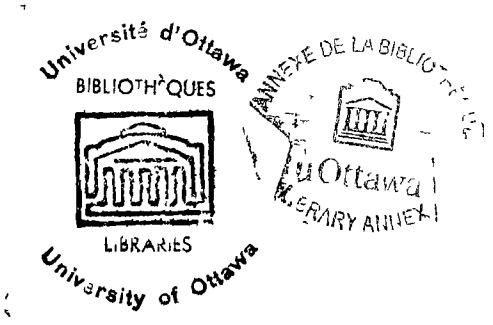
EFFECTS OF EARLY REARING IN DIFFERENTIAL ENVIRONMENTS ON THE ALBINO RAT'S PHOTIC EVOKED POTENTIALS

by Henry P. Edwards

Thesis presented to the Faculty of Psychology of the University of Ottawa as partial fulfillment of the requirements for the degree of Doctor of Philosophy



Ottawa, Canada, 1967

ACKNOWLEDGMENTS

This thesis was prepared under the supervision of Dr. William Barry, Ph.D., Associate Professor of Psychology, and of Dr. John Wyspianski, Ph.D., Associate Professor of Psychology. The writer gratefully acknowledges their advice.

The writer wishes also to thank Dr. John Ertl, Ph.D., Assistant Professor of Psychology, for his advice, and Mr. Edward Achorn for his technical assistance.

CURRICULUM STUDIORUM

Henry P. Edwards was born in Bogota, Colombia, on September 5, 1939. He received the Bachelor of Arts degree from Loyola College, Montreal, in 1961, and the Master of Arts degree in Psychology from the University of Ottawa, Ontario, in 1965.

TABLE OF CONTENTS

LIST OF TABLES

Table page

LIST OF FIGURES

INTRODUCTION

A significant relationship has been found by several investigators to exist between photic evoked potentials and psychometric intelligence measures, and in consequence the photic evoked potentials may soon assume great practical importance as a physiological measure of human intelligence.

In this context, it would be of great interest to know whether photic evoked potentials are shaped in a measurable way by the environment in which the individual has developed, for to that extent they cannot be said to be a culture-free measure of intelligence. However, a study of the effects of environment on photic evoked potentials must be longitudinal, and it is not at the moment feasible to carry out such a study on human subjects.

It is therefore the purpose of the present thesis to be a preliminary investigation of the effects of early environment on the photic evoked potentials of the albino rat. Its findings, it is hoped, will provide clues for further studies, with the eventual expectation that out of a series of studies will emerge results from which it will be possible to extrapolate with some confidence to the human realm.

The first chapter of this thesis presents a review of the literature. It reviews studies relating intelligence and measures of evoked cortical potentials in the first

section, and in the following two sections it reviews other relevant studies of the evoked cortical potentials. The latter part of the chapter reviews literature on the effects of early differential environment both upon animal behaviour and upon the structure and chemistry of the brain. The chapter ends with a statement of the experimental hypotheses.

The second chapter describes the actual procedure by means of which the hypotheses stated in the first chapter are tested experimentally. It sets forth the details of the experiment, including the statistical analysis of data.

The third and last chapter presents the numerical results of the experiment, and discusses their significance.

CHAPTER I

REVIEW OF THE LITERATURE

Several studies conducted at the University of Ottawa have demonstrated a significant relationship between intelligence test scores and photic evoked potentials in the human, thus raising the possibility of using the latter as a physiological measure of intelligence. In this context it is both of theoretical and of practical interest to explore the possible influence of early environment on the functioning of the brain as measured by PEP.[1]

Such an exploration must be a longitudinal study, and should be preceded by a series of preliminary studies on lower animals designed to assess whether the expectation that differential early environments have measurable effects on the PEP is reasonable and warrants investigation in the human. This is the first of a series of preliminary studies on the albino rat.

This chapter reviews the literature on the relationship between intelligence and evoked potentials, on evoked potentials in the rat, on factors that may contaminate the evoked potentials obtained, on the effects of differential environment on animal behaviour, and on the effects of

---

1 The abbreviation PEP will be used to denote photic evoked potentials.

differential environment on the nervous system. It ends with a statement of the hypotheses tested in the present study.

1. Evoked Potentials and Human Intelligence.

In this section, the writer wishes to review three studies carried out at the University of Ottawa.

In 1961, Ertl[2] for the first time explored the possible relationship between PEP and psychometrically measured intelligence, and obtained a highly significant correlation of -0.68 between PEP, expressed as intra-cortical delay, and intelligence scores on a sample of eleven graduate students. However, as was pointed out by Edwards[3] in a subsequent study on the relationship of electroencephalographic[4] variables and intelligence, Ertl's technique for the measurement of intra-cortical delay was difficult to cross-validate, and the results of his first study are therefore accepted with caution.

---

2 J.P. Ertl, "Intra-Cortical Delay and Intelligence", unpublished Master's thesis presented to the School of Psychology and Education of the University of Ottawa, Ontario, 1961, viii-41 p.

3 K.P. Edwards, "EEG and WAIS Intelligence in a Sample of Cultural-Familial Deficients", unpublished Master's thesis presented to the Faculty of Psychology and Education of the University of Ottawa, Ontario, 1965, vii-47 p.

4 Hereafter referred to as EEG.

In 1965, Ertl[5] described a zero crossing technique for the measurement of evoked potentials. Using this technique, Chalke and Ertl[6] studied forty-eight subjects, divided into groups of high, average and low intelligence. The authors found significant differences in the PEP of the groups. Specifically, they found significant differences in the mean latencies of the third, fourth and fifth wave components of the evoked responses, and therefore hypothesized that the delay of these components is a measure of the efficiency with which the organism processes information.

Based on Chalke and Ertl's study, Taylor[7] has recently found a significant correlation between Otis intelligence scores and PEP. Rather than using zero crossings, Taylor averaged the evoked responses of each subject directly on an enhancetron computer, displayed the averaged wave configuration on an oscilloscope, photographed it, and measured the latencies of each subject's PEP from the photographs. On a sample of eighty-four adults, he found a highly significant

---

5 J.P. Ertl, "Detection of Evoked Potentials by Zero Crossing Analysis", EEG and Clinical Neurophysiology, Vol. 18, 1965, p. 630-631.

6 F.R. Chalke and J.P. Ertl, "Evoked Potentials and Intelligence", Life Sciences, Vol. 4, 1965, p. 1319-1322.

7 N.A. Taylor, "Evoked Potential Latencies and Psychometric Intelligence", unpublished Master's thesis presented to the Faculty of Psychology and Education, University of Ottawa, Ontario, 1966, ix-76 p.

correlation of -0.68 between Otis I.Q. and the third event. He also studied other components of the evoked response, and attempted to separate speed and power variables in the intelligence test scores.

It must be pointed out that, historically, there have been many attempts to relate EEG variables and intelligence. With the exception of a study by Wyspianski,[8] they have been unsuccessful and contradictory. They are mentioned here only because they constitute the background for the studies reviewed in this section. The interested reader is referred to the comprehensive review by Voguel and Broverman,[9] and to the studies in this area by Wyspianski[10] and Edwards.[11]

2. Evoked Potentials and Cretinism in the Rat.

Two studies by Bradley and co-authors on cretinized rats are reviewed here because they show that one condition

---

8 J.O. Wyspianski, "Brain Wave Amplitude and Creative Thinking", unpublished doctoral thesis presented to the School of Psychology and Education of the University of Ottawa, Ontario, 1963, viii-105 p.

9 W. Voguel and D.M. Broverman, "Relationship Between EEG and Test Intelligence: A Critical Review", Psychological Bulletin, Vol. 62, 1964, p. 132-144.

10 Wyspianski, Op. Cit., viii-108 p.

11 Edwards, Op. Cit., vii-47 p.

which is known to be related to behavioural inefficiency gives rise to lengthening of evoked potential latency, in agreement with the results obtained on human beings as discussed in the preceding section. Secondly, these studies show that it is possible to obtain a reproducible evoked response from the laboratory rat, although the stimulus used was not photic.

In 1961, Bradley et al.[12] studied the recruiting response of thyroidectomized and control rats at twenty-four to twenty-six days of age. They found that rats which had been thyroidectomized at birth showed an increase in the latency and duration of the surface negative component of the recruiting response, which was recorded from the exposed cortex, during anesthesia, and in response to electrical stimulation of the thalamus. The authors found that the latency changes following thyroidectomy were reversible upon administration of thyroid hormone, and therefore probably reflect metabolic changes which produce an alteration in the transmitting properties of the synapses, rather than structural aberrations in the development of the nervous system.

---

12 P.B. Bradley, J.T. Mayrs, A. Glass and R.W. Heath, "The Maturational and Metabolic Consequences of Neonatal Thyroidectomy Upon the Recruiting Response in the Rat", EEG and Clinical Neurophysiology, Vol. 13, 1961, p. 577-586.

In a more recent study published in 1964, Bradley et al.[13] replicated and extended their first study. As before, they found that the cortical recruiting response to electrical stimulation of the nucleus mediodorsalis of the thalamus was of longer latency in the cretinous rats than in the control rats. A second finding was that the amplitude of the recruiting response was smaller in the cretinous rats than in the control rats.

3. Evoked Potentials and Possible Contaminants.

It is the purpose of this section to review studies which deal with variables that could, if ignored, bias the results of the present investigation. The variables considered will be arousal, the pupillary reflex, and the myogenic origin of evoked potentials.

The possible effects of different states of arousal on the evoked potentials were studied in 1962 by Schwartz and Shagass.[14] The authors studied different levels of arousal in cats. When studying somatosensory potentials, they

---

13 P.B. Bradley, J.T. Eayrs, and N.M. Richards, "Factors Influencing Potentials in Normal and Cretinous Rats", EEG and Clinical Neurophysiology, Vol. 17, 1964, p. 303-313.

14 M. Schwartz and C. Shagass, "Effects of Different States of Alertness on Somatosensory and Auditory Recovery Cycles", EEG and Clinical Neurophysiology, Vol. 14, 1962, p. 11-20.

found a decrease in amplitude with increasing arousal. No clear conclusions were drawn in the case of auditory evoked potentials, as amplitudes now seemed to increase in some animals and decrease in others with increasing arousal. The authors did not report latency changes.

Frommer and Livingston[15] in 1963 studied the evoked potentials to cerebellar stimulation recorded from the motor cortex of cats in different states of arousal. Their study verified the previous finding that evoked responses tend to decrease in amplitude and duration with increasing arousal measured in terms of behavioural and EEG criteria. In addition, the authors found that in response to cerebellar stimulation a short-latency component appeared in states of high arousal which was otherwise attenuated or absent. This component has not been reported in response to sensory stimulation.

Turning to the possible effects of pupillary reflexes on PEP, the writer wishes to review three relevant studies.

The initial study on this topic, published by Fernandez-Guardiola et al.[16] in 1961, concluded that

---

15 G.P. Frommer and R.B. Livingston, "Arousal Effects on Evoked Activity in a 'Nonsensory' System", Science, Vol. 139, No. 3554, 1963, p. 502-504.

16 A. Fernandez-Guardiola, E. Roldan R., M.L. Fanjul and C. Castells, "Role of the Pupillary Mechanism in the Process of Habituation of the Visual Pathways", EEG and Clinical Neurophysiology, Vol. 13, 1961, p. 564-576.

habituation of the PEP during repetitive stimulation may be largely inhibited through atropinization of the pupillary muscles, although reticular activation acting on the lateral geniculate bodies and visual cortex may be another factor in habituation to photic stimulation.

A more recent study by Steinberg[17] which controlled stimuls intensity was unable to demonstrate habituation effects in cats whose pupillary muscles had been immobilised with hyoscine hydrobromide. In this study, the author also studied the effects of different arousal states on the PEP, and found that, although arousal states significantly affected amplitude, latency was only affected by extreme variations in arousal. In such cases, increased arousal was accompanied by a shortening of latencies in the early components of the PEP. The author offers this as evidence for a facilitatory effect of the reticular activating system on transmission through the primary visual pathway.

A third study on the role of pupillary mechanisms on the habituation of the PEP was published in 1965 by Bergamini et al.[18] who studied human subjects with congenital aniridia,

---

17 R.H. Steinberg, "Alterations of Averaged Photic Evoked Potentials in Cat Visual Cortex During Repetitive Stimulation", EEG and Clinical Neurophysiology, Vol. 18, 1965, p. 378-391.

18 L. Bergamini, B. Bergamasco, A.M. Mombelli and G. Gandiglio, "Visual Evoked Potentials in Subjects with Congenital Aniridia", EEG and Clinical Neurophysiology, Vol. 19, 1965, p. 394-397.

a pathological condition one of whose characteristics is absence of pupillo-motor muscles. It was found that these subjects exhibited no diminution in amplitude nor change in morphology of their PEP during repetitive stimulation at the rate of two per second for as long as thirty minutes.

A number of studies reviewed to this point use amplitude as their dependent variable. For this reason, the writer has decided to include here mention of a recent publication by Ertl,[19] which indicates that changes in the amplitude of the evoked potentials under different experimental conditions are determined largely by the synchrony of the evoked responses to repetitive stimulation. The author goes on to state that this observation may have important implications for the interpretation of the many studies which use amplitude as dependent variable. It is suggested in this article that observed amplitude changes in such studies may simply reflect changes in the synchrony of the responses to repetitive stimulation, so that decreases in amplitude mean less synchrony. This publication does not suggest, however, that amplitude changes need be associated with systematic increases or decreases in latency.

There remain to be considered in this section two studies which claim that evoked responses from extra-cranial

---

19 J.P. Ertl, "Evoked Potential Recovery from Tape Recorded Zero Crossings of the EEG", EEG and Clinical Neurophysiology, Vol. 22, 1967, p. 367-368.

sites are myogenic, and two articles which conclusively refute this possibility.

Bickford et al.,[20] in a 1964 publication, reported a large, constant response to auditory stimulation, which could be recorded at the inion and was increased by tension in the neck muscles or abolished by relaxation of these muscles. This response was almost completely suppressed by partial curarization, and the authors therefore concluded that it was of muscular origin. It is the authors' conclusion that much of the evoked activity recorded from the surface of the scalp arises, not in the brain, but in the nearby musculature.

In agreement with the above, Prichard et al.[21] reported large muscle artifacts when attempting to record auditory evoked responses in cats with electrodes implanted in the musculature of the head and neck. Although the muscle artifacts found were not clearly time-locked to the stimulus and were not reliably reproducible in terms either of amplitude or of latency, the authors caution against the use of extra-cranial electrodes for the purpose of recording evoked responses in animals.

---

20 R.L. Bickford, J.L. Jacobson and D.T.R. Cody, "Nature of Averaged Evoked Potentials to Sound and Other Stimuli in Man", Annals of the New York Academy of Sciences, Vol. 112, Art. I, 1964, p. 204-223.

21 J.W. Prichard, J. Chimienti and R. Galambos, "Evoked Responses from Extracranial Sites in the Cat", EEG and Clinical Neurophysiology, Vol. 18, 1965, p. 493-496.

In opposition to the findings cited above have been the results of studies by Amassian et al.[22] and by Domino and Corssen.[23] The first of these studies is really an investigation on the nature of the primary evoked response. The relevant conclusion drawn in this article states that evoked potentials recorded at the scalp, though more difficult to interpret than those recorded from the cortex directly, are neural in origin and probably reflect synaptic potentials and after-potentials in many cortical elements.

The second study is a direct answer to Bickford's[24] publication. Domino and Corssen[25] here investigate the effects of complete skeletal muscle paralysis, induced on human patients by infusion of succinylcholine, on their visually evoked responses. Their conclusion, based on recordings of evoked responses with and without muscle paralysis made at various points on the scalp including the inion, is that skeletal muscle components of visually evoked responses in normal human subjects are negligible.

---

22 V.E. Amassian, H.J. Waller, and J. Macy, Jr., "Neural Mechanism of the Primary Somatosensory Evoked Potential", Annals of the New York Academy of Sciences, Vol. 112, Art. I, 1964, p. 5-32.

23 E.F. Domino and G. Corssen, "Visually Evoked Response in Anesthetized Man with and without Induced Muscle Paralysis", Annals of the New York Academy of Sciences, Vol. 112, Art. I, 1964, p. 226-237.

24 Bickford et al., Op. Cit., p. 204-223.

25 Domino and Corssen, Op. Cit., p. 226-237.

4. Differential Environment and Behaviour.

In this section the writer wishes to review a series of studies dealing with restriction or enrichment of the early environment in which animals are brought up, and the effects of such environments on later behaviour.

The original work on differential environment and its effects on behaviour was done by Hebb,[26] whose research has given rise to a number of related studies on rats and dogs. Hebb's original study simply compared the behaviour on the Hebb-Williams Test of Animal Intelligence[27] of rats reared as pets and rats reared in the laboratory. He found that the pet rats were considerably better problem-solvers.

Significant research projects which arose from the above will now be reviewed. The finding that restricted animals are duller than control or enriched animals in tests of animal "intelligence" is common to all of them, and in reviewing each study the writer will state only the additional findings of the study.

---

26 D.O. Hebb, "The Effects of Early Experience on Problem-Solving at Maturity", The American Psychologist, Vol. 2, 1947, p. 306-307.

27 D.O. Hebb and K. Williams, "A Method of Rating Animal Intelligence", The Journal of General Psychology, Vol. 34, 1946, p. 59-65.

In 1951, Clarke et al.[28] studied the effects of differential environment on Scottish terriers raised either in small, windowless cages, or as pets from the time of weaning to the age of seven and a half months. No differences in health were reported, but the restricted animals showed freezing behaviour in unfamiliar surroundings and were inferior problem-solvers.

Hebb's original experiments[29] were replicated by Hymovitch,[30] who published his results in 1952. In this publication, the free-environment box is described as a cage measuring 6 ft. by 4 ft. by 6 in. and containing blind alleys, inclined runways, and other articles designed to give rats extensive opportunity for varied experience. The author found that rats raised in the free-environment box were superior problem-solvers to rats raised in small enclosed cages or enclosed activity wheels. Furthermore, he found that experiences between thirty and seventy-five days of age were most important, resulting behaviour patterns being seemingly irreversible. His results are interpreted in terms of development in perceptual organization.

---

28 R.S. Clarke, W. Heron, M.L. Fetherstonaugh, D.O. Forgays and D.O. Hebb, "Individual Differences in Dogs: Preliminary Report on the Effects of Early Experience", Canadian Journal of Psychology, Vol. 5, 1951, p. 150-156.

29 Hebb, Op. Cit., p. 306-307.

30 B. Hymovitch, "The Effects of Experimental Variations on Problem-Solving in the Rat", The Journal of Comparative and Physiological Psychology, Vol. 45, 1952, p. 313-321.

An extension of the preceding study was published by Forgays and Forgays[31] in 1952. The authors confirmed previous results, and found that rats brought up in a free-environment box containing playthings were slightly superior in problem-solving ability to a group brought up together in a large cage without any playthings.

In a related study, Bingham and Griffiths[32] found that groups of enriched and deprived rats differed as expected in maze-solving ability, but showed no significant differences in discrimination, emotionality, or susceptibility to sound-induced seizures. The discrimination task employed was a black-white brightness discrimination using the Lashley jumping stand.

In 1954, Thompson and Heron[33] verified and extended the findings of Clarke et al.[34] The authors in their introduction state that they consider the study of early environment in relation to behaviour as very important in that it

---

31 D.G. Forgays and J.W. Forgays, 'The Nature of the Effect of Free-Environmental Experience in the Rat", The Journal of Comparative and Physiological Psychology, Vol. 45, 1952, p. 322-328.

32 W.R. Bingham and W.J. Griffiths, "The Effect of Different Environments During Infancy on Adult Behaviour in the Rat", The Journal of Comparative and Physiological Psychology, Vol. 45, 1952, p. 307-312.

33 W.R. Thompson and W. Heron, "The Effects of Restricting Early Experience on the Problem-Solving Capacity of Dogs", Canadian Journal of Psychology, Vol. 8, 1954, p. 17-31.

34 Clarke et al., Op. Cit., p. 150-156.

may shed light on the role of environment in the development of human intelligence. Their subjects were twenty-six Scottish terriers divided into a control group treated as pets, and experimental groups raised under conditions of isolation, moderate restriction, and slight restriction. The conclusion was drawn from this study, after administering a number of behaviour tests, that restriction of early perceptual experience has a definite and fairly permanent retarding effect on dog intelligence. Among the tests employed, it is significant that a delayed-reaction test yielded very large differences between control and restricted animals, thereby supporting the hypothesis that early environmental restriction affects the development of perceptual organization.

The most recent in this group of studies on the effects of early environment was published by Woods[35] in 1959. The object of this study was to investigate the effects of subsequent free-environmental experience on animals which, due to an early restricted environment, were inferior problem-solvers. The author found that rats raised in a restricted environment to the age of sixty days and then enriched during the next ninety days showed improvement in

---

35 P.J. Woods, "The Effects of Free and Restricted Environmental Experience on Problem-Solving Behaviour in the Rat", The Journal of Comparative and Physiological Psychology, Vol. 52, 1959, p. 399-402.

their performance, but not enough to match that of control animals raised in an enriched environment throughout the study.

The writer wishes at this point to add that a thorough review of literature on the effects of early experience upon the behaviour of animals was published by Beach and Jaynes[36] in 1954. In addition to the studies quoted here, the authors review studies dealing with the effects of extreme sensory deprivation on behaviour. These studies are not considered relevant to the present investigation.

5. Environment and the Brain.

This section will review a group of studies designed to assess the possible effects of early differential environment on the chemistry of the brain, and an additional study which will serve as a partial basis for the assumption that early differential environment has a measurable effect on the *PEP*.

In 1956, Krech *et al.*[37] published a study in which they reported that rats able to maintain a probabilistic

---

36 F.A. Beach and J. Jaynes, "Effects of Early Experience Upon the Behaviour of Animals", Psychological Bulletin, Vol. 51, 1954, p. 239-263.

37 D. Krech, M.R. Rosenzweig, and E.L. Bennett, "Dimensions of Discrimination and Level of Cholinesterase Activity in the Cerebral Cortex of the Rat", The Journal of Comparative and Physiological Psychology, Vol. 49, 1956, p. 261-266.

response pattern when confronted with light and dark alleys in a maze, only one of which allowed passage, showed on autopsy a higher cholinesterase level in the brain than rats which adopted a thorough commitment to one of the stimuli.

The above study led to authors to investigate the effects of early environmental enrichment on the chemistry of the brain, specifically cholinesterase activity as an indirect measure of acetylcholine, a substance known to be involved in synaptic transmission.

Thus, a second publication by Krech et al.[38] appeared in 1960. In this study, cholinesterase activity was treated as dependent variable, on the hypothesis that exposing rats to complex experience and training would affect their cerebral cholinesterase levels. Control rats were kept in isolation, the complex environment of the experimental subjects was that described by Hymovitch,[39] and their training consisted of exploration in the Hebb-Williams mazes.[40] Upon comparison of enriched and isolated groups of rats, the former exhibited a significantly lower cortical/subcortical ratio of cholinesterase activity than the latter. The authors state that

---

38 D. Krech, M.R. Rosenzweig and E.L. Bennett, "Effects of Environmental Complexity and Training on Brain Chemistry", Journal of Comparative and Physiological Psychology, Vol. 53, 1960, p. 509-519.

39 Hymovitch, Op. Cit., p. 314.

40 Hebb and Williams, Op. Cit., p. 63-69.

their results could not be explained on the basis of nutritional differences among the groups.

The above was followed by three related publications in 1962. In the first of these, Rosenzweig et al.[41] carried out a more careful analysis of cholinesterase activity and brain weight, and found that the enriched rats differed from their littermate controls in having greater brain weight, greater amounts of subcortical cholinesterase, and a lower cortical/subcortical cholinesterase ratio.

A related study by Krech et al.[42] in 1962 verified the previous finding that the enriched rats were superior problem-solvers, using the Krech hypothesis apparatus.[43] This apparatus consists of four successive units of two-point discrimination boxes. When the behavioural scores thus obtained were related to brain weight and cortical/subcortical cholinesterase ratio, a significant correlation was obtained for the enriched rats. However, the authors were unable to obtain significant differences between enriched and isolated

---

41 M.R. Rosenzweig, D. Krech, E.L. Bennett and C. Diamond, "Effects of Environmental Complexity and Training on Brain Chemistry and Anatomy: A Replication and Extension", Journal of Comparative and Physiological Psychology, Vol. 55, 1962, p. 429-437.

42 D. Krech, M.R. Rosenzweig and E.L. Bennett, "Relations Between Brain Chemistry and Problem-Solving Behaviour Among Rats in Enriched and Impoverished Environments", Journal of Comparative and Physiological Psychology, Vol. 55, 1962, p. 801-807.

43 Krech et al., 1956, Op. Cit., p. 263.

groups in brain measures taken at autopsy presumably because the discrimination testing permitted improvement in the brains of the deprived rats.

The last study published in 1962 by Rosenzweig et al.[44] compares a group of rats raised in an enriched environment from the time of weaning with an isolated control group and with a third group raised in isolation for thirty-three days, then in an enriched environment for the rest of the experiment, which lasted to the age of 105 days. It was found that the group which had been isolated and then enriched yielded intermediate values for tissue weight and cholinesterase, thus supporting the view that later exposure to environmental complexity can make up for the negative results of early isolation.

Since the publication of the preceding studies, two additional articles on the topic of environmental complexity and brain measures have been published by the same group of authors. Rosenzweig et al.[45] have carried out an investigation beginning with adult rats, and have obtained the same

---

44 M.R. Rosenzweig, D. Krech, E.L. Bennett and J.F. Zolman, "Variation in Environmental Complexity and Brain Measures", Journal of Comparative and Physiological Psychology, Vol. 55, 1962, p. 1092-1095.

45 M.R. Rosenzweig, E.L. Bennett and D. Krech, "Cerebral Effects of Environmental Complexity and Training Among Adult Rats", Journal of Comparative and Physiological Psychology, Vol. 57, 1964, p. 438-439.

results in terms of tissue weight and cholinesterase activity that had previously been obtained starting at the time of weaning. Their findings in this study appear to oppose the idea of a critical period early in the animal's life when differential environment is most influential. This study, which lasted eighty days, started when the rats were 105 days of age.

Finally, an investigation of the reliability of the findings discussed in this section has been conducted by Bennett et al.[46] The authors report that the chemical and anatomical effects of differential environment are highly repeatable, and that of all cortical regions the visual area shows the largest differences when comparing enriched and isolated groups of rats.

Having reviewed literature on the effects of differential environment on brain weight and chemistry, the writer now wishes to consider a 1964 publication by Melzak and Burns[47] which discusses possible neural mechanisms underlying

---

[46] E.L. Bennett, D. Krech and M.R. Rosenzweig, "Reliability and Regional Specificity of Cerebral Effects of Environmental Complexity and Training", Journal of Comparative and Physiological Psychology, Vol. 57, 1964, p. 440-441.

[47] R. Melzak and S.K. Burns, "Neuropsychological Effects of Early Sensory Restriction", First Conference on Neurobiology; Feedback Systems Controlling Nervous Activity, Sociedad Mexicana de Ciencias Fisiologicas, Mexico, 1964, p. 287-307.

the behavioural abnormalities of animals raised in very restricted environments.

The authors begin by stating that Scottish terriers raised in isolation become highly excitable, fail to attend selectively to environmental stimuli, often fail to respond to noxious stimulation, and have difficulty in performing cognitive tasks. Then, they look for a neural model which might explain such behaviour. They rule out neuronal degeneration as extremely unlikely, and hypothesize a process in which, as a result of prolonged restriction, there is inadequate filtering of sensory input based on previous memories of relevant stimuli, and consequently the total input bombarding the central nervous system produces excessive cortical arousal and prevents discrimination and adaptive response. It is proposed in this study that, in the normal animal, fast-conducting afferents, upon reaching the cortex, activate memory traces which in turn exert a dynamic control over slower afferent impulses. In this way, irrelevant information may be filtered out and selective attention permitted. The article concludes by suggesting that the EEG of restricted animals shows greater shifts to high frequency in the presence of a novel stimulus than that of control animals.

6. Cholinergic Synapses and Evoked Potentials.

The writer wishes at this point to link the studies reviewed concerning evoked potentials with those assessing the effects of differential environment on cholinesterase activity of the brain by summarizing here the results of an article by Szerb[46] which attempts to relate evoked potentials and cholinergic synapses.

In this project, the author hypothesizes that the later components of the evoked potential should reflect the activity of cholinergic synapses, and to test this studies the average evoked responses of cats to stimulation by shock on the forepaw while under the influence of various drugs known to have an effect on acetylcholine.

The results of this study reveal, first of all, that atropine decreases the amplitude of the later part of the evoked potentials, and secondly that cholinesterase inhibitors in small quantities increase the amplitude of the later part of the evoked potentials. This suggests to the author that cholinergic synaptic activity participates in the production of the later components of the evoked responses, but he does not provide a statistical analysis of data.

---

[46] J.C. Szerb, "Averaged Evoked Potentials and Cholinergic Synapses in the Somatosensory Cortex of the Cat", EEG and Clinical Neurophysiology, Vol. 18, 1965, p. 140-146.

The author proposes that the first component of the evoked response is due to the arrival of impulses from the subcortical structures to the deeper layers of the cortex, while later components are due to the spread of excitation to the more superficial layers, through cholinergic synapses.

7. Summary and Hypotheses.

This chapter has reviewed all major studies designed to investigate the relationship between evoked cortical potentials and behaviour, the variables which may bias the interpretation of the evoked potentials, differential environment and behaviour, differential environment and the brain, and the relationship between evoked potentials and cholinergic synaptic activity. The writer's purposes in covering these topics have been to show the reasons for the present study, to review facts relevant to the dependent and independent variables of the study, and to develop experimental hypotheses in terms of the literature reviewed.

The possible effects of differential environment on the evoked responses to photic stimulation are considered a topic worthy of investigation in view of the successful studies which have recently related human intelligence and PEP. Furthermore, the finding that cretinism in the rat is associated with lengthening of evoked potential latencies encourages the writer in hypothesizing that rats made

inferior through environmental impoverishment will show a similar lengthening of PEP latency.

The literature reviewed under the heading of evoked potentials and possible contaminants will be used in subsequent chapters when discussing the design of the experiment.

A series of studies dealing with the effects of early differential environment on behaviour has been reviewed at length in order to show their widespread agreement that animals brought up in enriched and isolated environments show definite and lasting differences in problem-solving ability, the enriched animals being superior problem-solvers.

The last two sections then review studies which link differential environments to brain functioning, and one study which attempts to link brain functioning in terms of cholinergic synaptic activity to evoked potentials. In view of these studies, the major hypothesis of the present thesis is that if animals raised in an impoverished environment are compared to animals brought up in an enriched environment, the two groups should show measurable differences in their PEP.

In its null form, the major hypothesis reads:

> When a group of rats raised in an impoverished environment is compared to a group raised in an enriched environment, no significant differences develop in the photic evoked potentials of the groups during the first three months of life.

Although differences in problem-solving ability of enriched and impoverished animals are well established, so that it is not considered essential to verify these in the present study, nonetheless the secondary hypothesis is advanced that enriched and impoverished groups of rats should differ in their performance on a brightness discrimination task. If the writer should be able to reject this hypothesis in its null form, this would lend support to the interpretation of differences between impoverished and enriched animals as attributable to different levels of perceptual organization. The writer feels that a discrimination test should be given because the studies reviewed have reported conflicting findings when discrimination tasks were administered.

In its null form the secondary hypothesis reads:

> When a group of rats raised in an impoverished environment is compared to a group raised in an enriched environment, there are no significant differences in the ability of the groups to solve a brightness discrimination problem at the age of three months.

The chapters that follow present a discussion of the tools, methods, and results of the present study.

CHAPTER II

EXPERIMENTAL DESIGN

This chapter describes in detail the research design whereby the experimental hypotheses stated in the preceding chapter are tested. The first two sections describe the sample and instruments used. The third and fourth sections set forth the experimental procedure and the statistics used in the analysis of data.

1. The Sample.

As stated in the first chapter, it was decided to carry out this preliminary investigation on lower animals, because a longitudinal study of this type is not feasible on human subjects at present. Consequently, a sample of Sprague-Dawley albino rats was chosen, both because they have been the species used in many previous studies and because they are less nervous and easier to handle than other varieties of rats.

More specifically, the sample chosen consisted of sixteen male rats belonging to four litters born within a period of twenty-four hours. The subjects were obtained immediately after weaning, at the age of twenty-one days.

2. The Tools.

In this section, the tools employed in obtaining the evoked responses to photic stimulation will be described first. Following this, the apparatus used for a brightness discrimination test, as required by the secondary hypothesis, will be described.

For the purposes of PER recording, all subjects were restrained in an E & M[1] transparent rat holder, and their head was immobilized with adhesive tape. Grass needle electrodes were then placed in the scalp, and the electrode leads were connected to a Tektronix Differential Amplifier Type 2A61, which contained a filter with an attenuation slope of 6 db per octave roll-off, set to filter responses 3 db down at 6 cps and 60 cps. This amplifier led to a second filter made in the laboratory as an active filter with an attenuation slope of 24 db per octave roll-off, set 3 db down at 100 cps.

This filter was in turn connected to the channel 1 input of a four-channel FM tape recorder, and by way of the tape recorder's output was connected to an oscilloscope and to a computer of average transients. The tape recorder, oscilloscope and averaging computer are described more specifically in the paragraphs that follow.

---

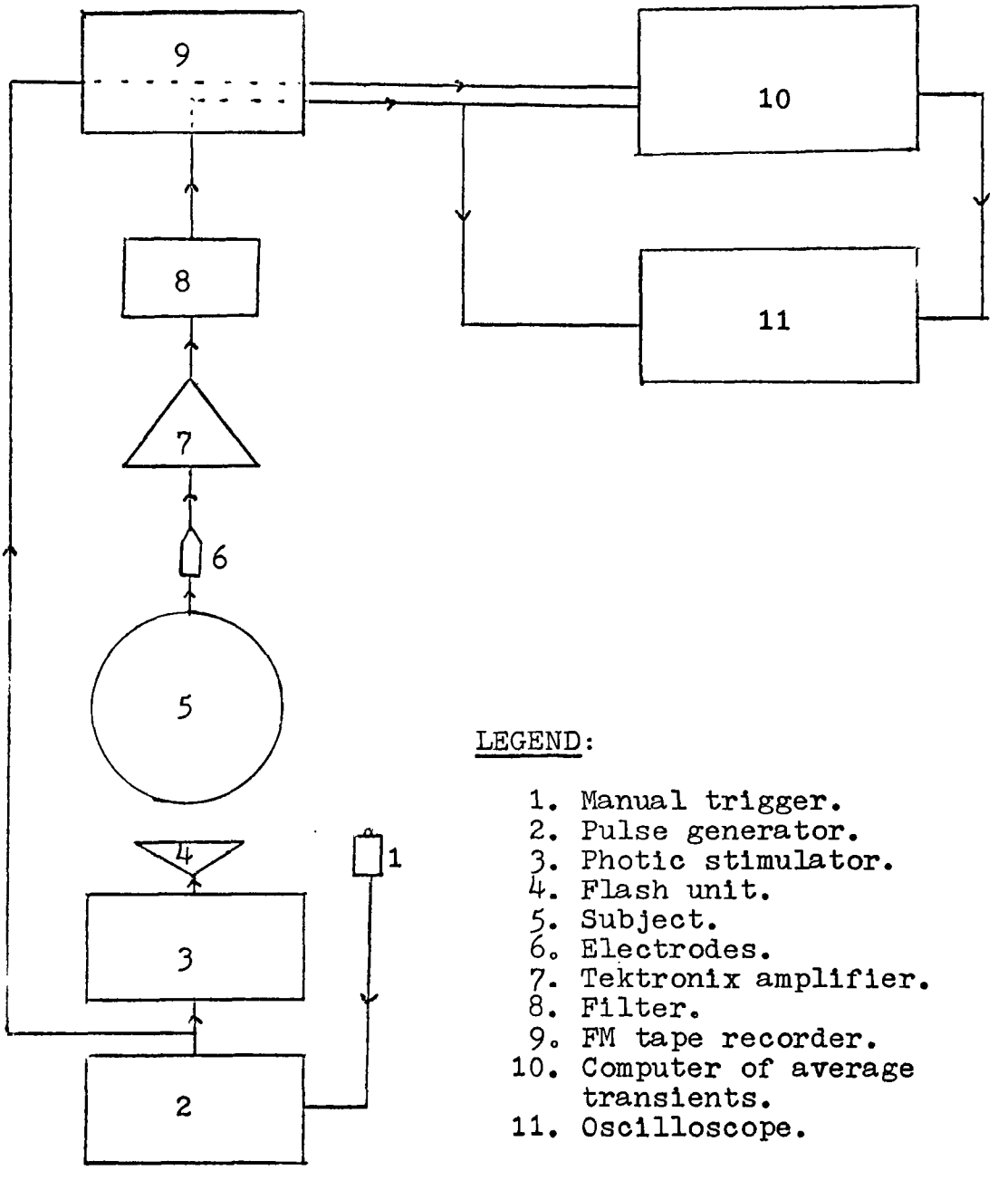
1 E & M denotes the manufacturer.

A Thermionic Products four-channel FM tape recorder Model T 3000 was used. Electrical activity of the brain was recorded on one channel, and the time of each photic stimulus was recorded on another. The recorder was set at a speed of 1-7/8, and Ampex magnetic tape was employed for the storage of data.

The data was averaged on a Nuclear Data 1024 Enhancetron computer of average transients, and displayed on a Tektronix Dual-Beam Oscilloscope Type RM565, equipped with two differential amplifiers type 2A63. The oscilloscope was also employed for monitoring the brain waves as they were recorded.

In order to obtain the PEP, photic stimuli were given by means of a Hilton Kohoen photic stimulator triggered manually with a Rutherford Model B14-R pulse generator, which was also connected to the tape recorder and to the averaging computer.

A diagramatic representation of the equipment described in the preceding section is given in Figure 1. Having now described the equipment employed in obtaining and recording each subject's PEP, the next section is devoted to the brightness discrimination apparatus used in the present investigation.



LEGEND:

1. Manual trigger.
2. Pulse generator.
3. Photic stimulator.
4. Flash unit.
5. Subject.
6. Electrodes.
7. Tektronix amplifier.
8. Filter.
9. FM tape recorder.
10. Computer of average transients.
11. Oscilloscope.

Figure 1.- Equipment Layout for the Recording of Photic Evoked Potentials on the Albino Rat.

Ability to solve a brightness discrimination problem was tested using an adaptation of the discrimination box first described by Thompson and Bryant[2] in 1955, consisting of a starting box, a choice chamber and a goal box, the last two inter-connecting only by two openings which may be covered with two windows of different brightness and left locked or unlocked. The subject's task in each trial is to reach the goal box in order to avoid electric shock.

The discrimination box used consisted of a starting box 9 in. long, 7 in. wide and 13 in. high. A sliding gate separated it from the V-shaped choice chamber which was 16 in. long, 11 in. wide at its widest end, and 13 in. high. The choice chamber was separated from the goal box by a wall 13 in. high containing two symmetrical 4 in. square windows, either of which could be locked. Between the windows, a division protruded 4 inches into the choice chamber. The goal box was 15 in. long, 11 in. wide and 13 in. high.

The apparatus was constructed of heavy cardboard mounted on a wooden base, and its entire inside, except for grids and windows, was painted with medium gray enamel.

---

2 R. Thompson and H. Bryant, "Memory as Activity of the Relevant Receptor", Psychological Reports, Vol. 1, 1955, p. 393-400.

The floor of both the starting box and the choice chamber was covered with a grid made from alpha wire strips 1/5 in. apart. The grid could be electrified at the will of the investigator by means of a Variac auto-transformer so as to deliver a 50 volt, 5 amp. shock. The grid section next to the windows could be activated independently of the grid covering the rest of the choice chamber. The goal box had a wooden floor.

3. The Experiment.

Stated in outline form, this experiment consisted in dividing a sample of albino rats into two groups, one of which was raised in an enriched environment and the other in an impoverished environment. The PEP of each subject was measured three times, the occasions being approximately a month apart. After the groups had been thus separated for eighty days, a discrimination task was administered to all subjects. Both the PEP and discrimination scores of the groups were compared by means of t tests. The paragraphs that follow will cover each of these steps in detail.

To begin, it must be made clear what the writer means by enriched and isolated or impoverished (in the present study the two terms are treated as synonyms) environments. An enriched environment is defined here as a large wooden cage, measuring 60 in. by 30 in. by 12 in., lined

completely on the inside with wire screen, covered on top only by a wire screen lid, filled with wood shavings, inhabited by a group of eight rats, and containing a variety of playthings. In its essentials, this corresponds to the free-environment box described by Hymovitch.[3]

An impoverished environment is defined by the writer as a small metal cage, measuring 12 in. by 7½ in. by 6½ in., so situated as to allow adequate light and air while providing for its single inhabitant no opportunity to view its surroundings except briefly whenever the cage is cleaned. The cage floor is lined with wood shavings. This fulfills the requirements for environmental impoverishment of most authors reviewed in the first chapter, including Krech et al.[4]

The first step in the present investigation consisted in splitting four litters of twenty-one-day old male albino rats of the Sprague-Dawley strain into enriched and impoverished groups according to the split-litter technique whereby equal numbers from each litter were assigned to each of the two environmental conditions. In this way, two groups

---

3 B. Hymovitch, "The Effects of Experimental Variations on Problem-Solving in the Rat", The Journal of Comparative and Physiological Psychology, Vol. 45, 1952, p. 314.

4 D. Krech, M.R. Rosenzweig and E.L. Bennett, "Effects of Environmental Complexity and Training on Brain Chemistry", The Journal of Comparative and Physiological Psychology, Vol. 53, 1960, p. 510.

of eight rats each were obtained, and the experiment was carried out on enriched and impoverished littermates.

An adequate supply of Master Laboratory Cubes and water was provided for all subjects throughout the experiment, based on a self-feeding schedule. All cages were thoroughly cleaned once a week. The enriched group was provided with the following playthings: an activity wheel, a topless metallic laboratory cage, several tunnels, an inverted plastic flower pot, several wooden obstacles, a brightly-colored plastic clown, a mirror and a toy turtle. In addition, despite inconclusive findings on the effects of fondling as reported by Weininger[5] and by Denenberg and Morton,[6] an effort was made to handle all the enriched rats everyday. Half of the playthings described above was placed in the enriched environment every second week and left there for a week.

The writer wishes to note, in closing his discussion of the experimental environments, that at the time of writing all sixteen rats are still living in the conditions described above. They are all in excellent health, and as a matter of

---

5 O. Weininger, "The Effects of Early Experience on Behaviour and Growth Characteristics", The Journal of Comparative and Physiological Psychology, Vol. 49, 1956, p. 1-9.

6 V.H. Denenberg and J.R.C. Morton, "Effects of Preweaning and Postweaning Manipulations Upon Problem-Solving Behaviour", The Journal of Comparative and Physiological Psychology, Vol. 55, 1962, p. 1096-1098.

fact each impoverished rat is a little heavier and bigger than its enriched littermate. This is in agreement with the results of previous studies which report that animals raised in isolation are as healthy as enriched animals.

Having discussed differential environment at some length, the writer now wishes to note that each subject's PEP was recorded three times at monthly intervals. The first record was obtained two weeks after the experimental groups had been formed in the fashion described in the preceding paragraphs. No PEP was recorded before the formation of groups, and it is assumed that since a split-litter technique was used, the PEP of the two groups did not differ significantly at the start of the experiment. The following paragraphs describe in detail the procedure whereby each subject's PEP was obtained.

The first step consisted in placing the rat in a transparent restraining apparatus which prevented escape while allowing it to breathe comfortably and see the photic stimulator. After an initial period of violent struggling lasting about five minutes, the rat was usually quiet enough to permit placement of two needle electrodes in its scalp and a reference electrode in its tail.

According to publications by Kimura[7] and by Pickenhain and Klingberg,[8] electrodes placed two to four mm. from the midline and five to six mm. posterior to the coronal suture yield the best evoked potential records from the rat's striate cortex. Since the present study did not implant electrodes surgically, such accuracy was not attainable. The placement suggested above was approximated, however, by placing the two head electrodes two mm. apart, on a sagittal plane half-way between the midline and the base of the right ear lobe, the posterior electrode being two to five mm. anterior to the inion depending on the size of the rat at the time.

Once the electrodes were securely in place, the rat was placed inside a small copper-shielded room facing the photic stimulator, which was placed six inches away. The room was then darkened, and the PEP to 120 light flashes triggered manually at the approximate rate of one every two seconds was recorded using the equipment described in the preceding section.

---

7 D. Kimura, "Multiple Response of the Visual Cortex of the Rat to Photic Stimulation", EEG and Clinical Neurophysiology, Vol. 14, 1962, p. 115-122.

8 L. Pickenhain and F. Klingberg, "Behavioural and EEG Changes During Avoidance Conditioning to Light Flashes in the Rat", EEG and Clinical Neurophysiology, Vol. 18, 1965, p. 464-476.

While recording, the subject's EEG was constantly monitored in order to avoid stimulating while the subject was struggling. If a subject tended to move excessively, the procedure was discontinued until it quieted and then repeated. In this way, myogenic contaminants were kept to a minimum. The system of filters previously described was thought necessary to eliminate minor movements which could not be avoided with anesthetizing all subjects and thereby introducing new artifacts. The writer's decision to obtained PEP from unanesthetized rats is based partly on his desire to avoid the unpredictable effects of anesthetics and partly on the articles by Amassian et al.[9] and by Domino and Corssen[10] showing that evoked responses recorded extra-cranially are not myogenic in origin.

In order to ensure that no record obtained was an artifact, whenever a subject's PEP seemed unclear a second set of stimuli was administered and the second PEP thus obtained was compared to the first. Only events found in both and of equal latencies in both were accepted. From such

---

9 V.E. Amassian, M.J. Waller and J. Macy, Jr., "Neuronal Mechanism of the Primary Somatosensory Evoked Potential", Annals of the New York Academy of Sciences, Vol. 112, Art. I, 1964, p. 29-31.

10 E.F. Domino and G. Corssen, "Visually Evoked Response in Anesthetized Man With and Without Induced Muscle Paralysis", Annals of the New York Academy of Sciences, Vol. 112, Art. I, 1964, p. 236.

cases, the writer concludes that the records obtained in the present study are highly repeatable, and that any myogenic artifacts are identifiable because they are not time-locked to the photic stimuli. It may be added here that eye-blinks as myogenic contaminants were ruled out by observation of a number of subjects, none of whom tended to blink in time to stimulation.

The first chapter discussed the possibility that not only muscle artifacts, but also arousal and pupillary reflexes could contaminate the PEP. As regards the latter, it was not considered necessary to atropinize the eyes prior to stimulation because the albino rat lacks pigmentation of the iris and thus resembles the condition studied by Bergamini et al.[11] who found no habituation effects in their study.

The possibility that enriched and impoverished subjects may have become differentially aroused during the recording session is not as easily dismissed. Therefore, an electrocardiogram of each subject was obtained immediately after the photic stimulation period to serve as a measure of autonomic arousal. Then, group differences in heart rate were

---

11 L. Bergamini, B. Bergamasco, A.M. Mombelli and G. Gandiglio, "Visual Evoked Potentials in Subjects with Congenital Aniridia", EEG and Clinical Neurophysiology, Vol. 19, 1965, p. 394.

assessed by means of a t test[12] of significance. The values obtained for the three recording sessions were t = 1.69, t = 1.08 and t = 1.12. None of these values is significant even at the 0.05 level, and therefore no differential arousal of the two groups is demonstrable through the analysis of heart rate. Since Schwartz and Shagass[13] report evoked potential changes only in relation to marked deviations in arousal, the writer considers that group arousal differences in the present study are not large enough to have acted as contaminants.

It was stated in the preceding section that the evoked responses were averaged in a computer of average transients. It may now be added that the computer was set to sweep for 250 milliseconds following each stimulus, and to add algebraically the 120 sweeps given to each subject. Input into the computer was set at a maximum of one volt. Its output was displayed on an oscilloscope, and was photographed with a Polaroid camera for subsequent analysis of each subject's PEP. On the photograph, the total width of the record represented 250 milliseconds. The latencies of

---

12 L.T. Dayhaw, Manuel de Statistique, Universite d'Ottawa, Ottawa, 1963, p. 364.

13 M. Schwartz and C. Shagass, "Effects of Different States of Alertness on Somatosensory and Auditory Recovery Cycles", EEG and Clinical Neurophysiology, Vol. 14, 1962, p. 14-20.

all events could therefore be estimated as fractions of this, against a grid representing 5 milliseconds per division.

Immediately after each photograph was obtained, it was labelled on the back for identification with the subject's group and number, and the exact date. No markings were placed on the front at the time. When the PEP of all subjects had been thus recorded on each occasion, the photographs were shuffled and stacked, and were then numbered on the front according to their position in the stack. During subsequent analysis they were identified by this number only, and the information at the back was used only when the PEP data was ready for statistical analysis.

At first, it was the writer's intention to number the various events according to latency, and compare the two groups according to the latencies of corresponding events. This, however, proved not to be feasible, as the writer could arrive at no truly objective criteria in terms of which to identify all events in all photographs.

He decided, therefore, based on the hypothesis of Melzak and Burns [14] that it is the slower afferents which convey perceptually meaningful information to the nervous

---

14 R. Melzak and S.K. Burns, "Neuropsychological Effects of Early Sensory Restriction", First Conference on Neurobiology: Feedback Systems Controlling Nervous Activity, Sociedad Mexicana de Ciencias Fisiologicas, Mexico, 1964, p. 237.

system, and on the findings of Szerb[15] that only the later components of the evoked potential reflect the activity of cholinergic synapses, coupled with the findings of studies on environment and brain chemistry that groups raised in different environments differ in cholinesterase levels, to investigate only events occurring later than twenty milliseconds after stimulation. It was the writer's further assumption that a meaningful event should be of high amplitude and well-defined relative to other events in the same record, and therefore he decided to measure the latency of the event of greatest amplitude and of latency greater than twenty milliseconds. An upper limit of seventy-five milliseconds was placed, because beyond this latency it was not found possible to reproduce events reliably. This conclusion was reached as the result of a pilot study on five rats who were not among the experimental subjects. Figure 2 shows the PEP records of two subjects, and the latencies obtained as described in this paragraph.

As described here, a PEP latency was obtained for each subject on each of three occasions. Based on this data, the statistical analysis for group differences was carried out. In this section, there remains now to discuss

---

15 J.C. Szerb, "Averaged Evoked Potentials and Cholinergic Synapses in the Somatosensory Cortex of the Cat", EEG and Clinical Neurophysiology, Vol. 18, 1965, p. 145.

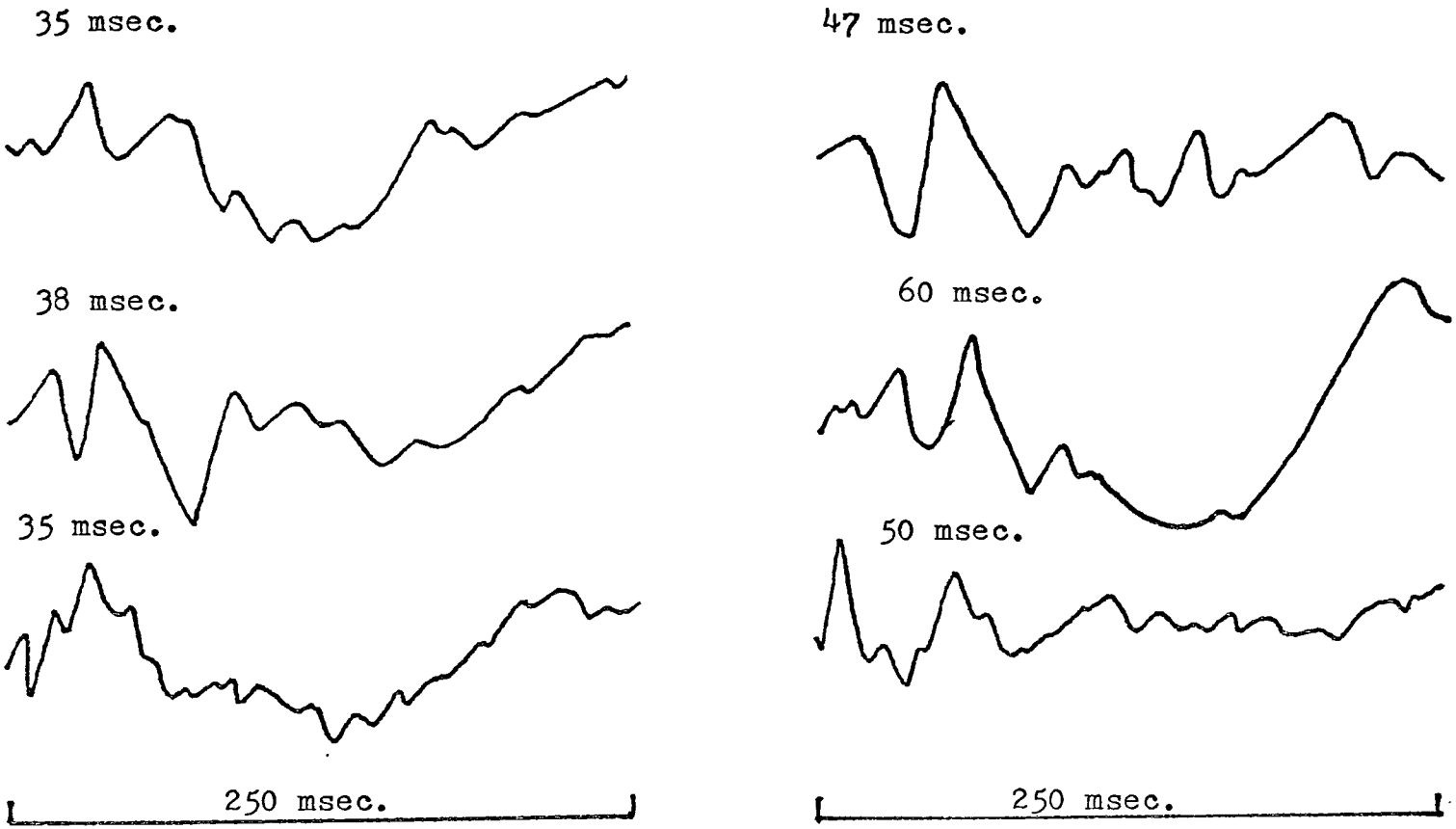


Figure 2.- Photic Evoked Potentials Obtained from Two Albino Rats, One Reared in an Enriched Environment and the Other in an Impoverished Environment, on Three Occasions at Monthly Intervals, Beginning Two Weeks After the Establishment of Differential Environments.

the discrimination task which was given to all subjects after all PEP data had been obtained.

The first step was to construct a discrimination test according to the specifications given in the preceding section. Following its construction, two days of pretraining were given. For the purposes both of pretraining and of testing on a black-white brightness discrimination, each group of subjects was divided in two, and for convenience half of all the subjects was tested to criterion before the pretraining on the other half was begun. As will be seen later, the writer decided to do a separate statistical analysis on each of the sub-groups thus formed, because the wire used for the grids was changed in favour of a stronger wire following completion of testing on the first sub-group.

The first day of pretraining consisted in teaching each subject to go from starting box to goal box in order to avoid shock. The subject was placed in the starting box and the barrier separating it from the choice chamber was lifted. If the subject failed to leave the starting box within five seconds it was given a brief shock. Twenty seconds later, if the subject had not crossed from choice chamber to goal box through the openings separating the two, which on this day were not covered in any way, it was again shocked. Each trial ended when the subject reached the goal

box. All subjects were trained on the first day to a criterion of three consecutive arrivals at the goal box without the aid of shock.

The second day of pretraining was similar to the first except that now the openings between choice chamber and goal box were covered with two cardboard windows painted with vertical black and white stripes. Both windows were unlocked, and the subject's task was now to push either one open in order to gain access to the goal box. No attempt was made to eliminate position habits. As before, all subjects were trained to a criterion of three consecutive arrivals at the goal box without the aid of shock.

On the third day, testing on a black-white discrimination began. Now, the openings between choice chamber and goal box were covered one with a white cardboard window and the other with a black cardboard window. The positions of the two cards were alternated according to a prearranged random sequence.[16] The white card constituted the positive stimulus. It was never locked, and the grid immediately in front of it was never used to shock the subject. The black card was always locked, and whenever a subject either touched it or stood next to it for more than two seconds, it was shocked.

---

16 Reference Data for Radio Engineers, International Telephone and Telegraph Corporation, 1956, p. 1114.

During the testing period, the exact procedure for administering each trial was as follows: The subject was placed in the starting box, and the gate separating it from the choice chamber was lifted. Failure to leave the starting box within five seconds was followed by a brief shock. Failure to choose one of the two windows within twenty seconds was followed by a brief series of shocks, which was repeated twenty seconds later if necessary. If the subject chose the black window, it was shocked and the trial was marked incorrect. If it chose the white window it was of course allowed access to the goal box without shock, and the trial was marked correct. The intertrial interval was kept constant at forty-five seconds.

Each subject was given eight trials daily, until it reached a criterion of six consecutive correct trials in a single day. When criterion performance was attained, the score was marked as the total number of trials required by the subject. The scores thus obtained were analyzed according to the statistics described in the last section of this chapter.

4. Analysis of Data.

The procedures whereby the raw data of this study was analyzed have already been described. It suffices in this section to state the independent and dependent variables,

and then to recapitulate the aforementioned procedures briefly.

The independent variable in the present study consists of the enriched and impoverished environments into which the subjects were divided at the start of the experiment, and in which they were raised. No control environment was considered necessary, because the writer is interested in differences between the two groups only, and not in their relationship to rats brought up in a "normal" environment.

The principle dependent variable studied in the present investigation is the PEP, and more specifically the latency of that component between twenty and seventy-five milliseconds after stimulation which exhibits the greatest amplitude in each PEP photograph of each subject. This data is expressed in milliseconds.

A second dependent variable is each subject's score on a brightness discrimination, expressed as the total number of trials required to reach a criterion performance of six consecutive correct trials in a single day.

b. Statistical Analysis.

In keeping with the purpose of the present investigation, which was simply to look for significant differences between two groups of rats in their PEP on three occasions

and in their discriminatory ability on one occasion, it was decided that all these differences could be validly assessed by means of a simple t test.

The two groups were formed at the start of the experiment using the split-litter technique, and therefore cannot be assumed to be independent of each other on the variables measured. The following t test formula, as suggested by Dayhaw,[17] is therefore employed:

$$t = \frac{M_D}{\sqrt{\frac{\sum(D-M_D)^2}{N(N-2)}}}$$

It has been the aim of this chapter to describe the sample and tools used in the present study, and to discuss in detail the experimental procedures and analysis of data. The results of the experiment will be presented and discussed in the following chapter.

---

17 Dayhaw, Op. Cit., p. 364.

CHAPTER III

PRESENTATION AND DISCUSSION OF RESULTS

This is the final chapter, devoted to the presentation and discussion of the results of this experiment. During the discussion, an effort will be made to point out the implications of the present study in terms of further research in this important area.

1. Results of the Tests of Significance.

In this section, the null hypotheses stated in chapter one will be repeated, and the statistical results will be presented following each null hypothesis.

The major hypothesis states that when a group of rats raised in an impoverished environment is compared to a group raised in an enriched environment, no significant differences develop in the photic evoked potentials of the groups during the first three months of life.

In accordance with the procedures discussed in chapter two, all PEP data was measured in milliseconds and in reference to the latency of that component in each photograph which was of greatest amplitude and between twenty and seventy-five milliseconds in latency. One PEP measure was thus obtained for every subject on each of three occasions.

In order to test the major hypothesis, a mean latency measure was obtained for each of the two experimental groups on each of the three occasions during which PEP was recorded, and each time the group means were compared using a t test. On the first occasion, which was two weeks after the start of the experiment, the mean PEP latency of the enriched group was 37.2 milliseconds, that of the impoverished group was 46.4 milliseconds, the difference between the means was 9.2 milliseconds, and the t test yielded a value of 3.99, which is significant beyond the 0.01 level.

On the second occasion, which occurred four weeks later, the mean PEP latency of the enriched group was 37.5 milliseconds, that of the impoverished group was 57.8 milliseconds, and the difference between the two was now 20.3 milliseconds. The t test for this difference gave a highly significant value of 8.14. This is significant beyond the 0.001 level of probability.

The third and last PEP records were obtained four weeks after the second occasion. This time the mean latency values obtained were 42.2 milliseconds and 52.2 milliseconds for the enriched and impoverished groups respectively. The difference between these values was found to be 10.0 milliseconds, and the t test yielded a value of 5.26, which was also significant beyond the 0.001 level of probability. These results are presented in Table I.

Table I.-

Comparison of Mean Photic Evoked Potential Latencies[a] in Enriched and Impoverished Groups of Rats, Using a t Test for the Significance of a Difference Between Means of Non-Independent Small Groups.

Occasion[b]	Enriched Group		Impoverished Group		Difference of Means	t	Significance
	N	M	N	M			
First	8	37.2	8	46.4	9.2	3.99	>0.01
Second	8	37.5	8	57.8	20.3	8.14	>0.001
Third	8	42.2	8	52.2	10.0	5.26	>0.001

a Mean Photic Evoked Potential Latencies are measured in milliseconds following the onset of photic stimulation.

b Evoked potentials were recorded on three occasions, the first, two weeks after the start of the experiment, and the next two at four-week intervals.

Although the discussion of results belongs properly in the next section, the writer wishes at this point to suggest that these significant differences in PEP, while they are encouraging, must be treated as preliminary findings to be verified in a further study, especially because the event which the writer has chosen to study does not correspond to the events which have been correlated with human intelligence. In a positive tone, the writer wishes to note that, based on the results stated in the preceding paragraphs, the major hypothesis of this investigation must be rejected.

The secondary hypothesis, in null form, states that when a group of rats raised in an impoverished environment is compared to a group raised in an enriched environment, there are no significant differences in the ability of the groups to solve a brightness discrimination problem at the age of three months.

According to the procedures described in chapter two, a black-white brightness discrimination problem was administered to all subjects after all PEP data had been gathered, and in this way each subject obtained a discrimination score representing the total number of trials it required to reach a criterion of six consecutive trials in a single day. Since, as the writer has stated in the second chapter, the subjects were tested as two sub-groups each comprised of

enriched and deprived rats, and since certain unavoidable repairs were performed on the discrimination apparatus before testing of the second sub-group could proceed, it was decided to compare the enriched and deprived subjects of each sub-group separately. The statistical comparison consists of a t test for the significance of a difference of means.

In comparing the first sub-group, it is found that the enriched subjects obtained a mean score of 64.5, while the deprived subjects obtained a mean score of 46.2. The difference between these values is 18.3, and the t test yields a value of 10.06. This is significant, beyond the 0.001 level of confidence.

A similar evaluation of the second sub-group discloses that the enriched subjects again ranked below the deprived, although there was a shift in the absolute scores of both groups of subjects. The mean now obtained by the enriched rats was 44.2, that obtained by the deprived was 32.8, the difference between the two means was 11.4, and comparison through a t test yielded a value of 3.06. This, in general agreement with the results obtained on the first sub-group, is significant at the 0.05 level of probability. Table II presents all discrimination test results.

The paradoxical results of the discrimination test will be discussed in the next section. It is noted here,

Table II.-

Comparison of Mean Brightness Discrimination Scores[a] in Enriched and Impoverished Groups of Rats, Using a t Test for the Significance of a Difference Between Means of Non-Independent Small Groups.

Sub-Group[b]	Enriched N	Enriched M	Impoverished N	Impoverished M	Difference of Means	t	Significance
First	4	64.5	4	46.2	18.2	10.66	>0.01
Second	4	44.2	4	32.8	11.4	3.06	>0.05

a The subjects' were obtained on a black-white brightness discrimination, as the total number of trials to reach a criterion performance of six consecutive trials in one day.

b The experimental subjects were tested as two sub-groups which were not subsequently pooled because the apparatus used to test the two sub-groups was not identical.

that the over-all results of the second sub-group were lower than those of the first. The writer attributes this difference to the improved wire grids employed when testing the second sub-group. These grids were of heavier alpha wire, and probably delivered a more powerful shock even though the current delivered was always of 50 volts and 5 amps. Before the new grids were installed, it sometimes happened that the subject's urine caused a temporary grid failure, and this effect may have been more detrimental to performance of the enriched group than to that of the impoverished. However, the direction of group differences was the same for both sets of trials, and this finding is therefore accepted at the 0.05 level of confidence.

2. Discussion of Results.

The three t tests applied to the PEP data showed significant differences. On the assumption, therefore, that the groups were initially equivalent because they had been formed by the split-litter technique, it is concluded that differential environment has a measurable effect on the PEP. This is a reasonable conclusion, in view of the finding by Szerb[1] that drugs which affect the activity of

---

1 J.C. Szerb, "Averaged Evoked Potentials and Cholinergic Synapses in the Somatosensory Cortex of the Cat", EEG and Clinical Neurophysiology, Vol. 18, 1965, p. 145.

acetylcholine in the brain have measurable effects on the later components of the evoked responses in cats, coupled with the results of a series of studies by Krech, Rosenzweig and co-authors, which show that differential environment affects the cholinesterase levels in the brain. Since cholinesterase is a physiological acetylcholine inhibitor the level of which rises whenever there are increases in acetylcholine activity, it was the writer's expectation that differential environment would have measurable effects on the later components of the PEP in the albino rat. Statistical rejection of the major hypothesis confirms this expectation.

The expectation of PEP differences between enriched and impoverished albino rats did not stem from the above source alone, however. It has been concluded by Hymovitch[2] and a number of subsequent investigators of differential environment that the basic effect of such environmental differences is upon the development of perceptual organization. Melzak and Burns,[3] in apparent agreement with this position, propose a neural model which suggests that as a

---

2 B. Hymovitch, "The Effects of Experimental Variations on Problem-Solving in the Rat", The Journal of Comparative and Physiological Psychology, Vol. 45, 1952, p. 319.

3 R. Melzak and S.K. Burns, "Neuropsychological Effects of Early Sensory Restriction", First Conference on Neurobiology; Feedback Systems Controlling Nervous Activity, Sociedad Mexicana de Ciencias Fisiologicas, Mexico, 1964, p. 287-307.

result of prolonged restriction there is inadequate filtering of sensory input based on memories of stimuli which were previously relevant, and consequently the total input reaches the cortex and by its very magnitude prevents discrimination of stimuli. The authors suggest that there are differences in EEG variables between normal and restricted, and extrapolating from their suggestion the writer expects differences in the later components of the PEP.

However, before an explanation of PEP in terms of development of perceptual organization can be accepted, it must be demonstrated that enriched and impoverished subjects differ in ability to solve a discrimination problem, such a difference being in favour of the enriched group. Previous findings on this topic are by no means unanimous. For example, Melzak and Burns[4] found that restricted dogs had greater difficulty than enriched dogs in discriminating between a black card and a white one. On the other hand, Bingham and Griffiths[5] found no differences in the abilities of rats raised in differential environments to solve a brightness discrimination problem using the Lashley jumping stand.

---

4 Ibid., p. 207-307.

5 W.E. Bingham and W.J. Griffiths, Jr., "The Effect of Different Environments During Infancy on Adult Behaviour in the Rat", The Journal of Comparative and Physiological Psychology, Vol. 45, 1952, p. 310.

In view of such conflicting results, therefore, it was decided to administer a black-white brightness discrimination problem to all subjects used in the present study. It was found, contrary to expectation, that the impoverished subjects obtained significantly better scores than their enriched littermates. Since, as has been pointed out, previous studies of environmental differences have yielded conflicting results on discrimination tests but have almost universally found enriched animals to be superior problem-solvers and impoverished animals to be inferior problem-solvers on a large variety of behavioural tests, the writer feels that the discrimination scores obtained here reflect something other than genuine ability differences between the experimental groups.

The most probable explanation for the paradoxical results of the discrimination test used in this study is as follows: For three months prior to the administration of the discrimination test, the enriched rats were storing in their brains traces of the stimuli with which they had daily contact, while the impoverished rats had very little opportunity for such memory storage. Similarly, when the test was being administered, the enriched rats enjoyed a greater wealth of experiences between sessions than their impoverished littermates. The writer suggests that, while the more complex environment enjoyed by the enriched group

contributed to their greater cerebral development, it also provided a source of interference with the retention of the brightness discrimination task, an interference which did not exist in the impoverished subjects, thereby permitting them to obtain higher scores, and obscuring true ability differences between the two groups.

The interference of which the writer speaks in the preceding paragraph is called proactive inhibition when referring to interference of prior experiences with the retention of a subsequent task, and retroactive inhibition when referring to interference with retention of a task by subsequent experiences. According to Deese,[6] both proaction and retroaction are important factors in explaining forgetting. In the present study, it is most probable that they were responsible for a higher rate of forgetting on the part of the enriched subjects, and thus explain the lower scores obtained by this group. This probability is increased by the finding of Thompson and Bryant[7] that retroactive inhibition has a measurable effect on the discrimination learning of rats.

---

6 J. Deese, The Psychology of Learning, McGraw-Hill, New York, 1958, p. 256-260.

7 R. Thompson and J.H. Bryant, "Memory as Affected by Activity of the Relevant Receptor", Psychological Reports, Vol. 1, 1955, p. 398-399.

It remains the task of future research to devise measures of perceptual development in lower animals which are free from the aforementioned inhibition effects. In the meantime, it is not possible to conclude with certainty that differential environment has its basic effect on the development of perceptual organization. Therefore, the writer interprets the PEP differences between enriched and impoverished subjects in terms of differences in the activity of cholinergic synapses, based on the group of studies in this area which have been reviewed and discussed previously.

To complete the discussion of results, it must be added that the latency of the PEP event studied was significantly shorter in the enriched group than in the impoverished group. This confirms the writer's expectations, based on previous studies which have demonstrated the behavioural superiority of enriched animals, on the findings of studies relating intelligence to evoked potentials that the latencies of more intelligent subjects are shorter, and on the finding of Bradley et al.[8] that cretinized rats, which are behaviourally inferior, exhibited longer latencies in their evoked responses than control rats. Any attempt to explain why diminished activity of cholinergic synapses

---

8 P.B. Bradley, J.T. Eayrs and N.M. Richards, "Factors Influencing Potentials in Normal and Cretinous Rats", EEG and Clinical Neurophysiology, Vol. 17, 1964, p. 312.

is associated with lengthening of PEP latencies is, however, beyond the scope of this project, although it is certainly a valid topic for future research.

The final paragraphs of this chapter will have as their aim to suggest areas in which related future research projects would be particularly desirable.

This is a preliminary study on a small number of subjects and, particularly because the event analyzed is not the same as those analyzed by previous investigators, a replication on a second group of albino rats would be highly desirable. It would be desirable for such a study to analyze the PEP through a zero-crossing analysis, as described by Ertl,[9] since this technique would make possible the objective measurement and comparison of all significant events in the evoked responses, and this data could be more thoroughly analyzed for group differences.

Secondly, the writer has observed that, although all the subjects remained healthy throughout the experiment, the impoverished rats tended to grow faster than the enriched. This suggests to him that there may be physiological differences between the groups, for example differences in endocrine functions, which may be worth future study. It is only

---

[9] J.P. Ertl, "Evoked Potential Recovery from Tape Recorded Zero Crossings of the EEG", EEG and Clinical Neurophysiology, Vol. 22, 1967, p. 630-631.

through a series of related studies that a thorough description of subjects raised in different environments may be achieved. Such a description seems valuable in attempting to explain evoked potential differences, since it is known that various systems in the organism, especially the nervous and endocrine systems, exert a mutual influence on each other.

Finally, for reasons which have been presented in an earlier section, the behaviour of enriched and impoverished animals when solving discrimination problems warrants further investigation.

The writer wishes to end this chapter with the statement that, whenever an attempt is made to link two variables of great complexity, such as environment and EEP, conclusive findings are to be expected from a series of related studies rather than from a single investigation. The present study is the first of such a series.

SUMMARY AND CONCLUSIONS

The present study was designed to assess the effects of differential environments on the photic evoked potentials of albino rats during the first three months of life, and secondarily to check whether the two experimental groups differed, at the end of three months in differential environments, in their ability to solve a discrimination problem.

The major hypothesis that was tested stated that, when a group of rats raised in an impoverished environment is compared to a group raised in an enriched environment, no significant differences develop in the photic evoked potentials of the groups during the first three months of life. A secondary hypothesis was also tested, which stated that, when a group of rats raised in an impoverished environment is compared to a group raised in an enriched environment, there are no significant differences in the ability of the groups to solve a brightness discrimination problem at the age of three months.

The t test was used as statistical test of significance for both hypotheses. The results of both were statistically significant, and both hypotheses were rejected. The direction of the difference found was as expected in the case of the major hypothesis, but in the case of the minor hypothesis the impoverished subjects obtained better results, probably due to proactive and retroactive inhibition.

BIBLIOGRAPHY

Amassian, V.E., M.J. Waller, and J. Macy, Jr., "Neuronal Mechanism of the Primary Somatosensory Evoked Potential", Annals of the New York Academy of Sciences, Vol. 112, Art. 1, 1964, p. 5-32.

This study investigates the nature of the primary evoked response, and concludes that evoked responses recorded at the scalp are neural in origin and reflect widespread synaptic activity.

Beach, F.A. and J. Jaynes, "Effects of Early Experience Upon the Behaviour of Animals", Psychological Bulletin, Vol. 51, 1954, p. 239-263.

In this general discussion on the effects of early experience, the authors review relevant literature and discuss previous findings. The view is advanced that the basic effects of differential environment are upon the developing perception of the animal.

Bennett, E.L., D. Krech and M.R. Rosenzweig, "Reliability and Regional Specificity of Cerebral Effects of Environmental Complexity and Training", Journal of Comparative and Physiological Psychology, Vol. 57, 1964, p. 440-441.

This is a recent publication by the authors of a series of studies on the effects of environment on brain structure and chemistry, which concludes that the chemical and anatomical effects of early experience are highly repeatable.

Bergamini, L., E. Bergamasco, A.M. Mombelli and G. Candiglio, "Visual Evoked Potentials in Subjects with a Congenital Aniridia", EEG and Clinical Neurophysiology, Vol. 19, 1965, p. 394-397.

The authors propose that the observed habituation of visual evoked responses is the result of pupillary adaptation, and support their hypothesis with a study of humans who lack the mechanism for pupillary adaptation.

Bickford, R.L., J.L. Jacobson, and D.T.R. Cody, "Nature of Average Evoked Potentials to Sound and Other Stimuli in Man", Annals of the New York Academy of Sciences, Vol. 112, Art. 1, 1964, p. 204-223.

The authors conclude that scalp evoked potentials recorded near the inion are myogenic and not neural in origin.

Bingham, W.E. and W.J. Griffiths, Jr., "The Effect of Different Environments During Infancy on Adult Behaviour in the Rat", The Journal of Comparative and Physiological Psychology, Vol. 45, 1952, p. 307-312.

This study, based on the original findings of Hebb, investigates the behaviour of enriched and isolated albino rats, and concludes that the enriched are superior in maze performance but do not differ from the deprived in ability to solve discrimination tasks, nor do they differ in emotionality.

Bradley, P.B., J.T. Eayrs, A. Glass and R.W. Heath, "The Maturational and Metabolic Consequences of Neonatal Thyroidectomy Upon the Recruiting Response in the Rat", EEG and Clinical Neurophysiology, Vol. 13, 1961, p. 577-586.

The authors, in this study on cretinized rats, find that neonatal thyroidectomy is associated in later life with an increase in the latency and duration of the surface negative component of evoked responses, called recruiting responses, in the rat. A reduction in amplitude is a second finding.

Bradley, P.B., J.T. Eayrs and N.M. Richards, "Factors Influencing Potentials in Normal and Cretinous Rats", EEG and Clinical Neurophysiology, Vol. 17, 1964, p. 308-313.

The relevant findings of this paper are that, when an evoked response is obtained to stimulation of a thalamic nucleus, its latency, duration and amplitude are different in normal and thyroidectomized rats. Latency and duration are lengthened, and amplitude diminished, in the cretinized rats.

Chalke, F.R. and J.P. Ertl, "Evoked Potentials and Intelligence", Life Sciences, Vol. 4, 1965, p. 1319-1322.

In this important study, the authors find that groups of human subjects classified as low, average or high in intelligence show significant differences in the latencies of their visual evoked responses. A zero crossing technique is used for the analysis of evoked responses.

Clarke, R.S., W. Heron, M.L. Fetherstonhaugh, D.G. Forgays and D.O. Hebb, "Individual Differences in Dogs: Preliminary Report on the Effects of Early Experience", Canadian Journal of Psychology, Vol. 5, 1951, p. 150-156.

This study is based on earlier work in this area by Hymovitch and Forgays. It concludes, on the basis of four tests of animal behaviour, that dogs reared under restricted conditions are inferior in problem-solving ability.

Denenberg, V.H. and J.R.C. Morton, "Effects of Preweaning and Postweaning Manipulations Upon Problem-Solving Behaviour", Journal of Comparative and Physiological Psychology, Vol. 55, 1962, p. 1096-1098.

This study confirms earlier findings that enriched animals perform better on the Hebb-Williams mazes than environmentally impoverished animals. The authors found that variations in the amount of handling during the preweaning period did not affect later problem-solving ability.

Domino, E.G. and G. Corssen, "Visually Evoked Response in Anesthetized Man With and Without Induced Muscle Paralysis", Annals of the New York Academy of Sciences, Vol. 112, Art. 1, 1964, p. 228-237.

The authors answer Bickford's objections concerning the myogenic origin of evoked responses. Having recorded visually evoked responses in man both in the presence and in the absence of skeletal muscle paralysis, they conclude that myogenic components are negligible.

Edwards, H.P., "EEG and WAIS Intelligence in a Sample of Cultural-Familial Deficients", unpublished Master's thesis presented to the Faculty of Psychology and Education of the University of Ottawa, Ontario, 1965, vii-47 p.

A review of the attempts to find a relationship between standard EEG variables and intelligence constitutes the bibliography of this thesis, which concludes that the EEG is too gross a measure of brain functioning for such a relationship to be found.

Ertl, J.P., "Intra-Cortical Delay and Intelligence", unpublished Master's thesis presented to the School of Psychology and Education of the University of Ottawa, Ontario, 1961, viii-41 p.

Ertl's thesis constitutes the first successful exploration of the relationship between visually evoked potentials and psychometric intelligence. However, its technique for analysis of evoked responses was difficult to cross-validate.

--------, "Evoked Potential Recovery from Tape Recorded Zero Crossings of the EEG", EEG and Clinical Neurophysiology, Vol. 22, 1967, p. 337-338.

This publication, in addition to describing a method for recording EEG data using an AM tape recorder, suggests that synchrony may play an important part in determining the amplitude of evoked potentials. This has implications for the interpretation of studies which use amplitude as dependent variable.

Fernandez-Guardiola, A., E. Roldan R., M.L. Fanjul and C. Castells, "Role of the Pupillary Mechanism in the Process of Habituation of the Visual Pathways", EEG and Clinical Neurophysiology, Vol. 13, 1961, p. 564-576.

During repetitive stimulation, gradual habituation changes are observed in the evoked responses. The authors study the effects of atropinization of the pupillary muscles on such habituation, and conclude that in the absence of pupillary adaptation no habituation occurs in the measurable characteristics of the evoked responses to repetitive stimulation.

Forgays, D.G. and J.W. Forgays, "The Nature of the Effect of Free-Environmental Experience in the Rat", The Journal of Comparative and Physiological Psychology, Vol. 45, 1952, p. 322-328.

In this extension of an earlier study by Hymovitch, the authors find that rats raised in a free-environment box are superior problem-solvers to rats raised in an impoverished environment.

Frommer, G.P., and R.B. Livingston, "Arousal Effects of Evoked Activity in a 'Nonsensory' System", Science, Vol. 139, No. 3554, 1963, p. 502-504.

This cat study verifies earlier findings that evoked responses become greater in amplitude and longer in latency when there is reduction of arousal measured through behavioural and EEG signs. In addition, it finds using cerebellar stimulation that a short-latency component of the evoked response at the motor cortex is present with high arousal but attenuated or abolished completely with diminishing arousal.

Hebb, D.O., "The Effects of Early Experience on Problem-Solving at Maturity", The American Psychologist, Vol. 2, 1947, p. 306-307.

In this brief report, Hebb outlines the original study on differential environment of rats. He compares laboratory rats to pet rats, and also studies the effects of blinding rats at various ages on their behaviour. He finds that pet rats and rats blinded late in their growth period perform better on the Hebb-Williams mazes than laboratory rats or rats blinded very young.

Hymovitch, B., "The Effects of Experimental Variations on Problem-Solving in the Rat", The Journal of Comparative and Physiological Psychology, Vol. 45, 1952, p. 313-321.

Based on Hebb's original work in this area, the author studies rats reared in environments differing in complexity. He concludes that enrichment of early experience undoubtedly has a beneficial effect on problem-solving.

He interprets his findings in terms of the greater opportunity of the enriched rates for perceptual learning.

Kimura, D., "Multiple Response of the Visual Cortex of the Rat to Photic Stimulation", EEG and Clinical Neurophysiology, Vol. 14, 1962, p. 115-122.
The relevance of this article is simply that it discusses the general characteristics of the wave train elicited to photic stimulation when recorded from the surface of the cerebral cortex, and suggests the placement of electrodes which give maximal response from the striate cortex.

Krech, D., M.R. Rosenzweig, and E.L. Bennett, "Dimensions of Discrimination and Level of Cholinesterase Activity in the Cerebral Cortex of the Rat", The Journal of Comparative and Physiological Psychology, Vol. 49, 1956, p. 261-266.
This is the first of a series of investigations on the relationships among behaviour, environment and the chemistry of the brain.

--------, "Effects of Environmental Complexity and Training on Brain Chemistry", Journal of Comparative and Physiological Psychology, Vol. 53, 1960, p. 509-519.
In this study, albino rats were raised in three degrees of environmental complexity, and the authors find systematic differences in the cholinesterase activity of the three groups.

--------, "Relations Between Brain Chemistry and Problem-Solving Among Rats Raised in Enriched and Impoverished Environments", Journal of Comparative and Physiological Psychology, Vol. 55, 1962, p. 801-807.
The authors first kept the animals in differential environments for a month, then tested their learning ability, and thirdly measured the cholinesterase activity in the brain. Enriched and impoverished rats differed in learning ability. But, at the end of the learning period, no differences in cholinesterase activity were found between the groups.

Melzak, R. and S.K. Burns, "Neuropsychological Effects of Early Sensory Restriction", First Conference on Neurobiology: Feedback Systems Controlling Nervous Activity, Sociedad Mexicana de Ciencias Fisiologicas, Mexico, 1964, p. 287-307.
This article attempts to explain the odd behaviour of dogs reared in a restricted environment through a

neurological model which hypothesizes that in the restricted animal sensory input cannot be adequately filtered since it has no memories of relevant stimuli, and in consequence its ability to discriminate is inferior.

Pickenhain, L. and F. Klingberg, "Behavioural and EEG Changes During Avoidance Conditioning to Light Flashes in the Rat", EEG and Clinical Neurophysiology, Vol. 18, 1965, p. 464-476.

This article is relevant only in that it shows that it is feasible to obtain an evoked potential to photic stimulation in the rat, and suggests electrode placements.

Prichard, J.W., J. Chimienti and R. Galambos, "Evoked Responses from Extracranial Sites in the Cat", EEG and Clinical Neurophysiology, Vol. 18, 1965, p. 493-499.

This paper agrees with an earlier publication by Bickford that evoked responses, when recorded extracranially, may be myogenic in origin. It is adequately refuted in the publications by Amassian et al. and by Domino and Corssen.

Rosenzweig, M.R., D. Krech, E.L. Bennett and C. Diamond, "Effects of Environmental Complexity and Training on Brain Chemistry and Anatomy: A Replication and Extension", Journal of Comparative and Physiological Psychology, Vol. 55, 1962, p. 429-437.

In this study on the effects of environment upon brain chemistry, the authors report that enriched and isolated rats differ in cholinesterase activity, cortical/subcortical cholinesterase ratio, and brain weight.

Rosenzweig, M.R., D. Krech, E.L. Bennett and J.F. Zolman, "Variation in Environmental Complexity and Brain Measures", Journal of Comparative and Physiological Psychology, Vol. 55, 1962, p. 1092-1095.

The data here presented replicate previous findings by the same group of authors, and in addition evidence is presented favouring the view that later exposure to complex environment can make up for early isolation.

Rosenzweig, M.R., E.L. Bennett and D. Krech, "Cerebral Effects of Environmental Complexity and Training Among Adult Rats", Journal of Comparative and Physiological Psychology, Vol. 57, 1964, p. 438-439.

This experiment shows that, if rats are separated into enriched and deprived environments for a time starting when they are already adults, the results at the end of the experimental period are the same as would have been obtained had the experiment started at the time of weaning. This appears to contradict the popular idea that there is a critical period during which the effects of differential environments are most pronounced.

Schwartz, M. and C. Shagass, "Effects of Different States of Alertness on Somatosensory and Auditory Recovery Cycles", EEG and Clinical Neurophysiology, Vol. 14, 1962, p. 11-20.

The authors of this study investigate on the cat the effects of different arousal states assessed through standard EEG criteria. With alerting, a diminution in amplitude of somatosensory evoked potentials is reported. No clear trends are apparent using auditory evoked potentials.

Steinberg, R.H., "Alterations of Averaged Photic Evoked Potentials in Cat Visual Cortex During Repetitive Stimulation", EEG and Clinical Neurophysiology, Vol. 18, 1965, p. 378-391.

The relevant part of this publication states that, when stimulus intensity is carefully controlled, no habituation effect of the evoked responses can be shown in animals whose pupillary muscles have been immobilized.

Szerb, J.C., "Averaged Evoked Potentials and Cholinergic Synapses in the Somatosensory Cortex of the Cat", EEG and Clinical Neurophysiology, Vol. 18, 1965, p. 140-146.

This publication investigates the relationship between the activity of cholinergic synapses in the cortex and electrical events recorded from the surface of the cortex, and concludes that amplitude of the later components of the evoked responses is related to the functioning of cholinergic synapses.

Taylor, N.A., "Evoked Potential Latencies and Psychometric Intelligence", unpublished Master's thesis presented to the Faculty of Psychology and Education of the University of Ottawa, Ontario, 1966, ix-76 p.

This is the most recent publication on the relationship between psychometric intelligence and photic evoked potentials. Its results show highly significant correlations to exist between intelligence scores and the evoked responses of the brain.

Thompson, W.R. and W. Heron, "The Effects of Restricting Early Experience on the Problem-Solving Capacity of Dogs", Canadian Journal of Psychology, Vol. 8, 1954, p. 17-31.

This article compares the behaviour of dogs reared as pets with that of dogs reared under several degrees of environmental restriction. Based on the results of six tests of animal behaviour, the authors conclude that environmental restriction results in inferior performance, and attribute this to lack of early perceptual experience.

Thompson, R. and J.H. Bryant, "Memory as Affected by Activity of the Relevant Receptor", Psychological Reports, Vol. 1, 1955, p. 393-400.

The relevance of this publication lies in the fact that it describes the apparatus which was adapted by the writer for testing his subjects on a brightness discrimination problem.

Woods, P.J., "The Effects of Free and Restricted Environmental Experience on Problem-Solving Behaviour in the Rat", The Journal of Comparative and Physiological Psychology, Vol. 52, 1959, p. 399-402.

This study verifies previous findings on the effects of differential environments on problem-solving, and in addition finds that the effects of early environment are far more important for later problem-solving ability than the effects of later environment.

Wyspianski, J.O., "Brain Wave Amplitude and Creative Thinking", unpublished doctoral thesis presented to the School of Psychology and Education of the University of Ottawa, Ontario, 1963, viii-108 p.

This publication is relevant in that it represents the one successful attempt to find a relationship between a psychological variable and a standard EEG variable. In it, the interested reader may find a review of the literature on early attempts to relate intelligence with standard EEG variables.

APPENDIX 1

PHOTIC EVOKED POTENTIAL LATENCIES

APPENDIX 1

PHOTIC EVOKED POTENTIAL LATENCIES[1]

Subject[2]	Five Weeks[3]	Nine Weeks	Thirteen weeks
1-E	36	37	42
2-E	43	43	62
3-E	35	35	33
4-E	50	40	35
5-E	35	33	37
6-E	30	29	42
7-E	35	47	32
8-E	32	40	55
1-I	42	63	51
2-I	37	62	56
3-I	62	67	52
4-I	47	60	50
5-I	32	50	60
6-I	52	60	57
7-I	47	40	52
8-I	52	60	60

1 All latency readings are shown in milliseconds.

2 Throughout the experiment, each subject bore an identifying number. The letter E signifies a subject from the enriched group, while I denotes an impoverished subject.

3 The number of weeks represents the actual age of the subjects when each photic evoked potential record was obtained.

APPENDIX 2

BRIGHTNESS DISCRIMINATION SCORES

APPENDIX 2

BRIGHTNESS DISCRIMINATION SCORES

Subject[1]	Score[2]
A1-E	70
A2-E	52
A5-E	56
A8-E	70
A5-I	46
A6-I	45
A7-I	47
A8-I	46
B3-E	46
B4-E	38
B6-E	47
B7-E	46
B1-I	31
B2-I	48
B3-I	22
B4-I	30

1 Each subject bore an identifying number throughout the experiment. The letters E and I denote enriched and impoverished respectively, while the letters A and B denote subgroup A and subgroup B, which were tested on somewhat different versions of the discrimination apparatus.

2 The score shown represents the total number of trials required by each subject to reach a criterion performance of six consecutive correct trials on a black-white brightness discrimination.

APPENDIX 3

ABSTRACT OF

Effects of Early Rearing in Differential Environments on the Albino Rat's Photic Evoked Potentials

APPENDIX 3

ABSTRACT OF

Effects of Early Rearing in Differential Environments on the Albino Rat's Photic Evoked Potentials[1]

This is a longitudinal study which has as its primary purpose to assess whether the early environment in which an organism is raised has measurable effects on the photic evoked potentials recorded from its brain. Its findings are to be considered as preliminary answers, providing clues for further research. The importance of the topic stems from the fact that, in the light of recent findings, the photic evoked potentials recorded from the human brain appear to be a valid physiological measure of intelligence.

The subjects for the present investigation were a sample of Sprague-Dawley albino rats. They were separated at weaning into two groups, and one was raised in an enriched environment while the other was raised in an impoverished environment, to the age of three months. During this time, three records of their photic evoked potentials were obtained, at monthly intervals. At the end of three

---

1 H.P. Edwards, doctoral thesis presented to the Faculty of Psychology of the University of Ottawa, Ontario, 1967, viii-73 p.

months, all subjects were required to solve a brightness discrimination problem.

The major hypothesis tested states that when a group of rats raised in an impoverished environment is compared to a group raised in an enriched environment, no significant differences develop in the photic evoked potentials of the groups during the first three months of life. A significant latency difference was found, and on this basis the writer rejects the major hypothesis.

A minor hypothesis which was also tested states that when a group of rats raised in an impoverished environment is compared to a group raised in an enriched environment, there are no significant differences in the ability of the groups to solve a brightness discrimination problem at the age of three months. Significant differences were found, but contrary to expectation the impoverished subjects proved better problem-solvers. This is interpreted in terms of proactive and retroactive inhibition having a detrimental effect on the performance of the enriched group.