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Functions of the Rat's Temporal Association Cortex in Higher Perceptual Functions

Summer L. Maki

Abstract

The role of the rodent temporal cortex in relational perception was investigated. Eighteen Long Evans rats were separated into three surgical groups (sham, partial striate, and Te2/3) and trained on a preoperative and postoperative discrimination task. The rats were then presented a series of relational judgement trials consisting of both between category judgements and within category judgements. It was hypothesized that the rats with Te2/3 lesions would perform as well as controls on the preoperative and postoperative discrimination task, but show a considerable behavioral dysfunction on the tests of visual relational perception. The results showed no differences across groups in the percentage of correct responses made in the visual relational perception task. These findings suggest that visual relational judgement does not appear to be a function of the Te2/3 area in the temporal cortex.

Functions of the Rat's Temporal Association Cortex in Higher Perceptual Functions

Research has found that the visual system in humans can be classified into two components. This dual visual cortical system consists of a dorsal stream pathway that innervates the posterior parietal region and is primarily occupied with visual spatial recognition, and a ventral stream that reaches the temporal lobe and functions to discriminate visual stimuli (Ungerleider & Mishkin,

1982). The ventral stream function is evidenced by deficits of visual perception, namely difficulty in organizing sensory inputs following temporal lobe injury. Inability to perform visual memory and discrimination tasks such as placing words or pictures into categories or recalling nonverbal material such as faces and shapes are indicators of damage to this area of the temporal lobe (Kolb & Whishaw, 1990).

These two cortical visual systems have also been identified in primates. A map of the functional visual system in primate using the [2-14C] deoxyglucose method revealed glucose utilization in the inferior temporal lobe on the ventral pathway and in the posterior portion of the parietal lobe on the dorsal pathway (Macko et.al., 1982). As in human patients, damage to the temporal lobe in primate leads to a loss in the ability to discriminate patterns and an impairment in visual memory. After lesions to the anterior part of the inferior temporal cortex, area TE, primate studies indicate impairment in the retention of visual discrimination tasks obtained both preoperatively and postoperatively (Mishkin, Ungerleider, & Mako, 1983).

Although there have been considerable amounts of research comparing human and primate visual systems, little comparative data exist for other species. The primary concern of our present study is the literature focusing on a homologous visual system in the posterior temporal cortex of rodent. Kolb, Buhrmann, McDonald and Sutherland (1994) conducted a comparative experiment to analyze rodent prefrontal, posterior parietal, and posterior temporal cortices. Lesions to the rat's posterior temporal cortex (area Te2) resulted in deficient learning in a nonmatch-to-sample task. This deficit in visual memory after Te2 lesions is analogous to the impairment seen from posterior temporal lobe injury in primate and human. As a result of these findings, Kolb et. al. (1994) suggested that the dual cortical visual system is as evident in the rodent cortex as in the primate cortex. Tees (1999) also found evidence to support this view. Rodents were assigned to one of three surgical groups: sham, posterior parietal cortex (PPC) lesions, or Te2/3

lesions. Animals with PPC lesions showed significantly less orientation to changes in the spatial arrangement of visual stimuli, whereas the Te2/3 lesion group showed deficits in recognition of auditory and visual stimuli's properties. Tees concluded that the temporal region in rodent is associated with visual memory tasks.

The previous suggestions of a homologous visual system in rodent have been challenged by Ellard (1998). Ellard points out that there have been both supportive (Kolb, Buhrmann, McDonald, & Sutherland, 1994; Tees 1999) and contradictory (Davis & McDaniel, 1993) results for the dual visual system hypothesis. He attributes the lack of conclusive experimental evidence for two cortical visual systems in rodent and other species to the collective conjecture that their visual systems are less differentiated as compared to presumably more advanced species. Ellard suggests that the temporal cortex in rat is not involved in higher order visual processes as it is in primates, meaning the rodent visual system has a more primitive organization.

An additional function of the human inferotemporal cortex has been suggested to be categorical perception. Patients with temporal lobe damage show impairment in their ability to categorize words, or even pictures of various stimuli (Kolb & Whishaw, 1990). This categorical perception function has also been demonstrated in primate (Wilson & DeBauche, 1981). Twelve monkeys were separated into three surgical conditions: lateral striate ablated (a brain injury control group), sham-operative, or inferotemporal-ablated group. The monkeys were trained preoperatively to discriminate between two extreme values, and retrained on the same discrimination task postoperatively. Once the animals mastered the discrimination task, they were given all possible combinations of varying orientation, length or texture of the stimulus. The animals were measured for their ability to discriminate between the various categorical presentations of the stimuli. The experimenters found no significant difference between the groups on the extreme discrimination task, however, the inferotemporal lesion group showed significant difficulty in discriminating the "between-category"

judgements (stimuli that belong to different categories). Wilson & DeBauche concluded that the inferotemporal cortex is involved in this aspect of visual perception as it is in humans.

Williams and McDaniel (1999) were the first to question the possible role of Te2 in the categorical perception of rodent. Their methodology followed many of the procedures utilized by Wilson and DeBauche, with the exception of the preoperative training task and sizes of the categorical stimuli. Contrary to the results observed in the monkeys with inferotemporal cortex lesions and humans with lesions of the inferior temporal gyrus, their data showed that rats with lesions within Te2 perform visual categorical or relational judgments just as effectively as non-brain injured rats. Their results, once again, question the existence of a homologous visual system in the rodent.

The purpose of this study is to settle the issue of whether or not the visual portion of the rat's temporal cortex (Te2) plays a role in categorizing visual stimuli as is the case in monkeys, apes, and man. The study is a follow-up to Williams & McDaniel's (1999) article and the methodology will be similar, however it will include the preoperative discrimination task and a less complicated visual stimulus to parallel further with Wilson and DeBauche's study.

Method

Subjects and Surgery

Subjects were eighteen male Long-Evans rats, purchased from a breeder, ranging in age from 80-95 days at the initiation of the preoperative training. The rats were housed in individual stainless steel cages and provided an ad-libitum schedule of food and water. The animals were maintained on a reversed light-dark cycle with light onset at 8:00 a.m. and offset at 8:00 p.m. All surgical and behavioral procedures were executed during the dark interval of the cycle. All aspects of the methodology were reviewed and approved by the University's Institutional Animal Care and Use Committee. The rats were divided into three surgical groups of six and matched on the basis of their pretraining scores. The three surgical condi-

tions were: partial striate (PS), inferotemporal (Te2/3), or sham. One animal was eliminated from the study due to complications during preoperative training. For details of surgical procedures refer to Williams and McDaniel's (1999) study.

Apparatus and Stimuli

Testing was conducted in a two-choice water maze fitted in an oval water tank. The galvanized steel water tank measured 213 cm in length. The two-choice maze consisted of two galvanized steel partitions. The shortest partition was placed 61 cm from the end of the tank and the remaining partition was arranged perpendicular to it. The tank was filled with water and Bromide tablets were added approximately every ten days to discourage microbiological growth. White nontoxic temptra paint was added to the water to obscure the view of a white escape platform that was slightly submerged 4 cm below the surface of the water. The distance between the start point and the escape platform was 152 cm.

The visual stimuli consisted of two black stripes constructed of pieces of wood and measuring 2.58 cm wide by 12 cm long attached to a 14 cm diameter circular white "clock face-like" background. The stripe could be manipulated on each stimulus to various positions between zero and 90 degrees.

Preoperative and Postoperative Training Procedures

Prior to surgery, the rats were trained to discriminate between two extreme values: a 0-degree black stripe and a 90-degree black stripe on a white background. The positive stimulus (0 degrees) served as the cue for the submerged escape platform. The left-right alley positions of the S- and S+ stimuli and the escape platform were randomized using a Fellows (1967) series. At the beginning of the trial, the rats were placed with heads facing the front wall of the tank. Once the animal rotated to face the stimuli, it swam toward the choice alleys. Correct responses were defined as entry into the alley containing the positive stimulus following escape onto the submerged platform. Errors were defined as entry into the alley containing the negative stimulus to the point where the root of the

tail crossed a predetermined mark on the tank. Animals were permitted to correct their incorrect choices and allowed to remain on the platform for 10 seconds. Animals were administered 12 trials per day until they reached a criterion of 11 out of 12 errorless alley choices within a single training session. Once the behavioral criterion was acquired, the animals underwent surgery.

After the recovery period from the operation, all animals were retrained on the visual discrimination task. After once again meeting the criterion of 11 out of 12 errorless choices, the animals began the visual relational perception task.

Visual Relational Perception Task

Utilizing the same construct for error identification, each animal received a series of trials wherein the angles of the stimuli, with reference to the horizontal axis, differed from those experienced during training. The animals were given 120 trials at a rate of 12 trials per day (three exposures to each stimulus pair per testing session) where the stripes were oriented 10 vs. 40, 20 vs. 50, 40 vs. 70, or 50 vs. 80. The stimulus that was most similar in orientation to the previously trained stimulus (0 degrees) cued the escape platform location. Some of the trials were considered "within category problems" (e.g., 10 vs. 40 and 50 vs. 80) and others were considered "between category problems" (e.g., 20 vs. 50 and 40 vs. 70).

Histology

After the completion of the experiment, the animals with PS and Te2/3 lesions received lethal injections of sodium pentobarbital. The animals were perfused through the heart with 50 cc of a saline, dextrose, sucrose, calcium chloride and sodium cacodylate solution followed by 50 cc of a paraformaldehyde, sucrose and sodium cacodylate solution. The rats were decapitated and placed in a container filled with perfusion fix solution for at least 24 hours to allow the brain to fully harden into the proper form. The brains were then extracted, photographed, and stored in the perfusion fix. The specimens were shipped overnight to NeuroScience Associates in Knoxville, Tennessee. At the neuro-histology lab, the brains

were embedded together, freeze-sectioned at 40 μ in the coronal plane through the posterior cortex (approximately 10 mm in length). Every eighth section (320 μ mm intervals) was stained using thionine to reveal cell bodies. Once brains were returned, they were analyzed for evidence of retrograde degeneration in the thalamus, for lesion accuracy, and for lesion depth.

Results

Lesion Analysis

Figure 1 displays representative photographs of PS lesions and Te2/3 lesions. The lesion locations appeared to be parallel to that described in previous studies (Davis & McDaniel, 1993; Meyer, Meyer & Cloud, 1986; Tees, 1999). Microscopic examination of the coronal sections revealed that the PS lesions removed amounts of Zilles' (1985) Oc1M and Oc2L, and portions of Oc2MM and Oc2ML. Patchy gliosis, cell loss, and cell shrinkage was often observed in the lateral geniculate nucleus.

Lesions of the temporal cortex invaded large portions of Zilles' (1985) Te2/3, the posterior region of Te1, and a small amount of the lateral border of lateral peristriate cortex (Oc2L). There was evidence of patchy gliosis or necrosis in the lateral, posterior, and medial geniculate nucleus in some animals. Topographical representations of the lesions in PS and Te2/3 are displayed in Figure 2.

Preoperative and Postoperative tasks

To accommodate the statistical program used (i.e., equal means for the factorial ANOVA program), scores were projected for a rodent that failed to learn the discrimination task preoperatively by calculating the mean of all scores. Thus, there were actually six animals in the two lesion groups and five in the sham control group.

Preoperative and postoperative errors are presented in Figure 3. The results indicate that the animals required on average 114 trials to learn to discriminate between two extreme values (0

degrees vs. 90 degrees). After surgery, the animals were retrained on the same tasks and required an average of 32 trials to reach the criterion. An analysis of variance for a 3 x 2 split-plot factorial (SPANOVA) indicated that all animals displayed a significant decrease in the number of errors preoperatively vs. postoperatively, $F(1,18) = 292.26$, $p < .0001$. There was no interaction between lesion placement and number of errors, $F(2,27) = 0.47$, $p > .05$ and no main effect between the lesion groups, $F(2, 17) = 0.65$, $p > .05$. This research shows that lesion placement did not adversely affect retention of the extreme discrimination task after surgery. As expected, a two-way ANOVA revealed no significant differences among the three surgical groups in the amount of savings between preoperative and postoperative tasks, $F(2, 17) = 2.98$, $p > 0.05$.

Visual Relational Perception Tasks

The test for categorical perception involved comparing the proportion of correct responses for between category stimuli vs. within category stimuli as a function of surgical group. As shown in Figure 4, a repeated measures 3 X 2 SPANOVA failed to reveal an interaction between lesion and categorical stimuli, $F(2, 18) = 0.73$, $p > .05$, or a main effect for lesion group $F(2, 17) = 0.03$, $p > .05$. There was a main effect for between category versus within category discriminations, $F(1, 18) = 4.62$, $p < .05$. Most animals performed slightly better on the between category groups (i.e., 40 vs. 70 and 20 vs. 50; 62% correct) than on the within category groups (i.e., 10 vs. 40 and 50 vs. 80; 59% correct). Behavioral observations indicated a decline in performance across trial days. As a more refined measure, a SPANOVA was used to analyze proportion correct across blocks of two days. There was a significant block main effect $F(4, 60) = 4.41$, $p < .01$. This effect showed that all groups performed at a higher level of accuracy on the initial days with novel stimuli (e.g. mean block, pooled across lesion groups = 66% accuracy) than on later blocks (e.g. mean blocks = 54% accuracy).

Discussion

This study explored the function of the rodent Te2/3 area in relational perception. Rats were trained to discriminate between two extreme stimuli (0 degrees vs. 90 degrees) and then matched to one of three surgery groups: sham, partial striate, and Te2/3 on the basis of the number of preoperative errors made before reaching criterion. The animals underwent surgery and then were retrained on the preoperative task. Once the behavioral criterion was met postoperatively, the rats were presented with 120 trials of paired novel stripe orientations. On this task, the pairs of stimuli were considered either between category problems (i.e., 40 vs. 70 and 20 vs. 50) or within category problems (i.e., 10 vs. 40 and 50 vs. 80).

It was hypothesized that the rats with Te2/3 lesions would perform as well as controls on the preoperative and postoperative discrimination task. Analysis of the data revealed no differences between surgical groups in retention rate of the preoperative task after surgery. This finding is consistent with previous studies on categorical perception in monkeys (Wilson & Debauch, 1981) and rats (Williams & McDaniel, 1999). Since these tasks do not involve the use of relational judgments, differences between the Te2/3 group and control groups were not anticipated. The difference was expected to manifest during the test of relational perception, however, the proportion of correct responses in the relational task was similar across groups. Not only were no differences seen between the groups, but no animal successfully performed the relational discrimination task with a high level of proficiency.

Generally, across groups the animals performed better on the between category judgments than the within category judgments and this finding parallels that of Wilson and Debauche (1981) and Williams and McDaniel (1999). Within category judgments appear to be more difficult to discriminate since both stimuli share much in common with one or the other of the original stimuli. Additionally, behavioral observations of the visual relational perception tasks indicated that as performance accuracy across trials eroded, animals seemed less motivated and swam slower. errors.

The findings in this study are consistent with the results from Williams and McDaniel's (1999) study of relational judgements in rat. This is the second experimental support for the suggestion that rodents, whether lacking temporal cortex areas or not, fail to possess the capacity to perceive relational judgements. Williams and McDaniel attempted to experimentally substantiate this relational perception in rats, yet their experiment revealed that rodents in all surgical groups were not able to perform the relational judgement tasks. It was thought that closer parallels between Wilson and Debauche's (1981) behavioral protocol in the present study would yield more positive results than the previous attempt. As opposed to this study, Williams and McDaniel did not include a preoperative task and their stimuli were not controlled for luminous flux as potential discriminanda. Despite these methodological differences between this experiment and Williams and McDaniel's experiment, there was no evidence that rodents were able to perform relational perception tasks. This leads to the suggestion that relational judgement, as defined here, is a higher order task not able to be accomplished in rodent. Rodent may not possess the visual abilities to perceive relations. Furthermore, this research also conveys additional knowledge regarding the proposed dual visual system in rodent. Although relational(categorical) perception seems to be a function of the temporal cortex in human and primate, this area in rodent may not be involved in tasks of relational perception. This suggests that the proposed ventral stream of the dual visual system in rodent is not homogenous to higher order species.

At the beginning of this study, there was an underlying assumption that the rodent would possess visual perception similar to higher order animals. As Dean (1990) points out in his review of visual perception functions in rodent, the visual cortex is "far from homogeneous but, as in other species, contains a number of representations of visual space." Naturally, as the term "higher order" implies, the specialized relational perception tasks that are accomplished by more developed species would not be seen in rodent. For this reason, the use of simple discriminanda was utilized in an attempt to uncover a much more simplistic form of relational perception.

Many researchers would argue a relational perception task for rodents would be too difficult because rodent visual ability is quite different than higher order species both functionally and anatomically. Dean (1990) goes on to point out that the primate visual cortex receives geniculostriate input, yet rats predominantly receive input from tectocortical projections. He hypothesized that the influence of the tectocortical projection corresponds to more primitive species and that inputs from geniculostriate evolved later in certain species. Dean says that the major use of vision by rats is to detect predators and prey and for navigational purposes. This requires rats to have a keen system for the visual detection of motion and the ability to attend to spatial cues. Rats, in other words, would not benefit from a highly organized system to recognize and categorize objects, therefore, even simplistic visual perception tasks would prove difficult for the rodent.

Trevarthen (as cited in Dean, 1990) also explored comparative visual systems and proposed that characteristics of the vision of primitive animals involved ambient vision. He described that animals with ambient vision possess a low resolution for fixed stimuli and a deficit in the ability to discriminate hues, orientation, or luminance. However, animals with ambient vision do possess an impeccable ability to perceive a change in motion of stimuli.

Ellard (1998) also suggested that rodent visual system is well suited to spatial and navigational tasks. He argued that rodents lack foveal vision for visual acuity. Therefore, a specialized area for object recognition in rats, again, would not prove to be beneficial since their vision lacks this acuity.

This evidence that rodents possess different visual perception abilities than more advanced species also calls into question the possibility of a homogenous dual visual system in rodent. Ellard (1998) attempted to behaviorally dissociate the dual visual system by studying predator behavior in gerbils. He found that the gerbils solved object identification problems on the basis of low frequency spatial information. Ellard contended that this information does not necessarily disprove the dual visual system hypothesis in rat. He proposed that the ventral stream in species with limited visual abil-

ities to recognize objects may be involved in the topographical representation of space and the dorsal stream may guide movements to targets. Therefore, in Ellard's view, both streams play a role in the coordination of movement in these species. Similarly, the function of the ventral stream for keen relational judgements may have evolved later.

Ellard's viewpoint may explain why the attempts to behaviorally dissociate the two streams by focusing on object recognition have been somewhat ambiguous. Meyer, Meyer and Cloud (1986) studied lesions of the temporal neocortex and visual areas in 17, 18, 18a, and 7 compared to sham controls. The rats were first given a black and white discrimination test and then the same stimuli was inverted as a measurement of visual perception. The temporal lesioned rats were able to solve the simple discrimination visual task, but when the same stimuli were inverted, the rats could not perform the task. The visual area lesioned rats were not able to perform the visual perception tasks. The researchers concluded that the temporal neocortical injuries in rats resulted in impairments of attention and not complex visual perception difficulties.

Davis and McDaniel (1993) also attempted to dissociate the visual pathways. They trained rats with PP, Te2, or sham lesions on a visual matching to sample task and a visual-spatial nonconceptual conditional problem. They failed to find a behavioral dissociation between the lesion groups. McDaniel and Skeel (1993) applied more stringent methodology to the above study by incorporating a less demanding visual-spatial tasks and the use of punishment upon incorrect choices. McDaniel and Steel obtained similar results despite alterations of the stimuli and behavioral criterion.

Although some studies have failed to behaviorally dissociate the two cortical pathways, others have detected behavioral differences. Tees (1999) conducted an experiment to compare performance of sham PPC, and Te2/3 groups. Tees introduced novel objects in an open field arrangement and looked at whether the animal habituated to the environment. This required the rodent to detect a difference from the old environment and the new environment. The sham and Te2/3 dishabituated in this environment, how-

ever, the PPC did not. His evidence also revealed that Te2/3 rodents took longer to make object-place associations. Tees concluded that these distinct differences between the two lesion groups further supports that there are two visual pathways in rodent that are involved in different perceptual functions.

The current study was another attempt to compare the function of the ventral pathway in higher order species to rodent. Relational judgement (categorical perception) has been hypothesized to be a function of the ventral cortical visual pathway. Specifically, efforts were made to establish whether relational judgements in Te2 lesioned rodents would be impaired. This project has advanced our knowledge concerning the comparative functional neurology of the temporal cortex. That is, although the dual visual system may exist in rat, the ventral stream does not appear to be involved in relational or categorical perception as is true of primate and humans. As Dean (1990) emphasized, the rodent visual system is not studied for only localized knowledge of the rat visual ability, but how it relates to other visual cortical organization in animals.

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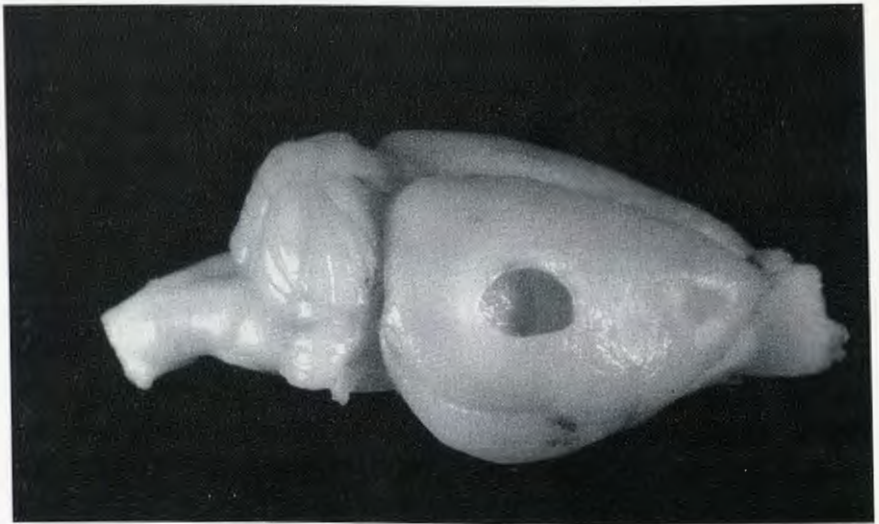
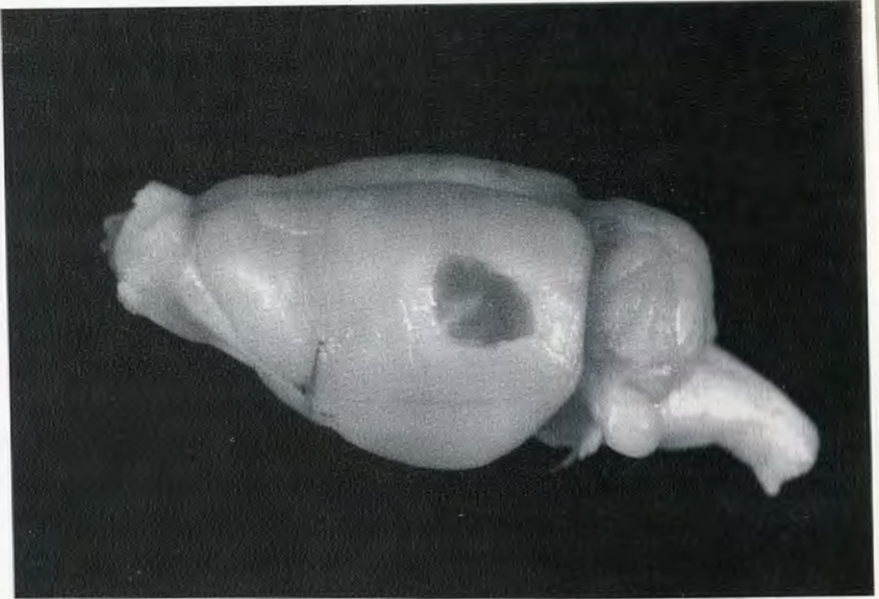


Figure 1a. Photograph depicting representative partial striate lesions as viewed from the dorsal perspective.



Figure 1b. Photographs depicting representative temporal lesions as viewed from the lateral perspective



Figure 2a. Coronal sections depicting topographical alterations induced by PS lesions. Approximate distance in mm posterior to Bregma ranges from -2.8, -3.6, - 4.6, -5.8.

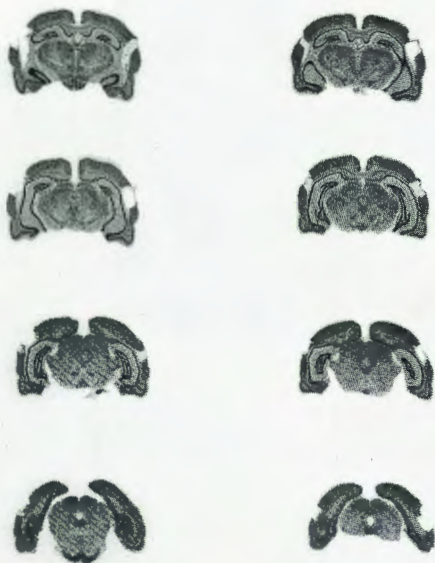


Figure 2b. Coronal section depicting topographical alterations induced by Te2/3 lesions. Approximate distance posterior to Bregma ranges from -2.8, -3.6, - 4.6, -5.8.

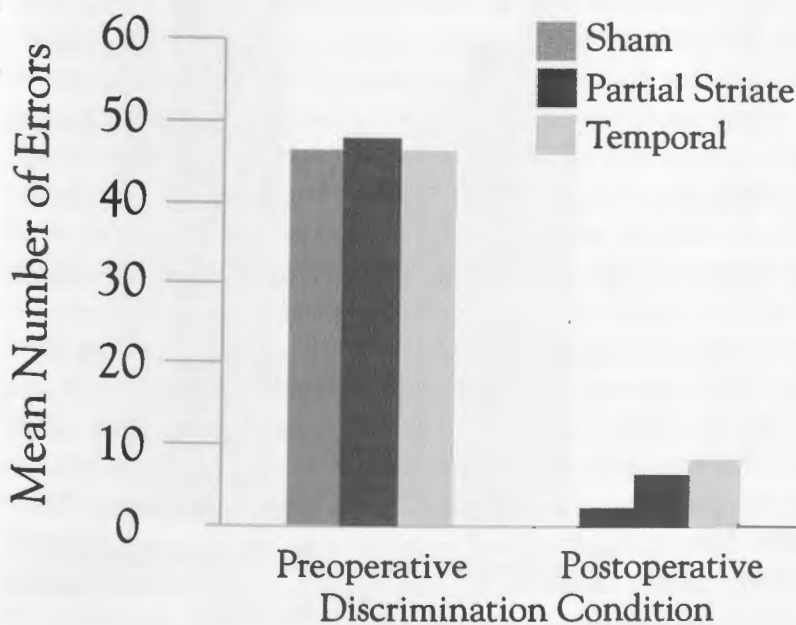


Figure 3. Mean and standard error of the number of errors committed through criterion across surgical conditions for the preoperative and postoperative task.

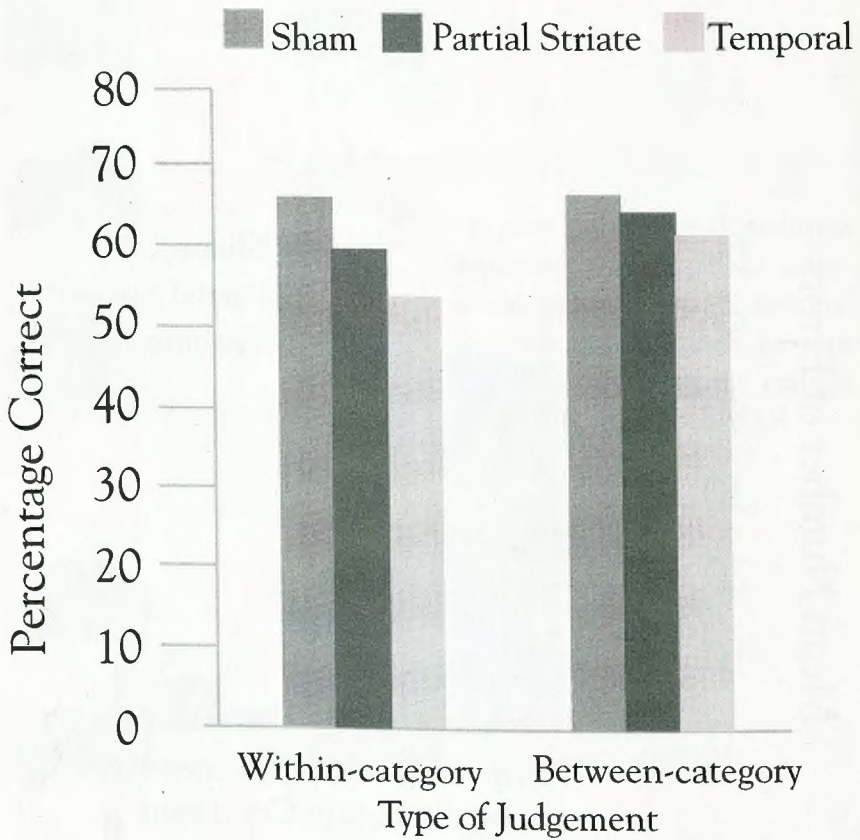


Figure 4. Mean and standard error of the percentage of correct responses across lesion groups for between-category (i.e. 10 vs. 40 and 50 vs. 80) and within-category judgements (i.e. 20 vs. 50 and 40 vs. 70).