A BEHAVIORAL AND ANATOMICAL EXAMINATION OF THE

INTRAMODAL AND INTERMODAL EFFECTS OF EARLY STIMULATION HISTORY

AND SELECTIVE POSTERIOR CORTICAL LESIONS IN THE RAT

By

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A B S T R A C T

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The aim of this study was to investigate the intra- and intermodal impact of different kinds of early sensory experience on the development of specific neural/perceptual systems. The manipulations of the rats' early experience involved a combination of early binocular deprivation through dark-rearing, somatosensory restriction through cauterization of mystacial vibrissae, and multimodal enrichment through rearing in a complex environment. Specific lesions to somatosensory (Par1) and visual (Oc2M) cortex in differentially reared animals were included in an attempt to gain further insight into the plasticity surrounding manipulations of early stimulation history.

Five tasks were used to assess these effects of early rearing condition in combination with later cortical lesions. Behavioral assessment focused on the ability of the animals to encode, abstract, and remember specific relationships between

stimuli within the deprived modality itself, their ability to do so with information presented in other modalities, and on the basic species specific behavior. The only effect found was a main effect for rearing condition. Basically, complex-reared rats were more competent on several of the behavioral tasks than were dark-reared rats. However, this result provided little behavioral support for ideas of modality interdependence.

Dendritic proliferation is considered to be a general mechanism supporting behavioral change. The subsequent neuroanatomical assessment focused on dendritic branching of neurons in specific cortical areas thought to be most affected by early environmental manipulations. Animals that were raised in a complex environment, but had experienced early tactile restriction through cauterization of vibrissae, showed significantly more dendritic branching than animals from all other rearing conditions in all cortical areas measured. This finding is consistent with ideas of both intra- and intermodal compensation following damage to an early developing modality, as well as behavioral demand acting as a significant factor in determining the impact of early somatosensory restriction.

It is reasonable to assume that anatomical changes should be manifested behaviorally. Suggestions for smaller, more restricted studies, that would be more effective in describing the behavioral impact of early manipulations of the environment, were outlined.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Introduction

For investigators interested in the general principles underlying behavioral plasticity, the effects of early stimulation history on the development of sensory and perceptual competencies have been an important and active area of study (Aslin, 1981; Greenough, 1976; Tees 1976, 1986). The role that environmental input plays in determining the course of perceptual development is multifaceted. Gottlieb (1976, 1983) defines three primary ways in which experiential and genetic factors could theoretically interact in the development of perceptual abilities. Maintenance describes the situation where a particular perceptual ability is already fully established, however, the subsequent appearance a specific environmental factor is necessary to maintain the ability. Should the organism not have the experience, the perceptual ability declines. In facilitation the development of a perceptual ability is accelerated or augmented by the availability of specific experiences. The role of experience is also important in the case of induction. Here, the nature of a perceptual ability would be altered depending on specific experiences available to the organism. Other investigators (Aslin, 1981; Tees, 1990) have contributed to further elaborations of the Gottliebian framework describing the interaction between experience and genetics. Aslin (1981) emphasizes that the nature of experience that is influential is different at different stages of development.

In any case, the use of three somewhat distinct manipulations of early experience - deprivation, biased rearing, and enrichment - have emerged as techniques to help expose some of the interactions between genetic and experiential factors. Differences, or lack of differences, found when comparing the behavior of animals reared under different conditions have established the relative contributions normally made by experiential factors to specific discriminative behaviors. With respect to competencies that could be measured shortly after birth, such techniques could be easily adapted to examine whether sensory experience played a role in their subsequent development. In many cases involving the impact of controlled rearing, there appears to be a common mammalian response to such environmental manipulations (Tees, 1990), and the altricial (immaturely born) rat with its rapid post-natal neural and behavioral development time frame have made it a useful animal model for controlled rearing research.

For a variety of reasons, including the relative ease with which one can alter early visual stimulation history, the role played by experience in the physiological and neuroanatomical development of the visual system and related behaviors has been the prime focus of much of the work utilizing controlled rearing paradigms (reviewed by Boothe, Vassdal, & Schenk, 1986; Mitchell & Timney, 1984; Tees 1986, 1990). Eliminating all visual stimulation by rearing in complete darkness has been a common environmental manipulation. Many of the effects of dark-rearing are observed at the level of the cortex (Mitchell & Timney,

1984). In part, dark-rearing leaves the cortex in a "nonspecified state", which retains considerable capacity for change when dark-rearing is followed by a period of visual stimulation (Freeman, Mallach, & Hartly, 1981). However, the extent of potential recovery often becomes less as the length of deprivation period increases. Visual deprivation appears to lead to some atrophy of cortical function (for review, see Mitchell & Timney, 1984).

Behaviorally, some abilities appear unaffected by dark-rearing. For example, no significant differences between light and dark reared animals have been found on their ability to resolve detail (Friedman & Green, 1982). Other abilities, however, are affected. On tests of depth perception, visually guided behavior, and form perception, the performance of dark reared rats is generally reduced in comparison to control animals (Tees, 1990). It is important to note that although the competence of dark reared rats is adversely affected, it is not eliminated.

For example, in a test of depth perception, dark reared rats are able to discriminate between the shallow and deep sides of a visual cliff provided the difference between the two sides is at least 20 cm. They perform significantly worse than light-reared controls, only when tested on smaller differential depths. Aspects of visually guided behaviors appear to be preserved in dark-reared rats in spite of their lack of visual experience. For example, dark-reared rats exhibit levels of light seeking behavior comparable to those of light-reared rats

(Tees, Midgley, & Bruinsma, 1980). However, when more complex visual stimuli are utilized, dark-reared rats exhibit some lack of orientational responsiveness over a wide part of their visual fields (Midgley & Tees, 1983). A specific effect of dark-rearing is also seen in form perception. Although, dark-reared rats are as able as light-reared rats to isolate figure from ground (Tees, 1968), acquire various kinds of discriminations involving differences in orientation of visual stimuli (Tees, 1979), and generalize along the dimension of angular orientation (Tees, 1972), such visually deprived animals take much longer than light-reared controls to learn pattern discriminations when the differences between patterns involve relational properties between sets of lines (Tees & Midgley, 1982).

Unimodal restrictive controlled rearing has also been utilized extensively but more selectively in respect to another sensory system, the somatosensory system. Although the somatosensory system has diverse inputs from a variety of unique receptor structures, most investigations have focused on the receptors stimulated by the mystacial vibrissae of rodents (Gustafson & Felbain-Keramidas, 1977; Kaas, Merzenich, & Killackey, 1983). The mystacial pad represents the single largest portion of the somatotopic map of the somatosensory cortex of the rat (Figure 1). Receptors located within the hair-follicle of each vibrissa project contralaterally to an individual field of cortical cells referred to as a "barrel" because of its distinctive shape (Welker, 1976; Woolsey & Van Der Loos, 1970). A great deal of physiological and anatomical

evidence (Kaas et al., 1983) has accumulated on the reorganization, or plasticity, that takes place following early sensory restriction resulting from the cauterization and removal of vibrissae in new born animals. Such deafferentation prevents the development of the barrel organization at the cortical level and there seems to be a sensitive period for these effects involving a "window of time", possibly closing between post natal days 7-10.

Although vibrissae are thought to play an important role in the interactions of the rat with its environment, the intermodal behavioral effects of vibrissae removal have not been comprehensively documented. Early research revealed few types of behavior that are guided solely by the vibrissae (Gustafson & Felbain-Keramidas, 1977), a result that is surprizing in light of the anatomical and physiological evidence. Rats appear to be able to adopt different behavioral strategies to compensate for vibrissae loss. Those behaviors for which vibrissae are considered important, such as tactile discrimination and several types of locomotion, have all, to some degree, survived vibrissal removal (Keramidas, 1976). The removal of vibrissae has been shown to decrease the size of gap in an elevated runway that a rat will jump across (Hutson & Masterton, 1986). The vibrissae extend the reach of the rat; removing them decreases their contact with the surrounding environment and thus decreases their range of movement. In a more recent study, a battery of sensorimotor tests was used in an attempt to illuminate some of the behavioral effects of early vibrissal

Figure 1. The representation of vibrissae receptors by their
corresponding barrel formations in the contralateral
primary somatosensory cortex (Par1) of the rat.

Normal Barrels
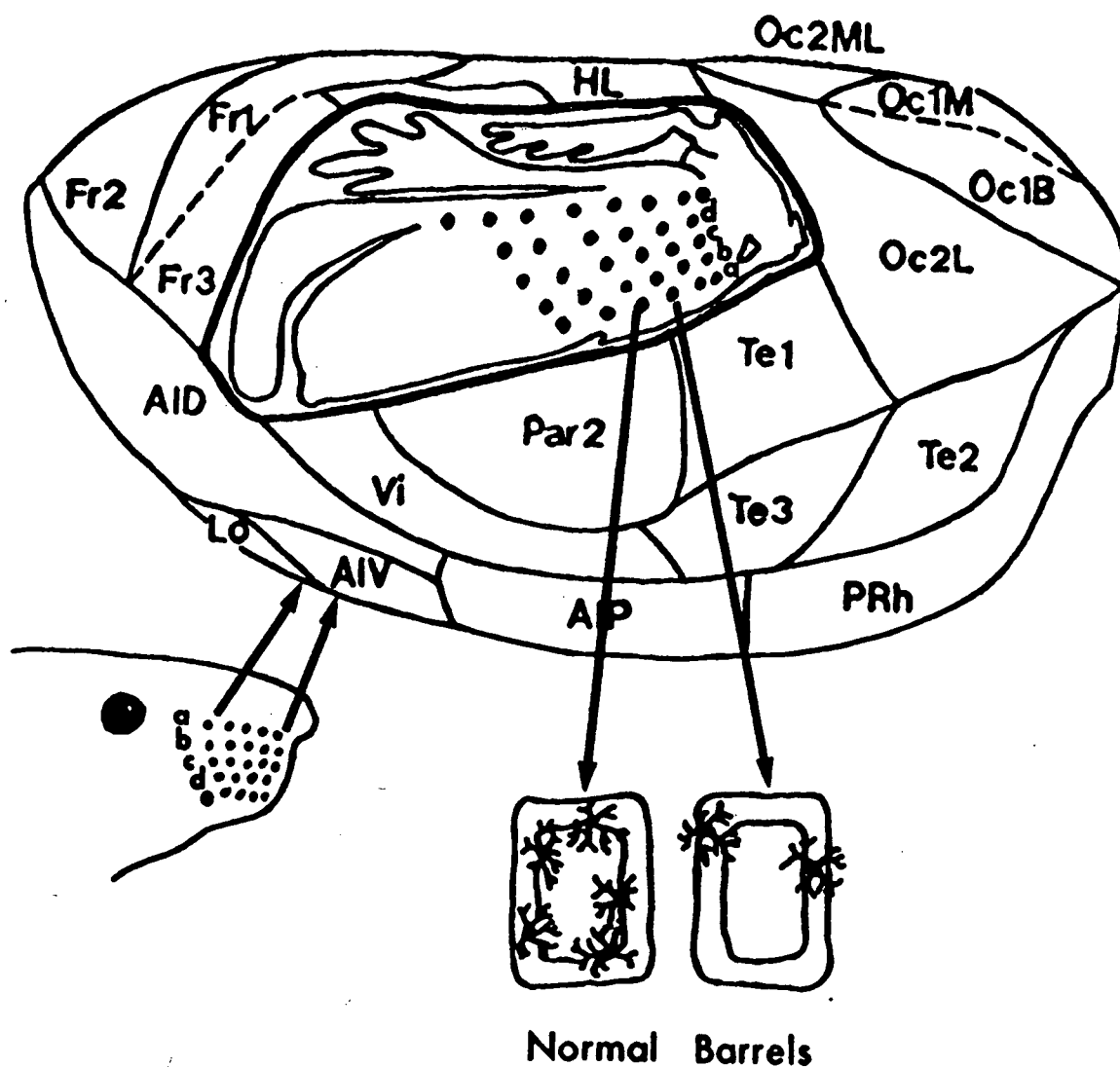
removal (Symons & Tees, in press). All early dewhiskered animals, regardless of rearing condition, displayed attenuated orientation to light tactile stimulation to the mystacial pads themselves.

In addition to intramodal consequences of unimodal deprivation there has been renewed interest in intermodal consequences of unimodal restriction. Differential experience in one modality could have consequences for the development and functioning of other sensory systems (Burnstine, Greenough & Tees, 1984; Gottlieb, 1971; Turkewitz & Kenny, 1982). Gottlieb (1971) outlined an invariant sequence in which sensory systems develop in vertebrates (Figure 2). The tactile system becomes functional first, followed by the olfactory and auditory systems, with the visual system coming on line last. Turkewitz and Kenny (1982) suggested that this sequence may facilitate the organization of sensory systems and provide the basis for subsequent perceptual development. Instead of having to contend with incoming information from all sensory systems at once, neonates would deal with limited information related to the sensory modalities that are functional at that stage in development. This filtering of information could also be observed with respect to the nature of signals within a single modality. When a system first becomes functional, the neural system is relatively primitive. Gradually, the system evolves and is able to encode and utilize progressively more complex information received within that sensory modality. These limitations, resulting from the staggered onsets of sensory

Figure 2. The ontogenetic sequence of emergence of sensory systems. (From Gottlieb, 1971).

visual

auditory

olfactory

vestibular

somatosensory

age
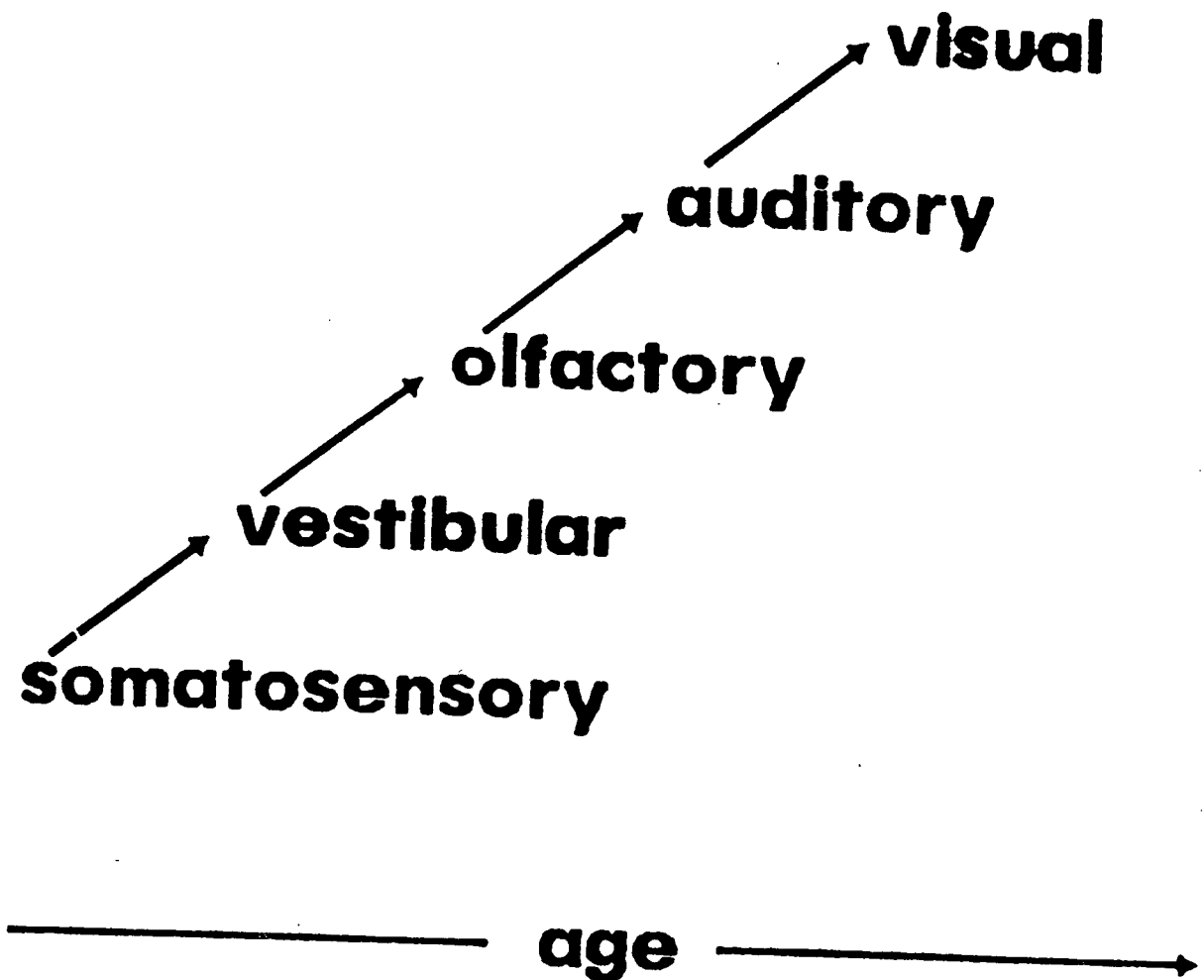
systems, provide an evolving structure into which environmental stimulation can be organized (e.g. Tees 1990).

Differential onset of functioning in each modality seems to reduce competition during development and results in relative independence between emerging systems (Turkewitz & Kenny, 1982). Competition, both intra- and intermodal, has an important impact on neural and behavioral ontogenies. For example, in kittens when one eye is placed at a competitive disadvantage through suturing, the nondeprived eye expands its "territory" into the neural space that normally receives stimulation from the deprived eye (Cynader 1979; Wiesel & Hubel 1963). A similar expansion is also observed in the somatosensory neural representation in rats. Eliminating a row or column of mystacial vibrissae in rodents leads to disruption of normal barrel formation. The barrels of the adjacent intact vibrissae expand into the neural space that normally receives stimulation from the cauterized vibrissae (Van Der Loos & Woolsey 1973).

Turkewitz and Kenny (1982) have suggested that the earlier stages of development of a system are characterized by increasing competition within that system and limited competition between different sensory systems. As a new sensory system comes "on line" intermodal competition becomes more prevalent. During this time, intermodal competencies may develop as a result of such competition. For example, with respect to neural development, Cynader (1979) found a decrease in the number of cells responding to visual stimulation in the deep (multimodal) layers of the superior colliculus of the cat

following dark rearing. Presumably, dark rearing would have put the visual system at a competitive disadvantage to the auditory and somatosensory systems, allowing these systems to have a greater influence on the responding of cells in that area, and take over groups of cells formerly responsive to the visual system. At the level of the cortex, limiting somatosensory or visual input can result in hypertrophy of areas representing other sensory modalities. In another study, blinding rats through enucleation, or limiting somatosensory input through cauterization of vibrissae at birth, led to an increase in dendritic spine density in the auditory cortex when examined at 25 days postnatally (Ryugo, Ryugo, Globus, & Killackey 1975). The somatosensory cortex of enucleated animals, and the visual cortex of cauterized rats did not show a similar increase. However, when long-term dewhiskered rats were studied at a more mature age (270 days), there was evidence of a thickening of the visual cortex (Keramidas, 1976).

There is limited evidence on the significance of intermodal competition at the behavioral level. Kittens with reduced tactile input through clipping of vibrissae were found to discriminate between shallow and deep sides of a visual cliff at younger ages and with greater consistency than controls (Turkewitz, Gilbert, & Birch, 1974). Rats that experienced early somatosensory restriction by vibrissae cauterization take longer to habituate to repeated visual stimuli and are more likely to orientate to subtle changes in these stimuli than are control rats (Symons & Tees, in press). This was true only for

animals reared with daily access to an enriched environment. In another study, long-term dewhiskered rats were faster to acquire two visual discriminations than were intact animals (Keramidas, 1976). Finally, blinded mice raised in tactile enriched early environments showed a vibrissae-triggered placing response to a greater distance than did sighted controls.

The normal pattern of competition between developing systems can also be altered by the premature availability of information from a sensory system. Kenny and Turkewitz (1986) examined the effects of early eyelid opening on the rat pups' homing behavior. Initially, homing has been shown to be under the control of thermal and olfactory cues (Freeman & Rosenblatt, 1978). Following eye opening, visual orientation to the home is gradually developed. Interestingly, these phases match the developmental sequence of sensory modalities. When visual information is made available earlier that normal through surgically opening the eyelids, homing behavior persists at an age when it normally declines (Kenny & Turkewitz, 1986). Availability of visual input before thermal and olfactory patterns of homing were established resulted in the development of an abnormal visually based pattern of homing. Early eye opening also affected later development of the olfactory system. Those pups receiving early visual exposure did not discriminate between shavings from the home cage and shavings with different odors at an age where their litter mate controls were making such discriminations (Celenza, Kenny, & Turkewitz, 1984).

Ideas about modality interdependence, such as the ones outlined above, lead to two hypotheses regarding potential outcomes of any early restriction of, or damage to, one modality, on the subsequent development of the remaining intact modalities: 1) early restriction of sensory input in one modality could result in intermodal compensation due to lack of competition from this restricted modality; 2) early restriction of sensory input into an early developing modality might disrupt the emerging organizational framework necessary for a competency which involves signals of a later developing modality. Evidence to support the first hypothesis has been presented above in the discussion of competition. Limited behavioral support for the second hypothesis is also available. For example, on a task of auditory localization, early blinded rats performed more poorly than late blinded or sighted rats (Spigelman, 1969). Obviously, in particular instances evidence for one of these hypotheses doesn't preclude the discovery of evidence for the other cases. Particular competencies and sensory systems could be differentially affected by the manipulations of early stimulation history (Tees, 1990). Presumably, because the somatosensory modality is the first to develop, the impact of early restriction of this modality could potentially be the greatest.

As mentioned earlier, the controlled rearing paradigm has also been used by investigators who have focused on the effects produced by multimodal complex rearing (Juraska, 1990; Rosenzweig & Bennett, 1977). Whereas restrictive manipulations

are hypothesized to impede the development of perceptual competencies and biased rearing to alter it in a specific way, exposure to a general complex environment is traditionally viewed as accelerating development. Typically, an complex environment consists of daily exposure, in groups, to a large cage in which there are a variety of visual, tactile, and auditory stimulus objects for the animals to interact with. Positive results from exposure to a complex environment have been reported regardless of the age at which exposure occurred; however, the most dramatic effects have resulted from exposure during the early developmental period.

In comparison to rats reared under normal laboratory cage conditions, rats reared in enriched environments show increases in the weight and thickness of the cortex, in the number of synapses and dendritic spines per neuron, as well as in the overall amount of dendritic branching in the cortex (Rosenzweig & Bennett, 1977). Interestingly, many of these same cellular indices decrease following dark rearing (Tees, 1990). However, the hypertrophy that results from early complex rearing is not seen in all cortical areas. Dark rearing and complex rearing seem to preferentially affect neurons in the temporal and parietal association cortex, but not those in the frontal cortex (Greenough, Volkmar, & Juraska, 1973). Behaviorally, rats reared in a complex environment are superior to control rats in their performance on a variety of tasks, including reversal, alternation, and especially maze (spatial) tasks (Greenough & Juraska, 1979).

Burnstine et al. (1984) have argued that increasing environmental complexity augments ongoing behavioral demand. Clearly, the demands placed on a subject living in a laboratory environment are different from those existing for animals living in a natural environment. Behavioral differences and deficiencies might go unnoticed simply because the demands placed on the animal are not sufficient to reveal them. Intermodal compensation, and its related neural substrates of functional reallocation and compensatory hypertrophy, resulting from deprivation of one kind of sensory input, might be more evident in animal studies with more demanding conditions, both in rearing environment and test situation (Burnstine et al., 1984; Tees, 1990). Whatever the underlying mechanisms, increasing behavioral demand would be an important investigative tool in looking at the changes resulting from controlled rearing situations.

The degree to which development of perceptual competencies was altered by manipulations of early experience including dewhiskering, dark rearing, and complex rearing, seems to be more diffuse than that observed with specific cortical lesions (Tees, 1990). However, some modules seem more affected than others (Table 1). The operations that were vulnerable to changes in early stimulation history could be characterized as requiring trade-offs between an appreciation of aspects of the environment and remembering specific features while ignoring others. These competencies seem to involve memory, attention and appreciation of spatial aspects of the environment. In this

Impact of Multimodal and Unimodal Environmental
Manipulations: Behavioral Evidence*

Limited Effect	Considerable Effect
1. Ability to resolve detail (Gratings)	Ability to recognize stationary patterns on the basis of relationship between lines (contour separation, contour interaction)
2. Ability to recognize visual stimuli on the basis of angular orientation cues	Ability to acquire and remember spatial map of environment and to navigate to invisible targets
3. Ability to orient (respond) to external movement	
4. Ability to localize and respond to large visual stimuli	Ability to orient to spatial and temporal changes in pattern or visual events
5. Ability to recognize crossmodal attribute of duration and intensity of auditory and visual events	Ability to recognize crossmodal attribute of location of auditory and visual events

* Partial list of competencies whose development is altered by multimodal complex rearing or unimodal restrictive rearing. The evidence supports the idea that the impact of early stimulation history is limited in the case of the abilities listed on the left where as it is considerable in the case of those listed on the right (from Tees, 1990).

Table 1. Description of the behavioral impact of multimodal and unimodal environmental manipulations.

regard, lesion studies on the functioning of extrastriate, posterior parietal, and temporal cortex suggest that these cortical regions may be important to the integrity of such competencies (Kolb, 1990).

Our knowledge of the intermodal consequences of early unimodal restriction is severely limited. Although there is limited neuroanatomical support for both of the Turkewitz and Kenny (1982) hypotheses on the potential outcomes of early restriction of one modality, little suitable behavioral evidence exists. Obviously, the anatomical and physiological differences should be reflected in behavioral differences. More behavioral evidence is required for a clearer picture of what cortical operations are involved in a rat's perceptual reactions.

One promising strategy to test ideas about the target of experientially induced plasticity is the direct use of specific surgical intervention in conjunction with manipulation of early stimulation history. In such an effort, we need to focus on those structures that behavioral (and neural) evidence indicate might be altered significantly by controlled rearing. In this study we have focused on two areas of the posterior cortex: somatosensory cortex (Par 1) and extrastriate cortex (Oc2M). Cortical and subcortical connections are shown in Figure 3.

1) Area Oc2M

Part of area Oc2M adjoins the medial border of Oc1, and has also been termed area 18, area 18b, or medial peristriate

Figure 3. Connections of primary and secondary sensory regions

to the posterior parietal cortex in the rat. (From

Kolb, 1990).
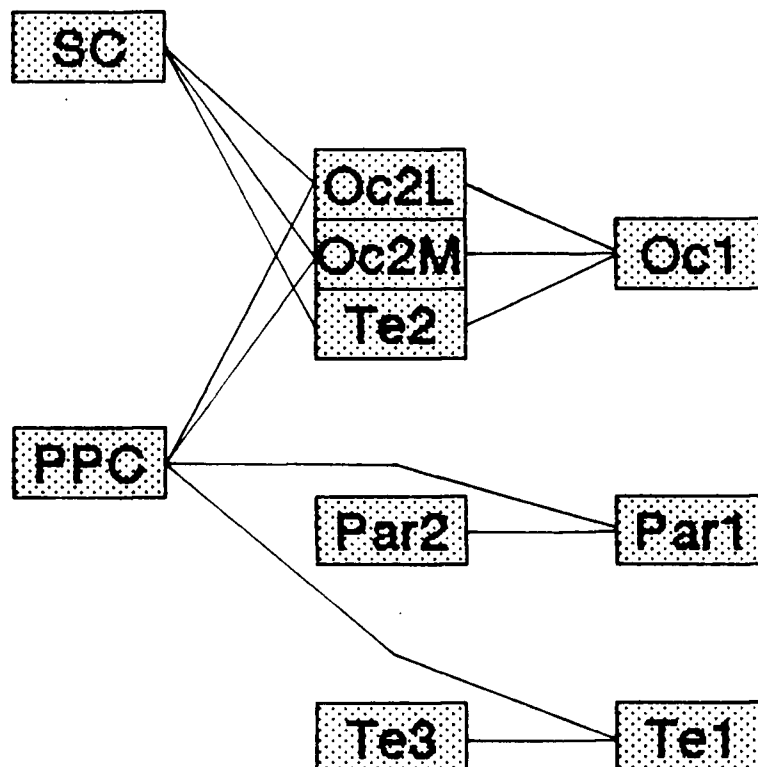
cortex. Further rostrally it adjoins the rostromedial boundary of Oc1 and there seems to correspond better with part of posterior parietal cortex (area 7). Area Oc2M receives a projection from Oc1 and from the lateral posterior nucleus (Dean, 1990). Two visual maps are contained within the area, both of which emphasize the peripheral field (Espinoza & Thomas, 1983; Olavarria & Montero, 1984).

The precise role of area Oc2M in rats can presently only be speculated on (Dean, 1990). In the majority of lesion studies area Oc2M is not removed alone, but as part of larger lesions in combination with other cortical visual areas. However, when area Oc2M is included in a given lesion, behavioral deficits appear on two types of tasks: those involving response to transient (suddenly appearing or moving) stimuli and those involving analysis of peripheral spatial cues for navigation. Midgley and Tees (1981) found posterior cortex lesions, including area Oc2M, reduced responsiveness to patterns of light flashes. Lesioning areas Oc1, Oc2M, and Oc2L together produced difficulty in detecting light onset, both peripherally and centrally (Overton cited in Dean, 1986). Recent findings (Overton & Dean, in press) suggest that lesions removing only area Oc2M may reduce sensitivity to dim light flashes. In another study where only area Oc2M was lesioned, rats were able to learn a brightness discrimination, but acquisition of a black-white pattern discrimination was retarded (McDaniel & Terrell Wall, 1988).

Both Goodale and Dale (1981) and Foreman and Stevens (1982) found large lesions to the posterior parietal cortex to impair learning on the radial arm maze spatial task. Smaller posterior parietal lesions, which included both the rostral portion of Oc2M and Oc2L produced deficits on both the water maze and the radial arm maze (Kolb & Walkey, 1987). More specific lesions which included only area Oc2M resulted in impaired performance by lesioned animals on the normal Morris water maze procedure as well as on the landmark version of the water maze task (Kolb, personal communication). Area Oc2M may also function to integrate spatial cues from different modalities. Following bilateral removal of area Oc2M, Pinto-Hamuy, Olvarria, Guic-Robles, Morgues, Nassal, and Petit (1987) found that rats were unable to discriminate between pairs of compound visual and somatic stimuli.

2) Area Par 1

Primary somatosensory cortex, area Par 1, contains a somatotopic representation or map of the rat's body. It is located anterior to visual cortex, adjacent to and actually partially overlapping the motor cortex. Par 1 appears to be selective for performance in sensory tasks which require an active movement component (Chapin & Lin, 1990). Hudson and Masterton (1986) found that the ability of the rat to collect situation-relevant information with its vibrissae is lost after the ablation of the corresponding cortical barrels. In their study, rats would jump a gap in an elevated runway after palpating the far side with their vibrissae only when

contralateral Par 1 remained intact. In addition, damage to this area appears to impair performance on tasks of palpitation, haptic exploration, active touch, tactile placing, and hopping (Chapin & Lin, 1990). In effect, area Par 1 is thought to be the sight of an integration of information from cutaneous and proprioceptive somatosensory submodalities with information from the motor cortex.

As mentioned earlier, complex rearing and dark rearing seem to affect functions in which extrastriate cortex would play a significant role. As far as dewhiskering is concerned, substantial cortical changes are observed in Par 1 with early dewhiskering; thus a surgical intervention that itself focuses on this region could provide interesting information. Will selective lesions of these cortical regions have more of an impact on dark-reared than on complex-reared? We certainly know that preoperative environments do have an effect on the impact of non-sensory cortical lesions and related tasks (Kolb 1990). Will Oc2M lesions have less of an impact on dark-reared than light-reared animals? The evidence suggests that the combination of dark-rearing and superior colliculus lesions (which projects to extrastriate cortex), but not the combination of dark rearing and Oc1 lesions, has a serious impact for the development of visuomotor orientation skills (Findlay, Marder, & Cordon, 1980). In looking at the impact of early developing modalities with respect to a later developing one, the somatosensory system is an ideal candidate if dewhiskering does

have intramodal consequences.   Exposure to complex rearing (ie.

increasing behavioral demand), should illuminate or augment the

effects of early somatosensory and/or visual restriction and

produce the greatest potential for evidence of intermodal

compensation.   Removal of area Oc2M will also serve to help

delineate the specific functions of this area.

In order to assess the consequences of early experience and

selective cortical lesions, a battery of five tests was used.

These tests encompassed both species specific and learned

behaviors.   The three species specific tasks were part of a

short test battery that was administered post-operatively.

There is some evidence to indicate that following early cortical

lesions, sparing of function is more common on learning tasks

than on tests of species typical behavior (Kolb & Whishaw,

1989).   This is possibly because on many tests of learning, more

than one strategy can be used.   The tests of species typical

behaviors are included in this study to determine if the impact

of early sensory deprivation on these behaviors is similar to

that of early cortical lesions.   Tasks included were measures of

grooming behavior, protection of food, and exploration of novel

objects in the environment.

The two learning tasks were selected on the basis of being

sensitive to posterior parietal cortex function.   A variation of

the Morris Water Maze task, developed by Symons and Tees (in

press), was used to assess spatial memory.   Variations of this

task have been used to assess the effects of various brain

lesions (Kolb & Walkey, 1987), and the ontogeny of spatial

behavior (Rudy, Stadler-Morris, & Albert, 1987). In this task rats are required to find a submerged platform hidden in a pool of water using the available proximal and distal cues. This task will assess differences in visual spatial behavior caused by differences in rearing condition and specific lesions.

To evaluate visual discrimination/memory, a second variation of the Morris Water Maze was used. Again, rats are required to find a submerged platform. However, in this version, the location of the platform is signaled by proximal cues of different patterns. Successful discrimination of, and memory for, two pairs of cues is required to locate the platform.

An increase in dendritic arborization has been correlated with enhanced behavioral abilities following complex rearing (Rosenzweig & Bennett, 1977), as well as with sparing of function following early cortical damage (Kolb, 1989, Kolb & Whishaw, 1989). In order to assess the effect of early rearing environment on cortical dendritic branching, brains of control animals from each rearing condition were stained by the Golgi-Cox method (Glaser & Van Der Loos, 1981; Kolb & McClimmons, 1986). Cells from somatosensory, visual, and auditory cortex were drawn and analyzed.

Methods

Subjects

The subjects were 84 male rats, from 19 litters, of the
Long-Evans (Rattus Norvegicus) strain, born and reared at the
biopsychology colonies at the University of British Columbia.
The general rearing conditions have been described previously
(Tees, 1968). The rats were raised in plastic maternity bins,
(25 x 47 x 20 cm), until 21 days of age. At this time they were
weaned and placed in groups of 3-6 in hanging wire mesh cages
(66 x 25 x 18 cm). Ad libitum food (Purina Rat Chow) and water
were available. At the time of testing, rats were separated
into single hanging mesh wire cages (20 x 25 x 18 cm). Testing
began at approximately 100 days of age. All rats weighed
between 350 and 500 g at the time of testing.

Environments and Rearing Conditions

Beginning on post-natal day 1-3, half of the animals (42
rats from nine litters) were assigned to be reared in complete
darkness. Conditions for dark rearing have been described
previously (Tees, 1968). Dark-reared (DR) animals remained in
dark conditions for the duration of the study.

The remaining animals (42 rats from ten litters) were
reared in the light and given enriched (complex) (CR) rearing
experience. The unique environmental conditions for complex
reared subjects began at 20 days of age. Exposure continued for
a minimum of two hours a day until the animals were 49 days of

age. This daily period of enriched environmental exposure has been reported to be as effective as long exposure, at least in terms of many neural and behavioral measures (Rosenzweig & Bennett, 1977; Rosenzweig, Love, & Bennett, 1968). The complex environment consisted of a tall, wire mesh chamber (180 x 92 x 62 cm) with a Sanicel covered floor and two Sanicel covered bridges, located approximately 20 and 40 cm above the floor. Wire mesh ramps connected the bridges with one another and with the bottom of the chamber. The environment was filled with an assortment of toys and objects of varying sizes, shapes, and textures, some of which also produced noise when manipulated by the animals. Objects were changed and moved around daily (Greenough & Green, 1981). Hanging from the shelves, ramps, and ceiling were bells and chimes which also produced sound when contacted. Two such environments existed. Groups were placed in each field on alternating days.

Complex reared animals maintained a 12:12 hour light/dark schedule throughout the experiment. Behavioral testing was performed during the animals' light cycle.

Surgery

One half of both the dark reared and complex reared animals underwent complete removal of their mystacial vibrissae through cauterization of the vibrissae follicles. In order to ensure that vibrissae removal occurs before the initial development of the posteromedial barrel field all animals were operated on within 3 days of birth (Kerimidas, 1976). To avoid placing

dewhiskered pups at a competitive disadvantage in comparison to intact littermates, animals were assigned to undergo the cauterization procedure by litter. Litters were assigned randomly. Five litters in the light reared condition (21 rats) and five litters in the dark reared condition (21 rats) underwent cauterization.

Pups were separated from their dams and anesthetized with a combination of cold (ice) and Halothane vapor. Animals were then maintained on ice during surgery. Each vibrissa was individually located with a dissecting microscope. A thin (98 micrometer) wire connected to a DC lesion maker (Grass) was inserted into the follicle. The follicle was then lesioned using a 150 V current with an intensity of 2 ma (Van Der Loos & Woolsey, 1973). The wire represented the negative source while the plate the animal rested on during the surgery was the positive source. Control animals were anesthetized as well, but the cauterization process was omitted. All pups were warmed to normal body temperature before being returned to their dams in their home cages.

At 90 days of age rats underwent a second set of surgical interventions. Animals were randomly assigned across litters to one of two lesion groups or to the lesion control group. Rats were anesthetized using sodium pentobarbital (100 mg/kg i.p.) and operated on under sterile conditions. The parietal cortex lesions were intended to bilaterally remove the area containing the barrel fields (Par 1). A skull opening was made from 1.5 mm to 3 mm posterior to bregma, and from 3 mm to 7 mm lateral from

the midline. The exposed brain was removed through aspiration.
The extrastriate cortex lesions were intended to bilaterally
remove area Oc2M (Zilles, 1990). The skull opening was made
from 3 mm to 7 mm posterior to bregma, and from 1.5 mm to 3 mm
lateral from the midline. Control animals were anesthetized and
the skin incised and sutured. Surgery was followed by a one
week recovery period.

The differences in early rearing conditions combined with
the early surgical intervention (cauterization) resulted in four
initial experimental groups. The groups were as follows: CR
normal, CR cauterized, DR normal, DR cauterized. There were 21
animals in each group. Animals from these original four groups
were then randomly assigned to one of the three "surgical"
conditions: Oc2M, Par 1, or control. The general design of the
study was a 4 x 3 factorial. The four environment types
represented one factor and surgical or lesion condition the
second. Thus, as shown in Figure 4, the final design had 12
experimental groups, with seven rats in each group.

Behavioral Tasks

The effects of early rearing and lesions on the animals
were behaviorally assessed by a variety of species specific and
discrimination tasks. Species specific behaviors were examined
through a short test battery administered following recovery
from surgery, at approximately 100 days of age. The battery
consisted of three separate tasks: grooming, dodging and

Figure 4.   Design of the experimental groups included in the study.
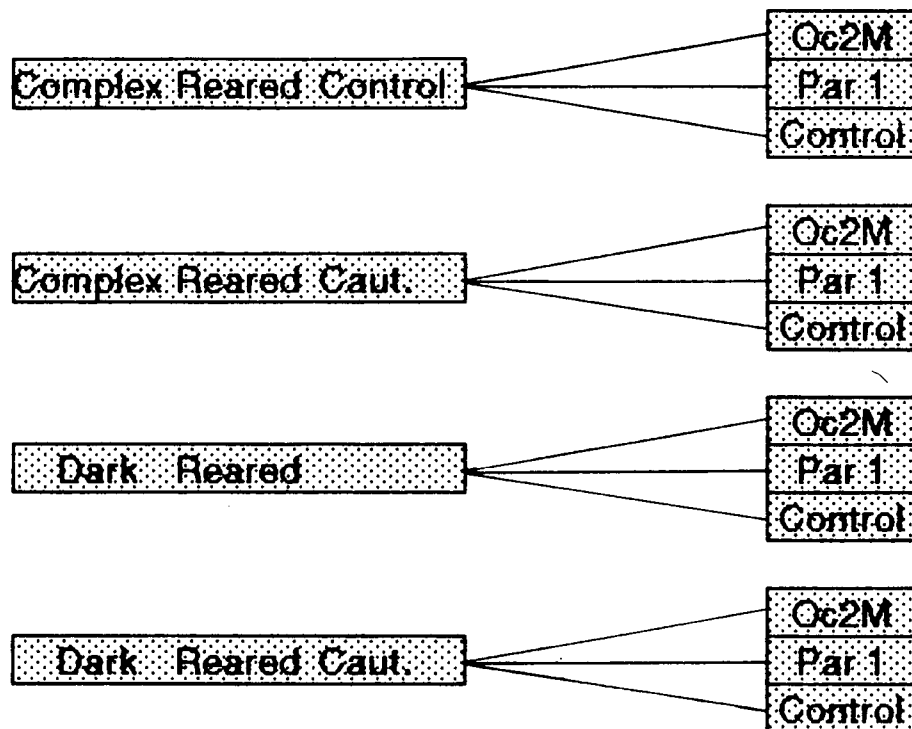
wrenching, and a visual/tactile discrimination task.

All tests in the battery were given in the same testing room, over a period of 4 days. The grooming, visual/tactile discrimination and dodging and wrenching tasks were all tested in the same cylindrical, Plexiglass chamber. The cylinder was 50 cm deep with a diameter of 50 cm. The rats were habituated to the cylinder and the test room individually for at least two 15 minute sessions in the days prior to testing.

Short Test Battery

1) Grooming

Rats were submersed in water to thoroughly wet their fur and then placed in the previously described chamber. Animals were then videotaped for 5 minutes. Videotapes were scored for the number of grooming sequences, the number of grooming components, and the total duration of grooming (Whishaw, Kolb, & Sutherland, 1983).

2) Dodging and Wrenching

The dodging and wrenching paradigm was originally developed by Whishaw and Tomie (1987) as a measure of a naturally occurring behavior observed when rats are group-housed. Basically, it involves competition for a limited amount of food. A rat without food will attempt to steal (rob) food from a rat with food. The rat with food will attempt to protect it by dodging away. A normal dodge is when the rat turns away 180 degrees contralateral to the approaching robber. Besides the

normal dodge, there are several other less frequently occurring responses to a robbery attempt. The victim can twist away (a contralateral dodge of less than 180 degrees), run forward, kick the approaching robber, or backward dodge (a dodge over and around the robber). A final response is the unsuccessful protection of the food pellet resulting in a robbery.

Rats were food deprived overnight to ensure that they were motivated to protect the food at the time of testing. Two animals were then placed in the testing chamber together and one was given a pellet of food (Purina Rat Chow). The first ten responses of the rat with the food pellet to the approach of the robber were videotaped. Responses were categorized as one of 6 possible responses, and the frequency of the normal dodge was compared to the frequency of all other responses.

3) Visual and Tactile "Novelty" Discrimination

A version of this task was recently described by Ennanceur and Delacour (1988). This task is predicated on the fact that rats normally prefer novel stimuli. When presented with two objects, one novel, the other familiar, the rat will tend to spend more time exploring the novel object. This indicates that they remember the original object and are able to distinguish it from the novel object. In our version of the task there were two separate discriminations tested, one visual, the second tactile.

Rats were exposed for three minutes to a pair of identical objects, in the cylindrical, Plexiglass chamber used in previous

testing. They were then removed for a 60 second inter-trial interval, and then were given a second three minute test. Exposure during this period was to a "mixed" pair of objects, one of which was identical to the two objects used in the first trial, while the other was a new object to which the rat had not previously been exposed.

The objects themselves were made of wood, and four exemplars of each different object were used. For the visual version of the task objects were different three-dimensional shapes: isosceles triangles and cylinders. All objects in this group were painted blue and had the same overall surface area and volume. The objects used for the tactile discrimination were two-inch cubes. Four exemplars are smooth surfaced and the remaining four, rough surfaced. The rough surface was achieved by glueing sand onto all sides. All cubes, smooth and rough were subsequently painted (black). To eliminate olfactory cues an object was used in only one trial for each rat and all objects were washed after each use.

The two discrimination tests were given over two consecutive days. The order of the tasks was varied randomly: half the rats were presented the visual discrimination task first, while the remainder the tactile discrimination task. The presentation of objects within each task was also randomly varied. The amount of time spent exploring each object on each test was measured. Behavior was identified as exploratory when the nose was at a distance of 2 cm or less to the object, or when the vibrissae were in contact with the object. The ratio

of total time spent exploring the new object to total time spent
exploring the old object was calculated and recorded.

Water-Based Spatial Memory Task

A procedural variation of the water maze task developed by
Morris (1981) was used to evaluate spatial memory. The
apparatus consisted of a white, circular fiber glass pool with a
diameter of 1.8 meters and a depth of 60 cm. The pool was
filled to 35 cm with water at room temperature (approximately 21
degrees C). White watercolor paint was added to the water to
make it opaque. The platform was a large plastic jar, 32 cm
tall and 9 cm in diameter at the lid. Wire mesh was attached to
the top of the jar and the jar was filled with stones for
weight. The entire platform structure was painted white to
render it invisible in the opaque water. A blue racquet ball
(Deuce Court) painted with white stripes was used as a proximal
cue and was attached by a 30 cm string to a sheet metal anchor.
This allowed the cue to be placed on the platform or to float
freely depending on the nature of the trial. The entire
apparatus resided in a testing room with a number of conspicuous
distal cues available.

The testing consisted of 18 trials conducted over three
days. A summary of trials is shown in Table 2. On the first
day each rat was given two 90 sec habituation trials with no
platform (P) or cue (C) present. On the second day, testing
began. The second day consisted of eight trials. For the first
four trials, the platform is located in quadrant 1 (North West)

trial number	trial type	description
1	C1/P1	Cue located on top of platform in quadrant 1 (northwest).
2	C1/P1	Cue located on top of platform in Q1.
3	C1/P1	Cue located on top of platform in Q1.
4	C1/P1	Cue located on top of platform in Q1.
5	C3/P1	Cue located in quadrant 3 (southeast). Platform in quadrant 1 (northwest).
6	C3/P1	Cue in Q3. Platform in Q1.
7	C3/P1	Cue in Q3. Platform in Q1.
8	C3/P1	Cue in Q3. Platform in Q1.
9	C3/P3	Cue located on top of platform in quadrant 3.
10	C3/P3	Cue on top of platform in Q3.
11	C3/P3	Cue on top of platform in Q3.
12	C3/P3	Cue on top of platform in Q3.
13	-/P3	No cue. Platform located in Q3.
14	-/P3	No cue. Platform located in Q3.
15	-/P3	No cue. Platform located in Q3.
16	-/P3	No cue. Platform located in Q3.

Table 2. Description of the trials in the Water-Based Spatial Learning Task

and the proximal cue is placed on top of it. On trials 5-8, the cue is placed in quadrant 3 (South East) while the platform remains in quadrant 1. On the second day of test trials 9-16 were run. For trials 9-12 the platform was moved beneath the cue in quadrant 3. On trials 13-16 the cue was removed from the pool.

The animals were released on each trial from one of the four poles in a pseudorandom sequence. Escape latency was recorded. Whether or not animals touched the cue during trials 5-8, when the cue was located in an "incorrect" quadrant, was also recorded. The entire trial was videotaped for a further more detailed analysis of behavior.

When a rat encountered the platform, it was permitted to remain there for 10 seconds. If the platform was not located within 90 seconds the trial was terminated, and the rat removed and given a score of 90 seconds.

Water-Based Concurrent Visual Discrimination Task

A second variation of the Morris Water Maze was used to evaluate visual discrimination/memory per se (Kolb, Buhrmann & McDonald, 1989). The apparatus and platform were the same as used for the spatial memory task. Four air filled rubber balls, approximately 10 cm in diameter were painted in different patterns in black and white and used as the cues with which to learn the task. The four stimuli were presented in pairs of two. In pair one the positive cue, (the cue signalling the location of the platform), was white with large black spots,

while the negative cue had black and white horizontal stripes approximately 1.5 cm wide. In the second pair the positive cue had black and white vertical stripes one centimeter wide while the negative cue was solid grey.

Training consisted of 80 trials run over 10 days. Over the eight trials in each test day, each pair of stimuli was used on alternate trials. Location of the positive cue (escape platform) and the negative cue were randomly switched between quadrants three (South East) and four (South West) of the pool. On each test day the platform was in each quadrant an equal number of times. Release point on each trial was varied. The rats were released from one of the four poles in a pseudorandom sequence. Rats were always released facing the wall of the pool.

A trial was over when the rat mounted the platform or after 90 seconds had elapsed, whichever came first. If the rat mounted the platform, it was allowed to remain on it for 10 seconds. The latency to find the platform was recorded. An error was recorded if the rat contacted or attempted to mount the negative cue or if the rat circled the negative cue as if searching for the escape platform.

Following the completion of training, an additional eight transfer trial were run on Day 11. Transfer tests were run to see what the rat learned during training and how it would react when confronted with conditions different from those that existed in training. The transfer day also consisted of 8 trials, summarized in Table 3. In the first two trials only the

Day 11-Transfer Trials

Trial 1   No negative cue. Platform cued only by the
           presence of the positive cue 1.
Trial 2   Same as Trial 1 using positive cue 2.

Trial 3   Normal trial to set up for next trial. Both the
           positive and negative cues (pair 2) present.
Trial 4   No positive cue. Platform cued only by the
           (distal) presence of the negative cue 2.

Trial 5   Original pairs mixed. Positive cue from Pair 1,
           negative cue from Pair 2.
Trial 6   Same as Trial 5, using the remaining two cues,
           positive cue 2 and negative cue 1.

Trial 7   Original pairing of pair 2. Location of cues and
           platform novel to those used in training.
Trial 8   Same procedure as Trial 8, using two additional novel
           locations.

Table 3.   Description of trials on Day 11 of the Water-Based

           Concurrent Discrimination Task.

positive was present. Negative cues were not present. Trial 3 and 4 tested the effects of removing the positive cue. The location of the platform was "cued" only by the location of the negative cue. In trials 5 and 6 the pairs were rearranged. The positive cue from the first pair was coupled with the negative cue from the second, and the negative cue from pair one was paired with the positive cue from pair two. The remaining trials tested the effects of changing the location of the cues and platform to novel positions in the pool.

Histology and Anatomy

Following the completion of behavioral testing animals in the complex-reared, complex-cauterized, dark-reared, and dark-reared cauterized control groups were anesthetized with sodium pentobarbital and perfused intercardially with 0.9% saline. The brains were removed and immersed whole in 50 ml of Golgi-Cox solution (Glaser & Van Der Loos, 1981). The solution was changed after two days and the brains were left in the dark for an additional 14-16 days. The brains were then placed in a 30% solution of sucrose for three to five days. The brains were then cut into 100 um sections with a vibratome and mounted onto 2% gelatine-coated slides.

Brains were numerically coded so neurons could be drawn "blind". Neurons were drawn using a Wild-Leitz Combistereo Scope, with a drawing tube attachment. Dendrites were clearly defined in the cortex. Ten pyramidal cells, five on each side, were drawn from layer V cells of somatosensory (Par 1), visual

Figure 5. A) Example of layer V Pyramidal cells drawn from

somatosensory (Area Par1), visual (Area Oc2M), and

auditory (Area Te1) cortex. B) Illustration of the

centrifugal ordering system; the root segment is the

order 0 segment.

A

Par1

Oc2M

Te1

B

1
1
2
2
3
3
3
3
4
4
5
5
6
6
7
7
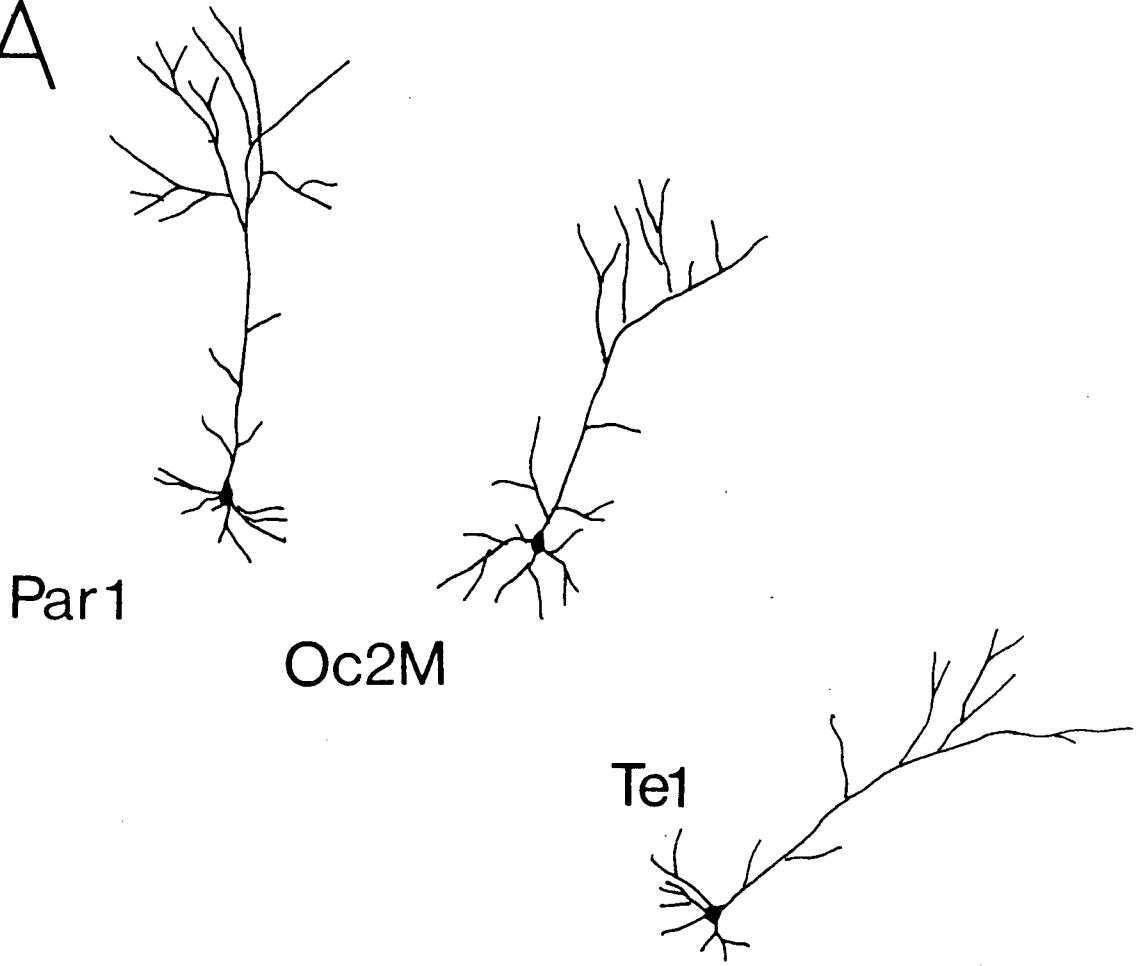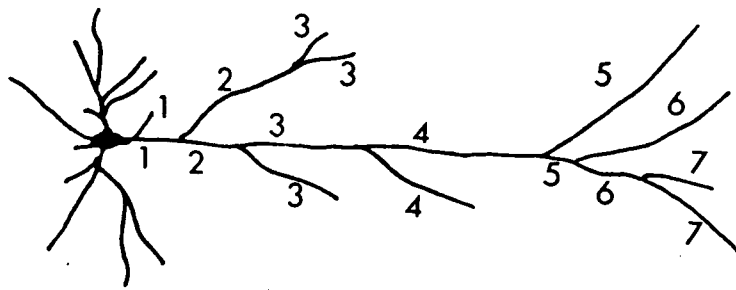
(Oc2M), and auditory (Te 1) cortex (Figure 5A). Layer V was selected because rearing condition has been shown to affect dendritic branching of layer V pyramidal cells in temporal and parietal cortex (Greenough, Volkmar, & Juraska, 1973). The dendritic branching pattern was quantified using the centrifugal ordering system (Uylings, Van Pelt, Verwer, & McConnel, 1989). Centrifugal ordering indicates the topological distance from the root. It starts with numbering order from the dendritic origin and increases the order by one beyond each bifurcation (Figure 5B). Higher order branching was considered to be all branching beyond order 6. Branching was summarized across higher orders. Because apical dendrites project through different layers while basilar dendrites project within the same layer as the cell body, apical and basilar dendrites were quantified and analyzed separately.

The animals in the remaining (lesioned) experimental groups were also anesthetized with sodium pentobarbital and perfused intercardially with 0.9% physiological saline followed by 10% formal saline. Brains were blocked around the lesion and sliced through the lesioned area at 40 um sections. Sections were mounted on 1% gelatin-coated slides. To verify the extent and location of the lesions, slides were analyzed and lesions reconstructed under a microscope.

Results

Behavioral Data

To reduce the probability of Type I error, the behavioral data were initially assessed with a multivariate analysis of variance (MANOVA). A repeated measures Rearing Condition x Lesion Group MANOVA was conducted on the data generated in all five behavioral tasks (30 dependent variables). Those animals for which there were incomplete data (15) were eliminated from the analysis. To create equal cell n's, data from an additional 9 animals were randomly eliminated (Glass & Hopkins, 1984). The total number of animals in the analysis was 60, 5 in each group.

Overall, the effect for Rearing Condition was significant, $F(6,53) = 1.521$, $p < 0.05$ (Wilks's lambda). However, no further significant effects were found for Lesion Group or Rearing x Lesion interaction. The significant result for Rearing Condition was followed up with univariate analyses of variance (ANOVA) for all dependent variables. For the univariate tests, data were collapsed across all Lesion Groups within each Rearing Condition.

Short Test Battery

1) Grooming

An analysis of variance was used to assess each of the three measures generated by the rats in the five minute grooming test. The three measures were: (1) the total number of grooming sequences; (2) the total latency spent grooming; (3)

the total number of grooming components. Although no significant effect was found for the total number of grooming sequences over the five minutes, the effect of Rearing Condition was significant on both the total latency spent grooming, $F(1,59) = 3.397$, $p < 0.05$, and the total number of grooming components, $F(1,59) = 3.055$, $p < 0.05$ (Figure 6). However, post-hoc comparisons (Tukey's HSD) did not find significant differences between any pairings of rearing condition groups for either variable. Significance was found for both measures using a planned orthogonal contrast which compared data pooled across dark-reared and complex-reared groups: total latency, $F(1,56) = 10.13$, $p < 0.01$; total number of components, $F(1,56) = 8.862$, $p < 0.01$. Thus, it appears that over the five minute grooming test, complex-reared (CR) rats groom longer, and demonstrate more grooming components than do dark-reared (DR) rats.

2) Dodging and Wrenching

Cauterization and/or dark-rearing (or selective posterior cortical lesions) did not seem to have any effect on the competence of a rat to protect its food from other rats attempting to steal it. The number of successful robberies across all the dodging and wrenching trials totalled less than 10 out of a possible 600. Did rats from different rearing conditions make different types of responses in avoiding food robbery attempts? The ratio of normal dodges to all other possible responses was analyzed, and no significant effect for Rearing Condition was found. It is interesting to note,

Figure 6.   A) Total duration of grooming in seconds over the
five minute grooming task for rats in all four
rearing conditions.   B) Total number of grooming
components (body parts) groomed over the total
duration of grooming.

A

B
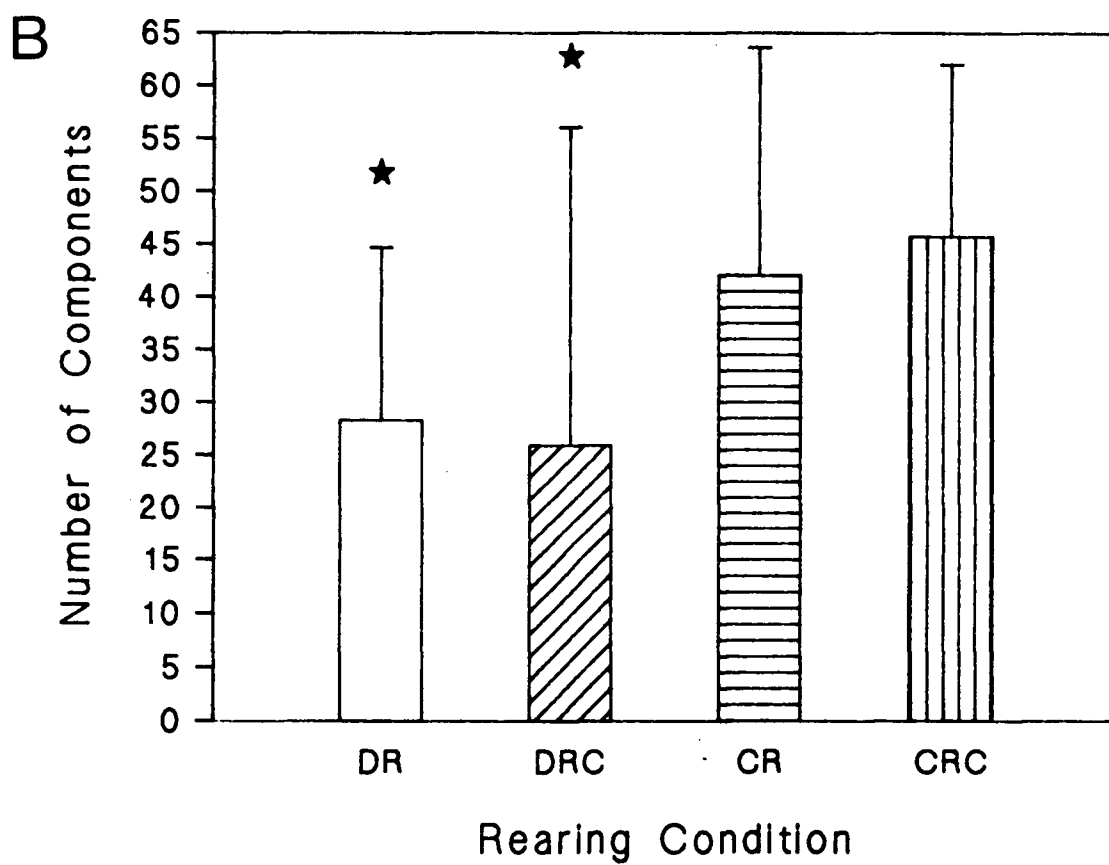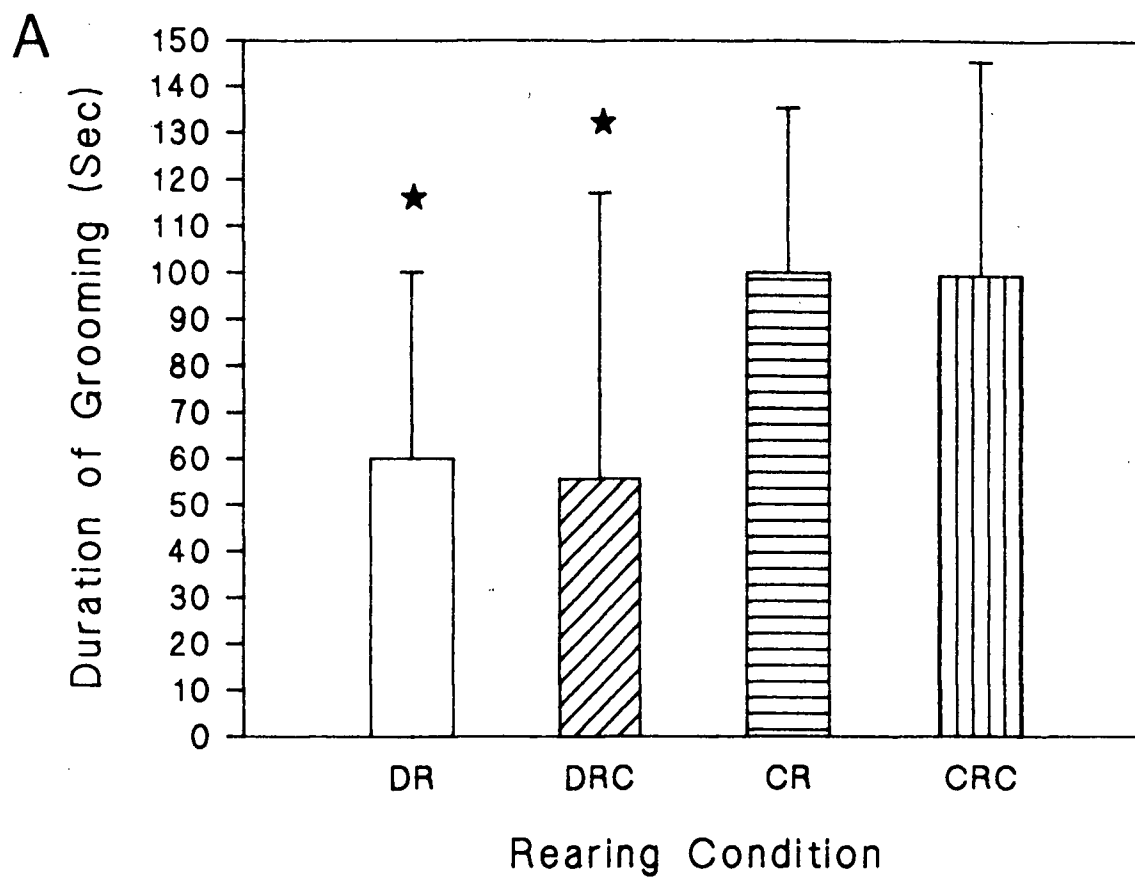
however, that the overall incidence of dodging responses observed here differed from that reported in the study by Whishaw (1988). In the original study by Whishaw, rats responded to the robber situation by a normal dodge more than 90% of the time. In this study, rats responded with a normal dodge only 66% of the time.

3) Visual and Tactile Novelty Discrimination

After a three minute exposure to pairs of identical objects, rats were simultaneously presented with a familiar and a novel object and given three minutes to explore the pair. A univariate analysis of variance was conducted on the ratio of total time spent exploring the novel object to total time spent exploring the familiar object. Overall, rats spent nearly twice as long exploring the novel object in both the visual (mean = 1.86) and the tactile (mean = 1.71) conditions. However, the impact of Rearing Condition was not significant for either condition. This indicates that the ability to discriminate between novel and familiar objects used in the tactile and visual conditions of this task is not affected by cauterization and/or dark rearing.

Although there was not a significant overall Lesion Group effect in the MANOVA, all univariate ANOVAS for type of lesion were run. One of the few significant results revealed, was on the tactile discrimination task, $F(2,48) = 4.356$, $p < 0.05$ (Figure 7). Post-hoc comparisons (Tukey's HSD) revealed that rats with Par1 (somatosensory) lesions spent less time exploring

Figure 7. Ratio of total time spent exploring the novel object over total time spent exploring the familiar object displayed by rats in the three surgical conditions on the Tactile Novelty Discrimination Task.
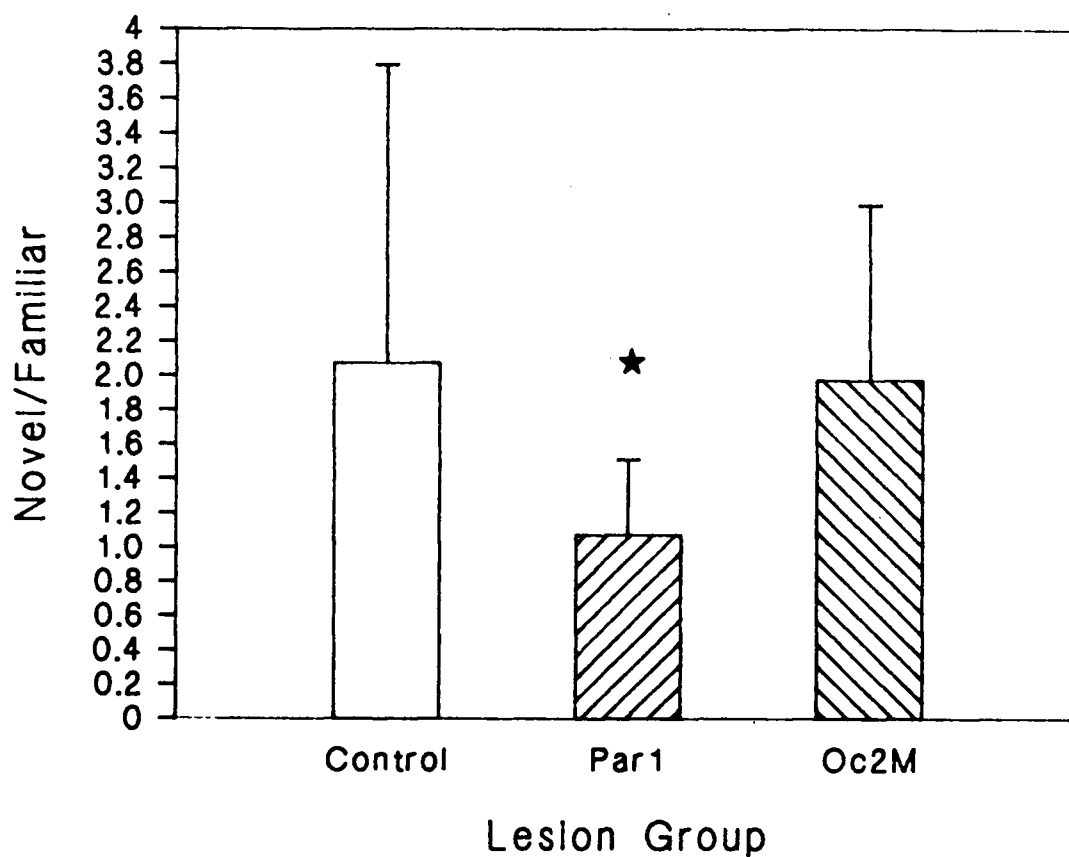
the novel object than did either Oc2M (visual) lesioned or control animals, p < 0.05. It should again be noted that because the overall test for rearing condition was not significant, this result for tactile discrimination, although interesting and predicted, is somewhat suspect, and could be the result of chance alone.

Water-Based Spatial Memory Task

The latency of rats from the four rearing conditions to find the submerged platform was compared on the fourth, eighth, twelfth, and sixteenth trials. As conditions were identical for trials 1-4, 5-8, etc., only the last trial in each block of four trials was assessed (Figure 8A). A significant effect for Rearing Condition was found for Trial Four, F(3,48) = 3.173, p < 0.05 (Figure 8B). Post-hoc comparisons (Tukey's HSD) did not reveal any significant differences between rats raised in the four rearing conditions. However, overall the two dark-reared groups were significantly different from the two complex-reared groups, F(1,56) = 8.588, p < 0.01 (Planned Orthogonal Contrast). It appears that CR rats showed faster escape latencies on trial four than did DR animals indicating that perhaps the CR rats had learned the initial test condition more thoroughly than did DR rats. No other significant differences were found on the remaining trials. On these trials DR rats did not appear to be more disrupted by the changing experimental conditions than were CR animals. Although DR rats did not learn the initial test condition as quickly as did CR rats, their learning of the

Figure 8. A) Latency in seconds to fimd the submerged platform
across trials 4, 8, 12, and 16 for animals in all
four rearing conditions. B) Latency and standard
deviation to find the platform on trial 4 for rats in
the four rearing conditions.
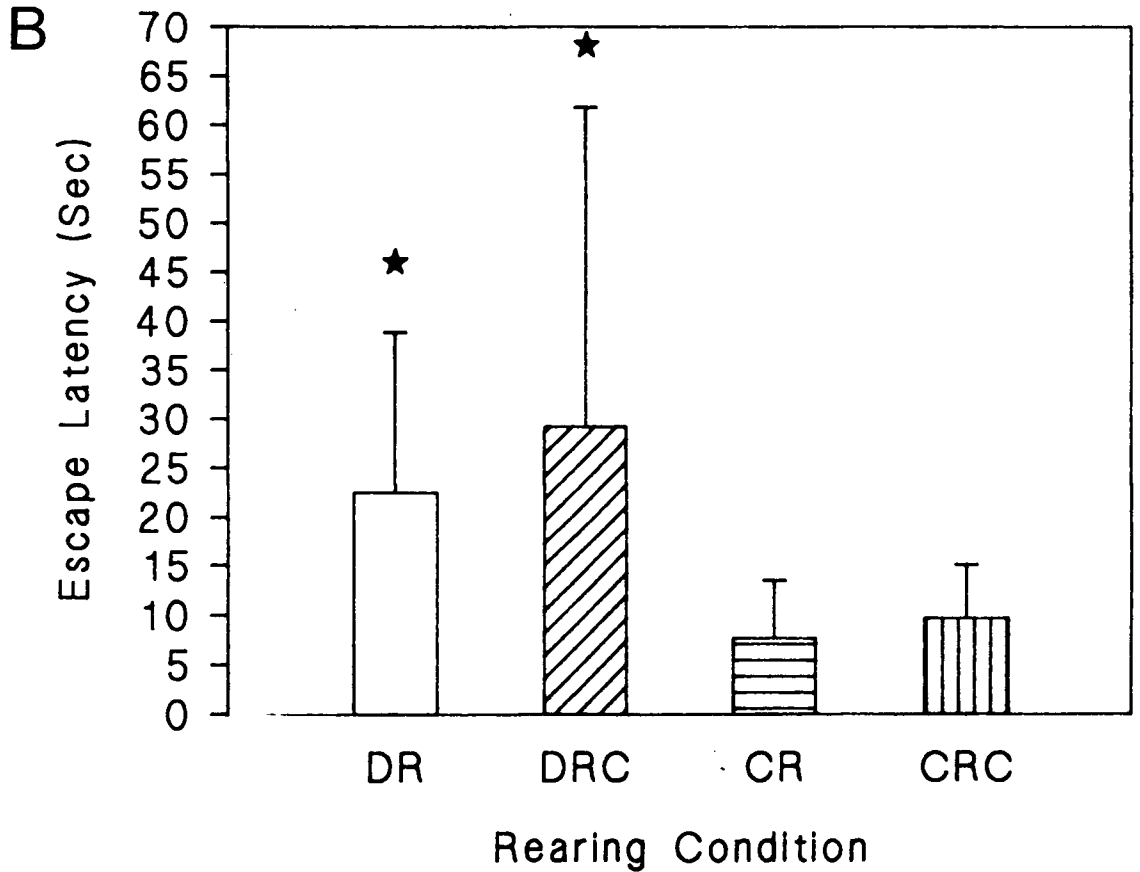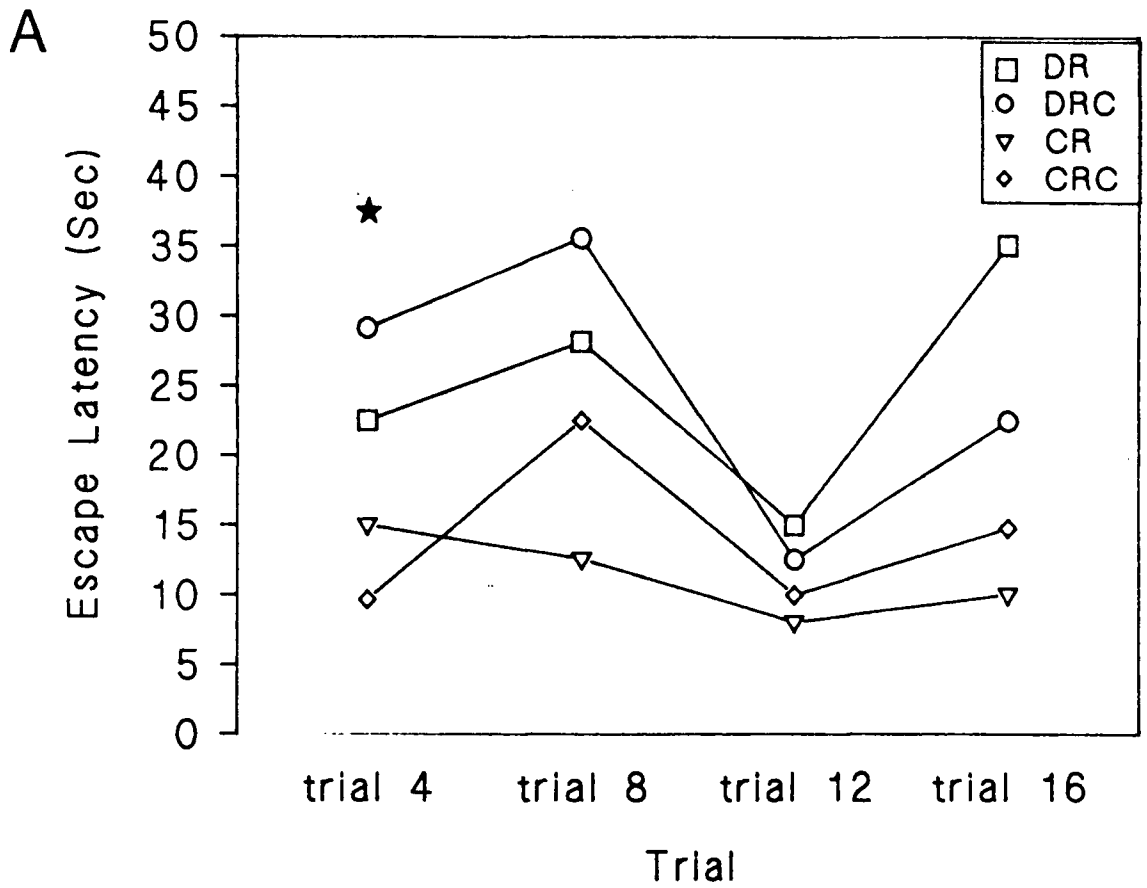
subsequent experimental conditions was not impaired.

Water-Based Concurrent Visual Discrimination

Over ten days of training, rats had to learn to discriminate between pairs of visual cues to locate the submerged platform. Following the completion of ten training days, rats were run (Day 11) on eight different transfer trials in which they were confronted with stimulus conditions different from those that existed during training. Univariate analyses were run for: (1) escape latency on training days 1, 5, and 10; (2) total errors on training days 1, 5, and 10; (3) escaped latency for all eight transfer trials; (4) total errors for transfer trials 3 through 8. Since no errors were committed by any rat on transfer trials 1 and 2, these conditions were eliminated from the original MANOVA analysis and all subsequent univariate analyses. The data for training days represent an average score of the eight trials run each day. For transfer trials each data point represents a single trial.

A significant effect for rearing condition was found on Training Day 1, $F(3,48) = 2.79$, $p < 0.05$, and on Training Day 5, $F(3,48) = 7.661)$, $p < 0.001$ (Figure 9). A planned comparison between both DR and both CR groups for Day 1 was significant, $F(1,56) = 7.998$, $p < 0.01$, indicating that rats from DR groups took longer to find the hidden platform than did rats from CR groups. Post hoc analysis (Tukey's HSD) did not reveal significant differences between any pair of rearing conditions for this training day. For Training Day 5 the post-hoc

Figure 9. Mean latency in seconds to find the cued submerged platform on Training Days 1, 5, and 10 for rats in four rearing conditions.
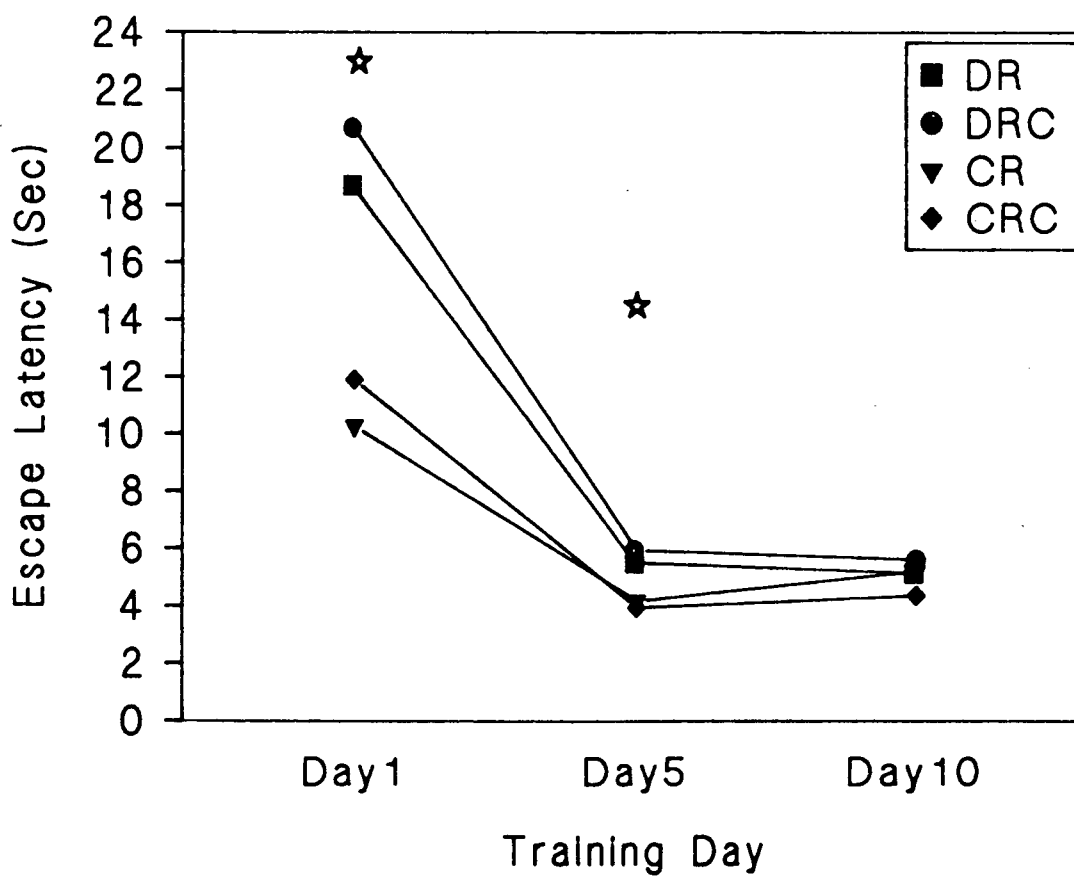
comparisons did find significant differences between individual groups. All pairings of CR and CRC groups with DR and DRC groups were significant (Tukey's HSD, all p's < 0.05). Again, all DR groups were less effective than CR groups. No significant differences in escape latencies were found between Rearing Conditions on Training Day 10. It appears that, although the DR groups were slower to acquire the task, by the last day of training, their escape latencies did not differ significantly from those of CR groups.

In analyzing the number of errors committed on the same training days, a significant effect for Rearing Condition was obtained only for Training Day 10, $F(3,48) = 3.505$, $p < 0.05$ (Figure 10). Post-hoc comparisons (Tukey's HSD) found the CR animals to make significantly more errors than the DR animals. This result is especially interesting in light of the nonsignificant result for escape latency on the same training day. It appears that by Day 10, although the CR group is as quick to find the platform as all other groups, they make significantly more errors than at least the DR group in the process. It should be noted that although this result for number of errors was significant, it was the only time that any of the groups differed significantly on errors across any of the training or transfer trials. Post-hoc univariate ANOVA's were conducted to assess errors committed on Training Days 8 and 9, days not included in the original analysis. No significant differences between rearing conditions were found, making the result for Day 10 somewhat suspect.

Figure 10. Mean number of total errors committed in finding the submerged platform on Training Days 1, 5, and 10 for rats in all rearing conditions.
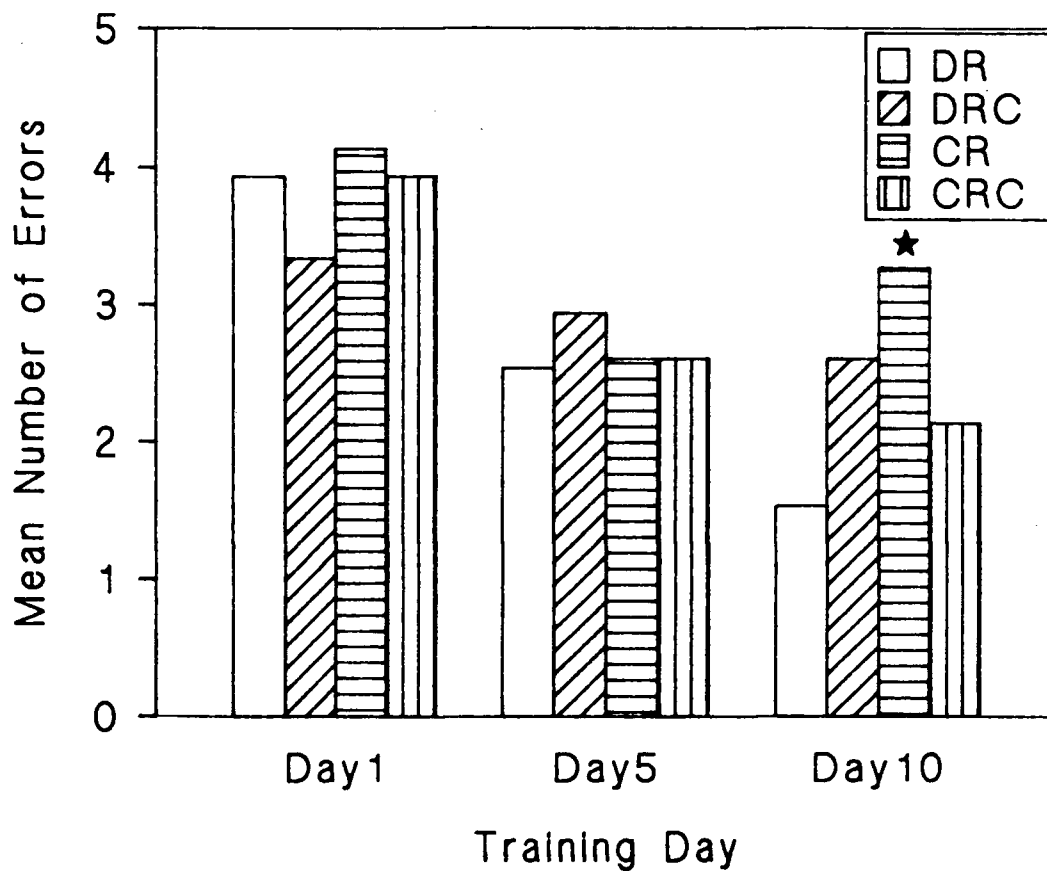
Analysis of escape latencies across the eight transfer trials revealed significant effect of Rearing Condition only on transfer trials where the original cue pairs were mixed: Trial 5, $F(3,48) = 5.187$, $p < 0.01$; trial 6, $F(3,48) = 3.714$, $p < 0.05$ (Figure 11). Post-hoc comparisons for Trial 5 found DRC animals to be significantly slower than both CR and CRC groups. On Trial 6, the DR group took significantly longer to find the platform than the CR group (Tukey's HSD, all p's < 0.05. No other significant effects for escape latency were found on any of the other transfer trial conditions, such as on Trials 7 and 8 where the locations of the cues and platform were novel to those used in training. From these results it appears that mixing the cue pairs disrupted the performance of the DR groups more than CR groups, but only in terms of escape latency.

Univariate analysis of variance for errors committed on transfer trials three through eight were all nonsignificant. Escape latency proved to be a more sensitive assay of early rearing conditions than errors.

Histological and Anatomical:

Verification of Lesion Location

Brains were blocked and sectioned at 40 microns through the extent of the cortical lesion. Mounted sections were analyzed visually to verify the extent of the lesion. Reconstructions of representative ablations are shown in Figure 12. Generally the lesions were well placed. However, some variation of lesion

Figure 11. Mean escape latency in seconds to find the cued

platform on Transfer Trials 5 and 6, for rats in all

rearing conditions.   These trials represent

situation where the original cue pairs from the

training portion of the Water-Based Concurrent
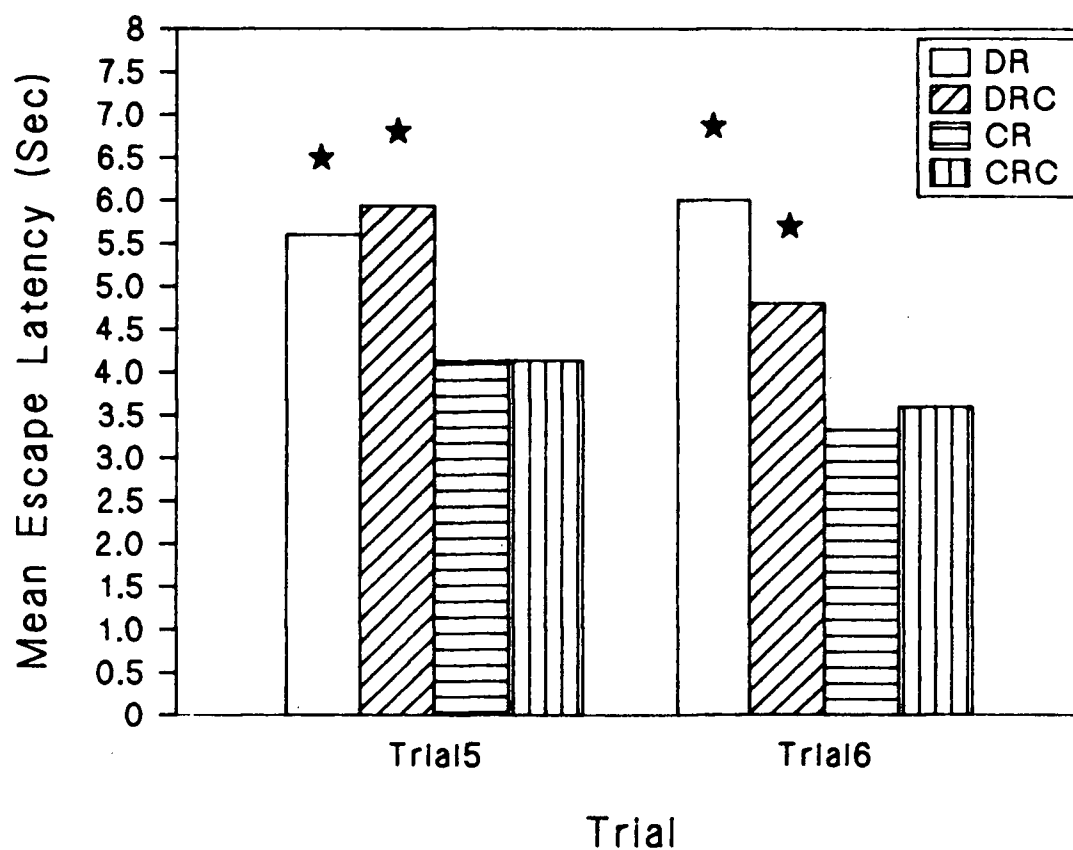
Discrimination Task are mixed.

Figure 12. Reconstruction of A) Par1, primary somatosensory cortex containing the vibrissae barrel fields, and B) Oc2M, extrastriate visual cortex lesions.

A
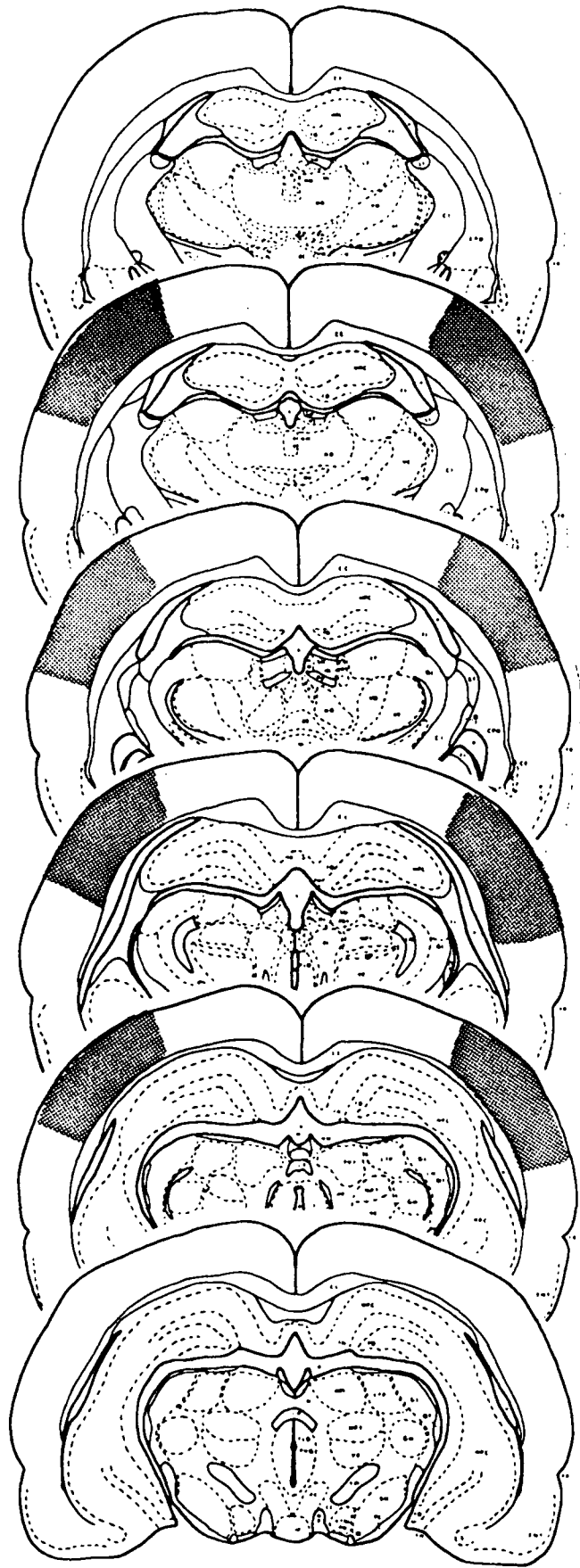
B

size was observed in both Par1 (somatosensory) and Oc2M (visual) lesions. Microscopic evaluations of the sectioned brains revealed that only a few of the injuries produced direct damage to structures below the level of the corpus collosum. As well, approximately one third of the lesions did not completely remove all of the intended cortical area.

To determine if variation in size of lesion was correlated with behavior, behavioral data for lesioned animals were reanalyzed. A repeated measures MANOVA compared the behavioral outcomes of rats classified as having "large", "complete", or "small" lesions within each Lesion Group. The analyses did not reveal a significant relationship between lesion size and behavior in the case of either Par1 or Oc2M lesioned animals. In general, lesion size was not seen to affect performance in any consistent way. The behavioral measures taken of rats with large or small lesions were not found to be quantitatively different from those of more accurately lesioned animals. Therefore, lesion size probably does not account for a significant amount of the behavioral variance found in this study.

Impact of Rearing Condition on Dendritic Arborization

The effect of different rearing conditions on dendritic arborization was assessed separately for apical and basaler dendrites. Data were obtained from five rats in each rearing condition for a total of 20 rats. The animals included in the anatomical assessment did were the lesion control animals.

These were the same as animals as those that did not receive cortical surgical intervention in the behavioral analysis.

1) <u>Apical Dendrites</u>

To assess extent of dendritic arborization in three sensory cortical areas a one factor (Rearing Condition) repeated measures MANOVA was conducted (total of 6 orders of branching x 3 areas = 18 dependant variables). The analysis revealed a significant effect of rearing condition on overall extent of arborization, $F(3,16) = 11.889$, $p < 0.001$. This result was followed up by a repeated measures ANOVA for each area.

In area Par1, somatosensory cortex, significant effects were found for rearing condition, $F(3,16) = 5.365$, $p < 0.01$, and for the interaction of rearing condition x order of branching, $F(5,80) = 4.212$, $p < 0.001$ (Figure 13A). Post-hoc analysis of these data indicated that the CRC group showed significantly more overall apical arborization averaged across all orders of branching in Area Par1 than the DR and the DRC group. As well, both CR groups showed significantly more high order (order 6) branching than both of the DR groups (Tukey's HSD, all p's < 0.05) (Figure 13B).

The analysis for area Oc2M, visual cortex, did not reveal a main effect for rearing condition. However, a significant interaction between rearing condition and order of branching was found, $F(5,80) = 2.037$, $p < 0.05$ (Figure 14A). Post-hoc comparisons (Tukey's HSD) found the CRC group to have significantly more higher order branching that any other group,

Figure 13. A) Mean of mean number of dendritic branches for
rats in all rearing conditions in area Par1.
B) Mean of mean number of higher order branching for
all rearing conditions in area Par1.

A

Mean Number of Branches

B

Mean Number of Branches

Rearing Condition

Order of Branching

DR
DRC
CR
CRC

61
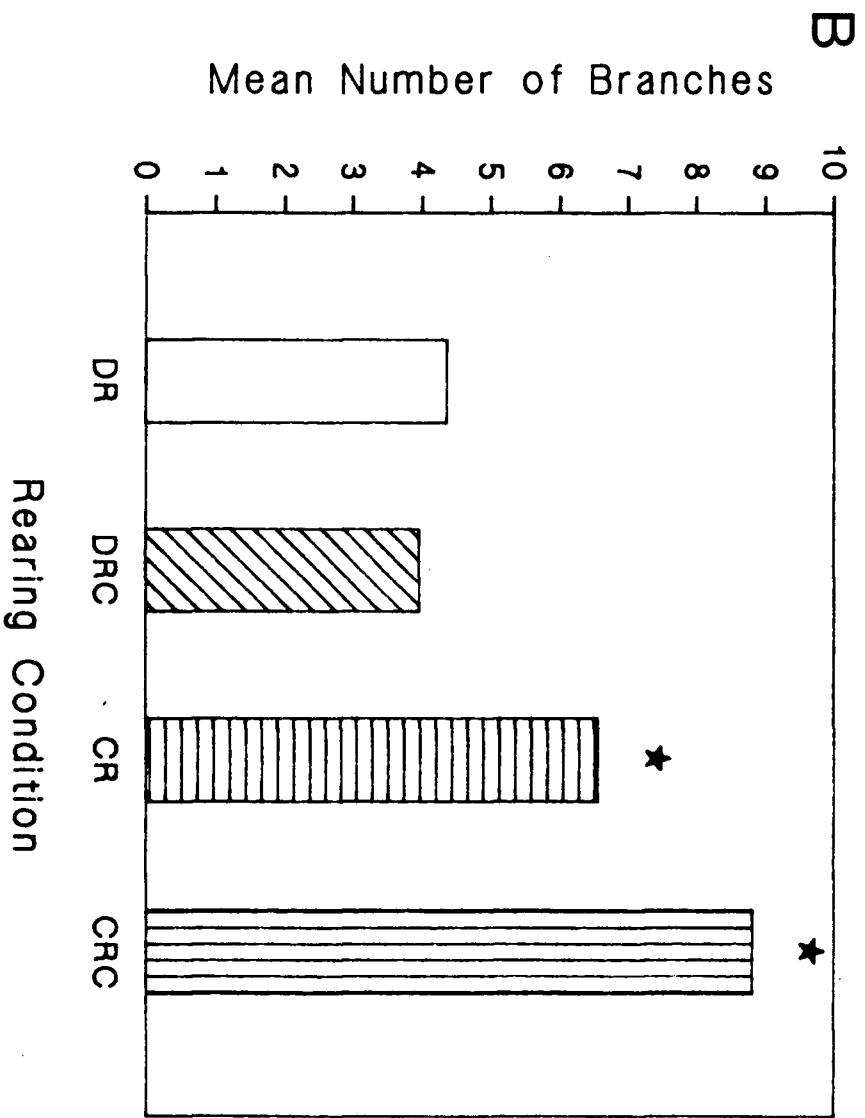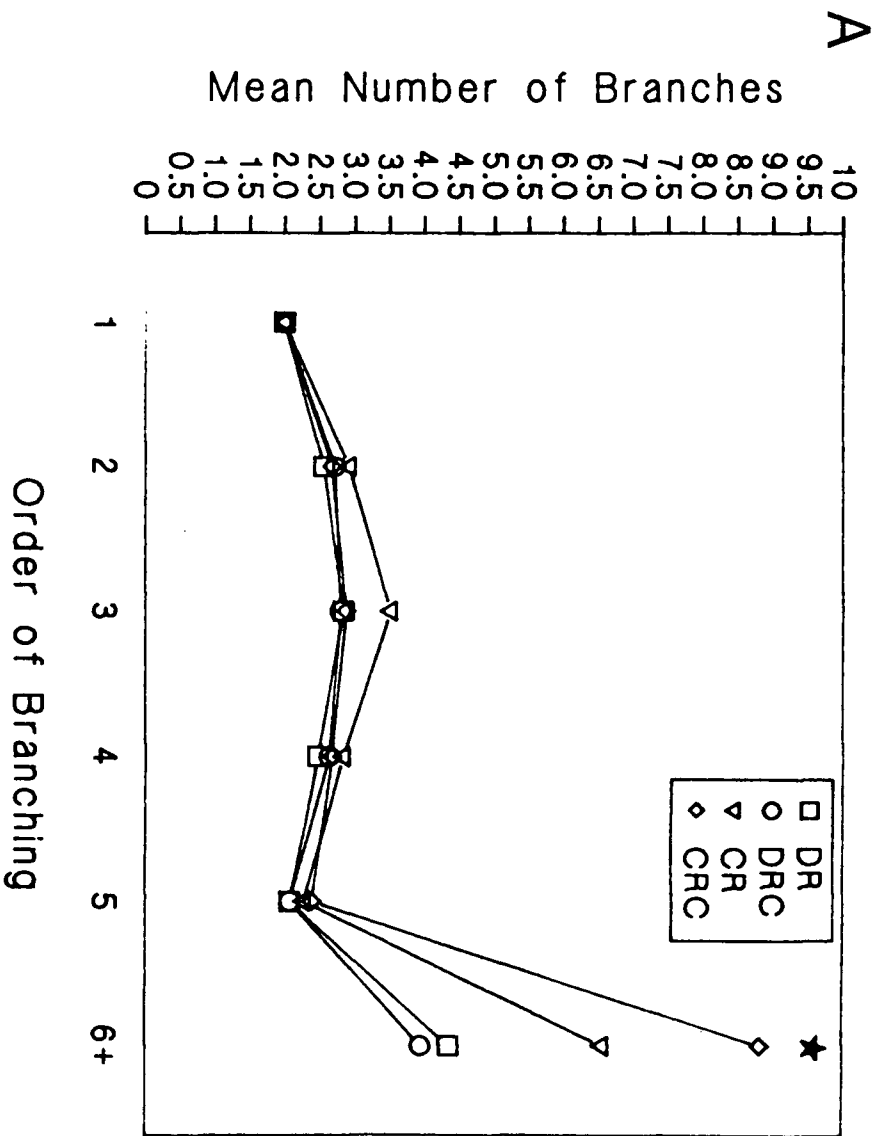
Figure 14. A) Mean of mean number of dendritic branches found in secondary visual cortex, area Oc2M, for rats in all rearing conditions. B) Summary of mean of mean number of higher order dendritic branches for rats in all rearing conditions in area Oc2M.
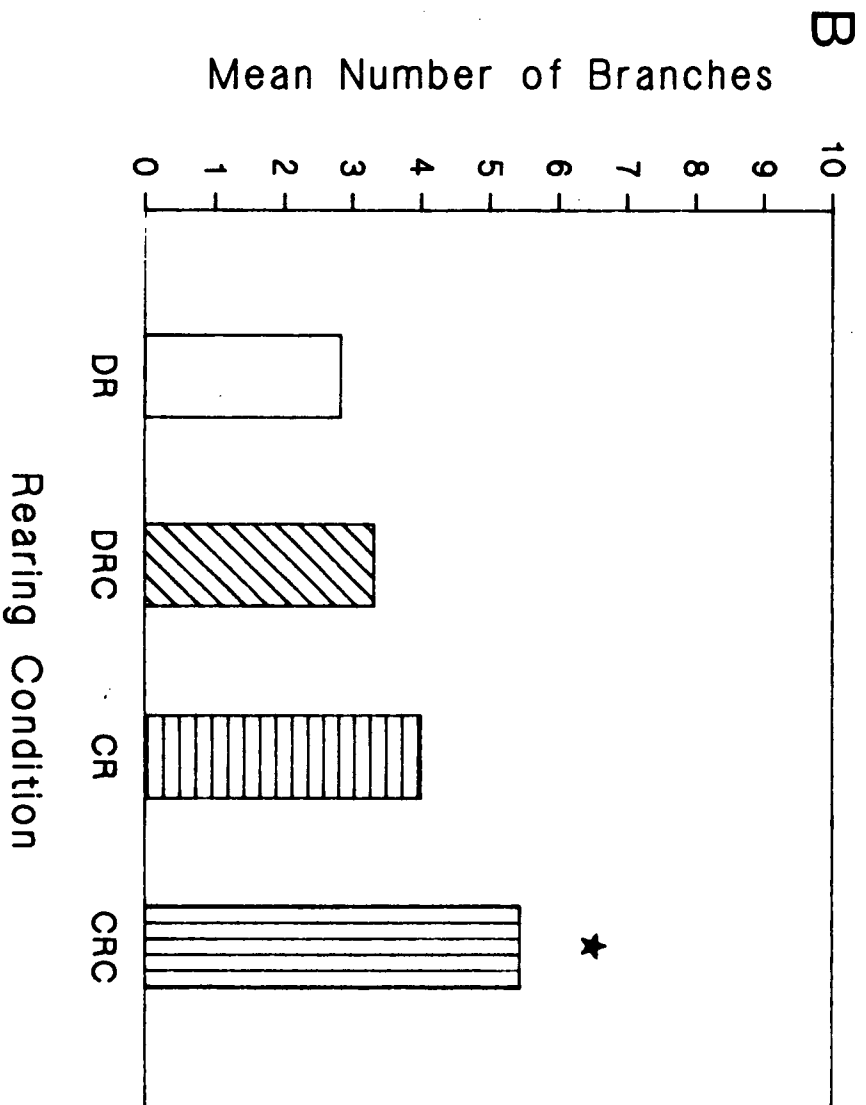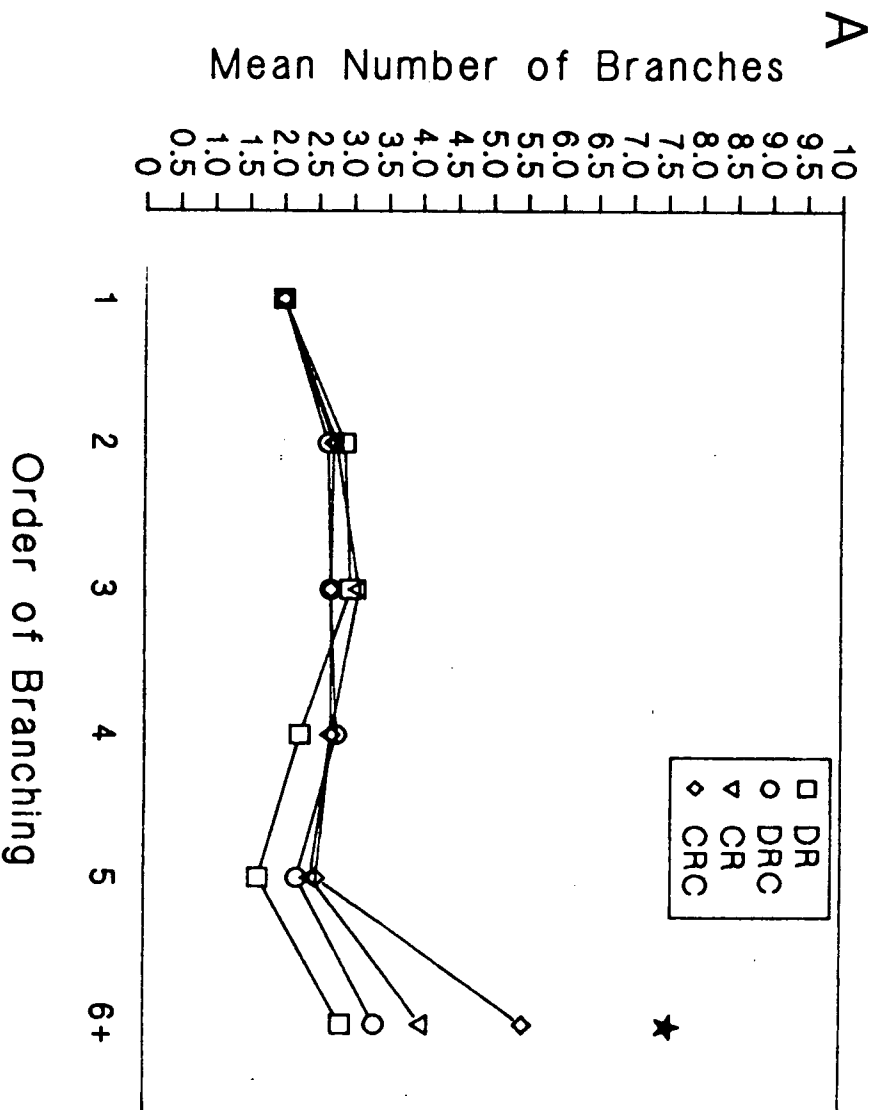
Figure 15. A) Mean of mean number of dendritic branching found
in primary auditory cortex, area Te1, a sensory
system not directly manipulated, for rats in all
rearing conditions. B) Summary of mean of mean
number of higher order dendritic branches for rats
in all rearing conditions in area Te1.
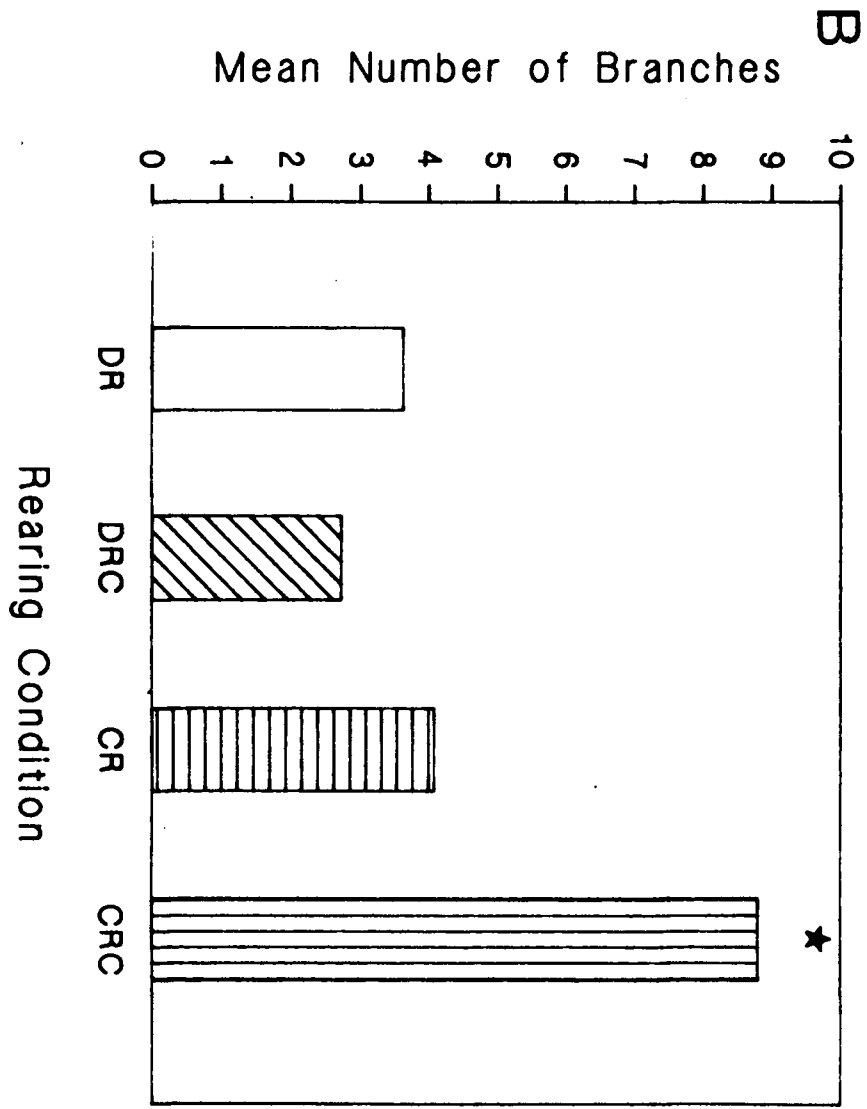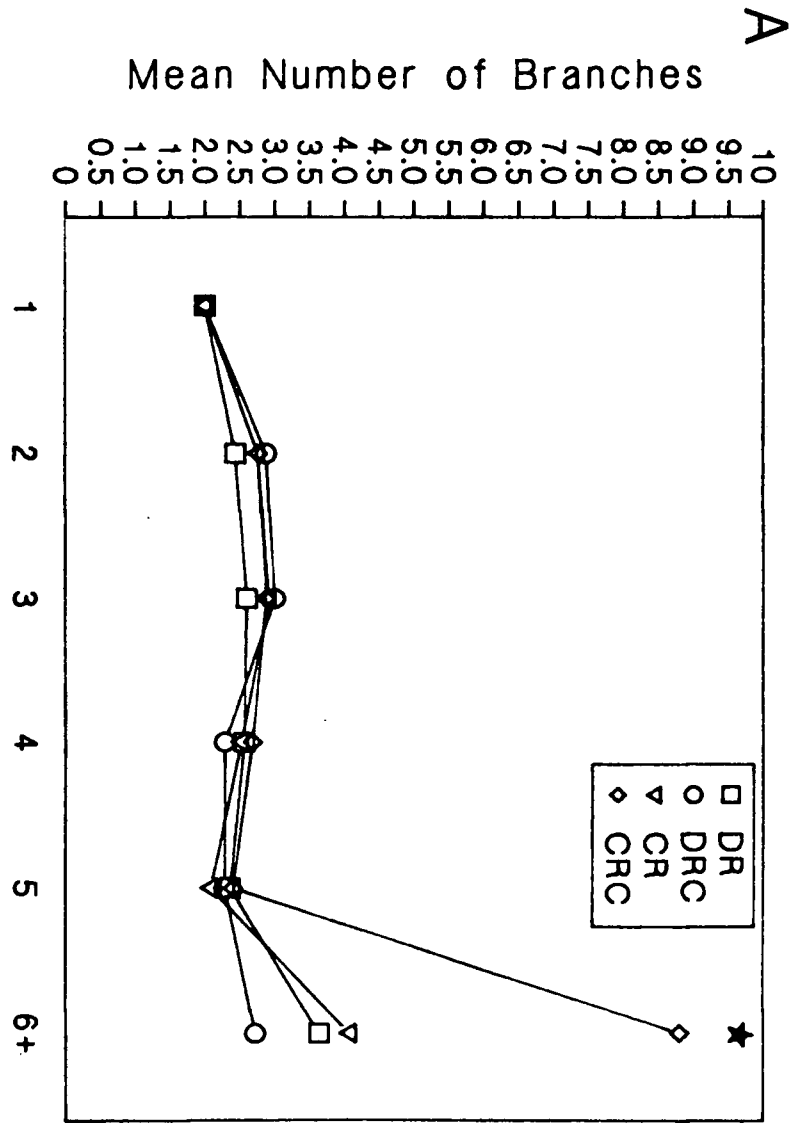
p < 0.05 (Figure 14B).

A significant effect for rearing condition was found in area Tel, auditory cortex, $F(3,16) = 8.115$, $p < 0.01$. The CRC group showed significantly more arborization across all orders of branching in primary auditory cortex than any other group (Tukey's, $p < 0.05$). As shown in Figure 15A the analysis again revealed a significant rearing condition x order of branching interaction, $F(5,80) = 7.532$, $p < 0.001$. Post-hoc comparisons found significantly more higher order branching in the CRC group than any other group (Tukey's, $p < 0.05$) (Figure 15B).

Dendritic arborization in all three cortical areas was significantly greater in the two CR groups than in the two DR groups: Area Parl, $F(1,16) = 15.417$, $p < 0.01$; Area Oc2M, $F(1,16) = 4.522$, $p < 0,05$; Area Tel, $F(1,16) = 11.829$, $p < 0.01$ (Planned Orthogonal Contrast). There were no significant differences in any cortical area when cauterized and intact groups were compared.

2) Basilar Dendrites

A one factor repeated measures MANOVA, the same as was used for apical dendrites, was conducted to assess arborization of basilar dendrites. No significant main or interaction effects were found.

Discussion

Impact of Early Simulation History on Behavior

In studying the relationship between brain and behavior one
approach is to alter the environment in which the brain normally
develops and then chart how neural and behavioral outcomes
change. The four rearing conditions included in this study
combined enhancement and deprivation of the somatosensory and/or
visual systems. One of the purposes for undertaking this study
was to determine the intra- and intermodal impact of the
differential rearing conditions on behavior. The overall effect
for Rearing Condition was significant, indicating that early
manipulation of the somatosensory and visual systems did have an
impact on performance of behavioral tasks.

Further analysis of the individual tasks assessed the
intramodal effects of early sensory restriction as well as
served as a direct test of the modality-interdependence model
proposed by Turkewitz and Kenny (1982). The two main hypothesis
arising from this model are: 1) early restriction of sensory
input in one modality could result in intermodal compensation
due to lack of competition from this restricted modality; 2)
early restriction of sensory input into an early developing
modality might disrupt the emerging organizational framework
necessary for a competency which involves signals of a later
developing modality. Little support for either hypothesis was
found in the present behavioral analysis.

Visual deprivation through rearing in total darkness has previously been shown to slow acquisition of various non visual-spatial tasks (Tees, Midgley, & Nesbit, 1981). As expected, a difference between dark and complex reared rats in escape latency to locate the hidden platform was found. Surprisingly, this difference was present only on trial four. Dark reared rats appeared to have more difficulty than complex reared rats only in learning the initial relationship between the proximal and distal cues and the platform. Following this phase, however, the relationship between cues was changed an additional three times. On subsequent trials, dark reared rats were not significantly worse at adapting to these changes and learning the new rules for locating the platform than were complex reared rats. The impact of dark rearing on the visual-spatial abilities and visually guided behavior in this study seems, at best, to be limited.

If restriction of sensory input to an early developing modality disrupts the organizational framework necessary for a spatial competency involving signals in a later developing modality, then the cauterized animals would be expected to be less capable. Early tactile restriction through cauterization of vibrissae had no effect on visual-spatial behavior as assessed by the present version of the water maze task. Even when early dewhiskered animals were also dark-reared, performance was not affected. However, expecting early somatosensory restriction to affect spatial behavior assumes developmental dependence between these capacities. It may be

that tactile input is unnecessary for the development of normal visual-spatial behavior. If the organization and development of spatial behavior is primarily dependent on the appropriate visual input, then tactile restriction would be of no consequence to spatial behaviors. It has been suggested in the literature that visual input is of primary importance for developing appropriate spatial behavior (Burnstine et al, 1984, Tees et al, 1981).

The Water-based Concurrent Discrimination Task produced similar results to those found with the Spatial Learning Task. Long term dewhiskering through cauterization did not qualitatively affect the ability to visually recognize and remember which object within the two pairs of visual stimuli was associated with the hidden platform. When cauterized rats were compared to intact groups in the same visual condition (ie. DR cauterized vs. DR, CR cauterized vs. CR), cauterized groups did not take longer to reach the platform, nor did they commit more errors in the process, than did intact rats. This was true for both training and transfer trials. Again, as far as stimuli are concerned, this is an almost purely visually based task. These results might indicate that tactile input is not necessary for the development of the ability to resolve visual detail, discriminate between different patterns, and remember differences between patterns. Furthermore, because tactile cues are not necessary to solve the problem facing the rats, tactile restriction was of no consequence to adult performance.

As expected, dark-rearing did seem to have an effect on performance on this task. Although dark-rearing has not been shown to affect the ability of rats to resolve detail per se (Friedman & Green, 1982), they do take longer to acquire various kinds of pattern discriminations (Tees, 1979). This delayed acquisition is reflected in the analysis of latency on training days 1, 5, and 10. CR rats are able to discriminate and remember the two pairs by day 5, while the same levels of performance are not achieved by DR groups until day 10. The poor performance of DR rats may reflect a problem in the ability to concurrently learn and remember two positive stimuli, not difficulty with resolving differences between stimuli.

The results of the analysis of transfer trials indicated that DR rats were more disrupted by mixing the original cue pairs than were CR rats. This too is consistent with the results of DR rats taking longer to acquire pattern discriminations (Tees, 1979). Although the rule didn't change for these trials, that is positive cues from previous trials remained as positive cues, the pairings did change, resulting in a novel pattern discrimination facing the rat.

One factor that may have influenced the results is that this task was run following the completion of the spatial learning task. Having had previous experience with a water maze task, rats had already learned that there was a submerged platform in the pool. Although it is unlikely that this had significant impact on the final outcome (Kolb & Walkey, 1987), it is possible different strategies to locate the platform may

have been employed in the initial acquisition phase. Naive animals may have taken longer to learn this task had they not have had previous experience with the water maze situation. Alternatively, having to switch from a place learning task to a visual discrimination task while in the same testing environment, could well have been expected to be more disruptive to specific animals with different early restrictive stimulation histories.

The remaining three tasks were tests of species specific behaviors. The results of the grooming task proved to be somewhat surprizing. Overall, CR rats groomed more body components and for longer period than did DR animals. DR and CR did not, however, differ in the number of grooming segments they initiated. There is some evidence to suggest that following early cortical lesions, sparing of function is more common on learning tasks than of tests of species typical behaviors (Kolb & Whishaw, 1989). Dark-rearing may have had a similar effect on the naturally occurring behavior of grooming. However, as the cortical impact of early dark or complex-rearing is thought to be more diffuse, (Tees, 1990), this is unlikely.

Although the rats had spent an equal amount of time being handled and habituated to the chamber, it is possible that the experience of being in the chamber, even under the dim lighting conditions, was much more distracting for the DR rats than it was for the CR rats, especially since this was the first behavioral task all animals were tested on. It is possibly for this reason that, although equal number of grooming sequences

were initiated for all groups, the DR rats did not carry through as thoroughly. Other experiments, however, show DR rats to be as successful as other groups on initial visual discrimination tasks (Tees, 1990).

Dewhiskering and/or dark-rearing had no significant impact on performance on the Dodging and Wrenching paradigm. The ability of rats to successfully defend their food was unaffected by rearing condition. The type of response elicited by a victim when challenged by a robber was also consistent across all rearing conditions, although different from the original findings by Whishaw and Tomie (1987). As acute dewhiskering and blinding have not been found to have an impact on performance in the Dodging and Wrenching task (Buhrmann & Tees, unpublished) it is unlikely that the results on this task can be explained by intermodal compensation occurring during development. It may be more plausable to conclude that success on this task is dependent on inputs not affected by visual or vibrissal sensory manipulations.

There was no significant effect for rearing condition in either the tactile or visual conditions of the novelty discrimination task. In both conditions rats did spend almost twice as long exploring the novel object as they did the familiar object. For the tactile condition, the presence of vibrissae during development did not appear to be important to the ability to recognize and remember the textural discrimination utilized in these cases. Since cauterization restricts sensory input only from the receptors located in the

vibrissae follicles intramodal compensation may have occurred.
To discriminate between novel and familiar tactilely distinct
objects, cauterized subjects could be relying on input from
other somatosensory receptors.

Results on the visual condition are in accordance with the
results of the water based visual discrimination task. DR rats
were not impaired in their ability to resolve the differences
between these shapes. Cauterization also had no effect on
performance on this task. Early tactile restriction does not
appear to intermodally impact on the development of this ability
either. Perhaps, if the test stimuli used for this task had
been more complex, differences between different rearing
conditions may have been revealed. In a cubic volume
discrimination task, enriched golden hamsters were able to make
learning transfers to more diversified test situations than were
standard subjects (Thinus-Blanc, 1982).

In comparing the behavioral outcomes of the four rearing
conditions, pairwise post-hoc comparisons often did not reveal
any significant differences between any of the groups.
Significant results for univariate ANOVA's were explained only
by combining the data from the DR and DRC groups and comparing
that to the combined data from the CR and CRC groups. There
were never any significant differences found between cauterized
and intact groups reared within the same "visual" rearing (dark-
reared or complex-reared) condition. The main rearing condition
effect can be narrowed down to an effect for dark-rearing
relative to complex-rearing.

The minimal behavioral effects for cauterization could be used as support for the idea of intermodal compensation. As the somatosensory system is the earliest system to develop, early restriction could be compensated for by other later developing systems. If intermodal compensation had occurred, the behavioral impact of early cauterization would be minimal, as was observed.

However, another possibility is that intramodal, not intermodal, compensation has occurred. Cauterization as a method of early restriction of the somatosensory system may not be a sufficient manipulation. Although intact vibrissae are believed to be very important to the normal functioning of the rat, and that the end points of their cortical projections (the cortical barrel fields) account for a full 30% of primary somatosensory cortex, 70% of primary somatosensory cortex is still receiving input from a wide variety of somatosensory receptors. Not even the restriction of input from the mystacial area is complete. Projections from sensory receptors located in the skin around the vibrissae are still inputting into the cortex (Kaas et al, 1983). Before it is necessary to consider intermodal compensation as an explanation for the lack of deficits demonstrated by the cauterized groups, the possibility of intramodal compensation occurring should be considered.

Previous research has shown that following vibrissae loss behaviors for which vibrissae are considered important all to some degree survive vibrissae removal (Kerimidas, 1976). For example, rats will learn to jump across a gap in an elevated

platform to receive a food reward (Hutson & Masterton, 1986).
Vibrissal removal decreases the width of the gap a rat would
jump, presumably because without their vibrissae, they could not
bridge (make contact with the other side) as large a gap.
However, as long as the far side could be contacted with the
snout (which contains many other somatosensory receptors besides
the vibrissae receptors), the rat would jump the gap. Thus, the
rat has compensated (although not completely) for vibrissal loss
by using input from other somatosenory receptors.

Perhaps when looking at the impact of early somatosensory
restriction on the development of other sensory systems, it
would be more effective to use a more complete form of
somatosensory restriction. Options such as cutting the common
somatosensory pathway through the thalamus, or later common
tracts projecting to the cortex, should be explored a means of
giving a more complete picture of the inter- and intramodal
effect of early somatosensory restriction.

Selective Posterior Cortical Lesions

A second approach to the study the relationship between
brain and behavior is to "perturb" the abilities of the rat by
inducing selective lesions, and observe how behavior changes.
Cortical areas are functionally distinct divisions of the brain.
Restricted lesions can produce very specific and irreversible
changes in behavior (Kaas, 1987). The later addition of select
lesions to Par1 (somatosensory) and Oc2M (visual) cortex was to
serve two purposes in this study. The first was an attempt to

gain further insight into the plasticity surrounding manipulations of early rearing environment. If there were an interactions between lesion group and rearing condition, then a clearer picture of the intra- and intermodal effects of early somatosensory and visual deprivation would be attained. The second purpose for including the lesion groups was an attempt to further delineate the functions that are localized in areas Par1 and Oc2M.

The analysis did not reveal a significant effect for lesion group. There was also no effect for the interaction of lesion type and rearing condition. In general, the behavioral abilities (as reflected in performance on the tasks) of rats with either visual or somatosensory cortical lesions were not significantly different from those of their comparable control groups. Inconsistency of lesion size as revealed by histological examination may have eliminated lesion effects. To assess this possibility, the behavioral performances of rats classified as having small, large, or accurate lesions were compared. The analyses were conducted separately for Par1 and Oc2M lesion groups. There were no consistent effects for either lesion. Although the performance of rats with different lesion sizes did differ significantly from each other on two or three out of the 32 dependent measures considered, these effects did not reveal a pattern. For instance, the rats with larger lesions were not always the worst off, nor were those with the smaller lesions the least impaired. This was true for both area Par1 (somatosensory) and area Oc2M (visual) cortex. For this

reason, it does not appear that the size and/or accuracy of the lesions played a central role in the overall outcome of this study.

A second possibility is that the behavioral tests were not sensitive to functions of the cortical areas focused on in this study, and therefore, no behavioral deficits were observed. Task selection is difficult when the behavioral impact of selective lesions is simply not well documented. For instance, as area Oc2M is most commonly part of a large cortical lesion in combination with other cortical visual areas, the precise function of area Oc2M can only be speculated on (Dean, 1990).

A final alternative is that the effect for lesion may not have been significant simply because there were so many factors included in the study (Glass & Hopkins, 1984). Subtle adverse effects could easily have been lost because of nature of the analysis. Furthermore, the nature of the dependent measures was such that not all the measures were expected to result in the same direction of an effect for each lesion group across all rearing conditions. Some of the tasks were included in the battery of behavioral tests because it was thought that they would specifically be sensitive to somatosensory cortex function, some were thought to be more visually based, while for others there was more of a possibility for an interaction between the factors of rearing and lesion. With so many variables, so many experimental groups, and limited numbers of subjects in each group, the power to find any differences between groups was severely diminished. Only the strongest and

most robust effects or interactions would have survived such an analysis.

One significant result worth mentioning in spite of the nonsignificant overall lesion effect is the result on the tactile condition of the novelty discrimination task. Rats with Par1 (somatosensory) cortex lesions spent less time exploring the novel object than did both the visually lesioned and control groups. Although this may be a chance finding, other researchers have found similar results following somatosensory lesions. An earlier study by Finger (1978) found rats with bilateral lesions of the somatosensory cortex to be less able to make textural discriminations than non-lesioned animals.

Dendritic Arborization

The final purpose of this study was to test ideas of modality interdependence and intermodal compensation at an anatomical level. Dendritic proliferation may be a general mechanism supporting behavioral change (Greenough, 1976, 1986; Kolb, 1989). Rearing condition was found to have a significant impact on dendritic arborization, but only for apical dendrites. In comparison to dark-rearing, environmental enhancement through rearing in a complex environment increased apical dendritic branching in somatosensory, visual, and auditory cortex. These findings extend previous reports of increased dendritic branching in animals reared in complex environments (Greenough & Juraska, 1979; Greenough & Volkmar, 1973; Juraska, 1990; Rosenzweig & Bennett, 1978).

To give a more complete picture of the intermodal effects
of dark-rearing, it would be interesting to raise DR rats in the
enclosed complex environment. Although input to the visual
system would still be restricted, input to remaining sensory
systems would be enhanced. This could potentially impact on the
development of these sensory modalities, possibly decreasing the
effect of dark-rearing.

Long term dewhiskering through cauterization also led to an
increase in dendritic branching, but only for CR animals. In
comparison to other rearing conditions, there was an increase in
higher order apical dendritic branching for the CR cauterized
group in all three cortical areas measured. The differences may
be confined to higher order branches because the lower order
branches are more fully developed at the time differential
rearing begins (Greenough & Volkmar, 1973).

These results provided anatomical evidence for modality
interdependence. Long-term tactile restriction through
cauterization led to increased higher order dendritic branching
in auditory and visual cortex. This finding is consistent with
two hypotheses about early experience and perceptual
development: 1) decreased competition during development from
an early developing system (in this case the somatosensory
system) leads to increased competency in a later developing
modalities (Burnstine et al, 1984; Turkewitz & Kenny, 1982); and
2) behavioral demand is a significant factor in determining the
impact of early somatosensory restriction (Burnstine et al,
1984). Neurons and neural connections are in competition with

each other for space and survival (Kaas, 1987). Experience activates and reinforces certain pathways, while others fall into disuse. Those not used by the system are gradually eliminated (Aoki & Siekevitz, 1988; Kolb & Whishaw, 1989). As dendritic proliferation has been proposed to be a general mechanism supporting behavioral change (Kolb, 1989; Kolb & Whishaw, 1989), increasing behavioral demand may be a significant factor in compensation for early damage.

The result for somatosensory cortex provides evidence for intramodal compensation for early sensory restriction. The prevailing view is that dendritic arborization is decreased by decreasing afferents to the cortex (Juraska, 1986, Kolb & Whishaw, 1989; Rosenzweig, Bennett & Diamond, 1972). If afferents are removed early in life, and dendritic atrophy fails to occur, then an increase in afferent stimulation from other sources is maintaining the dendritic integrity (Kolb & Whishaw, 1989). Since cauterization represents only partial deafferentation of all somatosensory afferents, the increase in higher order branching in somatosensory cortex may be supported by increased stimulation from other somatosensory afferents, undamaged by early cauterization.

It is reasonable to assume that anatomical changes are manifested behaviorally. CR rats were found to show increased dendritic branching in comparison to DR rats in all cortical areas measured. This difference was reflected in the behavioral results. On tasks where there were significant differences in level of performance, DR rats were generally worse off than were

CR rats. Given the extreme difference in rearing condition, however, these differences may not have been as great as one might expect. The behavioral data collected in this study did not completely parallel the anatomical results found for cauterized rats. Under anatomical examination, CRC rats showed increased branching overall in auditory cortex, and higher order in auditory and somatosensory cortex. On behavioral measures, they did not differ significantly from other groups. These results may be reflective of the behavioral tests used in this study not being sensitive enough to detect subtle differences that may follow cauterization.

Conclusions

At the anatomical level, the present study provides limited support for the idea of intermodal compensation following restriction of an early developing sensory modality. Animals experiencing early restriction to the tactile system through cauterization of the vibrissae show increased higher order branching in all sensory cortical areas measured. Decreasing competition during development leads to increased competency in later developing modalities. This difference, however, is present only when behavioral demand is augmented through rearing in a complex environment, indicating that rearing environment is a significant factor in determining the impact of early somatosensory restriction.

Although the anatomical differences due to early stimulation history were not mirrored by behavioral differences,

conducting anatomical and behavioral examinations in conjunction with each other will result in a clearer picture of the relationship between the brain and behavior (Kolb & Whishaw, 1989). Utilizing better behavioral assays of these selective cortical lesions will certainly help. In general, smaller studies more restricted in scope would probably be more effective in illuminating the relationship between the posterior cortex, behavior, and early environmental conditions.

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