-IC experiments, and the experiment on differential activity included only 8 pairs of rats. Furthermore, ECT had both more handling and greater locomotion, and the combination of these factors might be important. We therefore subsequently performed an experiment to test the effects of combined activity plus handling (A+H). The A+H group was handled daily and could locomote in individual running wheels, while littermate groups were in ECT or IC; the experiment extended for the standard length, from 25 to 105 days of age. The results (Rosenzweig, Krech, Bennett & Diamond, 1968) showed no effects of handling plus locomotion except perhaps in the somesthetic region of cortex. It was clearly established that the EC-IC effects could not be attributed either to the greater amount of handling or to the greater amount of locomotion or to the combination of these two factors in the enriched compared to the impoverished condition.

Subsequent experiments have offered further corroboration for this conclusion. In experiments on effects of formal maze training, rats in a runway control group have run back and forth in a 2.1 m long straight alley 50 times or more per day over a 30-day period, and this has not produced differences in cerebral measures (brain weights, AChE and ChE, and RNA and DNA) from rats not having this locomotor experience.

Concerning handling, two further kinds of experiments show that this treatment can be omitted from programs that, nevertheless, produce unusually large effects of environmental complexity. We will later report pronounced cerebral effects produced by placing rats in an outdoor field for 30 days; during this time they were not touched by the experimenters, but their brains showed enhanced EC effects at the end of the experimental period (Rosenzweig & Bennett, manuscript). Kuenzle and Knüsel (1974) set up a "superenriched environment" in which rats traversed a bridge between two complex environment cages, shuttling back and forth to get to food and water. Conditions were changed over the month-long experimental period so that the rats had to traverse a maze and open appropriate gates in the apparatus, but the rats were not handled. The superenriched environment, despite the lack of handling, was reported to produce greater brain effects than the usual Berkeley EC environment which includes handling.

A study on behavioral effects of handling in the context of EC and IC experience was reported by Greenough, Madden and Fleishman (1972). One group of rats was placed in EC, one in IC with no handling, and one in IC with daily handling. When tested subsequently for maze learning, the performance of EC rats was superior to that of the two IC groups which did not differ from each other.

Experiments to be reported below on stress also introduced the variable of handling. Some IC rats received the usual infrequent handling, while others were removed from their cages daily and carried to another room for a stress treatment. Handling plus stress did not cause these IC groups to differ from each other in our usual brain measures.

We conclude that neither postweaning handling, nor differential locomotion, nor the combination of the two, can give rise to the EC-IC effects.

Can Stress Account for the EC-IC Effects?

Stress has probably been the most frequently suggested alternative explanation for the EC-IC effects. As in the teapot story, some have seen stress as affecting the IC rats (e.g., Geller, 1971), while others, on the contrary, have suggested that the stimulation of the EC rats might be stressful (e.g., Welch et al., 1974).

In our Science paper of 1964 (Bennett et al.) we asked whether isolation stress of the IC rats could be the cause of the differences between them and their enriched-experience littermates. This seemed a hypothesis worth considering because isolation had been reported to be stressful for rats. According to a group of Canadian investigators (Balász et al., 1962; Hatch et al., 1963), isolated rats of the Wistar strain became so aggressive that they could not be handled with bare hands and they developed caudal dermatitis. A current review of the isolation syndrome will be found in Greenough (1975), and a comprehensive review of this syndrome with particular reference to mice has been prepared by Valzelli (1973).

The following two lines of evidence from our experiments made us doubt that isolation stress accounted in any large measure for the EC-IC

differences: (1) Rats of the strains we studied did not show any obvious symptoms of stress in the isolated condition. They did not become aggressive, did not develop caudal dermatitis, and their adrenal glands did not become enlarged. (2) Use of the Standard Colony condition showed that ECT rats differed significantly from SC littermates, and "the bulk of the effects on cerebral weight and on acetylcholinesterase activity is due to enriching rather than restricting the experience [in relation to that] of our colony animals" (Bennett et al., 1964, p. 615). (While later research has confirmed the existence of significant EC-SC differences, these may be either larger or smaller than SC-IC differences, depending both upon the brain measure considered and, for certain measures, upon the age of the rats at exposure to the environmental conditions. For example, in regard to depth of occipital cortex, the SC-IC difference exceeds the EC-SC when rats are in the conditions from 25 to 55 days of age, whereas the opposite is true when the experimental period runs from 60 to 90 days of age; see Figs. 7A and 7B in Rosenzweig, Bennett & Diamond, 1972c.)

Even if IC could be shown to be stressful, this would not prove that it caused the EC-IC effects. In fact, we had evidence to demonstrate that stress due to unavoidable electric shock does not produce cerebral effects similar to those of our differential environments. The results of five experiments, conducted in 1959-60, were reported at the International Congress of Psychology in 1966 and published later (Rosenzweig, 1968). In these experiments, each shock subject received intermittent unavoidable electrical shock for 12 minutes daily. At the same time, the littermate control was placed in a similar experimental enclosure but with no shock and in a different room. The first two experiments lasted two weeks and the other three, each four weeks. Two weeks or less of EC-IC suffices to

produce clear brain weight effects (Rosenzweig, 1968; Ferchmin et al., 1970; Bennett, 1975).

In all five experiments, employing a total of 42 littermate pairs of five different strains, the terminal body weight was lower in the shocked than in the control rats; overall the difference amounted to 6% ($P < .01$). Adrenal weights were taken in the first four of these experiments and were 6% greater in the shocked rats ($P < .10$); the ratio of adrenal to body weight was 14% greater in the shocked rats ($P < .001$). Although the stress of shock affected body weight and the ratio of adrenal weight to body weight, it had little effect on brain measures. None of the four cortical regions yielded a significant difference, the occipital and somesthetic areas showing somewhat greater weights in the shocked rats and the remaining dorsal cortex and ventral cortex weighing somewhat less in the shocked rats than in the controls. Total cortex weighed 2.3% less in the shocked rats ($P < .05$). When allowance was made, through analysis of covariance, for reduction of body weight by shock, the difference in cortical weight shrank and became non-significant. Even if the absolute weights are considered, the pattern of differences over cortical areas does not parallel that of EC-IC differences. AChE activity was analyzed in only one of these experiments. It showed no significant differences between shocked and control rats for any brain region.

Subsequently Geller and Yuwiler (1968) and Geller (1971) reported on effects of 30 days of EC or IC following weaning. Under their conditions IC, compared to EC, showed increases in norepinephrine in the caudate nucleus. There were also signs that the IC rats had been under stress early in the experiment, since IC showed increased values of transaminases and a 4% increase in adrenal weight ($P < .05$). Neither the serum nor the

adrenal corticosteroids were elevated at sacrifice, so Geller concluded "that some time during the 30 days of the experiment the ICs had adapted to the condition and were no longer responding with adrenal activation.... However, the adrenal weight change was not reversible and the transaminase activity remained at a higher basal level" (Geller, 1971, pp. 284-5). In a subsequent experiment, groups were kept in the differential conditions for 2-1/2 days, 6, 11, or 16 days. Geller reports that, "Adrenal corticoids were higher in the ICs during the first part of the exposure but by 11 days no difference could be seen" (1971, p. 286). The data show that the difference was never greater than 4% and never reached significance (Fig. 5, p. 287), so any effect on adrenal corticoids remains doubtful.

In considering these results of Geller, one aspect of the experiments requires mention--the unusually early age of weaning. The rats were weaned at approximately 19 days of age, some as young as 16 days and the oldest at 21 days. Sixteen days is only two days after the rat pup's eyes and ears open, and temperature regulation is still incomplete in such young rats. Most laboratories wean rats at about 25 days of age. It seems quite possible that isolation may be stressful for 19-day-old rats but not for rats weaned at a more normal age. Thus, it is not clear whether the findings of Geller on prematurely weaned rat pups are relevant to other studies in which rats were weaned at a normal age.

The possible role of stress on EC-SC-IC effects was studied experimentally in our laboratories by Riege and Morimoto (1970). They asked not only, "Does IC or, for that matter, EC entail stress?" but they also asked, "Even if overt stress is used, can this produce the brain differences

found in the EC-IC experiments?" In three experiments, environmental complexity and stress yielded a clear double differentiation in effects on brain weights and adrenal weights (Riege & Morimoto, 1970, Table 5). That is, EC vs. IC caused the usual significant differences in brain weight measures but no significant effects in adrenal weights. Stress (being tumbled each day in a rotating drum) did not cause any significant differences in brain weights, but it produced significant increases in adrenal weights. In regard to total acetylcholinesterase (AChE) activity, stress produced increases among both EC and IC rats, but these were only half the size of the EC-IC effects. In total cholinesterase (ChE) activity, stress also produced some effects but again they were generally smaller than the EC-IC effects. Concentrations of some biogenic amines (norepinephrine, dopamine, and serotonin) were also measured. Here both stress and environment produced effects, but the two patterns of effects were quite different. Thus, there was no indication that IC was stressful in these experiments (since there was no EC-IC difference in adrenal weight), and even when overt stress was employed it did not produce any brain weight effects nor a pattern of chemical effects that resembled those of EC vs. IC.

Up to now we have considered stress only as possibly occurring in the isolation condition. Elsewhere we have noted that the enriched condition might cause the stress of "information overload" (Rosenzweig et al., 1972c, p. 258). The possibility also exists that living in a grouped condition may be a cause of stress. An indication of this sort comes from the work of Welch and Welch (in preparation). They housed rats either singly or in groups for a one-year period following weaning. At the end

of the year the grouped rats "had elevated blood pressure, kidney pathology and endocrine change suggestive of greater stress." This result is opposite to that reported by Geller, but these results of the Welchs may be restricted to prolonged periods of group living, or, as we have pointed out earlier, Geller's results may be restricted to rats that are placed in the differential environments at a premature weaning age. Whether, in fact, the enriched condition, the condition of group living, or the impoverished condition represents a stress for the rat in certain experiments, this should not contradict the reasoning reported here. That is, neither our enriched nor our impoverished condition has produced symptoms of stress in comparison with animals raised in the standard colony condition, and furthermore, when overt stress of electrical shock or tumbling has been employed, it has not produced the patterns of alteration of cerebral measures seen with the enriched or impoverished conditions.

The weight of the evidence seems to us clearly to refute the hypothesis that EC-IC cerebral effects can be attributed to stress. We are not, of course, challenging the findings that stress can affect brain and behavior in many ways, but we wish to emphasize that Stress vs. Nonstress conditions do not yield effects like those produced by EC vs. IC.

Hormonal Mediation of Environmental Effects?

Although the experiments of the section above seem clearly to rule out stress as the cause of the cerebral EC-SC-IC effects, it might still be possible that hormonal functions mediated these effects of differential experience. That is, the differential experience might lead to alteration in hormonal activity which could, in turn, affect the nervous system. We

therefore tested the hypothesis that the pituitary gland is essential to occurrence of the EC-IC effects (Rosenzweig, Bennett & Diamond, 1972b). The pituitary gland was chosen not only to eliminate its secretions, but also to diminish and cut off from environmental influence the secretions of the glands controlled by the pituitary--the thyroid, the adrenal cortex, and the gonads.

Three experiments were run, two with male Fischer rats and one with male Long-Evans rats. In each case, some animals were hypophysectomized shortly after weaning. Then, five to ten days later, the animals were placed in one of four experimental conditions (to which they had been pre-assigned) and were kept there for 30 days. The four conditions were these: EC-Hypophysectomized, EC-Control, IC-Hypophysectomized, and IC-Control. Results of the operates were used only in the cases of those animals that showed verified complete hypophysectomy at sacrifice. The results of these experiments demonstrated that, although hypophysectomy stunts bodily growth and checks brain growth somewhat, significant EC-IC brain differences nevertheless occurred in both the brain weights and brain chemical measures of the operated animals. If the operation had prevented the occurrence of EC-IC effects, then it would have been necessary to determine which gland or glands are essential, to verify this by the procedures of replacement therapy, and so on. Since our results did not, however, implicate hormonal mediation of the experiential effects, we have not pursued work in the endocrine direction further; this may be someone else's cup of tea.

The one indication of possible hormonal effects upon these brain measures comes from work of Diamond, Johnson and Ingham (1971) on EC-IC effects in female rats. They reported that whereas EC-IC differences

in thickness of cortex occur in females, these effects can be obscured in the case of pregnant rats. Greenough (1975) has also commented on the possibility of hormonal mediation of EC-IC effects, pointing out that endocrine effects might be expected to occur rather generally throughout the cortex, whereas the EC-IC effects are seen to be strongly differentiated regionally.

Maturational Effects?

Brains from EC rats show, when compared to their IC littermates, greater cortical weight, a greater glial/neural ratio, and fewer neurons/unit of cortical volume. Similar changes are found when adult rats are compared to young. Very young (preweanling rats) raised in a complex environment open their eyes earlier than animals raised in a less complex environment (Malkasian & Diamond, 1971). It has been suggested (e.g., Sperry, 1968) that rats raised in EC would mature more rapidly than rats raised in IC, and it is therefore appropriate to inquire to what extent EC-IC brain differences merely reflect differences in rate of maturation.

In a recent review (Rosenzweig et al., 1972c), we summarized several lines of evidence which we believed made untenable the concept of more rapid maturation as a major factor contributing to the effects of differential environments. We have reported that there is no critical period for producing EC-IC effects in brain weight. During the last several years, additional data regarding this point have been accumulated, and a summary for several brain areas is given in Table 1. Rather similar effects are

 Table 1 around here

produced in brain weights with experiments extending over a variety of age ranges and durations, and there does not appear to be a critical age prior to which differential environments must be initiated. Cummins et al. (1973) have also reported brain weight differences among rats assigned to differential environments at weaning and kept in EC or IC for about 500 days. Maturation effects would be expected to become insignificant during such a lengthy period, but the obtained effects were as large as those found with the usual shorter periods. EC rats have also been shown to have thicker cortices in experiments run over a variety of age ranges and durations (Diamond, this volume).

The fact that many of the EC-IC differences are opposite in direction to changes produced by maturation is even more compelling evidence. Cortical thickness is greater in the EC rat than in the impoverished. However, while all regions of the cerebral cortex--dorsal, lateral, anterior, and posterior--increase rapidly in depth between 6 and 10 days postnatally, and more slowly to 26 days, after this age a gradual decrease in depth occurs (Diamond, Johnson & Ingham, in press). That is, after 26 days of age, maturation leads to reduced cortical thickness, whereas EC increases it. The ratio of cortical to subcortical weight has been a very reliable measure that distinguishes EC from IC animals; the EC rats have a greater cortex/subcortex weight ratio than do the IC littermates. However, maturation has been shown to lead to a marked decrease in this ratio (Bennett & Rosenzweig, 1971; Riege, 1971).

Several biochemical measures that distinguish EC rats from IC rats also show opposed EC-IC and maturational effects. The enzyme acetylcholinesterase shows a marked increase in activity/mg from 25 to 105 days

of age (Bennett et al., 1961; and unpublished), yet animals maintained in EC over this time period have lower levels of cortical AChE activity than do their IC littermates (Rosenzweig et al., 1972c). The nucleic acid concentration in occipital cortex is another measure that is responsive to differential environments as well as to maturation, as can be seen in Table 2. The ratio of RNA to DNA is significantly higher in occipital

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Table 2 about here

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cortex of EC rats compared to the impoverished. The higher ratio for the EC rats is obtained in both young and old rats and in experiments of several durations. The EC-IC difference in this ratio is caused primarily by a decrease in the DNA/mg of the EC rat, and partially by a very small but non-significant increase in RNA/mg. Although the RNA/DNA ratio increases with EC, it can be seen in the table to decrease with maturation. From 30 to 360 days, both EC and IC rats show decreases in RNA to DNA ratio of over 30% ($P < .001$). The decrease with age occurs primarily because of a relatively large decrease in RNA/mg. There is little or no change in DNA/mg with age after 40 days.

Thus it is clear that a number of anatomical and biological measures are differentially modified by maturation and by enriched environments, so we conclude that EC-IC differences cannot be attributed to maturational effects.

Can Differences in Water Content of Brain Account for EC-IC Effects?

Another tempest in the teapot concerns, appropriately enough, water. It is frequently suggested that cortical weight and depth changes are due

to an increase in water content or edema rather than an actual increase in tissue. Most recently this suggestion was made by Welch et al. (1974). Again, several different measures, some indirect and some direct, lead us to reject this suggestion.

The first indirect evidence is provided by our findings concerning AChE and ChE activities. Activity per unit of tissue weight typically goes down for AChE with enriched experience, whereas it goes up for ChE. Mere increases in water content of tissue would lead to similar decreases in both measures. Total cortical AChE activity is greater in the EC rat than in the IC rat. An even greater difference in favor of the EC rat is found when total ChE is determined (Rosenzweig et al., 1972). No changes in total activity would be anticipated if the major cerebral change were in the water content. The protein content, as a percentage of wet weight, is another indirect measure that argues against a mere increase in water content as a major factor producing the EC-IC weight differences. In 1962, in three experiments, protein content was determined in rats raised in differential environments. It was found to vary directly with tissue weight (Bennett et al., 1964). Occurrence of edema would be expected to reduce protein per unit of tissue weight, but this was not found.

A third indirect argument is provided by the RNA and DNA measures that we have recently obtained. Here again, if changes in water content were the primary cause of weight differences, both RNA and DNA would be expected to decrease, and by similar relative amounts, in the cortex of EC rats. Instead, we have found a differential effect; DNA has shown large and significant decreases per unit weight, whereas RNA has remained constant or even increased slightly. Thus the RNA/DNA ratio is increased in the EC rats when compared to the IC rats. This change, in the case of

the occipital cortex, has averaged about 7.5%, and has shown an increase in about 85% of the over 500 EC-IC pairs analyzed to date.

It should also be noted that biochemical and anatomical differences between EC and IC animals exhibit marked regional differences. For example, the effects found in the occipital cortex are generally large, while those in the somesthetic cortex are typically much smaller. Therefore, if edema is occurring, it must be highly localized.

Direct measures of EC-IC effects on wet weight and dry weight of brain were made in 1969. Both wet and dry weights were compared for 11 pairs of rats individually (Bennett, Rosenzweig & Diamond, 1969). More recently, wet and dry weights were determined for pooled tissue samples from 23 pairs of rats. Typical EC-IC differences were obtained using these dry weights. The data from both experiments have been summarized in Rosenzweig et al. (1972c).

Hoover and Diamond (in preparation) have recently shown that the occipital cortex of female rats maintained in differential environments from 60 to 90 days of age did not differ in water content as a percent of wet weight (N = 11 pairs). Geller (1971) has also reported that male rats raised in differential environments for 30 days beginning at weaning did not differ in water content (N = 8 pairs).

The only direct evidence that water content of brain may differ because of differential environments has come from a comparison made by de Feudis (1972) of mice living in grouped conditions with mice living in isolated conditions. In this case, aggregated mice were reported to have a 7.5% lower ratio of dry weight to wet weight than aggregated mice for the cortex, and a 4.8% lower ratio for the hemispheres. (Percentages were recalculated to correct errors in the original.) (It should be noted

that data from only 13 mice--7 aggregated and 6 isolated--were used for these determinations.)

While further investigation of the effect of aggregation on water content of mice may be justified, we do not believe that water content is a major factor in producing brain weight difference as a result of EC and IC environments that we have used for rats, mice, gerbils, or *peromyscus*.

Is Extracage Environment Effective?

In our initial design of experiments on the effects of differential environments on rat brain and behavior, we chose convenient, but not extreme, conditions which we believed would maximize the observed cerebral differences. We supposed that the varied activity of experimenters in the busy EC room would contribute to enrichment and that the lack of general stimulation in the separate isolation room would heighten the IC effect. Other investigators have also presented both intracage and extracage stimuli in their enriched conditions and have assumed that the results they obtained were due to both sources; this is true of the behavioral study of Gardner et al. (in press) to be discussed later and also of the paper of Mailloux et al. (1974) reporting effects of enriched visual experience on cortical evoked potentials in the rat. The latter group (Edwards et al., 1969) had already obtained significant effects with an EC condition similar to ours and apparently added extracage stimuli in the replication in an attempt to enhance the results.

The presumed effectiveness of extracage stimuli in the EC-IC experiments had to be subjected to experimental tests. (We had also supposed initially that the small amount of training in ECT contributed to the

cerebral effects, but we later found that the role of this factor was negligible.) We also had operational concerns with the necessity of using the isolation room--frequently it is convenient to house IC rats within the main colony rooms, e.g., when some animals are being given daily injections of drugs, or in case of limitation of space. A further reason for investigation was several reports, albeit somewhat contradictory, which suggested that extracage environment was an important factor in determining subsequent maze performance (Forgays & Forgays, 1952; Hymovitch, 1952).

Further experiments (1965-1966) showed that the usual extracage environment did not modify the results obtained with either EC or IC animals. That is, IC animals kept in the EC room had brain weights virtually identical with the IC animals run at the same time in the IC room, and vice versa. Additionally, clear EC-IC differences developed in an experiment in which the IC rats were kept in colony wire cages on the same racks on which 2-hour EC groups spent 22 hours per day.

Although rats raised in IC conditions in the main laboratory or in the isolation room did not differ in cerebral measures, rats isolated in an extremely impoverished environment/^(IEI) did have cerebral values that differed even more from the EC group than did the usual IC group (Krech et al., 1966). To obtain this extreme condition, cages were suspended individually in fiberglass boxes, and these boxes were placed in an audiometric test chamber.

Continuing concern with the possible influence of extracage perception on rats has been the subject of several recent articles. Some of the reports have been contradictory. For example, Lavallee (1969, 1970)

reported that rats given daily slide shows from weaning to 80 days of age were superior in problem-solving to the control rats which saw only a blank screen. Attempts in our laboratory to replicate these findings (Ricard, unpublished) were unsuccessful. In two experiments, using Fischer rats, Ricard found that the animals given the daily slide show were inferior to the controls on the Hebb-Williams maze. In addition, in a parallel experiment, no differences in cerebral weight or enzymatic measures were found between the visually deprived and stimulated rats.

Singh et al. (1967, 1970) reported that rats that could observe vertical stripes from their cage developed both behavioral and cerebral differences from rats whose cages faced a blank wall. Particularly large differences were reported in AChE activity; the group which had visualized the stripes had twice the AChE activity in posterior cerebral cortex as did the controls (1967). An attempt to replicate this experiment in our laboratory by Maki (1971) showed no cerebral differences as a consequence of the extracage stimuli.

Two experiments run during 1973 gave even clearer evidence that direct interaction of the rats with the stimulus objects is necessary to obtain the usual EC-IC cerebral effects (Ferchmin, Bennett & Rosenzweig, 1975). These experiments, termed the "observer" experiments, included three groups of animals--the usual EC rats, the IC rats, and the "Observer Condition" (OC) rats. The OC rats were placed in small wire-mesh cages inside the EC cage. Thus they were exposed to all of

Figure 1 around here

the general noises, sights, and smells of the laboratory. In addition, the OC group had a small amount of contact with the EC rats through the

wire mesh of the OC cages. In designing this experiment, it was thought, based on the literature of "observational learning," that the mere act of watching the EC animals at close hand might make the OC group more like EC rats than like IC rats in both brain weight and behavior. The results were clearly just the opposite. The brain weights of the OC rats were essentially identical to those of the IC rats. Behaviorally, when tested for exploratory behavior in a Greek cross apparatus, these observer rats, like the IC rats, showed a significantly lower level of exploration than the EC rats. For some measures, the scores were even more extreme than the ICs.

Our doubt that extracage stimuli are effective in the EC situation should not be taken to mean that we either ignore or do not believe reports that under certain circumstances certain types of animals can be affected strongly by visual stimuli with which they have no direct contact. Thus, there have been a number of papers reporting convincingly that early experience of kittens alters the receptive fields of cells in their visual system (Hirsch & Spinelli, 1970; Blakemore & Cooper, 1970; Pettigrew, 1975). It is not yet clear to what extent these phenomena will be found in other species. Rabbits did not show modification of cortical receptive fields when raised with exposure to only horizontal or vertical stripes (Mize & Murphy, 1973), although this is the situation that produced clear modification in the kittens of Blakemore and Cooper (1970). Earlier work with rats seem to show little effect of visual deprivation on perceptual capacity, as measured on tests of pattern discrimination or on the visual cliff. Recent experimenters have, however, found some perceptual changes in rats as a function of early

experience. Thus, Walk and Walters (1973) found that rats kept in the dark for 30 days after birth could not discriminate a 4-inch depth but could discriminate a 6-inch depth; controls reared in a normal light-dark cycle discriminated well on both the 4-inch and 6-inch tests. The rats reared in the dark for 30 days recovered the ability to discriminate the 4-inch depth after 48 hours of light, but rats kept in the dark for 60 days had not recovered after 12 days of light. Tees (1974) has found that differential ability to perceive depth does not depend upon experience in light at 20 days of age, but thereafter dark-reared rats did not improve at the same rate nor acquire the same degree of discriminative ability as did their light-experienced counterparts. It appears therefore that a complex story about effects of light experience on ability in the rodent is developing. It must be recalled, however, that rats in both the usual EC and IC situation have light experience; the differences are only in the complexity of their visual and other surroundings. We see no evidence to date that extracage stimuli, either visual or other, above the levels available in IC contribute independently to the EC-IC differences in behavior or especially in brain development. Any investigator who believes the extracage stimuli to be effective in determination of EC-IC differences is encouraged to present evidence that this is more than a fantasy.

Relative Effectiveness of Inanimate and Social Stimulation

Having just eliminated extracage stimulation as playing any important role in determining the EC-IC cerebral differences--and having previously eliminated such factors as handling, locomotion, and stress--we now come to the factors of social stimulation and stimulation from the varied

objects in the EC situation. We have considered the possible importance of social stimulation in previous papers (Rosenzweig, 1970; Rosenzweig, Bennett & Diamond, 1972c), but further findings and discussion suggest that this factor now requires more searching evaluation. Thus, Welch et al. (1974) have reported "...that mere group living sufficed to increase brain weight without a complex physical environment being involved... Our results suggest that the stimuli required for cerebral cortical enlargement are not as specific as the experience of learning to cope with structural complexity as Rosenzweig et al. suggest." (pp. 79-80). Welch et al. showed that rats that lived in a group of 12 for one year developed differences in brain weights and in brain RNA and DNA, compared to rats housed singly; environmental enrichment was not investigated.

Enrichment or Impoverishment from the Standard Colony Baseline

We had considered some effects of social grouping in our 1964 Science paper (Bennett et al.). In three experiments with S_1 rats we had included groups housed in colony conditions, three to a cage (SC). We had found that in weight of cortex and in total AChE "...the ECT group differed significantly from the SC group and differed further from them than did the IC group. Thus the bulk of the effects on cerebral weight and acetylcholinesterase activity is due to enriching rather than to restricting the experience of our colony animals." This was true both for animals assigned to the differential conditions at weaning (25 days of age) and for animals assigned at 105 days of age.

The relative contributions of enrichment and impoverishment to brain measures were discussed extensively in Rosenzweig et al. (1972c) by comparing EC to SC and IC to SC. Let us summarize briefly some of the

principal results for experiments of 80-day duration begun at weaning (in conditions from 25 to 105 days of age) and at 105 days (105-185), noting that the relative importance of enrichment and impoverishment differs both with age and with the brain measures considered. Since the overall EC-IC differences are small but significant, it should be apparent that results of partialling these differences between the two factors should be taken as indicative only. For the 5 experiments run from 25 to 105 days, the cortical brain weight differences were chiefly due to enrichment (EC-SC, 2.8%, $P < .001$; IC-SC, -0.9%, NS), the subcortical weight differences were chiefly the result of impoverishment (EC-SC, 0.5%, NS; IC-SC, 2.1%, $P < .01$), and the cortical/subcortical ratio should roughly equal results of both factors (EC-SC, 2.3%, $P < .001$; IC-SC, -3.0%, $P < .001$). Obviously the overall EC-IC differences are the sums of the two effects--for the cortical/subcortical ratio, 5.3%, $P < .001$. When experiments are started at weaning, the IC rats come to develop greater body weights than either EC or SC. When the percentage differences of brain weights are adjusted for covariance on body weight, the IC-SC differences then become somewhat greater than EC-SC in cortex as well as in subcortex. In several enzymatic measures--AChE per unit of weight, ChE/weight, and ChE/AChE--the effects were almost entirely due to impoverishment in the 25-105-day experiments. In contrast, for the three 105-185-day experiments, enrichment was clearly more effective than impoverishment in both cortical weight (EC-SC, 4.3%, $P < .001$; IC-SC, 1.6%, $P < .05$), and in the cortical/subcortical weight ratio (EC-SC, 3.2%, $P < .001$; IC-SC, -0.6% NS). For chemistry, only AChE/weight was determined for the older animals; the effects were small and were chiefly attributable to enrichment rather than to impoverishment.

Effects of EC, SC, and IC for still older rats were reported by Riege (1971). The brain weight measures were responsive to both enrichment above the SC baseline and to impoverishment. The cortical/subcortical ratio showed chiefly enrichment effects.

We have recently measured RNA and DNA in occipital cortex of rats assigned to EC, SC, and IC at weaning. For RNA/DNA, both EC and IC differed significantly from SC and in opposite directions. The effects of enrichment and of impoverishment were roughly similar in magnitude for these young rats. In experiments in which 100-day or 200-day old rats were assigned to the three conditions for 30 days, the RNA/DNA ratios were similar in the SC and IC groups but were significantly greater in the EC group.

Anatomical effects in EC, SC, and IC--cortical depths, cell size, and synaptic lengths--are discussed by Diamond in her chapter in this volume. As for the weight and chemical measures, the relative effectiveness of enrichment and impoverishment depends upon both the starting age and the measure considered. For still another anatomical measure, branching of cortical dendrites, Greenough and Volkmar (1973) have attributed the effects almost entirely to enrichment.

Concerning behavior, which is not our main focus in this paper, we have found both EC-SC and IC-SC differences, and these varied with both the age of exposure to the differential environments and the test employed. Both of these factors have also come out in studies by other laboratories (see review in Rosenzweig, 1971).

The foregoing studies show clearly that there are effects of both enrichment and impoverishment on a number of brain measures. One obvious way in which the EC, SC, and IC situations differ is in the size of the

social groups. Since the EC animals lived in groups of 12, whereas SC lived in groups of 3, the possibility remained that the EC-SC brain differences reflected mainly the sizes of the social groups rather than the differences in the inanimate environments. Two recent papers from other laboratories will be noted in which the most enriched situation has the largest group size, and so the two factors are confounded. Let us consider these studies briefly.

Kuenzle and Knüsel (1974) in Switzerland designed a "superenriched" environment. A group of 70 rats was housed in two large interconnected cages and had to shuttle back and forth across a bridge with changing gates and signals in order to find food and water. Over the 29-day experimental period the rats found successively more complicated problems and also had to perform athletic feats in order to survive. In two replications, groups were run simultaneously in the superenriched environment and in a reproduction of the Berkeley EC situation. The super EC rats were found to surpass the regular EC rats in weight of occipital cortex, in length of the cerebral hemispheres, in ChE/AChE in occipital cortex, but not in RNA/DNA in occipital cortex. While these results are encouraging in showing even greater brain plasticity than found heretofore, it is clear that this experiment confounds the factors of social and inanimate enrichment, since the super EC was greater along both dimensions. Also, the stress on agility in the super EC renders questionable the assertion of Kuenzle and Knüsel that the superenriched condition "is superior to the original [EC] in that it confronts the animal with true learning situations," whereas "the original setup mostly improves the animals' motor performance but does not provide for genuine learning situations."

Gardner et al. (1975) have measured separate effects of environmental and social enrichment on several behavioral tests. They kept male Long-Evans rats in one of four conditions, starting at 21 days and lasting for 60 to 70 days: (a) Perceptually enriched-socially enriched (PE-SE), in groups of 22 or 23 in large cages filled with varied objects that were moved or changed every 3 days; there were also extracage, visual and auditory stimuli (flashing Christmas-tree lights and intermittent radio music). (b) Perceptually enriched-socially isolated (PE-SI), in small individual cages with a single object that was changed every 3 days; extracage visual and auditory stimuli as for PE-SE. It is clear that the perceptual enrichment as well as group size differed between PE-SE and PE-SI. (c) Perceptually impoverished-socially enriched (PI-SE), in groups of 22 or 23 in large cages of the same size as for PE-SE, but without stimulus objects. The room was dark and the cages were surrounded by sound-attenuating material, and white masking noise was delivered constantly. (d) Perceptually impoverished-socially impoverished (PI-SI), in individual cages kept, like PI-SE, in the dark and with sound attenuation and masking noise. PI-SI is similar to our condition of Isolation in Extreme Impoverishment (Krech et al., 1966) and is thus more extreme than our usual IC condition.

On a one-trial passive avoidance step-down test, rats from all four conditions showed similar pretraining latencies, but there were significant differences in retention latencies. Both SE groups showed long latencies (excellent retention), and PE-SI showed good retention, but PI-SI gave little evidence of learning. Other animals from the same conditions were used to study memory consolidation by administering electroconvulsive

shock at varying intervals following a step-down trial. The investigators concluded that the socially impoverished rats suffered from a slowing of the consolidation process. All the rats were then tested for exploration in a Hebb-Williams maze used as an open field. The perceptually enriched groups explored more than the PI groups ($P < .01$), whereas the social variable had no effect. (It should be noted that this experiment did not distinguish between effects of intra- and extracage environmental stimulation.) On almost every measure, Gardner et al. found significant interaction between the perceptual and social factors. This may well be true, but it could be in part an artifact that occurred because the perceptual enrichment was distinctly unequal for the PE-SE and the PE-SI groups.

Inanimate and Social Stimulation

Our first experiments comparing IC with groups of 12 in either EC or in a large cage without varied stimulus objects was done with male inbred Fischer rats as subjects (Rosenzweig, 1971). In two experiments, animals were placed in the differential conditions at 60 days of age and remained there for 30 days until sacrifice at 90 days of age. In all, seven experimental conditions were used; this was a reason for employing Fischer rats as subjects, since they are inbred and a littermate design did not have to be used; it would not have been possible to obtain sufficient litters with seven S_1 rats, and the Fischer animals had shown generally similar effects to our S_1 and S_3 strains in previous experiments. The seven conditions were as follows: Rats of one group in each experiment remained isolated in individual colony cages (IC) for 24 hours per day. One group of 12 lived for 24 hours per day in the usual EC conditions, while another group of 12

lived in an empty EC cage; this was called the Large Cage (LC), and we have more recently referred to it as the Group Condition (GC). Further groups were also placed in LC or EC for only 2 hours per day, since we had found that 2 hours of enriched experience suffices to bring about many of the same brain effects as does 24 hours per day (Rosenzweig, Love & Bennett, 1968).

Brain weight measures at sacrifice showed that the animals placed in EC for either 24 hours per day or for 2 hours per day differed significantly from the IC rats; on the other hand, the animals placed in groups of 12 in LC for either 24 or 2 hours per day did not differ significantly from the IC animals. The animals placed singly in EC or LC did not differ from the IC animals. Since the animals placed in groups of 12 in LC did not come to show significant differences from the IC animals, we concluded that social stimulation was not sufficient to bring about major differences from IC. In retrospect, it seems that we should have been concerned about not finding any differences between LC and IC, since we had previously reported significant differences between SC and IC. It may be that the Fischer strain of rats is not as much affected by social stimulation as is the Berkeley S₁ strain.

In conjunction with recent experiments in which groups of animals are given access to a maze 24 hours a day and required to run through it as they shuttle back between food and water, we have included a control group placed in a large EC cage which is not furnished with the usual stimulus objects. Results of these experiments suggest that the subjects of the S₁ strain showed greater cerebral effects of grouping than did the Fischer subjects in the previous experiments reported above. Table 3 presents

Table 3 around here

some of the results of EC, GC, and IC on brain weights and RNA/DNA ratio from these recent experiments. It will be seen that GC vs. IC shows about half as large an effect as EC vs. IC in weight of occipital cortex and weight of total cortex but not in the cortical/subcortical ratio. The comparison of regular EC with the group condition shows that the regular EC produces significantly larger brain weight effects in all areas--occipital cortex, total cortex and in the cortical/subcortical ratio. For RNA/DNA the ratio in occipital cortex for animals raised in EC is significantly larger than for those raised in GC, and, in turn, the ratio for GC animals is significantly larger than for IC rats. [*Values for total cortex will be added in proof.*] Thus we can be sure that experience in the enriched condition produces significantly larger brain effects than does simple social living in a group of 12, but social living itself produces significant effects as compared with isolation.

The effects of living in the laboratory enriched environment themselves are smaller than living in a semi-natural environment, and this further shows that the stimulus situation is important as well as the size of the social group. The outdoor semi-natural environment (SNE) was described briefly in Rosenzweig, Bennett and Diamond (1972a). This condition has now been employed in a number of experiments where littermate S₁ male animals could be compared after either 30 days in SNE or 30 days in EC. The results show that to a high level of significance 12 animals in the outdoor environment develop larger cortical weights and cortical/subcortical weight ratios than do their littermates in the EC condition.

(In discussions of work with the semi-natural environment we have found that some investigators presume that rats placed in a relatively large area will scatter and avoid social contacts or conflicts. It may therefore be worth putting on the record that the two strains of laboratory rats that we have studied in this situation [Fischer and S₁] prefer to stay together. We find them resting together under boards, or staying together in tunnels that they burrow.)

Another way to show the importance of inanimate stimulation comes from experiments in which the social factor was excluded but in which the cerebral enrichment effects were obtained. In a series of experiments begun in 1967 we found that rats receiving a daily injection of methamphetamine, before being put in the enriched condition for 2 hours a day, developed larger than usual brain weight effects. In her doctoral thesis, Su-Yu Chang (1969) reported that the animals given methamphetamine showed less social interaction than animals given saline injections, whereas the methamphetamine animals showed a greater than usual amount of interaction with the stimulus objects. In further research along this line (Rosenzweig & Bennett, 1972) we found that placing rats singly in EC (SEC) for 2 hours per day resulted in significant differences from IC if the animals were given small injections of methamphetamine before the daily period in the enriched environment but not if they were given injections of saline. We therefore concluded that anatomical and chemical changes characteristic of EC will develop in the rat brain whenever the animal interacts with a relatively complex environment for at least a minimum daily period over at least a minimum duration of days. "Social stimulation, which heretofore has always been included in the enriched condition, is now found not to be necessary" (p. 304). Finding that social stimulation is not required to

produce the EC-IC effects, of course does not state whether or not social stimulation will contribute to the EC effect if the social condition is present.

We conclude that social living, while it has clear effects on brain measures, cannot account entirely for effects of our laboratory enriched condition. Furthermore, additional environmental enrichment, while holding the size of the group constant, brings about even larger cerebral effects. It is clear that the social condition itself warrants further study; perhaps the social condition is important in part because it provides opportunities for certain types of learning. And certainly the social condition is required as a control for other conditions in which animals are grouped together while effects of other factors are being studied.

DISCUSSION

Major Factors in Environmental Enrichment

From the research reviewed above it appears that some factors can now be set aside as having little or no importance in producing EC-IC cerebral effects. These factors that can now be safely disregarded include differential handling, differential locomotion, stress, and differential rates of maturation. Extracage stimulation seems to be of little importance, provided some light and sound are present as in IC; removal of all visual and auditory stimulation, as in IEI, did produce effects of sensory deprivation. On the other hand, it appears that both the stimulation of contact with varied stimulus objects and social stimulation contribute independently to the enrichment. The experiments reviewed above show that a number of investigators have manipulated either or both of these factors, as Figure 2 illustrates. Considerable progress has already been made in

Fig. 2 about here

mapping these two dimensions. Let us consider some of the results in terms of this figure.

The social dimension in this table is presented simply in terms of the number of animals living together, from one up. The enrichment of environment in terms of complexity of inanimate stimulus objects is more difficult to scale, and the ordinal scale presented here is purely intuitive. For example, how can one rank the relative enrichment of the large outdoor field (SNE), that of the Ferchmin procedure (FEC) with its variety of cages, (Ferchmin, Eterovic & Caputto, 1970) and that of the complex "superenriched" environment in the Swiss laboratory (SE)? They differ from each other in several dimensions, but, since we could not readily decide which was more complex, we have given them the same rating; later research may settle such a question.

Some investigators have attempted to disentangle the effects of these two factors by varying one and holding the other constant. For example, we have done this by exposing single rats to a number of different experimental environments, as shown in the left-hand column of the table. For single animals exposed under normal conditions of motivation, the inanimate environment apparently has relatively little effect; only extreme impoverishment (IEI) produced significantly different brain values from the IC condition. Even putting single rats in the enriched condition (SEC) did not bring about much difference, unless the single animals were exposed to it after having been administered an excitant drug which increased their interaction with the varied stimulus objects, and in that case they did differ from IC littermates in the EC direction. In the case of animals living in

a group of 12, it has been easier to show the effect of environmental enrichment on cerebral measures. Here we have found that rats in SNE exceed rats in EC in several cerebral measures, and the EC rats in turn surpass rats in GC in several measures. Thus there seems to be an interaction between environment and group size, the effects of environment showing up clearly with groups of 12 but being definitely smaller in the case of individual animals. We have discussed this previously (Rosenzweig & Bennett, 1972), pointing out that animals in a group tend to keep each other active, and this brings them into frequent contact with the inanimate stimulus objects as well as with each other; thus social grouping heightens the effects of inanimate enrichment.

This rather simple two-dimensional display could be complicated considerably by taking into account other variables and thus making a multi-dimensional display. Let us note some of these other variables. Age at which animals are exposed to the differential environments might well be taken into account. Even though we have found no critical period for these effects, it nevertheless seems to be true that somewhat larger effects are obtained when animals are placed in the differential environments at an early age than when they are already fully adult. The duration of exposure, both hours of exposure per day and number of days in the experimental period, also merits study. This will have to be investigated separately for different cerebral measures, since it appears that only a few days brings about clear effects in cerebral weights and nucleic acid concentrations whereas many weeks are required for clear effects in cholinesterase activity. The types of stimuli used could also be a subject of investigation. To date we have used a variety of readily obtainable

objects and gadgets without particular reference to the preferences of the animal subjects. One could well investigate the effectiveness of species-specific stimuli, such as odors produced by animals or animal products. One of the most important direction in which research should be extended, it seems to us, is to investigate the effects with other species of experimental animals. To date we have found rather similar effects in four species of rodents--laboratory rats, laboratory mice, gerbils, and feral *Peromyscus*. It seems important to extend this research to other orders of mammals. Many theorists already have seized upon the results obtained with rodents and have extrapolated them freely to other orders, including man. Clearly it is important to know whether the results obtained to date, or similar effects, will be found in other mammalian orders. We believe that an important next step will be to run similar experiments with cats. With this species we can use the same multiple litter designs that have been successful with rodents, and research with cats is both feasible and relatively economical. In the long run, of course, it would be important to extend this research further to primates.

The Role of Learning in Producing Effects of Environmental Enrichment

A much debated question has been whether differential opportunity for learning is one of the major causes of cerebral differences resulting from experience in differential environments. As we noted near the start of this paper, we embarked upon the research with the differential environment because of our unexpected early findings that training in different formal programs led to changes in brain chemistry. We set up the differential environments in order to increase the differential opportunity

to learn with the hope that this would enhance the brain differences, and in fact such increased differences were obtained. It is of course not certain that these larger cerebral effects could be attributed to learning and memory as such.

Others who have done research in this area have maintained that learning must be involved in producing these cerebral differences. Thus Greenough (1975) states that "...it would be much more difficult to argue that EC rats do not learn more than their cage housed counterparts than it is to argue that they do." He presents several specific reasons to support the conclusion that differential memory formation is at least one component in producing these cerebral effects: First, both the behavioral and the cerebral effects of environmental complexity appear to be potentiated by drugs that affect memory formation. In this regard, he cites our reports (Bennett, Rosenzweig & Wu, 1973; Rosenzweig & Bennett, 1972) that daily administration of excitant drugs potentiates the effects of environmental complexity upon brain measures. He also notes reports that effects of a complex environment upon maze learning are enhanced by daily administration of strychnine (LeBoeuf & Peeke, 1969; Peeke, LeBoeuf & Herz, 1971). Secondly, Greenough notes that our group and others have found effects of environmental complexity on brain weights and nucleic acids after only a few days in the differential environments, and thus the time scale is compatible with that of experiments on learning and memory (Ferchmin, Eterovic & Caputto, 1970). Furthermore, brain weight differences occur even when exposure to environmental complexity is restricted to as little as two hours per day for 30 days, again a daily period comparable to that of many learning experiments (Rosenzweig, Love & Bennett, 1968). Thirdly, Greenough

points out that behavioral effects of enriched experience seem to be greatest on tasks which are rather similar to the complex environment, especially mazes.

Gardner et al. (in press) consider a number of types of learning that probably take place in the enriched situation. They note that rats living in a social group sometimes display aggressive behavior and this provides opportunities for passive-avoidance learning that may then transfer to other situations. Perceptually enriched rats may learn to explore objects and spatial arrangements, and this may generalize positively to the open field and to maze situations. They also suggest that there may be specific alterations in brain mechanisms subserving learning and memory.

We can adduce further evidence that demonstrates that learning takes place in the enriched situation. Thus McCall (1969) has tested the responses of rats to objects that have previously been placed in their cages and novel objects. There are clear differences in the reactions to these classes of objects, thus showing that the animals have learned to distinguish them. Further evidence of learning in the EC situation comes from a recent study by Parsons and Spear (1972). In three experiments, two with weanlings and one with adult rats, the animals first learned in an active avoidance situation. Animals were then kept in either an enriched or a standard laboratory environment for 60 days before being given a retention test. Environmental enrichment in the interim period resulted in greater forgetting of the active avoidance response than did the standard laboratory environment. The experimenters concluded that learning in the complex situation resulted in extraexperimental interference with retention of the avoidance response.

The evidence and the reasoning summarized in this section of the discussion offers strong support for the concluding that learning and memory

formation are taking place at a greater rate in the EC than in the SC or IC situations. It remains to be shown how the learning and memory formation are tied to the observable changes in cerebral measures, and this will undoubtedly provide a fertile field for further research. In our own laboratory we are pursuing investigations of formal training in situations which we hope will produce cerebral effects in ways that can more readily be related to learning than has been true in the past.

L'ENVOI

The experimentation and conceptualization reviewed in this paper span many years, and, as we have noted, it rose out of the still earlier concerns that David Krech and we shared concerning the role of neurochemical variables in individual differences in problem-solving. We look back with pleasure to 1954 when we began a dozen years of interdisciplinary collaboration with David Krech who was responsible for many of the ideas and research techniques discussed here. While we remain cautious about the relations between learning and cerebral effects in our rats, we are certain of the stimulation and learning that we gained from our collaboration with David Krech, and we think back to many lively discussions, over many cups of tea.

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Table 1

EC-IC Percentage Differences in Brain Weights and Body Weights in Experiments with Different Starting Ages and Durations of 30 Days or More (1960 - 1974)

Age at Start	Duration (days)	<u>30</u>	<u>37</u>	<u>45</u>	<u>60</u>	<u>80</u>	<u>100</u>	<u>130</u>	<u>160</u>
	N (pairs)	267	24	23		206	46	58	22
25	Occipital Cortex	9.6***	6.1***	8.0***	--	7.3***	9.8***	8.5***	11.4***
	Total Cortex	5.2***	4.6***	6.4***		4.2***	6.6***	6.8***	2.5**
	Rest of Brain	0.1	0.9	2.6**		-0.8*	0.7	1.6*	-3.3**
	Total Brain	2.3***	2.4*	4.2***		1.2***	3.2***	3.7***	-0.9
	Cortex/Rest	5.0***	3.6***	3.6***		5.1***	5.8***	5.2***	6.1***
	Body Weight	-8.9***	-4.7*	1.1		-7.7***	-4.8**	-7.5***	-6.8*
	N (pairs)	133							
60	Occipital Cortex	7.2***	--	--	--	--	--	--	--
	Total Cortex	5.5***							
	Rest of Brain	1.9***							
	Total Brain	3.4***							
	Cortex/Rest	3.6***							
	Body Weight	-0.8							
	N (pairs)					45			
105	Occipital Cortex	--	--	--	--	10.9***	--	--	--
	Total Cortex					5.4***			
	Rest of Brain					1.7*			
	Total Brain					3.2***			
	Cortex/Rest					3.7***			
	Body Weight					-0.1			

Table 2

Influence of Age and Environmental Conditions on RNA/DNA Ratio
Occipital Cortex

Age (days) of Rats		Duration of EC-IC period	RNA/DNA		% Difference between EC and IC	No. pairs EC>IC ^a	P-Value
at: Start	Sacrifice		EC	IC			
26	30	4	2.224	2.060	8.0	13/14	.001
28	59	31	1.974	1.784	10.6	12/12	.001
25	150	125	1.730	1.633	6.0	10/12	.01
97	264	167	1.660	1.552	7.0	7/9	.01
330	360	30	1.638	1.559	5.0	9/11	.01

^aNumber of littermate pairs in which EC value was greater than IC value.

Table 3

Percentage Difference between Brain Values of Rats in Enriched Condition (EC), Group Condition (GC) and Impoverished Condition (IC)

(N = 35 per condition)

A. Brain Weights	Occipital Cortex	Total Cortex	Rest of Brain	<u>Cortex</u> Rest
EC vs IC	6.2****	5.3****	1.0	4.3****
GC vs IC	2.9**	2.5***	-0.6	3.1****
EC vs GC	3.2**	2.8*	1.6	1.2
B. RNA/DNA				
EC vs IC	9.7****		--	--
GC vs IC	5.9****			
EC vs GC	3.6****			

* P < .10 ** P < .05; *** P < .01; **** P < .001

FIGURE CAPTIONS

Fig. 1. Rats in the Observer Condition within an Enriched Environment cage.

Fig. 2. Representation of differential environments in terms of two main variables--inanimate stimulation and social grouping. The conditions have been described in the text, and the abbreviated designations are as follows:

Rosenzweig, Bennett and Diamond: EC (Environmental Complexity), FEC (Ferchmin EC), GC (Group Condition), HC (Home Cage), IC (Impoverished Condition), IEI (Isolated in Extreme Impoverishment), SC (Standard Colony), SEC (Single-Animal EC), SNE (Semi-Natural Environment).

Gardner et al.: PE-SE (Perceptually Enriched-Socially Enriched), PE-SI (Perceptually Enriched-Socially Isolated), PI-SE (Perceptually Isolated-Socially Enriched), PI-SI (Perceptually Isolated-Socially Isolated).

Kuenzle and Knüsel: SE (Superenriched Environment) and EC.

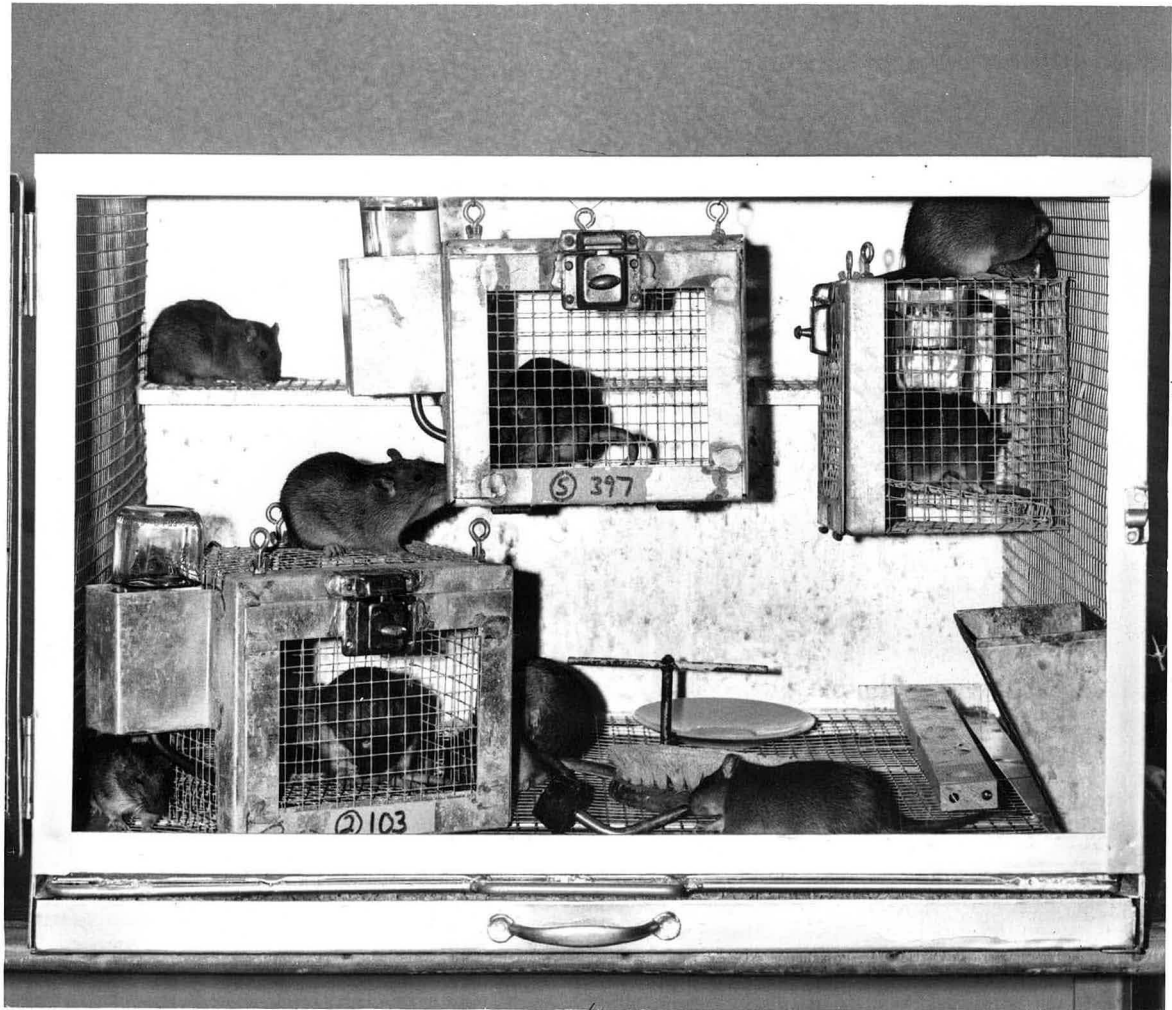



Fig. 1.

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Complexity of Inanimate Environment	High			SNE FEC		SE
		SEC		EC	PE-SE	
		PE-SI				
		HC	SC	GC		
		IC				
	Low	PI-SE IEI			PI-SE	
	1	3	12	22	70	
	Social Factor (Number of rats housed together)					

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Fig. 2. Representation of differential environments in terms of two main variables--inanimate stimulation and social grouping. The conditions have been described in the text, and the abbreviated designations are as follows:

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Kuenzle and Knüsel: SE (Superenriched Environment) and EC.

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