BILATERAL SURGICAL LESIONS WITHIN OCCIPITAL AND TEMPORAL REGIONS OF THE POSTERIOR NEOCORTEX AND VISUAL RELATIONAL LEARNING IN THE RAT

by

Laura Brewster Williams Sirotkin

(Under the Direction of Billy R. Hammond)

ABSTRACT

Research concerning the modular structure of the mammalian brain has sought to clarify how anatomically discrete regions of the neocortex underlie specific cognitive and behavioral functions. Historically, the laboratory rat has served as a valuable model organism in the study of cortical organization at the anatomical, chemical, physiological, and behavioral levels as a basis for comparative investigations. Findings from such studies suggest that the functional neuroanatomy of exclusive posterior neocortical regions in the rat resembles to a considerable degree that observed in more developed animals. Clinical observations and neurobehavioral experiments in primates indicate that injury to temporal regions results in marked deficits in visual analysis. The goal of the present study was to investigate the contributions of a purportedly homologous cortical region in the rat to such functions. The question of whether lesions in the rat temporal cortex impair performance on behavioral tasks that necessitate the use of visual relational learning was examined. In preoperative training, rats (n = 24) mastered a simple discrimination problem based on the relative luminance of two distinct visual cues and, after a 9-week hiatus, demonstrated retention of the acquired task. In the intervention phase, rats were separated into three surgical lesion groups defined as bilateral sham control (CON), partial striate (PS) or temporal (TE). In post-surgical retraining, rats (n = 21) re-mastered the original problem. In final testing, CON and PS rats generalized the original task to multiple, presumably more demanding, discrimination problems based on the relative luminance of novel, paired visual stimuli. In contrast, the TE group failed to attain behavioral criterion, exhibiting performance deficits on all measures compared to the other groups. The experimental data from the present study in the rat are consistent with research findings in primates that have suggested the presence of a specialized ventral occipitotemporal pathway subserving functions of higher visual processing.

INDEX WORDS: Rat, *Rattus norvegicus*, Posterior neocortex, Temporal cortex, Occipital cortex, Ventral pathway, Visual analysis, Visual discrimination, Visual relational learning

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TABLE OF CONTENTS

Page

LIST OF TABLES

Page

LIST OF FIGURES

Page

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Proposed Dual Visual Processing Pathways in Human

A large body of scientific research provides compelling evidence that two functionally dissociable corticocortical pathways for visual analysis, emanating from and extending beyond occipital cortex, exist in human (Chiaravalloti & Glosser, 2004; Damasio, Tranel, & Damasio, 1989; Gaddes & Edgell, 1994; Grady et al., 1992; Haxby et al., 1991; Hermann, Seidenberg, Wyler, and Haltiner, 1993; Horwitz et al., 1992; Nieuwenhys, Voogd, & van Huijzen, 1988; Newcombe, Ratcliff, & Damasio, 1987; Ungerleider, Courtney, & Haxby, 1998; Kolb, 1990) and in nonhuman primates (Baizer, Ungerleider, & Desimone, 1991; Goodale & Milner, 1992; Maunsell, 1992; Macko et al., 1982; Mishkin, Ungerleider, & Macko, 1983; Morel & Bullier, 1990; Ungerleider & Mishkin, 1982). In humans, an anterodorsal projection, coursing from occipital cortical areas (i.e., striate, medial peristriate and lateral peristriate) to the posterior parietal cortex (PPC), is reportedly critical to the processing of visuospatial stimuli and to the synchronization of motor responses related to visual spatial cues (Goldberg & Colby, 1989). Alternatively, a ventrorostral projection, originating in occipital cortex and extending to temporal (TE) regions, is purportedly specialized for visual object recognition, visual analysis, and visual memory (Adams, Victor, & Ropper, 1997; Cummings & Trimble, 1995; Kolb, 1990; Kolb & Whishaw, 1996; Kolb & Whishaw,

2003; Lindsley & Holmes, 1984; McCarthy & Warrington, 1990; Milner, 1968; Wilkins & Mosocovitch, 1978).

Temporal Cortex and Visual Analysis in Human

As is well documented in the human clinical neuropsychological and neurobehavioral literature, anatomical insult to integral regions of temporal cortex may be accompanied by cognitive and behavioral deficits, including those of visual analysis (Creutzfeldt, 1995; Kolb, Burhmann, McDonald & Sutherland, 1994; Kolb & Whishaw, 1996; Kolb & Whishaw, 2003), such as a loss of pattern recognition (Lindsley & Holmes, 1984; Nolte, 1993) and multiple distortions in visual perception (Adams et al., 1997; Kolb & Whishaw, 1996). Findings from clinical observations and from behavioral investigations reveal related impairments in complex visual perception (Huxlin & Merigan, 1998), visual perceptual categorization (Chan, Sze, & Cheung, 2004; Kolb & Whishaw, 2003) and visual memory (Wilkins & Moscovitch, 1978; Chiaravalloti & Glosser, 2004). Studies of the effects of temporal lobectomy in human patients have revealed deficits in the recognition and interpretation of faces, as well as impairments in verbal memory (Kolb & Whishaw, 1996; Milner, 1970).

Human clinical studies based on lesion effects are consistent with data from electrophysiological (Srebo, 1985) investigations, neuroimaging studies using positron emission tomography (Grady et al., 1992; Nakamaura et al., 2000), and functional and neuromagnetic measuring (MEG) techniques (Sams, Hietanen, Hari, Ilmoniemi, Lounasmaa, 1997; Wright et al., 2003), which have identified visually responsive regions within the ventral occipitotemporal cortex and have suggested the significance of the temporal cortex in functions of visual pattern discrimination and visual memory (Grady

et al., 1992; Haxby et al., 1991; Kawshima et al., 1998). In recent reviews (Ranganath, 2006) there are reports of experiments demonstrating activation of category-specific, inferior temporal subregions during mental imaging tasks (Ishai, Haxby, & Ungerleider, 2002; O'Craven & Kanwisher, 2000). Collectively, the human clinical neuropsychological, behavioral, and neurophysiological evidence strongly suggests that there exists an organizational and functional modularity of neural substrates in the posterior cortical visual system, implicating ventral occipitotemporal cortical circuitry in the mediation of visual identification and perception, visual analysis, and visual memory.

Proposed Dual Visual Processing Pathways in Non-Human Primate

In an attempt to further clarify the morphological and functional organization of the human posterior cortex, researchers have long turned to and relied upon evidence from experiments using nonhuman primates (Feinberg & Farah, 1997). An elaborate compilation of data, comprised principally of findings from empirical laboratory studies using rhesus macaque monkeys, has focused on the cytoarchitecture and functional neuroanatomy of the primate posterior neocortex (Creutzfeldt, 1995). Such studies have shown that a marked similarity exists in the anatomical and functional organization of the posterior neocortex between human and non-human primate.

It is well established (Baizer et al, 1991; Goodale & Milner, 1992; Macko et al., 1982; Maunsell, 1992; Mishkin et al., 1983; Morel & Bullier, 1990; Ungerleider & Mishkin, 1982) that two functionally distinguishable cortical pathways for visual analysis, diverge in and extend beyond occipital cortex in monkey. A cortical circuitry, originating in primary visual cortex and projecting anterodorsally to a posterior parietal area (PPC), is implicated in the integration of visuospatial perception. Conversely, a

ventrorostral projection, emanating from the occipital lobe and terminating in an inferior temporal (IT) region is implicated in the mediation of visual object recognition, visual analysis, visual relational learning, and visual memory (Mishkin et al., 1983; Ungerleider & Mishkin, 1982).

Inferotemporal Cortex and Visual Analysis in Non-Human Primate

Experiments investigating functional and behavioral deficits associated with IT lesions have yielded results converging, to a marked degree, with those obtained from clinical observations and behavioral investigations of humans with temporal lobe damage. Behavioral experiments involving IT lesions in monkey show impairment in the categorization of visual stimuli (Wilson & DeBauche, 1981), and recent electrophysiological recording studies have shown that IT is activated in tasks of visual analysis and visual categorization (Freedman, Riesenhuber, Poggio, & Miller 2003). Similarly, neurophysiological investigations of primate IT cortex have revealed neurons with selective characteristics for complex visual stimuli (Baylis & Rolls, 1987; Kreiman et al., 2006; Perrett et al., 1984; Perrett, Harries, Benson, Chitty, & Mistlin, 1990; Sobotka & Ringo, 1993). Other studies have shown that IT neurons can develop a complex receptive field organization as a consequence of extensive training in the discrimination and recognition of objects (Logothetis, Pauls & Poggio, 1995). Moreover, multiple lesion experiments (Buffalo et al., 1999; Buffalo, Ramus, Squire, & Zola, 2000) studying the functions of IT cortex have revealed visual modality deficiencies subsequent to anatomical insult, including impairments in complex visual discrimination, visual processing, and visual perception.

Other recent behavioral studies have examined the significance of IT cortex to specific functions, such as visual discrimination learning (Ridley, Warner, Maclean, Gaffan, & Baker, 2001), visual pattern discrimination (Weller et al., 2006), and categorization of visual stimuli (Buckley, Gaffan, & Murray, 1997; Freedman et al., 2003), and have produced findings indicating that this region is critical to the processing and analysis of visual cues. Collectively, the findings suggest that IT cortex is critical to visual analysis, visual perception, and visual memory and indicate considerable anatomical and functional similarity between human and non-human primate in posterior cortical organization.

Posterior Cortex and Purported Dual Visual Processing Pathways in Rat

Research conducted over the course of many years (Boyd & Thomas, 1977; Dean, 1981; Kolb, 1990; Kolb et al., 1994, Kolb & Walkey, 1987; McDaniel et al., 1995; McDaniel & Thomas, 1978; McDaniel & Wall, 1988; Tees, 1999; Thomas & Weir, 1975), involving lesions of anatomically dissociated regions of the posterior neocortex of the rat, has shared similar goals with human and primate research. As in investigations with more cortically developed animals, research with the rat has been concerned with the anatomical and functional organization of the neocortex and has had the goal of clarifying the relative contributions of exclusive neocortical regions to specific cognitive and behavioral functions. Findings from anatomical (McDaniel, McDaniel, & Thomas, 1978), behavioral (Kolb et al., 1994; McDaniel & Thomas, 1978; McDaniel & Wall, 1988; Myhrer, 2000), and neurophysiological (Zhu, Brown, & Aggleton, 1995; Zhu, McCabe, Aggleton, & Brown, 1996) studies of rats have shown that the organization of

the posterior association cortex resembles, to a considerable extent, that described in primate.

Based on the findings from studies investigating the effects of lesions in distinct neocortical regions (Dean, 1990; McDaniel & Thomas, 1978), it has been hypothesized (Kolb, 1990; McDonald & Mascagni, 1996) that a dual corticocortical pathway for visual analysis exists in the rat as well. Of the two projections originating in primary visual cortex (Striate Cortex, Area Oc1; Zilles [1985]), one is proposed to course anterodorsally, terminating in a putative posterior parietal region (Burcham, Corwin, Stoll, & Reep, 1997; McDaniel et al., 1995), while the other pathway projects rostroventrally, terminating in a more caudal portion of temporal cortex (Shi & Cassell, 1997), bearing notable resemblance to IT cortex in monkey.

Temporal Cortex and Visual Analysis in Rat

Similar to findings from experiments investigating the dissociation between the effects of PPC and TE/IT lesions in visual-spatial and visual-object recognition, results from studies examining these same effects in the rat have demonstrated that the PPC is critical to visual spatial navigation (e.g., Kolb et al., 1994; Kolb & Walkey, 1987; McDaniel, Williams, Attaway, & Compton, 1998) and that TE subserves functions of visual analysis, visual object recognition, and complex visual pattern discrimination (McDonald & Mascagni, 1996; Tees, 1999; Wortwein, Mogensen, Williams, Carlos, & Divac, 1994). Whereas there exists a sizeable body of literature concerning the PPC and visual spatial functions in the rat (DeCoteau & Kesner, 1998; McDaniel & Wall, 1988; Kolb & Walkey, 1987), there are only a limited number of experiments that have investigated anatomically localized TE in rat.

Of the investigations into a dual pathway for visual analysis and functions of TE in rat, findings have emerged that are markedly similar to those reported in the human and nonhuman primate literature. Kolb et al. (1994) demonstrated a double dissociation between the effects of PPC and TE lesions on visual-spatial and visual memory problems, respectively. More recently, Tees (1999) examined the functional consequences of PPC and TE lesions on spatial and non-spatial learning, with findings revealing a double dissociation of effects, as predicted. Investigations using electrophysiological, neurotoxic infusion, and protein product marking procedures (assays for the early gene *c-fos*), have also supported conclusions from neurobehavioral studies in rats that TE underlies functions of visual recognition and visual memory (Wan et al., 1999; Zhu et al., 1995; Zhu et al., 1996). A number of these experiments have demonstrated differential and significant neuronal activation produced by novel and familiar individual visual stimuli in the rat cortex. Others have demonstrated impeded visual memory following infusion of neurotoxins to temporal cortex (Myhrer & Anderson, 2001). Taken together, such results suggest that temporal cortex subserves visual recognition memory in rat.

Focus of the Present Study

Research in humans and primates has shown a unique function of TE/IT cortex in the categorization of visual information and in visual relational learning. The ability to categorize objects or to perform relational discriminations between visual stimuli is reportedly impaired in human patients who have sustained temporal lobe damage (Kolb & Whishaw, 2003), and in monkeys with lesions to IT cortex (Wilson & DeBauche, 1981). Recent investigations suggest that neurons in IT cortex have specificities that appear to contribute to the categorization of visual information (Freedman, Riesenhuber,

Poggio, & Miller, 2001). Following a review of the literature on this topic, there appear to be only a few neurobehavioral experiments that have investigated the involvement of exclusive posterior cortical regions, such as area TE, specifically to functions of visual relational learning in the rat (Maki et al., 2001; Williams & McDaniel, 1999). These investigations have suggested that further study is needed in resolving this topic.

The purpose of the present work was to examine whether temporal cortex lesions in the rat interfere with behavioral tasks that necessitate the use of visual relational learning. As it has been suggested that the rat serves as a valuable model for investigations of posterior cortex, and because similar hypotheses concerning visual analysis are being addressed in nonhuman primates, the findings from the current study using the rat should have broad applicability. A number of critical methodological considerations that are discussed in related neuroscientific studies and reviews, concerning visual acuity (Dean, 1978; Dean, 1981; Prusky, Harker, Douglas, & Whishaw, 2002; Prusky, West, & Douglas, 2000; Prusky & Douglas, 2003; Robinson, Bridge, & Riedel, 2001; Silveira, Heywood, & Cowey, 1987), spectral sensitivity (Birch & Jacobs, 1975; Jacobs, Fenwick & Williams, 2001; Muntz, 1967; Sokol, 1970), and brightness discriminative abilities of the rat (Hermann, 1958; Lashley, 1931), as well as control of stimulus luminance (Thomas, 1993), water maze performance (Kant, Yen, D'Angelo, Brown, & Eggleston, 1988), and behavioral criterion in two-choice discriminative tasks (Bogartz, 1965; Grant, 1946; Grant, 1947; Kalat, 1975; Runnels, Thompson, & Runnels, 1968), were carefully addressed in the experimental design of this research.

The present study had four experimental phases. In the initial training phase, it was anticipated that all animals would demonstrate acquisition and retention of a pre-operatively learned simple black-white visual discrimination based on the relative luminance of two constant visual cues. In the intervention phase, after being prepared with bilateral control (CON), partial striate (PS) or temporal (TE) cortex lesions, rats were expected to demonstrate re-mastery of the original problem. In the outcome phase, it was hypothesized that rats with TE lesions would display deficits in the ability to generalize the original discrimination problem to novel, presumably more complex, visual discriminations that were based solely on the relative luminance of paired cues. Following behavioral assessments, the animals were sacrificed, surgical lesions were mapped and quantified, and correlations between anatomical and behavioral variables were examined.

CHAPTER 2

EXPERIMENTAL PROCEDURES

Subjects and Maintenance

Twenty-four adult male black-hooded rats, from the Long-Evans Norwegian strain (*Rattus norvegicus*) and purchased from Harlan, Inc. (Indianapolis, IN), were used as experimental subjects (See Figure 1). Animals were individually housed in polycarbonate cages measuring 43.2 cm (length) x 21.6 cm (width) x 20.3 cm (height) in a humidity-controlled and temperature-regulated animal housing facility (Large Animal Research Unit, Department of Animal and Dairy Science, The University of Georgia) with food and water available *ad libitum*. Rats were maintained on a reversed 12-hr schedule (lights off at 0900h), with all behavioral procedures occurring during the dark phase of the cycle. The subjects were 112 days old at initiation of experimental procedures. The conditions of animal maintenance and research methodology were approved (Animal Use Proposal # A2005-10154-m1) by The University of Georgia, Office of The Vice President for Research, Institutional Animal Care and Use Committee (IACUC), whose research policies and procedures meet the standards of the Association for Assessment and Accreditation of Laboratory Animal Care International (AAALAC). All aspects of this research followed policies and procedures established in the *Ethical Standards for Use of Animals in Psychological Research* (American Psychological Association, 2002) and in the *Guide for the Care and Use of Laboratory Animals*

(Institute of Laboratory Animal Resources Commission on Life Sciences, National Research Council, 1996).

Apparatus

All behavioral procedures were conducted in a circular, aluminum, modified water tank (See Figure 2) measuring 1.37 m (diameter) x 0.46 m (height). Located directly opposite the single designated start position, the interior rear wall of the apparatus was fitted (at 90º) with a sheet of Plexiglas, measuring 61 cm (length) x 63.5 cm (height) x .75 cm (thickness) and extending 61 cm into the tank. The Plexiglas sheet served as a partition between the designated left and right goal quadrants (each 61 cm in length) where visual stimuli were consistently displayed against the interior rear wall during behavioral training and testing trials. The interior of the tank and all fitted components were painted with flat white, exterior, latex paint.

The apparatus was filled with water to a depth of 20 cm, with water temperature maintained at approximately $23^{o} \pm 1^{o}$ C and replaced every two days. Non-toxic, white powdered tempera paint (Fresco, Rich Art Color Co., Northvale, NJ) was added liberally to the water to obscure view of a white, weighted Plexiglas platform, measuring 26 cm (length) x 17 cm (width) x 17 cm (height), and submerged approximately 2 cm below the water surface. Across behavioral trials, the platform was located directly against the interior rear wall below one of two randomized visual stimuli. A Plexiglas sheet measuring 66 cm (length) x 20.5 cm (height) x .3 cm (thickness) was affixed to the rim of the apparatus above each of the two goal quadrants to prevent escape of rats from the tank from the mounted platform. The distance from the start position to each stimulus

was approximately 120 cm, and the distance from the start position to the accessible edge of the escape platform was approximately 103 cm.

Laboratory Environment and Illumination Conditions

All behavioral procedures were conducted in a laboratory room (Large Animal Research Unit, Department of Animal and Dairy Science, The University of Georgia), depicted in Figures 3 and 4. The laboratory environment measured 6.22 m in width x 6.55 m in length x 3.05 m in height, and was illuminated by six pairs of fluorescent tube lights encased in evenly dispersed, standard ceiling fixtures.

A supplemental lighting source (Regent, DTS1200, 1200-Watt Stand Light), consisting of two 600-watt manually adjustable professional work lamps containing halogen bulbs and mounted onto a weighted tripod, was employed during all behavioral trials. Lamps were positioned 106.7 cm above the floor and extended 34.3 cm from the laboratory wall and 3.5 m from the tank start position. Used as an intermediate filter between the lamps and the apparatus, an acrylic sheet measuring 118 cm (width) x 60 cm (height) x .4 cm (thickness) was suspended from a metal rack (150 cm in height x 81.3 cm in width x 45.7 cm in depth) and was placed 43 cm from the stand-light bulbs and 305 cm from the start position.

Quantification of Illumination Conditions

Since the illumination condition of the stimuli was one of the dependent measures in this experiment, precautions were taken to ensure that the ambient illumination in the left and right goal quadrants of the apparatus was strictly controlled and that the illumination of the stimuli was maintained at a constant level throughout the course of

behavioral procedures. To this end, the luminous flux generated by the light source (i.e., fluorescent and halogen bulbs) was measured in the left and right goal quadrants of the apparatus with an auto-ranging light meter (Oriel, Goldilux, Newport, Irvine, CA) for the duration of a trial (60 sec) during each of 10 random sessions in Experimental Phases 1-4. The light was quantified (in footcandles) and temporal stability was analyzed and compared between the apparatus goal quadrants.

Stimuli

Fourteen 2-dimensional solid squares (18 cm x 18 cm), differing only by photometric luminance (i.e., 74.4, 70.8, 63.6, 52.8, 49.2, 42, 38.4, 31.2, 24, 20.4, 16.8, 13.2, 9.6 and 6.48 cd/m^2; characterized as "white," "black," or graduated shades of "gray"), were used (See Table 1). The 14 discriminanda were selected from a larger group of stimuli consisting of consecutive, near-equal interval photometric luminance values, including and between 74.4 cd/m^2 and 6.48 cd/m^2, that were originally derived from 255 computer software-generated (Microsoft Word 2003) images. These images were individually and professionally laser printed on sheets of high-grade white paper, cut to identical measurements (18 cm x 18 cm) and laminated. Across trials, stimuli were systematically positioned and displayed in pairs within the apparatus, with each card suspended from a plastic hook and metal loop that were centered in the left or right goal quadrant against the interior rear wall (See Figure 5). Cues were set an equal horizontal distance from the center Plexiglas partition, with the bottom edges of cards set approximately 1 cm above the water surface.

Quantification and Preliminary Analyses of Stimulus Luminance

The luminance of each stimulus was quantified in preliminary measurements obtained via a telescopic-lens spectral photometer (SpectraScan Photometer, PhotoResearch, Model PR-650) under ambient fluorescent and halogen light conditions to which the subjects were exposed during behavioral procedures. A graphic depiction of the photometric luminance values of the fourteen visual stimuli employed in behavioral procedures is featured in Figure 6. An energy spectrum illustrating the amount of light (based on the ambient fluorescent and halogen light used during testing) reflected from a stimulus with intermediate (gray) shading is plotted graphically in Figure 7.

Collection of Behavioral Data

Data were recorded manually by one experimenter throughout behavioral procedures. Additionally, behavioral activity and navigational trajectories of animals across all trials were recorded by a digital video camera (Logitech Quick Cam Pro 4000, Logitech, Inc.) that was connected remotely to a computer (Dell, Intel Pentium III, Windows XP Professional Edition) equipped with licensed video-tracking software specifically engineered for use in laboratory experiments with animal subjects (ANY-maze^{TM} Video Tracking System, Application Version 4.20, 2005, Stoelting Co., Wood Dale, IL). This system provided a highly reliable and standardized system for systematically and consistently defining errors and correct responses. The camera was affixed to the laboratory ceiling, 3.05 m directly above the center of the tank, such that activity within the apparatus could be maximally visualized and optimally recorded from an overhead view. ANY-maze^{TM} was programmed to digitally map the perimeter and quadrants of the apparatus and to record subject navigational trajectories, by tracking the

center of the animal's body for the duration of a behavioral trial (e.g., 60 sec). During each trial, the computer screen image of respective left and right demarcated goal quadrants was highlighted upon animal entry, thus indicating an error or the beginning of a possible correct response (See Figure 8). Examples of systematically defined correct responses and errors, depicted in Track-Plot Diagrams that were generated during behavioral trials (n = 4,600) by ANY-maze™ Video Tracking System, are displayed in Figure 9.

Quantification of Behavior

Data in Experimental Phases 1-4 were obtained for the following behavioral variables: Terminal Performance (i.e., Percent Correct Response for the averaged final two sessions through criterion), Number of Errors Through Criterion, and Number of trials Through Criterion, per animal per session. Data were obtained via experimenter observation and documentation, using visualization enhancements and systematic video recording methods provided by the ANY-maze™ Video Tracking System.

All quantified behavioral variables were included in linear regression correlation matrices to produce a representative, composite behavioral variable for both the PS and TE lesion groups for use in subsequent correlation analyses.

Experimental Phase 1: Pre-Surgical Training

The purpose of Experimental Phase 1, Pre-Surgical Training, was to train subjects to solve a simple visual discrimination problem. It was hypothesized that all subjects would attain behavioral criterion and master the task with near-equivalent proficiency.

The stimuli employed in Pre-Surgical Training were two, 2-dimensional, square, solid images, with luminance values of 74.4 cd/m^2 ("white") and 6.28 cd/m^2 ("black"), selected from the collection of 14 visual stimuli. Across trials, rats were trained to discriminate between the paired stimuli ("white" vs. "black"), associating the less luminous cue ("darker"; 6.48 cd/m^2; S+) with escape from the water. The stimuli were presented for 10 trials per animal per training session through criterion performance. Behavioral criterion was defined as an average of 90% accuracy across two consecutive sessions. Throughout behavioral procedures, the left-right location of the S+ was randomized across trials using a Fellows (1967) series, such that an equal number of presentations of S+ (n = 5) and S- (n = 5) were represented within each of the two goal quadrants within each 10-trial session. The escape platform was positioned beneath the water, consistently below the S+.

At the beginning of a trial, the subject was placed in the water at the start location, facing the interior front wall of the tank. Correct responses were defined as initial navigational entry into the goal quadrant containing the S+, with subsequent mounting or attempted mounting of the platform. Errors were defined as navigational entry into the non-rewarded goal quadrant containing the S-, such that the center of the animal's body crossed the digitally mapped right-angle plane with respect to the center partition (See Figure 8). Subjects were permitted to self-correct initially incorrect choices, with an error recorded for the trial. During the inter-trial interval (up to 60 sec) the animal was placed in an opaque, polycarbonate holding cage, lined with towels and measuring 43.2 cm (length) x 21.6 cm (width) x 20.3 cm (height), while the stimuli, platform and ANY-maze™ Video Tracking System were prepared for the next trial. When behavioral

criterion was attained in Pre-Surgical Training, a 9-week hiatus was observed for all animals.

Experimental Phase 2: Pre-Surgical Testing

The purpose of Experimental Phase 2, Pre-Surgical Testing was to evaluate across all subjects the degree to which savings were demonstrated for the previously learned discrimination task. It was hypothesized that all subjects would demonstrate retention of the problem, and would commit significantly fewer errors through criterion and require significantly fewer trials through criterion in Pre-Surgical Testing than in Pre-Surgical Training. Subjects were expected to demonstrate near-equivalent terminal performances. All behavioral and procedural aspects of Experimental Phase 2, Pre-Surgical Testing, were identical to those described for Experimental Phase 1, Pre-Surgical Training. Upon demonstrating reacquisition and re-mastery of the task, animals were scheduled for surgery.

Surgery

Aspects of the surgical protocol have been described previously (Davis & McDaniel, 1993; Kolb et al., 1994; Maki et al., 2001; Williams & McDaniel, 1999). Surgery was performed by one experimenter, using sterile surgical instruments and under aseptic conditions (Large Animal Surgical Suite, Department of Animal and Dairy Science, The University of Georgia). Prior to surgery, each rat had been randomly pre-assigned (per preliminary data analysis of two behavioral measures in Experimental Phase 1, Pre-Surgical Training) to one of three lesion conditions: CON (n = 8), PS (n = 8) or TE (n = 8). Animals were weighed and administered sodium pentobarbital (65

mg/kg, i.p.) and ketamine hydrochloride (100 mg/kg, i.p.). Immediately following deep anesthetization, the scalp was shaved and scrubbed with Betadine solution and the animal was positioned in a stereotaxic instrument. Using a surgical scalpel, a midline incision was made to expose the dorsal cranium, and the temporalis muscle was retracted ventrolaterally to expose the *os temporale* cranial plate.

Of the eight rats assigned to the control (CON) group, four received cranial burr holes drilled bilaterally 3.0 mm anterior to the Lambda suture and 3.0 mm lateral to the sagittal suture; four received cranial burr holes drilled bilaterally 5.0 to 6.0 mm posterior to the coronal suture and 5.5 to 6.5 mm lateral to the sagittal suture. For rats receiving partial striate (PS) lesions, the skull was drilled bilaterally 3.0 mm anterior to the Lambda suture and 3.0 mm lateral to the sagittal suture. The drilled areas were expanded with microrongeurs, and the underlying tissues were aspirated using a 2 mm diameter glass micropipette attached to a commercial-grade, power-generated vacuum source and water receptacle. For animals assigned to the temporal (TE) lesion group, the skull was drilled bilaterally 5.0 to 6.0 mm posterior to the coronal suture and 5.5 to 6.5 mm lateral to the sagittal suture (i.e., immediately ventral to the temporal/parietal cranial plate juncture). The drilled areas were enlarged several millimeters along anterior-posterior (A/P) plane to expose area TE, and the underlying tissues were aspirated.

All cavities were packed with bone wax and scalp incisions were closed with stainless steel wound clips. Ointments containing antimicrobial-analgesic agents (Bacitracin Zinc, Neomycin Sulfate, Polymyxin B Sulfate, Pramoxine HCI) were applied generously to sutured sites. During the postoperative recovery period, rats were kept

warm by indirect light from a surgical lamp while respiration, motor activity, and food and water intake were monitored.

While in surgical recovery, two CON rats and one TE rat died from anesthesia-induced complications. Thus, the number of subjects in lesion groups used in subsequent behavioral training and testing was modified: CON (n = 6), PS (n = 8) and TE (n = 7). A 15-day postoperative recovery period was observed for each animal before behavioral procedures were resumed, in Experimental Phase 3, Post-Surgical Retraining.

Experimental Phase 3: Post-Surgical Retraining

The purpose of Experimental Phase 3, Post-Surgical Retraining, was to retrain the subjects on the original visual discrimination problem, examining the extent to which the rats re-mastered the task after receiving respective surgical lesions. All behavioral and procedural aspects of the Post-Surgical Retraining were identical to those described for Experimental Phases 1 and 2.

It was hypothesized that, due to compromised gross visual ability (i.e., a decrease in visual acuity and central vision as a result of PS lesions), the PS group would demonstrate a delay in attaining behavioral criterion, by committing a greater number of errors than the CON and TE groups. However, as is confirmed by evidence from the neurobehavioral animal research literature, laboratory rodents are generally able to compensate for the effects of striate lesions (via self-produced head movements intended to shift retinal images onto the fovea) in visual tasks involving navigation. Thus, it was predicted that the PS group would ultimately re-master the previously learned discrimination problem, demonstrating a terminal performance of at least 90%,

essentially equaling that of the CON and TE groups. After attaining criterion in Post-Surgical Retraining, subjects were introduced to the final behavioral procedure.

Experimental Phase 4: Relational Testing

The purpose of Experimental Phase 4, Relational Testing, was to examine the extent to which the CON, PS and TE lesioned rats were able to generalize the previously learned discrimination (from Experimental Phases 1, 2 and 3) to novel, presumably more challenging, visual relational discrimination problems. Relational Testing trials involved presentations of uniquely paired, novel stimuli (i.e., 6.48 vs. 38.4, 31.2 vs. 63.6, 20.4 vs. 74.4, 42 vs. 70.8, 9.6 vs. 42, 16.8 vs. 31.2, 13.2 vs. 52.8, 24 vs. 42, 16.8 vs. 49.2, and 24 vs. 63.6 cd/m^2) that were selected from the 14 stimulus images (See Table 2). The stimuli were grouped into 10 pairs that were presented sequentially throughout the Phase and that fulfilled all of the following conditions: (1) Each pair was comprised of two stimuli having a percent photometric luminance difference between them of at least 40% (e.g., 83%, 78%, 75%, 73%, 66%, 62%, 50%, 46%, 43% and 40%); (2) Stimuli were matched such that each of the 10 pairs represented one of five percentage categories including and between 40% and 80% (viz., 40%, 50%, 60%, 70%, and 80%); (3) At least four of the 10 pairs were composed of a versatile stimulus that would be considered to be the correct choice (S+) on one trial but the incorrect choice (S-) on another trial (e.g., 42 vs. 70.8 and 9.6 vs. 42; 31.2 vs. 63.6 and 16.8 vs. 31.2).

The presentation sequence of the paired stimuli (6.48 vs. 38.4, 31.2 vs. 63.6, 20.4 vs. 74.4, 42 vs. 70.8, 9.6 vs. 42, 16.8 vs. 31.2, 13.2 vs. 52.8, 24 vs. 42, 16.8 vs. 49.2, and 24 vs. 63.6 cd/m^2) was determined via a computer-generated random numbers table. For each testing session, the presentation sequence was altered by one stimulus-pair rotation,

as is shown in Table 3. As before, in Experimental Phases 1, 2 and 3, the left-right positions of the visual cues were randomized across trials using a Fellows (1967) series such that an equal number of S+ and S- presentations were represented within the left and right goal quadrants within a session, and such that the S+ was rewarded by escape via the platform. Behavioral criterion was identical to that described for previous Experimental Phases.

In Relational Testing, animals were required to generalize the previously learned discrimination (i.e., navigate to the darker of the two stimuli) to novel, relational discrimination problems that consisted of paired stimuli with differences in luminance. Subjects were required to solve the discrimination problems strictly on the basis of relative properties of visual cues rather than on the basis of absolute properties of the stimuli. Thus, the discrimination problems introduced in Phase 4 were presumed to be more challenging than the discrimination tasks presented in previous Phases.

Psychophysical research concerning vision in humans and neurobehavioral laboratory experiments involving visual abilities in rodents suggests an overlap and a quantifiable functional similarity between human scotopic spectral sensitivity and rodent spectral sensitivity (See Figure 10). Considering the general anatomical similarity in the retinal organization between human and rat, and given that the retina in the nocturnal rodent has a significantly greater rod than cone concentration, it was reasoned that the animals would be easily able to discriminate the luminance differences of the stimuli selected for use in this Phase (See Figure 11). Since the goal of the experiment was to evaluate rats' abilities to generalize a previously learned simple discrimination to novel visual relational problems as opposed to examining brightness discriminations from a

wide spectrum of distinct luminance values, cues were paired such that differences in luminance between stimuli would be large and, thus, presumably apparent. However, it was hypothesized that paired cues with a smaller percent luminance difference between them (e.g., 40%) might pose more of a discrimination challenge to rats than paired stimuli with a greater percent luminance difference between them (e.g. 83%).

In Relational Testing, it was expected that CON and PS rats would successfully generalize the previously mastered task to novel, relational discrimination problems. However, it was hypothesized that the TE lesioned group would demonstrate significant deficits in behavioral performance, compared to the other two groups. The TE group was predicted to demonstrate a terminal performance significantly inferior to that demonstrated by CON and PS groups, and was expected to commit a significantly greater number of errors than either the CON or PS group. These hypotheses were based on the recent clinical neuropsychological literature concerning temporal lobe damage in humans and the expanding neuroscientific research evidence regarding lesions in temporal (IT) cortex in primates, which indicate that temporal cortical regions are critical for functions of visual analysis and relational learning. Given the notable degree of neuroanatomical and neurobehavioral similarity between rat and primate sensory systems, it was hypothesized that rats with surgically induced temporal cortical lesions might demonstrate deficits similar to those reported in human and non-human primates with temporal lobe damage.

Experimental Phase 4, Relational Testing, was conducted for a maximum of 15 sessions per animal. Testing was performed at a rate of 10 trials per animal per session through behavioral criterion or, alternatively, for a maximum of 150 trials per animal.

Termination of Phase 4 at 15 sessions was determined by results from subject learning curve data that were generated and monitored across testing sessions throughout the Phase.

Histology

Upon completion of behavioral procedures in Experimental Phase 4, all subjects received injections of 1.0 ml sodium pentobarbital (i.p.). Upon deep anesthetization, Intracardial perfusions were performed by circulating 60 cc isotonic saline via a slow-cycle electrical perfusion pump, followed by 60 cc 10% formalin. Following manual decapitations with surgical scissors, brains were excised from the skull with microronguers, and guided with a stainless steel spatula into a 30% sucrose solution in 10% formalin mixture contained in individual, laboratory-grade chemical storage vials. CON, PS and TE brains were refrigerated for several days prior to being photographed with a tripod-secured, high-resolution digital camera. A metric device was positioned adjacently to each specimen at the time of image capture, so as to provide a measurement interval of reference for subsequent lesion quantification and analysis. After being blocked to include the lesion sites and thalamus, PS and TE specimens were frozen in dry ice and sectioned coronally on a sliding microtome (Model 860, America Optical; Buffalo NY) at 50µm, through the extents of the lesions. CON brains were also sectioned, with sections used as controls in subsequent histopathological verification and comparative analyses. Every fifth to eighth section in all specimens was mounted on a glass slide and stained with cresyl-violet.

Verification and Quantification of Lesions

Topographical examination. The previously captured digital photographic images of intact CON, PS and TE brains were imported into a photo-imaging computer software program (iPhotoPlus 4, Version 4.0, Ulead Systems, Inc.) for analysis. Photographs of perfused CON brains (n = 6) were included in the imaging process for purposes of verifying tissue integrity following bilateral cranial destruction from surgical burr holes. Brain images (CON, n = 6, dorsal; PS, n = 8, dorsal; TE, n = 14, left and right lateral) were enlarged such that topographical features could be adequately visualized and surface alterations could be inspected and verified.

Topometric quantification. Topometric quantification and analysis were performed via a computerized digital imaging technique (CDIT), using the imported digital photographs of the intact PS and TE brains. The perimeters of the PS and TE lesions were traced with photo-enhancing tools, after which a measurement grid (with units identical and proportionate to the metric device in each photograph) was superimposed onto each image. Lesions were verified and measured for both the left (L) and right (R) hemispheres. The following variables were quantified and used in analyses: Topographical A/P Lesion Length (L), Topographical A/P Lesion Length (R), Averaged Topographical A/P Lesion Length [(L+R)/2]; Topographical Lesion Width (L), Topographical Lesion Width (R), Averaged Topographical Width [(L+R)/2]. Topometric variables quantified by CDIT are shown in Table 4.

A computerized variation of the classic Dot Grid Method (Thomas & Peacock, 1965) was also used to evaluate the percent of surface cortex removed for each hemisphere. The Percent of Surface Cortex Removed (in percent) was calculated by first

totaling the number of intersections (in dots) on the superimposed measurement grid within the perimeter of each lesion. Then, the total number of intersections within the lesion was divided by total number of intersections within the corresponding cortical hemisphere, resulting in a quotient that defined the variable for each lesion. The following measures were quantified and used in analyses: Percent of Surface Cortex Removed (L), Percent of Surface Cortex Removed (R), Percent of Surface Cortex Removed [(L+R)/2]. Topometric variables quantified by the Dot Grid Method (DGM) are displayed in Table 4.

Morphometric quantification. Analyses by computerized digital-imaging techniques (CDIT) were also performed for each PS and TE brain tissue section (N = 301). Slides were scanned (Epson Perfection, Model 4490; 4800 dpi resolution) into a computer, and each tissue section image was enlarged and classified by µm interval with respect to Bregma, via reference to a standard rat brain atlas (Paxinos and Watson, 1986). Lesion widths (in mm) and lesion depths (in mm) were measured and recorded per hemisphere per tissue section per brain. Data were averaged across each applicable µm section, and were then averaged across all sections per brain to produce an averaged histological, morphometric representation for each subject. The following variables were quantified and used in analyses: Depth (L), Depth (R), Averaged Depth [(L+R)/2] (in mm); Width (L), Width (R), Averaged Width [(L+R)/2] (in mm); Greatest Depth (L), Greatest Depth (R), Averaged Greatest Depth [(L+R)/2] (in mm); Greatest Width (L), Greatest Width (R), Averaged Greatest Width [(L+R)/2] (in mm); Area (L), Area (R), Averaged Area [(L+R)/2] (in mm^2); Volume (L), Volume (R), and Averaged Volume

[(L+R)/2] (in mm^3). Tabular representation of morphometric variables may be reviewed in Table 4.

Morphological quantification. To examine accuracy of lesion placement and to quantify the percent of cortical tissue destroyed within each affected PS and TE region, illustrated atlas templates (categorized into μm intervals with respect to Bregma) were superimposed onto scanned images of tissue sections. Bilateral lesion images were traced onto respective templates, and the ablated tissue locations were identified and quantified (in percent). The estimated percent of tissue destroyed within each defined anatomical region was calculated for each tissue section and was subsequently averaged across all sections from within the same μm category for each hemisphere per brain. Data were averaged across sections per brain to produce an averaged histological, morphological representation for each subject. The following variables were quantified for lesioned regions in PS and TE brains, and were used in analyses: Percent of Anatomical Tissue Ablated (L), Percent of Anatomical Tissue Ablated (R) and Averaged Percent of Anatomical Tissue Ablated [(L+R)/2]. Morphological variables are exhibited in Table 4. All quantified histological variables were included in linear regression correlation matrices to produce a representative, composite histological variable for both the PS and TE lesion groups for use in subsequent correlation analyses.

Histopathological examination. Brain tissue sections were analyzed microscopically for histopathological alterations resulting from surgical ablations. Tissues were examined for evidence of retrograde degeneration and gliosis in the thalamus. CON tissue sections were used as controls in comparative analyses among the lesion groups.

The Experimental Subjects

Figure 1. A photograph of 24 adult male black-hooded Long-Evans, Norwegian strain (*Rattus norvegicus)* rats, purchased from Harlan, Inc. (Indianapolis, IN; D.O.B. 03/04/2005), used as experimental subjects (coded and identified as R1-R24). Animals were individually housed in polycarbonate cages in a humidity-controlled and temperature-regulated animal housing facility (Large Animal Research Unit, Department of Animal and Dairy Science, The University of Georgia) with food and water available *ad libitum*. Subjects were maintained on a reversed 12-hr schedule (lights off at 0900h). Rat R25, included pictorially, was not used in formal Experimental Procedures, but was utilized as a pilot subject in preliminary experimental testing of the apparatus, illumination conditions, stimuli, and computerized navigational tracking system, and as a model in surgical procedures and histological analyses.

The Experimental Apparatus

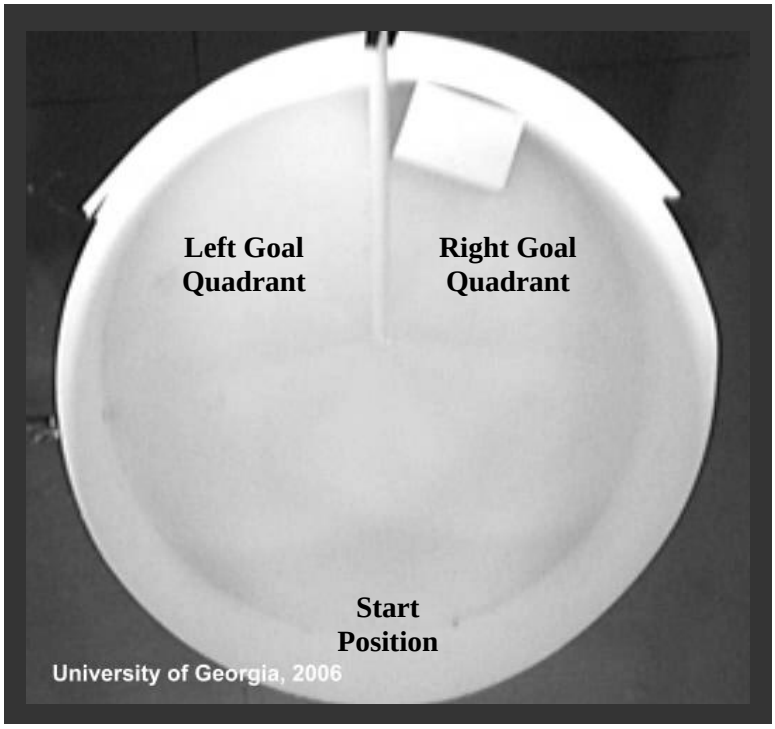


Figure 2. An overhead photograph of the modified experimental apparatus used during behavioral procedures in Experimental Phases 1-4. The interior of the tank and all fitted components were painted with flat white, exterior, latex paint. The apparatus was filled with water (not depicted photographically) to a depth of 20 cm, with water temperature maintained at approximately $23^{o} \pm 1^{o}$ C and replaced every two days. Non-toxic, white powdered tempera paint (Fresco, Rich Art Color Co., Northvale, NJ) was added liberally to the water to obscure view of a white, weighted Plexiglas platform submerged approximately 2 cm below the water surface.

The Laboratory Environment

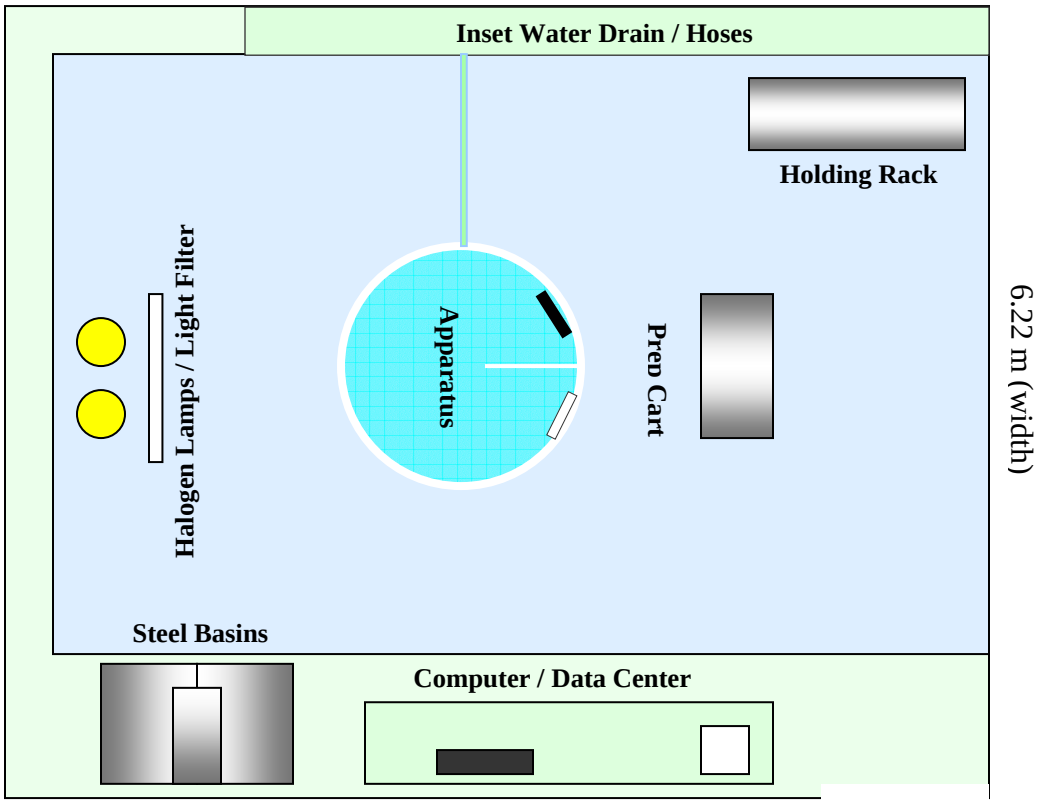


Figure 3. A schematic of the laboratory environment (from an overhead view) used in behavioral procedures in Experimental Phases 1-4 (Large Animal Research Unit, Department of Animal and Dairy Science, The University of Georgia). A digital video camera (not depicted schematically), connected remotely to a computer equipped with ANY-maze^{TM} Video Tracking System licensed software, was permanently affixed to the laboratory ceiling, 3.05 m directly above the center of the apparatus.

The Laboratory Environment and Illumination Conditions

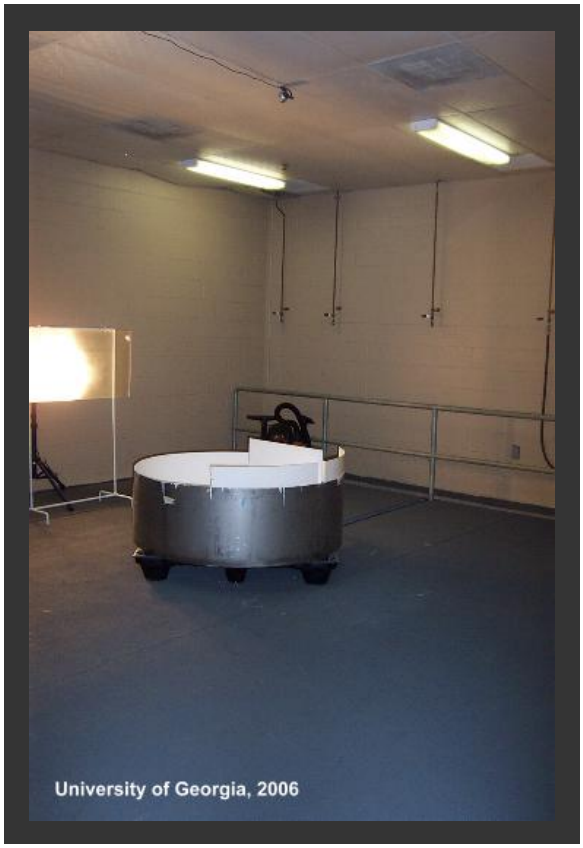


Figure 4. A photograph of the laboratory environment and illumination conditions to which experimental subjects were exposed during behavioral procedures in Experimental Phases 1-4. The laboratory environment was illuminated by fluorescent tube lights encased in evenly dispersed, standard ceiling fixtures, and by halogen bulbs contained in professional work lamps secured by a weighted tripod.

Table 1

The 14 Stimulus Images and Corresponding Photometric Luminance Values Used in Behavioral Procedures

Software-Defined Luminance (ordinal *n*s)	**Photometric Luminance Value (cd/m^2)**	**Stimulus Image**
255	74.4	
251	70.8	
231	63.6	
213	52.8	
212	49.2	
202	42.0	
184	38.4	
165	31.2	
151	24.0	
132	20.4	
117	16.8	
92	13.2	
63	9.6	
35	6.48	

The Systematic Placement and Standard Display of Paired Visual Stimuli in the Experimental Apparatus

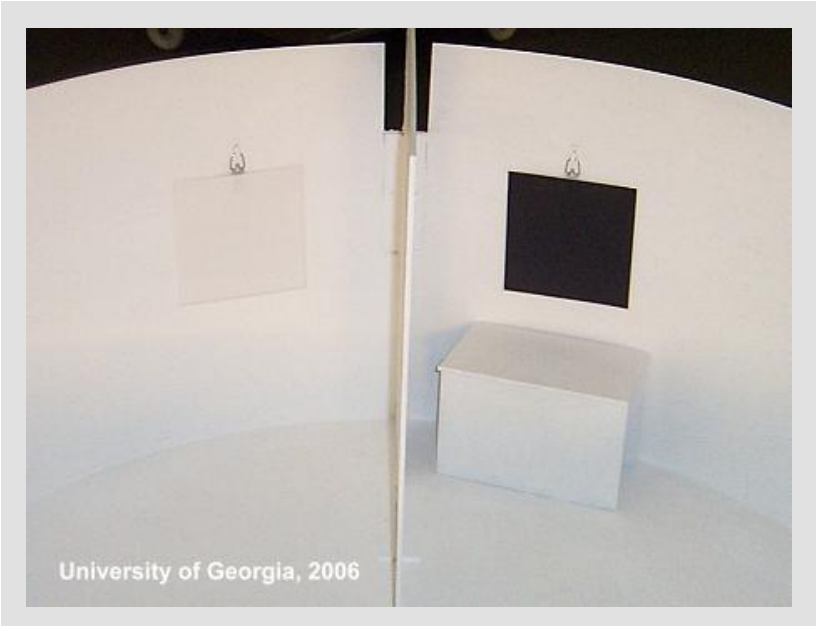


Figure 5. A photograph of the systematic placement and standard display of paired visual stimuli within the experimental apparatus. Across trials, stimuli were displayed in pairs, with each card suspended from a secured plastic hook and metal loop that were centered in the left or right goal quadrants against the interior rear wall of the apparatus. (The opaque water used for navigation during trials was removed at the time of image capture for viewing purposes).

The Photometric Luminance Values of the Visual Stimuli Employed in Behavioral Procedures

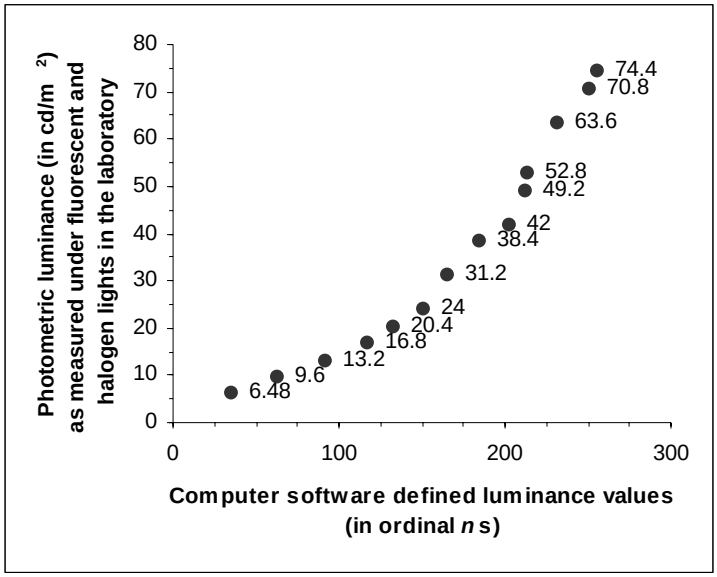


Figure 6. The photometric luminance values of the visual stimuli employed in behavioral procedures.

A Reflectance Spectrum of One of the Intermediate (Gray) Stimuli.

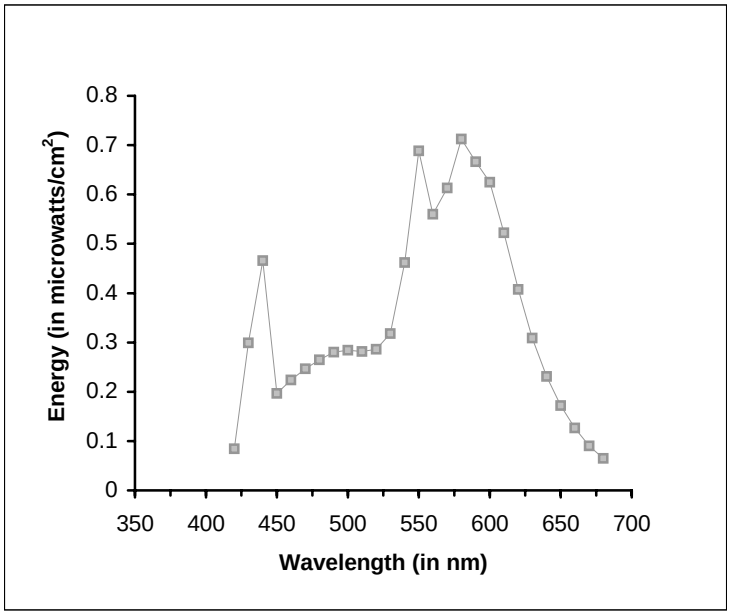


Figure 7. An energy spectrum illustrating the amount of light (based on the ambient fluorescent and halogen light used during testing) reflected from a stimulus with intermediate (gray) shading.

A Schematic Recreation of Computerized Digital Video Mapping of the Experimental Apparatus

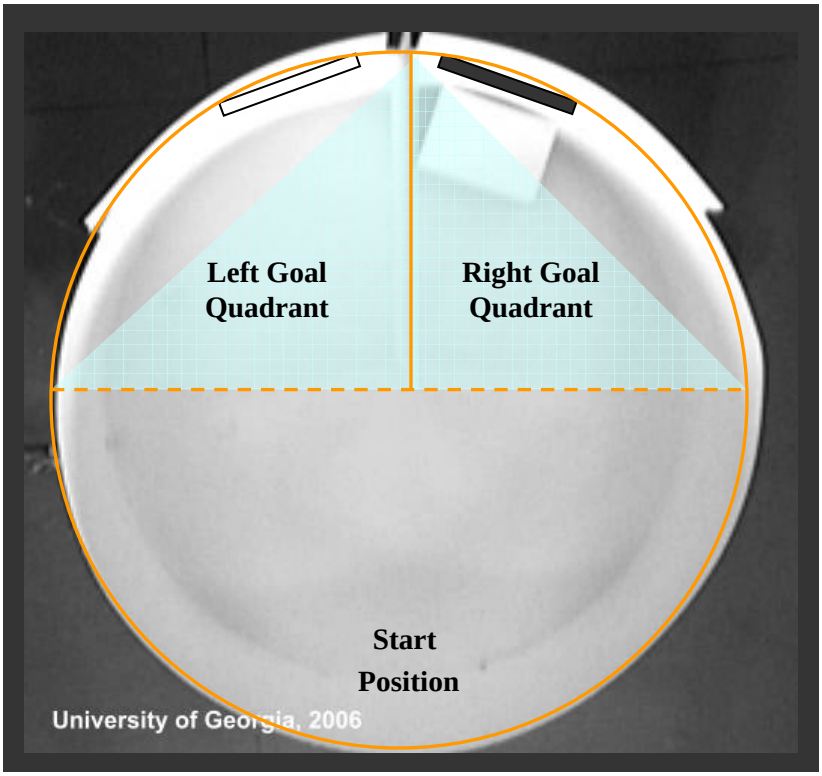
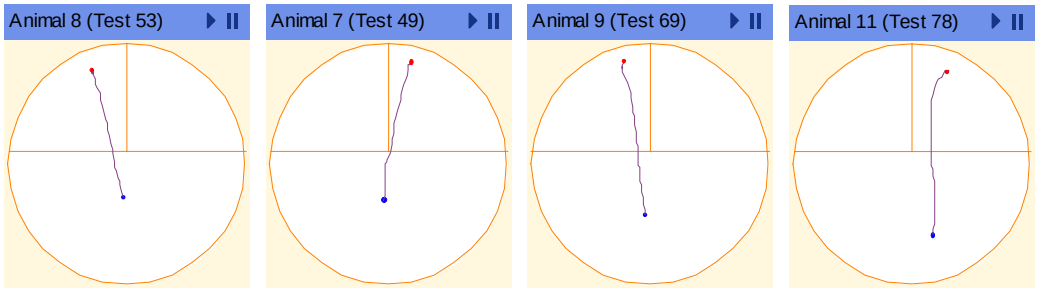
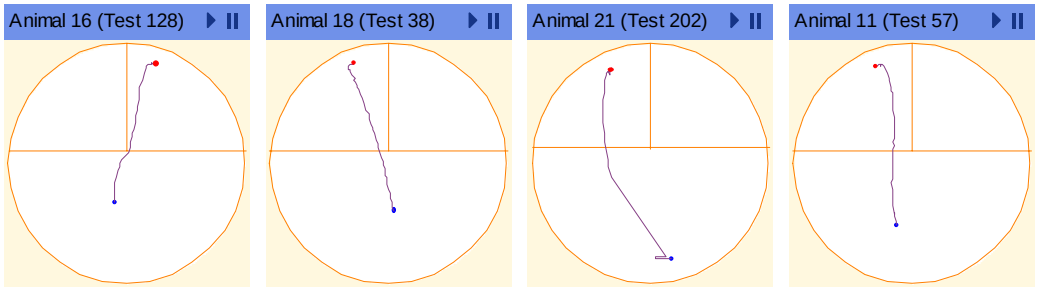


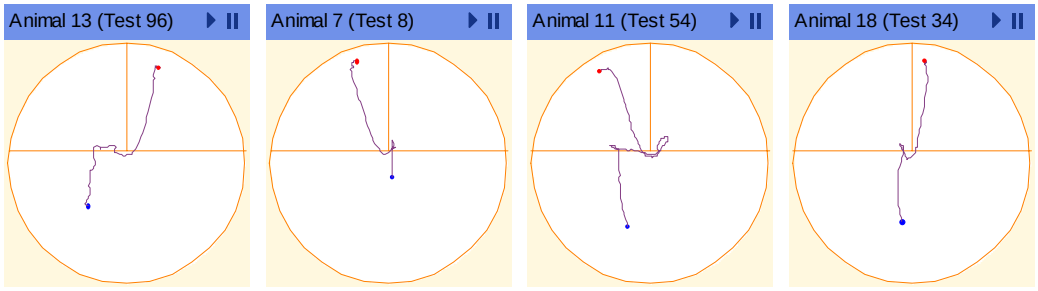
Figure 8. A schematic recreation of computerized digital video mapping of the experimental apparatus and interior components, as displayed during behavioral trials via computer by ANY-maze™ Video Tracking System. Left and right goal quadrants were defined by the intersection of the mapped vertical center partition and right angle plane, and by the marked tank perimeter. The computer screen image of respective left and right demarcated goal quadrants was highlighted upon animal entry, thus indicating an error or the beginning of a possible correct response. (The opaque water used for navigation during trials was removed at the time of image capture for viewing purposes).

(A)





(B)



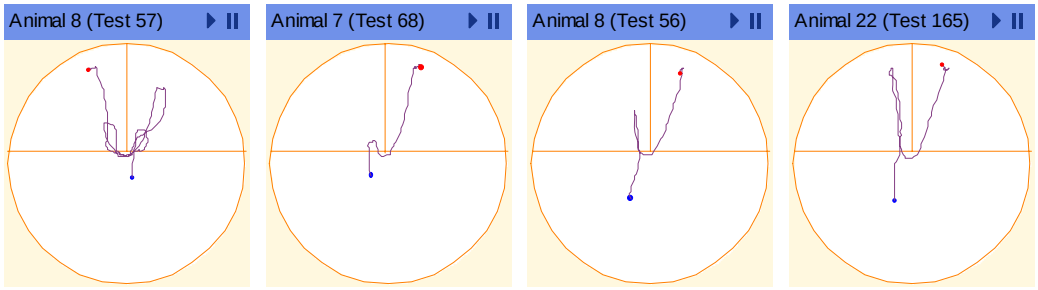


Figure 9. Examples of systematically defined (A) correct responses and (B) errors, as depicted in Track-Plot Diagrams that were generated in all behavioral trials (n = 4,600) by ANY-maze™ Video Tracking System. (The Test numbers are arbitrary and refer to the cumulative number of trials in the respective session with all rats at a rate of 10 trials per animal. Test numbers do not reflect the actual training trial number in a session).

Table 2

Photometric Luminance Values, Percent Difference in Luminance Between Paired Stimuli, and Paired Images Employed in Experimental Phase 4, Relational Testing

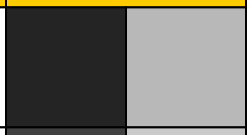
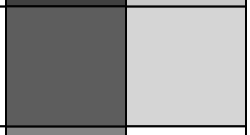
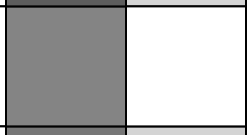
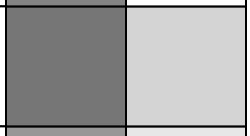
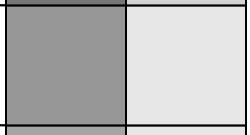
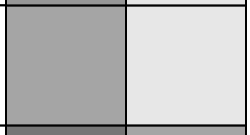
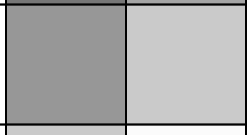
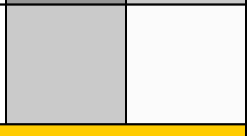
Photometric Luminance (cd/m^2)	**Percent Difference in Luminance (*P*)**	**Paired Images**
6.48 vs. 38.4	83%	
9.6 vs. 42 *	78%	
13.2 vs. 52.8	75%	
20.4 vs. 74.4	73%	
16.8 vs. 49.2	66%	
24 vs. 63.6	62%	
31.2 * vs. 63.6	50%	
16.8 vs. 31.2 *	46%	
24 vs. 42 *	43%	
42 * vs. 70.8	40%	
**** A versatile stimulus***		

Table 3

The First 4 of 15 Sessions of Paired-Stimuli Sequence Presentations and Rotations Employed in Experimental Phase 4, Relational Testing

Session 1	*Session 2*	*Session 3*	*Session 4*
6.48 vs. 38.4	31.2 vs. 63.6	20.4 vs. 74.4	42 vs. 70.8
31.2 vs. 63.6	20.4 vs. 74.4	42 vs. 70.8	9.6 vs. 42
20.4 vs. 74.4	42 vs. 70.8	9.6 vs. 42	16.7 vs. 31.2
42 vs. 70.8	9.6 vs. 42	16.7 vs. 31.2	13.2 vs. 52.8
9.6 vs. 42	16.8 vs. 31.2	13.2 vs. 52.8	24 vs. 42
16.8 vs. 31.2	13.2 vs. 52.8	24 vs. 42	16.8 vs. 49.2
13.2 vs. 52.8	24 vs. 42	16.8 vs. 49.2	24 vs. 63.6
24 vs. 42	16.8 vs. 49.2	24 vs. 63.6	6.48 vs. 38.4
16.8 vs. 49.2	24 vs. 63.6	6.48 vs. 38.4	31.2 vs. 63.6
24 vs. 63.6	6.48 vs. 38.4	31.2 vs. 63.6	20.4 vs. 74.4

Note. The first pair from each session was rotated and reintroduced as the last pair of the presentation sequence for the subsequent session (Total sessions = 15).

The Human Scotopic Spectral Sensitivity Curve and the Rat Electroretinogram Spectral Sensitivity Function

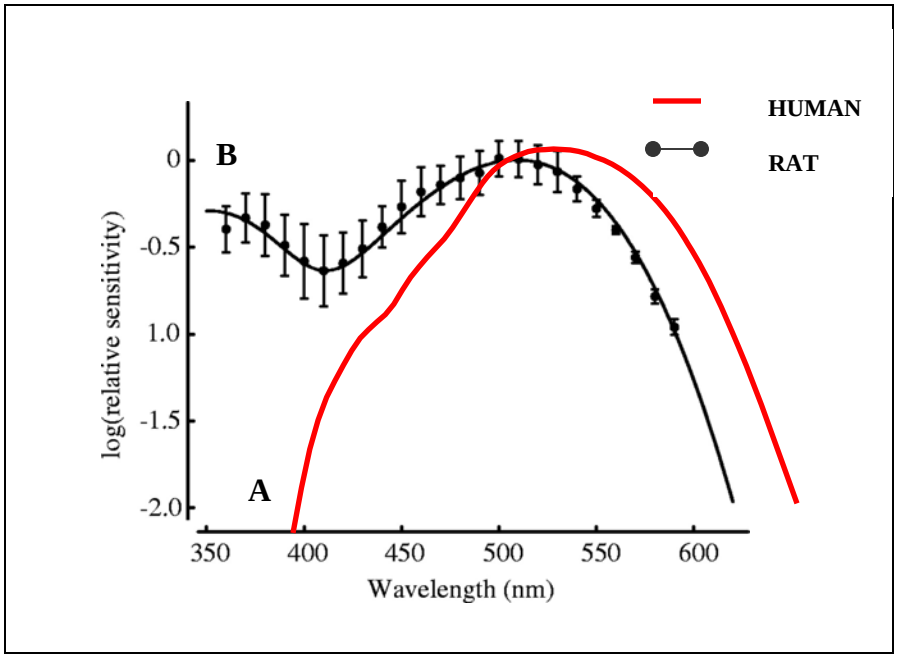


Figure 10. A depiction of (A) the human scotopic spectral sensitivity curve and (B) the rat electroretinogram spectral sensitivity function. The graph illustrates the general overlap and quantified functional similarity between human scotopic spectral sensitivity and rat spectral sensitivity.

The Reflectance Spectrum of One of the Intermediate (Gray) Stimuli Used in Behavioral Procedures and the Rat Electroretinogram Spectral Sensitivity Function

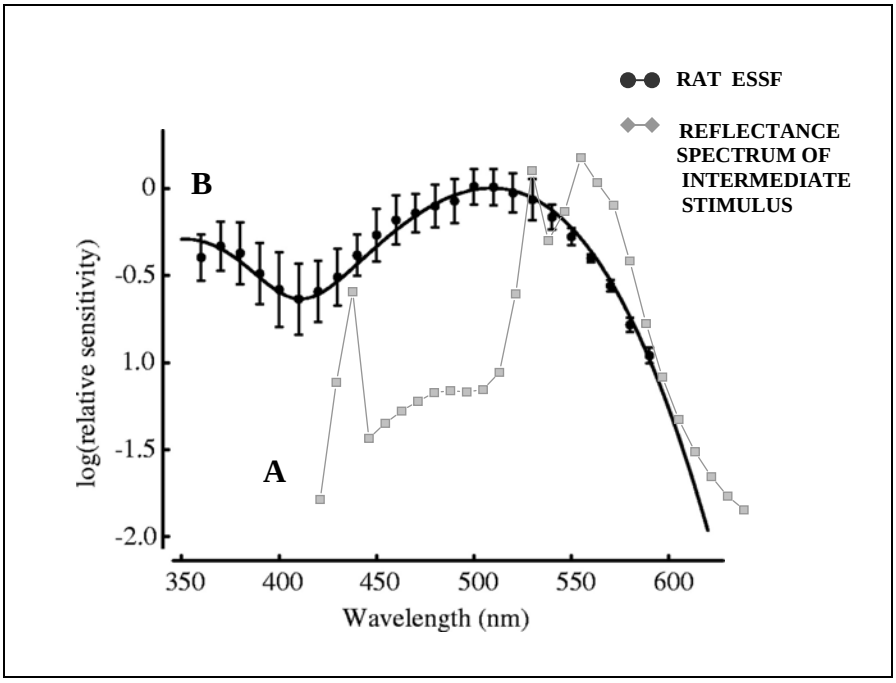


Figure 11. A graph depicting the overlap between (A) the reflectance spectrum of one of the intermediate (gray) stimuli used in behavioral procedures and (B) the rat electroretinogram spectral sensitivity function (ESSF).

Table 4

The Quantified Variables in Experimental Procedures

QUANTIFIED VARIABLES IN EXPERIMENTAL PROCEDURES		
	METHOD	**UOM**
LIGHT AND STIMULUS VARIABLES		
ILLUMINATION WITHIN APPARATUS (L)	AR LIGHT METER	fc
ILLUMINATION WITHIN APPARATUS (R)	AR LIGHT METER	fc
ILLUMINATION WITHIN APPARATUS [(L+R)/2]	AR LIGHT METER	fc
STIMULUS LUMINANCE	SPEC PHOTOMETER	cd/m^2
BEHAVIORAL VARIABLES (Per Group, Per Experimental Phase)		
CON, PS AND TE SUBJECTS		
TERMINAL PERFORMANCE	ANY-maze™/EXPERIMENTER/SCORING	*n*
NUMBER OF ERRORS THROUGH CRITERION	ANY-maze™/EXPERIMENTER/SCORING	*n*
PERCENT CORRECT RESPONSE THROUGH CRITERION	ANY-maze™/EXPERIMENTER/SCORING	%
NUMBER OF TRIALS THROUGH CRITERION	ANY-maze™/EXPERIMENTER/SCORING	*n*
HISTOLOGICAL VARIABLES		
PS AND TE BRAINS/LESIONS		
TOPOGRAPHICAL/TOPOMETRIC VARIABLES (Per Brain, per Hem)		
TOPOGRAPHICAL A/P LESION LENGTH (L)	CDIT	mm
TOPOGRAPHICAL A/P LESION LENGTH (R)	CDIT	mm
TOPOGRAPHICAL A/P LESION LENGTH [(L+R)/2]	CDIT	mm
TOPOGRAPHICAL LESION WIDTH (L)	CDIT	mm
TOPOGRAPHICAL LESION WIDTH (R)	CDIT	mm
TOPOGRAPHICAL LESION WIDTH [(L+R)/2]	CDIT	mm
PERCENT OF SURFACE CORTEX REMOVED (L)	DGM	%
PERCENT OF SURFACE CORTEX REMOVED (R)	DGM	%
PERCENT OF SURFACE CORTEX REMOVED [(L+R)/2]	DGM	%
MORPHOMETRIC VARIABLES (Per Tissue Section, per Hem)		
AREA (L)	CDIT	mm^2
AREA (R)	CDIT	mm^2
AREA [(L+R)/2]	CDIT	mm^2
VOLUME (L)	CDIT	mm^3
VOLUME (R)	CDIT	mm^3
VOLUME [(L+R)/2]	CDIT	mm^3
DEPTH (L)	CDIT	mm
DEPTH (R)	CDIT	mm
DEPTH [(L+R)/2]	CDIT	mm
WIDTH (L)	CDIT	mm
WIDTH (R)	CDIT	mm
WIDTH [(L+R)/2]	CDIT	mm
GREATEST DEPTH (L)	CDIT	mm
GREATEST DEPTH (R)	CDIT	mm
GREATEST DEPTH [(L+R)/2]	CDIT	mm
GREATEST WIDTH (L)	CDIT	mm
GREATEST WIDTH (R)	CDIT	mm
GREATEST WIDTH [(L+R)/2]	CDIT	mm
MORPHOLOGICAL VARIABLES (Per Tissue Section, Per Anatomical Location, per Hem)		
PERCENT OF TISSUE ABLATED (L)	CDIT/TEMPLATE	%
PERCENT OF TISSUE ABLATED (R)	CDIT/TEMPLATE	%
PERCENT OF TISSUE ABLATED [(L+R)/2]	CDIT/TEMPLATE	%

CHAPTER 3

RESULTS

Histological Data Analyses

Histological impressions of PS and TE lesioned brains were characterized in quantified topometric, morphometric, and morphological variables, with lesion extent and anatomical placement calculated for each tissue specimen and defined for each brain. Data were used to examine differences among brains within respective lesion groups and to investigate general correlations between histology and behavior. An alpha level of .05 was used for all statistical tests. Condensed histological data and corresponding tabulated statistical analyses may be consulted in Appendix A, Tables A1-A8.

Topographical verification. Digital photographic images of PS and TE lesioned brains are featured in Figures 12 and 13, respectively. As was anticipated, topographical alterations were observed in all PS and TE lesioned brains. Inspection of CON brains revealed no evidence of surface tissue damage from bilateral surgical cranial destruction (e.g., burr holes). A representative CON brain is exhibited in Figure 14.

Topometric data analyses. The topographical alterations observed in PS lesioned brains were systematically quantified (in mm) with computer digital imaging techniques. Although all PS lesions were placed generally within intended occipital cortical regions, topometric analyses of the lesion data revealed a significant difference among PS brains in the averaged left/right hemisphere anterior-posterior (A/P) Topographical Lesion Length, ($p < .0001$), as well as a significant difference among brains in the averaged

left/right hemisphere Topographical Lesion Width, ($p < .001$). In contrast, no significant difference in Topographical A/P Lesion Length between the left and right hemispheres, ($p > .05$), or in Topographical Lesion Width between the left and right hemispheres, ($p > .05$), was found for the PS group as a whole. The results are illustrated in Figures 15 and 16. Quantified topographical variables are contained in Appendix A, Table A1. Corresponding statistical data tables may be found in Appendix A, Table A2.

For TE lesioned brains, topographical alterations were also systematically quantified (in mm) with computer digital imaging techniques. Although all TE lesions were placed generally within temporal regions, topometric analyses of the lesion data revealed a significant difference among TE brains in the averaged left/right hemisphere A/P Topographical Lesion Length, ($p < .0001$), as well as a significant difference among TE brains in the averaged left/right hemisphere Topographical Lesion Width, ($p < .0001$). In contrast, no significant difference in Topographical A/P Lesion Length between the left and right hemispheres, ($p > .05$), or in Topographical Lesion Width between the left and right hemispheres, ($p > .05$), was found for the TE group as a whole. The findings are characterized pictorially in Figures 17 and 18. Quantified topographical variables may be seen in Appendix A, Table A3. Corresponding statistical data tables are presented in tabular form in Appendix A, Table A4.

Topographical alterations in each cortical hemisphere were also evaluated via a computerized variation of the classic Dot Grid Method (Thomas & Peacock, 1965). Consistent with all findings obtained by computerized digital imaging techniques (CDIT), the Dot Grid Method (measuring the variable Percent of Surface Cortex Removed) also revealed significant differences among PS brains in averaged left/right

hemispheres, but no significant differences between left and right hemispheres for the group as a whole. Similarly, measurements obtained with the Dot Grid Method (DGM) revealed significant differences among TE brains in averaged left/right hemispheres, but no significant differences between left and right hemispheres for the group as a whole. Specifically, a one-sample *t*-Test used to compare the Percent of Surface Cortex Removed in averaged left/right hemispheres among brains in the PS group revealed a statistically significant difference among brains, ($p < .0001$), but no significant difference between the hemispheres for the PS group as a whole, ($p > .05$). Similarly, a one-sample *t*-Test was also used to compare the Percent of Surface Cortex Removed in averaged left/right hemispheres among brains in the TE group. The analysis revealed a statistically significant difference among TE brains, ($p < .0001$), but no significant difference between the hemispheres for the TE group as a whole, ($p > .05$). The results are represented in Figures 19 and 20. The quantified topometric variable is contained in Appendix A, Table A5. Corresponding statistical data tables are presented in Appendix A, Table A6.

Morphometric data analyses. Morphometric analysis of each PS histological tissue section ($n = 171$) was systematically conducted, with results averaged for both the left and right hemispheres of each PS brain, and described in lesion volume (in mm^3). Analyses by *t*-Tests revealed a significant difference in the averaged left/right hemisphere Lesion Volume among brains in the PS group, ($p < .001$), but indicated no significant difference in Lesion Volume between the left and right hemispheres for the PS group as a whole, ($p > .05$). The findings are pictured in Figure 21. Quantified morphometric

variables (e.g., volume) are contained in Appendix A, Table A1; Corresponding statistical data are tabulated in Appendix A, Table A2.

Morphometric analysis of each TE histological tissue section (n = 130) was systematically conducted, with results averaged for both the left and right hemispheres of each TE brain, and described in lesion volume (in mm^3). Analyses by t-Tests revealed a significant difference in the averaged left/right hemisphere Lesion Volume among brains in the TE group, ($p < .0001$) and a significant difference in Lesion Volume between the left and right hemispheres for the TE group as a whole, ($p < .05$). Illustrative depictions appear in Figure 22. Quantified morphometric variables may be viewed in Appendix A, Table A3; Corresponding tabulated statistical data are featured in Appendix A, Table A4.

Morphological data analyses. Morphological analysis of all PS tissue sections (n = 171) indicated that lesions were generally located in delineated territories of occipital/striate cortex. The results from the analyses indicated that bilateral PS lesions invaded substantial portions of Oc1M (M = 71%; range = 11%-100%), Oc2MM (M = 82%; range = 58%-94%) and Oc2ML (M = 88%; range = 68%-100%), and considerable portions of Oc1B (M = 41%; range = 0%-89%) and Oc2L (M = 35%; range = 2%-63%). In all cases, there was bilateral damage to retrosplenial agranular cortex, and some PS brains sustained either unilateral or bilateral damage to the corpus callosum and to dorsomedial or dorsolateral portions of the hippocampus. Superficial and inconsequential damage to minor portions of dorsolateral parietal cortex (Par1) and to frontal cortex (Fr1) was also observed in PS brains. The results from morphological analyses are displayed in Figure 23. Digital images of representative coronal PS

histological tissue sections, depicting the bilateral lesions, are featured in Figure 24. Tabulated corresponding statistical data may be appreciated in Appendix A, Table A7.

Specifically, a one-way ANOVA was used to determine whether there were statistically significant differences in the Percent of Tissue Destroyed between the averaged left/right hemispheres of each affected, anatomical region of occipital/striate cortex for the PS lesion group as a whole (i.e., Oc1M, Oc1B, Oc2MM, Oc2ML and Oc2L). The analysis revealed significant differences in the Percent of Tissue Destroyed among the various sub-regions, [t (4, 35) = 8.42, $p < .0001$]. Two-sample Independent t-Tests indicated that the percent of tissue destroyed in Oc2MM (M = 82%, SD = 12%) was significantly greater than that destroyed in Oc1B (M = 41%, SD = 34%), [$p < .01$], and in Oc2L (M = 35%, SD = 21%), [$p < .0001$], that the percent of tissue destroyed in Oc2ML (M = 88%, SD = 11%) was significantly greater than that destroyed in Oc1B (M = 41%, SD = 34%), [$p < .01$] and in Oc2L (M = 35%, SD = 21%), [$p < .0001$], and that the percent of tissue destroyed in Oc1M (M = 71%, SD = 29%) was significantly greater than that destroyed in Oc2L (M = 35%, SD = 21%), [$p < .05$]. In addition, one-sample t-Tests were used to evaluate whether there were significant differences in the Percent of Tissue Destroyed within the anatomical subregions among all PS brains. The findings indicated significant differences among brains in the Percent of Tissue Destroyed in Oc1M ($p < .001$), Oc1B ($p < .05$), Oc2MM ($p < .0001$), Oc2ML ($p < .0001$), and in Oc2L ($p < .01$). Finally, two-sample Independent t-Tests were used to compare the Percent of Tissue Destroyed between the left and right hemispheres within each lesioned region of occipital/striate cortex among PS brains, the results of which indicated no significant

difference between the left and right hemispheres of affected, anatomical sub-regions for the PS group as a whole, (All *p*s > .05).

Morphological analyses of all TE histological tissue sections (n = 130) revealed that lesions were located generally within subregions of temporal cortex. Analyses indicated that bilateral TE lesions invaded substantial portions of Te1 (M = 67%; range = 53%-86%) and variable amounts of dorsal medial and dorsal lateral portions of Te3 (M = 12%; range = 3%-24%). Temporal area Te2 (- 8.30 mm to - 6.30 mm, Bregma) was not surgically ablated in any of the 7 TE lesioned brains. In all cases, there was minor damage sustained to ventrolateral borders of the hippocampus and to ventromedial portions of lateral peristriate cortex (Oc2L), and damage to insignificant portions of ventromedial/lateral and dorsomedial/lateral parietal cortex (Par1 and Par2, respectively). The results from the analyses are characterized in Figure 25. Digital images of representative coronal TE histological tissue sections, depicting the bilateral lesions, are featured in Figure 26.

Specifically, two-sample Independent t-Tests were used to determine whether significant differences existed in the Percent of Tissue Destroyed between the averaged left/right hemispheres of affected sub-territories of temporal cortex (i.e., Te1 and Te3) for the TE lesion group as a whole. The results indicated that the percent of tissue destroyed in Te1 (M = 67%, SD = 13%) was significantly greater than that destroyed in Te3 (M = 11%, SD = 8%), [t (12) = 9.67, p < .0001]. In addition, one-sample t-Tests were used to evaluate whether there were significant differences in the Percent of Tissue Destroyed within the anatomical subregions among all TE brains. The findings revealed significant differences among brains in the Percent of Tissue Destroyed in Te1 (p < .0001) and in

Te3 ($p < .05$). Finally, two-sample Independent *t*-Tests used to compare the Percent of Tissue Destroyed within sub-territories Te1 and Te3 between the right and left hemispheres showed no significant difference between the left and the right hemispheres of subregions Te1 or Te3, for the group as a whole, (Both *p*s > .05). Corresponding tabulated statistical data are represented in Appendix A, Table A8.

Histopathological verification. As was expected, microscopic examination of PS tissue section samples revealed evidence of cell shrinkage, patchy necrosis and variable gliosis in the dorsal lateral geniculate nucleus of the thalamus compared to CON tissue section samples.

Illumination Conditions Data Analyses

The illumination and temporal stability of illumination within the apparatus were measured and compared between the left and right stimulus-display quadrants. Illumination measurements were averaged for each of the two locations across 60 seconds for each of 10 random, non-consecutive sessions in Experimental Phases 1-4. While it was anticipated that statistically significant, yet inconsequential, temporal variations in illumination (produced by electrically generated sources) would inevitably exist (Left: range = 39.6 - 42.8, [$p < .0001$]; Right: range = 39.5 - 42.6, [$p < .0001$]), comparative analyses by two-sample Independent *t*-Tests confirmed no significant differences in temporal stability of illumination between the left and right stimulus-display quadrants in each of the 10 sessions, ($p > .05$). The findings confirmed that the illumination in the left ($M = 41.34$, $SD = 1.23$) and right ($M = 40.93$, $SD = 1.01$) quadrants was essentially equal. Illustrative findings may be observed in Figure 27.

Behavioral Data Analyses

Behavioral data were used to examine whether differences existed among the subject groups and between specific Experimental Phases. In particular, data obtained in Relational Testing were analyzed to investigate whether the TE group demonstrated a performance significantly inferior to that of CON and PS groups, and whether there existed correlations between behavioral and histological variables. An alpha level of .05 was used for all statistical tests. Condensed behavioral data and corresponding tabulated statistical analyses may be consulted in Appendix B, Tables B1-B9.

Experimental Phase 1: Pre-Surgical Training. Statistical analyses of behavioral data obtained in Experimental Phase 1, Pre-Surgical Training, indicated that all subjects mastered the original, simple visual discrimination problem. Terminal Performances and Number of Trials Through Criterion were evaluated for all rats, after which scores were placed in ordinal rank and subjects were pre-assigned to future lesion groups (See Appendix B, Table B1) via a computerized randomization application. Further statistical analyses of the pre-surgical training behavioral data were conducted for the grouped animals, the findings of which showed that the subject groups performed with near-equivalent proficiency on all behavioral measures. No statistically significant differences were found.

Specifically, a one-way ANOVA was used to analyze Terminal Performance, the results of which indicated a performance accuracy exceeding 90% for each group, [CON (M = 93%, SD = 4%); PS (M = 94%, SD = 4%); TE (M = 93%, SD = 3%)], and no statistically significant difference among groups, [F (2, 21) = 0.28, $p >> .05$]. Likewise, one-way ANOVAs examining Mean Number of Errors Through Criterion and Mean

Number of Trials Through Criterion also indicated equivalent performances and no significant difference among groups for either variable, (Both *p*s >> .05). Depictions of the findings may be seen in Figure 28. Corresponding, condensed statistical results are included in Appendix B, Table B2. Representative Track-Plot Diagrams generated by the ANY-maze™ Video Tracking System are depicted in Figure 29.

Experimental Phase 2: Pre-Surgical Testing. Statistical analyses of the behavioral data obtained in Experimental Phase 2, Pre-Surgical Testing, indicated that all animals demonstrated excellent savings for the original visual discrimination following a 9-week hiatus from the pre-surgical training task. Additionally, all subject groups re-mastered the problem with equivalent proficiency, and no statistically significant differences among groups surfaced on any behavioral measures. In order to examine more closely the extent of savings and performance improvement, further analyses were used to compare scores on all behavioral measures between the pre-surgical training and testing phases for each subject group. As was expected, significant differences in performance between the two experimental phases were observed for each group, with all groups committing significantly fewer errors through criterion and requiring significantly fewer trials through criterion in Pre-Surgical Testing than in Pre-Surgical Training.

Specifically, a one-way ANOVA used to analyze Terminal Performance revealed group performance accuracies exceeding 90%, [CON (M = 93%, SD = 4%); PS (M = 94%, SD = 2%); TE (M = 94%, SD = 2%)] and indicated no significant difference among groups, [F (2, 21) = 0.13, p >> .05]. Similarly, one-way ANOVAs used to evaluate Mean Number of Errors Through Criterion and Mean Number of Trials Through Criterion yielded findings showing near-equivalent scores and no differences among groups, (Both

*p*s >> .05). Illustrated results may be observed in Figure 30. Corresponding, condensed statistical findings are displayed in Appendix B, Table B3. Representative Track-Plot Diagrams generated by the ANY-maze™ Video Tracking System are depicted in Figure 31.

To examine the extent of savings, two-sample Independent *t*-Tests were used to compare both Mean Number of Errors Through Criterion and Mean Number of Trials Through Criterion between Experimental Phase 1, Pre-Surgical Training and Experimental Phase 2, Pre-Surgical Testing. As was anticipated, the findings indicated a statistically significant difference in the Mean Number of Errors Through Criterion between the pre-surgical training and testing phases for each of the three subject groups, (CON, PS, and TE), [All *p*s << .0001], with each group committing significantly fewer errors through criterion in Pre-Surgical Testing [CON (*M* = 2.63, *SD* = 1.92); PS (*M* = 1.88, *SD* = 1.13; TE (*M* = 1.75, *SD* = .89)] than in Pre-Surgical Training [CON, (*M* = 21.5, *SD* = 3.89); PS, (*M* = 23, *SD* = 5.13); TE, (*M* = 22, *SD* = 2.93)]. As was also expected, the analyses showed a significant difference in the Mean Number of Trials Through Criterion between the two experimental phases for each subject group, (CON, PS, and TE), [All *p*s << .0001], with each group requiring significantly fewer trials through criterion in Pre-Surgical Testing [CON (*M* = 26.25, *SD* = 9.16); PS (*M* = 23.75; *SD* = 7.44); TE (*M* = 22.5, *SD* = 4.63)] than in Pre-Surgical Training [CON (*M* = 75.0, *SD* = 14.14); PS (*M* = 77.5, *SD* = 16.69); TE (*M* = 72.5, *SD* = 14.88)]. Pictographic results may be reviewed in Figure 32. Corresponding condensed statistical data may be found in Appendix B, Table B4.

Experimental Phase 3: Post-Surgical Retraining. Statistical analyses of the behavioral data obtained in Experimental Phase 3, Post-Surgical Retraining, indicated that all animals ultimately re-mastered the original simple visual discrimination problem subsequent to CON, PS or TE lesion surgery. While all rats demonstrated equivalent Terminal Performances, the findings did reveal significant differences among the lesion groups for the other behavioral measures. In particular, the TE group committed a significantly greater number of errors through criterion than the CON and PS groups. In addition, both the PS and TE groups required a significantly greater number of trials through criterion than the CON group, with the TE group also requiring a significantly greater number of trials through criterion than the PS group.

Specifically, a one-way ANOVA was used to analyze Terminal Performance in the post-surgical retraining phase, the results of which revealed that all animals demonstrated re-mastery of the discrimination problem, with similar success in performance observed among groups, [F (2, 18) = 0.24576, $p >> .05$]. Next, a one-way ANOVA examining Mean Number of Errors Committed Through Criterion produced findings showing a statistically significant difference among groups, ($p << .001$), with the TE group committing a significantly greater number of errors through criterion (M = 7.43, SD = 3.26) than the CON (M = 2.00, SD = 1.26), [$p << .001$] and PS (M = 3.38, SD = 2.26), [$p << .01$] groups. A one-way ANOVA evaluating the Mean Number of Trials Through Criterion also revealed significant differences among groups, ($p << .01$), with the PS group requiring a significantly greater number of trials through criterion (M = 27.5, SD = 7.07) than the CON group (M = 21.67, SD = 4.08), [$p < .05$], and with the TE group (M = 37.14, SD = 11.13) requiring a significantly greater number of trials through

criterion than the CON (M = 21.67, SD = 4.08), [$p << .01$], and PS (M = 27.5, SD = 7.07), [$p << .05$], groups. The results are depicted graphically in Figure 33. Corresponding condensed statistical data is provided in Appendix B, Table B5. Representative Track-Plot Diagrams generated by the ANY-maze^{TM} Video Tracking System are depicted in Figure 34.

Next, to examine behavioral performance between Experimental Phase 1, Pre-Surgical Training and Experimental Phase 3, Post-Surgical Retraining, comparative analyses were conducted using *t*-Tests. As was anticipated, the results revealed no significant difference in Terminal Performance between Post-Surgical Retraining and Pre-Surgical Training among the three lesion groups, (All *p*s >> .05). Additionally, a statistically significant difference in the Mean Number of Errors Through Criterion between the two Experimental Phases was observed for each lesion group, (All *p*s << .0001), with each group committing significantly fewer errors through criterion in Post-Surgical Retraining [CON (M = 2.00, SD = 1.26); PS (M = 3.38, SD = 2.26); TE (M = 7.43, SD = 3.26)] than in Pre-Surgical Training [CON (M = 21.5, SD = 3.89); PS (M = 23, SD = 5.13); TE (M = 22, SD = 2.93)]. Analyses also uncovered a significant difference in the Mean Number of Trials Through Criterion between the two Experimental Phases for each lesion group, (All *p*s << .0001), with each group requiring significantly fewer trials through criterion in Post-Surgical Retraining [CON (M = 21.67, SD = 4.08); PS (M = 27.5, SD = 7.07); TE (M = 37.14, SD = 11.13)] than in Pre-Surgical Training [CON (M = 75.0, SD = 14.14); PS (M = 77.5, SD = 16.69); TE (M = 72.5, SD = 14.88)]. Graphed data may be viewed in Figure 35. Corresponding statistical data are tabulated in Appendix B, Table B6.

Finally, to examine effects strictly of lesion on the retained task, comparative analyses by two-sample *t*-Tests were used to compare behavioral performance for each group between Experimental Phase 2, Pre-Surgical Testing and Experimental Phase 3, Post-Surgical Retraining. The analyses revealed no significant difference in Terminal Performance for the CON and PS groups between the two Phases. Though the TE group re-mastered the Post-Surgical Retraining task by attaining a Terminal Performance behavioral criterion of at least 90%, a significant difference in Terminal Performance between Pre-Surgical Testing and Post-Surgical Retraining was found, [t (13) = 2.75, $p << .01$], with the TE group demonstrating a Terminal Performance in Post-Surgical Retraining (M = 90.71, SD = 1.89) that was inferior to that demonstrated in Pre-Surgical Testing (M = 93.75, SD = 2.31). In addition, a significant difference in Mean Number of Errors Through Criterion between the two Experimental Phases was found for the PS, ($p << .05$), and TE, ($p << .001$), groups, with both groups committing a significantly greater number of errors through criterion [PS (M = 3.38, SD = 2.26) and TE (M = 7.43, SD = 3.26)] in Post-Surgical Retraining than in Pre-Surgical Testing. Analyses indicated that the TE group also required a significantly greater number of trials through criterion (M = 37.14, SD = 11.13) in Post-Surgical Retraining than in Pre-Surgical Testing (M = 22.5, SD = 4.63), [$p << .01$]. The findings, which are graphed with Pre-Surgical Training data for reference, are characterized pictorially in Figure 36. Corresponding statistical data may be consulted in Appendix B, Table B7.

Experimental Phase 4: Relational Testing. Statistical analyses of the behavioral data obtained in Experimental Phase 4, Relational Testing, revealed a statistically significant difference among the lesion groups on each behavioral measure. CON and PS

groups successfully attained behavioral criterion and generalized the discrimination to novel relational problems, demonstrating mastery of the task and a Terminal Performance exceeding 90%. In contrast, the TE group not only demonstrated a Terminal Performance that was significantly inferior to that of the CON and PS groups, but also, as a group, failed to attain behavioral criterion, despite being given 150 trials. As was anticipated, the TE group also committed a significantly greater number of errors than the CON and PS groups, and required a significantly greater number of trials in an attempt, though failed, to attain behavioral criterion, compared to CON and PS groups. The results are featured graphically in Figure 37. The corresponding tabulated statistical data may be found in Appendix B, Table B8. Representative Track-Plot Diagrams generated by the ANY-maze^{TM} Video Tracking System are depicted in Figure 38.

Specifically, results from a one-way ANOVA used to analyze Terminal Performance in Relational Testing indicated a statistically significant difference among lesion groups, [F (2, 18) = 3.90, $p << .01$]. Findings from subsequent two-sample Independent t-Tests revealed that the Terminal Performance of the TE group was significantly different from that of CON and PS groups, (Both ps << .05), with the TE group (M = 82.14, SD = 12.86) performing with considerably less performance accuracy than the CON (M = 93.33, SD = 4.08), and PS (M = 91.88, SD = 3.72) groups.

Likewise, results from a one-way ANOVA evaluating the Mean Number of Errors Through Criterion revealed a significant difference among lesion groups, ($p << .01$), with findings from subsequent two-sample Independent t-Tests demonstrating a statistically significant difference in the Mean Number of Errors between the TE and CON groups, ($p << .01$), and between the TE and PS groups, ($p << .05$), and with the TE group

committing a significantly greater number of errors (M = 36.43, SD = 19.76) than the CON (M = 8.5, SD = 7.94) and PS (M = 15.75, SD = 15.87) groups. Similarly, a one-way ANOVA evaluating Mean Number of Trials (through criterion or, alternatively, through testing termination) indicated a statistically significant difference among lesion groups, ($p << .01$), with two-sample Independent *t*-Tests revealing a significant difference in the Mean Number of Trials between the TE and CON groups ($p << .01$) and between the TE and PS groups, ($p << .05$), and with the TE group requiring a significantly greater number of trials in the failed attempt to attain criterion (M = 117.14, SD = 48.55) than the CON (M = 41.67, SD = 19.41) and PS (M = 67.5, SD = 51.48) groups. During the relational testing phase, behavioral learning curves were generated and followed across sessions for all subjects. Based on subject performance trends, testing was terminated after a total of 15 sessions (150 trials) per animal. Applicable corresponding data are exhibited in Appendix B, Table B9.

Versatile Stimuli Analyses. Four pairs of stimuli in Experimental Phase 4, Relational Testing, each composed of a versatile stimulus (i.e., a stimulus considered to be the correct choice (S+) on one trial but the incorrect choice (S-) on another trial [e.g., 42 vs. 70.8 and 9.6 vs. 42; 31.2 vs. 63.6 and 16.8 vs. 31.2]), were analyzed for Mean Percent Correct Response per stimulus for the subject groups averaged. Specifically, two-sample Independent *t*-Tests were conducted to (a) compare the Mean Percent Correct Response on trials in which 42 cd/m^2 was the correct (S+) choice versus trials in which 42 cd/m^2 was the incorrect (S-) choice and (b) compare the Mean Percent Correct Response on trials in which 31.2 cd/m^2 was the correct (S+) choice versus trials in which 31.2 cd/m^2 was the incorrect (S-) choice. Analyses revealed that, for subject groups

averaged, the Mean Percent Correct Response was significantly greater for trials in which 42 cd/m^2 was the S+ choice (M = 70.33, SD = 5.13) than for trials in which it was the S- choice (M = 13, SD = 8), ($p < .001$). Similarly, analyses revealed that, for subject groups averaged, the Mean Percent Correct Response was significantly greater for trials in which 31.2 cd/m^2 was the S+ choice (M = 76, SD = 12.77) than for trials in which it was the S- choice (M = 39, SD = 5.57), ($p < .01$). The results are shown graphically in Figure 39.

Correlation Analyses: Histology and Behavior

Linear regression correlation matrices were generated from quantified histological and behavioral variables (Per PS and TE groups) to produce a representative composite histological variable (viz., lesion volume) and a representative composite behavioral variable (viz., mean number of errors). Composite variables were used in examining whether general correlations existed between histology and behavior for either of the two lesion groups. Correlation matrices appear in Appendix C, Tables C1, C2, C3 and C4. Condensed statistical data for correlation analyses are charted in Appendix C, Tables C5 and C6.

Linear regression analyses were conducted to examine whether a correlation existed between morphometric (i.e., averaged left/right hemisphere lesion volume) and behavioral variables (i.e., mean number of errors) in Post-Surgical Retraining or in Relational Testing for the PS group. No statistically significant correlation emerged between the two variables for the PS group in Post-Surgical Retraining, [F (1, 6) = 0.26, $p > .05$], or in Relational Testing, [F (1, 6) = 1.38, $p > .05$]. Analyses were also performed to assess whether there was a correlation between the two variables (i.e., averaged left/right hemisphere lesion volume and mean number of errors) in Post-

Surgical Retraining or in Relational Testing for the TE group. Again, no correlation emerged between the two variables for the TE group in either Post-Surgical Retraining, [F (1, 5) = 3.91, p > .05], or Relational Testing, [F (1, 5) = 2.50, p > .05].

Linear regression analyses were also performed to investigate whether correlations would emerge between morphological (i.e., averaged left/right hemisphere Anatomical Lesion Location [i.e., Oc1M, Oc1B, Oc2MM, Oc2ML and Oc2L]) and behavioral (i.e., mean number of errors) variables in Post-Surgical Retraining or in Relational Testing for the PS group. No statistically significant correlation was observed between variables for the PS group in either Phase (Post-Surgical Retraining: Oc1M, Oc1B, Oc2MM, Oc2ML, and Oc2L), [All ps > .05]; Relational Testing: (Oc1M, Oc1B, Oc2MM, Oc2ML, and Oc2L), [All ps > .05]).

Similarly, analyses were performed to investigate whether a correlation existed between morphological (i.e., averaged left/right hemisphere Anatomical Lesion Location [i.e., Te1 and Te3]) and behavioral (i.e., mean number of errors) variables in Post-Surgical Retraining or in Relational Testing for the TE group. No statistically significant correlation was found between the histological and behavioral variables for the TE group in Post-Surgical Retraining: Te1, [p > .05] and Te3, [p > .05]. For the Relational Testing Phase, no significant correlation was found between Anatomical Lesion Location Area Te1 and Mean Number of Errors, (p >> .05) or between Anatomical Lesion Location Area Te3 and Mean Number of Errors, (p >> .05).

Microanalysis of the TE Lesion Group

Microanalysis of the TE Lesion Group was performed in order to examine the degree of variability in histological features and in behavioral performance among the TE

subjects. Rats were first compared across behavioral measures in Relational Testing (RT) via a one-sample *t*-Test. The results indicated a statistically significant difference among TE rats on measures of terminal performance, ($p < .0001$), number of errors, ($p < .01$) and number of trials, ($p < .001$). Then, based on terminal performance scores, subjects were matched and assigned to one of two groups: *TE Group 1* [RT Criterion Attained, ($n = 3$)] or *TE Group 2* [RT Criterion Not Attained, ($n = 4$)]. The two groups were subsequently compared across both behavioral and histological measures.

Comparative data analyses: Relational Testing. Two-sample Independent *t*-Tests were used to compare TE Groups 1 and 2 on behavioral variables in Relational Testing, the findings of which revealed a significant difference for measures of Terminal Performance, ($p < .05$), Mean Number of Errors, ($p < .01$), and Mean Number of Trials, ($p < .01$). Illustrative findings appear in Figure 40. Corresponding statistical data may be viewed in Appendix D, Table D1.

Comparative data analyses: Post-Surgical Retraining. To determine whether differences between the two groups were confined to behavioral performance only in Relational Testing, a comparative analysis between groups was conducted for performances in Post-Surgical Retraining. Two-sample Independent *t*-Tests confirmed performance equivalency between TE Groups 1 and 2 on all behavioral measures in Post-Surgical Retraining [Terminal Performance, ($p > .05$), Mean Number of Errors Through Criterion, ($p > .05$), and Mean Number of Trials Through Criterion, ($p > .05$)], with no statistically significant difference between groups observed. A graphic representation of the results is shown in Figure 41. Corresponding statistical data are represented in Appendix D, Table D1.

Comparative morphometric data analyses. Comparative analyses of morphometric (i.e., lesion volume) differences between TE Groups 1 and 2 were performed. Two-sample Independent *t*-Tests revealed no significant difference between the two groups in averaged left/right hemisphere Lesion Volume, ($p > .05$), and, furthermore, indicated no significant difference between TE Groups 1 and 2 in left Lesion Volume, ($p > .05$), or in right Lesion Volume, ($p > .05$). The findings are illustrated in Figure 42.

Comparative morphological data analyses. Comparative analyses of morphological (i.e., Percent of Tissue Ablated within Area Te1 or Te3) differences between TE Groups 1 and 2 were conducted. Two-sample Independent *t*-Tests revealed no significant difference between TE Groups 1 and 2 in the Percent of Tissue Ablated in Te1, ($p > .05$), or in the Percent of Tissue Ablated in Te3, ($p > .05$). Results are depicted pictorially in Figure 43. Finally, two-sample Independent *t*-Tests were used to evaluate the Percent of Tissue Ablated in the left and in the right hemispheres of Te1 between groups. No significant difference between TE Groups 1 and 2 was found for either factor, (Both *p*s > .05). Similarly, two-sample *t*-Tests were used to assess the Percent of Tissue Destroyed in the left and in the right hemispheres of Te3 between TE Groups 1 and 2, the findings of which also indicated no significant difference between the two groups for either hemisphere, (Both *p*s > .05). Corresponding statistical data are provided in Appendix D, Table D2.

Correlation Analyses: Lesion Quantification Methods

Linear regression analyses were performed to analyze the extent to which the topometric aspects of the Computer Imaging Technique (CDIT) and the Dot Grid Method

(DGM) were correlated. As was predicted, the analyses revealed that the two methods were significantly correlated for variables for the PS group, (*p*s at least << .05), and for the TE group, (*p*s at least << .05). Corresponding tabulated statistical data may be observed in Appendix E, Tables E1 and E2.

Correlation Analyses: Stimulus Luminance and Behavior

Linear regression analyses were performed to evaluate whether a significant correlation existed for CON, PS and TE groups between (a) Percent Difference in Photometric Luminance between novel, paired stimuli in Relational Testing and (b) Mean Percent Correct Response. The findings indicated a statistically significant correlation between variables (a) and (b) for the PS ($p << .05$) and TE ($p << .05$) groups, indicating that the PS and TE group performance accuracies were, on average, greater for presentations of paired stimuli with a larger percent luminance difference between them (e.g., 83%) than for presentations of paired stimuli with a smaller percent luminance difference between them (e.g., 40%). The correlation between variables (a) and (b) for the CON group was non-significant, ($p >> .05$). A graphic characterization of the results is featured in Figure 44.

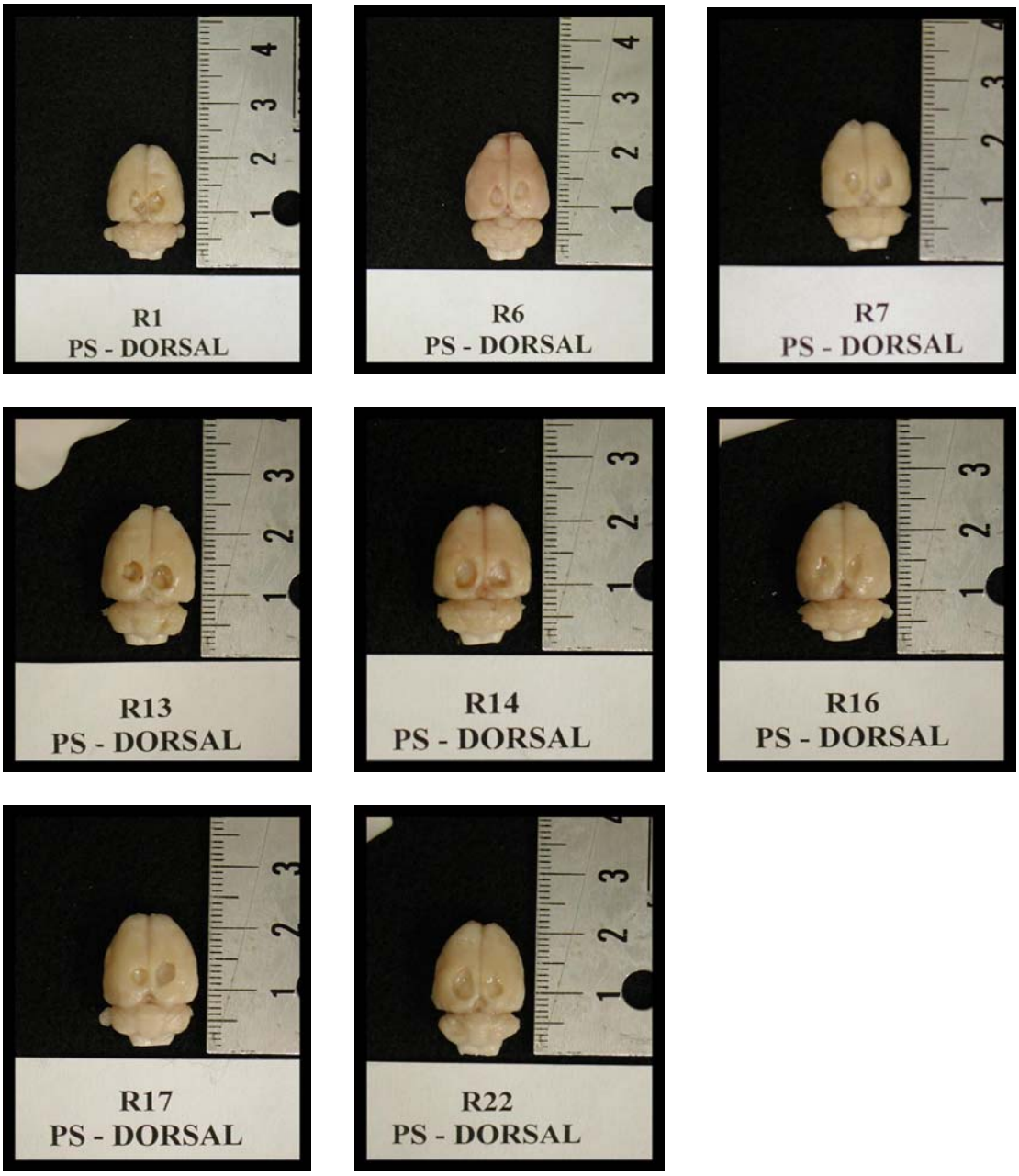


Figure 12. Digital photographs of topographical alterations in PS lesioned brains, as viewed from dorsal perspectives and with metric reference (in mm).

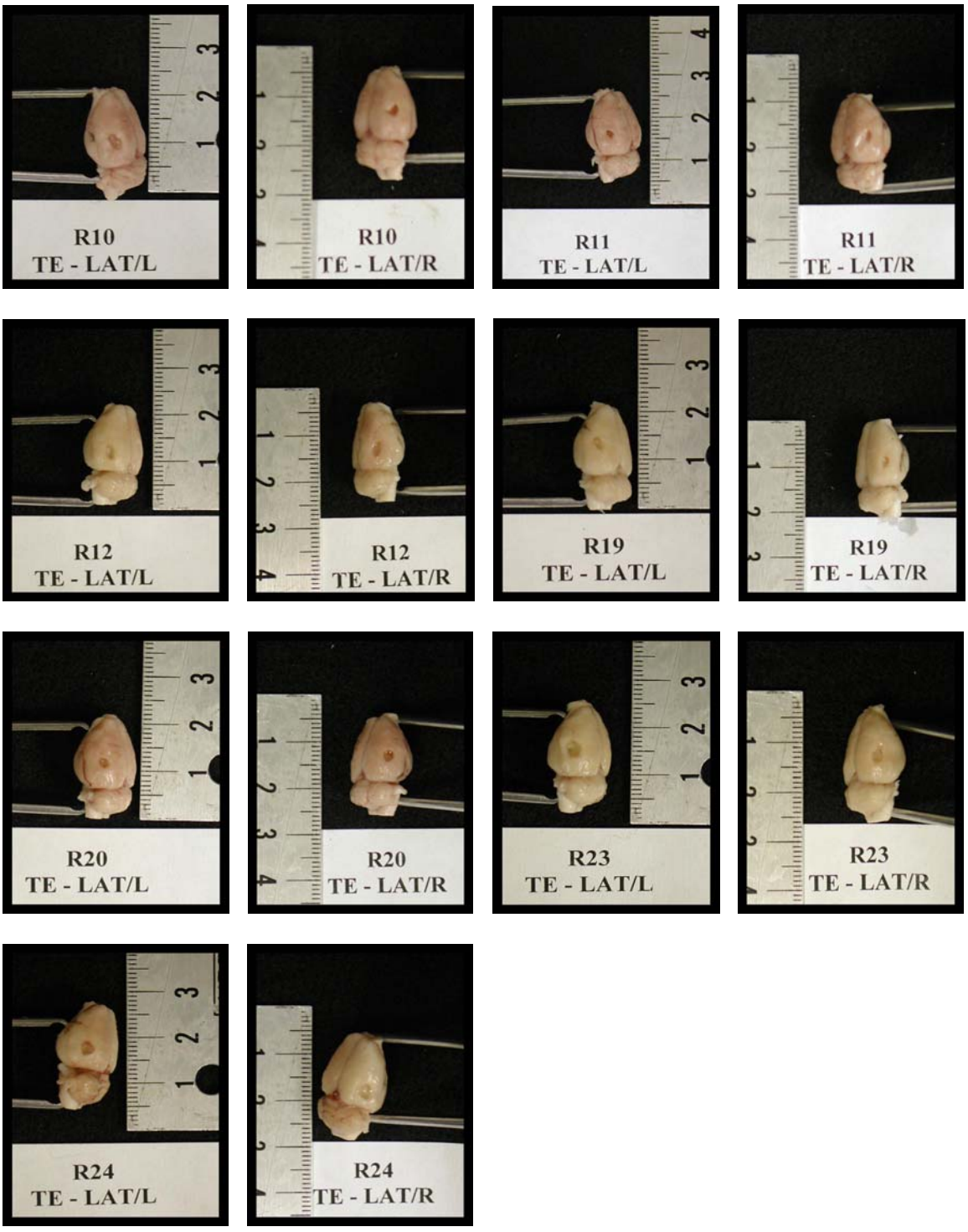
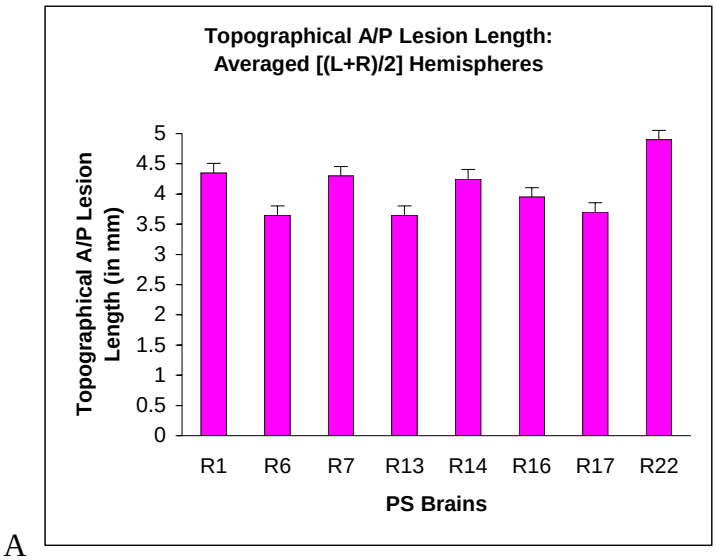
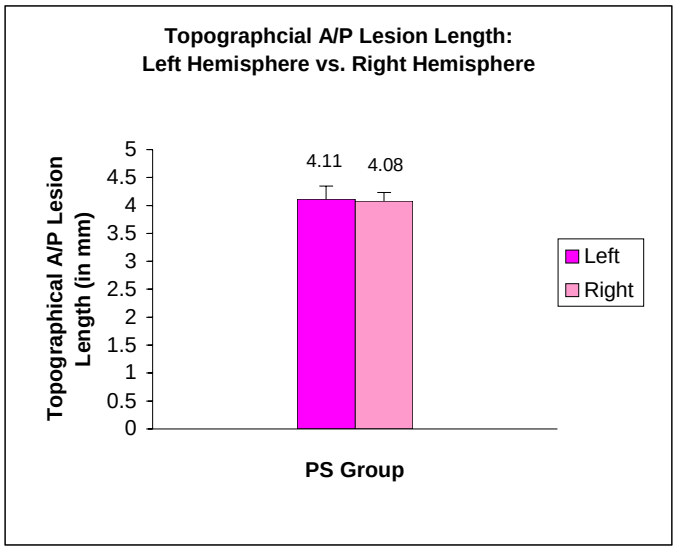


Figure 13. Digital photographs of topographical alterations in TE lesioned brains, as viewed from lateral perspectives and with metric reference (in mm).

Figure 14. A digital photograph of a representative CON brain, as viewed from the dorsal perspective and with metric reference (in mm). No topographical alterations resulting from surgical bilateral cranial destruction were observed in CON brains.



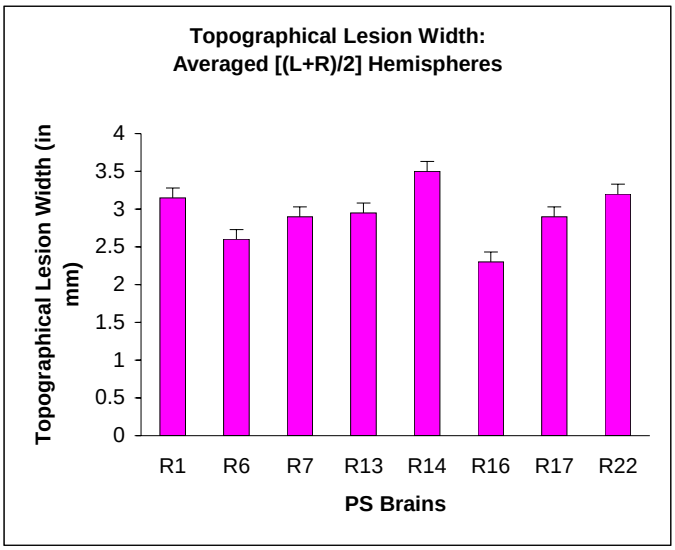
A



B

Figure 15. Graphs A and B represent topometric data ($M \pm SEM$) analyzed for the PS group (n = 8). A statistically significant difference in (A) Topographical A/P Lesion Length of Averaged Left/Right Hemispheres was observed among PS brains, ($p < .0001$), by one-sample *t*-Test. A two-sample Independent *t*-Test revealed no significant difference in (B) Topographical A/P Lesion Length Between the Left and Right Hemispheres for the PS group as a whole, ($p > .05$).

A



B

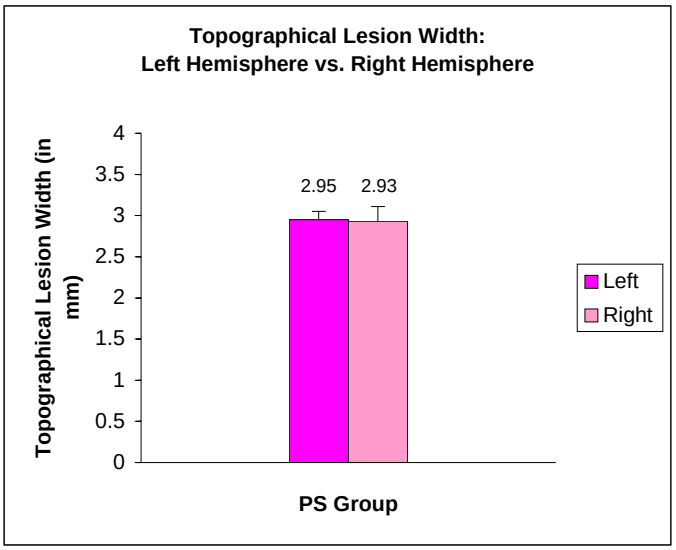
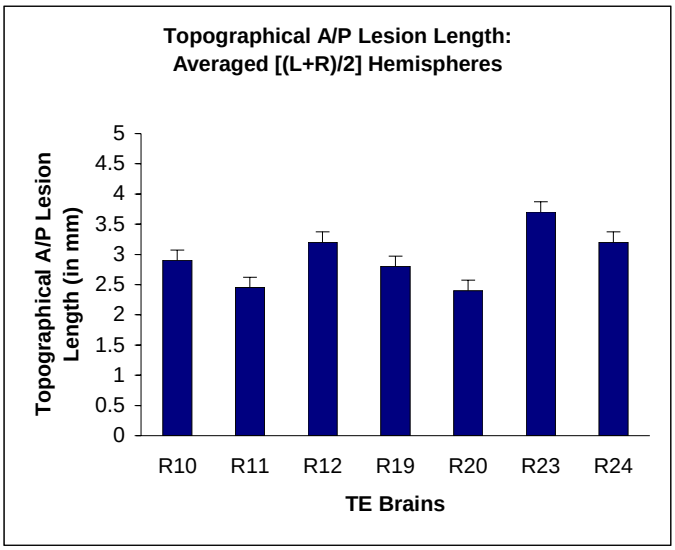
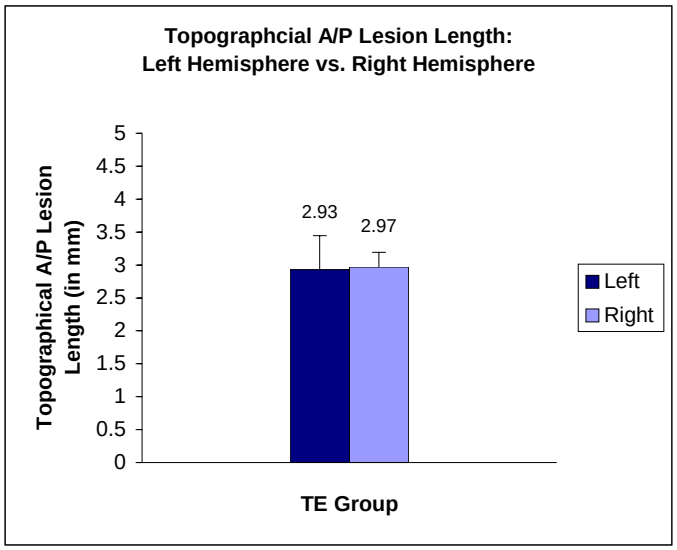


Figure 16. Graphs A and B represent topometric data ($M \pm SEM$) analyzed for the PS group ($n = 8$). A one-sample *t*-Test indicated a statistically significant difference among PS brains in (A) Topographical Lesion Width of Averaged Left/Right Hemispheres, ($p < .0001$). A two-sample Independent *t*-Test showed no significant difference in (B) Topographical Lesion Width Between the Left and Right Hemispheres for the PS group as a whole, ($p > .05$).

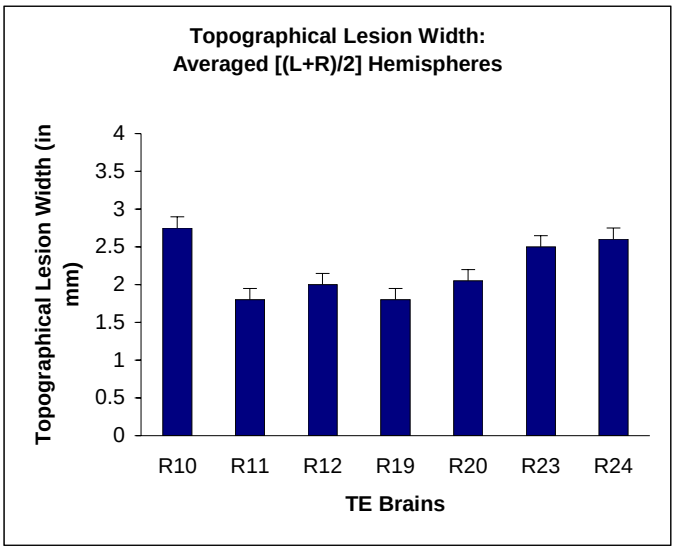


A

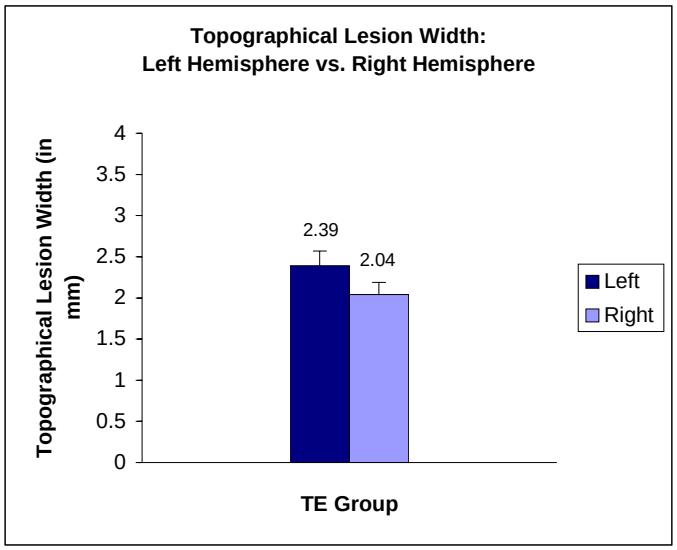


B

Figure 17. Graphs A and B represent topometric data ($M \pm SEM$) analyzed for the TE group ($n = 7$). A statistically significant difference in (A) Topographical A/P Lesion Length of Averaged Left/Right Hemispheres was observed among TE brains, ($p < .0001$), by one-sample t-Test. A two-sample Independent *t*-Test revealed no significant difference in (B) Topographical A/P Lesion Length Between the Left and Right Hemispheres for the TE group as a whole, ($p > .05$).

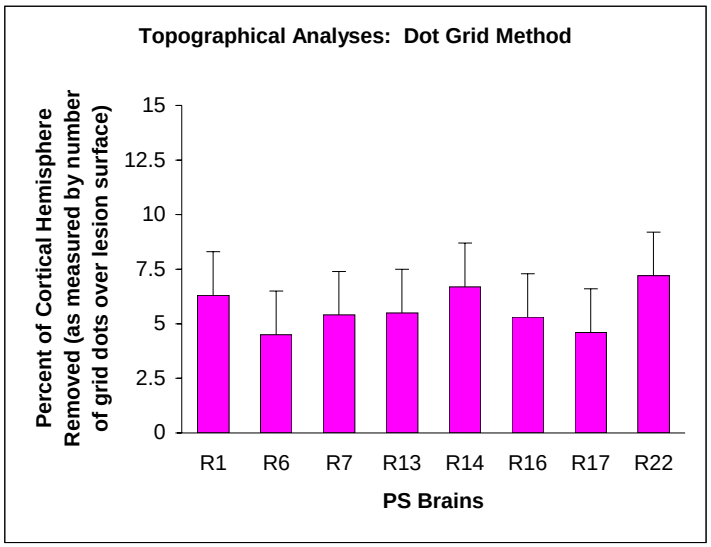


A

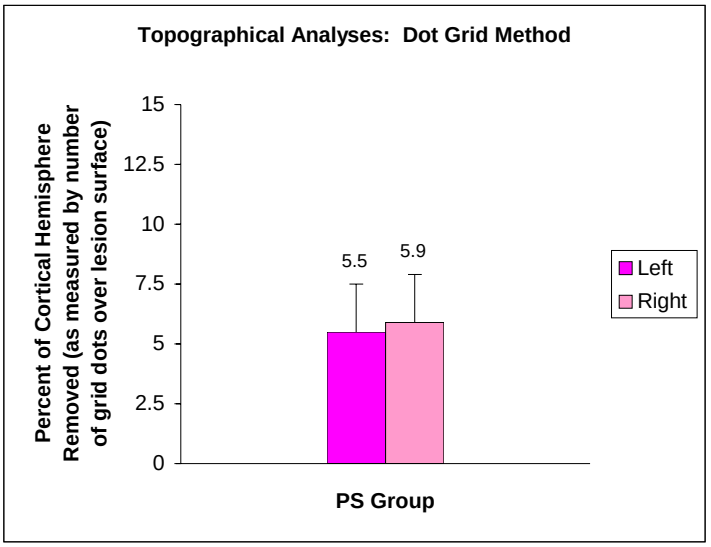


B

Figure 18. Graphs A and B represent topometric data (*M* ± *SEM*) analyzed for the TE group (*n* = 7). A statistically significant difference in (A) Topographical Lesion Width of Averaged Left/Right Hemispheres was observed among TE brains, ($p < .0001$), by one-sample *t*-Test. A two-sample Independent *t*-Test indicated no significant difference in (B) Topographical Lesion Width Between the Left and Right Hemispheres for the TE group as a whole, ($p > .05$).

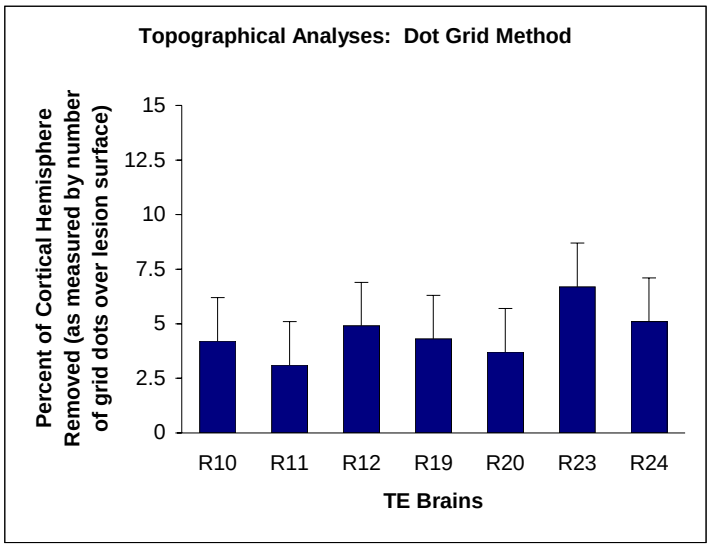


A

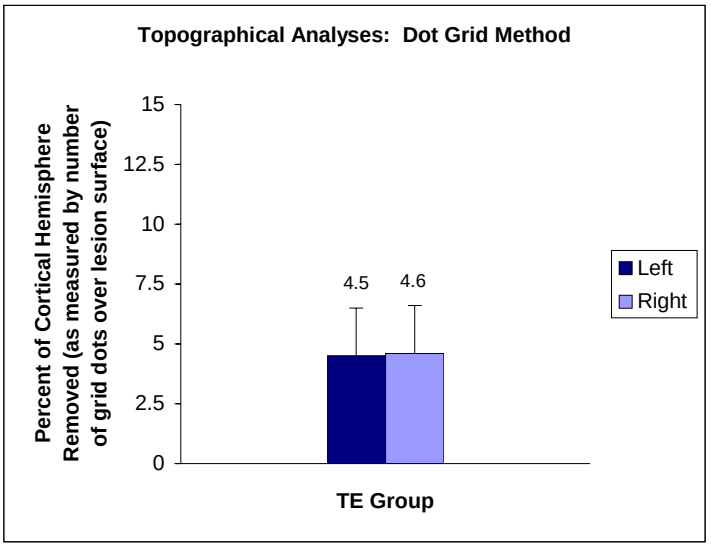


B

Figure 19. Graphs A and B represent topometric data (*M* ± *SEM*) analyzed for the PS group (*n* = 8), obtained via the DGM. A statistically significant difference in (A) Percent of Surface Cortex Removed in Averaged Left/Right Hemispheres was found among PS brains, (*P* < .0001), by one-sample *t*-Test. A two-sample Independent *t*-Test revealed no significant difference in (B) Percent of Surface Cortex Removed Between the Left and Right Hemispheres for the PS group as a whole, (*p* > .05).

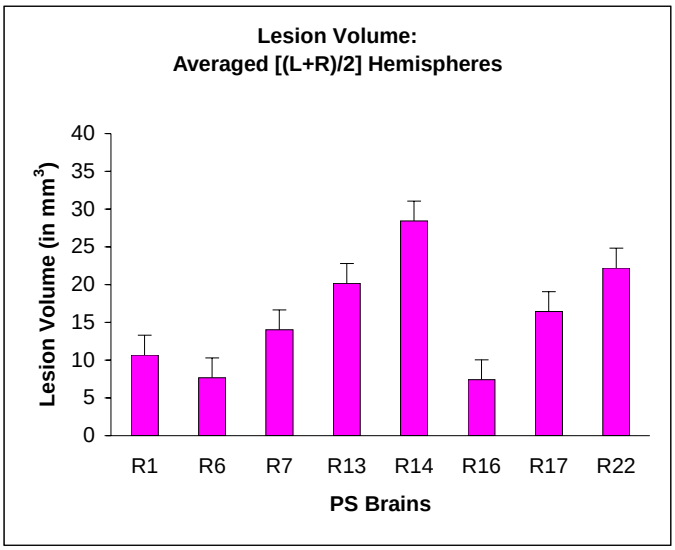


A

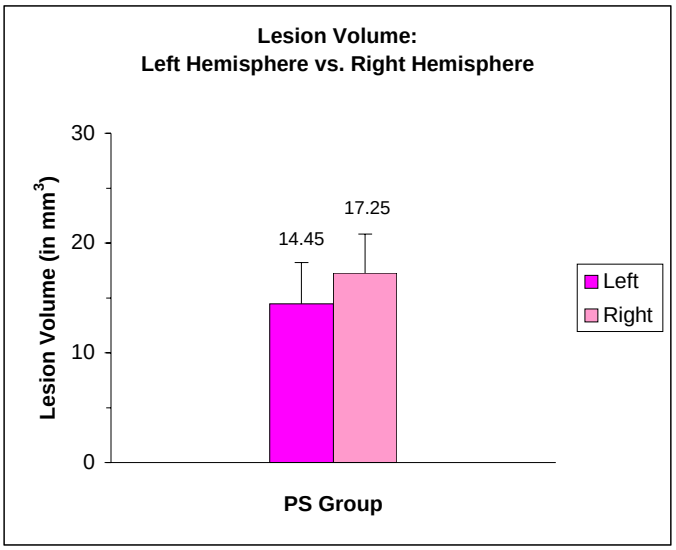


B

Figure 20. Graphs A and B represent topometric data (*M* ± *SEM*) analyzed for the TE group (*n* = 7), obtained via the DGM. A statistically significant difference in (A) Percent of Surface Cortex Removed in Averaged Left/Right Hemispheres was found among TE brains, (*P* < .0001), by one-sample *t*-Test. A two-sample Independent *t*-Test revealed no significant difference in (B) Percent of Surface Cortex Removed Between the Left and Right Hemispheres for the TE group as a whole, (*p* > .05).

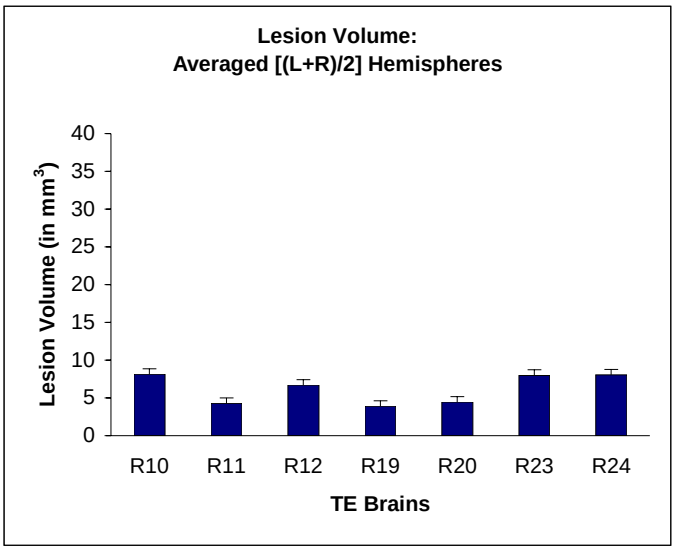


A

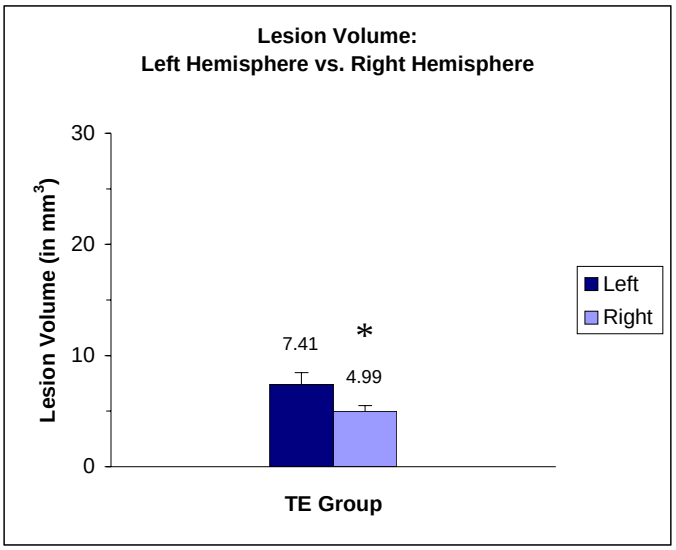


B

Figure 21. Graphs A and B represent morphometric data ($M \pm SEM$) analyzed for the PS group (n = 8). A statistically significant difference in (A) Lesion Volume of Averaged Left/Right Hemispheres was revealed among brains in the group, ($p < .001$), by one-sample *t*-Test. A two-sample Independent *t*-Test indicated no significant difference in (B) Lesion Volume Between the Left and Right Hemispheres for the PS group as a whole, ($p > .05$).



A



B

Figure 22. Graphs A and B represent morphometric data ($M \pm SEM$) analyzed for the TE group (n = 7). A statistically significant difference in (A) Lesion Volume of Averaged Left/Right Hemispheres was revealed among brains in the group, ($p < .0001$), by one-sample *t*-Test. A two-sample Independent *t*-Test indicated a significant difference in (B) Lesion Volume Between the Left and Right Hemispheres for the TE group as a whole, ($p < .05$).

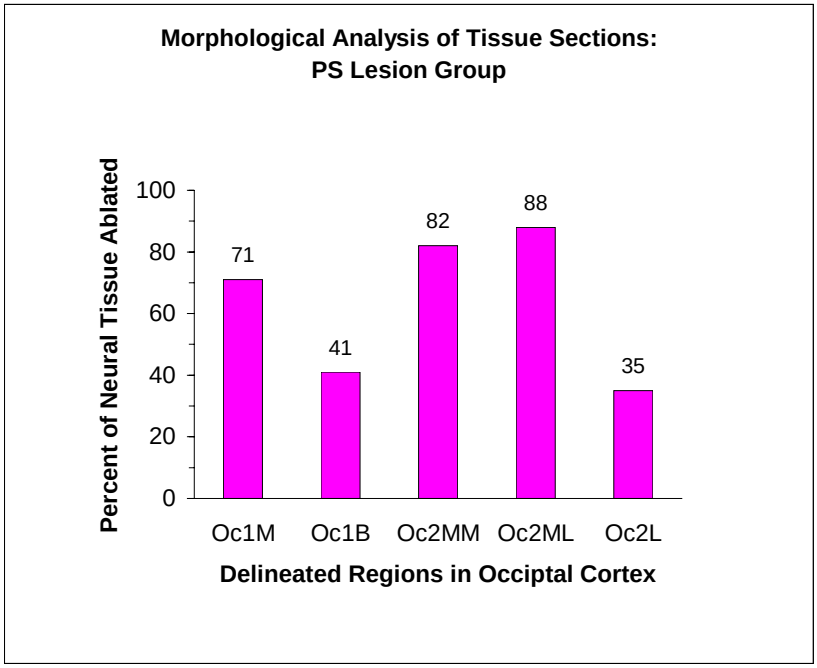


Figure 23. Morphological data (*M* ± *SEM*) analyzed across all PS histological tissue sections and averaged for the PS group (*n* = 8), representing the percent of tissue ablated within distinct anatomical divisions of Occipital/Striate Cortex. One-sample *t*-Tests indicated that bilateral PS lesions invaded substantial portions of Oc1M (*M* = 71%; range = 11%-100%), Oc2MM (*M* = 82%; range = 58%-94%) and Oc2ML (*M* = 88%; range = 68%-100%), and considerable portions of Oc1B (*M* = 41%; range = 0%-89%) and Oc2L (*M* = 35%; range = 2%-63%). Two-sample Independent *t*-Tests revealed that the percent of tissue destroyed in Oc2MM was significantly greater than the percent of tissue destroyed in Oc1B, ($p < .01$), and in Oc2L, ($p < .0001$); the percent of tissue destroyed in Oc2ML was significantly greater than that destroyed in Oc1B, ($p < .01$) and in Oc2L, ($p < .0001$); and the percent of tissue ablated in Oc1M was significantly greater than that ablated in Oc2L, ($p < .01$).

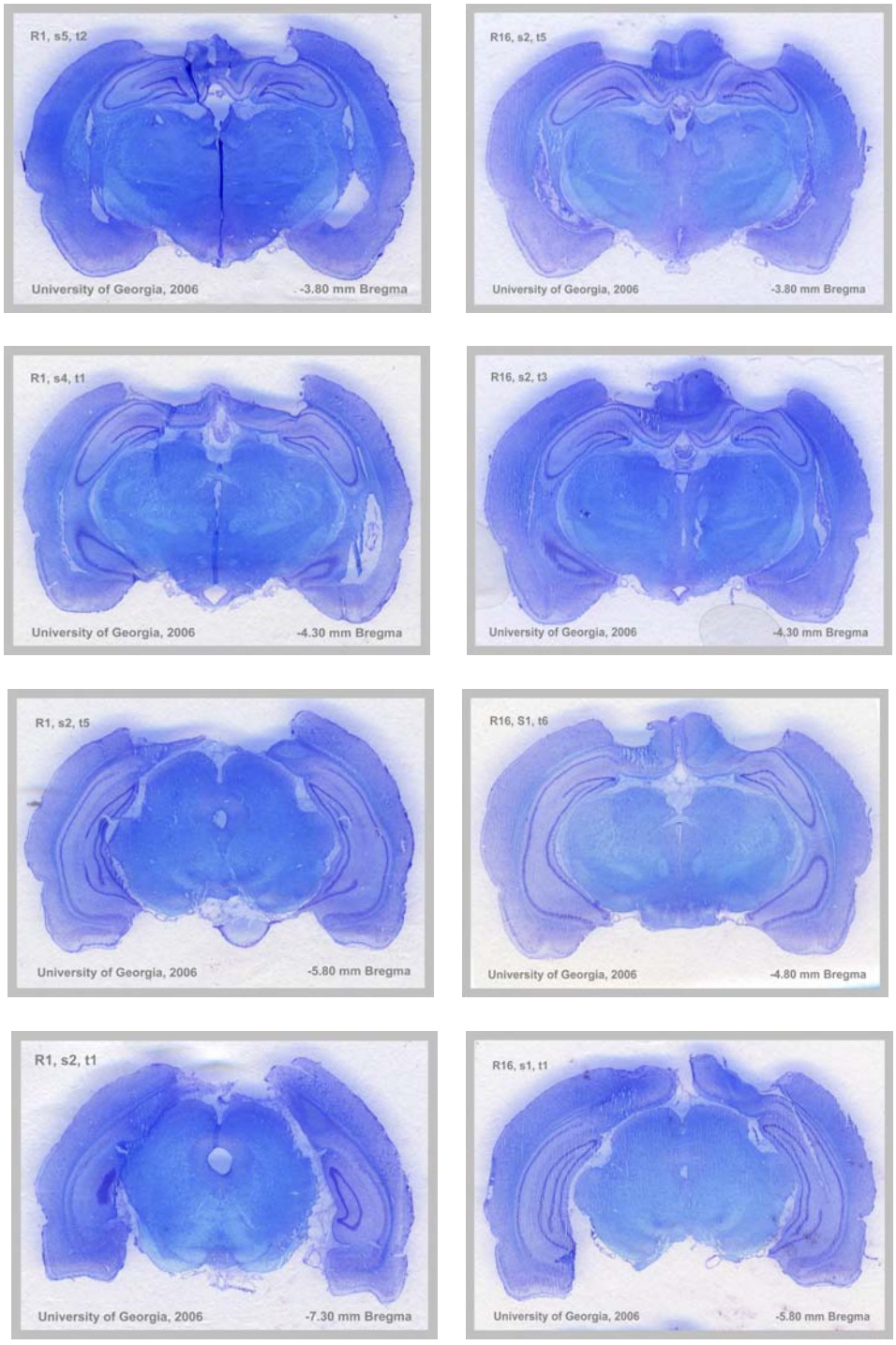


Figure 24. Digital images of coronal tissue sections from two PS lesioned brains, through approximate extents of lesions, displayed in columns. Specimen identification details and distance (in mm) posterior to Bregma are indicated pictorially.

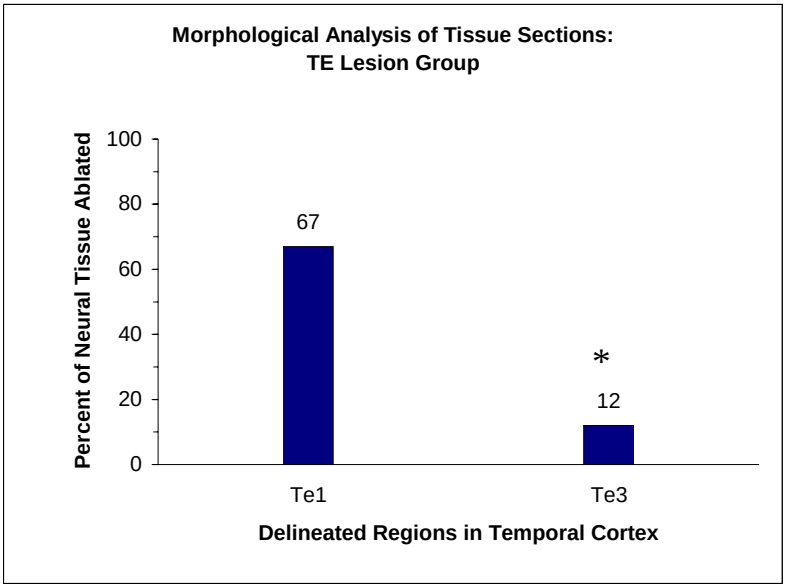


Figure 25. Morphological data ($M \pm SEM$) analyzed across all TE histological tissue sections and averaged for the TE group ($n = 7$), representing the percent of tissue ablated within delineated regions of temporal cortex. One-sample *t*-Tests indicated that bilateral TE lesions invaded considerable portions of Te1 ($M = 67\%$; range = 53%-86%) and variable portions of the dorsal medial and dorsal lateral regions of Te3 ($M = 11\%$; range = 3%-24%). From a two-sample *t*-Test, a statistically significant difference emerged in the percent of tissue destroyed between the two temporal regions, in which the percent of tissue destroyed in Te1 was significantly greater than that lesioned in Te3, ($p < .0001$).

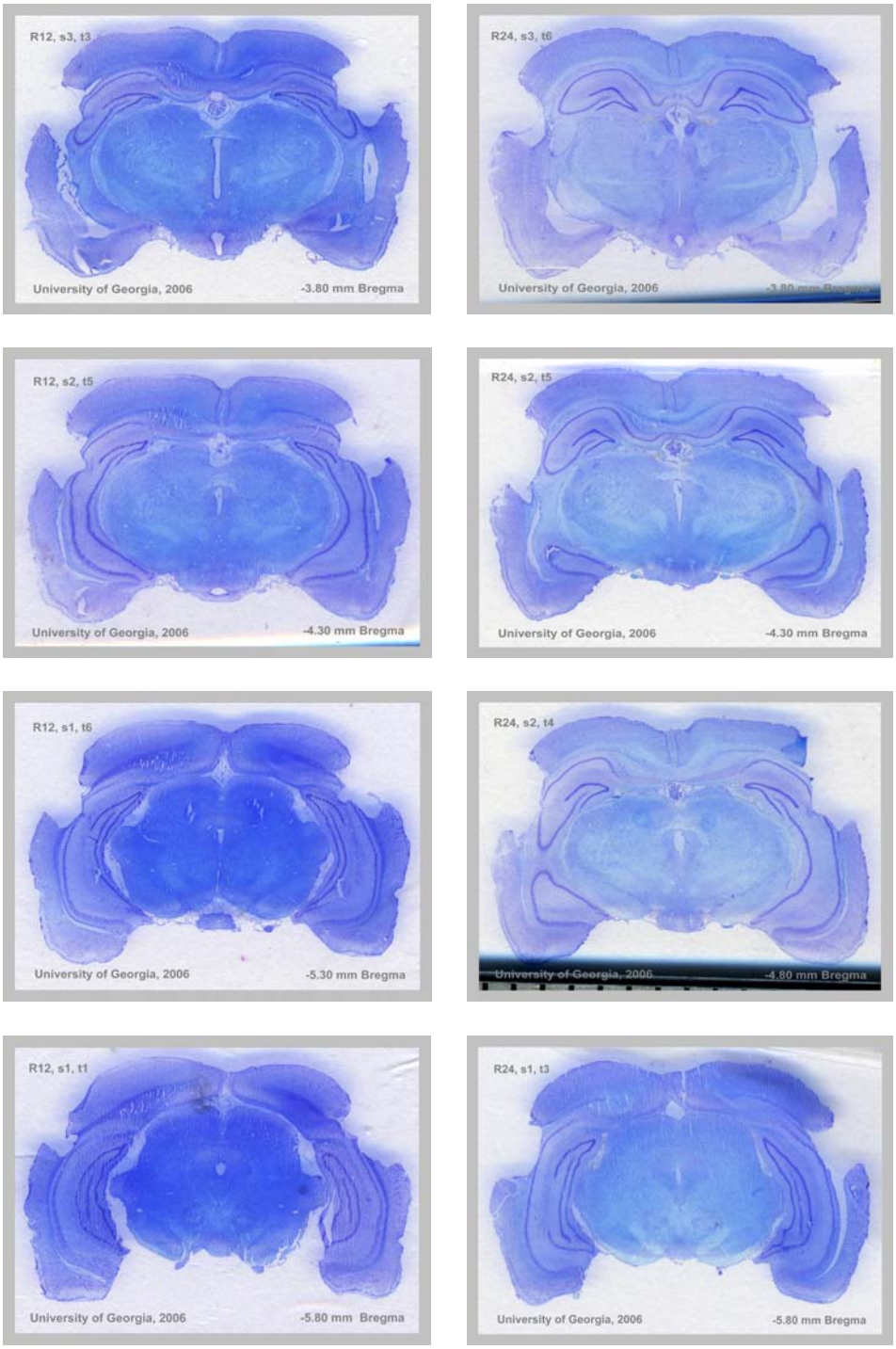


Figure 26. Digital images of coronal tissue sections from two TE lesioned brains, through approximate extents of lesions, displayed in columns. Specimen identification details and distance (in mm) posterior to Bregma are indicated pictorially.

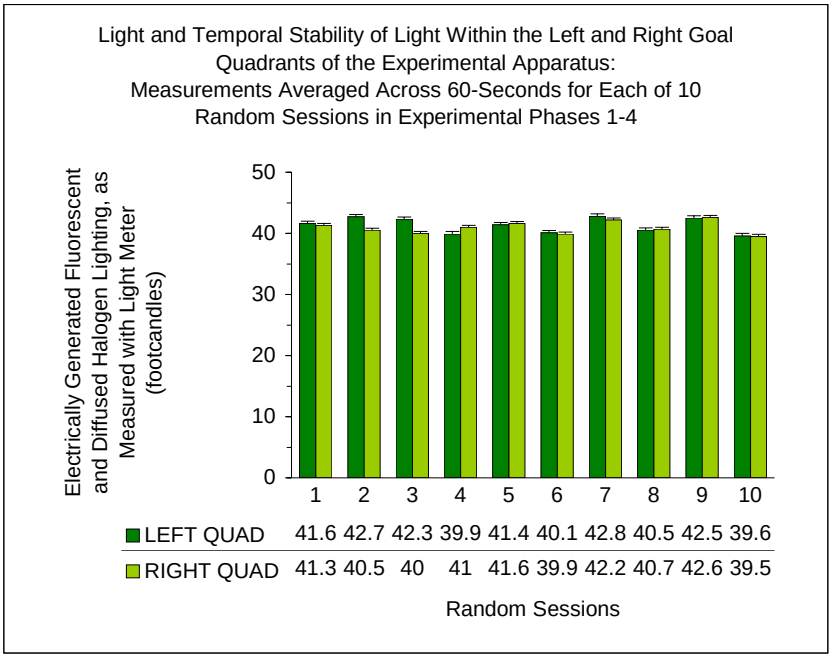


Figure 27. Light data (*M* ± *SEM)* analyzed for temporal stability and compared between the left and right stimulus-display quadrants within the experimental apparatus. Light measurements were averaged for each quadrant across 60 seconds for each of 10 random, non-consecutive sessions in Experimental Phases 1-4. While it was anticipated that statistically significant, yet inconsequential, temporal variations in light would inevitably exist (Left: range = 39.6 - 42.8, [$p < .0001$]; Right: range = 39.5 - 42.6, [$p < .0001$]), comparative analyses by two-sample Independent *t*-Tests confirmed no significant differences in the temporal stability of light between the left and right stimulus-display quadrants in each of the 10 sessions, [$p > .05$]. The results confirmed that the average light measurements in the left ($M = 41.34$, $SD = 1.23$) and right ($M = 40.93$, $SD = 1.01$) quadrants were essentially equal.

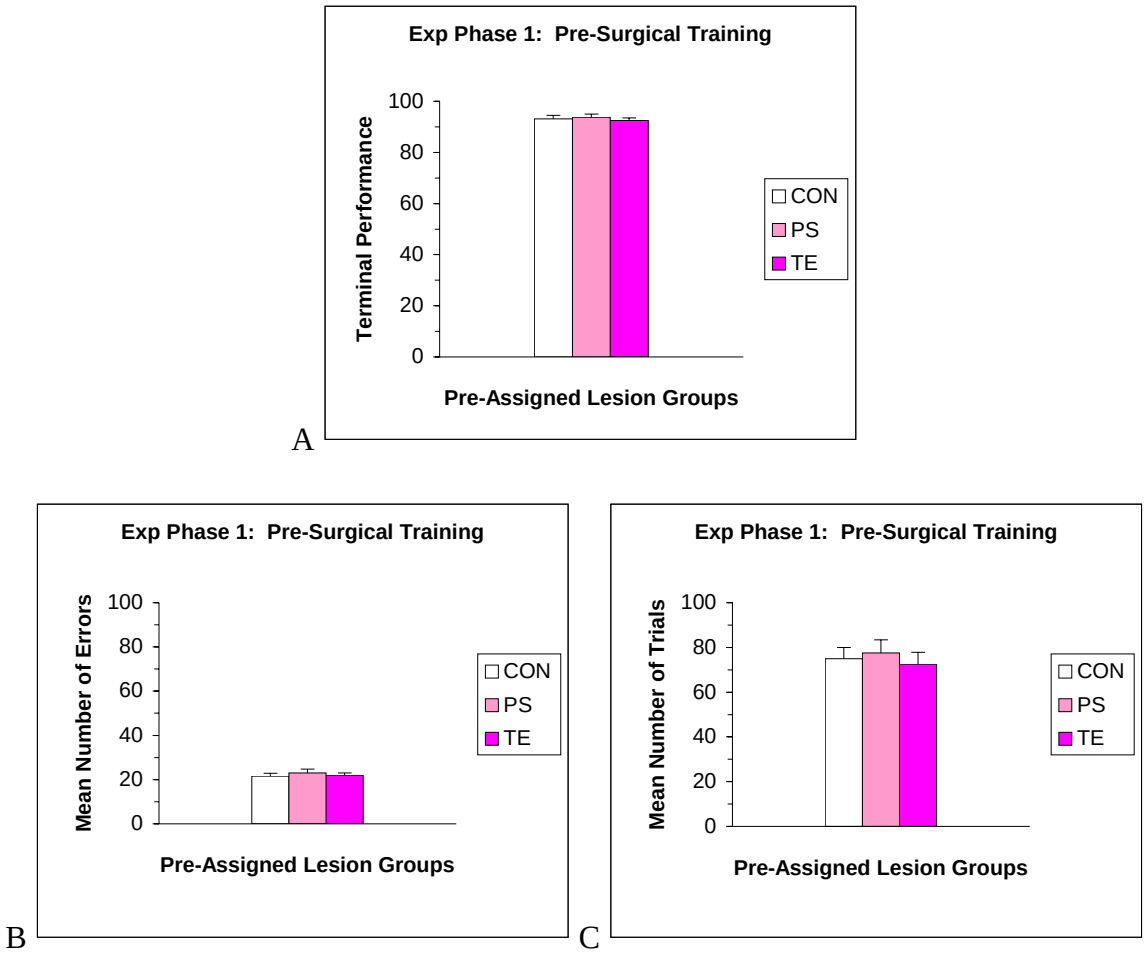
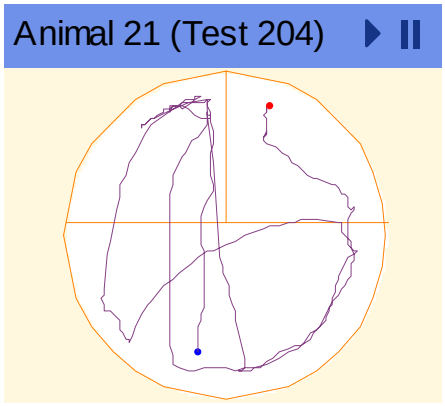


Figure 28. Graphs A, B and C represent behavioral data (*M* ± *SEM*) analyzed for Experimental Phase 1, Pre-Surgical Training for pre-assigned CON (*n* = 8), PS (*n* = 8) and TE (*n* = 8) subject groups. As was predicted, all rats demonstrated acquisition and mastery of the original, visual discrimination problem. Near-equivalent performances were found among subject groups on behavioral measures of (A) Terminal Performance, (B) Mean Number of Errors through Criterion and (C) Mean Number of Trials through Criterion, by one-way ANOVA. Statistically significant differences were not observed among subject groups on any behavioral measures, (All *p*s >> .05).

(A)



(B)

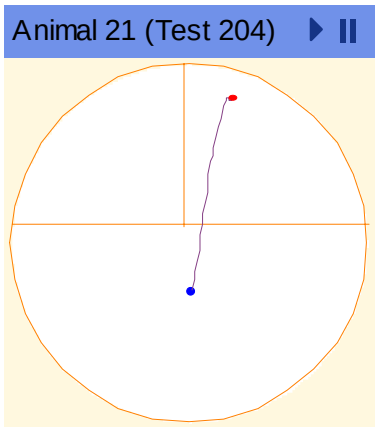


Figure 29. Navigational trajectory and performance within a 60-second trial in (A) Session 1 and in (B) the Final Session through behavioral criterion in Experimental Phase 1, Pre-Surgical Training by a representative, cortically intact rat (R21), as depicted in Track-Plot Diagrams by ANY-maze™ Video Tracking System. A comparison of the pictorial data in (A) and (B) illustrate the significant improvement in visual discrimination performance between the initial and final training sessions in the Pre-Surgical Training Phase. (The Test number above refers to the cumulative number of trials in the daily session (n = 240) with all rats (n = 24) at a rate of 10 trials per animal. Thus, Tests 201-210 were Trials 1-10 for Rat R21).

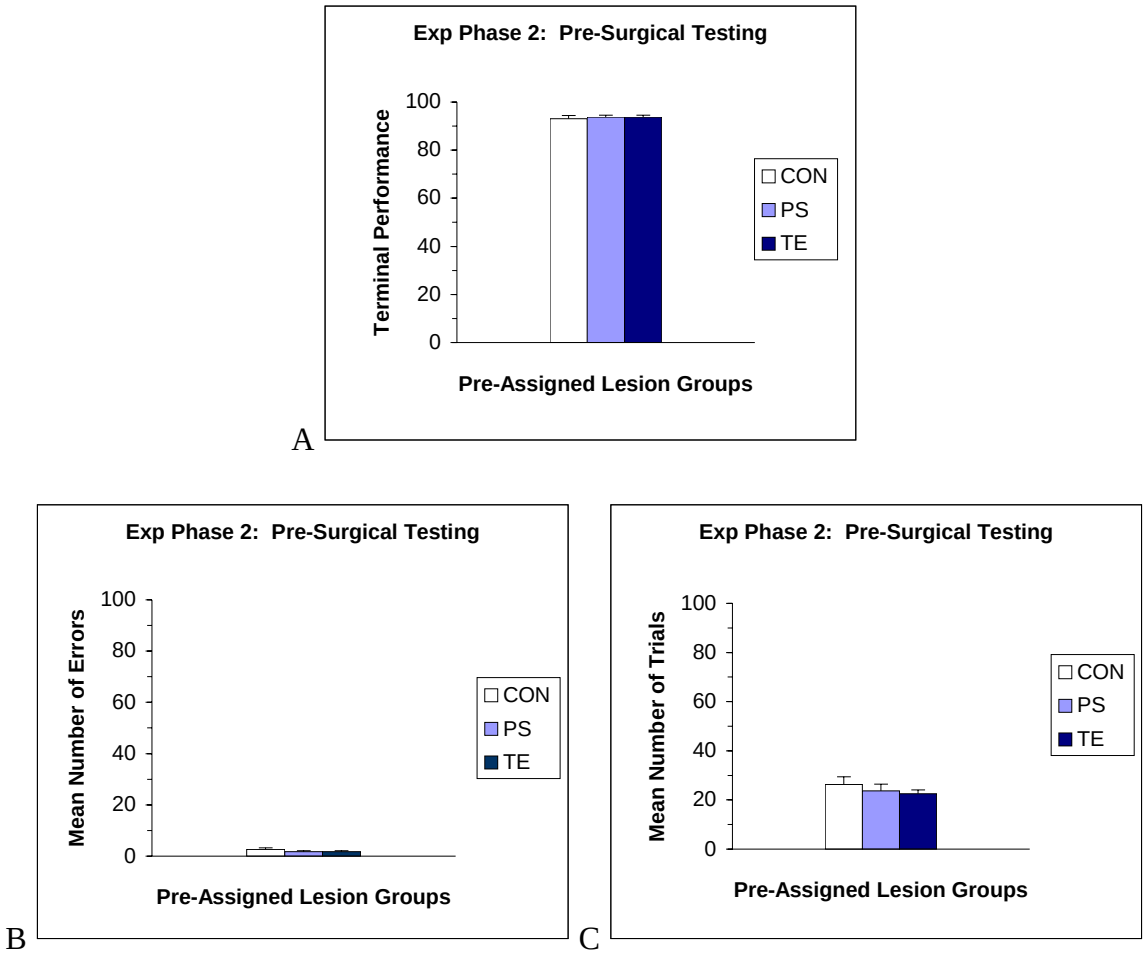
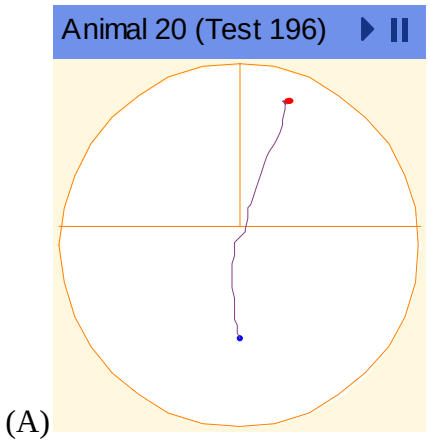
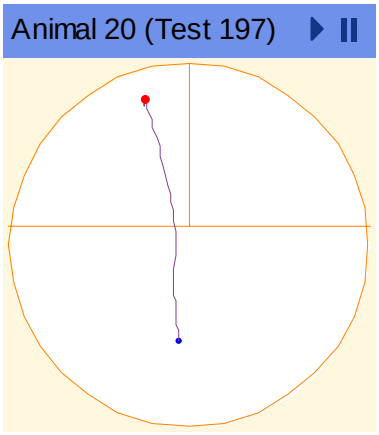


Figure 30. Graphs A, B and C represent behavioral data ($M \pm SEM$) analyzed for Experimental Phase 2, Pre-Surgical Testing for pre-assigned CON (n = 8), PS (n = 8) and TE (n = 8) subject groups. As was expected, all rats demonstrated excellent savings for the previously learned visual discrimination problem, with near-equivalent performances among subject groups on behavioral measures of (A) Terminal Performance, (B) Mean Number of Errors through Criterion and (C) Mean Number of Trials through Criterion. No statistically significant differences were observed on any behavioral measures among groups, (All ps >> .05).



(A)



(B)

Figure 31. Navigational trajectory and performance within a 60-second trial in (A) Session 1 and in (B) the Final Session through behavioral criterion in Experimental Phase 2, Pre-Surgical Testing by a representative, cortically intact rat (R20), as depicted in Track-Plot Diagrams by ANY-maze™ Video Tracking System. Diagrams (A) and (B) illustrate the finding that, even after a 9-week hiatus, there was excellent savings for the original discrimination task. (The Test number above refers to the cumulative number of trials in the daily session (n = 240) with all rats (n = 24) at a rate of 10 trials per animal. Thus, Tests 191-200 were Trials 1-10 for Rat R20).

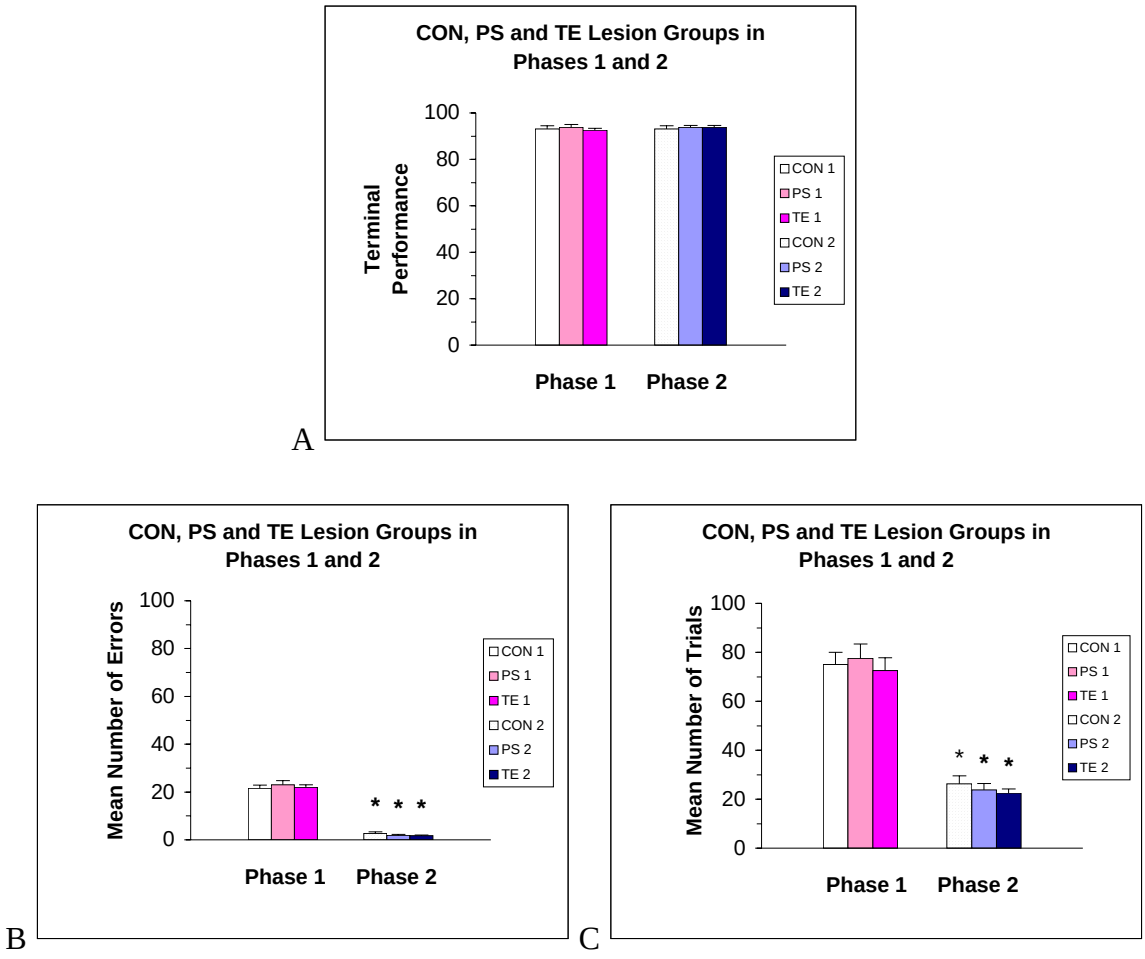


Figure 32. Graphs A, B and C represent data (*M* ± *SEM*) compared between Experimental Phase 1, Pre-Surgical Training, and Experimental Phase 2, Pre-Surgical Testing, across pre-assigned CON (*n* = 8), PS (*n* = 8) and TE (*n* = 8) subject groups. For each group, no significant difference was observed between the two Experimental Phases on the measure of (A) Terminal Performance. As was expected, a statistically significant difference between Experimental Phases was found on measures of (B) Mean Number of Errors Through Criterion, ($p << .0001$), and (C) Mean Number of Trials Through Criterion, ($p << .0001$), with CON, PS and TE groups each demonstrating performance accuracy in Experimental Phase 2, Pre-Surgical Testing significantly superior to that demonstrated in Experimental Phase 1, Pre-Surgical Training.

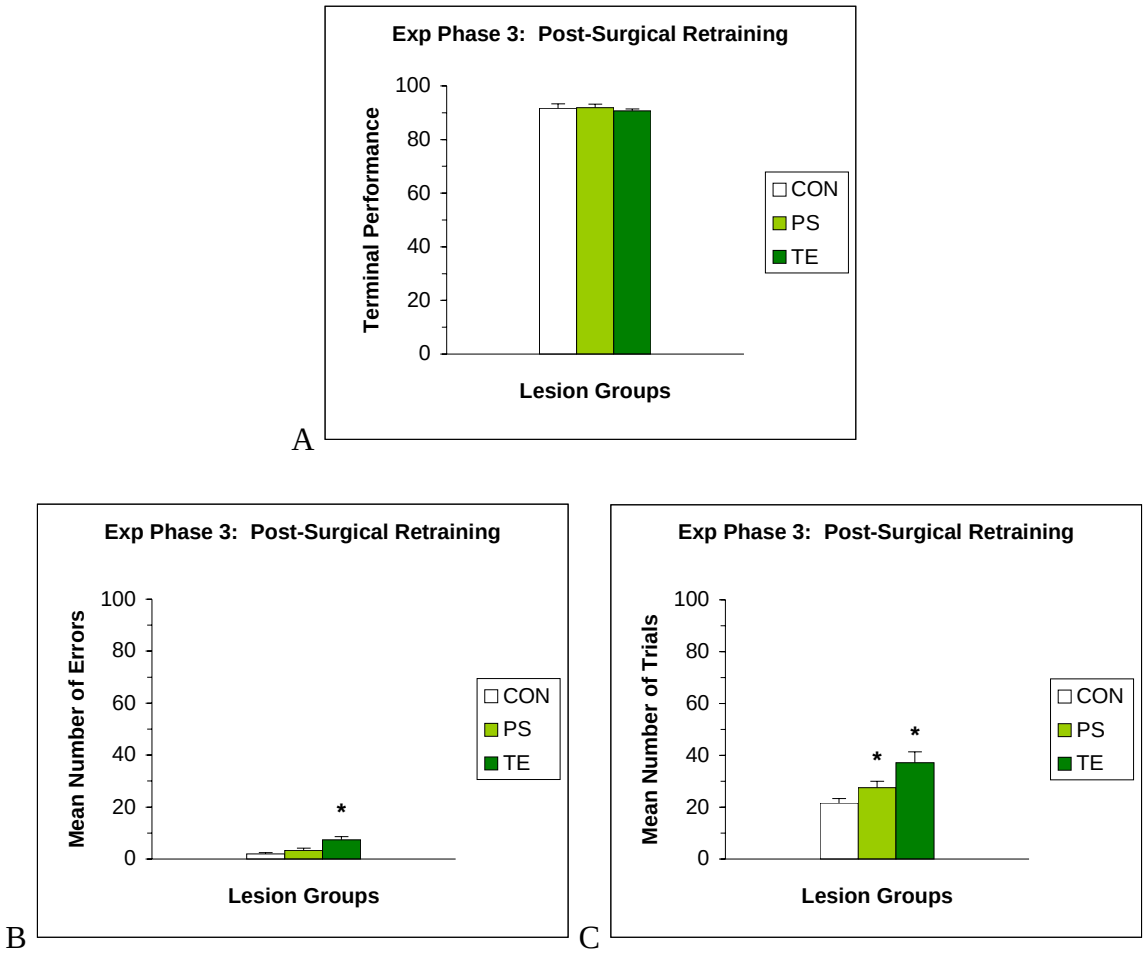


Figure 33. Graphs A, B and C represent behavioral data ($M \pm SEM$) analyzed for Experimental Phase 3, Post-Surgical Retraining for CON (n = 6), PS (n = 8), and TE (n = 7) groups, indicating that subjects re-mastered the original discrimination problem (subsequent to surgeries) in (A) Terminal Performance, ($p >> .05$). The TE group demonstrated a significantly greater (B) Mean Number of Errors Through Criterion than the CON ($p << .001$) and PS ($p << .01$) groups. PS and TE groups demonstrated a significantly greater (C) Mean Number of Trials Through Criterion than the CON group ($p << .05$; $p << .01$), and the TE group demonstrated a significantly greater (C) Mean Number of Trials Through Criterion than the PS group ($p << .05$).

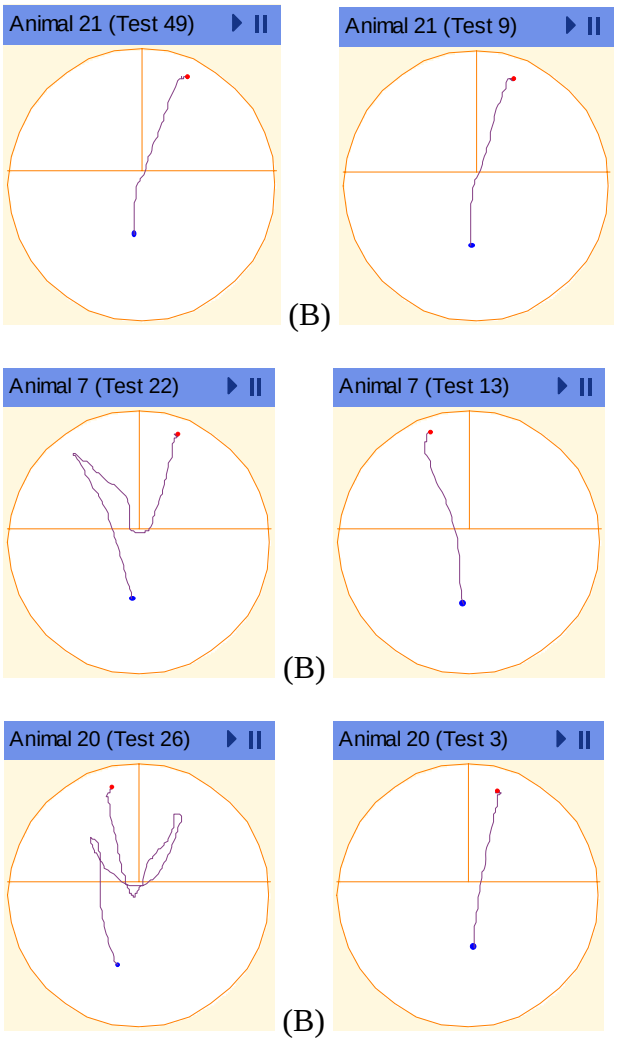


Figure 34. Navigational trajectory and performance within a 60-second trial in (A) Session 1 and in (B) the Final Session through behavioral criterion in Experimental Phase 3, Post-Surgical Retraining by representative CON, PS and TE rats, as depicted in Track-Plot Diagrams by ANY-maze™ Video Tracking System. Diagrams (A) and (B) for a PS and a TE rat illustrate the main finding that, despite initial delays, PS and TE subjects ultimately demonstrated re-mastery of the original problem to a degree equaling that of the CON group and essentially equaling that which was demonstrated in the pre-surgical training and testing phases. (The Test numbers above do not reflect the actual training trial number).

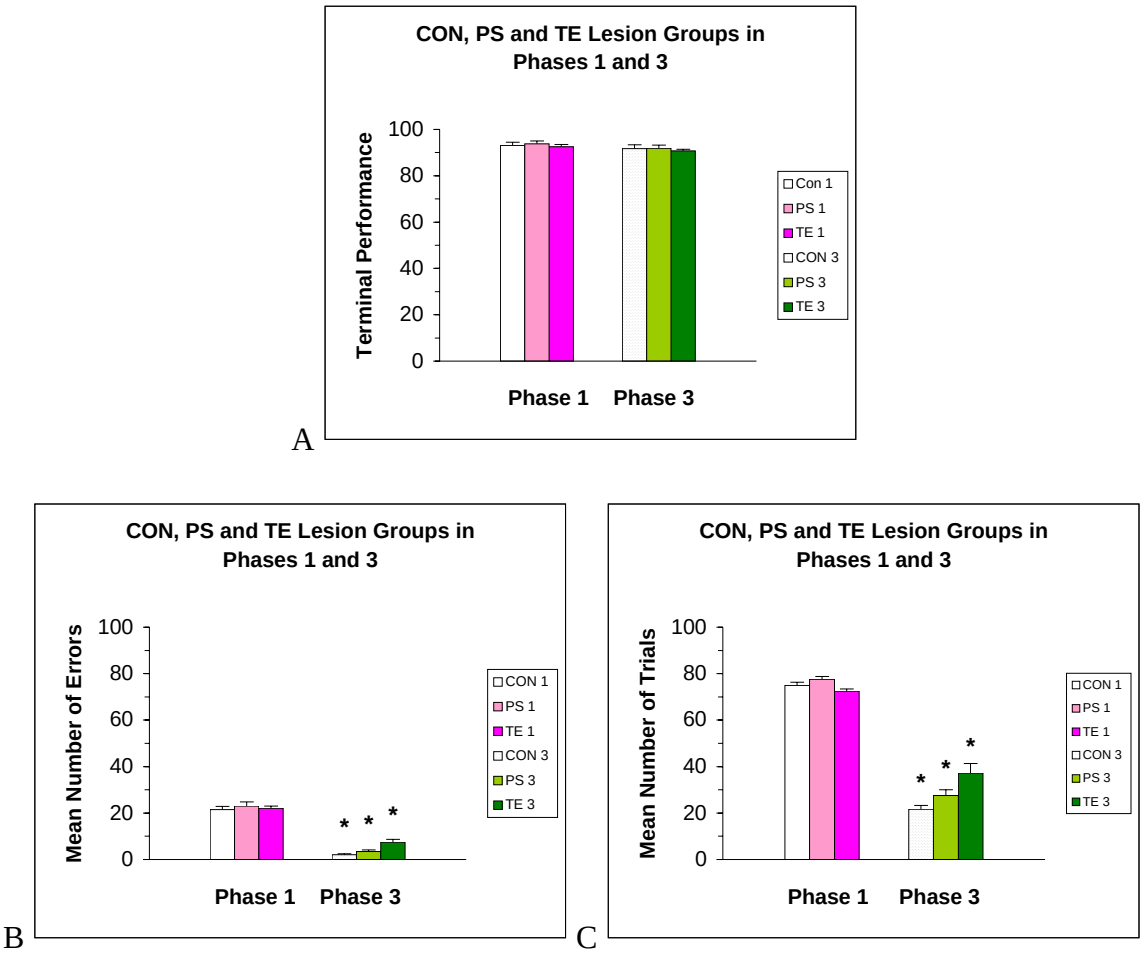


Figure 35. Graphs A, B and C represent behavioral data (*M* ± *SEM*) compared between Experimental Phase 1, Pre-Surgical Training and Experimental Phase 3, Post-Surgical Retraining for CON (*n* = 6), PS (*n* = 8) and TE (*n* = 7) lesion groups. Equivalent (A) Terminal Performance between Phases was observed for each group, (All *p*s >> .05). A statistically significant difference surfaced for each group between Phases on measures of (B) Mean Number of Errors Through Criterion, (All *p*s < .001), and (C) Mean Number of Trials Through Criterion, (All *p*s << .001), with all groups demonstrating significantly greater proficiency in Experimental Phase 3, Post-Surgical Retention than in Experimental Phase 1, Pre-Surgical Training.

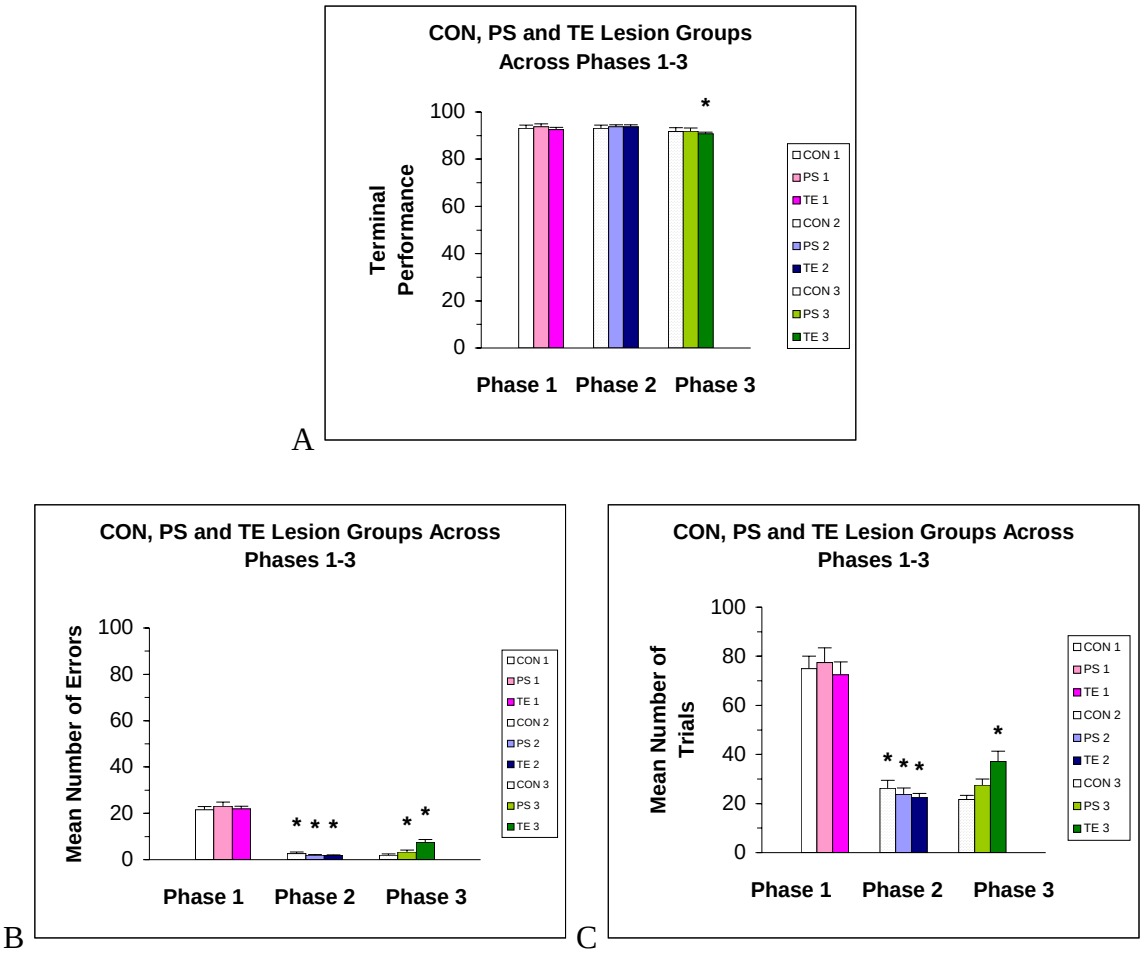


Figure 36. Graphs A, B and C represent data ($M \pm SEM$) compared between Experimental Phase 2, Pre-Surgical Testing and Experimental Phase 3, Post-Surgical Retraining for CON (n = 6), PS (n = 8) and TE (n = 7) lesion groups (with Exp Phase 1 included for reference). Though all three subject groups attained at least a 90% (A) Terminal Performance, the TE group demonstrated a significantly lower score in Phase 3 than in Phase 2 ($p << .01$). In addition, a significantly greater (B) Mean Number of Errors Through Criterion in Phase 3 than in Phase 2 was found for both the PS ($p << .05$) and TE ($p << .001$) groups. The TE group also demonstrated significantly greater (C) Mean Number of Trials Through Criterion in Phase 3 than in Phase 2 ($p << .01$).

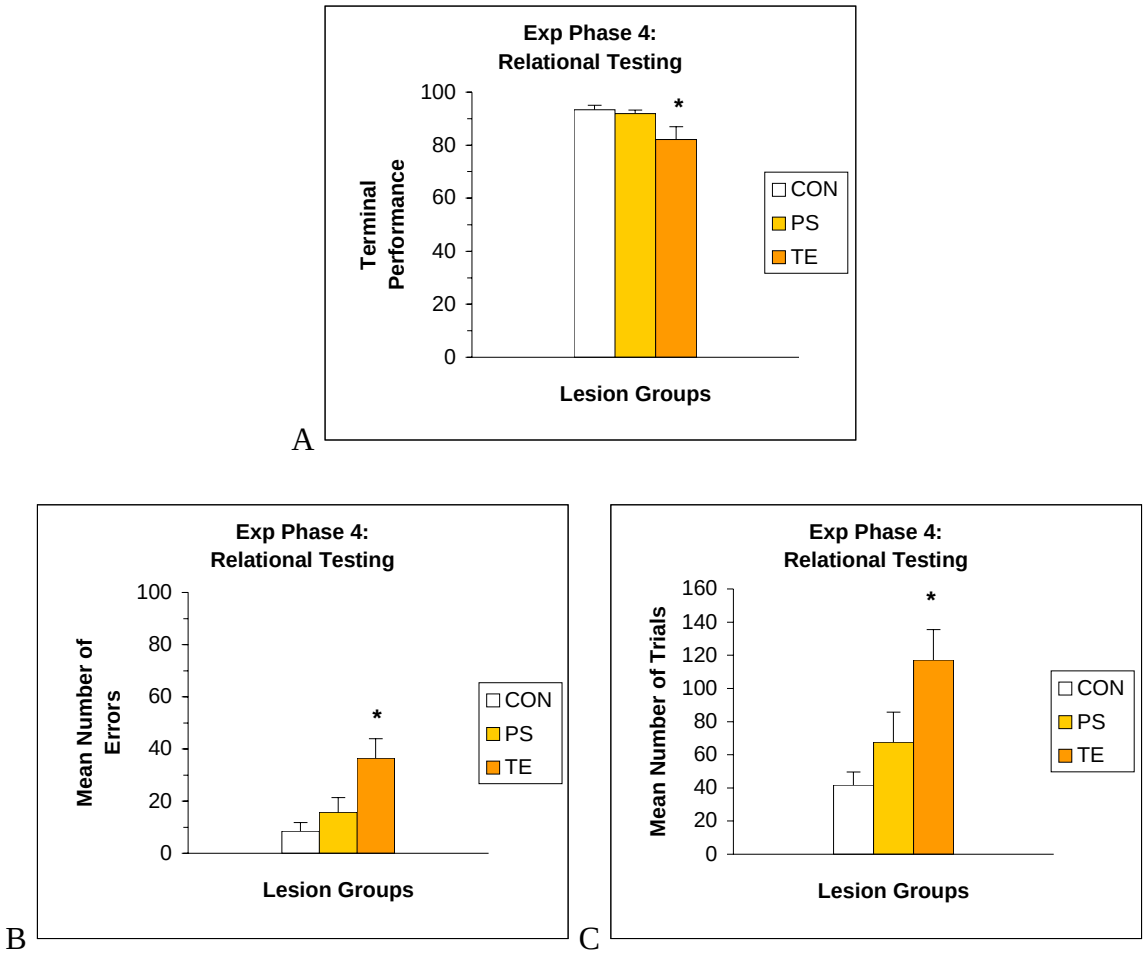


Figure 37. Graphs A, B and C represent behavioral data ($M \pm SEM$) analyzed for Experimental Phase 4, Relational Testing for CON (n = 6), PS (n = 8) and TE (n = 7) groups. As was hypothesized, statistical analyses revealed a significant difference among groups for the behavioral measure of (A) Terminal Performance ($p << .01$), with the TE group failing to attain behavioral criterion and performing with significantly less accuracy than CON and PS groups, (All ps $<< .05$). The TE group demonstrated a significantly greater (B) Mean Number of Errors through Criterion than the CON, ($p << .01$) and PS ($p << .05$) groups, and a significantly greater (C) Mean Number of Trials through Criterion than the CON ($p << .01$) and PS ($p << .05$) groups.

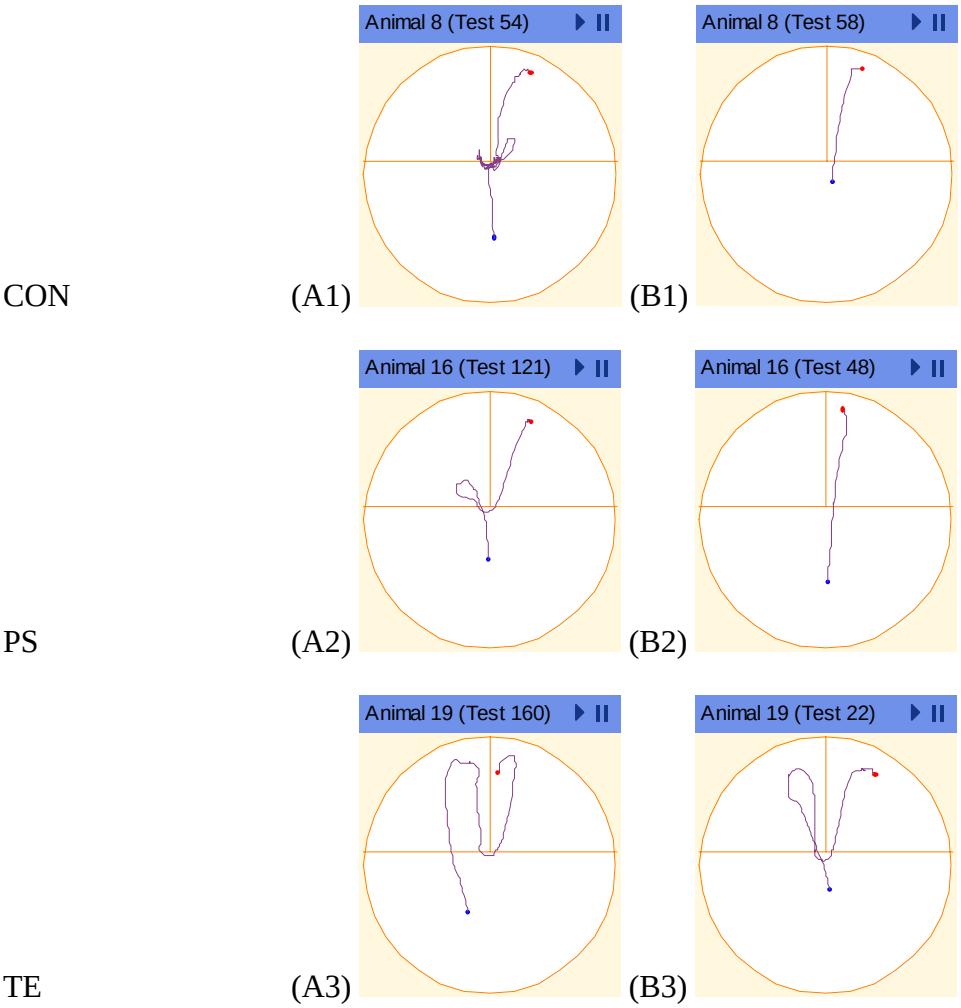
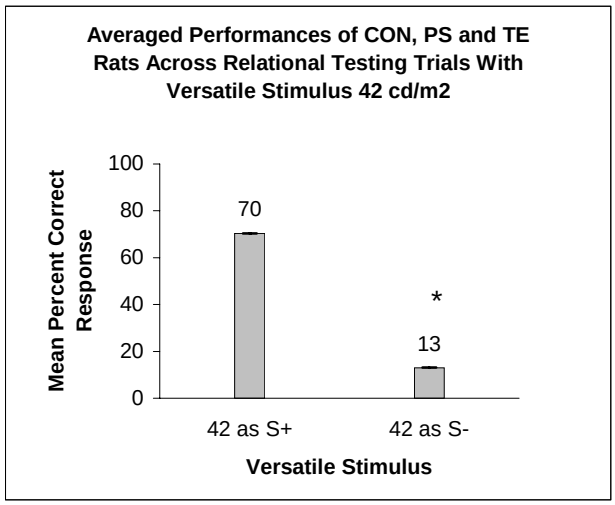
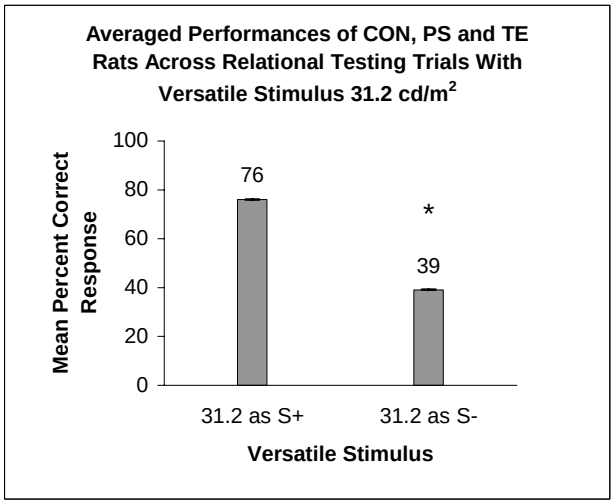


Figure 38. Navigational trajectory and performance within a 60-second trial in (A) Session 1 and in (B) the Final Session in Experimental Phase 4, Relational Testing by representative CON, PS and TE rats, as depicted in Track-Plot Diagrams by ANY-maze™ Video Tracking System. Diagrams (A1 and B1; A2 and B2) illustrate the performance improvement across sessions and illustrate the main finding that CON and PS rats mastered the novel relational task with proficiency. Diagrams (A3 and B3) illustrate the overall lack of improvement in the TE group and illustrate the failed attempt to attain behavioral criterion. (The Test numbers above do not reflect the actual training trial number).



(A)



(B)

Figure 39. Graphs A and B represent behavioral data (*M* ± *SEM*) averaged for CON, PS and TE Rats across trials in Experimental Phase 4, Relational Testing, that included presentation pairs with versatile stimuli (A) 42 cd/m^2 vs. 70.8 and 9.6 vs. 42 and (B) 31.2 cd/m^2 vs. 63.6 and 16.8 vs. 31.2. Of the averaged performances of CON, PS and TE rats, the (A) Mean Percent Correct Response was significantly greater for trials in which 42 cd/m^2 was the S+ choice than for trials in which it was the S- choice, ($p < .001$), and the (B) Mean Percent Correct Response was significantly greater for trials in which 31.2 cd/m^2 was the S+ choice than for trials in which it was the S- choice, ($p < .01$).

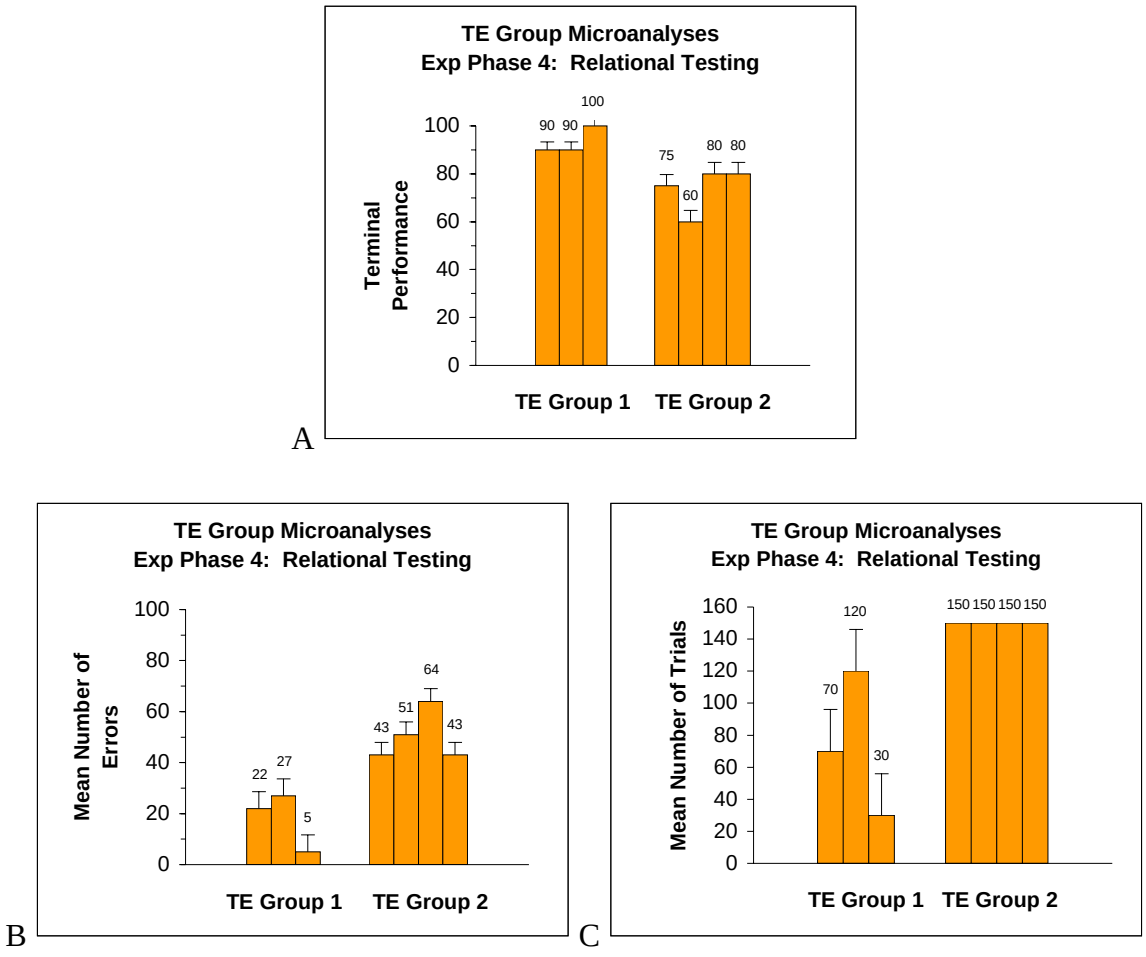


Figure 40. Graphs A, B and C represent behavioral data ($M \pm SEM$) analyzed for rats in TE Groups 1 and 2. Significant differences were found between the groups in Experimental Phase 4, Relational Testing, for (A) Terminal Performance, ($p < .05$), (B) Mean Number of Errors ($p < .01$), and (C) Mean Number of Trials, ($p < .01$). The findings indicated that (A) Terminal Performance was significantly lower for Group 2 than for Group 1. Group 2 also demonstrated a significantly greater (B) Mean Number of Errors than Group 1 and significantly greater (C) Mean Number of Trials than Group 1, in a failed attempt to reach behavioral criterion.

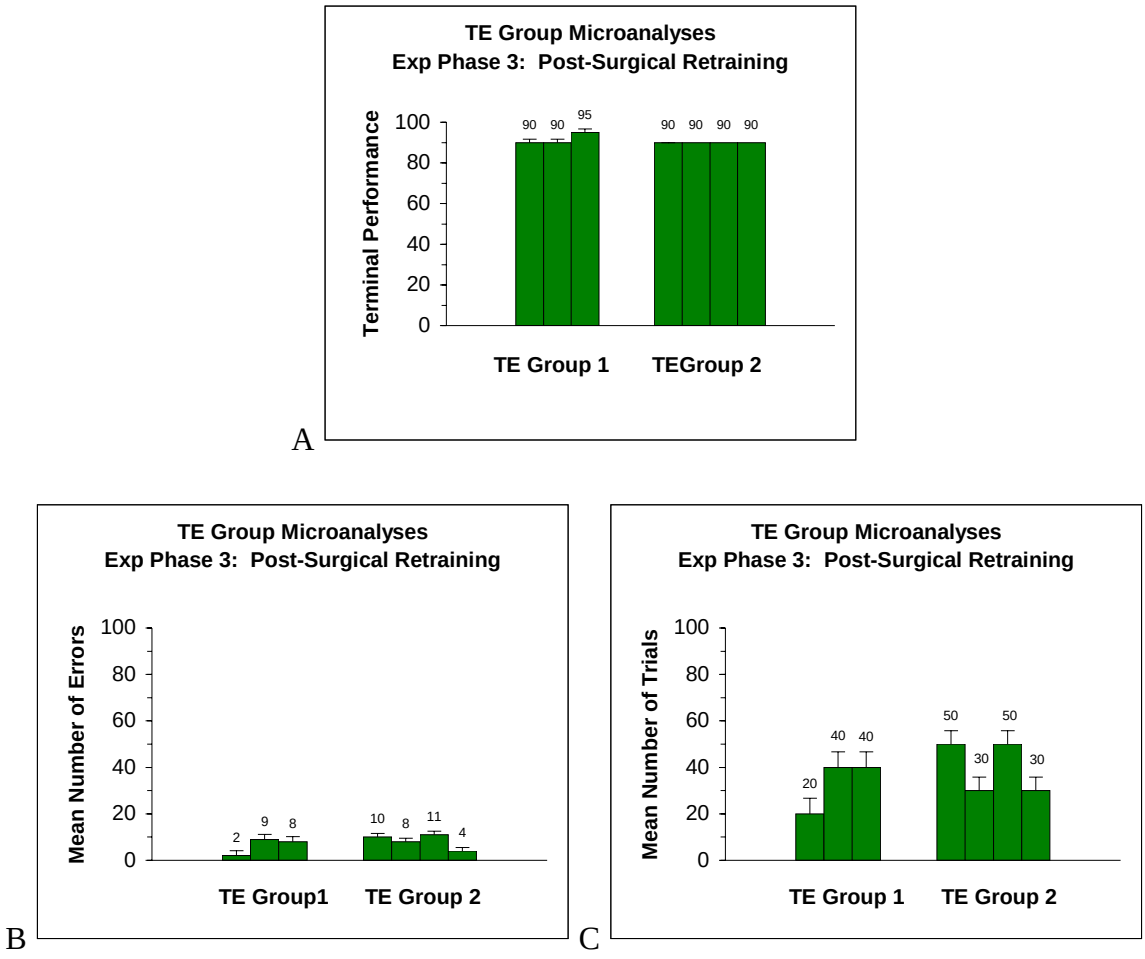
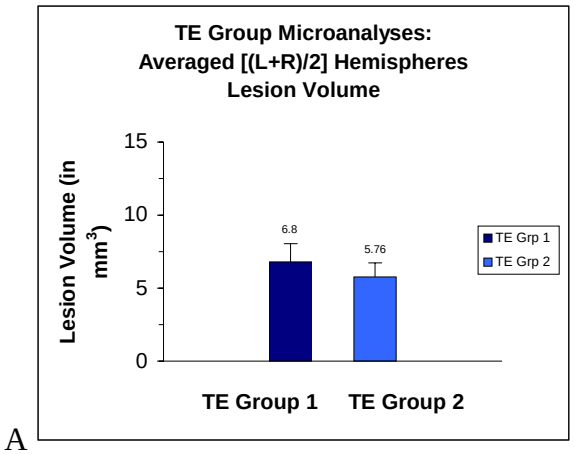
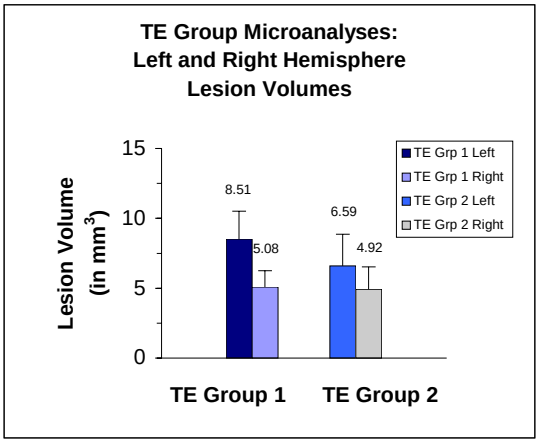


Figure 41. Graphs A, B and C represent behavioral data ($M \pm SEM$) analyzed for rats in TE Groups 1 and 2. No significant difference in performance was found between TE Groups 1 and 2 in Experimental Phase 3, Post-Surgical Retraining, on the variables (A) Terminal Performance, (B) Mean Number of Errors or (C) Mean Number of Trials, (All *p*s > .05).

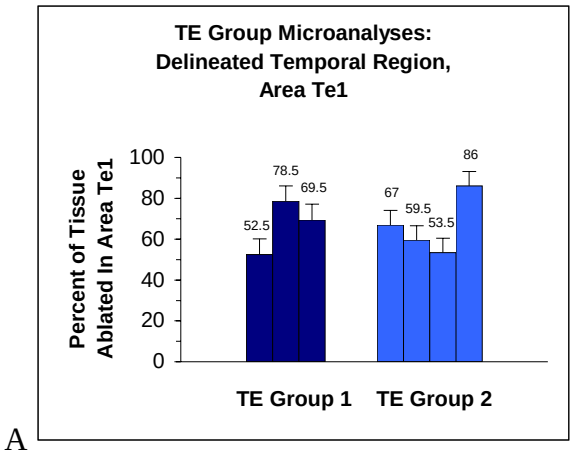


A

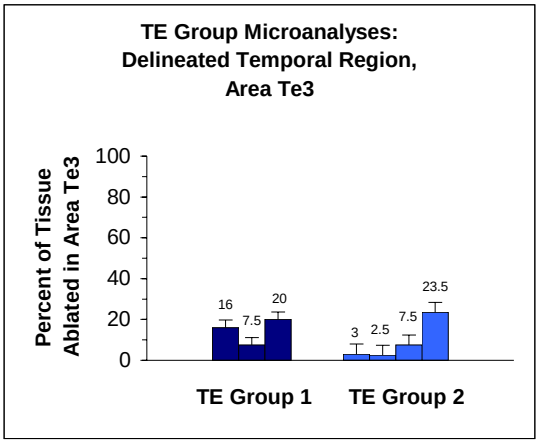


B

Figure 42. Graphs A and B represent morphometric data (*M* ± *SEM*) analyzed for TE Groups 1 and 2. As indicated by one-sample *t*-Test, no difference in (A) Lesion Volume of Averaged [(L+R)/2] Hemispheres between TE Groups 1 and 2 was observed ($p > .05$). Similarly, a two-sample Independent *t*-Test indicated no significant difference between the TE Groups 1 and 2 for (B) Left Hemisphere Lesion Volume ($p > .05$) or for Right Hemisphere Lesion Volume, ($p < .05$).



A



B

Figure 43. Graphs A and B represent morphological data ($M \pm SEM$) analyzed for TE Groups 1 and 2. As indicated by two-sample *t*-Tests, no difference between TE Groups 1 and 2 was observed for the (A) Percent of Tissue Ablated in Te1 ($p > .05$) or for the (B) Percent of Tissue Ablated in Te3, ($p > .05$).

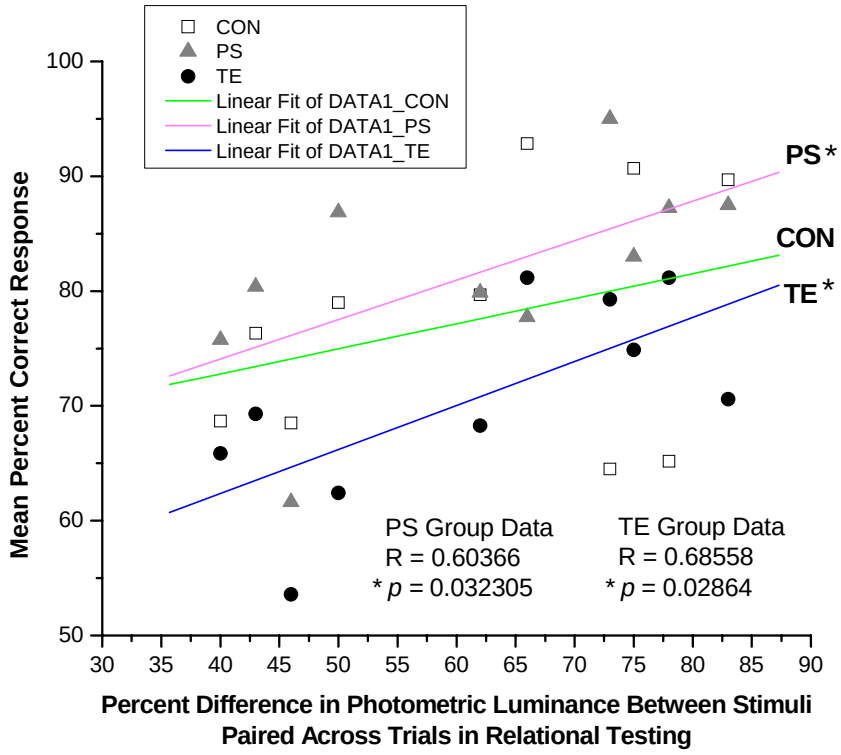


Figure 44. The correlation between (X) Percent Difference in Photometric Luminance Between Paired Stimuli Across Trials in Experimental Phase 4, Relational Testing and (Y) Mean Percent Correct Response. Linear regression analyses revealed a statistically significant correlation between the two variables for the PS ($p << .05$) and TE ($p << .05$) groups, indicating that PS and TE group performances were, on average, higher for presentations of paired stimuli with a greater percent luminance difference between them (e.g., 83%) than for presentations of paired stimuli with a smaller percent luminance difference between them (e.g., 40%). The correlation data between the two variables for the CON group was non-significant ($p >> .05$).

CHAPTER 4

DISCUSSION

Review of the Rationale

Research involving the posterior neocortex of the rat has examined the involvement of exclusive neocortical regions in specific cognitive and behavioral functions (Boyd & Thomas, 1977; Dean, 1981; Kolb, 1990; Kolb et al., 1994, Kolb & Walkey, 1987; McDaniel et al., 1995; McDaniel & Thomas, 1978; McDaniel & Wall, 1988; Tees, 1999; Thomas & Weir, 1975). Findings from anatomical (McDaniel et al., 1978), behavioral (Dean, 1981; Dean, 1990; Kolb et al., 1994; McDaniel & Thomas, 1978; McDaniel & Wall, 1988; Myhrer, 2000; Thomas & Weir, 1975), and neurophysiological (Zhu et al., 1995; Zhu et al., 1996) studies of rats have revealed that the organization of the posterior neocortex resembles that which has been described in human (Chiaravalloti & Glosser, 2004; Damasio et al., 1989; Gaddes & Edgell, 1994; Grady et al., 1992; Haxby et al., 1991; Hermann et al., 1993; Horwitz et al., 1992; Nieuwenhys et al., 1988; Newcombe et al., 1987; Ungerleider et al., 1998; Kolb, 1990) and non-human primates (Baizer et al., 1991; Goodale & Milner, 1992; Macko et al., 1982; Maunsell, 1992; Mishkin et al., 1983; Morel & Bullier, 1990; Ungerleider & Mishkin, 1982).

Clinical neuropsychological observations, behavioral investigations, and neuroimaging studies of posterior cortex in humans (Adams et al., 1997; Chan et al., 2004; Chiaravalloti & Glosser, 2004; Creutzfeldt, 1995; Cummings & Trimble, 1995;

Grady et al., 1992; Haxby et al., 1991; Huxlin & Merigan, 1998; Ishai et al., 2002; Kawshima et al., 1998; Kolb, 1990; Kolb et al., 1994; Kolb & Whishaw, 1996; Kolb & Whishaw, 2003; Lindsley & Holmes, 1984; McCarthy & Warrington, 1990; Milner, 1968; Milner, 1970; Nakamaura et al., 2000; Nolte, 1993; O'Craven & Kanwisher, 2000; Ranganath, 2006; Sams et al., 1997; Srebo, 1985; Wilkins & Mosocovitch, 1978; Wright et al., 2003) and experimental data on non-human primates (Baizer et al., 1991; Baylis & Rolls, 1987; Buckley et al., 1997; Buffalo et al., 1999; Buffalo et al., 2000; Freedman et al., 2003; Goodale & Milner, 1992; Kreiman et al., 2006; Logothetis et al., 1995; Macko et al., 1982; Maunsell, 1992; Mishkin et al., 1983; Morel & Bullier, 1990; Perrett et al., 1984; Perrett et al., 1990; Ridley et al., 2001; Sobotka & Ringo, 1993; Ungerleider & Mishkin, 1982; Weller et al., 2006; Wilson & DeBauche, 1981) provide convincing evidence that temporal regions of the posterior neocortex subserve functions of visual object recognition, visual memory, and visual analysis.

Investigations into the temporal cortex and visual analysis in the rat have yielded results that are markedly similar to those reported in humans and non-human primates. Experiments using electrophysiological, neurotoxic infusion, and protein product marking procedures support conclusions from neurobehavioral studies in rats that temporal areas underlie visual object recognition, complex pattern discrimination (McDonald & Mascagni, 1996; Tees, 1999; Wortwein et al., 1994) and visual memory (Wan et al., 1999; Zhu et al., 1995; Zhu et al., 1996). A number of these studies have demonstrated differential and significant neuronal activation in the rat cortex produced by novel versus familiar individual visual stimuli. Others have revealed evidence of impeded visual memory following infusion of neurotoxins to temporal areas (Myhrer &

Anderson, 2001). Taken together, these findings demonstrate that the rat appears to be a useful model for the experimental study of the role of the posterior cortex in higher visual processing.

Focus of the Present Study

Research concerning posterior neocortex and visual analysis indicates that temporal regions are also involved in tasks requiring categorization of visual information and visual relational learning. Such investigations have demonstrated that the ability to categorize objects on the basis of visual cues or to perform relational discriminations between visual stimuli is impaired in humans who have sustained temporal lobe damage (Chan et al., 2004; Kolb & Whishaw, 1996) and in monkeys with surgical IT lesions (Buckley et al., 1997; Wilson & DeBauche, 1981). In a review of the literature on this topic, it appears that only a few neurobehavioral experiments have examined the involvement of area TE specifically in functions of visual relational learning in the rat (Maki et al., 2001; Williams & McDaniel, 1999), and indicate that further study is needed.

The present experiment was conducted to determine whether TE lesions in the rat interfere with performance on behavioral tasks that require the ability to generalize a previously learned discrimination to novel problems involving relational judgments of two stimuli. In the present case, the discrimination was based on approaching one (black) of two visual targets (black and white) that consistently guaranteed subsequent escape from the water. In the initial training and testing phases, it was anticipated that all animals would demonstrate acquisition and retention of the task. In the intervention phase, after being prepared with either bilateral control (CON), partial striate (PS) or

temporal (TE) cortex lesions, rats were expected to demonstrate re-mastery of the original training. In the testing and outcome phase, it was hypothesized that rats with TE lesions would display significant deficits in the ability to generalize the original discrimination problem to novel, presumably more demanding visual discriminations. This final task was considered to be more demanding than the initial discrimination problems because the luminance difference between each set of paired stimuli, while still easily visible, was varied along a continuum ranging from considerably similar (e.g., 40% luminance difference) stimulus combinations to clearly dissimilar (83% luminance difference) stimulus combinations under conditions designed to minimize or prevent the use of absolute cues.

Experimental Phases 1 and 2: Pre-Surgical Training and Testing

In the preoperative phase, rats were trained to solve a simple black-white discrimination problem based on the luminance (6.48 cd/m^2 vs. 74.4 cd/m^2) of two distinct, constant visual stimuli. As was hypothesized, all rats mastered the task with proficiency, demonstrating terminal performance accuracies ranging between 93% and 94%. Results in the neurobehavioral literature, similar to those described here, concerning general visual discriminative abilities of normal, cortically intact rats have been documented and reviewed extensively (Dean, 1990; Kolb et al., 1994, Lashley, 1931). Based on such findings and reviews, the successful performance by rats on this task was fully expected. Following an extended interval, savings for the problem was assessed. As was projected, all animals demonstrated excellent retention of the previously mastered problem. This finding is supported by data indicating that group performances on pre-surgical testing (retention) behavioral measures (i.e., mean number

of errors [*M*s = 2.63, 1.88 and 1.75, respectively] and mean number of trials through criterion [*M*s = 26.25, 23.75 and 22.5, respectively]) were significantly superior to those [Error *M*s = 21.5, 23 and 22, respectively; Trial *M*s = 75, 77.5 and 72.5, respectively] in pre-surgical training. Furthermore, group terminal performance accuracies in pre-surgical testing (*M*s = 93% to 94%) were at least equal to those in pre-surgical training (*M*s = 93% to 94%). Thus, the results from preoperative training and testing appear to be consistent with well-documented findings concerning general visual discriminative abilities in rodents, revealing that the cortically intact rats were capable of performing a simple black-white discrimination problem based on the luminance of two, constant visual cues.

Experimental Phase 3: Post-Surgical Retraining

Following bilateral CON, PS or TE surgical lesions and a standard post-surgical recovery period, animals were retrained on the original discrimination task. As was hypothesized, all rats re-mastered the problem, with group terminal performance accuracies each exceeding the 90% behavioral criterion requirement (*M*s = 92%, 92% and 91%, respectively). Closer assessment of these findings revealed that although the PS group attained behavioral criterion and demonstrated a terminal performance accuracy (*M* = 92%) essentially equaling that of the CON (*M* = 92%) and TE groups (*M* = 91%), the PS group required a significantly greater mean number of trials through criterion (*M* = 27.5) than the CON group (*M* = 21.67). These results were anticipated in light of previous reports in the rodent research literature concerning the consequences of partial striate and total striate lesions. Specifically, as has been reviewed and demonstrated experimentally (Goldstein & Oakley, 1987, Hughes, 1977; McDaniel & Noble, 1984),

rats with partial striate lesions are reported to perform well on tests of visual discrimination and, even in cases of total striate ablations, eventually solve visual discriminations. Dean (1990) concluded that, following an initial decline in visual acuity and central vision, rodents ultimately compensate for the effects of striate lesions via self-produced head movements and cue scanning that are intended to shift retinal images onto the fovea in visual tasks involving navigation. Clearly, the findings here are consistent with previous data concerning visual discriminative abilities of partial striate and de-striate rats.

Further appraisal of post-operative retraining results indicated that, while the TE group demonstrated a terminal performance accuracy (M = 91%) that exceeded the behavioral criterion requirement and essentially equaled that of the CON (M = 92%) and PS (M = 92%) groups, it also demonstrated a significantly greater mean number of errors (M = 7.43) and mean number of trials (M = 37.14) through criterion than the CON (Error M = 2, Trial M = 21.67) and PS (Error M = 3.38, Trial M = 27.5) groups. However, these findings were anticipated, as they are consistent with previous neurobehavioral studies reporting that damage to TE in rats may produce a generalized disruptive effect on visual memory (Davis & McDaniel, 1993; Kolb et al., 1994; Myhrer, 1996), specifically interfering with performance in retraining of preoperatively acquired visual discrimination tasks (Meyer & Meyer, 1977; Myhrer, 1991; Myhrer, 1992; Myhrer, 2000). Also, the findings described here are reconcilable with those from the primate literature concerning monkeys with IT lesions and performance of pre-operatively learned visual discrimination tasks. From these investigations it has been shown that, due to retroactive visual memory impairments, monkeys with surgical IT lesions are initially

delayed in re-mastering visual discriminations that were acquired prior to brain damage (Dean & Cowey, 1977; Dean & Weiskrantz, 1974). The results here illustrate that, despite demonstrating a significantly greater mean number of errors and trials through criterion in performing the postoperative discrimination compared to the other two groups, the TE group ultimately re-mastered the problem, with a terminal performance (91%) exceeding the established behavioral criterion requirement of 90% and essentially equaling that of the CON (92%) and PS (92%) groups. Collectively, these data indicate that rats with CON, PS and TE lesions were capable of re-mastering a preoperatively learned simple black-white discrimination based on the luminance of two, constant visual cues.

Experimental Phase 4: Relational Testing

The final testing phase was conducted to examine whether the TE lesion group would demonstrate deficits in the ability to generalize the previously mastered discrimination to novel, presumably more demanding, discrimination problems based solely on the relative luminance of paired, intermediate (gray) stimuli (i.e., 6.48 vs. 38.4, 31.2 vs. 63.6, 20.4 vs. 74.4, 42 vs. 70.8, 9.6 vs. 42, 16.8 vs. 31.2, 13.2 vs. 52.8, 24 vs. 42, 16.8 vs. 49.2, and 24 vs. 63.6 cd/m^2). On the basis of previously reported clinical observations and primate research describing impairments in humans with temporal lobe damage and behavioral deficits in monkeys with surgical IT lesions on tasks of visual categorical or relational learning, it was hypothesized that rats with TE lesions would demonstrate significant deficits in performance on relational testing problems. As was predicted, the CON and PS groups exhibited mastery of the task, each demonstrating excellent terminal performance accuracy (M = 93% and M = 92%, respectively). No

significant differences between the CON and PS groups were observed across any behavioral measures in the testing phase. In contrast, the TE group failed to attain behavioral criterion, and demonstrated a significantly greater mean number of errors (*M* = 36.43) and a significantly greater mean number of trials (*M* = 117.14) than the CON (Error *M* = 8.5; Trial *M* = 41.67) and PS (Error *M* = 15.75; Trial *M* = 67.5) groups, with a terminal performance (*M* = 82%) that was significantly inferior to that of the CON (*M* = 93%) and PS (*M* = 92%) groups. That the TE group showed significant performance deficits on all behavioral measures compared to CON and PS groups is consistent with findings from previous experiments comparing the performances of monkeys with lesions to lateral striate (LS) or to IT cortex (Wilson & DeBauche, 1981). The data here suggest that the temporal region in the rat is involved in the processing of relationships between visual stimuli, and would imply that some cognitive and behavioral functions of the ventral occipitotemporal pathway, described in primates, generalize to rodents.

Such a conclusion, however, must be considered in the light of several caveats. Although the terminal performance of the TE group was significantly inferior to that of the CON and PS groups in relational testing, it was, nonetheless, significantly higher (82%) than would be expected by chance (50%). A more robust deficit than that demonstrated here in rats was observed in IT-lesioned monkeys in a similar study investigating visual categorical and relational learning (Wilson & DeBauche, 1981).

Additionally, microanalysis revealed significant variability in behavioral performance among subjects in the TE group. That is, although the majority of TE subjects (*n* = 4) failed to attain behavioral criterion in relational testing (Group 2), three TE subjects did attain behavioral criterion (Group 1). Terminal performance averages of

Group 1 (93%) and Group 2 (74%) differed significantly from one another, as did the corresponding mean number of errors (*M*s = 18 and 50, respectively) and mean number of trials (*M*s = 73 and 150, respectively). That Group 2 averaged a terminal performance of 74% indicates that even rats with the most pronounced behavioral deficits performed at a level above 50%. Although significant variability in morphometric and morphological variables existed among TE rats, it does not account for behavioral performance variability among subjects in the TE group or between TE Groups 1 and 2 in relational testing, as no statistically significant correlations between histological variables and behavioral performance emerged. For example, microanalysis of TE Groups 1 and 2 clearly showed that, while a number of rats in Group 2 had a significantly greater percent of tissue destroyed in Area Te1 than some rats in Group 1, two rats in Group 1 had significantly greater percent of tissue ablated in Area Te1 compared to three of the four rats in TE Group 2. Likewise, while one rat in Group 2 had a significantly greater percent of tissue destroyed in Area Te3 compared to rats in Group 1, three animals in Group 1 had significantly greater percent of tissue ablated in Area Te3 compared to three of the four rats in Group 2.

In addition, while variability in behavioral performance within the TE group was observed in relational testing, it was not observed in previous training and testing phases, which suggests that the significant deficits observed in TE rats in relational testing were not a result of gross functional impairments or general traumatic effects from lesions (such impairments would have emerged in the post-surgical retraining phase). Furthermore, the finding that rats with extensive striate lesions were able to overcome initial impairments in visual ability and ultimately master retraining and relational

learning tasks with accuracies of 92% indicates that the significant decline in performance observed in the TE rats in the relational testing phase cannot be attributed to generalized visual impairments, to random deficits in visual acuity, nor to cortical trauma *per se*.

Finally, the finding of a significant correlation between the percent difference in luminance between paired stimuli and mean percent correct response in the relational testing phase was anticipated. It was hypothesized that paired stimuli with a smaller percent difference in luminance between them (e.g., 40%) might pose more of a challenge than paired stimuli with a greater percent difference in luminance between them (e.g., 83%). Though the findings were non-significant for the CON rats, the performances of the PS and TE groups on problems with more challenging combinations of stimuli is consistent with that which would be expected to accompany the respective lesions. That is, although the PS rats were able to rapidly overcome the global effects of extensive striate lesions and subsequently master tasks in post-operative retraining and in relational testing through compensatory behaviors, it was likely the case that the discriminative abilities of the extensively lesioned PS rats were not as refined as those of the CON rats. Thus, the PS group, on average, demonstrated inferior performances on some stimulus pairs compared to others. However, it is clear from the data that partial striate lesions did not affect the performance of these rats to a degree that it precluded mastery of the relational learning task or the post-operative retraining problem, as the PS group demonstrated excellent performances (92%) in post-operative training and relational testing phases. Likewise, the data indicated that the TE rats performed with greater accuracy on problems with larger percent differences in luminance between

stimuli than on problems with smaller percent differences in luminance between stimuli. Unlike that of the PS group, the TE group performance cannot be attributed to residual deficits in visual acuity. As reviewed by Kolb et al., 1994 (p. 677-678), it has been demonstrated that rats with temporal cortex lesions have greater difficulty processing details of visual stimuli that demand close attention than those that require minimal attention. It is reasonable to conclude that the performance problems, on average, with smaller luminance differences between stimuli demanded more attention to detail and were, thus, more challenging to TE rats than problems with stimuli having greater percent differences in luminance between them. Despite this correlation, however, it is apparent that the inferior performance on tasks with the less discriminable stimuli cannot account for the overall failure to meet behavioral criterion on the relational task by the TE group, as a similar overall failure by the PS group would have emerged in relational testing, as well. Clearly, this was not the case.

General Conclusions

The behavioral data from the present study indicate that rats generalized a previously learned simple visual discrimination to novel, relational discrimination conditions. As was shown here, control and partial striate lesioned rats demonstrated terminal performance accuracies in the relational testing phase on tasks involving the discrimination of novel stimuli that well exceeded a behavioral criterion requirement of 90%, and transferred the initial discrimination to novel, even more challenging, problems with relative ease. This latter point is evidenced by the observation that the CON and PS groups demonstrated a lower mean number errors through criterion and a lower mean number of trials through criterion in relational testing than in pre-surgical training.

Additionally, the CON group demonstrated terminal performance accuracy in relational testing (*M* = 93%) that was even higher than that in post-surgical retraining (*M* = 92%). Similarly, the terminal performance by PS lesioned rats in the relational testing phase (92%) was as high as that demonstrated in post-surgical retraining (92%).

This general ability of rats to transfer from a previously acquired simple visual discrimination task to subsequent, novel discrimination problems was also demonstrated in one of two experiments in an earlier, related study (Williams & McDaniel, 1999). Across a series of initial, graduated transfer trials (introduced prior to problems with the most demanding paired stimuli), rats successfully transferred from a post-operatively acquired simple visual discrimination (i.e., two, black, circular images differing in diameter by 14 cm; 17 cm versus 3 cm) to subsequent discrimination problems (i.e., where the difference in size between compared stimuli was reduced gradually; 15 cm versus 5 cm; 13 cm versus 7 cm) that required application of a previously learned discrimination to relational judgments between novel stimuli (p. 347-348). In a review of the findings, however, it was determined that the successful performance by rats may have been attributable to several factors, such as a training experience that heavily facilitated the use of the relational rule or to a design in which the subsequent, graduated stimuli differed from the original cues by only a small amount (p. 348). It was also possible that the relational judgments were based on more than one inherent characteristic of the visual stimuli (e.g., the cues differed with respect to both size and luminance). With this latter issue in mind, the present study aimed to isolate one stimulus dimension (i.e., luminance), such that mastering the relational testing task depended purely on the application of the previously acquired discrimination to novel relational problems with

stimuli differing only by one feature (i.e., luminance). Using this methodology, the present study produced findings indicating that the transfer from a simple visual discrimination task to novel, more demanding discriminations that required the use of relational judgments between stimuli was successfully performed by CON and PS rats, but was impaired in the majority of rats with lesions to area TE. These data are consistent with reports of subsequent impairments in visual processing in humans with temporal lobe damage and monkeys with IT lesions (Buckley et al., 1997; Freedman et al., 2003). Taken together, these data indicate that the temporal region in the rat is involved in the processing of relationships between visual stimuli.

Ultimately, the extent of this involvement is open to question. Although significant impairments were observed for the TE lesioned group, the ability to generalize the initial discrimination to novel, relational discrimination problems was not completely lost in all TE rats. Of course, some variability among subjects is expected based on the inherent nature of behavioral tasks, as well as on the small size of the rodent cortex and the limits of surgical precision that typically preclude placement of mutually exclusive lesions. Perhaps it was the case that some retained ability (i.e., 82% or 74% terminal performance accuracy, as opposed to a 50% chance level performance) was due to mediation of other neural regions, wherein TE is a part of a larger cortical network subserving functions of visual processing. This possibility was proposed in earlier investigations (Maki et al., 2001; Williams & McDaniel, 1999), wherein it was suggested that one or more of the various retinotopically organized visual cortical regions adjacent to area TE, such as distinct subterritories of the lateral peristriate cortex, might be involved in mediating such functions. It might be useful to examine whether lesions in

these contiguous distinct subregions, in conjunction with area TE, would abolish visual relational learning entirely. Other meaningful directions for study might also focus on whether the behavioral deficits in TE lesioned rats would improve over the course of time with extensive training or if there are specific behavioral methods useful in restoring function. Obviously, further research is needed to address relevant questions concerning this topic that are undoubtedly important to the goal of clarifying the neural mechanisms involved in higher visual processing in the rat.

Findings from the neuroscientific research demonstrate a reasonable degree of neuroanatomical and behavioral similarity between rodents and primates. Given the extent of species similarity and the significant advantages of using rodents in laboratory studies, it has been suggested (Kolb, 1990) that the rat is a valuable alternative to the primate model in preliminary investigations of cortical function. Studies using the rodent model support the postulation that dual visual processing pathways, described extensively in primates, also exist in the rat. An anterodorsal pathway is critical to the processing of visuospatial stimuli and navigation based on visual cues and a rostroventral projection is purportedly specialized for visual object recognition, visual processing, and visual memory. The findings from this study suggest an involvement of temporal cortex in visual relational learning and are consistent with investigations in primates that suggest the presence of a ventral occipitotemporal pathway subserving functions of higher visual processing. The extent of this involvement in the rat remains to be determined.

REFERENCES

Adams, R. D., Victor, M., & Ropper, A. H. (1997). *Principles of neurology* (6th ed.). New York: McGraw-Hill.

American Psychological Association. (2002). *Publication manual of the American Psychological Association* (5th ed.). Washington, DC.

Baizer, J. S., Ungerleider, L. G., Desimone, R. (1991). Organization of visual inputs to the inferior temporal and posterior parietal cortex in macaques. *The Journal of Neuroscience, 11(1),* 168-190.

Baylis, G. C., & Rolls, E. T. (1987). Responses of neurons in the inferior temporal cortex in short term and serial recognition memory tasks. *Experimental Brain Research, 65,* 614-622.

Birch, D. & Jacobs, G. H. (1975). Behavioral measurements of rat spectral sensitivity. *Vision Research, 15(6),* 687-691.

Bogartz, R. S. (1965). The criterion method: Some analyses and remarks. *Psychological Bulletin, 64(1),* 1-14.

Boyd, M. G., & Thomas, R. K. (1977). The effects of posterior association cortex lesions in rats: Mazes, pattern discrimination, and reversal learning. *Physiological Psychology, 5,* 455-461.

Buckley, M. J., Gaffan, D., Murray, E. A. (1997). Functional double dissociation between two inferior temporal cortical areas: Perirhinal cortex versus middle temporal gyrus. *Journal of Neurophysiology, 77(2),* 587-598.

Buffalo, E. A., Ramus, S. J., Clark, R. E., Teng, E., Squire, L. R., Zola, S. M. (1999). Dissociation between the effects of damage to perirhinal cortex and area TE. *Learning and Memory, 6(6),* 572-599.

Buffalo, E. A., Ramus, S. J., Squire, L. R., & Zola, S. M. (2000). Perception and recognition memory in monkeys following lesions of area TE and perirhinal cortex. *Learning and Memory, 7(6),* 375-382.

Burcham, K. J., Corwin, J. V., Stoll, M. L., & Reep, R. L. (1997). Disconnection of medial agranular and posterior parietal cortex produces multimodal neglect in rats. *Behavioural Brain Research, 86(1),* 41-47.

Chan, A. S. Sze, S. L. M., Cheung, M. (2004). Neuroanatomical basis in the temporal lobes for processing living things. *Neuropsychology, 18(4),* 700-709.

Chiaravalloti, N. D., & Glosser, G. (2004). Memory for faces dissociates from memory for location following anterior temporal lobectomy. *Brain and Cognition, 54(1),* 35-42.

Creutzfeldt, O. D. (1995). The neocortical temporal association cortex. In *Cortex cerebri: Performance, structural and functional organization of the cortex* (pp. 397-420). Oxford: Oxford University Press.

Cummings, J. L., & Trimble, M. R. (1995). *Neuropsychiatry and behavioral neurology.* Washington, DC: American Psychiatric Press.

Damasio, A. R., Tranel, D., & Damasio, H. (1989). Disorders of visual recognition. In H. Goodglass & A. R. Damasio (Eds.), *Handbook of neuropsychology* (pp. 317-332). Amsterdam: Elsevier.

Davis, B. K., & McDaniel. W. F. (1993). Visual memory and visual spatial functions in the rat following parietal and temporal cortex injuries. *Physiology and Behavior, 53,* 145-151.

Dean, P. (1978). Visual acuity in hooded rats: Effects of superior collicular or posterior neocortical lesions. *Brain Research, 156(1),* 17-31.

Dean, P. (1981). Grating detection and visual acuity after lesions of striate cortex in hooded rats. *Experimental Brain Research, 43,* 145-153.

Dean, P. (1981). Visual pathways and visual acuity in hooded rats. *Behavioural Brain Research, 3,* 239-271.

Dean, P. (1990). Sensory cortex: Visual perceptual functions. In B. Kolb & R.C. Tees (Eds.), *The cerebral cortex of the rat* (pp. 275-307). Cambridge, MA: The MIT Press.

Dean, P., & Cowey, A. (1977). Inferotemporal lesions and memory for pattern discriminations after visual interference. *Neuropsychologia, 15(1),* 93-98.

Dean, P., & Weiskrantz, L. (1974). Loss of preoperative habits in rhesus monkeys with inferotemporal lesions: Recognition failure or relearning deficit? *Neuropsychologia, 12,* 299-311.

DeCoteau, W. E., and Kesner, R. P. (1998). Effects of hippocampal and parietal cortex lesions on the processing of multiple-object scenes. *Behavioral Neuroscience, 112(1),* 68-82.

Fellows, B. J. (1967). Chance stimulus sequences for discrimination tasks. *Psychological Bulletin, 67,* 87-92.

Feinberg, T. E., & Farah, M. J. (1997). Amnesia: Neuroanatomic and clinical aspects. In *Behavioral neurology and neuropsychology* (pp. 449-461). McGraw Hill: New York.

Freedman, D. J., Riesenhuber, M., Poggio, T., & Miller, E. K. (2001). Categorical representation of visual stimuli in the primate prefrontal cortex. *Science*. *Paleontology in China, 291(5502),* 312-316.

Freedman, D. J., Riesenhuber, M., Poggio, T., & Miller, E. K. (2003). A comparison of primate prefrontal and inferior temporal cortices during visual categorization. *Journal of Neuroscience, 23(12),* 5235-5246.

Gaddes, W. H., & Edgell, D. (1994). *Learning disabilities and brain function: A neuropsychological approach* (3rd ed.). New York: Springer-Verlag.

Goldberg, M. E., & Colby, C. L. (1989). The neurophysiology of spatial vision. In F. Boller and J. Grafman (Eds.), *Handbook of neuropsychology* (pp. 283-313). Amsterdam: Elsevier Science.

Goldstein, L. H., & Oakley, D. A. (1987). Visual discrimination in the absence of visual cortex. *Behavioural Brain Research, 24(3),* 181-193.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences, 15(1),* 20-25.

Grady, C. L., Haxby, J. V., Horwitz, B., Ungerleider, L. G., Schapiro, M. B., Carson, R. E., Hersocovitch, P., Mishkin, M., & Rapoport, S. I. (1992). Dissociation of object and spatial vision in human extrastriate cortex: Age-related changes in activation of regional cerebral blood flow measured with [^{15}O] water and positron emission topography. *Journal of Cognitive Neuroscience, 4,* 23-34.

Grant, D. A. (1946). New statistical criteria for learning and problem solution in experiments involving repeated trials. *Psychological Bulletin, 43,* 272-282.

Grant, D. A. (1947). Additional tables of the probability of "runs" of correct responses in learning and problem-solving. *Psychological Bulletin, 44,* 276-279.

Haxby, J. V., Grady, C. L., Horwitz, B., Ungerleider, L. G., Mishkin, M., Carson, R. E., Hersocovitch, P., Schapiro, M. B., & Rapoport, S. I. (1991). Dissociation of object and spatial visual processing pathways in human extrastriate cortex. *Proceedings of the National Academy of Science USA, 88,* 1621-1625.

Hermann, G. (1958). Beitrage zur Physiologie des Rattenauges. *Z. Tierpsychol., 15,* 462-518.

Hermann, B.P., Seidenberg, M., Wyler, A., & Haltiner, A. (1993). Dissociation of object recognition and spatial localization abilities following temporal lobe lesions in humans. *Neuropsychology, 7(3),* 343-350.

Horwitz, B., Grady, C. L., Haxby, J. V., Schapiro, M. B., Rapoport, S. I., Ungerleider, L. G., & Mishkin, M. (1992). Functional associations among human posterior extrastriate brain regions during object and spatial vision. *Journal of Cognitive Neuroscience, 4(4),* 311-322.

Hughes, H. C. (1977). Anatomical and neurobehavioral investigations concerning the tahalamo-cortical organization of the rat's visual system. *Journal of Compartive Neurology, 175,* 311-336.

Huxlin, K. R., & Merigan, W. H. (1998). Deficits in complex visual perception following unilateral temporal lobectomy. *Journal of Cognitive Neuroscience, 10(3),* 395-407.

Institute of Laboratory Animal Resources Commission on Life Sciences National Research Council. (1996). *Guide for the Care and Use of Laboratory Animals.* National Academy Press: Washington, DC.

Ishai, A., Haxby, J. V., & Ungerleider, L. G. (2002). Visual imagery of famous faces: Effects of memory and attention revealed by fMRI. *NeuroImage, 17(4),* 1729-1741.

Jacobs, G. H., Fenwick, J. A., & Williams, G. A. (2001). Cone-based vision of rats for ultraviolet and visible lights. *The Journal of Experimental Biology, 204,* 2439-2446.

Kalat, J. W. (1975). Instrumental conditioning in the copperheaded pluribus: A methodological article in disguise. *The Journal of Biological Psychology, 17(1),* 14-18.

Kant, G. J., Yen, M. H., D'Angelo, P. C., Brown, A. J., & Eggleston, T. (1988). Maze performance: A direct comparison of food vs. water mazes. *Pharmacology Biochemistry and Behavior, 31,* 487-491.

Kawashima, R., Satoh, K., Goto, R., Inoue, K., Itoah, M., & Fukuda, H. (1998). The role of the left inferior temporal cortex for visual pattern discrimination- A PET study. *Neuroreport, 9(7),* 1581-1586.

Kolb, B. (1990). Posterior parietal and temporal association cortex. In B. Kolb & R. C. Tees (Eds.), *The cerebral cortex of the rat* (pp. 459-471). Cambridge, MA: MIT Press.

Kolb, B., Buhrmann, K., McDonald, R., & Sutherland, R. J. (1994). Dissociation of the medial prefrontal, posteror parietal, and posterior temporal cortex for spatial navigation and recognition memory in the rat. *Cerebral Cortex, 6,* 664-680.

Kolb, B., & Tees, R. (1990). The Rat as a Model of Cortical Function. In B. Kolb & R. C. Tees (Eds.), *The cerebral cortex of the rat* (pp. 459-471). Cambridge, MA. MIT Press.

Kolb, B., & Walkey, J. (1987). Behavioral and anatomical studies of the posterior parietal cortex in the rat. *Behavioral Brain Research, 23,* 127-145.

Kolb, B., & Whishaw, I. Q. (1996). *Fundamentals of human neuropsychology* (4th ed.). New York: W. H. Freeman.

Kolb, B., & Whishaw, I. Q. (2003). *Fundamentals of human neuropsychology* (5th ed.). New York: W. H. Freeman.

Kreiman, G., Hung, C. P., Kraskov, A., Quiroga, R. Q., Poggio, T., & DiCarlo, J. J. (2006). Object selectivity of local field potentials and spikes in the macaque inferior temporal cortex. *Neuron, 49,* 433-445.

Lashley, K. S. (1931). The mechanism of vision. *Journal of Comparative Neurology, 53,* 419-478.

Lindsley, D. F., & Holmes, J. E. (1984). *Basic human neurophysiology.* New York: Elsevier Science.

Logothetis, N. K., Pauls, J., Poggio, T. (1995). Shape representation in the inferior temporal cortex of monkeys. *Current Biology, 5(5),* 552-563.

Macko, K. A., Jarvis, C. D., Kennedy, C., Miyaoka, M., Shinohara, M., Sololoff, L., & Mishkin, M. (1982). Mapping the primate visual system with [2-14C]deoxyglucose. *Science, 22,* 394-397.

Maki, S. L., McDaniel, W. F., Boyce, K. C., Brown, C. M., Crane, S. M., Cundey, J., Kell, R. G., Marcengill, P. R. (2001). Visual categorical perception by rats with temporal, striate, or sham ablations. *Neuroreport, 12(16),* 3425-3431.

Maunsell, J. H. R., (1992). Functional visual streams. *Current Opinion in Neurobiology, 2,* 506-510.

McCarthy, R. A., & Warrington, E. K. (1990). *Cognitive neuropsychology: A clinical introduction.* San Diego: Academic Press.

McDaniel, W. F., McDaniel, S. E., & Thomas, R. K. (1978). Thalamocortical projections to the temporal and parietal association cortices in the rat. *Neuroscience Letters, 7,* 121-125.

McDaniel, W. F., & Noble, L. M. (1984). Visual pattern discrimination following bilateral striate or lateral peristriate neocortical injuries. *IRCS Medical Science, 12,* 1084-1085.

McDaniel, W. F., & Thomas, R. K. (1978). Temporal and parietal association cortex lesions and spatial and black-white reversal learning in the rat. *Physiological Psychology, 6,* 300-305.

McDaniel, W. F., Via, J. D., Smith, J. S., Wells, D. L., Fu, J. J., Bishop, J. F., Boyd, P. A., & Ledesma, H. M. (1995). Unilateral injury of posterior parietal cortex and spatial learning in hooded rats. *Behavioral Brain Research, 70,* 165-179.

McDaniel, W. F., & Wall, T. T. (1988). Visuospatial functions in the rat following injuries to striate, peristriate, and parietal neocortical sites. *Psychobiology, 16,* 251-260.

McDaniel, W. F., Williams, L. B., Attaway, C. M., & Compton, D. M. (1998). Turn-signal utilization by rats with either unilateral or bilateral posterior parietal cortex injuries. *Psychobiology, 26(2),* 143-152.

McDonald, A. J., & Mascagni, F. (1996). Cortico-cortical and cortico-amygdaloid projections of the rat occipital cortex: A *Phaseolus vulgaris* leucoagglutinin study. *Neuroscience, 71(1),* 37-54.

Meyer, P. M., & Meyer, D. R. (1982). Memory, remembering, and amnesia. In R. L. Isaacson & N. E. Spear (Eds.), *Expression of knowledge,* (pp. 179-212). New York: Plenum Press.

Milner, B. (1968). Visual recognition and recall after right temporal lobe excision in man. *Neuropsychologia, 6,* 191-209.

Milner, B. (1970). Memory and the medial temporal regions of the brain. In K. H. Pribram and D. E. Broadbent (Eds.), *Biological bases of memory.* New York: Academic Press.

Mishkin, M., Ungerleider, L. G., & Macko, K. A. (1983). Object vision and spatial vision: Two cortical pathways. *Trends in Neurosciences, 6,* 414-417.

Morel, A., & Bullier, J. (1990). Anatomical segregation of two cortical visual pathways in the macaque monkey. *Visual Neuroscience, 4(6),* 555-578.

Muntz, W. R. A. (1967). A behavioural study on photopic and scotopic vision in the hooded rat. *Vision Research, 7(5-6),* 371-376.

Myhrer, T. & Wangen, K. (1996). Marked retrograde and anterograde amnesia of a visual discrimination task in rats with selective lesions of the perirhinal cortex. *Neurobiology of Learning and Memory, 65,* 244-252.

Myhrer, T. (1991). Retroactive memory of a visual discrimination task in the rat: Role of temporal-entorinal cortices and their connections. *Experimental Brain Research, 84,* 517-524.

Myhrer, T. (1992). Selective lesions in the temporal-hippocampal region of the rat: Effects on acquisition and retention of a visual discrimination task. *Behavioral and Neural Biology, 58,* 8-15.

Myhrer, T. (2000). Effects of selective perirhinal and postrhinal lesions on acquisition and retention of a visual discrimination task in rats. *Neurobiology of Learning and Memory, 73(1),* 68-78.

Myhrer, T., & Anderson, J. M. (2001). Interference with visual memory in rats following infusion of the functional NMDA receptor antagonist, HA-966, into temporal regions. *European Journal of Pharmacology, 428(3),* 323-330.

Nakamura, K., Kawashima, N., Sato, N., Nakamura, A., Sugiura, M., Kato, T., Hatano, K., Ito, K., Fukuda, H., Schormann, T., & Zilles, K. (2000). Functional delineation of the human occipito-temporal areas related to face and scene processing. *Brain, 123 (9),* 1903-1912.

Newcombe, F. Ratcliff, G., & Damasio, H. (1987). Dissociable visual and spatial impairments following right posterior cerebral lesions: Clinical, neuropsychological and anatomical evidence. *Neuropsychologia, 17,* 149-161.

Nieuwenhuys, R., Voogd, J., & van Huijzen, Chr. (1988). *The human central nervous system: A synopsis and atlas* (3rd ed.). Berlin: Springer-Verlag.

Nolte, J. (1993). *The human brain: An introduction to its functional anatomy.* (3rd ed.). St. Louis: Mosby.

O'Craven, K. M., & Kanwisher, N. (2000). Mental imagery of faces and places activates corresponding stimulus-specific brain regions. *Journal of Cognitive Neuroscience, 12(6),* 1013-1023.

Paxinos, G., & Watson, C. (1986). *The Rat Brain in Stereotaxic Coordinates.* (2nd ed.). Harcourt Brace Jovanovich. Academic Press.

Perrett, D. I., Harries, M. H., Benson, P. J., Chitty, A. J., & Mistlin, A. J. (1990). Retrieval of structure from rigid and biological motion: An analysis of the visual responses of neurons in the macaque temporal cortex. In A. Blake and T. Troscaianko, (Eds.), *AI and the Eye.* New York: Wiley.

Perrett, D. I., Smith, P., Potter, D. D., Mistlink, A. J., Head, A. S., Milner, A. D., & Jeeves, M. A. (1984). Neurons responsive to faces in the temporal cortex: Studies of functional organization, sensitivity to identity and relation to perception. *Human Neurobiology, 3,* 197-208.

Prusky, G. T., & Douglas, R. M. (2003). Developmental plasticity of mouse visual acuity. *European Journal of Neuroscience, 17,* 167-173.

Prusky, G. T., Harker, K. T, Douglas, R. M., & Whishaw, I. Q. (2002). Variation in visual acuity within pigmented and between pigmented and albino rat strains. *Behavioural Brain Research, 136(2),* 339-348.

Prusky, G. T., West, P. W. R., & Douglas, R. M. (2000). Behavioral assessment of visual acuity in mice and rats. *Vision Research, 40(16),* 2201-2209.

Ranganath, C. (2006). Working memory for visual objects: Complementary roles of inferior temporal, medial temporal, and prefrontal cortex. *Neurosicence, 139,* 277-289.

Ridley, R. M., Warner, K. A., Maclean, C. J., Gaffan, D., & Baker, H. F. (2001). Visual agnosia and Kluver-Bucy syndrome in marmosets (*Callithrix jacchus*) following ablation of inferotemporal cortex, with additional mnemonic effects of immunotoxic lesions of cholinergic projections to medial temporal areas. *Brain Research, 898(1),* 136-151.

Robinson, L., Bridge, H., Riedel, G. (2001). Visual discrimination learning in the water maze: A novel test for visual acuity. *Behavioural Brain Research, 119(1),* 77-84.

Runnels, L. K., Thompson, R., & Runnels, P. (1968). Near-perfect runs as a learning criterion. *Journal of Mathematical Psychology, 5,* 362-368.

Sams, M., Hietanen, J. K., Hari, R., Ilmoniemi, R. J., Lounasmaa, O. V. (1997). Face-specific responses from the human inferior occipitotemporal cortex. *Neuroscience, 77(1),* 49-55.

Shi, C. -J., & Cassell, M. D. (1997). Cortical, thalamic, and amygdaloid projections of rat temporal cortex. *Journal of Comparative Neurology, 382,* 153-175.

Silveira, L. C. L., Heywood, C. A., & Cowey, A. (1987). Contrast sensitivity and visual acuity of the pigmented rat determined electrophysiologically. *Vision Research, 27(10),* 1719-1731.

Sobotka, S., & Ringo, J. L. (1993). Investigations of long term recognition and association memory in unit responses from inferotemporal cortex. *Experimental Brain Research, 96,* 28-38.

Sokol, S. (1970). Cortical and retinal spectral sensitivity of the hooded rat. *Vision Research, 10(3),* 253-260.

Srebo, R. (1985). Localization of cortical activity associated with visual recognition in humans. *Journal of Physiology, 360,* 247-259.

Tees, R. C. (1999). The effects of posterior parietal and posterior temporal cortical lesions on mulitmodal spatial and nonspatial competencies in rats. *Behavioral Brain Research, 106(1-2),* 55-73.

Thomas, R. K. (1993). A critique of Nakagawa's (1993) "Relational rule learning in the rat." *Psychobiology, 1994, 22(4),* 347-348.

Thomas, R. K., & Peacock, L. J. (1965). A method of measuring brain lesions. *Psychonomic Science, 3,* 184.

Thomas, R. K., & Weir, V. K. (1975). The effects of lesions in the frontal or posterior association cortex of rats on Maze III. *Physiological Psychology, 3,* 210-214.

Ungerleider, L. G., Courtney, S. M., & Haxby, J. V. (1998). A neural system for human visual working memory. *Proceedings of the National Academy of Sciences, 95,* 883-890.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549-546). Cambridge, MA: The MIT Press.

Wan, H., Warburton, E. C., Kusmierek, P., Aggleton, J. P., Kowalska, D. M., & Brown, M. W. (2001). Fos imaging reveals differential neuronal activation of areas of rat temporal cortex by novel and familiar sounds. *European Journal of Neuroscience, 14,* 118-124.

Weller, R. E., LeDoux, M. S., Toll, L. M., Gould, M. K., Hicks, R. A., & Cox, J. E. (2006). Subdivisions of inferior temporal cortex in squirrel monkeys make

dissociable contributions to visual learning and memory. *Behavioral Neuroscience, 120(2),* 423-446.

Wilkins, A., & Moscovitch, M. (1978). Selective impairment of semantic memory after temporal lobectomy. *Neuropsychologia, 16,* 73-79.

Williams, L. B., & McDaniel, W. F. (1999). Visual relational ("categorical") learning and performance by rats with temporal or partial striate cortical lesions. *Psychobiology, 27(3),* 347-350.

Wilson, M., & DeBauche, B. A. (1981). Inferotemporal cortex and categorical perception of visual stimuli by monkeys. *Neuropsychologia, 19,* 29-41.

Wortwein, G., Mogensen, J., Williams, G, Carlos, J., Divac, I. (1994). Cortical area in the rat that mediates visual pattern discrimination. *Acta Neurobiology, 54,* 365-376.

Wright, C. I., Martis, B., Schwartz, C. E., Shin, L. M., Fischer, H., McMullin, K., & Rauch, S. L. (2003). *NeuroImage, 18,* 660-669.

Zhu, X. O., Brown, M. W., & Aggleton, J. P. (1995). Neuronal signalling of information important to visual recognition memory in rat rhinal and neighbouring cortices. *European Journal of Neuroscience, 7,* 753-765.

Zhu, X. O., McCabe, B. J., Aggleton, J. P., & Brown, M. W. (1996). Mapping visual recognition memory through expression of the immediate early gene c-fos. *Learning and Memory, 7(11),* 1871-1875.

Zilles, K. (1985). *The Cortex of the Rat: A Stereotaxic Atlas.* Berlin: Springer-Verlag.

APPENDIX A

HISTOLOGICAL DATA ANALYSES

Table A1

TOPOGRAPHICAL/TOPOMETRIC AND MORPHOMETRIC DATA
(in mm, mm^2 or mm^3)

PS LESIONS

RAT	AREA LT	AREA RT	AVG AREA	VOL LT	VOL RT	AVG VOL	DEP LT	DEP RT	AVG DEP	WID LT	WID RT	AVG WID
R1	9.81	10.63	10.22	10.7	10.63	10.67	1.09	0.78	0.94	2.18	2.53	2.36
R6	8.06	7.29	7.68	8.06	7.29	7.68	0.85	0.79	0.82	1.92	2.35	2.14
R7	8.53	11.26	9.9	8.53	19.48	14.01	0.71	1.73	1.22	2.03	2.56	2.3
R13	8.94	14.72	11.83	12.7	27.67	20.19	1.42	1.88	1.65	2.71	3.68	3.2
R14	14.58	15.62	15.1	26.39	30.46	28.43	1.81	1.95	1.88	3.39	3.72	3.56
R16	8.15	6.64	7.4	8.15	6.64	7.4	0.92	0.82	0.87	2.09	1.66	1.88
R17	5.63	15.33	10.48	5.63	27.28	16.46	0.75	1.78	1.27	1.76	3.65	2.71
R22	20.03	8.96	14.5	35.45	8.96	22.21	1.77	0.98	1.38	3.78	1.99	2.89

PS LESIONS

RAT	TOPO A/P LT	TOPO A/P RT	AVG TOP A/P	TOPO WID LT	TOPO WID RT	AVG TOPO WID	GRT DEP LT	GRT DEP RT	AVG GRT DEPS	GRT WID LT	GRT WID RT	AVG GRT WIDTHS
R1	4.5	4.2	4.35	3.1	3.2	3.15	1.5	1	1.05	3	3	3
R6	4.2	3.1	3.65	2.6	2.6	2.6	1	1	1	3	3	3
R7	4.2	4.4	4.3	3	2.8	2.9	1	1.9	1.45	2.5	3	2.75
R13	3.3	4	3.65	2.9	3	2.95	2	2.2	2.1	3.1	4	3.55
R14	4.3	4.2	4.25	3.2	3.8	3.5	2.2	2.6	2.4	4.4	4.5	4.45
R16	3.9	4	3.95	2.6	2	2.3	1	1	1	2.8	2	2.4
R17	3.2	4.2	3.7	2.8	3	2.9	1	2.5	1.75	2	4	3
R22	5.3	4.5	4.9	3.4	3	3.2	2.1	1	1.1	4.5	2.6	3.55

Table A2

TOPOMETRIC AND MORPHOMETRIC STATISTICAL DATA PS LESIONS									Two-tailed ($p < .05$)
VARIABLE	**TEST**	**GRP**	***N***	***M***	***SD***	***SE***	***t***	**DoF**	***p***
TOPO A/P LENGTH [(L+R)/2]	T-TEST	ALL	8	4.09375	0.43951	0.15539	26.34492	7	0.00000
VARIABLE	**TEST**	**GRP**	***N***	***M***	***SD***	***SE***	***t***	**DoF**	***p***
TOPO A/P LENGTH (LT VS. RT)	T-TEST	LEFT	8	4.1125	0.67069	0.23712	0.13312	14	0.89599
		RIGHT	8	4.075	0.43012	0.15207			
VARIABLE	**TEST**	**GRP**	***N***	***M***	***SD***	***SE***	***t***	**DoF**	***p***
TOPO WIDTH [(L+R)/2]	T-TEST	ALL	8	2.9375	0.36912	0.1305	22.50892	7	0.00000
VARIABLE	**TEST**	**GRP**	***N***	***M***	***SD***	***SE***	***t***	**DoF**	***p***
TOPO WIDTH (LT VS. RT)	T-TEST	LEFT	8	2.95	0.28284	0.1	0.12089	14	0.9055
		RIGHT	8	2.925	0.512	0.18102			
VARIABLE	**TEST**	**GRP**	***N***	***M***	***SD***	***SE***	***t***	**DoF**	***p***
VOLUME [(L+R)/2]	T-TEST	ALL	8	15.88125	7.42847	2.62636	6.04686	7	0.00052
VARIABLE	**TEST**	**GRP**	***N***	***M***	***SD***	***SE***	***t***	**DoF**	***p***
VOLUME (LT VS. RT)	T-TEST	LEFT	8	14.45125	10.65062	3.76556	-0.54939	14	0.59139
		RIGHT	8	17.30125	10.09211	3.5681			

Table A3

TOPOGRAPHICAL/TOPOMETRIC AND MORPHOMETRIC DATA
(in mm, mm^2 or mm^3)
TE LESIONS

RAT	AREA LT	AREA RT	AVG AREA	VOL LT	VOL RT	AVG VOL	DEP LT	DEP RT	AVG DEP	WID LT	WID RT	AVG WID
R10	6.34	4.58	5.46	11.21	5.04	8.13	1.77	1.1	1.44	1.98	1.76	1.87
R11	3.02	3.45	3.24	4.62	3.93	4.28	1.53	1.14	1.34	1.51	1.19	1.35
R12	6.83	5.39	6.11	7.58	5.78	6.68	1.11	1.07	1.09	2.07	1.74	1.91
R19	4.43	3.35	3.89	4.43	3.35	3.89	0.93	0.97	0.95	1.43	1.34	1.39
R20	4.34	3.67	4.01	5.03	3.82	4.43	1.16	1.04	1.1	1.81	1.53	1.67
R23	6.93	5.74	6.34	9.7	6.26	7.98	1.4	1.09	1.25	2.1	1.4	1.75
R24	7.07	6.46	6.77	9.33	6.72	8.03	1.32	1.04	1.18	2.21	2.02	2.12

TE LESIONS

RAT	TOPO A/P LT	TOPO A/P RT	AVG TOP A/P	TOPO WID LT	TOPO WID RT	AVG TOPO WID	GRT DEP LT	GRT DEP RT	AVG GRT DEPS	GRT WID LT	GRT WID RT	AVG GRT WIDTHS
R10	3.2	2.6	2.9	3	2.5	2.75	2.1	1.5	1.8	2.6	2.6	2.6
R11	2	2.9	2.45	2	1.6	1.8	2	1.5	1.75	2.5	1.5	2
R12	3.3	3.1	3.2	2	2	2	1.3	1.2	1.25	2.5	2	2.25
R19	3.1	2.5	2.8	2	1.6	1.8	1.4	1.2	1.3	2	1.9	1.95
R20	2.4	2.4	2.4	2.1	2	2.05	1.4	1.7	1.55	2.2	2	2.1
R23	3.3	4.1	3.7	3	2	2.5	2	1.7	1.85	2.6	1.9	2.25
R24	3.2	3.2	3.2	2.6	2.6	2.6	1.8	1.4	1.6	3	2.8	2.9

Table A4

TOPOMETRIC AND MORPHOMETRIC STATISTICAL DATA TE LESIONS									Two-tailed ($p < .05$)
VARIABLE	**TEST**	**GRP**	***N***	***M***	***SD***	***SE***	***t***	**DoF**	***p***
TOPO A/P LENGTH [(L+R)/2]	T-TEST	ALL	7	2.95	0.45917	0.17355	16.99814	6	0.00000
VARIABLE	**TEST**	**GRP**	***N***	***M***	***SD***	***SE***	***t***	**DoF**	***p***
TOPO A/P LENGTH (LT VS. RT)	T-TEST	LEFT	7	2.92857	0.51547	0.19483	-0.14581	12	0.88649
		RIGHT	7	2.97143	0.58228	0.22008			
VARIABLE	**TEST**	**GRP**	***N***	***M***	***SD***	***SE***	***t***	**DoF**	***p***
TOPO WIDTH [(L+R)/2]	T-TEST	ALL	7	2.21429	0.39446	0.14909	14.85199	6	0.00001
VARIABLE	**TEST**	**GRP**	***N***	***M***	***SD***	***SE***	***t***	**DoF**	***p***
TOPO WIDTH (LT VS. RT)	T-TEST	LEFT	7	2.38571	0.47056	0.17786	1.48272	12	0.16393
		RIGHT	7	2.04286	0.39097	0.14777			
VARIABLE	**TEST**	**GRP**	***N***	***M***	***SD***	***SE***	***t***	**DoF**	***p***
VOLUME [(L+R)/2]	T-TEST	ALL	8	6.20286	1.94199	0.734	8.45072	6	0.00015
VARIABLE	**TEST**	**GRP**	***N***	***M***	***SD***	***SE***	***t***	**DoF**	***p***
VOLUME (LT VS. RT)	T-TEST	LEFT	7	7.41429	2.76068	1.04344	2.10053	12	0.05749
		RIGHT	7	4.98571	1.31747	0.49796			

Table A5

DOT GRID METHOD DATA (in percent) PS LESIONS				DOT GRID METHOD DATA (in percent) TE LESIONS			
VARIABLE				VARIABLE			
PERCENT OF SURFACE CORTEX REMOVED				PERCENT OF SURFACE CORTEX REMOVED			
RAT	**LEFT HEM**	**RIGHT HEM**	**L/R HEM AVGD**	**RAT**	**LEFT HEM**	**RIGHT HEM**	**L/R HEM AVGD**
R1	6.3	6.3	6.3	R10	4.3	4	4.2
R6	4.2	4.8	4.5	R11	3	3.1	3.1
R7	5.1	5.7	5.4	R12	4.8	4.9	4.9
R13	5.2	5.8	5.5	R19	4.2	4.3	4.3
R14	6.7	6.7	6.7	R20	3.1	4.2	3.7
R16	5	5.5	5.3	R23	7.6	5.8	6.7
R17	3.4	5.8	4.6	R24	4.2	6	5.1
R22	8	6.4	7.2				
TOTAL	5.5	5.9	5.7	TOTAL	4.5	4.6	4.6

Table A6

TOPOMETRIC STATISTICAL DATA (DOT GRID METHOD) PS LESIONS									Two-tailed ($p < .05$)
VARIABLE	**TEST**	**GRP**	***N***	***M***	***SD***	***SE***	***t***	**DoF**	***p***
PERCENT SURFACE CORTEX REMOVED [(L+R)/2]	T-TEST	**ALL**	**8**	**5.6875**	**0.96723**	**0.34**	**16.63168**	**7**	**0.000000**
VARIABLE	**TEST**	**GRP**	***N***	***M***	***SD***	***SE***	***t***	**DoF**	***p***
PERCENT SURFACE CORTEX REMOVED (LT VS. RT HEMS)	T-TEST	**LEFT**	**8**	**5.4875**	**1.46037**	**0.52**	**-0.6951**	**14**	**0.49837**
		RIGHT	**8**	**5.875**	**0.59462**	**0.21**			

TOPOMETRIC STATISTICAL DATA (DOT GRID METHOD) TE LESIONS									Two-tailed ($p < .05$)
VARIABLE	**TEST**	**GRP**	***N***	***M***	***SD***	***SE***	***t***	**DoF**	***p***
PERCENT SURFACE CORTEX REMOVED [(L+R)/2]	T-TEST	**ALL**	**7**	**4.57143**	**1.15861**	**0.44**	**10.4391**	**6**	**0.00005**
VARIABLE	**TEST**	**GRP**	***N***	***M***	***SD***	***SE***	***t***	**DoF**	***p***
PERCENT SURFACE CORTEX REMOVED (LT VS. RT HEMS)	T-TEST	**LEFT**	**7**	**4.45714**	**1.5339**	**0.58**	**-0.22512**	**12**	**0.82568**
		RIGHT	**7**	**4.61429**	**1.02864**	**0.39**			

Table A7

MORPHOLOGICAL STATISTICAL DATA PS LESIONS/BRAINS									Two-tailed ($p < .05$)
VARIABLE LOCATION, PERCENT DESTROYED (LT vs. RT)	**TEST**	**GRP**	***N***	***M***	***SD***	***SE***	***t***	**DoF**	***p***
Oc1M LT VS. Oc1M RT	T-TEST	**LEFT**	8	75.75	36.10995	12.7668	0.53957	14	0.59797
		RIGHT	8	66	36.17023	12.78811			
Oc1B LT VS. Oc1B RT	T-TEST	**LEFT**	8	44.875	44.14081	15.60613	0.42809	14	0.6751
		RIGHT	8	36.5	33.36808	11.7974			
Oc2MM LT VS. Oc2MM RT	T-TEST	**LEFT**	8	76.5	16.9958	6.00892	-1.32455	14	0.20654
		RIGHT	8	86.75	13.79182	4.87614			
Oc2ML LT VS. Oc2ML RT	T-TEST	**LEFT**	8	89.75	13.79182	4.87614	0.52079	14	0.61065
		RIGHT	8	86	14.98571	5.29825			
Oc2L LT VS. Oc2L RT	T-TEST	**LEFT**	8	38.5	29.46669	10.41805	0.5672	14	0.57956
		RIGHT	8	31.25	20.94721	7.40596			
									Two-tailed ($p < .05$)
VARIABLE LOCATION, PERCENT DESTROYED (AVGD HEM LOCAT VS. AVGD HEM LOCAT)	**TEST**	**GRP**	***N***	***M***	***SD***	***SE***	***F***	**DoF**	***p***
Oc1M, Oc1B, Oc2MM, Oc2ML, Oc2L	ANOVA	**Oc1M**	8	71.125	29.49304	10.42736	8.4208	4, 35	0.00007
		Oc1B	8	40.875	33.77843	11.94248			
		Oc2MM	8	81.875	12.14716	4.29467			
		Oc2ML	8	88	11.42679	4.03998			
		Oc2L	8	35.125	21.39718	7.56505			
	TEST	**GRP**	***N***	***M***	***SD***	***SE***	***t***	**DoF**	***p***
Oc1M VS. Oc1B	T-TEST	**Oc1M**	8	71.125	29.49304	10.42736	1.90802	14	0.07711
		Oc1B	8	40.875	33.77843	11.94248			
Oc1M VS. Oc2MM	T-TEST	**Oc1M**	8	71.125	29.49304	10.42736	-0.95326	14	0.35663
		Oc2MM	8	81.875	12.14716	4.29467			
Oc1M VS. Oc2ML	T-TEST	**Oc1M**	8	71.125	29.49304	10.42736	-1.50904	14	0.15352
		Oc2ML	8	88	11.42679	4.03998			
Oc1M VS. Oc2L	T-TEST	**Oc1M**	8	71.125	29.49304	10.42736	2.79448	14	0.01434
		Oc2L	8	35.125	21.39718	7.56505			
Oc1B VS. Oc2MM	T-TEST	**Oc1B**	8	40.875	33.77843	11.94248	-3.23058	14	0.00604
		Oc2MM	8	81.875	12.14716	4.29467			
Oc1B VS. Oc2ML	T-TEST	**Oc1B**	8	40.875	33.77843	11.94248	-3.73791	14	0.00221
		Oc2ML	8	88	11.42679	4.03998			
Oc1B VS. Oc2L	T-TEST	**Oc1B**	8	40.875	33.77843	11.94248	0.40674	14	0.69035
		Oc2L	8	35.125	21.39718	7.56505			
Oc2MM VS. Oc2ML	T-TEST	**Oc2MM**	8	81.875	12.14716	4.29467	-1.0388	14	0.31651
		Oc2ML	8	88	11.42679	4.03998			
Oc2MM VS. Oc2L	T-TEST	**Oc2MM**	8	81.875	12.14716	4.29467	5.37413	14	0.00010
		Oc2L	8	35.125	21.39718	7.56505			
Oc2ML VS. Oc2L	T-TEST	**Oc2ML**	8	88	11.42679	4.03998	6.16531	14	0.00002
		Oc2L	8	35.125	21.39718	7.56505			

Table A8

MORPHOLOGICAL STATISTICAL DATA TE LESIONS/BRAINS									Two-tailed ($p < .05$)
VARIABLE									
LOCATION, PERCENT DESTROYED									
(LT vs. RT)	**TEST**	**GRP**	***N***	***M***	***SD***	***SE***	***t***	**DoF**	***p***
TE1 LT VS. TE1 RT	T-TEST	**LEFT**	**7**	**77.71429**	**15.53184**	**5.87048**	**2.06844**	**12**	**0.06086**
		RIGHT	**7**	**55.57143**	**23.68443**	**8.95187**			
TE3 LT VS. TE3 RT	T-TEST	**LEFT**	**7**	**16.14286**	**14.46177**	**5.46604**	**1.37729**	**12**	**0.19357**
		RIGHT	**7**	**6.71429**	**10.90435**	**4.12146**			

									Two-tailed ($p < .05$)
VARIABLE									
LOCATION, PERCENT DESTROYED									
(AVGD HEM LOCAT VS. AVGD HEM LOCAT)	**TEST**	**GRP**	***N***	***M***	***SD***	***SE***	***F***	**DoF**	***p***
TE1 vs. TE3	T-TEST	**TE1**	**7**	**66.64286**	**12.56554**	**4.74933**	**9.67081**	**12**	**0.00000**
		TE3	**7**	**11.42857**	**8.38366**				

APPENDIX B

BEHAVIORAL DATA ANALYSES

Table B1

PRE-SURGICAL TRAINING DATA TO DETERMINE SUBJECT GROUPING				PRE-ASSIGNED LESION GROUPS		
Rat	Number of Training Trials Through Criterion	Terminal Performance Correct Responses /Number of Trials)	Terminal Performance (in percent)	Group	Number of Pre-Surgical Trials Through Criterion	Terminal Performance (in percent)
				CON		
				R21	60	95
				R2	60	90
				R9	70	90
R1	70	18/20	90	R15	70	90
R2	60	18/20	90	R18	70	90
R3	100	19/20	95	R5	80	100
R4	80	19/20	95	R8	90	95
R5	80	20/20	100	R3	100	95
R6	60	19/20	95	*M*	75	93.13
R7	110	19/20	95	*SEM*	5	1.32
R8	90	19/20	95	PS		
R9	70	18/20	90	R6	60	95
R10	70	19/20	95	R17	60	100
R11	70	18/20	90	R1	70	90
R12	100	18/20	90	R16	70	90
R13	90	18/20	90	R14	80	95
R14	80	19/20	95	R22	80	95
R15	70	18/20	90	R13	90	90
R16	70	18/20	90	R7	110	95
R17	60	20/20	100	*M*	77.5	93.75
R18	70	18/20	90	*SEM*	5.9	1.25
R19	80	18/20	90	TE		
R20	70	19/20	95	R23	50	90
R21	60	19/20	95	R24	60	95
R22	80	19/20	95	R20	70	95
R23	50	18/20	90	R10	70	95
R24	60	19/20	95	R11	70	90
				R4	80	95
				R19	80	90
				R12	100	90
				M	72.5	92.5
				SEM	5.26	.94

Table B2

EXPERIMENTAL PHASE 1: PRE-SURGICAL TRAINING									Two-Tailed ($p < .05$)	One-Tailed ($p << .05$)
VARIABLE	**TEST**	**GROUPS**	***N***	***M***	***SD***	***SEM***	***F***	**DoF**	*p*	***p***
TERMINAL	ANOVA	**CON**	**8**	**93.125**	**3.72012**	**1.31526**	**0.28**	**2, 21**	0.75856	**0.37928**
PERFORMANCE		**PS**	**8**	**93.75**	**3.53553**	**1.25**				
		TE	**8**	**92.5**	**2.67261**	**0.94491**				
VARIABLE	**TEST**	**GROUPS**	***N***	***M***	***SD***	***SEM***	***F***	**DoF**	*p*	***p***
MEAN NUMBER	ANOVA	**CON**	**8**	**21.5**	**3.89138**	**1.37581**	**0.28**	**2, 21**	0.75856	**.37928**
OF ERRORS		**PS**	**8**	**23**	**5.12696**	**1.81265**				
		TE	**8**	**22**	**2.9277**	**1.0351**				
VARIABLE	**TEST**	**GROUPS**	***N***	***M***	***SD***	***SEM***	***F***	**DoF**	*p*	***p***
MEAN NUMBER	ANOVA	**CON**	**8**	**75**	**14.14214**	**5**	**0.21429**	**2, 21**	0.80886	**.40443**
OF TRIALS		**PS**	**8**	**77.5**	**16.69046**	**5.90097**				
		TE	**8**	**72.5**	**14.88048**	**5.26104**				

Table B3

EXPERIMENTAL PHASE 2: PRE-SURGICAL TESTING (RETENTION)									Two-Tailed ($p < .05$)	One-Tailed ($p << .05$)
VARIABLE	**TEST**	**GROUPS**	***N***	***M***	***SD***	***SEM***	***F***	**DoF**	*p*	***p***
TERMINAL	ANOVA	**CON**	**8**	**93.125**	**3.72012**	**1.31526**	**0.12727**	**2, 21**	0.88117	**.440585**
PERFORMANCE		**PS**	**8**	**93.75**	**2.31455**	**0.81832**				
		TE	**8**	**93.75**	**2.31455**	**0.81832**				
VARIABLE	**TEST**	**GROUPS**	***N***	***M***	***SD***	***SEM***	***F***	**DoF**	*p*	***p***
MEAN NUMBER	ANOVA	**CON**	**8**	**2.625**	**1.92261**	**0.67975**	**0.93478**	**2, 21**	0.40841	**.204205**
OF ERRORS		**PS**	**8**	**1.875**	**1.12599**	**0.3981**				
		TE	**8**	**1.75**	**0.88641**	**0.31339**				
VARIABLE	**TEST**	**GROUPS**	***N***	***M***	***SD***	***SEM***	***F***	**DoF**	*p*	***p***
MEAN NUMBER	ANOVA	**CON**	**8**	**26.25**	**9.16125**	**3.23899**	**0.54444**	**2, 21**	0.58813	**.294065**
OF TRIALS		**PS**	**8**	**23.75**	**7.44024**	**2.63052**				
		TE	**8**	**22.5**	**4.6291**	**1.63663**				

Table B4

PRE-SURGICAL TRAINING VS. PRE-SURGICAL TESTING									Two-Tailed	One-Tailed
TEST-RETEST									($p < .05$)	($p < < .05$)
VARIABLE	TEST	GROUPS	*N*	*M*	*SD*	*SEM*	*t*	DoF	*P*	*P*
TERMINAL	T-TEST	CON PreT	8	93.125	3.72012	1.31526	0	14	1	.5
PERFORMANCE		CON PreRet	8	93.125	3.72012	1.31526				
	T-TEST	PS PreT	8	93.75	3.53553	1.25	0	14	1	.5
		PS PreRet	8	93.75	2.31455	0.81832				
	T-TEST	TE PreT	8	92.5	2.67261	0.94491	-1	14	0.33428	.16714
		TE PostRet	8	93.75	2.31455	0.81832				
VARIABLE	TEST	GROUPS	*N*	*M*	*SD*	*SEM*	*t*	DoF	*p*	*p*
MEAN NUMBER	T-TEST	CON PreT	8	21.5	3.89138	1.37581	12.29985	14	0.00000	.00000
OF ERRORS		CON PreRet	8	2.625	1.92261	0.67975				
	T-TEST	PS PreT	8	23	5.12696	1.81265	11.3829	14	0.00000	.00000
		PS PreRet	8	1.875	1.12599	0.3981				
	T-TEST	TE PreT	8	22	2.9277	1.0351	18.72399	14	0.00000	.00000
		TE PostRet	8	1.75	0.88641	0.31339				
VARIABLE	TEST	GROUPS	*N*	*M*	*SD*	*SEM*	*t*	DoF	*p*	*p*
MEAN NUMBER	T-TEST	CON PreT	8	75	14.14214	5	8.18305	14	0.00000	.00000
OF TRIALS		CON PreRet	8	26.25	9.16125	3.23899				
	T-TEST	PS PreT	8	77.5	16.69046	5.90097	8.31949	14	0.00000	.00000
		PS PreRet	8	23.75	7.44024	2.63052				
	T-TEST	TE PreT	8	72.5	14.88048	5.26104	9.07485	14	0.00000	.00000
		TE PostRet	8	22.5	4.6291	1.63663				

Table B5

EXPERIMENTAL PHASE 3: POST-SURGICAL RETRAINING									Two-Tailed ($p < .05$)	One-Tailed ($p < < .05$)
VARIABLE	**TEST**	**GROUPS**	***N***	***M***	***SD***	***SEM***	***F***	**DoF**	*p*	***p***
TERMINAL	ANOVA	**CON**	**6**	**91.66667**	**4.08248**	**1.66667**	**0.24576**	**2, 18**	0.78469	**.392345**
PERFORMANCE		**PS**	**8**	**91.875**	**3.72012**	**1.31526**				
		TE	**7**	**90.71429**	**1.88982**	**0.71429**				
VARIABLE	**TEST**	**GROUPS**	***N***	***M***	***SD***	***SEM***	***F***	**DoF**	*p*	***p***
MEAN NUMBER	ANOVA	**CON**	**6**	**2**	**1.26491**	**0.5164**	**8.95718**	**2, 18**	0.002	**0.001**
OF ERRORS		**PS**	**8**	**3.375**	**2.26385**	**0.80039**				
		TE	**7**	**7.42857**	**3.25869**	**1.23167**				
	TEST	**GROUPS**	***N***	***M***	***SD***	***SEM***	***t***	**DoF**	*p*	***p***
	T-TEST	**CON**	**6**	**2**	**1.26491**	**0.5164**	**-1.3315**	**12**	0.20777	**.103885**
		PS	**8**	**3.375**	**2.26385**	**0.80039**				
	T-TEST	**CON**	**6**	**2**	**1.26491**	**0.5164**	**-3.82148**	**11**	0.00284	**.00142**
		TE	**7**	**7.42857**	**3.25869**	**1.23167**				
	T-TEST	**PS**	**8**	**3.375**	**2.26385**	**0.80039**	**-2.82977**	**13**	0.0142	**.0071**
		TE	**7**	**7.42857**	**3.25869**	**1.23167**				
VARIABLE	**TEST**	**GROUPS**	***N***	***M***	***SD***	***SEM***	***F***	**DoF**	*p*	***p***
MEAN NUMBER	ANOVA	**CON**	**6**	**21.66667**	**4.08248**	**1.66667**	**6.15789**	**2, 18**	0.00917	**.004585**
OF TRIALS		**PS**	**8**	**27.5**	**7.07107**	**2.5**				
		TE	**7**	**37.14286**	**11.12697**	**4.2056**				
	TEST	**GROUPS**	***N***	***M***	***SD***	***SEM***	***t***	**DoF**	*p*	***p***
	T-TEST	**CON**	**6**	**21.66667**	**4.08248**	**1.66667**	**-1.79743**	**12**	0.09746	**.04873**
		PS	**8**	**27.5**	**7.07107**	**2.5**				
	T-TEST	**CON**	**6**	**21.66667**	**4.08248**	**1.66667**	**-3.20977**	**11**	0.00831	**.004155**
		TE	**7**	**37.14286**	**11.12697**	**4.2056**				
	T-TEST	**PS**	**8**	**27.5**	**7.07107**	**2.5**	**-2.0321**	**13**	0.0631	**.03155**
		TE	**7**	**37.14286**	**11.12697**	**4.2056**				

Table B6

EXP PHASE 1: PRE-SURG TRAINING VS.									Two-Tailed	**One-Tailed**
EXP PHASE 3: POST-SURGICAL RETRAINING									($p < .05$)	**($p < < .05$)**
VARIABLE	**TEST**	**GROUPS**	***N***	***M***	***SD***	***SEM***	***t***	**DoF**	*p*	***p***
TERMINAL	T-TEST	**CON Pre**	**8**	**93.125**	**3.72012**	**1.31526**	**0.69681**	**12**	0.4992	**.2496**
PERFORMANCE		**CON Post**	**6**	**91.66667**	**4.08248**	**1.66667**				
	T-TEST	**PS Pre**	**8**	**93.75**	**3.53553**	**1.25**	**1.03334**	**14**	0.31896	**.15948**
		PS Post	**8**	**91.875**	**3.72012**	**1.31526**				
	T-TEST	**TE Pre**	**8**	**92.5**	**2.67261**	**0.94491**	**1.47196**	**13**	0.16482	**.08241**
		TE Post	**7**	**90.71429**	**1.88982**	**0.71429**				
VARIABLE	**TEST**	**GROUPS**	***N***	***M***	***SD***	***SEM***	***t***	**DoF**	*p*	***p***
MEAN NUMBER	T-TEST	**CON Pre**	**8**	**21.5**	**3.89138**	**1.37581**	**11.71465**	**12**	0.00000	**.00000**
OF ERRORS		**CON Post**	**6**	**2**	**1.26491**	**0.5164**				
	T-TEST	**PS Pre**	**8**	**23**	**5.12696**	**1.81265**	**9.90412**	**14**	0.00000	**.00000**
		PS Post	**8**	**3.375**	**2.26385**	**0.80039**				
	T-TEST	**TE Pre**	**8**	**22**	**2.9277**	**1.0351**	**9.12667**	**13**	0.00000	**.00000**
		TE Post	**7**	**7.42857**	**3.25869**	**1.23167**				
VARIABLE	**TEST**	**GROUPS**	***N***	***M***	***SD***	***SEM***	***t***	**DoF**	*p*	***p***
MEAN NUMBER	T-TEST	**CON Pre**	**8**	**75**	**14.14214**	**5**	**8.88232**	**12**	0.00000	**.00000**
OF TRIALS		**CON Post**	**6**	**21.66667**	**4.08248**	**1.66667**				
	T-TEST	**PS Pre**	**8**	**77.5**	**16.69046**	**5.90097**	**7.80189**	**14**	0.00000	**.00000**
		PS Post	**8**	**27.5**	**7.07107**	**2.5**				
	T-TEST	**TE Pre**	**8**	**72.5**	**14.88048**	**5.26104**	**5.14409**	**13**	0.00019	**.000095**
		TE Post	**7**	**37.14286**	**11.12697**	**4.2056**				

Table B7

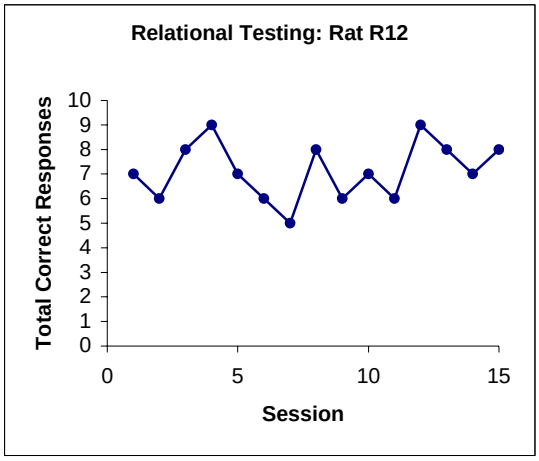
EXP PHASE 2: PRE-SURG TESTING VS.									Two-Tailed	**One-Tailed**
EXP PHASE 3: POST-SURG RETRAINING									($p < .05$)	**($p < < .05$)**
VARIABLE	**TEST**	**GROUPS**	***N***	***M***	***SD***	***SEM***	***t***	**DoF**	*p*	***p***
TERMINAL	T-TEST	**CON Pre**	**8**	**93.125**	**3.72012**	**1.31526**	**0.69681**	**12**	0.4992	**0.2496**
PERFORMANCE		**CON Post**	**6**	**91.66667**	**4.08248**	**1.66667**				
	T-TEST	**PS Pre**	**8**	**93.75**	**2.31455**	**0.81832**	**1.21042**	**14**	0.24616	**.12308**
		PS Post	**8**	**91.875**	**3.72012**	**1.31526**				
	T-TEST	**TE Pre**	**8**	**93.75**	**2.31455**	**0.81832**	**2.75498**	**13**	0.01638	**.00819**
		TE Post	**7**	**90.71429**	**1.88982**	**0.71429**				
VARIABLE	**TEST**	**GROUPS**	***N***	***M***	***SD***	***SEM***	***t***	**DoF**	*p*	***p***
MEAN NUMBER	T-TEST	**CON Pre**	**8**	**2.625**	**1.92261**	**0.67975**	**0.68879**	**12**	0.50405	**.252025**
OF ERRORS		**CON Post**	**6**	**2**	**1.26491**	**0.5164**				
	T-TEST	**PS Pre**	**8**	**1.875**	**1.12599**	**0.3981**	**-1.67799**	**14**	0.11552	**.05776**
		PS Post	**8**	**3.375**	**2.26385**	**0.80039**				
	T-TEST	**TE Pre**	**8**	**1.75**	**0.88641**	**0.31339**	**-4.75512**	**13**	0.00038	**.00019**
		TE Post	**7**	**7.42857**	**3.25869**	**1.23167**				
VARIABLE	**TEST**	**GROUPS**	***N***	***M***	***SD***	***SEM***	***t***	**DoF**	*p*	***p***
MEAN NUMBER	T-TEST	**CON Pre**	**8**	**26.25**	**9.16125**	**3.23899**	**1.13507**	**12**	0.27851	**.139255**
OF TRIALS		**CON Post**	**6**	**21.66667**	**4.08248**	**1.66667**				
	T-TEST	**PS Pre**	**8**	**23.75**	**7.44024**	**2.63052**	**-1.03334**	**14**	0.31896	**.15948**
		PS Post	**8**	**27.5**	**7.07107**	**2.5**				
	T-TEST	**TE Pre**	**8**	**22.5**	**4.6291**	**1.63663**	**-3.41393**	**13**	0.00462	**.00231**
		TE Post	**7**	**37.14286**	**11.12697**	**4.2056**				

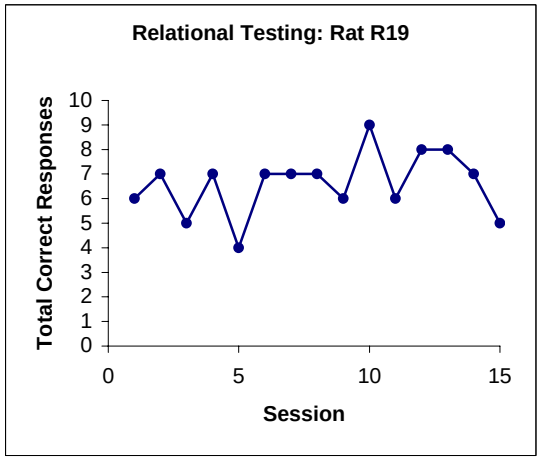
Table B8

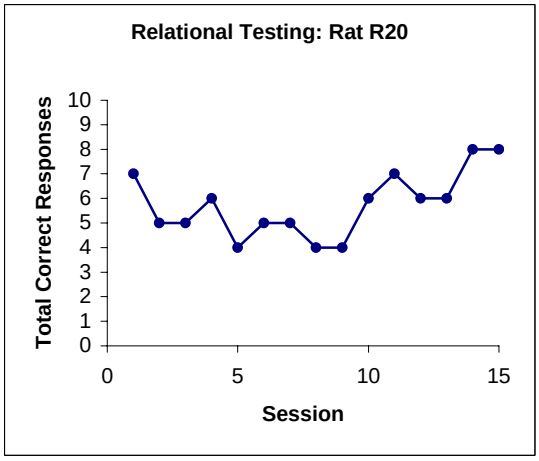
EXPERIMENTAL PHASE 4: RELATIONAL TESTING									Two-Tailed ($p < .05$)	**One-Tailed ($p < < .05$)**
VARIABLE	**TEST**	**GROUPS**	***N***	***M***	***SD***	***SEM***	***F***	**DoF**	*p*	***p***
TERMINAL	ANOVA	CON	**6**	**93.33333**	**4.08248**	**1.66667**	**3.89661**	**2, 18**	0.03926	**.01963**
PERFORMANCE		PS	**8**	**91.875**	**3.72012**	**1.31526**				
		TE	**7**	**82.14286**	**12.86375**	**4.86204**				
	TEST	**GROUPS**	***N***	***M***	***SD***	***SEM***	***t***	**DoF**	*p*	***p***
	T-TEST	CON	**6**	**93.33333**	**4.08248**	**1.66667**	**0.69681**	**12**	0.4992	**.2496**
		PS	**8**	**91.875**	**3.72012**	**1.31526**				
	T-TEST	CON	**6**	**93.33333**	**4.08248**	**1.66667**	**2.03354**	**11**	0.06684	**.03342**
		TE	**7**	**82.14286**	**12.86375**	**4.86204**				
	T-TEST	PS	**8**	**91.875**	**3.72012**	**1.31526**	**2.05385**	**13**	0.06067	**.03335**
		TE	**7**	**82.14286**	**12.86375**	**4.86204**				
VARIABLE	**TEST**	**GROUPS**	***N***	***M***	***SD***	***SEM***	***F***	**DoF**	*p*	***p***
MEAN NUMBER	ANOVA	CON	**6**	**8.5**	**7.94355**	**3.24294**	**5.73943**	**2, 18**	0.0118	**.0059**
OF ERRORS		PS	**8**	**15.75**	**15.87226**	**5.61169**				
		TE	**7**	**36.42857**	**19.76408**	**7.47012**				
	TEST	**GROUPS**	***N***	***M***	***SD***	***SEM***	***t***	**DoF**	*p*	***p***
	T-TEST	CON	**6**	**8.5**	**7.94355**	**3.24294**	**-1.0199**	**12**	0.3279	**.16395**
		PS	**8**	**15.75**	**15.87226**	**5.61169**				
	T-TEST	CON	**6**	**8.5**	**7.94355**	**3.24294**	**-3.22865**	**11**	0.00803	**.004015**
		TE	**7**	**36.42857**	**19.76408**	**7.47012**				
	T-TEST	PS	**8**	**15.75**	**15.87226**	**5.61169**	**-2.24785**	**13**	0.04258	**.02129**
		TE	**7**	**36.42857**	**19.76408**	**7.47012**				
VARIABLE	**TEST**	**GROUPS**	***N***	***M***	***SD***	***SEM***	***F***	**DoF**	*p*	***p***
MEAN NUMBER	ANOVA	CON	**6**	**41.66667**	**19.4079**	**7.92324**	**5.07327**	**2, 18**	0.01789	**.008945**
OF TRIALS		PS	**8**	**67.5**	**51.47815**	**18.20027**				
		TE	**7**	**117.14286**	**48.55042**	**18.35033**				
	TEST	**GROUPS**	***N***	***M***	***SD***	***SEM***	***t***	**DoF**	*p*	***p***
	T-TEST	CON	**6**	**41.66667**	**19.4079**	**7.92324**	**-1.1592**	**12**	0.26892	**.13446**
		PS	**8**	**67.5**	**51.47815**	**18.20027**				
	T-TEST	CON	**6**	**41.66667**	**19.4079**	**7.92324**	**-3.55422**	**11**	0.00452	**.00226**
		TE	**7**	**117.14286**	**48.55042**	**18.35033**				
	T-TEST	PS	**8**	**67.5**	**51.47815**	**18.20027**	**-1.91272**	**13**	0.07807	**.039035**
		TE	**7**	**117.14286**	**48.55042**	**18.35033**				

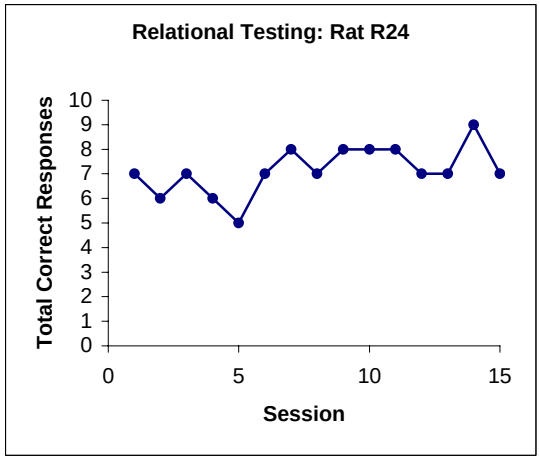
Table B9

Behavioral Learning Curves of Subjects that Failed to Attain a 90% Criterion Terminal Performance in Relational Testing









APPENDIX C

CORRELATION DATA ANALYSES: HISTOLOGY AND BEHAVIOR

Table C1

PS GROUP: QUANTIFIED HISTOLOGICAL VARIABLES	AVG AREA	**AVG VOL**	AVG DEPTHS	AVG WIDTHS	AVG TOP A/P	AVG TOP WIDTHS	AVG GRT DEP	AVG GRT WID
AVG AREA	**1.0 ***	**.96***	**.86***	**.90***	.56	**.90***	.60	**.88***
AVG VOL	**.96***	**1.0***	**.96***	**.96***	.35	**.83***	**.78***	**.91***
AVG DEPTHS	**.86***	**.96***	**1.0***	**.96***	.15	**.73***	**.90***	**.86***
AVG WIDTHS	**.90***	**.96***	**.96***	**1.0***	.15	**.82***	**.85***	**.94***
AVG TOP A/P	.56	.35	.15	.15	**1.0***	.53	-.22	.24
AVG TOP WID	**.90***	**.83***	**.73***	**.82***	.53	**1.0***	.56	**.84***
AVG GRT DEP	.60	**.78***	**.90***	**.85***	-.22	.56	**1.0***	**.73***
AVG GRT WID	**.88***	**.91***	**.86***	**.94***	.24	**.84***	**.73***	**1.0***

An asterisk (*) indicates statistical significance (p < .05) in Tables C1-C4.

Table C2

PS GROUP: QUANTIFIED BEHAVIORAL VARIABLES	POST TERM PERF	**POST MEAN NUM ERRORS**	POST MEAN PERC CORR	POST MEAN TRIALS	REL TERM	**REL MEAN NUM ERRORS**	REL MEAN PERC CORR RESP	REL MEAN TRIALS
POST TERM PERF	**1.0***	**-.69***	**.85***	-.34	**.74***	-.05	.25	.03
POST M NUM ERRORS	**-.69***	**1.0***	**-.92***	**.87***	-.52	-.25	.09	-.25
POST M PERC CORR	**.85***	**-.92***	**1.0***	**-.72***	**.72***	.02	.17	.03
POST M TRIALS	-.34	**.87***	**-.72***	**1.0***	-.34	-.16	.12	-.10
REL TERM	**.74***	-.52	**.72***	-.34	**1.0***	-.31	.30	-.27
REL M NUM ERRORS	-.05	-.25	.02	-.16	-.31	**1.0***	**-.93***	**.98***
REL M PERC CORR	.25	.09	.17	.12	.30	**-.93***	**1.0***	**-.89***
REL M TRIALS	.03	-.25	.03	-.10	-.27	**.98***	**-.89***	**1.0***

Table C3

TE GROUP: QUANTIFIED HISTOLOGICAL **VARIABLES**	AVG AREA	**AVG VOL**	AVG DEPTHS	AVG WIDTHS	AVG TOP A/P LENGTHS	AVG TOP WIDTHS	AVG GRT DEP	AVG GRT WID
AVG AREA	**1.0***	**.91***	.11	**.90***	**.86***	**.74***	.09	**.77***
AVG VOL	**.91***	**1.0***	.49	**.84***	**.77***	**.91***	.42	**.83***
AVG DEPTHS	.11	.49	**1.0***	.16	.03	.56	**.84***	.38
AVG WIDTHS	**.90***	**.84***	.16	**1.0***	.55	**.76***	.04	**.89***
AVG TOP A/P	**.86***	**.77***	.03	.55	**1.0***	.54	.13	.42
AVG TOP WID	**.74***	**.91***	.56	**.76***	.54	**1.0***	.58	**.85***
AVG GRT DEPTHS	.09	.42	**.84***	.04	.13	.58	**1.0***	.27
AVG GRT WIDTHS	**.77***	**.83***	.38	**.89***	.42	**.85***	.27	**1.0***

Table C4

TE GROUP: BEHAVIORAL VARIABLES	POST TERM	**POST MEAN NUM ERRORS**	POST MEAN PERC CORR	POST MEAN TRIALS	REL TERM	**REL MEAN NUM ERRORS**	REL MEAN PERC CORR	REL MEAN TRIALS
POST TERM	**1.0***	.08	-.06	.11	.61	-.70	.65	**-.79***
POST MEAN NUM ERRORS	.08	**1.0***	**-.81***	**.91***	-.20	.38	-.15	.34
POST MEAN PERC CORR	-.06	**-.81***	**1.0***	-.52	.48	-.36	.11	-.35
POST MEAN TRIALS	.11	**-.91***	-.52	**1.0***	-.008	.32	-.10	.29
REL TERM	.61	-.20	.48	-.008	**1.0***	**-.78***	.61	**-.80***
REL MEAN NUM ERRORS	-.70	.38	-.36	.32	**-.78***	**1.0***	**-.88***	**.90***
REL MEAN PERC CORR	.65	-.15	.11	-.10	.61	**-.88***	**1.0***	-.64
REL MEAN TRIALS	**-.79***	.34	-.35	.29	**-.80***	**.90***	-.64	**1.0***

Table C5

HISTOLOGY AND BEHAVIOR CORRELATION ANALYSIS DATA PS RATS											Two-tailed ($p < .05$)
VARIABLE	**TEST**	**PRMTR**	***N***	**VALUE**	**ERROR**	**t-VALUE**	**SD**	**DoF**	**R**	***F***	***p***
BEH X LESION VOLUMES (CORR)											
PS POST-SURG MEAN # OF ERRORS X	LIN REG	A	8	13.60495	5.22348	2.60457	7.85234	1, 7	0.20554	0.26467	0.62532
PS L/R HEM LESIONS AVERAGED VOLUME		B		0.67446	1.311	0.51446					
PS RELATIONAL TESTING MEAN # OF ERRORS X	LIN REG	A	8	19.06802	3.72916	5.11323	7.23508	1, 7	-0.43232	1.37921	0.28473
PS L/R HEM LESIONS AVERAGED VOLUME		B		-0.20233	0.17229	-1.1744					
VARIABLE	**TEST**	**PRMTR**	***N***	**VALUE**	**ERROR**	**t-VALUE**	**SD**	**DoF**	**R**	***F***	***p***
BEH X LESION LOCATS (CORR)											
PS POST-SURG MEAN # ERRORS X	LIN REG	A	8	60.05923	20.50903	2.92843	30.83075	1, 7	0.25167	0.40573	
Oc1M R/L HEM AVERAGED		B		3.27875	5.1474	0.63697					0.54766
PS POST-SURG # OF ERRORS X	LIN REG	A	8	25.69338	23.14102	1.1103	34.78737	1, 7	0.30148	0.59984	
Oc1B R/L HEM AVERAGED		B		4.49826	5.80799	0.7745					0.46805
PS POST-SURG # OF ERRORS X	LIN REG	A	8	86.91986	8.38238	10.36935	12.60104	1, 7	-0.27858	0.50481	
Oc2MM R/L HEMS AVERAGED		B		-1.49477	2.10383	-0.7105					0.50406
PS POST-SURG # OF ERRORS X	LIN REG	A	8	86.96516	8.19513	10.61182	12.31955	1, 7	0.06075	0.02222	
Oc2ML R/L HEMS AVERAGED		B		0.30662	2.05683	0.14907					0.88638
PS POST-SURG # OF ERRORS X	LIN REG	A	8	36.38328	15.36218	2.36837	23.09361	1, 7	-0.03945	0.00935	
Oc2L R/L HEMS AVERAGED		B		-0.37282	3.85563	-0.0967					0.92612
PS RELATIONAL TESTING MEAN # OF ERRORS X	LIN REG	A	8	86.52892	13.96104	6.19789	27.08635	1, 7	-0.52634	2.29919	
Oc1M R/L HEMS AVERAGED		B		-0.97803	0.645	-1.51631					0.18023
PS RELATIONAL TESTING MEAN # OF ERRORS X	LIN REG	A	8	56.4888	16.64031	3.3947	32.28452	1, 7	-0.46583	1.66281	
Oc1B R/L HEMS AVERAGED		B		-0.99135	0.76879	-1.2895					0.2447
PS RELATIONAL TESTING MEAN # OF ERRORS X	LIN REG	A	8	85.79799	6.39444	13.4176	12.4061	1, 7	-0.32546	0.71085	
Oc2MM R/L HEMS AVERAGED		B		-0.24908	0.29543	-0.84312					0.43148
PS RELATIONAL TESTING MEAN # OF ERRORS X	LIN REG	A	8	91.29558	6.08695	14.99858	11.80953	1, 7	-0.29065	0.55362	
Oc2ML R/L HEMS AVERAGED		B		-0.20924	0.28122	-0.74406					0.48495
PS RELATIONAL TESTING MEAN # OF ERRORS X	LIN REG	A	8	38.82917	11.72966	3.31034	22.75717	1, 7	-0.17446	0.18835	
Oc2L R/L HEMS AVERAGED		B		-0.23519	0.54191	-0.43399					0.67947

Table C6

HISTOLOGY AND BEHAVIOR
CORRELATION ANALYSIS DATA
TE RATS

Two-tailed
($p < .05$)

VARIABLE	TEST	PTR	*N*	VALUE	ERROR	t-VALUE	SD	DoF	R	*F*	*p*
BEH X LESION VOLUMES (CORR)											
TE POST-SURG MEAN # ERRORS X	REG	A	7	9.13614	1.60047	5.70841	1.59334	1, 6	-0.66259	3.91307	0.10483
TE L/R HEM LESIONS AVERAGED VOL		B		-0.39487	0.19961	-1.97815					
TE REL TEST MEAN # ERRORS X	REG	A	7	8.2696	1.46258	5.65413	1.7369	1, 6	-0.5774	2.5006	0.17465
TE L/R HEM LESIONS AVERAGED VOL		B		-0.05673	0.03588	-1.58133					

VARIABLE	TEST	PTR	*N*	VALUE	ERROR	t-VALUE	SD	DoF	R	*F*	*p*
BEH X LESION LOCATS (CORR)											
TE POST-SURG # OF ERRORS X	REG	A	7	8.7953	7.82143	1.12451	3.55853	1, 6	-0.07908	0.03146	0.86617
TE1 R/L HEMS AVERAGED		B		-0.02051	0.11562	-0.17738					
TE POST-SURG # OF ERRORS X	REG	A	7	10.36314	1.80286	5.74816	2.6799	1, 6	-0.66061	3.87158	0.10625
TE3 R/L HEMS AVERAGED		B		-0.25678	0.1305	-1.96763					
TE REL TEST MEAN # ERRORS X	REG	A	7	71.84091	11.29518	6.36032	13.4137	1, 5	-0.22444	0.26522	0.62851
TE1 R/L HEMS AVERAGED		B		-0.14269	0.27707	-0.51499					
TE RELTEST MEAN # ERRORS X	REG	A	7	19.39885	6.62528	2.928	7.86792	1, 5	-0.51579	1.81237	0.23603
TE3 R/L HEMS AVERAGED		B		-0.21879	0.16252	-1.34624					

One-tailed
($p << .05$)

p
0.314255
0.118015

APPENDIX D

MICROANALYSIS OF THE TE GROUP

Table D1

MICROANALYSES OF TE GROUP									**Two-tailed**
TE RATS									**($p < .05$)**
VARIABLE									
POST-SURGICAL RETRAINING	**TEST**	**GROUP**	***N***	***M***	***SD***	***SEM***	***t***	**DoF**	***p***
POST-SURG RETRAINING TERM PERF X	T-TEST	**1 CRIT**	**3**	**91.66667**	**2.88675**	**1.66667**	**1.19523**	**5**	**0.28559**
POST-SURG RETRAINING TERM PERF		**2 NO CRIT**	**4**	**90**	**0**	**0**			
POST-SURG RETRAINING MEAN # ERRORS X	T-TEST	**1 CRIT**	**3**	**6.33333**	**3.78594**	**2.18581**	**-0.74055**	**5**	**0.49226**
POST-SURG RETRAINING MEAN # ERRORS		**2 NO CRIT**	**4**	**8.25**	**3.0957**	**1.54785**			
POST-SURG RETRAINING MEAN # TRIALS X	T-TEST	**1 CRIT**	**3**	**33.33333**	**11.54701**	**6.66667**	**-0.75593**	**5**	**0.48376**
POST-SURG RETRAINING MEAN # TRIALS		**2 NO CRIT**	**4**	**40**	**11.54701**	**5.7735**			
VARIABLE									
RELATIONAL TESTING	TEST	**GROUP**	***N***	***M***	***SD***	***SEM***	***t***	**DoF**	***p***
RELAT TEST TERM PERF X	T-TEST	**1 CRIT**	**3**	**93.33333**	**5.7735**	**3.33333**	**3.13055**	**5**	**0.02594**
RELAT TEST TERM PERF		**2 NO CRIT**	**4**	**73.75**	**9.46485**	**4.73242**			
RELAT TEST MEAN # ERRORS X	T-TEST	**1 CRIT**	**3**	**18**	**11.53256**	**6.65833**	**-3.98723**	**5**	**0.01046**
RELAT TEST MEAN # ERRORS		**2 NO CRIT**	**4**	**50.25**	**9.91211**	**4.95606**			
RELAT TEST MEAN # TRIALS X	T-TEST	**1 CRIT**	**3**	**73.33333**	**45.0925**	**26.03417**	**-3.51977**	**5**	**0.01692**
RELAT TEST MEAN # TRIALS		**2 NO CRIT**	**4**	**150**	**0**	**0**			

Table D2

MICROANALYSES OF TE GROUP TE RATS									Two-tailed ($p < .05$)
VARIABLE									
(AVERAGED LESION VOLUMES) [(L+R)/2]	TEST	GROUP	*N*	*M*	*SD*	*SEM*	*t*	DoF	*p*
AVGD L/R LESION VOLUMES X	T-TEST	1 CRIT	3	6.79667	2.18079	1.25908	0.66746	5	0.53404
AVGD L/R LESION VOLUMES		2 NO CRIT	4	5.7575	1.93779	0.96889			
VARIABLE									
(LT LESION VOL VS. RT LESION VOL)	TEST	GROUP	*N*	*M*	*SD*	*SEM*	*t*	DoF	*p*
LT LESION VOLUMEX	T-TEST	1 CRIT	3	8.51	3.4524	1.99325	0.89408	5	0.41224
LT LESION VOLUME		2 NO CRIT	4	6.5925	2.27939	1.1397			
RT LESION VOLUME X	T-TEST	1 CRIT	3	5.07667	1.16543	0.67286	0.1447	5	0.8906
RT LESION VOLUME		2 NO CRIT	4	4.9175	1.59734	0.79867			
VARIABLE									
(LESION LOCATIONS)	TEST	GROUP	*N*	*M*	*SD*	*SEM*	*t*	DoF	*p*
TE1 X	T-TEST	1 CRIT	3	66.83333	13.20353	7.62306	0.03171	5	0.97593
TE1		2 NO CRIT	4	66.5	14.12445	7.06222			
TE3 X	T-TEST	1 CRIT	3	14.5	6.38357	3.68556	0.81569	5	0.45177
TE3		2 NO CRIT	4	9.125	9.84357	4.92178			
VARIABLE									
(LT LESION LOCAT VS. RT LESION LOCAT)	TEST	GROUP	*N*	*M*	*SD*	*SEM*	*t*	DoF	*p*
LEFT LESION TE1 X	T-TEST	1 CRIT	3	86	12.52996	7.23418	1.2876	5	0.25426
LEFT LESION TE1		2 NO CRIT	4	71.5	16.052	8.026			
RIGHT LESION TE1 X	T-TEST	1 CRIT	3	47.66667	21.5484	12.44097	-0.73482	5	0.49544
RIGHT LESION TE1		2 NO CRIT	4	61.5	26.51415	13.25707			
LEFT LESION TE3 X	T-TEST	1 CRIT	3	25.66667	18.33939	10.58825	1.74864	5	0.14077
LEFT LESION TE3		2 NO CRIT	4	9	5.94418	2.97209			
RIGHT LESION TE3 X	T-TEST	1 CRIT	3	3.33333	5.7735	3.33333	-0.67765	5	0.52807
RIGHT LESION TE3		2 NO CRIT	4	9.25	13.98511	6.99256			

APPENDIX E

CORRELATION DATA ANALYSES: LESION QUANTIFICATION METHODS

Table E1

LESION QUANTIFICATION METHODS CORRELATION ANALYSIS DATA PS RATS											Two-tailed ($p < .05$)	One-tailed ($p << .05$)
VARIABLE **DOT GRID METHOD X COMPUTER DIGITAL IMAGING TECHNIQUE (LT/RT HEMS AVGD)**												
	TEST	**PRMTR**	***N***	**VALUE**	**ERROR**	**t-VALUE**	**SD**	**DoF**	**R**	***F***	***p***	***p***
CDIT Top A/P Lesion LENGTH [(L+R)/2] X	LIN REG	**A**	**8**	**-2.09129**	**1.86471**	**-1.12151**	**0.52702**	**1, 7**	**0.86344**	**17.57755**	**0.00573**	**0.002865**
DGM Percent Cortex Removed [(L+R)/2]		**B**		**1.90016**	**0.45322**	**4.19256**						
CDIT Top A/P Lesion WIDTH [(L+R)/2] X	LIN REG	**A**	**8**	**0.16284**	**2.20318**	**0.07391**	**0.72746**	**1, 7**	**0.71774**	**6.37488**	**0.04499**	**0.022495**
DGM Percent Cortex Removed [(L+R)/2]		**B**		**1.88073**	**0.74489**	**2.52485**						
VARIABLE **DOT GRID X COMPUTER IMAGING (LT VS. RT HEMS)**												
	TEST	**PRMTR**	***N***	**VALUE**	**ERROR**	**t-VALUE**	**SD**	**DoF**	**R**	***F***	***p***	***p***
CDIT Top A/P Lesion LENGTH LT HEM X	LIN REG	**A**	**8**	**-1.85427**	**2.11723**	**-0.8758**	**0.9031**	**1, 7**	**0.81988**	**12.30433**	**0.01271**	**0.006355**
DGM Percent Cortex Removed LT HEM		**B**		**1.78523**	**0.50894**	**3.50775**						
CDIT Top A/P Lesion LENGTH RT HEM X	LIN REG	**A**	**8**	**1.48533**	**1.4485**	**1.02542**	**0.40255**	**1, 7**	**0.7792**	**9.27341**	**0.02265**	**0.011325**
DGM Percent Cortex Removed RT HEM		**B**		**1.07722**	**0.35374**	**3.04523**						
CDIT Top A/P Lesion WIDTH LT HEM X	LIN REG	**A**	**8**	**-7.60313**	**3.19162**	**-2.38221**	**0.80639**	**1, 7**	**0.85945**	**16.95811**	**0.00623**	**0.003115**
DGM Percent Cortex Removed LT HEM		**B**		**4.4375**	**1.07758**	**4.11802**						
CDIT Top A/P Lesion WIDTH RT HEM X	LIN REG	**A**	**8**	**3.3485**	**0.93938**	**3.56457**	**0.42933**	**1, 7**	**0.74374**	**7.42749**	**0.0344**	**0.0172**
DGM Percent Cortex Removed RT HEM		**B**		**0.86376**	**0.31694**	**2.72534**						

Table E2

LESION QUANTIFICATION METHODS
CORRELATION ANALYSIS
DATA
TE RATS

											Two-tailed	One-tailed
											($p < .05$)	($p << .05$)
VARIABLE												
DOT GRID METHOD X COMPUTER DIGITAL IMAGING TECHNIQUE (LT/RT HEMS AVGD)												
	TEST	**PRMTR**	***N***	**VALUE**	**ERROR**	**t-VALUE**	**SD**	**DoF**	**R**	***F***	***p***	***p***
CDIT Top A/P Les LENGTH [(L+R)/2] X	LIN REG	**A**	7	**-2.62284**	**0.86341**	**-3.03778**	**0.32582**	**1, 6**	**0.96649**	**70.8710**	**0.000000**	**0.000000**
DGM Perc Cortex Removed [(L+R)/2]		**B**		**2.43874**	**0.28969**	**8.4185**						
CDIT Top A/P Les WIDTH [(L+R)/2] X	LIN REG	**A**	7	**1.23221**	**2.52973**	**0.48709**	**1.08915**	**1, 6**	**0.51342**	**1.78977**	**0.23857**	**0.119285**
DGM Perc Cortex Removed [(L+R)/2]		**B**		**1.50803**	**1.12723**	**1.33782**						
VARIABLE												
DOT GRID X COMPUTER IMAGING (LT VS. RT HEMS)												
	TEST	**PRMTR**	***N***	**VALUE**	**ERROR**	**t-VALUE**	**SD**	**DoF**	**R**	***F***	***p***	***p***
CDIT Top A/P Les LENGTH LT HEM X	LIN REG	**A**	7	**-1.43674**	**2.90862**	**-0.49396**	**1.23772**	**1, 6**	**0.67632**	**4.21515**	**0.09527**	**0.047635**
DGM Perc Cortex Removed LT HEM		**B**		**2.01254**	**0.98026**	**2.05308**						
CDIT Top A/P Les LENGTH RT HEM X	LIN REG	**A**	7	**1.08989**	**1.76813**	**0.61641**	**0.83507**	**1, 6**	**0.67141**	**4.104**	**0.09863**	**0.049315**
DGM Perc Cortex Removed RT HEM		**B**		**1.1861**	**0.58549**	**2.02583**						
CDIT Top A/P Les WIDTH LT HEM X	LIN REG	**A**	7	**-0.38355**	**2.76699**	**-0.13862**	**1.3151**	**1, 6**	**0.62246**	**3.1626**	**0.13548**	**0.06774**
DGM Perc Cortex Removed LT HEM		**B**		**2.02903**	**1.14095**	**1.77837**						
CDIT Top A/P Les WIDTH RT HEM X	LIN REG	**A**	7	**1.81729**	**2.08451**	**0.87181**	**0.96222**	**1, 6**	**0.5204**	**1.85695**	**0.23114**	**0.11557**
DGM Perc Cortex Removed RT HEM		**B**		**1.36916**	**1.00474**	**1.3627**						