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THE EFFECTS OF SUPERIOR COLLICULUS AND/OR STRIATE CORTEX ABLATIONS ON VISUAL SPACE LOCALIZATION BY MONKEYS

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by

STEPHEN JAY SOLOMON

A dissertation submitted to the Graduate
Faculty in Psychology in partial fulfillment of
the requirements for the degree of Doctor of
Philosophy, The City University of New York.

1980

This manuscript has been read and accepted for the Graduate Faculty in Psychology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

August 20, 1980
Date

Chairman of Examining Committee

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Abstract

THE EFFECTS OF SUPERIOR COLLICULUS AND/OR STRIATE CORTEX ABLATIONS ON VISUAL SPACE LOCALIZATION BY MONKEYS

by

Stephen Jay Solomon

Adviser: Professor Pedro Pasik

Recent experiments have demonstrated that destriated rhesus monkeys could be trained to reach accurately for visual targets presented at random in space. Although the superior colliculi were considered to be the most likely candidates for subserving spatial localization in the normal animal, this function persisted after colliculus removals. In the absence of striate cortex, however, the colliculi have been shown necessary for monkeys to perform a brightness and/or area discrimination when the figures were equated for total luminous flux, since the animals failed to discriminate between flux differing targets when the latter structures were subsequently destroyed. The primary purpose of this study was to determine whether the integrity of the superior colliculus was critical for spatial localization, as measured by accurate reaching, in destriated monkeys. Since striatectomies and colliculectomies were performed in a counterbalanced order with inter-operative testing, there was also the opportunity to re-examine the effects of individual lesions on spatial localization.

The subjects were 12 monkeys (Macaca mulatta), ranging in weight from 2.3 -2.9 kg, which were tested under normal room illumination. The Task required the animal to reach for a target randomly placed in one of eight octants, and having an apple cube affixed to the center. A correct response consisted of an initial contact with either the target or apple cube directly, the latter serving as the reward. Therefore, the discriminanda, manipulanda, and reinforcement were congruent thereby maximizing the possibilities of successful performance. Each monkey was trained sequentially to a criterion level of 90% correct responses in four consecutive 56-trial sessions using black disks of decreasing diameters (viz. 90 mm, 55 mm, 35 mm and 15 mm) and finally for the apple cube (about 10 mm on a side) presented alone. All ablations were made by visualization through an operating microscope, under general anesthesia and aseptic conditions. The lesions were reconstructed from serial histological sections.

Five animals with only bilateral colliculectomies, of which four were complete, performed just as accurately as before the lesions. In contrast, six of the monkeys with only bilateral striatectomies, all of which were complete, could be trained to reach accurately for all targets but with marked deficits on the first and last tests. The ablations were combined in seven of the subjects. The four animals with total collicular destruction and/or degeneration, failed to solve the task in almost 6,000 trials (i.e., 107 testing sessions). The other three monkeys, with as much as 60% of the colliculus volume aspirated and almost 80% of the surface area destroyed, showed a minimal deficit only on the first task.

These results indicate that the superior colliculi are critical structures for spatial localization in the absence of striate cortex. In addition, the findings confirm previous studies which showed that monkeys with total bilateral striatectomies could reacquire the ability for visually guided accurate reaching, and that the superior colliculi were not crucial structures for this capacity in otherwise intact animals. Together with earlier findings, the outcome of the present study emphasizes the primary importance of the geniculostriate system for the function explored, and moreover does not support a sharp dichotomy of two independent visual systems in the monkey.

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CHAPTER I

INTRODUCTION

Residual vision in monkeys with complete bilateral destruction of the striate cortex has been demonstrated through the relearning of both visual discrimination and spatial localization tasks. Initially, Klüver (1941, 1942) concluded that destriated monkeys had lost all "approximate perceptual constancies" in that spatial relationships were no longer effective in directing behavior. These animals could not solve most visual discriminations, except for those in which the stimuli differed in total luminous flux, and consistently failed to localize targets when their position was varied at random. Later studies confirmed and extended Klüver's observations with respect to the severity of the disruptive effect on previously learned visual tasks, the exclusive use of luminous flux cues when available to the animal as part of the testing procedure, and the initial loss of visual localization capacities. In contrast with Klüver's conclusions, however, it was shown subsequently that destriated monkeys were able to relearn visual discriminations using transilluminated figures differing in area and brightness but equated either for flux alone (Pasik, Pasik, & Schilder, 1969), flux and total overall area, or flux and contour (Schilder, Pasik, & Pasik, 1971). Other monkeys with similar lesions mastered a triangle vs circle task in which area, perimeter and brightness were systematically varied (Pasik & Pasik, 1971; Schilder, Pasik, & Pasik, 1972). They could be trained also to discriminate the orientation of vertical vs horizontal bars of equivalent dimensions (Pasik, Pasik, Nolan, & Solomon, 1976; Pasik, Pasik, Nolan, Solomon, & Feinberg, 1977), and could solve problems using multi-element stimuli equated for flux, contour, corners and number of elements (Keating & Dineen, 1980, in press). Some of the earlier results do not preclude the possibility that flux differences were created behaviorally by the animal in the process of scanning the targets, in which case gradients in the rate of luminous flux change possibly served as the effective cues mediating successful performance. Nervertheless, this explanation cannot apply to the demonstration of relative constancies, such as brightness/area (Schilder et al., 1971), color (Keating, 1979; Schilder et al., 1972), and pattern (Pasik & Pasik, 1971; Schilder et al., 1972).

Even though the striatectomized monkey was able to perform many visual discriminations, there was a marked decrement in the capacity for processing incoming visual information. The photopic spectral sensitivity curve became displaced in the direction of the scotpic range in these animals (Leporé, Cardu, Rasmussen, & Malmo, 1975) and threefold increases occurred in differential achromatic thresholds determined under both scotopic and photopic levels of illumination (Leporé, Ptito, Cardu, & Dumont, 1976). Comparable findings have been reported with respect to the large increments in the stimulus intensity that were required to reinstate the detection of a punctate light presented within a scotoma of cortical origin (Mohler & Wurtz, 1977; Weiskrantz & Cowey, 1970). Moreover, monkeys with complete bilateral striate cortex removals demonstrated an increased threshold for detecting a deviation from the vertical (Pasik et al., 1976; Pasik et al., 1977), a decrease in the maximum resolvable spatial frequency, and higher contrast thresholds for the individual supraliminal gratings (Miller, Pasik, & Pasik, 1980).

Discriminative capacities were also investigated in the tree shrew after resection of the striate cortex. These animals, considered to be prosimians, failed to exhibit postoperative deficits in the initial acquisition or relearning of: simultaneous and successive discriminations of vertical vs horizontal stripes (Snyder, Killackey, & Diamond, 1969; Ware, Casagrande, & Diamond, 1972; Ware, Diamond, & Casagrande, 1974); reversal learning sets using pairs of black-white, blue-red, and horizontal-vertical striped stimuli; and the discrimination of successively finer stripes (Snyder et al., 1969; Ware et al., 1972; Ware et al, 1974). Striatectomized tree shrews, however, did suffer significant acuity losses (Ward, Frank, & Moss, 1975; Ward & Masterton, 1970), were unable to discriminate a triangle embedded in an annulus, and failed to master tasks in which either irrelevant background features were added or the rewarded stimulus was varied across testing sessions (Killackey, Snyder, & Diamond, 1971; Killackey, Wilson, & Diamond, 1972).

In addition to the residual discriminative abilities shown by destriated monkeys, some capacity for spatial localization was suggested by the work of Humphrey (Humphrey, 1974; Humphrey & Weiskrantz, 1967) who conducted an in-depth study on one monkey with an almost complete striate lesion. The animal gradually began to pursue visually, to reach accurately for small targets, and avoided obstacles in its path. The histology, however, revealed the preservation of a small remnant of striate cortex within the depths of the calcarine fissure that corresponded to the far peripheral field. These behaviors were subsequently observed in monkeys complete deprived of striate cortex (Feinberg, Pasik, & Pasik, 1977, 1978; Keating, 1980; Weiskrantz, Cowey, & Passingham, 1977). Although the accuracy of making oculomotor saccades was not studied in these preparations, Mohler and Wurtz (1977) reported that monkeys with partial striate cortex lesions regained the ability to perform accurate saccadic eye movements to the location of a punctate light flashed for 150-200 msec within the limits of the scotoma.

In summary, while the complete removal of striate cortex in primates constricted the scope of sensory functioning, relearning differential responses to a variety of visual stimuli was not only possible but in some instances very remarkable. The total destruction of the geniculostriate system did not abolish visually guided reaching accuracy or the orientation of gaze toward visual stimuli. It is interesting to note that Orbach (1959) has reported a deficit in maze learning following visual cortex removals in monkeys previously blinded by enucleation. In the final analysis, such non-specific effects of striatectomy cannot be ignored particularly in relation to the retention and reacquisition of previously learned habits.

Attempts have been made to determine which critical structures subserve the residual visual capacities in the absence of striate cortex. Traditionally, the superior colliculus was believed to be the most likely candidate on anatomic and physiologic bases. In fact, the optic tectum of submammalian vertebrates has been considered the homologue of visual cortex, anatomically in terms of the laminar arrangement and physiologically with respect to the receptive field organization. Anterograde degeneration (Pollack & Hickey, 1979; Wilson & Toyne, 1970) and autoradiographic techniques (Hubel, LeVay, & Wiesel, 1975; Pollack & Hickey, 1979) have revealed a topographic representation of the visual fields upon the surface of the superior colliculus, which in addition was shown to receive indirect visual input from striate cortex in both the monkey (Lund, Lund, Hendrickson, Bunt, & Fuchs, 1976; Wilson & Toyne, 1970) and the tree shrew (Casseday, Jones, & Diamond, 1979). The superior colliculus in turn projects to the lateral geniculate nucleus pars dorsalis and pars ventralis, inferior pulvinar and prectectum (Benevento & Fallon, 1975; Benevento & Rezak, 1976; Harting, Casagrande, & Weber, 1970), as well as to other "non-visual" thalamic nuclei (Benevento & Fallon, 1975). The deeper strata receive spinotectal fibers from high cervical levels (Mehler, Feferman, & Nauta, 1970) and send efferents back to this region of the spinal cord and, at least in the cat, to the brain stem reticular formation (Altman, 1962).

Unilateral stimulation of the superior colliculus elicited a contralateral conjugate deviation of the eyes (Adamük, 1870; Faulkner & Hyde, 1958; Schiller & Stryker, 1972). This finding led to the conclusion that the tectum was a "visual grasp reflex center" responsible for foveation (Hess, Bürgi, & Bucher, 1946). Electrical recordings support this hypothesis. Thus neurons with the shortest latency and maximal discharge rates preceding eye movements of a specific amplitude and direction were identified in the intermediate and deep layers of the colliculus (Mohler & Wurtz, 1976; Robinson & Jarvis, 1974; Sparks, 1975; Sparks, Holland, & Guthrie, 1976; Wurtz & Goldberg, 1971, 1972). Other units in these lamina were differentially responsive to voluntary, as opposed to reflexive, saccades (Mohler & Wurtz, 1976). Finally, similar experiments corroborated the topographical representation of the visual field upon the surface of the colliculus (Cynader & Berman, 1972; Goldberg & Wurtz, 1972) and have studied the influence of the corticotectal input (Schiller, Stryker, Cynader, & Berman, 1974).

In contrast to the anatomical and physiological evidence offered above, destruction of the colliculus in the otherwise intact brain did not produce gross defects in visually guided behaviors or in oculomotor responsiveness (Pasik, Pasik, & Bender, 1966). Notwithstanding a variety of qualitative disturbances which have been described in bilaterally colliculectomized monkeys (e.g., losses of object identification, binocular fixation, and visuo-social behavior, Denny-Brown & Fischer, 1976), the initial learning of a simple pattern discrimination (Rosvold, Mishkin, & Szwarcbart, 1958), or the retention of other visual problems (Anderson & Symmes, 1969; Thompson & Myers, 1971; Vetter, 1975) were not affected by superior colliculus ablations. Subtle quantitative deficits did emerge, however, when the demands of the task were made more difficult (Anderson & Symmes, 1969; Butter, 1974a; Keating, 1976; Vetter, 1975), and when absolute (Latto, 1977) or differential brightness thresholds were determined (Leporé, Ptito, Cardu, & Dumont, 1976). It must be emphasized that recovery to the preoperative performance levels was possible in all cases.

Spatial localization following colliculus lesions has been investigated in several ways. Using the accuracy of oculomotor responses, Schiller and Koerner (1971) observed that these ablations were accompanied by a "persistent inability to acquire visual targets" through saccadic eye movements. More recently, however, Schiller, True, and Conway (1979) found only subtle deficits in the accuracy, number, size, and velocity of saccades, while Mohler and Wurtz (1974, 1977) reported just slight increases in the response latency and in the frequency of small secondary saccades required to fixate. A marked impairment of this response occurred when either the duration of the stimulus was reduced to 50 msec, or the location was beyond 43° from the fovea (Butter, Weinstein, Bender, & Gross, 1978). Accurate saccades were reinstated by presenting the stimulus within the central 43° of fixation or by increasing the duration of the flash to 1 sec. Apparently, therefore, this deficit was related more to the detection of briefly presented lights than to an impairment in localization. The conclusion of Latto and Marzi (1975) that colliculectomized monkeys have a "deficit in absolute localization and an impairment in spatial attention," was not confirmed by other investigators (MacKinnon, Gross, & Bender, 1976; Keating, 1974; Vetter, 1975). Since the defect was revealed only when the duration of the discriminative cue was reduced to 1 sec., the impairment was attributed to an alteration in oculomotor function rather than to an underlying disturbance in spatial orientation (MacKinnon et al., 1976). This interpretation, however, is inconsistent with the findings that colliculus-lesioned monkeys were no more impaired than normals in reaching for objects while wearing displacement prisms (Bossom, 1972) or in saccadic accuracy to light flashes briefer than 1 sec. (Butter et al., 1978; Mohler & Wurtz, 1977).

In summary, ablation of the primate superior colliculi does not permanently affect the accuracy of performing spatial localization and orientation tasks. The conditions under which deficits occur are related to manipulating the likelihood of detecting the stimulus and, therefore, it cannot be concluded that the superior colliculi are necessary for mediating the visual capacities thus far studied.

In spite of the above findings, it is still possible that the superior colliculi are critical for the residual vision observed after striatectomies. In fact, combined, complete, bilateral striate cortex and superior colliculus resections had a severely disruptive impact on a wide range of visually guided behaviors. In such monkey preparations, however, discriminations between stimuli differing in total luminous flux could be established, but only after extensive retraining (Anderson & Symmes, 1969; Pasik & Pasik, 1971; Pasik, Pasik, Schilder, & Wininger, 1973; Wininger, Pasik, & Pasik, 1972). Preoperative criterion performance levels were attained on a light vs no-light discrimination following complete bilateral striatectomy and also after superior colliculus ablations (Pasik & Pasik, 1973). This latter task required the animal to reach out and press one of two randomly lit neon lights which appeared in fixed locations. The integrity of the accessory optic system was shown to be essential for this residual vision (Pasik & Pasik, 1973; Pasik & Pasik, 1971, 1973). In another experiment, the discrimination between two transilluminated stimuli equated for surface area but differing in brightness and flux could be re-established, but the monkeys were unable to distinguish flux-equated targets of unequal area and brightness (Pasik et al., 1973; Wininger et al., 1972). Anderson and Symmes (1969) concluded that the cortical lesions potentiated the loss from prior colliculus ablations, changing the deficit qualitatively from one of a rate detection impairment to a generalized inability to make difficult discriminations (see Orbach, 1959).

Monkeys with partial lesions of the colliculi and striate cortex did not show deficits in the retention of pattern, size, and brightness discriminations, and it was assumed that this was due to the preservation of some collicular tissue (Butter, 1974b). Although incomplete lesions of either the striate cortex or the superior colliculus did not eliminate the detection of or the ability to direct accurate saccades to a brief punctate light stimulus, neither response was possible when light appeared within a region of overlapping scotomata of cortical and collicular origins (Mohler & Wurtz, 1977). Commenting on these findings, Feinberg et al. (1978) observed that leaving large portions of the visual system intact or the relatively taxing nature of the stimulus parameters could account for these results since failure to detect the stimulus would logically preclude its localization.

The effect of combined ablations of striate cortex and colliculi have been investigated also in non-primate species. In the cat, Sprague (1966) has demonstrated the partial recovery of vision in a hemianopic field due to a unilateral striatectomy, by the subsequent removal of the contralateral superior colliculus. A similar result was obtained in the rat (Kirvel, Green, & Meyer, 1974). After more extensive combined bilateral lesions in the cat, a retention deficit occurred on a light-dark discrimination task with subsequent relearning (Fischman & Meikle, 1965; Urbaitis & Meikle, 1967). Inasmuch as the eventual magnitude of this impairment was not substantially affected by the ablation sequence, the cortical lesions alone always produced the most severe defect. Radical resections removing both structures in one stage did not prevent cats from relearning brightness and flicker discrimination problems (Norton & Clark, 1963). Although rats retained a flux discrimination following the addition of colliculus lesions to prior visual cortex excisions (Thompson & Rich, 1963; Horel, 1968), visual cliff performances were impaired (Cheney & Crow, 1969). Moreover, Lashley (1926) observed severe behavioral deficits in rats which sustained extensive concurrent damage to both structures.

From the foregoing, it is clear that in destriated monkeys, the superior colliculi appear crucial for solving visual discrimination tasks using flux-equated figures (Pasik et al., 1973; Wininger et al., 1972) whereas the accessory optic system is essential for performing tests with flux-differing targets (Pasik & Pasik, 1973). The critical structure(s) responsible for mediating spatial localization in the absence of striate cortex have yet to be identified. The primary purpose of the present endeavor was to determine whether the superior colliculi were necessary for accurate reaching in the destriated monkey by combining these ablations in the same animal. Since the excisions were performed in a counterbalanced order with intervening testing, there was also the opportunity to re-examine the effects of each individual lesion.

A preliminary report of these findings has been presented earlier (Solomon, Pasik, & Pasik, 1979).

CHAPTER II

METHOD

Subjects

Six male and six female adolescent rhesus monkeys (Macaca mulatta), ranging in weight from 2.3 kg to 2.9 kg at the beginning of training, participated in this experiment. Table 1 provides individual data on these animals. Eight of them were experimentally naive. Five of these eight sustained bilateral superior collicular ablations first followed by bilateral occipital lobectomies, two were given the same lesions in the reverse order, and the last sustained a lesion of the cerebellum and then occipital lobectomies. The remaining four monkeys had prior visual training in a two-choice visual discrimination using transilluminated targets in which a pulling-in response was required (Schilder et al., 1971) and underwent operations of the brain in the general region of the superior colliculi in addition to their initial occipital lobe removals. The eight naive monkeys were tested beginning on the seventh postoperative day, while the latter animals had three to five months postoperative recovery, after each surgical procedure, before they participated in this experiment.

The monkeys were individually caged in a colony room in which the light dark cycle was 12/12 hr. and the temperature was regulated between 68° and 72°. Their diet consisted of Purina Monkey Chow, micromixture, supplemented daily with 1 ml of liquid vitamins (Poly Vi-Sol Multivitamins, Mead Johnson), and fresh fruit, as testing permitted. During formal testing, the monkeys were maintained between 85-90% of their free-feeding weight, determined initially upon entry into the experiment and recalculated following each surgical procedure.

Table 1. Information About Individual Subjects

Monkey Number	Sex	Weight[a] (Kg)	Ablation Sequence	Postop-Test[b] Period (Days)	Survival[c] (Days)
848*	Female	2.30	STR.	151	
			THA.	113	128
849*	Male	2.35	STR.	120	
			THA.	81	132
850	Female	2.40	S.C. Bil.	7	
			STR.	7	364
852*	Female	2.40	STR.	93	
			THA.	27	333
853*	Male	2.50	STR.	106	
			THA.	34	202
862	Male	2.40	CER.	7	
			STR.	7	154
863	Female	2.60	STR.	7	
			S.C. Bil.	7	39
864	Female	2.70	S.C. Left	7	
			S.C. Right	7	
			STR.	7	150
865	Male	2.60	STR.	7	
			S.C. Bil.	7	50
875	Female	2.60	S.C. Left	7	
			S.C. Right	7	
			STR.	7	127
876	Male	2.90	S.C. Left	7	
			S.C. Right	7	
			STR.	7	86
884	Male	2.75	S.C. Bil.	7	
			STR.	7	143

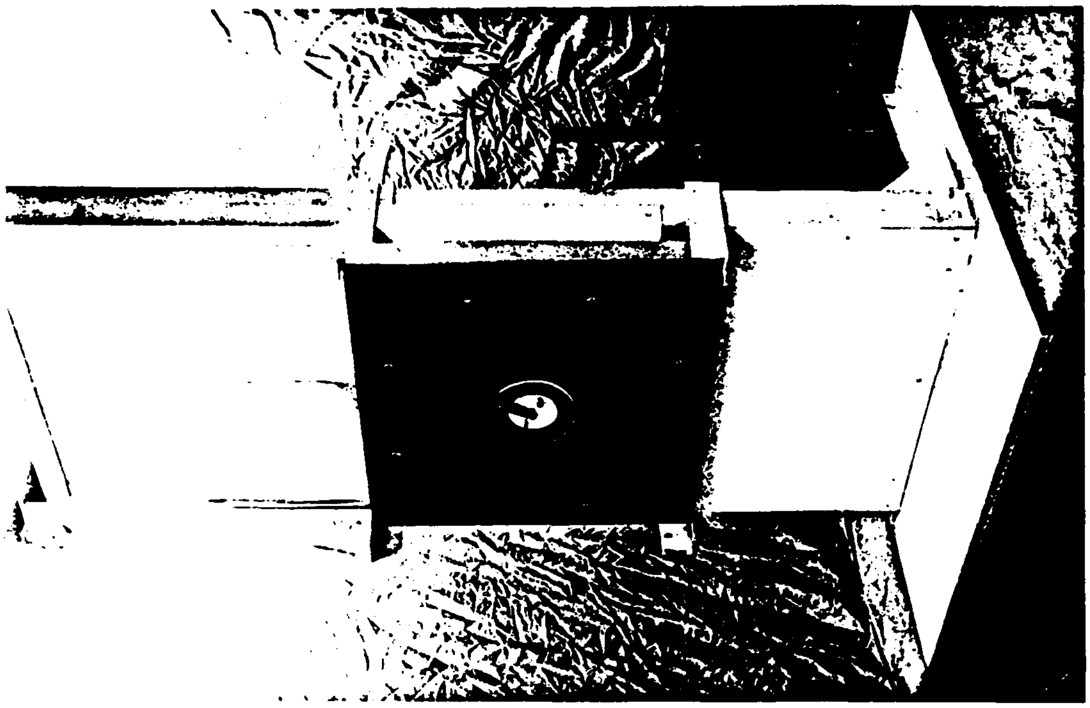
a - Just prior to entry into the study.
b - Interval between surgery and onset of formal testing.
c - Period between the last surgical procedure listed and the date of sacrifice.
* - Denotes animals with prior visual discrimination training.
Ablations indicated by: STR., Bilateral striatectomy; THA., bilateral posterior thalamic lesions; S.C., superior colliculectomy; CER., bilateral cerebellar lesion; bil., bilateral.

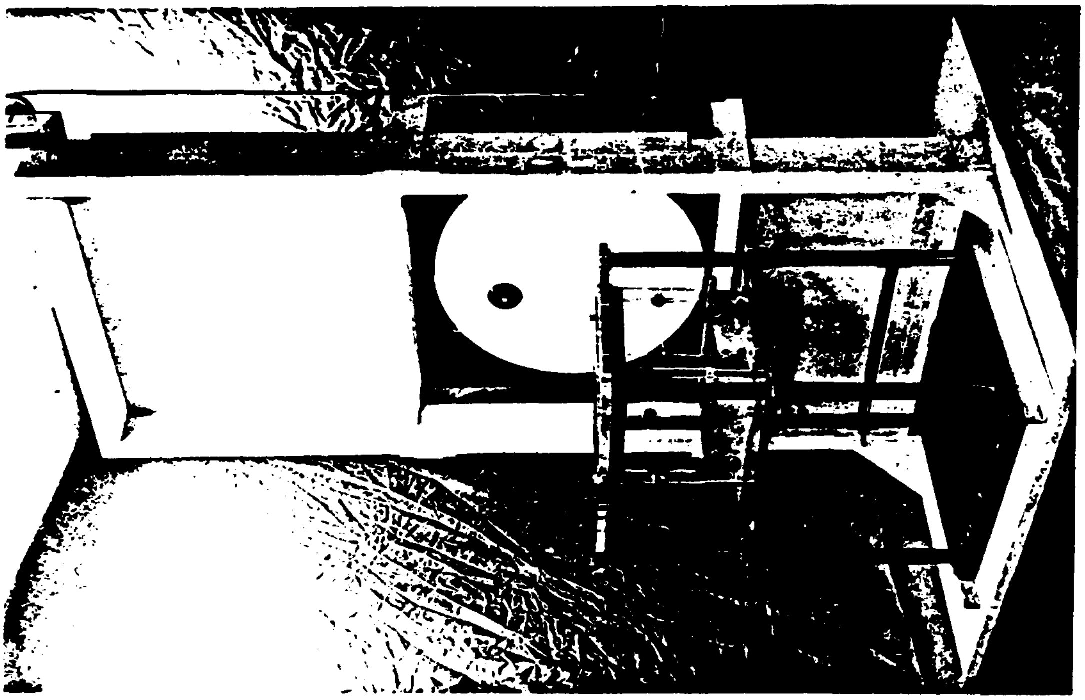
Apparatus

The testing apparatus, illustrated in Figure 1, was a modified version of the "spin-wheel" described by Feinberg et al. (1977, 1978). An opaque guillotine door, mounted on a frame, was interposed between the monkey and the stimulus display. Facing the animal, the display consisted of a circular disk of white matte lucite (457 mm in diameter X 6.5 mm thick) with a 10-32 stainless steel, flat head, machine screw threaded through the white disk 125 mm from the center and protruded 13 mm from the surface of the disk. The tip of the screw was milled to a fine point, 6.5 mm in length, leaving an additional 6.5 mm of thread remaining upon which targets could be affixed through 10-32 holes tapped in their center. The four targets used consisted of black matte lucite disks, 6.5 mm thick and 90 mm, 55 mm, 35 mm and 15 mm in diameter, respectively, which were beveled at a 45° angle along the circumference, in order to minimize extraneous shadows. The reward was a cube of apple, approximately 10 mm on a side, placed on the finely milled point of the screw, which protruded through the hole in the center of the black target.

On the back side of the apparatus (see Figure 1), facing the experimenter, a clear cylindrical lucite hub (76 mm in diameter x 19 mm high) was glued center to center onto the back of the white lucite disk, fitted into a hole of similar dimensions in the center of a plywood square (534 mm on a side and 19 mm thick), and secured in place with a clear lucite collar. An indicator arm was fastened to the collar with its point oriented directly behind the stainless steel screw-pin. This mounting arrangment permitted the rotation of the white disk by turning the indicator arm. On the back of the plywood board, eight equally spaced

Figure 1. The testing apparatus is illustrated frontally (left) featuring the primate restraining chair with the 90 mm black target and apple cube located at position P3 of the stimulus display. The photograph on the right shows the back of the apparatus with the eight positions marked and the indicator-rotator arm placed at position P3.





positions were designated such that there were two in each Cartesian quadrant at 22.5° from either the vertical or horizontal axes, respectively. Aligning the point of the indicator arm with any of these positions placed the screw-pin in that same location.

The plywood board with the stimulus display on the frame of the guillotine door was held in a fixed position with respect to the monkey. When the door was raised, the subject's eyes were tangential to, and at 203 mm from, the center of the white disk which subtended 115° of visual angle. The black targets subtended 21°, 13°, 8°, and 3° and the apple cube was 2°. Testing was conducted in an isolated room illuminated by two overhead 48" flourescent light tubes (General Electric f40W main-lighter white). The mean luminances of the white disk, black targets, and apple cube, measured in four different locations with a Macbeth Illuminometer (model 6800, Leeds & Northrup Company), were 16.5 ft-L (56.5 cd/m^2), 0.19 ft-L (0.65 cd/m^2), and 13.35 ft-L (45.72 cd/m^2), respectively. Therefore, the contrasts as computed from $\frac{\text{Lmax-Lmin}}{\text{Lmax+Lmin}}$ were 0.98 between the white disk and black targets, 0.97 between the apple cube and the black targets, and 0.10 between the white disk and the apple cube.

Testing Procedure

This study used a multifactor experimental design, having repeated measures on each experimental subject at different levels of task difficulty and after several surgical treatments. The task was designed to assess reaching for a stationary object, the location of which varied randomly on successive presentations. The sites of stimulus, response and reward were made spatially congruent in order to facilitate learning. These conditions were chosen because of the demonstration of deficits in orienting to visual stimuli after collicular and cortical lesions when stimulus and response sites were separated (Butter, 1974a).

The monkeys were tested preoperatively and after each surgical stage in 56-trial sessions, five days per week. A trial began when the guillotine door was raised, exposing the stimulus display. The subject was permitted to scan for as long as it wished and to reach until it made contact, whereupon the trial was terminated with the lowering of the guillotine door. A response was scored correct if the monkey touched either the black target or the apple cube whereas any other contact with the white disk was scored incorrect. The animal obtained the apple following all correct responses. The eight target positions were presented seven times each during the session in two different random sequences alternately used on successive days. The sequences were prepared into seven blocks with the stipulation that the same position did not occur twice on successive trials.

The first test used the 90 mm target. When the monkey achieved a strict criterion level of accuracy, which was set at 90% correct reaches over 224 consecutive trials, this target was replaced with the next smaller one. The procedure was repeated for all of the black targets and finally only the apple cube was presented on the white disk thus serving as both target and reward. This design was chosen to maximize the probability of successful performance and as such did not allow the evaluation of the influence of target size. Training was terminated if the monkey failed to attain criterion within 107 testing sessions (i.e. 5992 trials) at any stage. The animals that sustained occipital lobectomies, either as a first or as a second procedure required special shaping before being presented with the 90 mm target. This shaping was carried out in two stages. First, the monkey was presented with a larger cube of apple, 15 mm on a side and placed at the tip of a 150 mm stylette, which was moved into the visual field horizontally (from the right and from the left) and vertically (from above and from below) in order to determine whether the animal would spontaneously reach out for a slowly moving stimulus. Initially, it was necessary to contact the face of the monkey or the vibrissae with the apple in order to induce reaching. However, after several repetitions of these contacts, it would spontaneously grope in space until the apple cube was found. In the second stage, a more formal attempt was made to shape the reaching of the animal with a modified stimulus display: the white disk had four pins bearing large apple cubes 125 mm from the center and positioned in each quadrant equidistant from the horizontal and vertical axes. When the guillotine door was raised, the monkey was encouraged to grope until all of the apples were obtained at which time the door was lowered. At first, it was often necessary to guide the subject's hand toward one or more of the four positions. Twenty five such presentations were given daily until the monkey succeeded in obtaining all apple cubes on two consecutive sessions.

When criterion performance was attained postoperatively on the last test, i.e. the apple cube alone, two types of control trials were given to rule out nonvisual cues in the guidance of reaching behavior. The first consisted of 10 trials of approximately 60 sec duration, with the room lights off. Without exception, the monkeys were quiescent in the dark and never groped for the apple. A second procedure consisted of a 112-trial session during which the apple was randomly replaced by a white matte lucite cube, 7 mm on a side, six times per position. The animal was handed a piece of apple if its first response was to touch the lucite cube. All subjects that reached this level of testing satisfied these controls without impairment.

Surgical Procedures

The monkeys were anesthetized with sodium pentobarbital, 30-45 mg/kg of body weight, injected two-thirds intraperitoneally and one-third intramuscularly. All operations were performed under aseptic conditions and immediately after surgery the animals were given 600,000 units of penicillin intramuscularly.

One-Stage Bilateral Superior Colliculus Ablations

Two monkeys sutained single-stage bilateral lesions of the superior colliculi as the first surgical procedure (850 and 884). While the animal was under a moderate level of anesthesia, the head was shaved and an IV catheter inserted into the saphenous vein. A hypertonic solution of sterile urea (30% urea reconstituted in 10% inverted surgar) was administered through the catheter (1 g urea/kg of body weight) over a 30-minute interval just prior to surgery. The urea acted to reduce brain volume making the surgical approach easier, and consequently less adverse effects of intracranial edema resulted from the manipulation of the occipital lobes during the collicular approach. In order to keep the vein patent, the animal was maintained throughout surgery on dextrose 5% in water administered through an IV microdrip at a slow flow rate of 1 drop/15 seconds (60 drops/ml).

The monkey was mounted in a David Kopf U frame, a skin incision made along the interaural plane, and the subcutaneous and muscular layers reflected. Two trephine holes were bored in the midline, one directly on the inion and the other about 4 cm forward, and a bilateral bone flap removed using a compressed nitrogen driven turbine osteotome. The dura covering the left hemisphere was incised and reflected on the superior sagittal sinus. The exposed brain tissue of the dorsolateral and mesial surfaces of the left occipital area were protected with cottonoid strips, moistened in physiological saline. While gently retracting the brain with silver elevators, and after teasing away the arachnoid of the quadrageminal cistern, the superior colliculus was visualized using a Zeiss operating microscope at X 10 magnification. The colliculus was identified in relation to the surrounding brain structures, i.e. the pineal gland, splenium of the corpus callosum, and the sulcus separating the superior from the inferior colliculus. The pia covering the left collicular surface was cauterized with a bipolar coagulator and the underlying left superior colliculus was removed with a curved 22 gauge suction tip. In the case of monkey 884, the right colliculus was visualized and aspirated across the midline. Upon completing the lesion, a dural substitute made of dacron coated with silicone rubber (No. 01-61-0001, Extracorporeal Specialties, Inc.), was placed over the exposed brain tissue to minimize postoperative dural adhesions resulting from the surgical intervention, and the dura sutured closed with 5-0 silk. In monkey 850, the right superior colliculus was then exposed and aspirated according to the same protocol.

The bone flap was replaced, the soft tissue reapproximated in anatomical layers using 4-0 and 3-0 silk to suture the muscular layer and scalp, respectively. These animals were given IM steroid injections, Depo-Medrol (methylprenisolone acetate, 40 mg/ml, Upjohn Company), on the day of surgery and, in decreasing doses, over the succeeding six postoperative days according to the following schedule: 10 mg-10 mg, 10 mg-5 mg, 5 mg-5 mg, 5 mg-5 mg, 5 mg, 2.5 mg and 2.5 mg, with one dose in the morning and one in the evening when two were indicated, or just one dose in the afternoon. The steroids acted to reduce intracranial edema and obviate systemic rebound through gradual withdrawal from the drug. On the seventh postoperative day, the scalp sutures were removed and testing commenced.

Two-Stage Bilateral Superior Colliculus Ablations

Monkeys 864, 875 and 876, sustained successive left and right superior collicular ablations. The preoperative preparation, craniotomy, surgical approach, and postoperative treatment for each unilateral lesion were essentially the same as described above except that the left superior colliculus was always lesioned first through a unilateral bone flap that extended up to the interparietal suture. Formal testing began on the seventh postoperative day and after criterion performance on the final condition, i.e. control sessions, the right colliculus was removed and testing resumed one week later.

Bilateral Striate Cortex Ablations

Both occipital lobes were ablated in a single stage. In six monkeys (848, 849, 852, 853, 863 and 865) this was the first surgical procedure, whereas the other six received it after collicular or control lesions. A bilateral bone flap was removed and the dura reflected exposing the dorsolateral surface of the occipital lobe. The lobe was amputated 1 mm behind the lunate sulcus, perpendicular to the surface, with a 20 gauge suction tip and bipolar cauterization of the pia and connecting blood vessels to maintain hemostasis. The residual striate cortex within the rostral end of the calcarine fissure was aspirated with a 22 gauge suction tip using the operating microscope. When the lobectomy was the first procedure, a piece of dural substitute was inserted between the medial aspect of the hemisphere and the falx, in addition to the usual piece placed under the dural sutures. This facilitated the subsequent collicular approach.

Bilateral Superior Colliculus or Posterior Thalamus Lesions as a Second Procedure

A total of six monkeys (848, 849, 852, 853, 863 and 865) sustained either bilateral collicular or posterior thalamic control lesions in a single operative stage. These animals were also given urea through a 23 gauge butterfly infusion set to facilitate the surgical approach. Since the occipital lobes were removed in a previous operation, the brain had sufficient room to expand after the midbrain or diencephalic lesion making an IV drip or steroid treatment unnecessary. The colliculi were aspirated as described above. The diencephalic lesions were accomplished by using the superior colliculi as reference points, directing a straight 22 gauge suction tip into the thalamus, particularly the posterior nuclear group. Four of these animals (848, 849, 852 and 853) participated in another experiment on vision requiring about two months before being tested in this experiment.

Histological Verification of the Lesions

At the conclusion of the experiment, the monkeys were deeply anesthetized (50 mg pentobarbital sodium/kg of body weight) and sacrificed for histological verification of the lesions. The axillary arteries were ligated. The abdominal cavity was opened along the left costal margin and the left kidney retracted toward the midline in order to expose the descending aorta in the retroperitoneal space. Two silk ligatures were placed around the artery and the distal one tied immediately. The artery was temporarily clamped proximal to the ligature. A small opening was made in the wall and a cannula (K-30 feeding tube, size 8 French, Pharmecal) inserted 55 mm into the aorta toward the heart while releasing the clamp. The cannula was then secured in place with sutures. The following solutions were passed in sequence through the indwell tube: 1 ml of Heparin (1000 units, Panheparin, Abbott Laboratories), 1000 ml of physiological saline, and 1000 ml of 5% formalin. Ample drainage was insured by sectioning the inferior vena cava. The brains were removed, placed in 10% formalin for seven days, photographed, cut into an anterior and posterior block at a level rostral to the lateral geniculate nucleus, and embedded in celloidin. Sections were cut on a sliding microtome at 40 µm and every tenth, stained with cresyl violet, was used for the reconstruction of the midbrain lesions and the examination of the thalamus, including the lateral geniculate nuclei. The cortical ablation was reconstructed from every 40th section.

Statistical Considerations

As stated earlier, this experiment was a complex multifactorial study because it evaluated the performances of the monkeys on five tests, with eight positions per test, before and after six surgical conditions. In order to simplify the data analysis, the larger design was collapsed around the main effects, i.e. those of surgery, tests and positions, at the expense of sacrificing the interaction effect which were of little value to the study. The computations involved an analysis of variance as proposed by Winer (1962) for evaluating the outcome of experiments having repeated measures on a group or on a single element. Upon obtaining a significant F ratio with this procedure, a Scheffé test

(1953) was applied. This test makes <u>any and all</u> comparisons of interest between a set of *k* treatment means without having to make any *a priori* stipulations (see Edwards, 1969, Ch. 10 for computation formulas). The Scheffé test is a more conservative statistic than others that evaluate specific planned orthogonal comparisons and, as such, it requires larger mean differences for significance. For this reason, Scheffé has suggested adoption of an alpha level of 0.10 in which case the probability that all statements made about the treatment means are correct is greater than or equal to 0.90.

The results were analyzed in several ways. First, for each lesion group in which an impairment occurred, performances were compared among the five targets on measures of total errors and trials through criterion. Second, on those targets where a deficit was observed, reaching accuracy was assessed by comparing the total number of correct responses per target position, since the absence of accurate reaches to individual positions or to multiple position aggregates might reflect a disturbance in a particular region of the visual field. Third, the performances of individual monkeys were analyzed for reaching accuracy. Fourth, acquisition curves for each subject were determined on those targets and the linear and logarithmic least squares fit to the data were computed. The line of better fit was determined by the equation which resulted in the smaller error function [F(E)]. F(E) is defined as the squared difference between the observed cummulative errors and those determined from the equation and summed over the domain of the independent variable.

CHAPTER III

RESULTS

Anatomic Observations

Superior Colliculi

The superior colliculus ablations varied in extent. The portions destroyed were surrounded by regions of marked gliosis and absence of neurons. In order to quantify the amount of damage, drawings were made at 400 µm intervals from slides which were either projected through a Bausch & Lomb Tri-Simplex microprojector with a 40 mm luminar lens, at X 10 magnification, or through a microscope equipped with a Zeiss drawing tube at X 31.7 magnification. The latter method was needed to delimit the small amount of collicular tissue that contained a few "normal looking" neurons in monkeys 864, 875, 876, and 884. The remaining tissue, without degenerative changes, was measured from these drawings by means of an electronic graphic calculator (Numonics Co., No. 274-117). Both area and linear surface extent values were obtained and from these data the volume (V) and surface (A) of the "viable tissue" were calculated according to the general formula:

$$V \text{ or } A = 1/3\ d\ [4\ (X) + 2\ (Y)],$$

where d is the distance between sections and X and Y are the sums of the values from even and odd numbered sections, respectively. These values consisted of areas to compute V and linear distances to obtain A. V and A were then compared with similar data from a series of slides of a normal monkey processed in the same way, which served as a standard to derive an estimate of the percent collicular damage. The total volume of the normal colliculi was 82.390 mm^3 (40.940 mm^3 on the right and 41.450 mm^3 on the left) and the total surface area was 49.58 mm^2

(24.57 mm^2 on the right and 25.01 mm^2 on the left).

Table 2 gives the estimates of the percent collicular destruction for each side separately as well as for the total damage. It is clear that four animals (864, 875, 876, and 884) suffered almost total destruction of the collicular mass. Moreover, one of these monkeys (864) with nearly complete destruction of the surface area, had viable tissue in the deep layers. Two animals (875 and 876) also showed major pretectal damage (Figures 2 and 3). Monkey 884 (Figure 4) sustained only minimal damage to the pretectum, and in animal 864 (Figure 5) the pretectum was intact. In the other three subjects (850, 863, and 865) the collicular lesions were partial varying in severity from 49% to 58% by volume, and 53% to 78% by surface area (Figures 6-8). Monkey 865, in addition, suffered major damage to the pretectum and splenium of the corpus callosum (Figures 8 and 10).

Occipital Lobes

The bilateral occipital lobectomies, in all 12 monkeys, were relatively symmetrical and the procedure consistently removed the entirety of striate cortex on both the dorsolateral surface and within the depths of the rostral extension of the calcarine fissure (Figure 10). There was also partial involvement of the circumstriate cortices, the extent of which was estimated to be 80% and 20% destruction of areas OB and OA respectively, consulting with v. Bonin and Bailey's maps (1947). The expected retrograde degeneration changes were found in the lateral geniculate nuclei pars dorsalis, and in the pulvinars, particularly the inferior and lateral divisions (e.g. Figure 10). The changes consisted of absence of nerve cells and intense gliosis with the exception of the few neurons present in the LGNd. These have been shown to

Table 2. A Summary of the Subcortical Lesions

Monkey No.	Superior Colliculus						Central Grey	Pretectum	Inferior Colliculus	N. Limitans	Area Tegmentalis	Splenium	Midbrain Tegmentum	Thalamus	Cerebellum
	V			A											
	R	L	T	R	L	T									
875	100	100	100	100	100	100	rL	X	l	L					
876	100*	99	100*	100	100	100	x	X					x		
884	98	94	96	100	94	97		x		r					
864	89	88	88	100	91	96	r				l				
863	49	67	58	73	83	78	x								
865	56	49	53	67	49	58	x	X				X			
850	44	54	49	49	57	53	x								
848	0	0	0	0	0	0				R				rL	
849	0	0	0	0	0	0				r	r			rL	
852	0	0	0	0	0	0	x			l		X	R	rL	
853	0	0	0	0	0	0	x			r	r		L	R	
862	0	0	0	0	0	0									x

Note: Under the heading Superior Colliculus V and A = volume and area, R, L and T = right, left and total, respectively. Numerical values give the percent destruction and the * indicates that less than 1% of the tissue was preserved. X, R, L = marked bilateral, right and left involvement; x, r and l = minimal bilateral, right and left damage.

Figure 2. Subcortical lesions in 875. Black shading indicates absence of tissue, and the stippled areas denote gliosis. The numbers identify the serial sections which were cut at 40 µm. Note the destruction of the superior colliculus with additional damage to the central grey, pretectum, and slight invasion of the inferior colliculus.

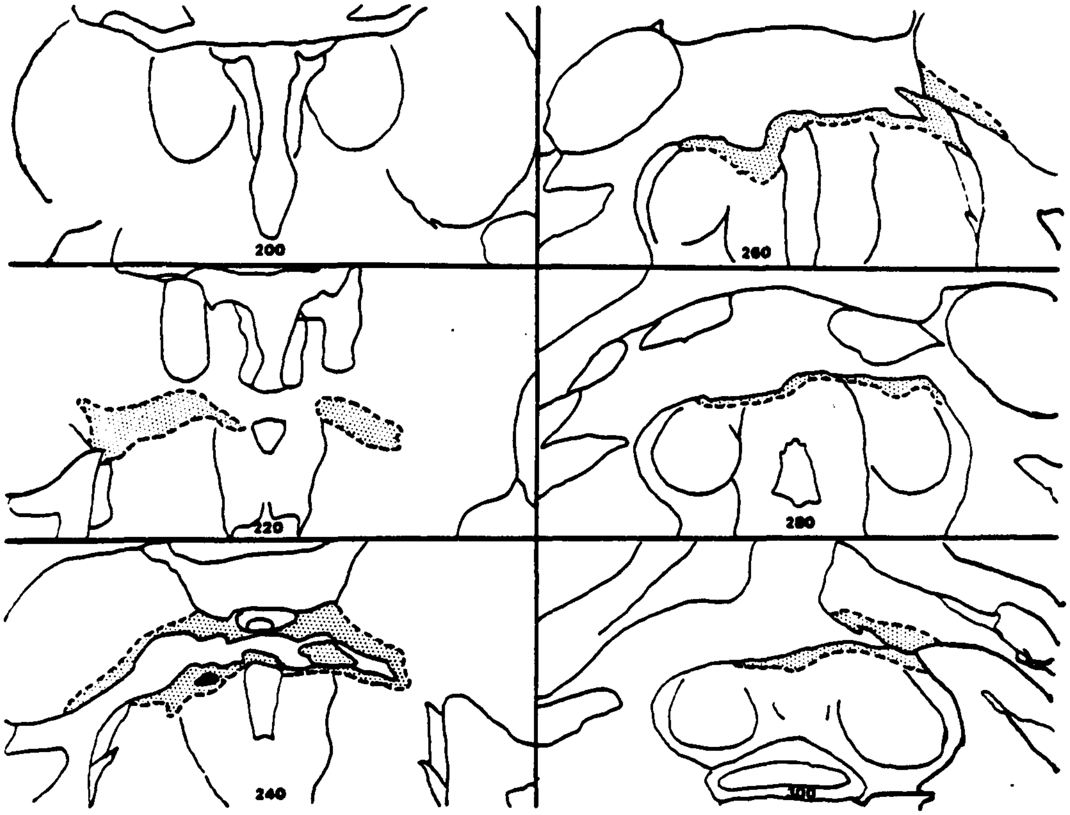

200
260
220
280
240
300

Figure 3. Subcortical lesions in 876. Notation as in Figure 2. Note the nearly complete collicular destruction with the additional damage to the medial pretectum and central grey.

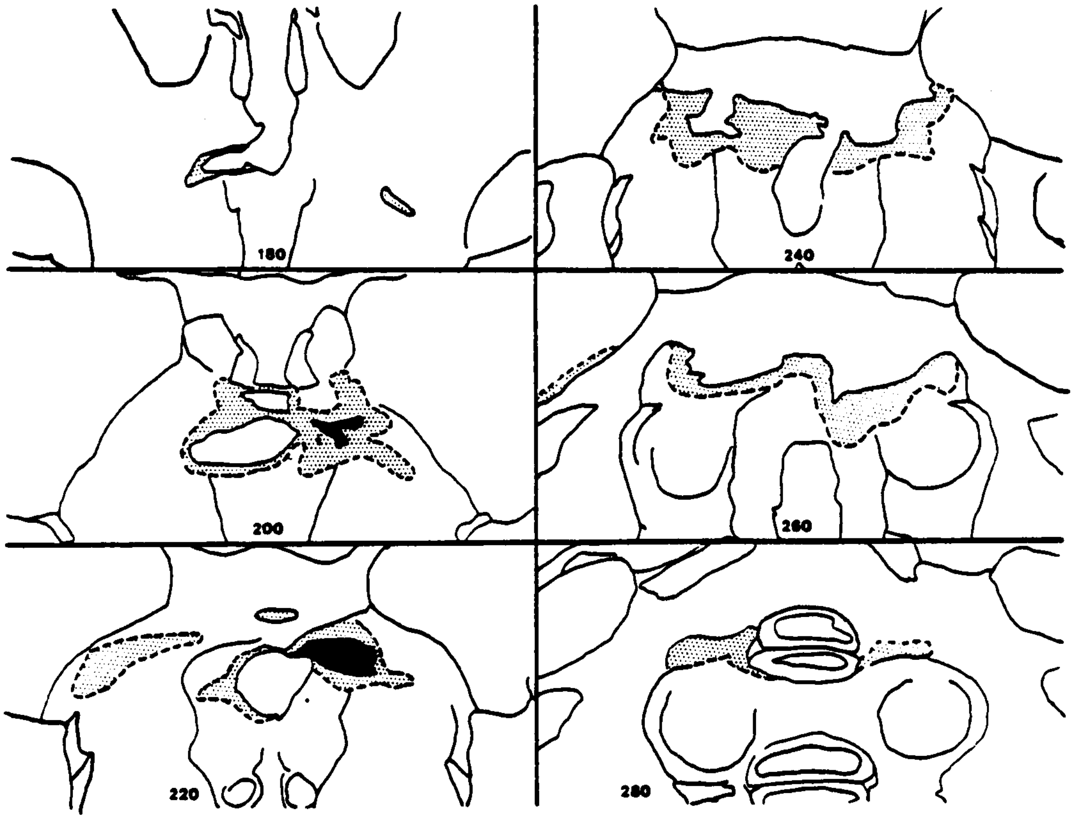

180
240
200
260
220
280

Figure 4. Subcortical lesions in 884. Notation as in Figure 2. Note that the damage in this animal was limited almost exclusively to the collicular mass with only a slight invasion of the central grey.

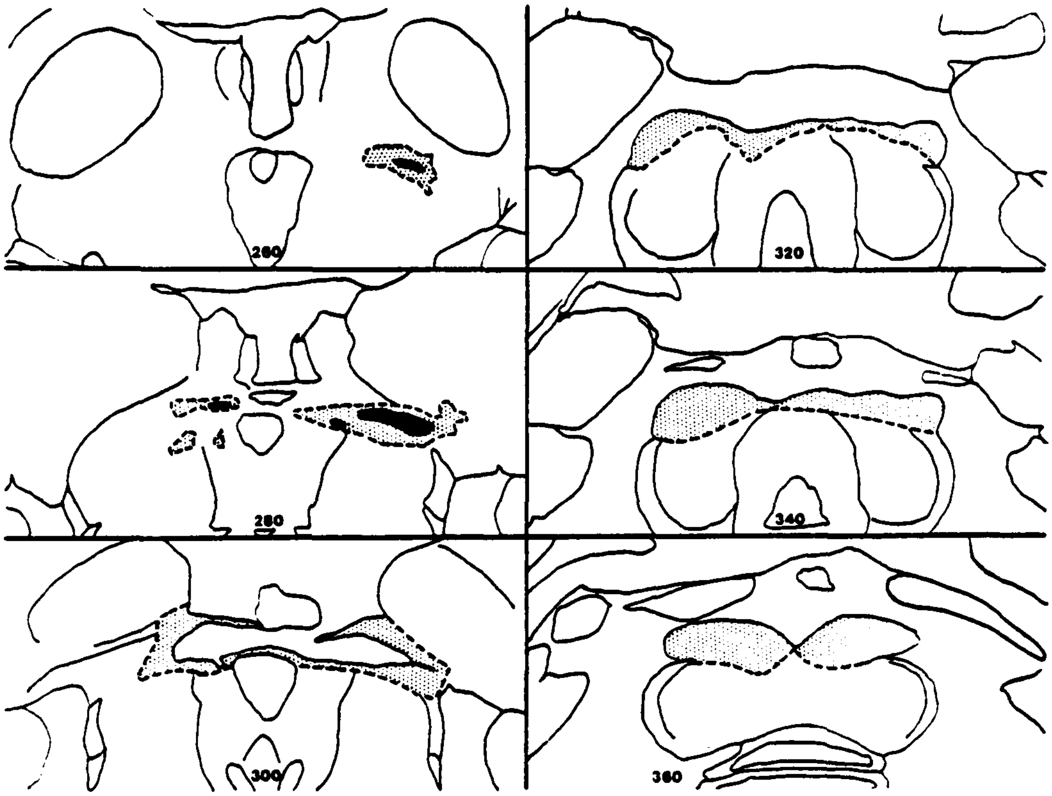

280
320
280
340
300
360

Figure 5. Subcortical lesions in 864. Notation as in Figure 2. Note that the lesion included most of the colliculus and only minimal encroachment into the central grey.

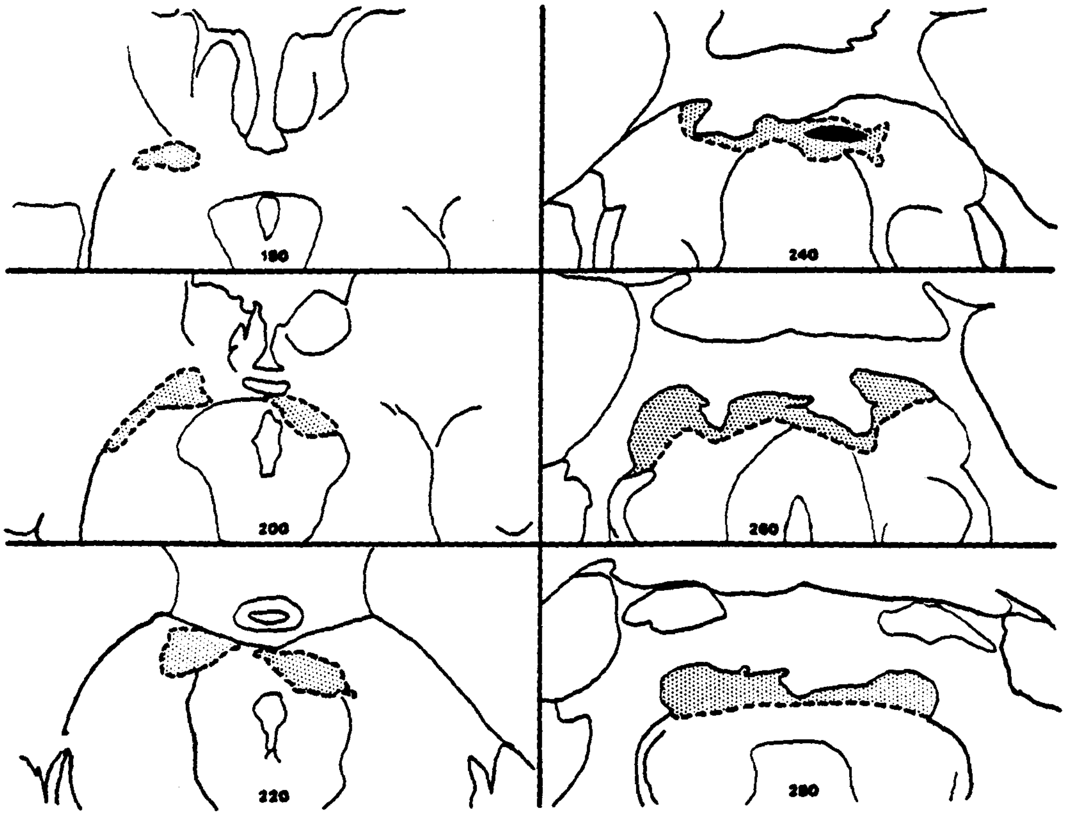

180
240
200
260
220
280

Figure 6. Subcortical lesions in 850. Notation as in Figure 2. There is partial superior collicular destruction and a slight invasion of the central grey.

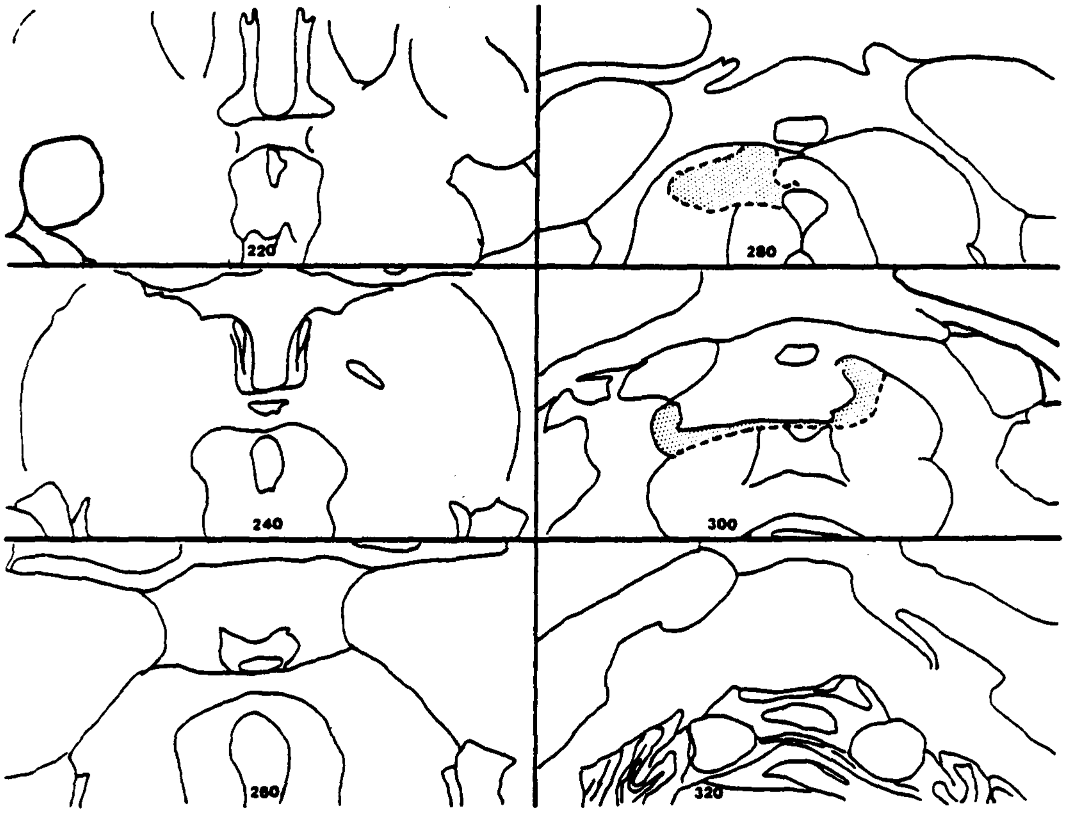

220
280
240
300
260
320

Figure 7. Subcortical lesions in 863. Notation as in Figure 2. The damge is restricted almost exclusively to the collicular mass with only minor damage to the central grey.

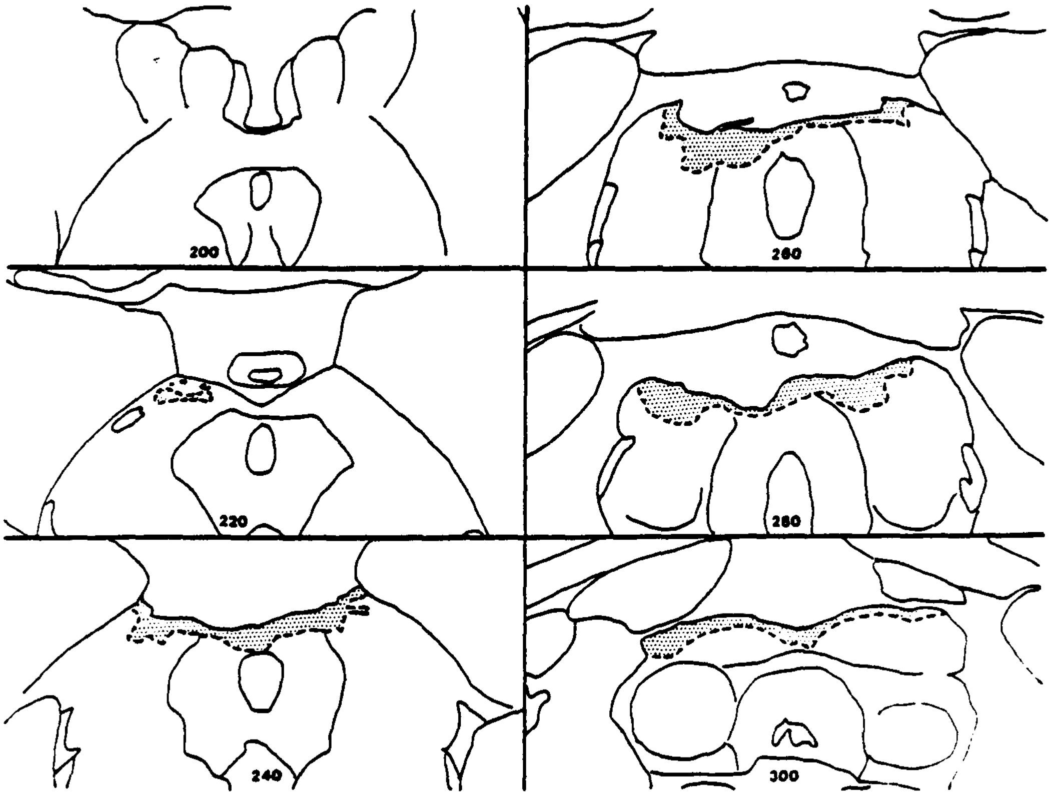

200
260
220
280
240
300

Figure 8. Subcortical lesions in 865. Notation as in Figure 2. The damage to the superior colliculus, <u>per se</u>, is incomplete but there is extensive destruction of the posterior commissure, some involvement of the central grey, and, in addition, the splenium of the corpus callosum is partially transected and gliotic.

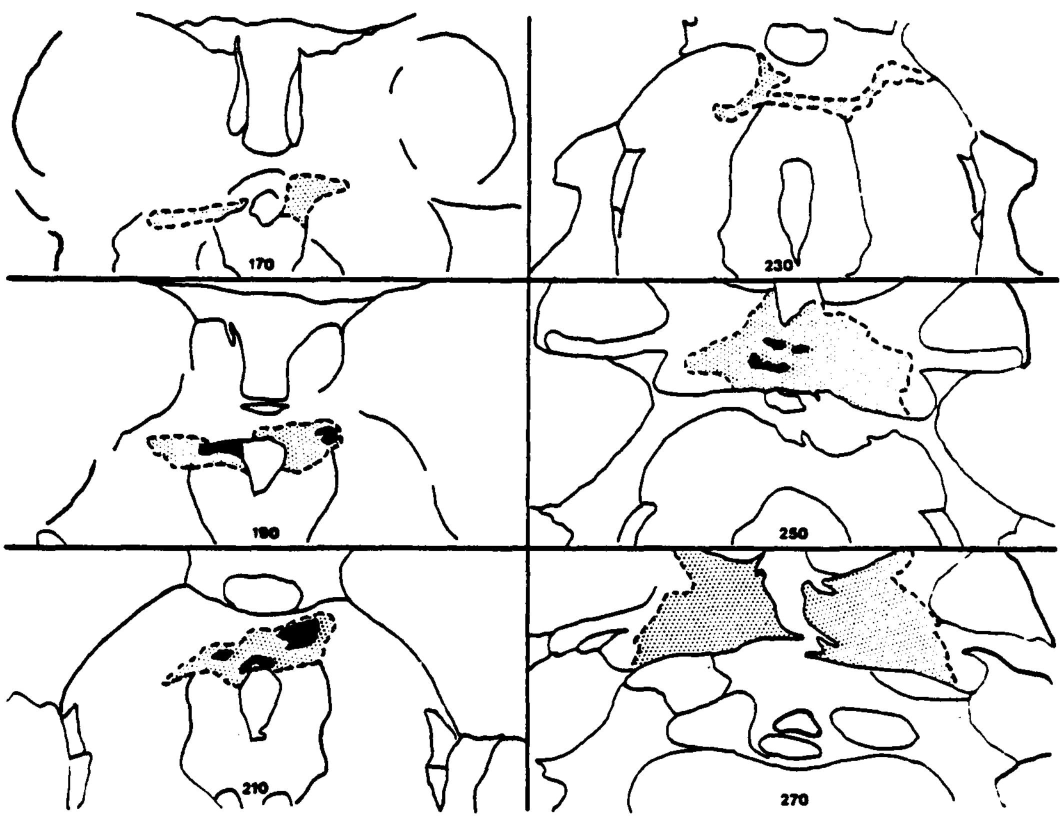
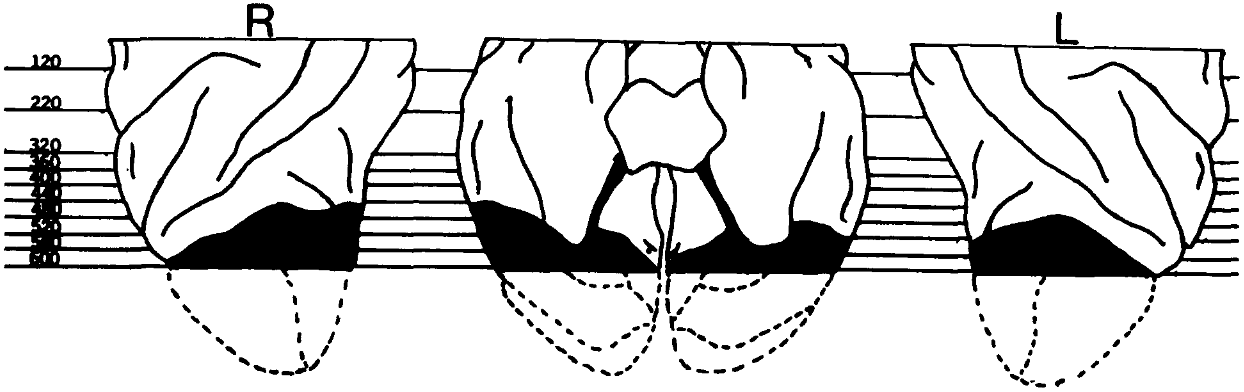

170
230
190
250
210
270

Figure 9. Subcortical lesions in 848. Notation as in Figure 2. This is a surgical control showing damage restricted mainly to a small region of the thalamus with the superior colliculi and pretectum completely intact.

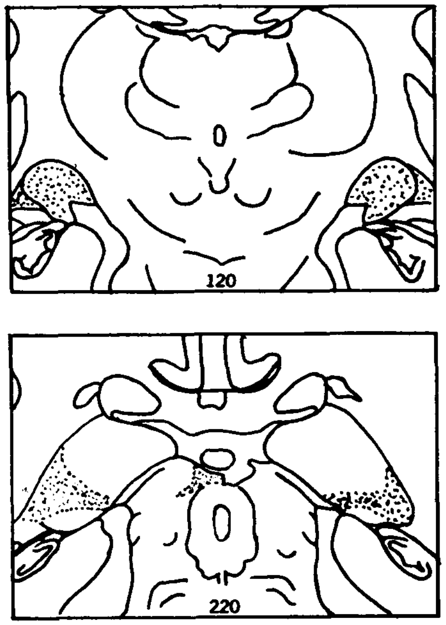

140
260
180
300
220
340

Figure 10. Surface views, representative cross-sections and mesodiencephalic regions of 865. Absence of occipital lobes indicated by dashed lines. Absence of cortex is shown by black in the surface views and by fine lines in the sections. Intact cortex in the sections is represented by the thicker black shading. In the framed enlargements, degeneration with dense gliosis is indicated by stippling. The numbers identify serial sections which were cut at 40 µm. Similar findings were present in all other subjects.


R
L
120
220
320
360
400
440
480
520
560
600

No. 865


320
360
400
440
480
520


120
220

Golgi type II interneurons (Pasik, Pasik, Hámori, & Szentágothai, 1973).

Surgical Control-Lesions

Four of the control-lesion animals (848, 849, 852, and 853) sustained varying degrees of damage which were rather asymmetric (e.g. Figure 9). All of these monkeys had thalamic lesions. In addition, two of them (852 and 853) showed marked unilateral destruction in the midbrain tegmentum and one of these animals (852) also suffered major damage to the splenium of the corpus callosum.

The last control-lesion animal, monkey 862, sustained bilateral ablations of the cerebellar vermis that were comparable in size and extent to the amount of tissue removed in producing complete colliculectomies.

Qualitative Observations

Unilateral Superior Colliculus Lesions

Three monkeys (864, 875 and 876) sustained total or almost total removal of the left superior colliculus as a first surgical procedure. As soon as the monkeys recovered from the anesthesia, all exhibited ipsilateral symptoms of varying degrees. Head and eye deviation to the left were observed in 864 and 875, just the eye deviation in 876, and a tendency to fall to the left only in 864. Spontaneous nystagmus was seen in 875, and 876 exhibited pupillary dilation accompanied by a slight retraction of the upper eyelids.

During the first postoperative day, all animals were alert and reactive, although the ocular symptoms persisted together with a tendency to circle in the direction ipsilateral to the lesion. At this time, visual responsiveness was assessed with single and double simultaneous stimulation (DSS). An apple cube was moved across the visual field entering from the right, left, below and above. Monkeys 875 and 876 were unable to move their eyes past the midline when the apple entered from the left and showed a unilateral neglect of the right half of space. In addition, 875 exhibited a startle response to stimuli presented on the left and had a paresis of upward gaze. The animal oriented to objects presented from above by dorsiflexion of the head. DSS was performed in two ways. In the first, two pieces of apple were suddenly exposed on a counter top at arms length approximately 45 cm apart. In the second, the experimenter faced the monkey with an apple cube in each hand. Under both conditions, all of the animals reached for the apple on the left and only after great effort located the one on the right. Extinction was elicited by introducing competing visual stimuli. A reaching response already in progress to an apple presented on the right was immediately abandoned when a competing stimulus appeared on the left. If an apple cube was held in front of monkeys 875 or 876 and then moved laterally with the onset of a response, they continued the full sequence of reaching and grasping to the general area of space where the apple originally appeared. In contrast, 864 compensated for the lateral displacement of the object.

From the 2nd to the 6th postoperative day, the rate of recovery varied. After the 2nd day, 864 did not exhibit any signs of laterality preference, but 875 and 876 had more enduring impairments that extended into the formal testing period. Monkey 876 was the most severely affected, lying either on the side or on the back while holding the head and eyes with the hands. Pupils were widely dilated and these symptoms persisted for the 3rd and 4th postoperative days. Although the responses to stimuli presented on the right were more brisk on the 6th day, the asymmetry and extinction on DSS could still be elicited, albeit less frequently.

On the 7th day, the animals started formal testing. Monkey 864 behaved normally. Monkey 875 was quantitatively unimpaired but qualitatively the right-left asymmetry persisted through testing with the second target. The asymmetry appeared as an initial reaching out to the left when the guillotine door was raised, but no contact was made with the white disk. This was followed by orienting and reaching toward the target. Formal testing was completed in the minimum time required by normals. In contrast, 876 had a more prolonged quantitative deficit characterized by a high error rate and a lack of dexterity in obtaining the reward. The performance initially was below criterion at all target positions and the typical reaching response was a stereotyped contact with the lower left quadrant of the display.

Two-Stage Bilateral Superior Colliculus Lesions

This group comprises the same animals of the previous heading which received subsequent total removal of the right colliculus. Monkey 864 was relatively unaffectecd, but 875 and 876, which had also major damage to the medial pretectum, exhibited pronounced signs of this involvement, namely paresis of upward gaze, pupillary alterations and eyelid retraction. These disturbances remained until sacrifice. In addition, there were transient unilateral behavioral and oculomotor symptoms. This time the neglect was of the left half of space, selecting the right apple cube, extinguishing to the left stimulus, pastpointing the target site, and having poor eye/hand coordination.

On formal testing, 864 reached without error and exhibited exquisite dexterity in responding to the apple cube. In contrast, 875 made more initial contacts with the target and showed a tendency to reach to the right when the guillotine door was lifted. Impaired head, eye and hand coordination continued through testing on the 15 mm target. Monkey 876 performed accurately with the first two targets, but made progressively more errors on the remaining three, although not exceeding 10%. This animal also had difficulty on the control sessions. The reaching was accurate, but the monkey tried to pull the lucite cube from the apparatus as if it were the apple. This tendency was characteristic of destriated monkeys (see below).

One-Stage Bilateral Superior Colliculus Lesions

Two monkeys (850 and 884) sustained single-stage superior collicular ablations. The colliculi of 850 were only partially removed through two dural incisions, whereas those of 884 were almost totally ablated through the left dural incision. The latter animal did not exhibit any postoperative disturbances in behavior or in oculomotor responsiveness. There was no selective neglect of the visual space or deficits on DSS. In addition, there were no quantitative impairments on formal testing.

In contrast, 850 exhibited semidilated pupils that reacted incompletely and sluggishly to a pen light, with slight eyelid retraction, upon awakening from anesthesia. The animal had difficulty moving the eyes downward, both in pursuit and spontaneously. Even though a horizontal tonic left deviation of the eyes developed, conjugate eye movements were possible to the right as well as to the left. By the end of the first day, there was a reduction of the eyelid retraction and the pupillary light reflex returned to normal, but the oculomotor symptoms persisted through the 3rd day. During this period, the signs of intracranial hypertension slowly developed reaching a maximum on the 3rd day. The animal was lethargic and sat with the head bowed, was not easily aroused by loud noises, and exhibited a startle response when touched. On the 4th day there was marked improvement. The monkey was more alert, active, and all of the oculomotor responses were intact. On the 7th day the animal was tested formally and performed without error on all targets.

Bilateral Striate Cortex Lesions

Monkeys 848, 849, 852, 853, 863 and 865 received total bilateral excision of striate cortex and partial damage to prestriate cortex as a first procedure. The behavioral changes observed immediately after surgery were similar to those described in earlier studies (Pasik et al., 1969). The animals tended to remain in the back of the cage and did not attempt to escape when the door was opened. Destriated monkeys did not withdraw until actually touched and did not respond to threatening or rapidly approaching stimuli. In an open field, the animals typically walked on the hind legs with the forelimbs outstreatched in front of them as if to avoid obstacles. Initially, they failed to track large targets that traversed the visual field and were unable to localize the apple cubes mounted on a stylette. Observed after a longer postoperative period, these monkeys were dramatically improved. They exhibited visual pursuit of slowly moving stimuli, reached toward the apple cubes on the stylette, and required fewer pretest-shaping sessions in preparation for formal testing.

On formal testing, most of these animals showed marked deficits, particularly on the first and last tests, but all eventually attained criterion performance. It is interesting to note that they attempted to retrieve the lucite cube on control trials as if it was the apple cube.

Combined Striate Cortex and Superior Colliculus Lesions

These monkeys were divided into two groups on the basis of the lesion sequence. Two animals (863 and 865) sustained the sequence striatectomy-partial colliculectomy. The tectal lesion did not exacerbate the qualitative effects of the striate cortex removal. On formal testing, there was a moderate initial decrease in reaching accuracy which was rapidly reinstated. Correct responses were under the direct control of visual guidance (see Figure 11) since accurate reaches were always preceeded by head and eye orientation in the direction of the target. Monkey 865 exhibited an obvious prectectal syndrome that remained until sacrifice and that correlated with extensive pretectal damage.

The second group of animals (850, 864, 875, 876, and 884) were given the lesion sequence colliculectomy-striatectomy. Only 850, which had just a partial collicular ablation, was able to attain criterion performance on formal testing, but the process was greatly prolonged as compared to that of 863 or 865 who received the reverse lesion sequence. At first, 850 responded with groping and extensive tactual exploration of the stimulus display. After corrective procedures were instituted to discourage this inappropriate behavior, accurate reaching returned as in the monkeys 863 and 865. In contrast, the other four monkeys in this group with practically total colliculectomies, appeared disoriented, with a paucity of spontaneous eye movements, and never demonstrated accurate visually guided reaching. Unlike the destriated or combined-lesion animals which passed the test, these monkeys never exhibited pursuit of targets traversing the visual fields.

Figure 11. Monkey 863 following the complete removal of the striate cortices and the partial destruction of the superior colliculi. These are three frames from a motion picture taken during a control session using the white lucite cube. Note the precision with which the response was executed and the orientation toward the target. The monkey reached with the right hand for a target located at the upper left position, P3.

Surgical-Control Lesions

Of the five control monkeys (848, 849, 852, 853, and 862), four sustained rather asymmetric posterior thalamic aspirations after initial striatectomies (848, 849, 852, and 853). The second lesion had little effect on the qualitative visual status of these animals. One monkey (852), however, developed a partial left hemiparesis and hemisensory syndrome immediately after surgery that improved somewhat over time. All animals were unimpaired on the first four targets. When the apple cube was presented, the effect ranged from a slight decrease in accurate responses in two animals (848 and 852) to a rather marked deficit in the performance of the other two (849 and 853). It should be noted that these monkeys were tested formally 1-4 months after surgery during which they were subjects of another experiment involving visual discrimination training. By this time the hemiparesis present in 852 did not hamper its performance.

Using the collicular approach, the fifth control monkey (862) suffered a cerebellar lesion as a first-stage procedure and there was no impairment whatever in qualitative or quantitative observations. On the first postoperative day, the animal showed integrated motor behaviors that included ambulatory and visuomotor activities. After the occipital lobectomies, there was a marked deficit on the first two targets with the more severe impairment on the first. On the subsequent tests, however, criterion was attained in the minimum amount of time.

Quantitative Analyses

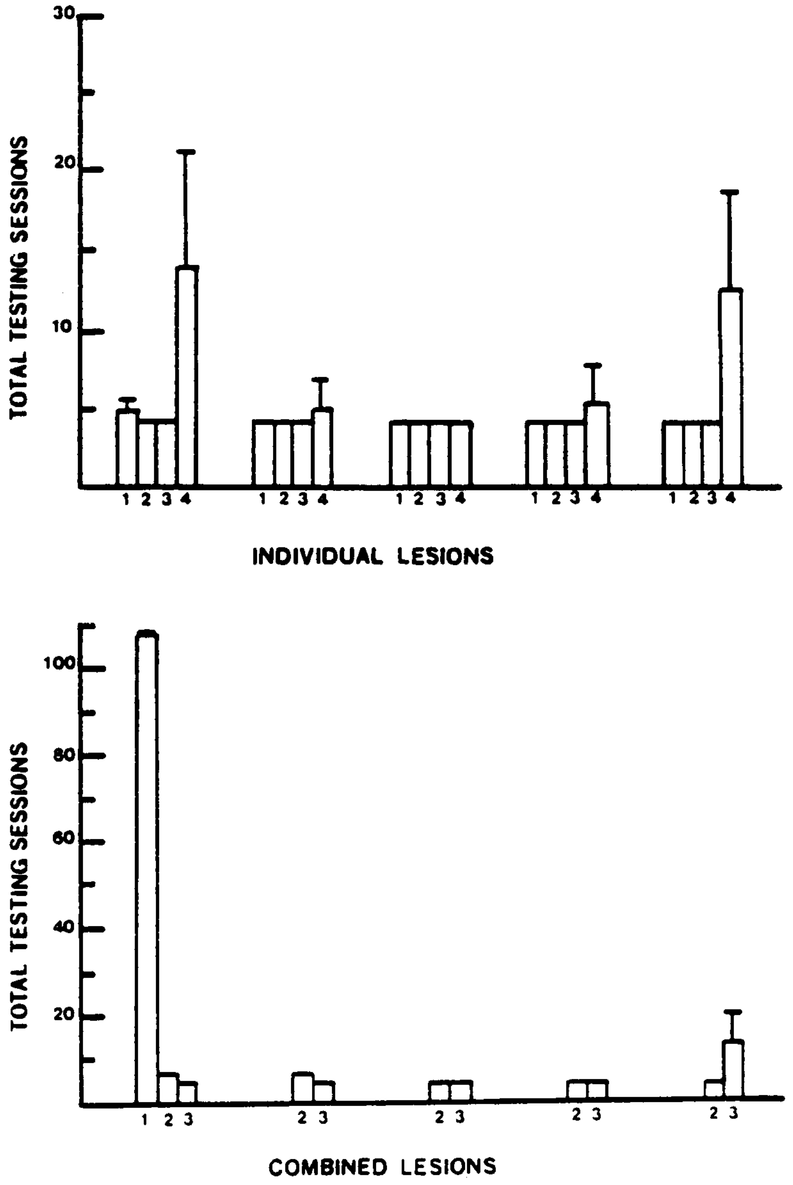
The main experimental findings of this study are given in Table 3, and Figure 12 depicts a diagram of the mean total testing sessions through criterion with respect to target and lesion groups. There follows a

Table 3. Mean Number of Trials and Errors Through Criterion Per Target and Operative Stage

Operative Stage	90 mm	55 mm	35 mm	15 mm	Apple Cube
Normals (12)	224 ± 0 0 ± 0	224 ± 0 0 ± 0	224 ± 0 0 ± 0	224 ± 0 0 ± 0	224 ± 0 0 ± 0
S.C. left (3)	261 ± 53 18 ± 25	224 ± 0 2 ± 2	224 ± 0 1 ± 1	224 ± 0 0 ± 0	224 ± 0 0 ± 0
S.C. bil. (5)	224 ± 0 3 ± 6	224 ± 0 3 ± 8	224 ± 0 4 ± 8	224 ± 0 2 ± 4	224 ± 0 4 ± 6
STR. (6)	775 ± 413 267 ± 179	271 ± 104 18 ± 20	224 ± 0 11 ± 7	289 ± 146 28 ± 36	700 ± 355 247 ± 209
STR. + S.C. (2) (passed)	336 ± 0 55 ± 18	336 ± 0 55 ± 18	224 ± 0 7 ± 0	224 ± 0 12 ± 3	224 ± 0 15 ± 0
S.C. + STR. (1) (passed)	1568* 701*	224 19	336 36	1680 537	2016 753
S.C. + STR. (4) (failed)	5978 ± 25 4867 ± 413				
STR. + THA. (4)	224 ± 0 13 ± 8	224 ± 0 7 ± 7	224 ± 0 4 ± 3	224 ± 0 8 ± 6	728 ± 425 165 ± 142
CER. + STR. (1)	3864 2237	1008 410	224 6	224 11	224 10

Figures in parenthesis indicate N. In each set mean trials and errors are given at top and bottom, respectively, ± standard deviations. Notation of lesions as in Text Table 1. Asterisks are on values obtained in last 28 sessions with modified procedure.

Figure 12. Total number of sessions through criterion or to a maximum of 107 on each of five target conditions. Height of bars and segments indicate means and standard deviations, respectively. Top: 1, unilateral colliculectomy; 2, two-stage bilateral colliculectomy; 3, one-stage bilateral colliculectomy; 4, one-stage bilateral striatectomy. Bottom: 1, striatectomy and complete colliculectomy; 2, striatectomy and partial colliculectomy; 3, striatectomy and control subcortical lesion.


TOTAL TESTING SESSIONS
30
20
10
1 2 3 4
1 2 3 4
1 2 3 4
1 2 3 4
1 2 3 4
INDIVIDUAL LESIONS
TOTAL TESTING SESSIONS
100
80
60
40
20
1 2 3
2 3
2 3
2 3
2 3
COMBINED LESIONS

more detailed analyses of the data by operative stage.

Superior Colliculus Lesions

As a group, the monkeys with only unilateral or bilateral colliculectomies were relatively unaffected when tested formally. Figure 13 shows that the mean correct responses made by the animals with bilateral lesions almost reached the 100% level for all positions of the 90 mm disk. Although no quantitative analyses were made, it is noteworthy that bilateral one-stage removals did not produce a measurable effect, but two of the monkeys with two-stage operations exhibited a slight impairment in reaching accuracy on the initial task. After a right unilateral lesion, 875 showed a slight depression in the number of correct responses to the lower left section (Appendix 1, top), although its overall performance was at or above the 90% level. Following a left unilateral colliculectomy, 876 was most accurate when the target appeared in the lower left sector and least accurate when it was presented in the lower right (Appendix 1, bottom).

Bilateral Striate Cortex Lesions

Inspection of Figures 12 and 14 clearly indicate all monkeys (848, 849, 852, 853, 863,and 865) achieved criterion performance on all tests. Initially, however, there was a relatively large deficit on the 90 mm disk, not found on the intermediate targets (viz. 55 mm, 35 mm, and 15 mm), but which reappeared when the apple cube was presented alone. Analyses of variance (ANOVAR) demonstrated significant differences in the mean total errors and trials through criterion across targets (Appendix 2, lines 1 and 2, respectively). The Scheffé test of multiple comparisons applied to these results indicated that the performances on the 90 mm and apple cube targets were impaired as compared to each intervening test.

Figure 13. Graph illustrating the group data for the bilateral colliculectomized monkeys (850, 864, 875, 876, and 884) on the 90 mm target. The radial plot consists of a series of unit radii which correspond to the locations of the eight target positions, 1-8, respectively. The frequency of correct responses to each position is expressed as a proportion of the total length of the radius. The interconnecting lines join the total scores through criterion which required the minimum number of sessions. Deviations from a regular octagon represents the relative location of impaired performances.

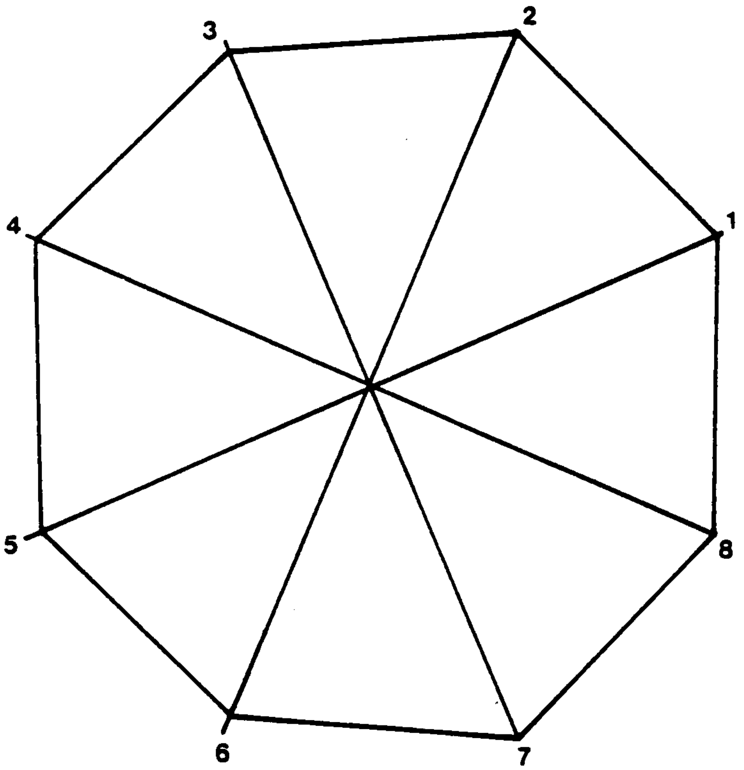
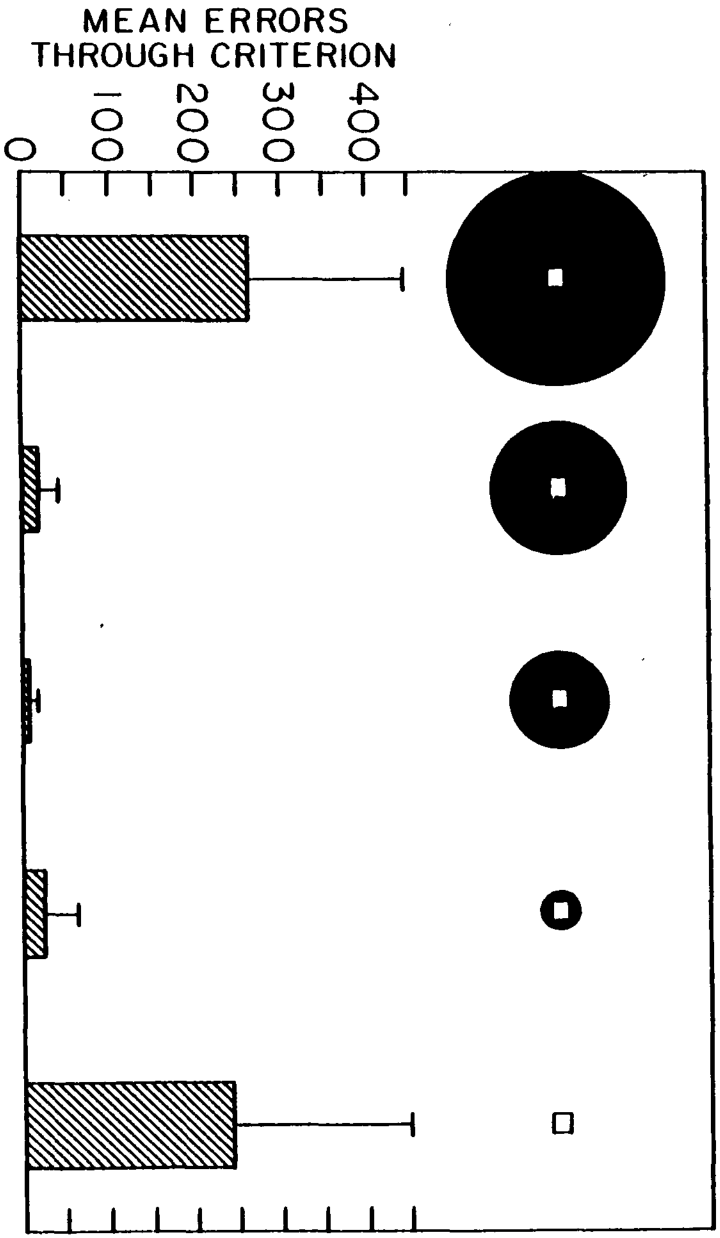

3
2
4
1
5
8
6
7

Figure 14. Mean errors of destriated monkeys on the 90, 55, 35 and 15 mm disks, and the apple cube target. Means and standard deviations represented by the height of bars and segments, respectively. Target conditions are drawn to scale above the appropriate bar. Note the deficit on the 90 mm disk, absent in the remaining black targets, and reinstated to a similar degree when the apple cube was presented alone. This was confirmed statistically by the following comparisons: 90 vs 55, 90 vs 35, 90 vs 15, apple vs 55, apple vs 35 ($p < 0.01$), and apple vs 15 ($p < 0.05$).

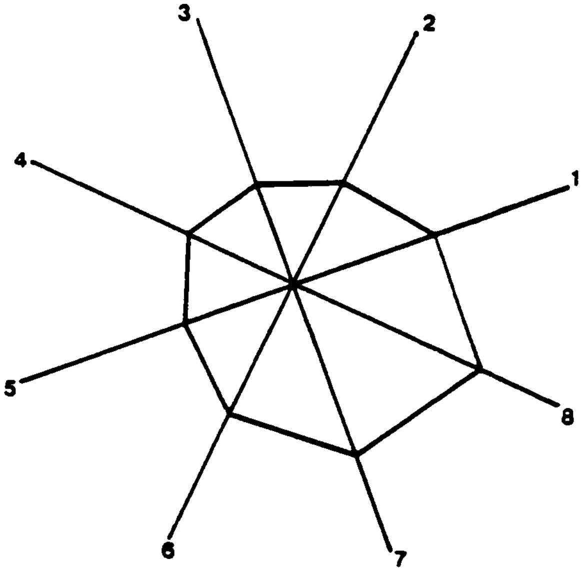

MEAN ERRORS THROUGH CRITERION
0
100
200
300
400

Significant differences were not found between the overall deficits with the 90 mm and apple cube, as well as between the three other tests.

The group performance of the destriated monkeys was assessed for reaching accuracy to the eight positions (1-8) on the 90 mm and apple cube targets. A group position effect was found for the performance on the 90 mm disk (Appendix 2, line 3). The Scheffé test failed to confirm significant differences between individual comparisons. However, when contiguous position performances were aggregated, differences ($p < 0.05$) were found (i.e. 7+8 vs 2+3 and 7+8 vs 2+3+4+5; $p < 0.05$) and graphically represented in Figure 15 top. The destriated monkeys reached more accurately when the 90 mm target appeared in the lower positions, particularly in the lower right quadrant. The individual performances of four of the six monkeys (848, 849, 863, and 865) demonstrated significant position effects (Appendix 2, lines 4, 5, 6, and 7, respectively) with only one of these animals (865) showing a right-left difference rather than the lower-upper disparity characteristic of the group (Appendix 3).

Reaching accuracy on the apple cube target suggested a tendency for better performance in the upper quadrants (Figure 15, bottom). It must be emphasized, however, that the overall performance on this target was impaired and highly correlated to the magnitude of the deficit observed on the 90 mm target using total errors ($\underline{r} = 0.99$) and trials through criterion ($\underline{r} = 0.88$). Of the four striatectomized monkeys which demonstrated a position effect on the apple cube target (849, 852, 863, and 864) (Appendix 2, lines 8, 9, 10, and 11, respectively), three responded significantly better when the apple cube appeared in the extreme upper positions (852, 863, and 865) while the other animal (849) responded better in the lower positions (see Appendix 4).

Figure 15. Mean reaching accuracy of striatectomized monkeys on the 90 mm (top) and apple cube targets (bottom) where impairments were observed. Graph as in Figure 13, except that interconnecting lines do not represent through criterion scores but precriterion performance in order to make the location of the deficit more noticeable. Note that the performance of these animals was superior in the lower right section on the 90 mm disk, whereas reaching accuracy to the apple cube was better in the upper quadrants.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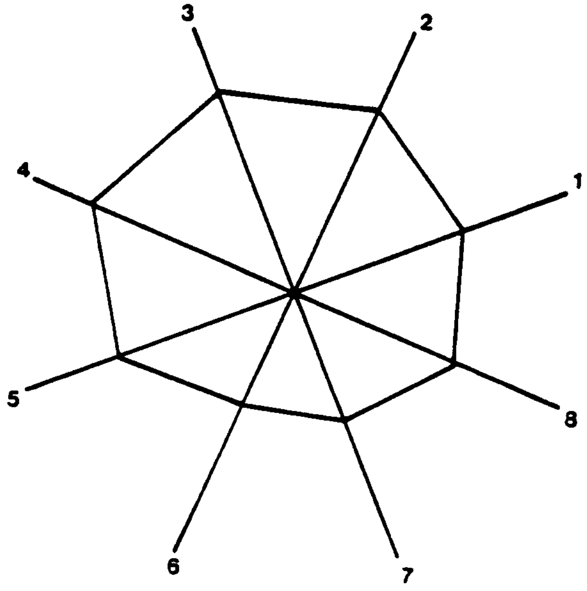
8
6
7


3
2
4
1
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6
7

The acquisition curves, i.e. cummulative precriterion errors, are plotted for the five destriated monkeys (848, 849, 852, 863, and 865) which demonstrated a deficit on the 90 mm target (Figure 16). The sixth monkey (853) does not appear for as much as precriterion performance consisted of a single testing session. All of the data plots shown in Figure 16 were better fitted by a linear least squares solution (see Appendix 5). The various parameters of these curves, e.g. total errors, number of precriterion sessions and rate of error commission, do not offer a clear indication for the subdivision of the group according to the interval between surgery and formal testing (Table 1). This distinction, however, becomes apparent in a single measure of overall performance (P) which combines and weighs the effects of the three parameters. P is defined as the shortest distance between the total precriterion errors and the minimum criterion line, i.e. a 10% error rate. For 56-trial sessions, the slope of this line is 5.6. Computed in this way (Appendix 6), the mean P values are significantly different in the two groups of animals ($t = 4.65$, $p. < 0.05$).

The learning curves for the impaired monkeys using the apple cube target (848, 849, 852, 863, and 865) are presented in Figure 17. Four of these data plots were better fitted by logarithmic least squares solutions (Appendix 5), and the fifth one (863) by a linear solution. It can be seen from the graphs that the deficit was more severe in the monkeys with short intervals between surgery and formal testing (viz. 863 and 865).

Combined Striate Cortex and Superior Colliculus Lesions

The animals which sustained both striatectomies and colliculectomies (850, 863, 864, 865, 875, 876, and 884) fell into one of two categories

Figure 16. Individual learning curves for accurate reaching to the 90 mm target by destriated monkeys. Note that the scores for 848, 852, 863 and 865 are similar, but that 848 and 852 required fewer sessions. Monkey 863 was most impaired with respect to both total errors and sessions. Monkey 865 committed more errors but required less precriterion testing than 849.

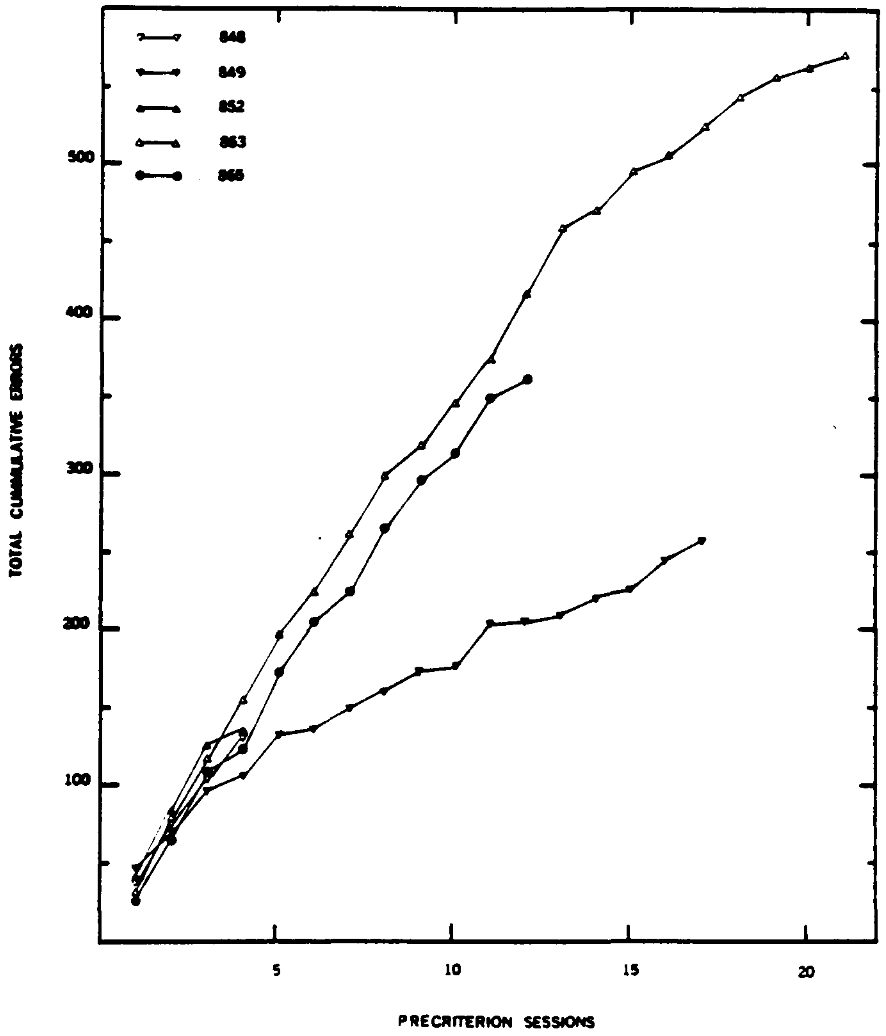
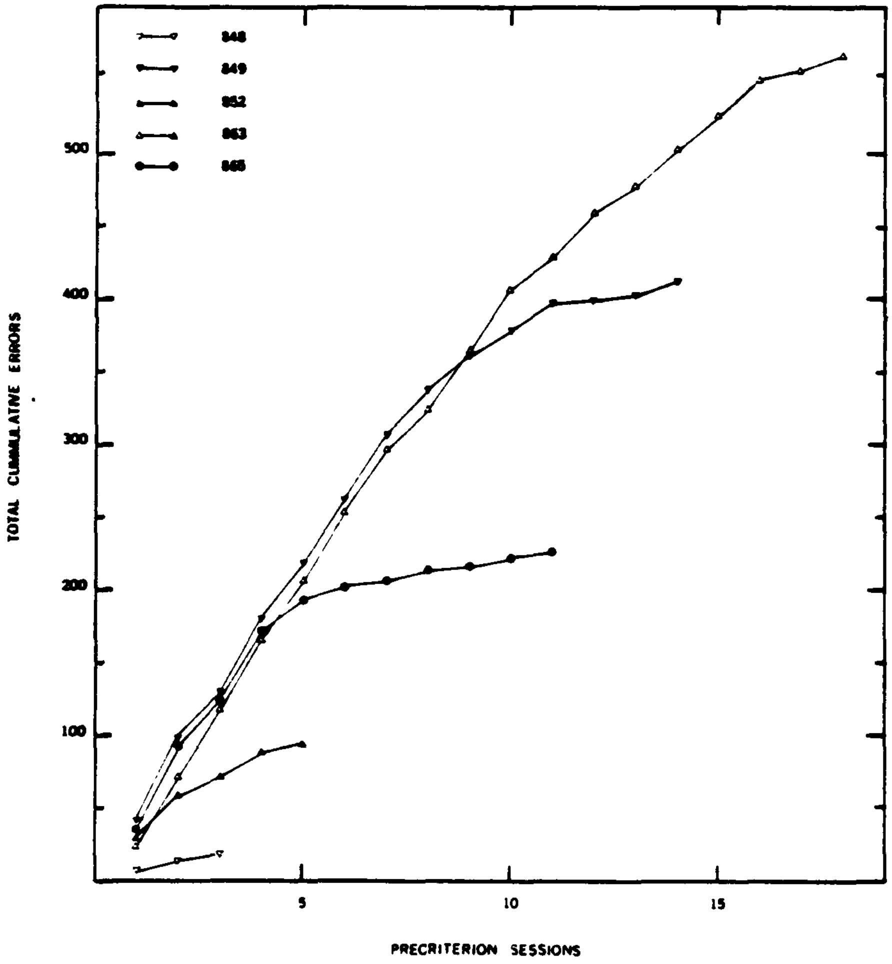

848
849
852
863
865
TOTAL CUMMULATIVE ERRORS
100
200
300
400
500
5
10
15
20
PRECRITERION SESSIONS

Figure 17. Learning curves to criterion performance on the apple cube tasks for the destriated monkeys (848, 849, 852, 863, and 865) which demonstrated an impairment. Note the direct relationship between total number of errors and number of precriterion testing sessions.


848
849
852
863
865
500
400
300
200
100
TOTAL CUMMULATIVE ERRORS
5
10
15
PRECRITERION SESSIONS

depending on whether or not they mastered the tests. Four of the monkeys (864, 875, 876 and 884) with practically complete destruction of the superior colliculi, failed to meet the criterion for successful performance on the 90 mm disk within 107 testing sessions, and consequently no other target was presented. As a group, the analysis of position effects was not statistically significant (Figure 18). All individual analyses, however, were significant (Appendix 2, lines 12, 13, 14, and 15, respectively) and the radial plots of these data are presented in Appendix 7. It can be seen from the graphs that there was no consistent response pattern among these animals, e.g. less errors occurred in upper positions for 864, the extreme right for 875 and 876, and to the left for 884, which would explain the non-significant group findings. These results, taken together with informal observations, suggest that the animals adopted a stereotyped reaching mode (i.e. a position habit) which could not be corrected. None of these monkeys approached the 90% correct level at any target position, and in fact the best performance was only 50% correct at a single location.

Three of the combined-lesion animals (850, 863 and 865), with incomplete colliculectomies, mastered the entire battery of targets. The data of two (863 and 865), which received the sequence striatectomy-colliculectomy, will be treated together whereas the results of the third animal (850), with a reversed operative order, will be considered separately.

A significant target effect was found for 863 and 865 using trials but no errors to criterion (Appendix 2, lin3 16). The Scheffé comparisons revealed that this was due to the performance on the 90 mm disk compared to each and all of the other targets ($p < 0.05$). A group position analysis was not computed since errors to criteron failed to reach a significant depending on whether or not they mastered the tests. Four of the monkeys (864, 875, 876 and 884) with practically complete destruction of the superior colliculi, failed to meet the criterion for successful performance on the 90 mm disk within 107 testing sessions, and consequently no other target was presented. As a group, the analysis of position effects was not statistically significant (Figure 18). All individual analyses, however, were significant (Appendix 2, lines 12, 13, 14, and 15, respectively) and the radial plots of these data are presented in Appendix 7. It can be seen from the graphs that there was no consistent response pattern among these animals, e.g. less errors occurred in upper positions for 864, the extreme right for 875 and 876, and to the left for 884, which would explain the non-significant group findings. These results, taken together with informal observations, suggest that the animals adopted a stereotyped reaching mode (i.e. a position habit) which could not be corrected. None of these monkeys approached the 90% correct level at any target position, and in fact the best performance was only 50% correct at a single location.

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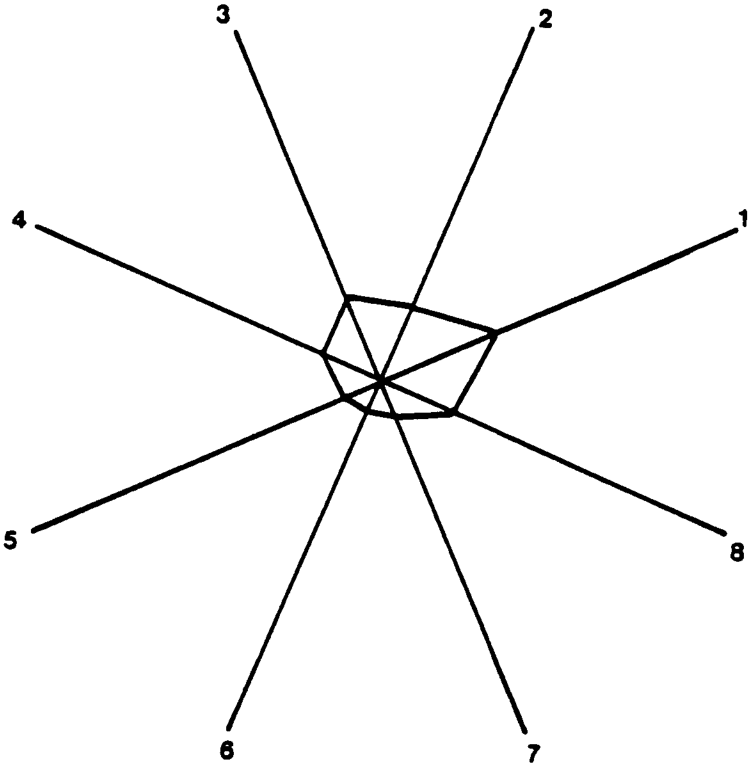
Figure 18. Group accuracy plot for the combined-lesion animals (864, 875, 876 and 884) which failed on the 90 mm test. The graph is constructed as in Figure 13, but the interconnecting line denotes failure to attain criterion within 5992 trials. Note the very low proportion of accurate reaches at all positions.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level. The individual ANOVARs for 863 on the 90 mm and 55 mm targets were significant (Appendix 2, lines 17 and 18, respectively). When the 90 mm disk was presented, more correct responses occurred in the lower left sector, whereas the effect on the 55 mm target consisted of more correct reaches to the left as compared to the right (Appendix 8). The analysis of the position data from 865 was significant for the 90 mm target only (Appendix 3, line 19). No individual or contiguously aggregated combination of comparisons achieved significance. This would indicate that the effect was distributed over the eight positions, but no necessarily in relation to adjacent cluters.

Since these two animals required only two precriterion sessions on the 90 mm target, and a single such session on the 55 mm disk, learning curves were not generated. In fact, there were positive savings on most of the targets after the second-stage collicular lesion that ranged from 56%-97% in 863, and 17%-94% in 865.

In contrast, 850 failed to attain criterion on the 90 mm target in the prescribed 107 testing sessions. After altering the testing procedure to discourage grouping, the animal mastered the task in an additional 28 sessions. Only the performance on the latter sessions was used for statistical analysis which showed a significant position effect (Appendix 2, line 20). Additional impairments were also demonstrated on the 35 mm, 15 mm, and apple cube targets (Appendix 2, lines 21-23, respectively). The learning curves (Appendix 9) on the 90 mm and 15 mm disks were better fitted by linear least squares solutions, while the performance on the apple cube target was better described by a logarithmic reduction (Appendix 5).

Striate Cortex and Surgical Control-Lesions

Five monkeys served as operated controls. Four had posterior thalamic lesions after prior striatectomies (848, 849, 852 and 853), whereas the fifth animal (863) sustained cerebellar damage before the striate cortices were ablationed.

As a group, the animals with posterior thalamic lesions mastered the first four tests in the minimum number of trials, but showed a marked impairment with the apple cube target (Figure 3 and Table 3) as evidenced by both the errors and trials to criterion (Appendix 2, lines 24 and 25, respectively). The mean reaching accuracy on the latter task did not predominate in any particular region, but two of the individual analyses resulted in a significant position effect (849 and 853) (Appendix 2, lines 26 and 27, respectively). The learning curves of these latter two monkeys are presented in Appendix 10. In both cases, the data were better described by linear least square solutions. The remaining two animals (848 and 849) required only one and two precriterion sessions respectively, and no functions were generated.

The performance of the last lesion-control monkey (862) was unaffected following the first-stage cerebellar lesion. After the striate cortex removal, however, a large deficit occurred with the 90 mm and 55 mm disks (Table 3) which was not found when the subsequent targets were presented. Further analyses of these data revealed significant position effects (Appendix 2, lines 28 and 29). The learning curves were better fitted by linear solutions and they appear in Appendix 11.

CHAPTER IV

DISCUSSION

The Effects of Complete Combined Bilateral Striate Cortex and Superior Colliculus Ablations

The primary purpose of this study was to assess the accuracy of reaching for visual targets by destriated monkeys with complete bilateral superior colliculus resections, a task presumably testing the capacity for spatial localization. The animals prepared in this way were unable to attain criterion performance levels, and their reaches were stereotyped responses that lacked any suggestion of visual guidance. The behavior persisted even after extensive postoperative training. It should be emphasized that in this experiment the stimulus, response, and reward were made congruent, thereby maximizing the possibility of success. Other studies have shown that comparable conditions significantly reduced many deficits caused by lesions of the visual system (Butter, 1974a, 1979; Butter et al., 1978).

Although it can be hypothesized that the animals suffered from a general impairment in stimulus detection, it appears unlikely inasmuch as similarly lesioned monkeys: (a) made visual discriminations between transilluminated figures differing in total luminous flux using Klüver's pulling-in technique (Pasik et al., 1973; Wininger et al., 1972); (b) solved a light vs no-light problem (Pasik & Pasik, 1973); and (c) retained some capacity for a simple flicker discrimination and responded differentially to changes in total luminous flux (Anderson & Symmes, 1969). The aforementioned demonstrations of residual vision, however, were conducted using transilluminated targets under conditions of relative dark adaptation, whereas the animals in the present study were tested in normal room light with reflected figures. The issue of whether these procedural variants are important can be resolved by training a single group of such combined-lesioned monkeys on: (1) a discrimination task using flux-differing transilluminated figures, and (2) a localization test with a similar target in randomly varying positions. Consistently mastering the former problem and failing the latter would suggest that the ability to perceive differences in the total amount of radiant energy impinging on the retina is not sufficient for the animal to maintain the dimensions of its spatial environment.

Our findings are consistent to some extent with those of Mohler and Wurtz (1977) who used another measure of spatial localization. In their experiment, monkeys with partial unilateral lesions of striate cortex and superior colliculus showed a permanent deficit in both detecting and directing oculomotor saccades to a brief punctate light when flashed within overlapping scotomata. These results, however, may not be conclusive since the stimuli used could have been subliminal for the affected region of the field. In fact, it has been demonstrated that monkeys with total combined ablation can still detect a light (Pasik & Pasik, 1973) but according to the present study, failed localization tests.

In a recent experiment, Keating (1980) reported on the behavior of a single monkey which sustained extensive cortical and midbrain ablations. He observed the animal over a six-week period, and after testing it for only 500 trials concluded that the monkey appeared blind and was unable to execute accurate reaches for visual targets. This finding, however, is of relative value in determining the critical structures for space localization because the cortical resection not only removed the entirety of striate cortex but also damaged almost all of areas OA, OB and TEO. Moreover, the lesions of the superior colliculi invaded the posterior commissure, midbrain tegmentum, and posterior thalamus. Interestingly, Myers (1964) found that cats with just superior colliculus ablations that extended into these same subcortical regions, exhibited an apparent loss of visual responsiveness that was absent if the destruction was restricted to the colliculus and pretectum alone.

The present findings do not preclude the possibility that structures other than the superior colliculi assume a critical role for spatial localization in monkeys completely deprived of striate cortex. Several brain regions, however, can be excluded, as for instance, the medial pretectum. It should be recalled that one of our destriated monkeys (865) which sustained extensive pretectal damage in the course of a partial colliculus lesion, was only minimally impaired on the initial postoperative test (i.e., 90 mm disk) in spite of showing the characteristic <u>pretectal</u> syndrome, viz. paresis of upward gaze, eyelid retraction and pupillary alterations (Pasik, Pasik, & Bender, 1966, 1969; Pasik & Pasik, 1975). Preoccipital areas and portions of temporal neocortex are also non-essential for many visually guided behaviors such as accurate reaching, both in the presence and in the absence of striate cortex (Keating, 1975, 1980). Keating (1980) proposed that these residual capacities were mediated subcortically by the tectum inasmuch as most of the visual cortex had been removed (see also Humphrey, 1974). The possible importance of motor cortex in subserving these behaviors cannot be ignored. Monkeys subjected to unilateral ablations of the premotor and supplementary motor areas, including the adjoining rostral half of the precentral gyrus, were unable to direct the contralateral arm around a transparent barrier for a food reward, although they could reach directly toward the object (Moll & Kuypers, 1977). It is possible that combining these lesions with striatectomies would markedly disrupt accurate reaching without barriers. On the other hand, after adding bilateral accessory optic system ablations to complete striate cortex resections, monkeys failed to solve even a simple light vs no-light discrimination (Pasik & Pasik, 1973), and most probably they must have also been incapable of accurate reaching. The latter results suggest that an intact accessory optic system is necessary to modulate or regulate the function of the remaining visual system in the destriated monkey. This relationship, if it exists, could be demonstrated through electrophysiological procedures.

The Effect of Complete Bilateral Superior Colliculus Ablations Alone

The group performance of bilaterally colliculectomized monkeys was unimpaired and all tests were mastered in the minimum number of sessions. Moreover, these animals exhibited a differential reaction to the presence of the plastic cube as compared to the apple target on control trials which confirms other studies reporting that colliculus-lesioned monkeys could make complex visual discriminations (Anderson & Symmes, 1969; Butter, 1974a; Keating, 1974, 1976; Rosvold et al., 1958; Thompson & Myers, 1971).

The lack of clear cut deficits following colliculectomies perhaps indicates that either the appropriate questions are not being asked about the role of the colliculus in the otherwise intact brain, or that not all of the available techniques are being used to measure the extent of the defect, especially when the integrity of the striate cortex is preserved. In fact, colliculus removals may produce subtle underlying visual disturbances, such as: (a) a slight increase in the differential achromatic threshold (Leporé et al., 1976); (b) some alterations in saccadic eye movements (Schiller et al., 1979; Mohler & Wurtz, 1974, 1977); and (c) impairments in reaching toward or detecting lights briefly flashed in the far peripheral field (Butter et al., 1978; MacKinnon et al., 1976). In any event, the superior colliculi do not appear to be the necessary or sufficient structure for mediating accurate reaching.

The Effect of Striate Cortex Ablations Alone

Confirming the original observations on an almost totally striatectomized monkey (Humphrey, 1974; Humphrey & Weiskrantz, 1967), subsequently verified in completely destriated animals (Feinberg et al., 1977, 1978; Keating, 1980, Weiskrantz et al., 1977), our monkeys deprived of striate cortex could be trained to reach accurately for visual targets that varied in location, size, and contrast. This restitution of accurate reaching may reflect either new learning using available visual cues that acquire meaning through schedules of differential reinformcement, or the re-establishment of a morphological-physiological substrate, that is a physical change in the brain, which mediates the behavior. The data from the various measures of performance, i.e. reaching accuracy and acquisition curves, suggest the operation of both processes.

Selective and specific defects in performance on the first and last postoperative tests cannot be explained solely on the basis of some physical alteration in the central nervous system. An analysis of the demands of the two tasks reveals somewhat different requirements for successful performance, and these differences are reflected in the observed behaviors. For example, on the initial task (90 mm black disk), the animal had to withhold the reaching response and scan the field to detect the target, and then to localize it. The linear nature of the individual acquisition curves suggests that the two aspects of the learning process, namely response-suppression and detection-localization, developed concurrently, since no improvement in performance occurred during the precriterion sessions. This conclusion is supported by the observation that most animals reached in a "reflexive" pattern to the lower right quadrant and this was primarily due to their using the right hand, and the greater possibility for contacting the lower sections of the display. After a period of this type of response, accurate reaching was rapidly instated and generalized to the other disks. In contrast, the demands of the last test (apple cube alone) probably did not entail a response-suppression since "reflexive" reaching to the lower right quadrant was not a common occurrence. Presenting a low contrast target, therefore, transformed the task into a problem of just detection-localization. The difference in the learning process as compared to that of the previous tests was apparent in the negatively accelerated acquisition curves which showed a progessive improvement in reaching accuracy during the precriterion sessions. The complete transfer effects observed across the black targets, and from the apple cube to the plastic control cube, are consistent with a learning hypothesis.

The reinstatement of reaching accuracy in destriated monkeys cannot be primarily or exclusively dependent upon learning either, because the period separating the striate cortex removal and formal testing in the spatial localization problem proved to be a significant factor in the severity of the observed defects. In favor of a physical change hypothesis, there is some evidence of "sprouting" or "reactive synaptogenesis" in subcortical structures of the destriated rat, although no such findings are available for the monkey as yet. Schiller et al. (1974) explored some electrophysiological aspects of the problem by recording colliculus unit activity in acute monkey preparations after unilateral ablations or reversible cooling of visual cortex. They found that the units in the optic strata were relatively unaffected by both lesion procedures, but neurons in the deeper layers showed a marked decrement in responsivity to visual stimuli. These findings offer at least some physiological evidence for a functional change in the primate extrageniculostriate system pursuant to visual cortex excisions.

The process must begin relatively soon after striatectomy, inasmuch as the most severely impaired of our monkeys demonstrated reaching accuracy on the first target within one month after surgery. From the results of the present experiment, it can be adduced that the deficits were relatively smaller in the animals with a more prolonged lesion-test interval. The evidence, however, is not conclusive because the subjects with the longest recovery had also a considerable amount of discrimination training prior to this study. In any event, specific practice within a region of anopia has been shown to improve the accuracy of saccadic eye movements, which suggest that time is not the only determinant (Mohler & Wurtz, 1977; Weiskrantz & Cowey, 1963, 1970). In the final analysis, theories of anatomical and physiological plasticity of the nervous system must account also for the "non-specific" effect of striate cortex removals on performance (e.g. see Orbach, 1959). It is interesting to note that there have been demonstrations of residual visual capacities within scotomata in humans with lesions of the geniculostriate system. It had been shown that the method of testing influenced the relative size of the anopic region (Teuber, Battersby, & Bender, 1960), and more recently, that patients could accurately reach (Weiskrantz, Warrington, Sanders, & Marshall, 1974) or make oculomotor saccades to stimuli (e.g. Zihl, 1980) presented within the scotomata.

Theoretical Implications

From the results following single lesions, an important issue emerges regarding the functional organization of the primate visual system, viz. is the processing of information hierarchical or parallel? There are electrophysiological data in support of both points of views. In their original work, Hubel and Wiesel have proposed the former type of organization as a chain of neuronal connectivity, in the cat (Hubel & Wiesel, 1962) and in the monkey (Hubel & Wiesel, 1968), whereby the cells of the lateral geniculate nucleus project their axons to cortical neurons having "simple receptive field" characteristics. The next higher order elaboration is mediated by the "complex cortical cells" that receive their input from numerous simple cells and in turn transmit this information to "hypercomplex cells." In contrast, however, more recent physiological findings support the existence of separate systems of retinal ganglion cells (viz. X-, Y-, and W-cells). In both the cat and monkey, each system has a specific distribution across the receptor surface with characteristic receptive field properties (Enroth-Cugel & Robson, 1966; DeMonasterio, 1978); and a relatively insulated course to the lateral geniculate nucleus and superior colliculus (Cleland, Rubin, & Levick, 1971; Dreher, Fukada, & Rodieck, 1976; Marrocco, 1976; Sherman, Wilson, & Kaas, 1976) and to visual cortex (Campbell, Cooper, Robson, & Sachs, 1969; Schiller, Finlay, & Volman, 1976).

From behavioral work with the golden hamster, Schneider (1969) concluded that the retinogeniculostriate system subserves visual discriminative capacities whereas the retinotectal system mediates orientation and localization in space. Similar comparisons have been drawn also with regard to primate vision (Trevarthen, 1968). Such a hypothesis of two visual systems operating in the monkey requires experimental verification through a double dissociation of deficit and locus of lesion. From the results of the present experiment and the flavor of the research cited throughout this disseration, however, such a dichotomy of structure and function cannot be supported in the primate. Specifically, monkeys sustaining either complete bilateral colliculectomies or striatectomies demonstrated the capacity for both exquisite spatial localization as well as many visual discriminations. In fact, a recent study has questioned the importance of this distinction even in the hamster (Mort, Cairns, Hersch, & Finlay, 1980). More importantly, however, there is evidence for neuroanatomical and electrophysiological interactions between the striate cortex and superior colliculus (Cynader & Berman, 1972; Schiller et al., 1974; Wilson & Toyne, 1970), and, therefore, it does not seem parsimonious to ascribe mutually exclusive functions to these two structures.

Incidental Observations

While some investigators have found relatively severe visual deficits in colliculectomized animals (Denny-Brown, 1962; Denny-Brown & Fischer, 1976; Sprague, Berlucchi, & Di Berardino, 1970; Sprague & Meikle, 1965; and see also Sprague, Berlucchi, & Rizzolatti, 1973), several others, including the present author, have observed that the gross alterations in visual behaviors rapidly disappeared within the first postoperative month (Anderson & Symmes, 1969; McKinnon et al., 1976; Rosvold et al., 1958). The more permanent defects in the monkey seemed to reflect subtle changes, as in the aforementioned oculomotor responses (Mohler & Wurtz, 1977; Schiller et al., 1971; Schiller et al., 1979) and in the problems of stimulus detection or in threshold determinations (Butter et al., 1976; Leporé et al., 1976; McKinnon et al., 1976). The reason for these seemingly divergent findings may be due to some task related or species specific variables. Moreover, since our animals just manifested the marked disturbances in vision during the acute postoperative period, the cause could have been due to the non-specific effects of brain edema. It should be noted, in this regard, that the progressive restitution of function and the eventual remission of the visual deficits, corresponded to the reversal and the disappearance of the signs of intracranial hypertension.

Denny-Brown (1962) concluded that the severity of the impairment following superior colliculus ablations was related to the amount of associated pretectal involvement; however, two of his animals also suffered "patchy" superficial damage to the occipital pole. This latter result is more consistent with our observations that the cortical involvement, whether direct or indirect, was the most crucial determinant of the defects found in colliculus-lesioned monkeys.

As reported earlier in the cat (Fischman & Meikle, 1965; Urbaitis & Meikle, 1968), the single lesion most disruptive to behavior in the monkey was the complete destruction of the striate cortices, and the subsequent partial removal of the superior colliculi did not exacerbate the nature of the impairment. This was even true in the present experiment if the latter lesion also extended into the pretectum and corpus callosum. Unlike the above investigations using the cat, reversing the lesion sequence was an important factor as this resulted in a marked decrement in the overall visual responsiveness that could not be explained solely on the basis of adding the occipital damage alone. Other factors must have influenced the eventual restitution of accurate reaching in the destriated animal with partial colliculectomies, such as physical changes in the nervous system and new learning. In fact, if a morphological substrate were not involved, the lesion sequence would not infleuence the results because the remaining collicular tissue would be structurally similar. However, this latter hypothesis cannot exclusively explain these findings either, since accurate reaching could be demonstrated after modifying the reinformcement contingencies to discourage tactual exploration of the stimulus display. Extending the findings of Butter (Butter, 1974a, 1974b; Butter et al., 1978), it was necessary to force the animal to maximize the probability of visual input. Therefore, if a sufficient amount of collicular tissue was present in the destriated monkey, an impressive capacity for spatial localization could be demonstrated even when presenting low contrast stimuli.

Areas For Future Research

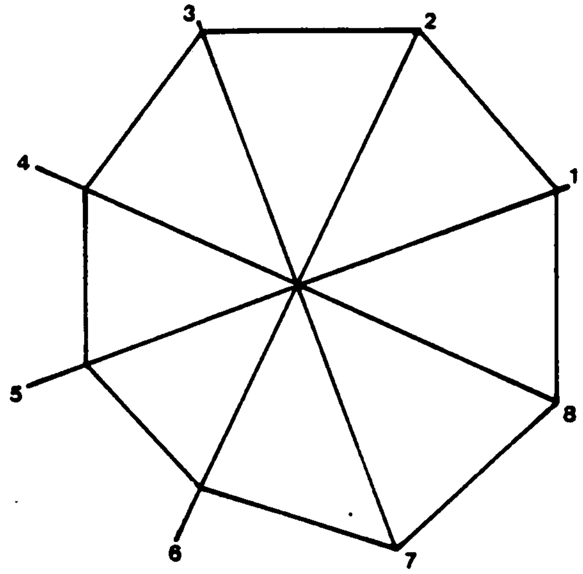
Including the experiments alluded to above, two other areas for future research should also be mentioned. First, the present study was primarily concerned with whether the superior colliculi were critical structures for mediating spatial localization using the accuracy of reaching as the dependent variable. Since the magnitude and direction of inaccurate responses could not be obtained under these testing conditions, no correlation could be obtained relating them to the process of re-establishing precise spatial localization. An analysis of these data in terms of differential position effects would provide additional useful information. An experiment designed to quantify these measures may shed some light on the progress of restitution of function and be of value in evaluating how the destriated monkey learns to use the available visual cues in the solution of this problem. Second, the effect of the time interval separating the striatectomy and formal testing, both with and without practice on other discrimination tasks, should be investigated in a study specifically designed to assess the effect of these parameters. This could be accomplished by examining two groups of animals. One group would be tested on the spatial localization problem at variable intervals after the striate cortices were removed, and the second group would be given interposed visual discrimination training. The procedure would permit the examination of inter-group as well as intra-group differences with respect to time (T) and practice (P), in which case a meaningful main effects interaction (TxP) could be evaluated.

Conclusions

The results of the present investigations, taken together, demonstrate that the primate superior colliculi are dispensable structures for accurate reaching toward objects appearing at random in space with the integrity of the striate cortices preserved. They are critical for mediating this behavior in the destriated monkey, inasmuch as the complete excision of both structures is required to eliminate the response. These findings do not preclude, however, comparable effects following the ablation of other structures in animals completely deprived of striate cortex (e.g. the accessory optic system). Moreover, the existence of two independent visual systems operating in the primate, is not supported by the present findings and they further emphasize the primary importance of the geniculostriate vision in the intact organism for the behaviors explored. Learning and physical changes within the brain structures are possible factors influencing the restitution of function represented by extrageniculostriate vision.

Appendix 1. Top: Peformance of 875 on the 90 mm target after right colliculectomy. For explanation of the radial plot see Text Figure 13. Note the occurrence of some errors on the lower left quadrant (positions 5 and 6).

Bottom: Performance of 876 on the 90 mm target after left colliculectomy. In this and all following graphs the interconnecting lines indicate only precriterion scores to make more evident the location of the deficit. Note a marked asymmetry of responses with predominance of errors in the right field (positions 1, 2, 7, 8).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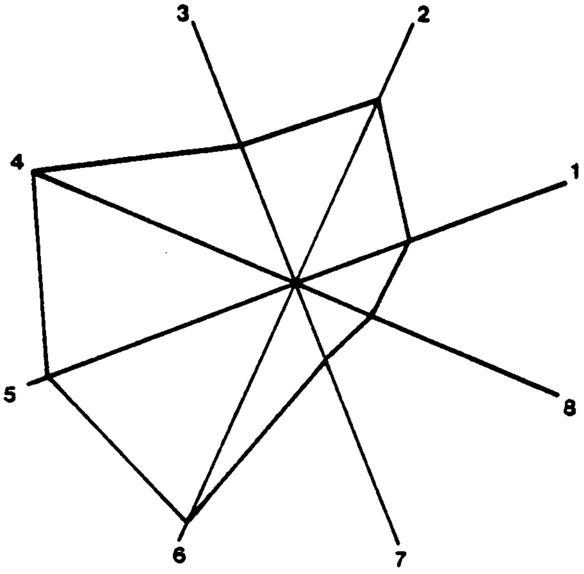
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Appendix 2. The significant F ratios from the ANOVARs of the experiment are enumerated by line number reference and give the corresponding degrees of freedom for the respective treatments and error components.

Line No.	Degrees of Freedom Treatments	 Error	F
1	4	20	8.03
2	4	20	14.94
3	7	35	2.80
4	7	49	3.18
5	7	140	4.63
6	7	178	7.12
7	7	105	13.45
8	7	119	7.00
9	7	56	7.07
10	7	147	14.74
11	7	98	7.97
12	7	735	61.44
13	7	742	100.95
14	7	742	134.86
15	7	742	37.04
16	7	4	15.00
17	7	35	7.72
18	7	28	6.10
19	7	35	2.76*
20	7	189	23.86
21	7	35	8.20
22	7	203	9.86
23	7	245	10.42
24	7	12	3.79
25	7	12	4.23
26	7	140	6.67
27	7	126	17.38
28	7	476	31.76
29	7	119	11.17

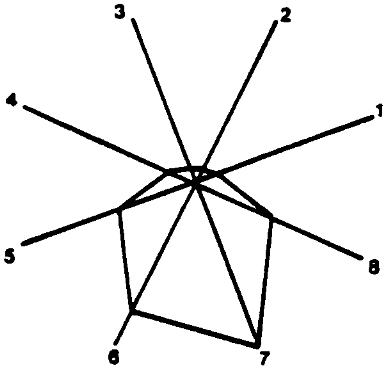
* Denotes $p < 0.05$. All other values are significant at $p < 0.01$ level.

Appendix 3. Individual accuracy plots, as described in Appendix 1 bottom, for the destriated monkeys which demonstrated a position effect on the 90 mm target. The following Scheffé comparisons of interest were found significant.

Monkey 848	2+3	vs	6+7	*
	1+2+3+4	vs	5+6+7+8	**
Monkey 849	2+3	vs	1+4+5+6	*
Monkey 863	3+4	vs	6+7	**
	3+4	vs	7+8	**
	1+2+3+4	vs	5+6+7+8	**
	2+3+4	vs	6+7+8	**
Monkey 865	4+5	vs	1+8	**
	5+6	vs	1+2	**
	3+4	vs	7+8	**
	3+4+5+6	vs	1+2+7+8	**

*$p < 0.5$

**$p < 0.01$



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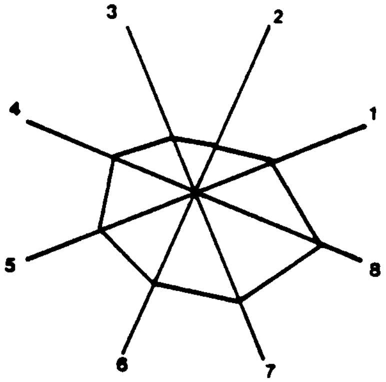

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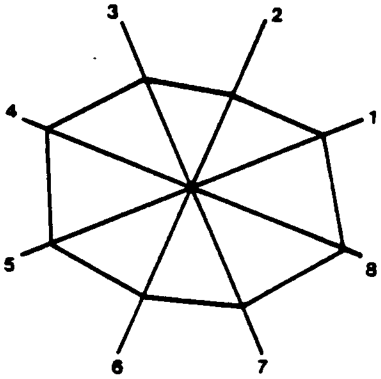

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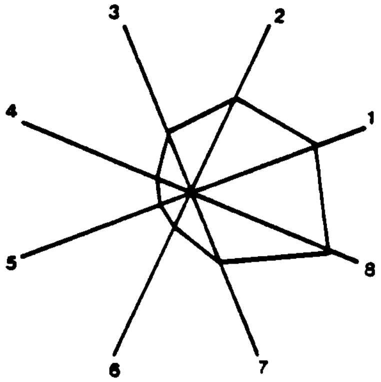

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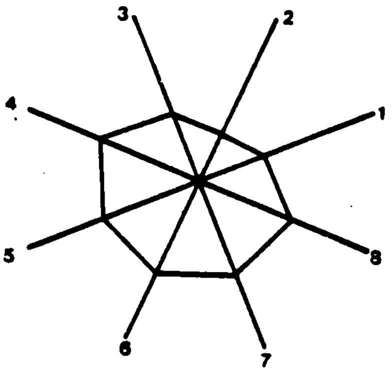
Appendix 4. Individual accuracy plots, as constructed in Appendix 1, bottom, for the striatectomized animals which exhibited a significant position effect for the apple cube target. The following Scheffé comparisons of interest were found to be significant:

Monkey 849	2+3	vs	6+7	**
	1+2	vs	5+6	**
	1+2+3+4	vs	5+6+7+8	
Monkey 852	6+7	vs	2+3	**
	5+6	vs	1+2	**
	7+8	vs	3+4	**
	5+6+7+8	vs	1+2+3+4	**
Monkey 863	6+7	vs	2+3	**
	5+6	vs	1+2	**
	7+8	vs	3+4	**
	5+6+7+8	vs	1+2+3+4	**
Monkey 865	6+7	vs	2+3	**
	6+7	vs	1+2+3+4+5+8	*

*$p < 0.05$

**$p < 0.01$



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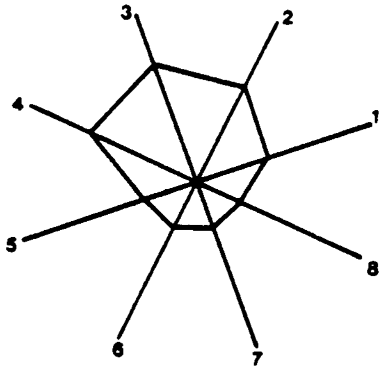

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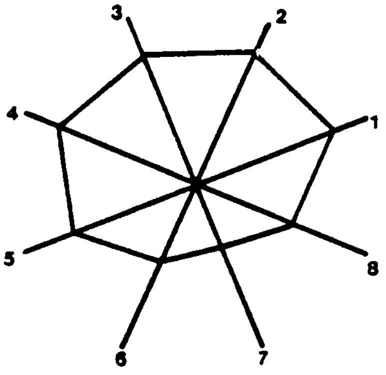

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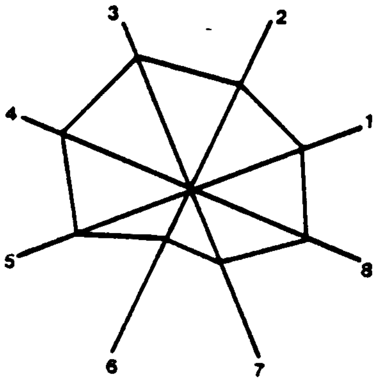

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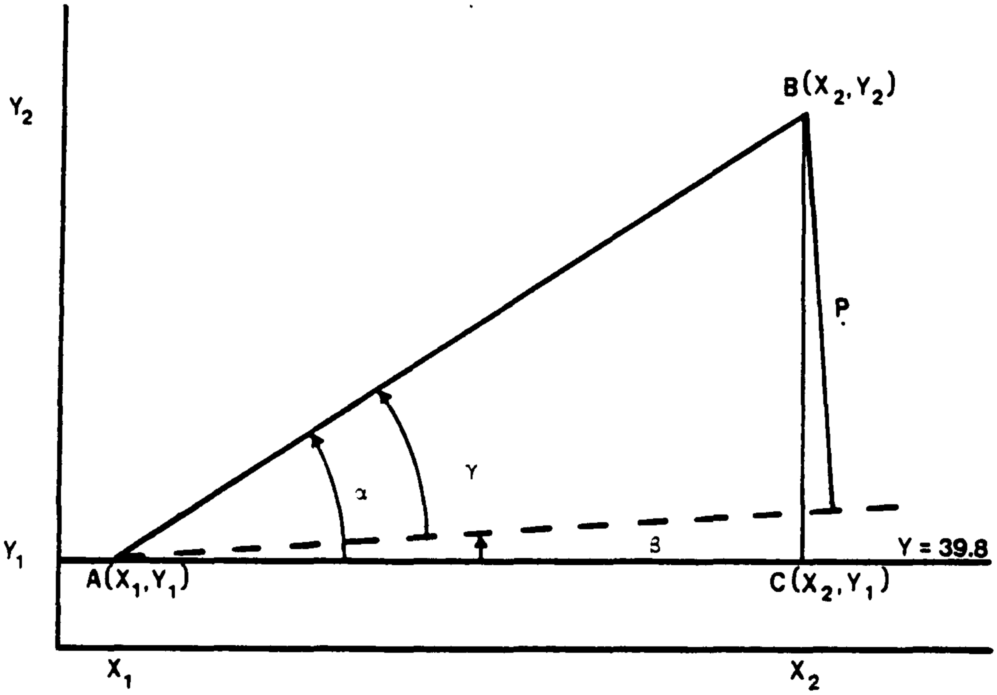
Appendix 5. The linear and logarithmic least squares solution for the slope (A), Y-intercept (B), and predicted error function [F (E)] on selected postoperative targets are listed by monkey and operative stage using those targets which required at least three precriterion sessions. Notation of lesions as in Text Table 1.

			Linear Regression			Logarithmic Regression		
Monkey	Lesion	Target	A	B	F (E)	A	B	F (E)
848	Str.	90 mm	32.8	7.5	13.8	159.7	34.4	178.0
	Str.	Apple	7.0	2.3	0.7	29.0	8.8	0.5
849	Str.	90 mm	12.4	55.0	1393.8	164.9	20.9	1849.1
	Str.	Apple	29.4	62.8	15026.2	371.7	-7.6	7982.1
	Str. + Tha.	Apple	17.8	57.6	3933.8	269.3	-10.2	7199.7
852	Str.	90 mm	33.4	13.5	88.2	164.9	40.1	103.0
	Str.	Apple	13.9	28.7	85.1	81.3	36.6	2.6
853	Str. + Tha.	Apple	12.4	3.9	96.0	154.4	-21.9	33192.9
863	Str.	90 mm	27.6	54.4	15927.4	470.8	-83.0	42956.1
	Str.	55 mm	8.3	-3.9	13.1	45.5	2.1	71.6
	Str.	15 mm	13.3	-4.6	199.4	95.2	-1.8	329.1
	Str.	Apple	32.4	45.1	16436.5	490.1	-77.4	30073.9
865	Str.	90 mm	30.9	13.5	674.2	326.8	-22.24	10318.7
	Str.	Apple	16.1	81.9	6453.3	191.1	43.7	636.0
850	S.C. + Str.	90 mm	26.9	80.1	17642.0	515.0	-94.6	54441.3
	S.C. + Str.	15 mm	20.6	32.0	21759.2	425.8	-125.2	44486.0
	S.C. + Str.	Apple	21.9	133.1	107584.0	562.9	-128.4	63119.0
862	Cer. + Str.	90 mm	36.1	169.7	833996.4	1652.3	-950.2	3618230.5
	Cer. + Str.	55 mm	30.3	-29.3	1986.3	347.6	-73.5	33631.6

Notation same as Text Figure 1

Appendix 6. The mathematical derivation of P and its value for the performance on the 90 mm target by striatectomized monkeys.



B(X2, Y2)
Y2
P
Y
α
β
Y1
A(X1, Y1)
Y = 39.8
C(X2, Y1)
X1
X2

Let: $A(X_1,Y_1)$ = the errors on the first testing session and

$B(X_2,Y_2)$ = cummulative number of precriterion errors.

Since on the first testing session the striatectomized monkeys scored an average of 39.8 ± 3.82 errors with the 90 mm target, indicating a relatively homogeneous group, the minimum criterion line (i.e. the dashed line) is shown to originate from point A which facilitates the mathematics. Note that the slope of this line still equals 5.6 (viz. a 10% error rate per 56 trial sessions).

Then: the length of line segment $\overline{AB} = \sqrt{(X_2-X_1)^2 + (Y_2-Y_1)^2}$; the tangent of $\alpha = \frac{Y_2-Y_1}{X_2-X_1}$ or the slope of $\overline{AB}$; the tangent of $\beta = 5.6$ or the slope of the dashed line; and angle γ = angle α = angle β.

Therefore: $P = \overline{AB}\,[\text{sine}\ (\gamma)\ ]$.

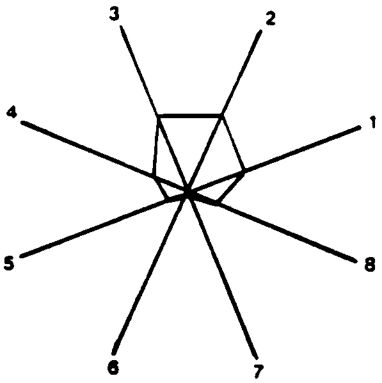
Values of P

848	--	18.66
849	--	18.90
852	--	19.14
863	73.79	--
865	48.71	--
$\bar{x}$	61.25	18.90
SD	17.73	0.25
t	4.530	
$p < 0.05$		

Appendix 7. Individual accuracy graphs on the 90 mm target for the combined lesion animals. The interconnecting lines denote that the animals never attained criterion in 107 testing sessions. The Scheffé analyses of the position effects revealed the following significant differences:

Monkey 864	6+7	vs	2+3	**
	5+6	vs	1+2	**
	7+8	vs	3+4	**
	5+6+7+8	vs	1+2+3+4	**
Monkey 875	4+5	vs	1+8	**
	5+6	vs	1+2	**
	3+4	vs	7+8	**
	3+4+5+6	vs	1+2+7+8	**
	2+3+4+5+6+7	vs	1+8	**
Monkey 876	4+5	vs	1+8	**
	5+6	vs	1+2	**
	3+4	vs	7+8	**
	3+4+5+6	vs	1+2+7+8	**
Monkey 884	1+8	vs	4+5	**
	1+2	vs	5+6	**
	7+8	vs	3+4	**
	1+2+7+8	vs	3+4+5+6	**

**$p < 0.01$



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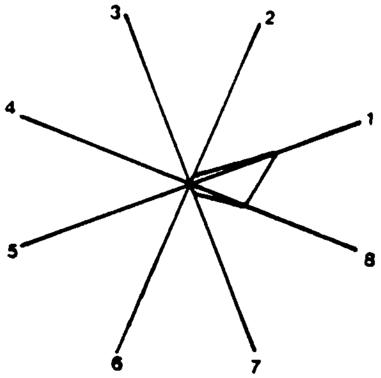

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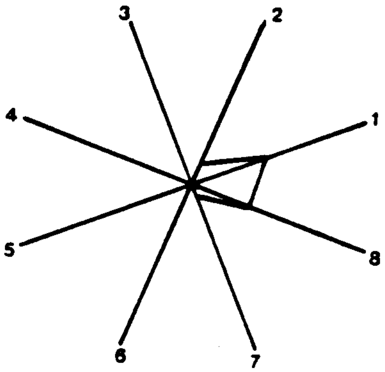

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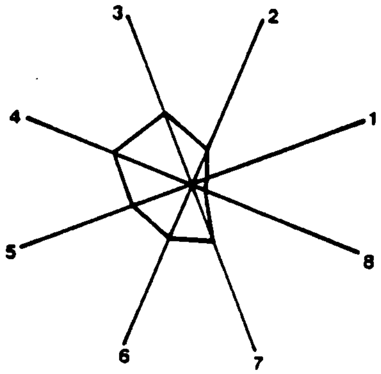

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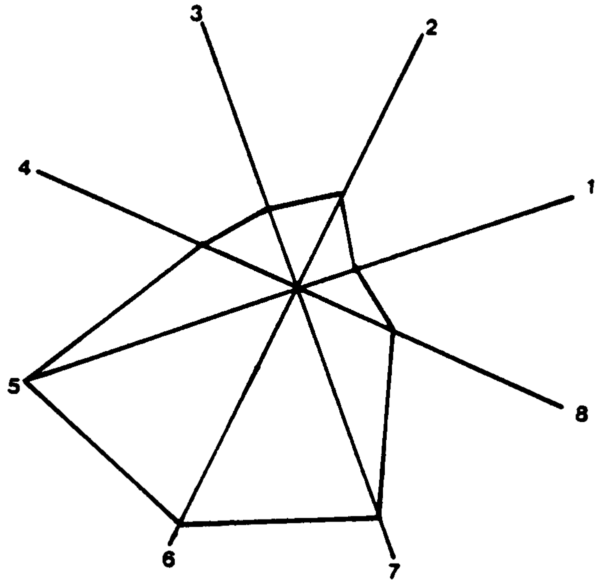
Appendix 8. Reaching accuracy of 863 on the 90 mm (top) and 55 mm target (bottom) after the combined ablations. Notation as in Appendix 3. The significant Scheffé comparisons for the 90 mm target positions were:

1+8	vs	4+5	**
1+2	vs	5+6	**
1+2+3+8	vs	4+5+6+7	**
1+2+3+4+8	vs	5+6	**

and for the 55 mm target:

1+8	vs	4+5	**
1+2+7+8	vs	3+4+5+6	*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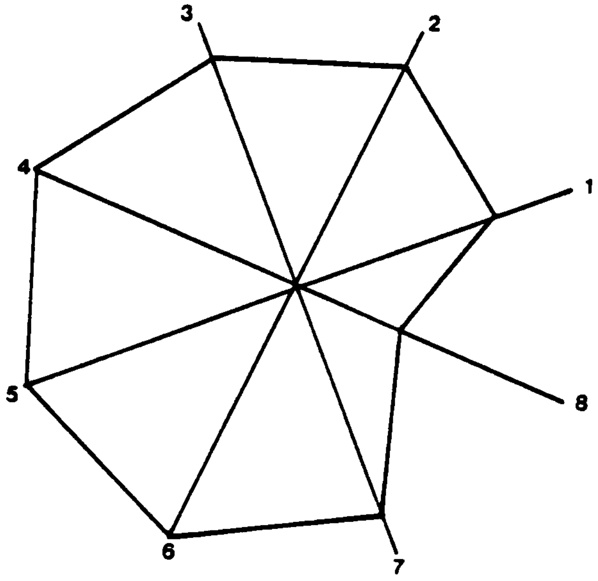
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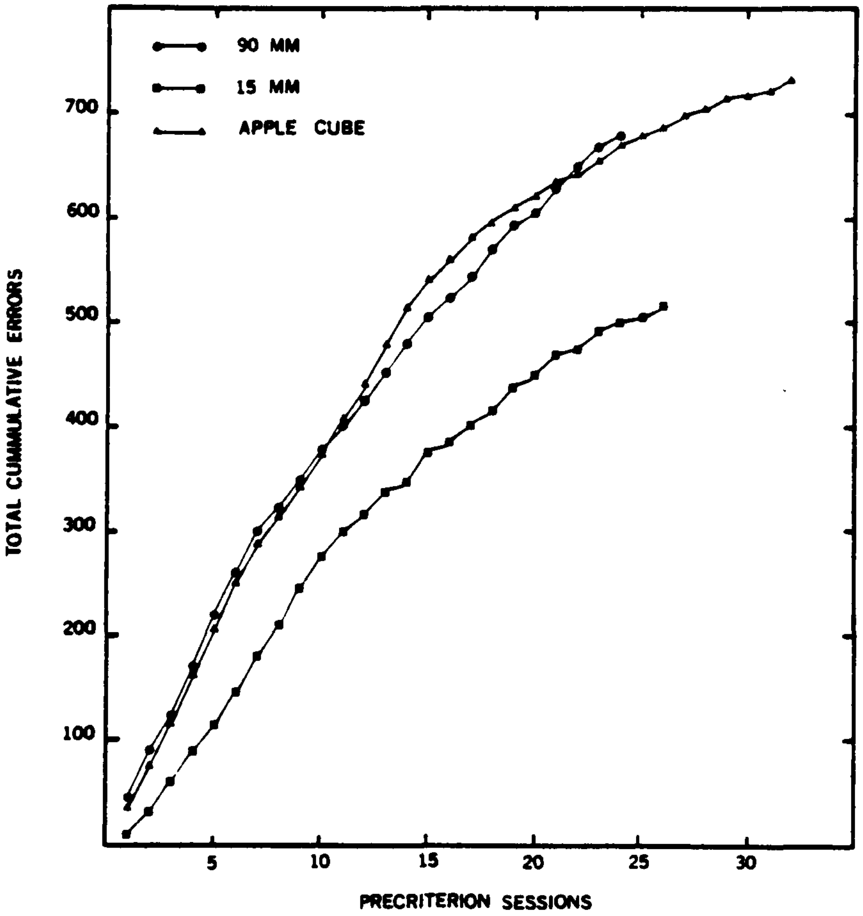
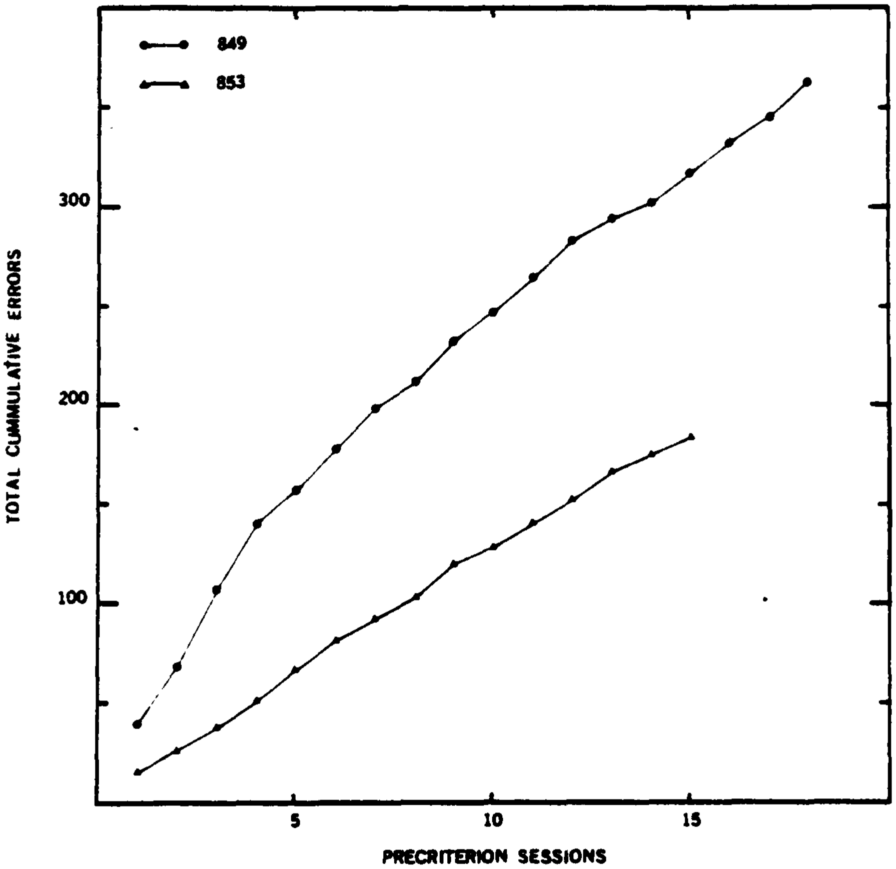
Appendix 9. Learning curves of 850 on the 90 mm, 15 mm, and apple cube targets after the combined lesions.

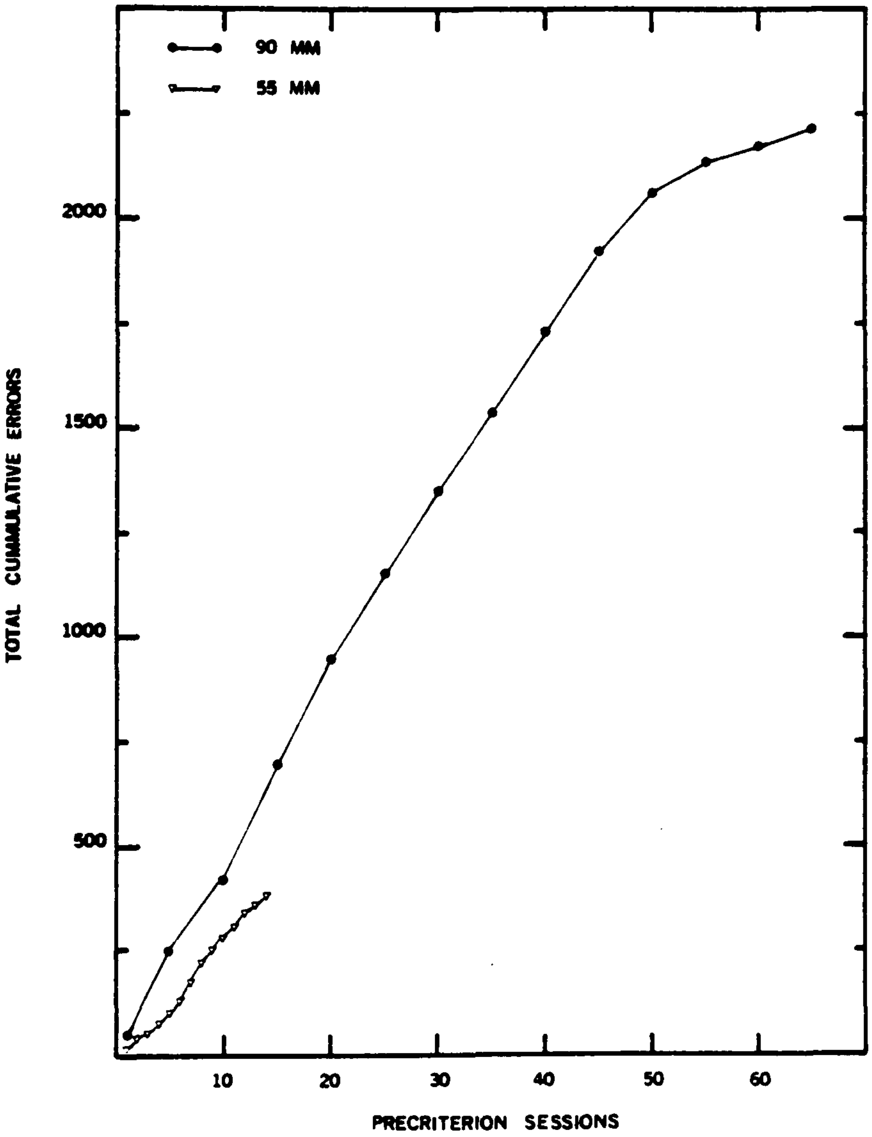

90 MM
15 MM
APPLE CUBE
TOTAL CUMMULATIVE ERRORS
100
200
300
400
500
600
700
5
10
15
20
25
30
PRECRITERION SESSIONS

Appendix 10. Learning curves of monkeys 849 and 853 on the apple cube target after the second lesion in the posterior thalamus. Note that 853 was less affected than 849 in both the total errors committed and the amount of precriterion testing.



●—● 849
▲—▲ 853
TOTAL CUMMULATIVE ERRORS
300
200
100
5
10
15
PRECRITERION SESSIONS

Appendix 11. Learning curves of monkey 862 on the 90 mm and 55 mm tasks following the second lesion (i.e. striatectomy). Note the rather large deficit on the 90 mm target evidenced by the total amount of errors committed and the prolonged precriterion testing. The impairment on the 55 mm target was relatively severe, although not so pronounced.



90 MM
55 MM
TOTAL CUMMULATIVE ERRORS
2000
1500
1000
500
10
20
30
40
50
60
PRECRITERION SESSIONS

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