EFFECTS OF MONOCULAR ENUCLEATION
IN THE VISUAL CORTEX
OF THE RAT

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ABSTRACT

Research using visual deprivation has suggested that early experience mediates neural development. Previous research in rats has revealed significant effects of dark-rearing on the growth pattern of stellate cells in the visual cortex. Although it has been suggested that monocular enucleation has similar effects, this has never been quantitatively examined. The present study evaluated the quantitative effects of monocular enucleation in rat visual cortex.

Fourteen hooded rats were monocularly enucleated at birth and reared under normal diurnal laboratory conditions. Rats were sacrificed at day 30, the brains stained with Golgi-Cox solution. Twelve stellate cells from layers III-IV of the visual cortex were traced in each hemisphere with a computer-based tracking system. A Polar Analysis, in which three-dimensional cones radiate from the somata, indicated that no orientation change is involved with the differential growth pattern. The results do indicate, however, a sexual dimorphism in rat visual cortex. Results from the present study indicate that visual deprivation effects may in fact be quite small. It is suggested that the results from dark-rearing studies may be due in part to factors other than altered activity levels in the visual system.
Introduction

The capacity of the nervous system to adapt to its environment is a major component of the ability to deal with environmental variation in more advanced species. A good example of neural adaptation to the environment is seen in the development of the visual system in higher mammals, which is particularly dependent on normal visual experience for proper maturation. The visual system has been extensively studied as it is both easy to manipulate and is of critical importance to the survival of these organisms in the natural environment. Electrophysiological experiments have demonstrated that neural functioning in the visual cortex may be profoundly affected by the visual experience of the developing organism. Similarly, anatomical studies have quantified neural changes subsequent to experience manipulations. Much data are consistent with the concept that the environment may "fine-tune" the connections of the developing visual system.

Gottlieb (1976) has noted that there are several ways in which experience may act upon the development of a behavioral process and upon corresponding neural development. The first role of experience is concerned with maintaining the system which, if deprived, would degenerate; the second involves a facilitative role in which the rate of development is enhanced by stimulation; the third involves an inductive role in which the environment may direct the course of development. A combi-
nation of these mechanisms constitutes a fourth possibility. At a mechanism level, one theory has dominated the recent literature. Changeux and Danchin (1976) have proposed a selective stabilization model in which major cortical structures may be determined genetically, while specific patterns of connectivity may be determined experientially, through selective preservation of appropriate neural connections, and loss of others. (This is described in a later section.) The Changeux and Danchin proposal implies that experience brings about a selective maintenance of connections, and suggests that Gottlieb's separate experience effects may in fact describe a single process. The following section review results of research on the effects of experience manipulations upon the development of the visual system, focusing upon rodents, the subject of the present investigation.

Effects of Visual Deprivation

The most prevalent methods by which the visual system has been experimentally deprived include dark-rearing, lid-suturing, and enucleating animals. (Enucleation is a surgical technique whereby the eye is made non-functional.) These manipulations with rats, cats, and monkeys have demonstrated that deprivation during the sensitive period of growth significantly affects the visual system's development. Many connectivity patterns are affected by environmental modifications during this sensitive period, after which time the environment has
much less influence. Work with cats by Hubel and Wiesel (1963a, 1963b, 1973) and others has demonstrated that certain characteristics of cortical neurons are determined prenatally, while others require visual experience (Blakemore and Van Sluyters 1974). It now appears that, at least for cats, some neurons are specified prior to experience, while other neurons need experience to "fine-tune" their properties. The Changeux and Danchin (1976) selective preservation model proposes that experience may stabilize a subset of active connections, while inactive connections subsequently degenerate. It is this progressive elimination of redundancy which may explain the diminution of plasticity as the animal develops.

At a behavioral level, various sorts of support for such a process have been generated. For example, a study by Tees and Midgely (1978) showed that dark-reared rats did not improve in complex pattern discrimination learning following visual experience. This suggests that there exists a sensitive period during which time visual experience is required for normal visual development. At the anatomical level, direct evidence for loss of connections has been described. LeVay, Hubel, and Wiesel (1975) have shown that overlapping connections are lost as the binocular visual system of a cat or monkey develops.
Behavioral Effects of Visual Deprivation. Behavioral capacities of visually deprived animals are the ultimate criteria for the quality of sensory function. Unfortunately, it is technically difficult to teach young rats and other developing animals to both perform a discrimination task and respond in a reliable fashion. However, behavioral effects of visual experience manipulations during development have been demonstrated quantitatively in several ways.

Much of the rodent research deals with various forms of discrimination and the capacity to learn or recall various tasks. One of the simpler forms of discrimination used with rodents involves varying the absolute brightness of the stimuli. This discrimination is known as luminance flux. Luminance, on the other hand, is a quantitative measure of brightness equal to luminance flux per unit solid angle emitted per unit projected area of its surface. It is suggested that luminance cues require a higher level of discrimination than luminance flux cues. Tees (1968) showed that there is not a significant difference in dark-reared rats in their ability to discriminate using luminance flux cues. Tees did, however, find significant differences, compared to light-reared rats, when the animals had to use luminance as the cue. Similarly, Tees found a significant difference between control and dark-reared rats with respect to pattern discrimination tasks. One pattern discrimination involved differentiating between an "X" and an "N." Tees suggested
that pattern discrimination is a "higher order" level of functioning compared to luminance flux cues. Walk and Gibson (1965) developed a "cliff test" in which they measured depth perception for several species. They concluded that the development of depth perception occurred at an age in which the organism began to move about. Tees (1974) and Walk and Walters (1973) analyzed the effects of light deprivation on depth perception. Both researchers reported that at 20-21 days there was no significant difference among the animals in their ability to discriminate depth due to rearing conditions. Both studies noted deficiencies in dark-reared rats with at least 30 days of light deprivation after birth. The behavioral differences in the light- and dark-reared groups became more pronounced with increases in the duration of deprivation. Both researchers found some recovery to occur in the deprived group following visual experience, though there was a general trend for the dark-reared group to remain behaviorally impaired relative to the control group.

Schwartz and Rothblat (1980) attempted to relate long-lasting behavioral deficits to decrements in spine density. Spines are extensions of dendrites, which generally terminate with a synapse, the structural mechanism of neural communication. Hence, quantification of spine density of dendrites is a reasonable anatomical estimate of the number of synapses per nerve cell. The experiment
involved monocular deprivation in rats from the time of normal eye-opening until day 45. As has been found in other studies, Schwartz and Rothblat (1980) reported a significant decrease in the density of dendritic spines in the visual cortex contralateral to the deprived eye. Some animals were given 30 days of visual experience with the deprived eye after testing. They did not report any significant behavioral recovery as a result. The behavioral task consisted of discriminating between columns and rows of 5 mm squares. No spine recovery was observed in either the deprived group or the group given 30 days of visual experience subsequent to the deprivation.

The data suggest that some basic visual abilities exist early in a mammal’s development, and that these abilities are affected by experience. These points form the basis for the conclusion that behavioral ability is subject to "critical" and/or "sensitive" periods for experience effects upon development.

Electrophysiological Effects of Visual Deprivation. Electrophysiological studies have provided insight concerning the response properties of individual neurons in the developing visual system. Blakemore and Van Sluyters (1975), for example, measured orientation selectivity in the visual cortex of cats. They found that approximately 20% of the neurons in kittens responded selectively to oriented visual stimuli at eye-opening, while another 20% showed some tendency toward orientation
selectivity, although these cells were not as specific in their preferences as those of adults. Blakemore and Van Sluyters reported that these response properties diminished quickly when the kittens were kept in darkness.

Similarly, it has been found that pattern deprivation in cats produces electrophysiological effects. In monocularly pattern-deprived cats, cortical cells were found to be unresponsive to stimulation of the deprived eye (Ganz et al 1968; Hubel and Wiesel 1970; Wiesel and Hubel 1963b). These physiological changes were paralleled by behavioral defects, as these animals had severe difficulties in learning various perceptual tasks, such as pattern discrimination and depth perception with the deprived eye. These results have been interpreted as indicating a loss of control over binocularly innervated cortical neurons by axons associated with the deprived eye. This point is supported by a study by Fregnac and Imbert (1976) in which monocular and binocular cortical cells in dark-reared kittens were analyzed. The results indicated that monocularly-driven cells were unaffected by visual deprivation, whereas binocularly-driven cells were adversely affected. This suggests that monocular deprivation has its strongest effects on binocular parts of the visual system due to competitive advantages of experience.

In rats, in which the visual system is highly decussated, binocular competition should be minimal. Yinon
and Auerbach (1973) have provided the only electrophysiological work of visually deprived rats. They unilaterally lid-sutured rats for 70-170 days and recorded visual evoked potentials (VEPs) in the visual cortex. The authors believed that the VEP is related to single unit responses as found in cats (Minke and Auerbach 1972). They found that the VEP derived from the deprived striate cortex of the rat was smaller in amplitude than the VEP from the hemisphere with "normal" input. This finding demonstrated a localized electrophysiological consequence of monocular deprivation on the central nervous system. They also found that the VEP recorded from the control animals was always larger than the VEP recorded from the "normal" hemisphere in rats monocularly deprived. They suggested that this may indicate that commissural connections play an important part in visual interaction. They concluded that the difference in VEPs in normal and deprived animals is likely to reflect changes in the characteristics of single neurons as a result of the absence of patterned light stimuli in the postnatal animal.

Structural Effects of Visual Deprivation. The structural basis of these functional effects of visual experience manipulations has been the subject of several studies. Visual deprivation studies have demonstrated structural consequences in various regions of the brain. Modification of functionally connected nuclei and cortical areas have been observed in dark-reared and lid-sutured
animals. Gyllensten et al (1965; 1966) found a significant decrease in internuclear material per neuronal nucleus in the lateral geniculate nucleus (LGN) and superior colliculus following 2, 3, and 4 months of dark-rearing. Internuclear material includes dendrites and synapses, and they suggested that this result implies reduced numbers of interneuronal connections.

Fifkova (1967, 1968, 1969, 1970) has studied the effects of unilateral deprivation in rats at the gross level (volume of visual structures), the fine structural level (density of spines), and the ultrastructural level (size and frequency of synapses). Fifkova reported that monocular lid-suture in young rats caused a significant decrease in the volume of the contralateral LGN and visual cortex, but did not affect the optic tract and superior colliculus. Fifkova found 11.5% more cells per unit volume in layer IV of the visual cortex contralateral to the deprived eye. Similarly, Gyllensten et al (1965; 1967) found a reduction in thickness of layers II, III, and IV of the striate cortex following dark-rearing. Diminution of the volume of a brain structure may be caused by either a decrease in cell numbers or a reduction in the size of specific parts of neurons. Since cell density was increased, Fifkova proposed that a decrease in dendritic material resulted in greater cell density in the deprived side of the visual cortex. Fifkova also analyzed the spines of apical dendrites of pyramidal
neurons in layer V of the visual cortex. She found a significant decrease in the density of spines in the deprived half of the visual cortex, again suggesting decreased interneuronal connectivity. Fifkova (1970) further compared volume changes in rat visual cortex after varying age of onset of unilateral deprivation. Fifkova reported that the changes were of the same magnitude in both previously visually experienced and visually naive rats. Fifkova concluded that the observation that the changes were of the same magnitude whether the lids were sutured on the 15th or the 60th day post-natal argued in favor of the idea that the assymetrical changes were not due to any growth inhibition caused by the deprivation, but were of a degenerative nature. This assertion seems to conflict with functional studies which have indicated a decrement in sensitivity to visual deprivation as a function of the system's maturation (Hubel and Wiesel 1970). Fifkova attempted to explain this discrepancy as a species difference. However, a number of other scientists have reported developmental differences in visual deprivation effects in rodents (Valverde 1971, Rothblat and Schwartz 1979, Borges and Berry 1978).

Valverde extensively examined anatomical effects of dark-rearing in mice. His quantitative work focused on spine counts of apical dendrites of layer V pyramids as they traversed the visual cortex. Valverde (1967) reported that light deprivation in the mouse caused a significant reduction in the number of spines in layer IV.
Comparing the changes in the visual cortex to the absence of such effects in the somatosensory cortex, he proposed that sensory deprivation specifically affected the fine structure of the visual system and did not reflect an overall effect of the type which might result from hormonal or metabolic mediation. Valverde believed that these results were especially significant since the observed changes occurred in an intact animal. He stated, "We think that this proves further that the normal function of the specific cortical afferents, supposing they exist normally in visually deprived animals, must be necessary for the maintenance of the dendritic spine complex."

Later studies by Valverde tended to emphasize mathematical models for spine growth. The basic concept involved the point that dendritic spines along the apical dendrite develop exponentially. This model also showed that dendritic spine development occurs similarly across several species, and the model can be used to predict average growth patterns in both light- and dark-reared animals. Valverde (1971), presented a summary of his research, which was concerned with the rate and extent of recovery from dark-rearing in the visual cortex of the mouse. He restated his previous position that, "mice raised in complete darkness from birth show a marked diminution of the number of dendritic spines in the apical shafts of layer V pyramidals in the visual cortex. The loss of dendritic spines is greatest during the first week after the spontaneous opening of the eyes."
cluded that visual deprivation profoundly affected spines, some of which would not grow in the absence of normal visual inputs. The data indicated that animals maintained in darkness followed the normal sequence of development until day 15, where the mean values of spines stabilized until day 25. "Thereafter the number of spines increased at a slow rate towards normal values which, however, they never reached." This statement appears to be a misrepresentation of the data. Valverde's comparison of animals at day 50 showed no significant difference between normal and dark-reared mice. Therefore his data suggest that spine density will reach normal levels, with a latent period of growth. Moreover, a first derivative chart on spine rates indicated that dark-rearing may only temporarily restrain the growth pattern. Based on his questionable assertion of permanently arrested development of dendritic spines, Valverde proposed that the "distribution clearly indicates the existence of at least two populations of segments in different pyramidal cells: Those that we assumed to have recovered a normal number of spines (having a mode of 80) and those that retained a low number of spines (having a mode of 28)." He also presented "representative examples," photographs of dendrites of light- and dark-reared animals. If these "representative examples" were in fact accurate representation of the effects of the differential manipulations, the differences reported would have been much more pronounced. Valverde suggested, on the basis of these examples, that, "the absence of dendritic spines in mice raised in dark-
ness is demonstrable not only along the entire apical shaft but also in the basal dendrites which in many cases appear almost devoid of spines." This latter assertion was not supported by any data in the paper.

Coleman and Riesen (1968) analysed the effect of dark-rearing on cortical dendritic fields in cats. The results indicated that there were no length differences in first- and second-order dendrites of layer IV stellates of the visual cortex. However, it was reported that third-order dendrites were significantly shorter in the dark-reared animals. The general trend suggested that dark-rearing decreased the probability of branching of stellate cell dendrites in layer IV. Layer V stellates were not significantly affected by dark-rearing. Coleman and Riesen did not propose a specific mechanism for the significant alteration of layer IV stellates, but they suggested that, "neuronal systems deprived of input or stimulation show a greater variability in quantitative aspects of their dendrites than do their normal controls." They further speculated that lack of stimulation may allow a greater manifestation of genetic variability, while stimulation may tend to drive neuronal systems toward some common point. This speculation is consistent with the selective preservation model in which experience is thought to "fine-tune" the inherent genetic variability during neural development by stabilising synapses which would otherwise be lost.

Borges and Berry (1976) reported that in dark-reared albino rats, stellate cell dendritic fields were oriented
primarily above the soma. This was seen in three layers in the visual cortex, whereas in controls the dendritic material was primarily localized below the cell body. Borges and Berry's (1978) measurements suggested that these field changes resulted from differential branching and growth and not from the reorientation of existing dendrites. This change in polarization permits speculation as to the underlying mechanism whereby superficial dendrites showed precocious growth, relative to controls, while deeper dendritic growth was retarded in the dark-reared group. Borges and Berry (1976) suggested that this effect was mediated by greater synaptogenic activity in the superficial laminae, relative to the lower layers.

**Effects of Enucleation.** Physical damage to the periphery is an extreme form of visual deprivation, but one which has provided further insight into the role of peripheral input in the growth and maintenance of the visual system. Tsang (1937) observed a reduction in the diameter of the optic nerve, a substantial reduction in the size of the LGN, and a diminution of the visual cortex in neonatally enucleated rats. Rosenzweig et al (1969) observed a 6% reduction in the weight of the visual cortex in rats enucleated at weaning. Similarly, Gyllensten et al (1967) found a significant reduction in cortical thickness at two and four months after bilateral enucleation. They also found decreases in internuclear material per cell nucleus in each layer of the visual cortex compared to dark-reared rats, as well as more marked decreases in the LGN and
superior colliculus. The effects of enucleation may involve both reduced specific afferent input (due to retinal axon degeneration) and a decrement in trophic or metabolic factors to the denervated cells.

Fine structural changes have also been observed in enucleated animals. Valverde (1968) unilaterally enucleated mice at birth and studied the effects after 24 and 48 days. He counted spines in several regions along layer V apical dendrites. Valverde found 25% and 12% fewer spines per unit length in layers IV and III, respectively, of the deprived hemispheres at 24 days relative to controls. This difference was attenuated in layer IV at 48 days, while no differences were found in any samples taken in layer V.

Valverde (1968) analysed stellate neurons with ascending axons from layers III and IV of unilaterally enucleated mice. At day 48 Valverde observed that in the hemisphere contralateral to the enucleated eye stellate cell dendritic fields were oriented away from layer IV. That is, stellates in the layer III/IV boundary had the majority of their dendritic fields in layer V, whereas in controls the dendritic fields were equally distributed above and below the soma. This contrasts with the Borges and Berry (1976; 1978) results discussed above in which dendrites of stellate cells were generally oriented upwards in dark-reared rats. Valverde stated, "The major difference is obvious; stellate cells from the affected area striata of enucleated animals showed a clear ten-
dency to direct dendrites towards layers III and V as if they were looking for other axonal relations outside layer IV." Unfortunately Valverde did not support this statement quantitatively, but rather based this point on the appearance of a few "randomly" drawn cells from normal and enucleated hemispheres. These "randomly" drawn cells are technically not equivalent across groups, for it is apparent from the figures presented that there exist marked differences in the locations of the cell bodies in each condition. Because Valverde (1968) did not provide a quantitative analysis, the question of dendritic orientation of stellates remains unresolved.

Proposal

This study is a quantitative analysis of the effects of unilateral enucleation upon stellate dendrites in layers III and IV of the striate cortex of rats. Borges and Berry (1976, 1978) have quantified stellate dendrites in the visual cortex in rats subsequent to dark-rearing. They provided evidence that in dark-reared rats stellate neurons have a significantly higher dendritic density present in the upper-half of the averaged dendritic field in layers III-IV, IV, and IV-V, relative to light-reared controls. Their measurements of branching indices have suggested that these field changes resulted from increased branching and growth in the superficial domain, rather than the reorientation of dendrites. Valverde believed that the changes observed in dendritic fields were due to
orientation changes as a consequence of unilateral enucleation. Unfortunately, Valverde did not provide quantitative data on stellate neuron dendritic fields.

This study was designed to quantitatively examine the hypothesis that stellate cells in the layer III-IV region of the visual cortex of unilaterally enucleated rats have dendrites which are oriented away from layer IV, relative to controls, and to attempt to determine by quantitative comparison with controls whether this represents a shift in dendritic mass (reorientation) or a relative increase in superficial material (growth). The present study differs from that of Valverde in that a stratified sample of visual cortex stellate cells is used. In addition, a sufficiently large sample of subjects and neurons is used to prevent intra- and inter-subject variability from influencing the overall pattern. Finally, the data collection system used here allows three-dimensional analysis of dendritic fields, in contrast to the prior studies. Two dimensional analysis would increase the apparent polarity of neurons, since for dendrites traveling in the vertical direction as well as in the horizontal direction (toward or away from the microscope lens), only the vertical component is recorded.

Methods

Subjects

Fourteen hooded rats (Stock source: Simonsen laboratories, Gilroy, CA.) were born and reared on a normal diurnal light/dark cycle. Male and female subjects were
housed with their mother and littermates throughout the
experiment. Each litter was housed in an opaque plastic
tub cage (46x24x14 cm) with a wire top and was given
Purina Laboratory Chow and water ad libitum. On the day
after birth the litters were culled to nine rat pups
per litter and were unilaterally enucleated. Each litter
contained approximately equal numbers of male and female
subjects. All animals were sacrificed on day 30. Subjects
were derived from three separate litters.

Histological Procedures

On the day of sacrifice each animal received an
overdose of sodium pentobarbital. The brain was then
quickly removed without perfusion and put into Golgi-
Cox solution for 21 days. 4 to 5 mm thick coronal slabs
were embedded in 16% cellodoin. Coronal sections 150
microns thick were obtained, developed with ammonia,
and mounted on slides in Permount with a coverslip.

Neuron Sample

Twelve stellate neurons from each hemisphere were
drawn from the fourteen animals, for a total of 336 cells.
Stellate cells were traced from area 17 in a region
comprising the lower aspect of layer III and the upper
aspect of layer IV. Cortical ratios were determined
from comparable Nissl stained sections. The neurons
were sampled by two microscopists using a stratified
sampling procedure. The cells were located at approxi-
mately 2500, 3000, and 3500 micron distances lateral
to the midline. The microscopists traced only stellate cells within a 50 micron radius of these distances, which corresponded to approximately half the field of view under the power in which the cells were drawn. This technique reduced selection bias as very few traceable cells were located in these small regions. A traceable cell was defined as a stellate cell of any type which were impregnated well and were centered in the section, such that truncation of dendrites was minimal. The slides were coded such that neither microscopist had knowledge of the treatment condition of individual hemispheres.

**Data Collection**

Neurons were traced at 500X magnification. A Zeiss Universal microscope linked to a Nova 3/12 minicomputer was used for data acquisition. This system (DeVoogd et al, 1981) allows the experimenter to store in the computer three dimensional coordinates of the dendritic processes emanating from the stellate cells.

**Data Analysis**

The drawings were analyzed in two ways. First, the number of intersections of the dendrites with each of a series of concentric shells at 10 micron intervals from the cell body was recorded (after Sholl, 1956). This gave a general indication of dendritic branching patterns and a good estimate of the dendritic processes. The second analysis involved a computer program in which
the three-dimensional dendritic field was divided into conical sections at 30 degree intervals starting from the dorsal position. The number of intersections of dendrites within sections of shells in this compartment was analyzed. Data were statistically evaluated by ANOVA.

RESULTS

Enucleation effects

The factor of enucleation was not statistically significant. The treatment condition did not affect the number of intersections in any of the individual bins. Similarly, treatment effects were not found in either the evaluation of the dorsal or in the ventral domain of the dendritic fields. Additionally, no effects of enucleation were found in the analysis of the entire dendritic field.

Subject effects

The effects for the factor of subjects was not statistically significant in any of the analyses. The probabilities for this factor is presented in Table 1.

Sex effects

The factor of sex was statistically significant in the majority of parameters evaluated. The dendritic pro-
cesses were significantly affected in the region of bins 2, 3, and 4. This result is demonstrated in Figure 3.

Similarly, significant sex effects were found throughout the entire dendritic field as well as the dorsal region. No statistically significant effects were found in the ventral domain of the dendritic field. These data are presented in Table 1.

**Interaction effects**

Effects were not found in any analysis concerning treatment x subject or treatment x sex. The statistical results of these analyses are presented in Table 1 and shown graphically in Figures 4 and 5.

**DISCUSSION**

The results of this study are not consistent with much of the prior literature. Valverde (1968) observed that the dendritic processes of stellate neurons localized within and around layer IV of the visual cortex contralateral to the enucleated eye were oriented such that the majority of their mass was directed away from layer IV. In this paper Valverde suggested the existence of compensatory mechanisms which affect significantly the intrinsic organization of the visual cortex. The results of the present study indicate that unilateral enucleation does not significantly affect dendritic orientation. Valverde (1968)
did not provide quantitative evidence to support this orientation effect. Valverde provided only a composite drawing of a few stellate cells located around layer IV. This diagram does not detail whether there was in fact any statistical difference between stellate neurons from normal and enucleated subjects. Additionally, these "randomly" drawn cells do not appear to be equivalent across groups as there exist marked differences in the sublaminar locations of the cell bodies in the two conditions. The present study used a sufficiently large stratified sample to permit statistical analysis. The analysis in the present study does not indicate that enucleation causes differential orientation of stellate cell dendrites in the area striata.

Borges and Berry (1976; 1978) described a shift in dendritic polarisation subsequent to dark-rearing. In these papers they reported that dark-rearing caused the highest dendritic density to shift from below the soma to above it. Their branching indices suggested that these field changes resulted from increased growth in the superficial region and not from the reorientation of dendrites. The present study is not entirely consistent with this differential growth pattern: no change in dendritic density subsequent to enucleation is evident. Comparison between Borges and Berry (1976; 1978) and the present study is clouded by three issues. First, the manipulation in the former studies was dark-rearing, whereas the present study used enucleation. Enucleation completely eliminates
transmission of neuronal activity from the retina to the LGN, as the retina is surgically removed. Dark-rearing does not surgically alter the visual system; spontaneous activity, in addition to trophic factors, still are transmitted between the retina and the LGN. While both manipulations involve severe visual deprivation, one can not consider the manipulations to be equivalent. Second, Borges and Berry (1976; 1978) used albino rats; the present study used hooded rats. For the present study hooded rats were chosen because several anatomical anomalies have been noted in the visual system of albino animals (Montero et al 1973; Guillery et al 1971; Hubel and Wiesel 1971). Finally, dark-rearing appears to have metabolic consequences which enucleation does not. Mos (1976) reported that dark-reared rats weighed less than those reared in the light. This could affect neuronal growth.

The results of this study are more compatible, however, if sex differences are considered. Similar to Borges and Berry (1976; 1978), the male rats in this study have a greater dendritic density localised above the somata, and this tendency is somewhat more pronounced in the cortex opposite the enucleated eye. The females in this study have a greater dendritic density below the cell body regardless of condition and there is no apparent enucleation effect. These data are consistent with some reports indicating that various conditions affect males to a greater extent than their female counterparts. Sackett (1970; 1972) demonstrated a sex difference in the behavioral response to isolation rearing in rhesus mon-
keys. The data of these reports suggested that females are more resilient to the manipulation than are males. Similarly, Juraska and Greenough (1979) demonstrated differential sexual susceptibility in a neuroanatomical study following various postweaning environments. Juraska and Greenough (1979) noted a significant sex by environment interaction in a complex environment in which males had more outer dendritic material than females. While the present study does not demonstrate a significant sex by treatment interaction, there is a significant sex difference. The present study suggests that there is a sexual dimorphism in rat visual cortex. Continuing research may provide evidence that rodent brains are more sexually dimorphic than has previously been believed.

The question regarding the effects of dark-rearing remains unresolved. Prior research has demonstrated that dark-rearing brings about changes outside the visual system. These effects include changes in total body weight as well as various organs (Eayrs and Ireland 1950; Mos 1974; Mos 1976). Similarly, changes subsequent to dark-rearing of rats have been demonstrated behaviorally, emotionally, and physiologically (Eayrs and Ireland 1950; Mos 1974; Mos 1976). It has not been demonstrated that the reduced visual system activity involved in dark-rearing is the factor affecting the neuronal growth pattern in the cortex; metabolic, hormonal, cyclic or other factors may be important or even causal in nervous system effects of dark-rearing. Monocular enucleation, on the other hand, has not been shown to produce the additional consequences
that dark-rearing has, and, in fact, body weight deficits were not apparent in the animals used in the present investigation. Prior to the present study no one has measured total dendritic length following enucleation. The present study demonstrates that the effects of enucleation are very small. It is suggested that dark-rearing may bring about more changes than those arising from reduced visual system activity; the effects of visual deprivation may in fact be very subtle.
REFERENCES


Minke, B., and Auerbach, E. Latencies and correlation in single units and visual evoked potentials in the cat striate cortex following monocular and binocular stimulations. Experimental Brain Research, 1972, 14: 409-422.


Figure Captions

Figure 1. Method used to determine dendritic distribution in the visual cortex. Conical sections represent boundaries used to quantify the amount of dendritic mass in various orientations around the somata.

Figure 2. Relationship between mean number of ring intersections and bin orientation in enucleated and non-enucleated stellate neurons.

Figure 3. Relationship between mean number of ring intersections and bin orientation in stellate neurons from male and female subjects. (p < .009).

Figure 4. Relationship between mean number of ring intersections and bin orientation in enucleated and non-enucleated stellate neurons from male and female subjects.

Figure 5. Relationship between total mean ring intersections and bin orientation in enucleated and non-enucleated stellate neurons from male and female subjects.
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FIGURE 1
Pie meter

White matter
FIGURE 3

Mean ring intersections per neuron

BINS
FIGURE 5

Mean ring intersections for enucleated and non-enucleated groups, separated by gender.