THE EFFECTS OF ENVIRONMENTAL COMPLEXITY ON THE HIPPOCAMPAL FORMATION OF THE ADULT RAT

Evan R. SUSSER and Robert B. WALLACE

Laboratory of Developmental Psychobiology, University of Hartford
West Hartford, Connecticut 06117, USA

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Abstract. In an effort to determine the plasticity of the proliferative matrix of the hippocampus in an adult rat to environmental manipulation, the following study was conducted. Fifteen adult male Long-Evans rats (6 months old at the start of the experiment) were placed into two different environments for 3 months. Seven animals represented the enriched condition and 8 represented the condition of isolation. At the conclusion of exposure to the different environments, the animals were sacrificed by transcardial perfusion and the dorsal hippocampi examined in matched sections for all animals. Results indicated heavier total brain weights and larger numbers of granule cells in the dorsal hippocampus for animals exposed to the enriched environment. Implications for CNS plasticity were discussed.

The concept of neuronal plasticity has been a focal point of much research in the past two to three decades. Classic studies by Hubel and Wiesel (7, 8) as well as studies by Blakemore and Cooper (4) and Blakemore and Mitchell (5) have demonstrated that environmental manipulation can alter the visual system of cats, and in fact, the development of the brain may depend on the visual environment. In addition, environmental complexity studies carried out by Rosenzweig, Krech, Bennett, and Diamond (9) indicated that raising experimental animals in either
enriched or deprived environments induced substantial and lasting changes in the central nervous system. When the brains of the enriched and deprived rats were compared, three major differences were observed: (i) the enriched rats had heavier brain weights; (ii) although the number of neurons was not different, the enriched rats were found to have more glial cells; (iii) the enzyme contents of the brains of the two groups were different; this was especially noted in the case of AChE.

In a more recent environmental complexity study carried out by Walsh, Budiz-Olsen, Penny, and Cummins (12), one group of rats was reared under conditions of complexity or enrichment, while their littermates served in an isolated or deprivation condition. These researchers noted thicker occipital cortices (4.90/o) and hippocampi (5.70/o) in the enriched versus deprived animals.

The study mentioned above, Walsh et al. (12) was carried out with rat pups as the experimental animals and therefore at the time of experimentation the hippocampus was undergoing behavioral maturation. Previous investigations have indicated that the bulk of the short-axon-ed neurons that make up the granule cell layer of the hippocampal dentate gyrus come into existence in the first weeks after birth (1, 2). If the hippocampus is in process of maturation and undergoing neurogenesis, the environmental manipulation might be expected to result in permanent anatomical changes. Will, however, the proliferative matrix of the hippocampus in the adult animal retain the capacity to similarly respond to environmental change? If so, then this may represent one answer to the observed behavioral plasticity of the adult. In an effort to answer this question, the following study was conducted.

Fifteen adult male (6 month old) Long-Evans hooded rats were used as subjects in this experiment. Seven animals represented the enriched condition and 8 represented the isolated control condition.

The experimental animals were placed in a large communal cage, 90 X 75 X 60 cm; four sides were constructed of plywood with a plexi-glas top and a wire mesh floor. Placed inside the “enriched environment” was an assortment of objects such as an activity wheel, wooden blocks, ramps leading to a bi-level platform, metal toys, a rope and colored discs. Additionally, a radio placed over the communal cage was turned on according to a random schedule. Every week the interior design of the communal cage was changed. The animals were handled every other day and they received food and water ad lib.

The isolated control animals were placed in individual stainless steel cages (18 X 18 X 19 cm). These animals were housed in an isolated room and no two cages on the holding rack were adjacent. These isolated rats were given minimal stimulation; weights were taken every other week (handling) and food and water were available ad lib.
Both groups of rats were on a 12–12 h schedule of light-dark. All animals were kept in their respective environments for 3 months at which time they were sacrificed and the brains processed for anatomical evaluation.

![Figure 1](image_url)

**Fig. 1.** Schematic illustration of a rat brain indicating the points on each hemisphere where the measurements of antero-posterior length were taken.

All animals were given an overdose of sodium pentobarbital and perfused transcardially with 10% buffered formalin. Prior to post fixation, hemispheric length measurements were taken from the right and left hemisphere (see Fig. 1); measurements were taken using a metric rule microforceps and a thread. Brain/body weight ratios were also calculated. Following post fixation, brains were embedded in para-plant sectioned at 7 μm in the coronal plane and stained using the H and E procedure of Harris. Matched sections containing the dorsal hippocampus were examined at 400 X magnification using a 12 X12 matrix grid and the number of granule cells in the dentate gyrus counted for each animal.

It is known that the granule cells of the dentate gyrus originate postnatally and are therefore susceptible to induced anatomical change through environmental manipulation (11, 12). Neurogenesis within the hippocampal formation, however, comes to a halt by approximately one month after birth and by two to three months basic connectivity within this structure has been accomplished (1). Since a number of studies, however, have suggested the effects of environmental manipulation on brain structure (6) it was determined to manipulate this variable in an adult. Table I indicates the results of the various statistical comparisons that were made. Right and left hemispheric lengths were measured since an earlier investigation (3) had suggested that environmental manipulation might produce increases in hemispheric length in animals exposed to environmental enrichment. These increases in length were attributed to increased rates of neurogenesis in the regions of the frontal pole in the enriched animals although no definitive conclusions were reached. No such differences, however, were observed in the present study in
either group of animals. Brain/body weight rations were calculated and no significant differences were seen between the enrichment and isolated control animals. The brain weights, however, were significantly different with the animals exposed to the enriched environment having heavier wet brain weights. Finally, hippocampal cell counts in matched sections of the dorsal hippocampus revealed a significantly greater number of

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<th>Description</th>
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<th>Significance</th>
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<tr>
<td>A. Hemispheric lengths</td>
<td>1.38</td>
<td>13</td>
<td>not significant</td>
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<tr>
<td>B. Brain/body weight ratios</td>
<td>0.19</td>
<td>13</td>
<td>not significant</td>
</tr>
<tr>
<td>C. Brain weights</td>
<td>3.42</td>
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<td>significant</td>
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<tr>
<td>D. Hippocampal cell counts</td>
<td>2.53</td>
<td>10</td>
<td>significant</td>
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granule cells in animals from the enriched condition. Thus these data would seem to suggest a capacity for the proliferative matrix of the hippocampus to retain the ability to respond to environmental manipulation well into adult life. This evidence offers additional support for observations we made some time ago in a totally different system — the cerebellum (10). There we noted that in cases of degranulation of the IGL in infancy by up to 80% of normal base line levels through use of X-irradiation, the matrix showed some recovery potential in animals with better than 1 year survival times post irradiation.

It is conceivable that the behavioral plasticity so long observed by psychologists may well be explainable in terms of an underlying structural plasticity not only within the juvenile animal but also, albeit to a lesser degree, in the adult. Further experimentation exploring the limits of this phenomenon will be pursued.

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