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Original Research Article

Effects of MT lesions on visuomotor performance in macaques☆

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ABSTRACT

Monkeys with selective bilateral lesions of area MT were trained on tasks designed to examine visuomotor function. They were required to: 1- retrieve a small food pellet from a narrow slot; 2- locate and retrieve a loose peanut mounted on a background of fixed peanuts; and 3- retrieve an erratically moving food pellet from a spinning bowl. After the lesions, these monkeys were behaviorally impaired relative to their own preoperative performances and also relative to the postoperative performances of the control monkeys with lesions in optic radiation fibers (OR) under MT or lesions in the posterior parietal cortex (PP). Although their performance improved with practice and time, the MT-lesioned monkeys showed long-term impairments twenty weeks after surgery. Control monkeys performed no worse on the tasks after their lesions. Another task which required the monkeys to retrieve a food pellet without visual guidance revealed that all the animals performed equally poorly when visual cues were unavailable, but that only the control monkeys benefited when visual cues were available. None of the monkeys were impaired on a pattern discrimination learning task. Besides that, direct observations revealed that the MT-lesioned animals grasped peanuts in a manner different from the control animals.

1. Introduction

Our goal here is to explore the functions of a portion of prestriate cortex known as the middle temporal area (MT) or V5. Area MT has been clearly identified and delimited (Ungerleider and Mishkin, 1979; Zeki, 1974a,b; Gattass and Gross, 1981), and lies in the posterior bank and fundus of the superior temporal sulcus (STS). The extrastriate cortex in primates contains multiple visual areas (Van Essen and Zeki, 1978; Gattass and Gross, 1981; Gross et al., 1981; Gattass et al., 1988, 2005, 2015; Kaas, 1989; Neuenschwander et al., 1994). Indeed, while the processing of visual attributes is distributed across multiple areas (Zeki, 1969a, b; Van Essen and Zeki, 1978) and streams (Ungerleider and Mishkin, 1982), receptive field size becomes gradually larger at each successive hierarchical stage (Gattass et al., 1985). Other areas which have been implicated in visual functions, but which are not purely visual are posterior parietal cortex (PP), the superior temporal polysensory area (STP), and the frontal eye fields (FEF).

MT was first described in the owl monkey (*Aotus trivirgatus*) by Allman and Kaas (1971). Homologous areas have been identified in several other species, including the Galago (Allman et al., 1973) and the squirrel monkey (Spatz et al., 1970), marmoset (Spatz and Tigges, 1972), capuchin (Fiorani et al., 1989) and rhesus (Cragg and Ainsworth, 1969; Ungerleider and Mishkin, 1979; Weller et al., 1978; Zeki, 1971; Gattass and Gross, 1981) macaques. Although MT is not located in the middle of the temporal lobe of the macaque, the term has been adopted for the present study based on the similarity of architectural features, visuotopic organization, and anatomical connections of the area.

In the macaque, MT lies in the posterior bank and fundus of the superior temporal sulcus (STS) within cytoarchitectonic area 19 of Brodmann (Brodmann, 1905; Gattass and Gross, 1981). It can be myeloarchitectonically distinguished from surrounding cortex, since fiber staining shows heavy myelination in layers IV-VI. It receives a topographically organized projections from V1 (Ungerleider and Mishkin, 1979; Weller and Kaas, 1978), and also receives projections from V2, V3, V4, PO, POm, MST, FST, DI, DM, LIP, PIP, VIP and FEF (Zeki, 1976; Rosa et al., 1993). MT also receives projections from the inferior and lateral pulvinar (Benevento and Rezak, 1976; Soares et al., 2001).

Early work of extrastriate areas attributed color processing to a region in the pre-lunate gyrus (Zeki, 1973), while visual motion was processed at the STS (Zeki, 1974a,b). Furthermore, initial investigations on the posterior portion of the STS revealed at least three distinct visual areas: MT (Gattass and Gross, 1981; Ungerleider and Desimone, 1986;

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Fiorani et al., 1989; Diogo et al., 2003) and two middle superior temporal (MST) areas (Newsome and Wurtz, 1981; Newsome et al., 1986; Desimone and Ungerleider, 1986). Analysis of their receptive field properties indicated that visual motion processing becomes more elaborate as one progress from area MT to area MST (Zeki, 1974a,b; Albright, 1984; Albright et al., 1984; Albright et al., 1984; Movshon et al., 1985; Rodman et al., 1989, 1990; Newsome and Wurtz, 1981; Hikosaka et al., 1985; Tanaka et al., 1986; Wurtz et al., 1990).

Gattass and Gross (1981) have investigated the visuotopic organization of MT in *Macaca fascicularis.* MT contains a first-order transformation of the visual field (Allman, 1977), with the upper visual field represented anteriorly in the sulcus and the lower visual field posteriorly. The representation of the vertical meridian runs along the outer border of MT, while the horizontal meridian splits the area in two halves. The representation of the lower visual field is slightly larger than that of the upper visual field.

The visuotopic organization of MT is cruder than that found in V1 or V2. Additional, receptive field sizes increase a great deal with eccentricity. A large proportion of them are sensitive to direction of movement of a stimulus and are relatively insensitive to color, form, size, and orientation (Zeki, 1974a,b, 1978). Some neurons in MT respond best to changing disparity or to stimuli with expanding or contracting contours, possibly signaling movement in depth (Zeki, 1974a,b). Maunsell and Van Essen (1983) showed that a majority of MT cells were disparity selective. This neuronal disparity sensitivity could account for the abilities of primates to perform coarse disparity discrimination tasks and make perceptual decisions concerning depth (Uka and DeAngelis, 2003, 2004).

The purpose of the present study is to determine the behavioral impact of selective, bilateral, and complete MT lesions on easy-to-learn, visually-guided motor tasks. Among other aspects, the tasks we employed involved eye-hand coordination, visual search and depth discrimination. Our rational was that any behavioral impairment observed on these tasks would provide us with some insight into MT's visuomotor function (if any). The past decades have provided us with a detailed picture of MT's visual properties. Understanding MT's role in visuomotor function will extend our understanding of the prestriate cortex and its role in visually guided behavior.

2. Materials and methods

2.1. Subjects

Nine adult male cynomolgus monkeys (*Macaca fascicularis*) weighing between 3.0 and 6.0 kg were used in this study. Four subjects underwent selective, bilateral, and complete MT lesions (experimental group). There were two control groups. In the first control group, three monkeys underwent partial lesions of the posterior parietal cortex (PP). In the second control group, two monkeys underwent lesions of the white matter located under the superior temporal sulcus (STS). Note that the latter included lesions of the optic radiation (OR) fibers (Polyak, 1957). The behavioral performance of each animal was accessed during three phases (20 test sessions each): **1-** before the lesions, **2-** two weeks after the lesion, and **3-** 20 weeks after the lesions. All experimental protocols followed the National Institutes of Health guidelines for animal care and use and were approved by the Institutional Animal Care and Use Committee of Princeton University. The subjects, lesions and tests are depicted in Table 1.

2.2. Surgical procedures

The animals were anesthetized with ketamine hydrochloride (Ketaset, 20 mg/kg), and secured in a head holder under aseptic conditions. The scalp was incised along the midline and the skin and underlying muscle retracted, exposing the skull, which was then removed using a dental drill and rongeurs. The dura was opened exposing the STS from the top of the sulcus to a few millimeters below the junction of STS with the lateral fissure.

For the MT-lesioned animals, the dura was retracted and the blood vessel running the length of the STS was cauterized. Codman surgical

Table 1
Experimental Design. The procedures and tests used in each animal (cases) are presented. Procedures are listed in chronological order.

Lesion	*Case1* MT	*Case2* MT	*Case3* MT	*Case4* MT	*Case5* PP	*Case6* PP	*Case7* PP	*Case8* OR	*Case9* OR
Preoperative Testing									
Slot task	√	√	√	√	√	√	√	√	√
Peanut board	√	√	√	√	√	√	√	√	√
Spinning	√	√	√	√	√	√	√	√	√
Videotaped				√			√	√	√
Retrained	√	√							
Recovery period	2 wks	2 wks	2 wks	2 wks	2 wks	2 wks	2 wks	2 wks	2 wks
1st Posoperative Test									
Slot task	√	√	√	√	√	√	√	√	√
Peanut board	√	√	√	√	√	√	√	√	√
Spinning	√	√	√	√	√	√	√	√	√
Videotaped				√			√	√	√
Pattern discrim.	√	√	√	√	√	√	√		
Videotaped				√			√	√	√
Retrained	3 wks	3 wks	3 wks		2 wks	2 wks			
Videotaped	√	√	√		√	√			
Barrier Task	√	√	√	√	√	√	√	10 wks	10 wks
Videotaped	√	√	√	√	√	√	√	10 wks	10 wks
2nd Posoperative Test									
Slot task	√	√	√	√	√	√	√		
Peanut board	√	√	√	√	√	√	√		
Spinning	√	√	√	√	√	√	√		
Videotaped	√	√	√	√	√	√	√		

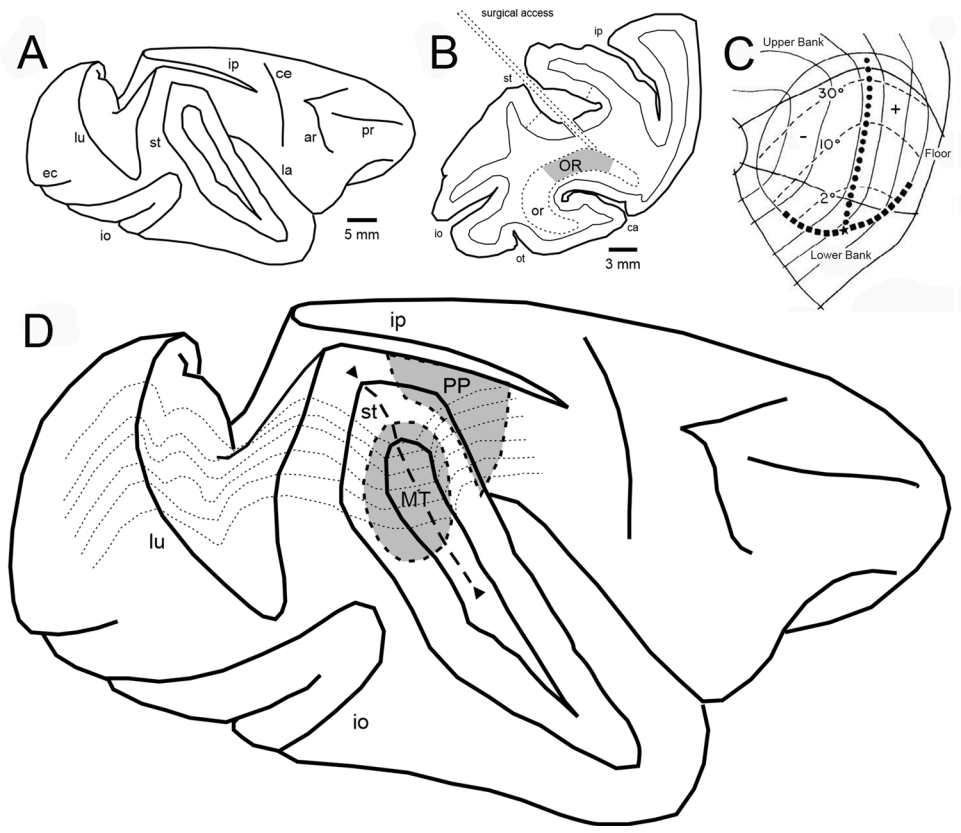

Fig. 1. Lesions were aimed at area MT, posterior parietal cortex (PP) and optical radiation (OR). **(A)** Lateral view of the monkey brain with the lunate (**lu**) and superior temporal (**st**) sulci opened. **(B)** Coronal section passing through area MT showing the surgical access to the OR. Fibers under area MT were lesioned using a scalpel. **(C)** Flattened representation of **st** showing the visual topography of MT, based on receptive field centers. **(D)** Expanded view of the monkey brain as shown in A. Shaded areas indicate areas MT and PP, the target of the lesions. MT lies at the bottom and posterior bank of the **st**, while PP lies on the brain surface, between **st** and the intraparietal sulcus (**ip**). The dashed line running at the bottom of **st** and delimited by arrow heads indicate the trajectory of the scalpel blade during lesion of the OR. Thin dotted lines indicate levels of parasagittal sections used for analysis of the 3D cortex. ***Abbreviations***: **ar**, arcuate sulcus; **ca**, calcarine sulcus; **ce**, central sulcus; **ec**, external calcarine sulcus; **io**, inferior occipital sulcus; **la**, lateral sulcus; **ot**, occipital temporal sulcus; **pr**, principal sulcus.

strips were carefully inserted into the sulcus to pry it gently open. The strips were subsequently removed, exposing both banks and the fundus of the sulcus. Using subpial suction, we removed the cortical tissue located on the floor and lower third of the posterior bank of the STS, extending from the top of the sulcus to a few millimeters below the junction of STS and the lateral fissure. For the first control group, three monkeys received partial bilateral lesions of area 7 (Bonin and Bailey, 1947) located in the posterior parietal cortex (PP). To this aim, the STS was opened in the same manner as above, to control for bruising of the cortex along the sulcus. Again, the blood vessel was cauterized first. The lesions were also made using aspiration, which took a portion of the inferior parietal lobule. The idea was to take similar amounts of gray matter from area MT and PP. For that reason, the posterior parietal lesions did not destroy the whole of area 7.

The white matter under MT is partially composed of optic radiation (OR) fibers (Polyak, 1957). To control for damage to these fibers inflicted during the MT surgeries, two subjects received bilateral lesions, which were intended to spare MT cortex, but to transect the white matter under the corresponding segment of the STS. The sulcus was opened with surgical strips in order to expose its banks and fundus, and a scalpel blade was passed through the floor of the sulcus, from the top of the STS to its junction with the lateral fissure. The intention was to transect the white matter under STS down to the ventricle, while sparing as much gray matter as possible. The blood vessel running along the STS was not cauterized during this procedure. The intended lesions are illustrated in Fig. 1.

When the lesion was completed, the dura was sutured, and the soft tissues closed in anatomical layers. The wound was sprayed with topazone or betadine, and biocillin (1000 ui) was given intramuscularly.

2.3. General apparatus and testing procedures

The animals were trained in a Wisconsin General Test Apparatus (WGTA) on several tasks intended to measure eye-hand coordination. Their ability to perform visual pattern discriminations was also tested. The WGTA was equipped with an electronic timing device capable of measuring two events. Twenty pairs of infrared light emitting diodes (LEDs) and infrared phototransistors placed 0.25 in. apart created a "gate" of infrared beams just inside the opaque door of the WGTA (Fig. 2A-C). The phototransistor diodes generated high-power infrared pulse beams, pulsing at a frequency of 200 Hz. This "gate" was interfaced with two electronic stopwatches which could be manually reset by the experimenter. The interruption of the beams was checked at a frequency of 100 Hz allowing the measurement of the interruption to an accuracy of 100 ms.

At the beginning of each trial, the guillotine door was opened, exposing the task to the monkey. Lifting the door opened a microswitch, which started one of the stopwatches (Time 1 or T1). When the monkey reached through the bars of its cage to reach for a peanut or banana pellet, its arm interrupted one or more of the infrared beams, which provided the signal to stop the first stopwatch (T1) and start a second stopwatch (Time 2 or T2). When the monkey withdrew its hand to put his reward in his mouth, the infrared beams were no longer broken, and the second stopwatch (T2) stopped.

T1 thereby measured the interval between the opening of the microswitch when the door of the WGTA was opened, and the breaking of one or more infrared beams when the monkey reached through the bars of the cage. This measure presumably reflected the time it took for the animal to complete whatever visual search operations were required to locate the target pellet or peanut. T2 began when the monkey reached past the row of infrared LEDs, breaking at least one beam in order to grasp the peanut or pellet, and ended when the animal withdrew his hand (to eventually put the reward in his mouth). This measure then reflects the amount of time taken to perform the necessary manipulations, or visually guided hand movements, to grasp the pellet or the peanut.

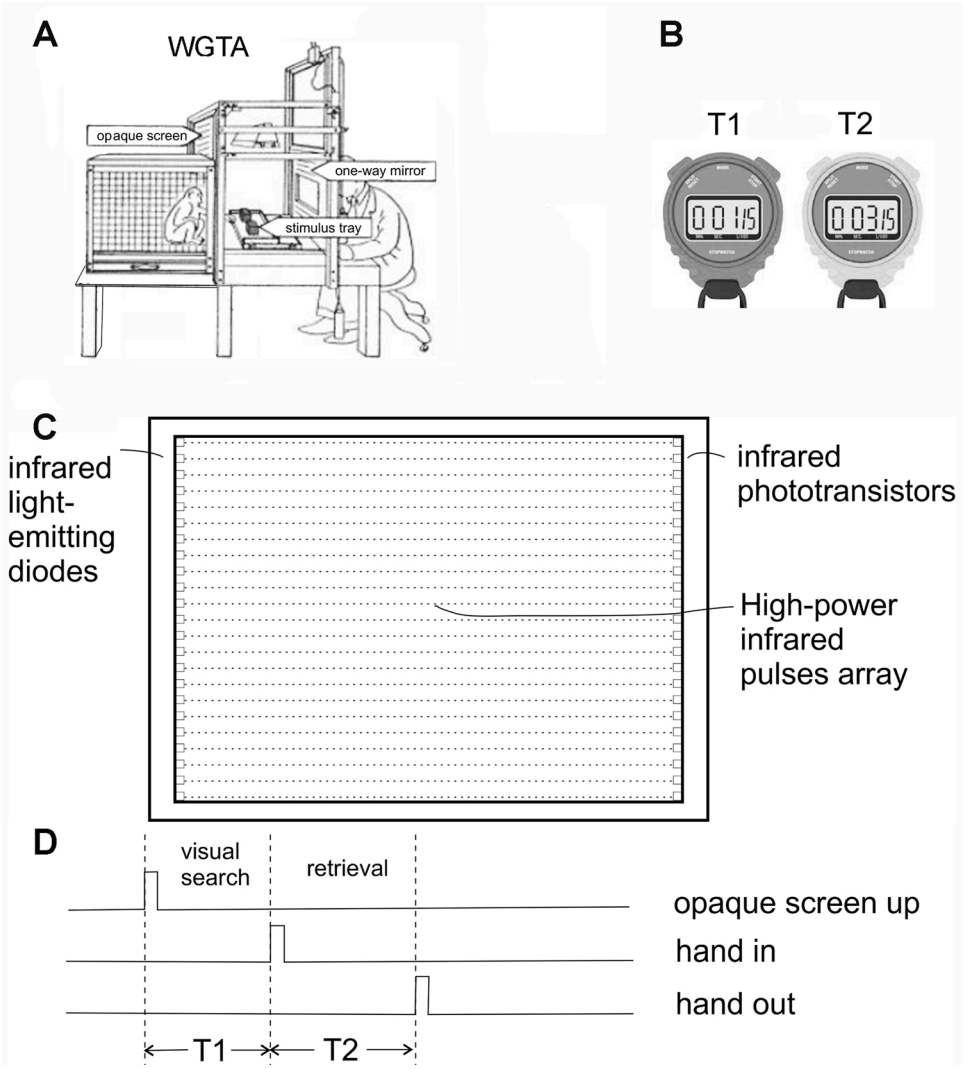

Fig. 2. Behavioral testing was done on a Wisconsin General Test Apparatus (WGTA) adapted with a timing system using infrared arrays. **(A)** The typical two compartments of the WGTA, with the monkey housed on the left and the stimulus presentation tray located on the right. The experimenter can visually access the monkey's behavior through a one-way mirror. **(B)** Two chronometers were used to control events related to the start of the trial (presentation of the stimulus tray), the passage of the monkey's hand through an infrared array, and the withdrawal of the hand from the infrared array. The infrared array, which was located in front of the opaque sliding door, is shown in (**C**). The Time 1 or T1 period starts when the compartment door of the WGTA (an opaque screen) is opened. The pulse described in (**D**) as the start of the 'visual search' indicates when the stimulus tray is presented to the monkey. T1 ends when the monkey reaches out to the stimulus tray, specifically when its hand first crosses the array of infrared beams. The Time 2 or T2 period starts when T1 ends, depicted in (**D**) as 'hand in' and marks the start of the 'retrieval' of the reward (food pellet). T2 ends when the hand is withdrawn from the infrared array.

2.4. Time measuring system

The time measuring system was composed of an aluminum frame containing pairs of photo diodes and phototransistors placed in front of the animal's cage and two digital timers. The diode-transistor photo pairs were placed and aligned on the vertical bars of the frame, spaced 0.25 in. apart. To generate infrared pulse beams the diodes and phototransistors were mounted on pvc tubes on either side of the frame, as shown in Fig. 2B. Each test had 30 trials. Each trial began by the opening of the opaque window and ended with its closure. Fig. 2C shows the relationship of the corresponding pulses that generated visual search time (T1) and visuomotor coordination time (T2).

2.5. Specific test procedures

2.5.1. Slot task

The animal faced a horizontal board with three inset discs. Each disc had a well in the center, and slots on either side, which could be positioned at four different orientations. A banana flavored monkey chow pellet (Noyes, Indiana, USA 300 mg) was placed in the central well, and the animals were required to place two fingers into the slots and pinch the pellet in order to retrieve it. Distracting slots, which did not lead to the pellet were also oriented around the hole, making the task difficult to perform using tactile information alone. One banana pellet was placed in one of the three discs on each trial. Each disc was tested at each orientation three times every day (36 trials), following a balanced, semi-random schedule. This task is a modification of one described by Haaxma and Kuypers (1974, 1975), and is illustrated in Fig. 3A.

2.5.2. Peanut board task

The peanut board task consisted of a 16cm × 45cm array of peanuts glued to a board which could be raised to face the monkey at a 45° angle. A pin could be inserted into any of 24 different positions on the peanut board, and retrieve a free peanut impaled on the end of the pin. Three different lengths of pins were used. The short pins (21 mm long) were just long enough that a peanut impaled on the end stuck out 1 mm from the background peanuts. The medium length pins made the free peanut stick out 7 mm from the background nuts, and peanuts on the long pins stuck out 15 mm from the background.

Each kind of pin was tested eight times daily. The 24 daily trials tested each of the 24 different positions on the peanut board. The positions of the long, medium, and short pins were roughly balanced over the board. When the door of the WGTA was opened, the monkey made a visual search of the array, and a visually guided hand movement to retrieve the free peanut. The animals quickly learned not to try to locate the free peanut by running their hands over the board; if they tried to do so, the WGTA door was closed and the trial terminated. This task is illustrated in Fig. 3B.

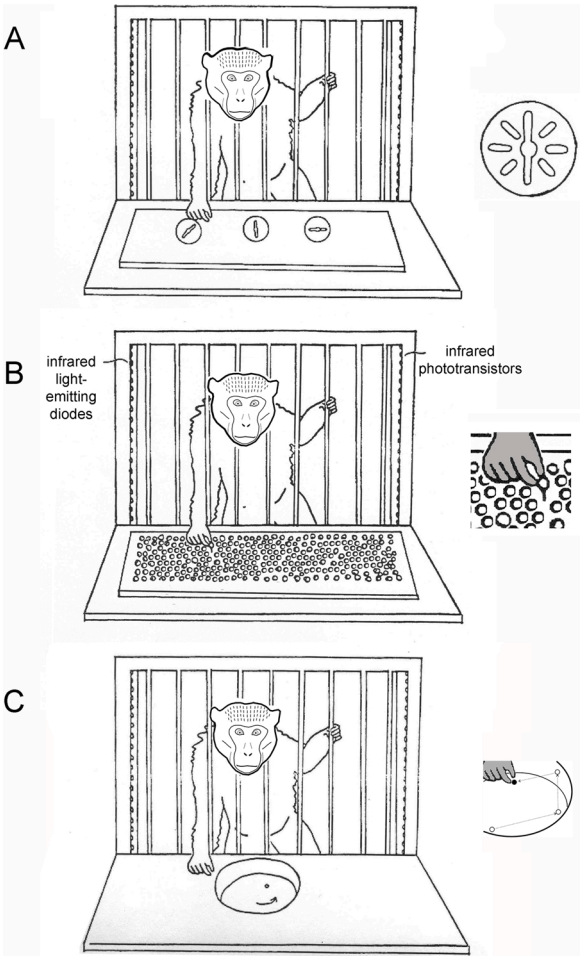

Fig. 3. The tasks used tested behavioral abilities such as visual perception of oriented stimuli, visual search, visual perception of moving stimuli and visuomotor coordination to retrieve a reward. **(A)** The Slotted Task had three differentially oriented slots. A solid reward (peanut or pellet) was placed on one of the slots, while the two other slots served as distractors. It tested the monkey's ability to discriminate a visual stimulus and shape its hand appropriately in order to retrieve the pellet from an oriented slot. **(B)** The Peanut Board Task used an array of small objects distributed on a horizontal tray in order to test the monkey's ability to search for a single randomly placed peanut. Note here the position of the infrared light-emitting diodes and the corresponding phototransistors. **(C)** The Spinning Pellet Task consisted of a banana pellet erratically moving inside a bowl. The monkey's task was to interpret the movement of the pellet in order to adequately plan and execute an efficient grasping procedure.

2.5.3. Spinning pellet task

The setup included was a bowl, the bottom of which was rotating like a roulette wheel. The monkey's task was to reach into the bowl in order to retrieve an erratically moving banana pellet (Fig. 3C). This task required some training. At first the animals were trained simply to reach into the stationary bowl to retrieve the pellet (~40 trials per day). Subsequently, the monkeys were given 20 trials for each slow speed of rotation. For example, they retrieved 20 pellets from the bowl rotating at 0.5 revolutions per second (rps) and so on in eight steps until the bowl was rotating at 2 rps. The speed of rotation was then increased to 4 rps. The monkeys were able to obtain 40 pellets per day from the bowl rotating at this speed.

In summary, we designed a battery of visuomotor tasks in order to differentiate between the visual search component (T1) and visuomotor performance (T2) in monkeys with complete bilateral MT lesions. Accordingly, we developed an experimental apparatus capable of precisely measuring the corresponding response latencies. The peanut board test, which was previously used by Kuypers and collaborators (Haaxma and Kuypers, 1974, 1975), was intended to be simpler to perform than the slot test. On the other hand, the spinning pellet task was expected to be harder since the animal was required to anticipate the trajectory of the pellet in order to carry out the appropriate grasping movement. However, we observed that the animal may have adopted a passive motor posture, grasping the pellet only when it eventually touched the hand.

2.5.4. Other neurological testing

After completing 40 trials on the spinning pellet task, the monkeys were observed picking up single banana pellets placed on the table next to the stationary bowl for 10 trials per day.

2.5.5. Barrier task

The barrier task was similar to the slot task, with some modifications. A 14cm × 20.5cm black plexiglass barrier was placed in front of the central disc of the stimulus board and the side discs were covered. The monkey was required to reach around the barrier to obtain the pellet reward. The barrier was large enough that the monkeys were unable to see around it to locate the pellet visually; they had to locate the pellet using tactile cues alone. Alternatively, a distinct barrier of clear plexiglass of the same dimensions could instead be placed in front of the disc. In this case, the monkey had visual cues available but was forced to use the same awkward hand posture to obtain the pellet. The barrier task had four components: (a) the animals reached behind the black barrier to retrieve pellets from the slot. The slot was tested in each position six times, according to a random schedule, resulting in 24 trials per day, (b) the animals reached behind the clear barrier to retrieve pellets from the slot, again for 24 trials per day, according to the same schedule, (c) the animals reached around the black barrier to grasp peanuts resting on a plain surface for 15 trials per day, and (d) the animals reached behind the clear barrier to grasp pellets resting on a plain surface for 15 trials per day.

2.5.6. Pattern discrimination task

To determine whether they could perform standard pattern discriminations, the MT and PP-lesioned animals were trained in an automatic testing apparatus, which has been described elsewhere (Cowey and Gross, 1970). The experimental chamber was sound-insulating and lightproof. The animal's compartment was 44cm × 47cm x 73 cm. In one wall of the compartment a light source, a liquid feeder, and two response keys were mounted. The stimuli were patterns of light projected onto the response keys (composed of transparent Lucite with 3.0 cm in diameter). Pressing the key with the correct stimulus activated a relay that produced a click and delivered a liquid reward through the feeder. The monkeys learned an intensity discrimination (light vs dark) task and a pattern discrimination (horizontal lines vs vertical lines) task. The animals were trained until they reached a criterion of 90 trials correct (out of 100) on two consecutive days.

2.6. Experimental design

2.6.1. Preoperative training

Before receiving their lesions, the monkeys were trained daily on the slot, peanut board, and spinning pellet tasks until they showed no improvement with practice for ten consecutive days (Table 1). It was assumed that the animals had reached an asymptotic level of performance when a linear regression analysis showed that the response times rather than becoming shorter were staying fairly steady ($r = 0.50$) for the ten-day period.

Two of the monkeys (Cases 1 and 3) were originally selected as pilots in this study. They were trained on the Slot, Peanut Board, and Spinning Pellet tasks until they reached asymptotic levels of performance on each task. They then had a two-week resting period, after which they were retested on the three tasks again, until they showed no improvement

with practice for ten days. The purpose of this was to see whether a two-week resting (or recovery) period would affect performance on the tasks.

Six monkeys underwent their assigned lesions within two weeks of completing their preoperative testing. Two monkeys (Cases 1 and 2) were operated after completing their second training periods, while one monkey (Case 9) was operated five weeks after completing the preoperative testing. If a monkey finished training on one task before completing the others, or if he reached criterion on all three tasks more than a few days before his surgery was scheduled, he was trained on the completed task(s) once every three days.

2.6.2. Postoperative training

After undergoing their assigned lesions, the monkeys were given a two-week recovery period. After this they were retrained on the Slot Task, Peanut Board Task, and Spinning Pellet Task. Again, training was continued daily until the animals reached asymptotic levels of performance. Eight weeks after lesion, the MT- and PP-lesioned groups were tested on the pattern discrimination task. The OR-lesioned monkeys were not tested on pattern discrimination.

The MT- and PP-lesioned monkeys were trained on the barrier task 14–16 weeks after receiving their lesions. The OR monkeys began training on the barrier task 9–10 weeks after surgery. Training continued until the animals reached asymptotic levels of performance on all parts of the task.

To observe the long-term effects of the lesions, the MT and PP-lesioned groups were retested on the Slot, Peanut Board, and Spinning Pellet tasks again 20 weeks after surgery. Six animals were sacrificed after completing this final testing period. One of the OR-lesioned monkeys was sacrificed after completing the barrier task. Two of the monkeys, Case 4 (MT) and Case 9 (OR), were spared for further testing.

2.6.3. Videotaping procedures

During the first postoperative training phase it was noticed that the MT-lesioned monkeys grasped pellets in a manner that was qualitatively different from the manner in which normal and control monkeys grasped pellets. Only five monkeys (Cases 1, 2, 4, 6 and 8) had been included in the experiment at the time of this discovery. When these five monkeys completed the pattern discrimination tasks, they were retested in the WGTA during 2–3 days in order to determine whether the effects of the lesions remained (a session was videotaped). The other four monkeys (Cases 5–8) were added to the experiment later on. They were videotaped before and after receiving their lesions. All nine monkeys were videotaped while performing the barrier task. The videotapes were evaluated by two observers that independently endeavored to evaluate the qualitative differences between groups of animals. Only one of the observers knew which experimental group each monkey belonged to.

When a monkey picked up pellets from the table, or when he plucked peanuts from the pins of the peanut board, we evaluated the posture of his hand upon grasping the pellet or peanut. On the Slot Task and Barrier Task, we scored the number of times each monkey put his fingers in the distracting slots and the number of times he had trouble orienting his hand, dropped the pellet, etc., as well as the number of times he retrieved the pellet without difficulty. On the Spinning Pellet Task, we observed whether the monkey cupped his hand by the side of the bowl and waited for the pellet to roll in, or whether he actually made distinct visually guided hand movements to obtain the pellet while it was moving erratically about. We also noted whether the monkeys looked at their hands while they grasped their rewards.

2.7. Histological procedures

At the end of the testing period, each animal was anesthetized with an overdose of sodium pentobarbital, and perfused through the heart with saline followed by formalin solution. The brain was removed from the skull and sectioned (40 μm-thick) at the coronal plane. Alternate sections were stained either for myelin or for cell bodies using the Gallyas' (1979) or the Nissl method, respectively. MT boundaries were determined based on its characteristic myeloarchitecture (Gattass and Gross, 1981; Ungerleider and Mishkin, 1979; Van Essen et al., 1981; Fiorani et al., 1989).

3. Results

Here, we will describe in distinct sections the anatomical, behavioral, and videotape results.

3.1. Anatomical results

Histological data were obtained from six of the monkeys used in this experiment. Two monkeys (Cases 3 and 9) were spared for further testing and the histology for one monkey (Case 6) was not available for analysis. Representative coronal selections and reconstruction of the lesions are presented for five of the cases in Figs. 4 and 5. Also presented in the figures are sections through the dorsal lateral geniculate nucleus (LGN), which were examined for degeneration caused by damage to the optic radiation (OR) fibers running in the white matter underneath MT cortex. Scotomata produced by OR damage were reconstructed by comparing patches of degeneration to the known topography of the LGN (Malpeli and Baker, 1975).

3.2. MT lesions

Cases 1 and 2 had complete bilateral lesions of MT. As shown in Fig. 4, all gray matter was removed from the floor and posterior bank of the upper half of the STS. These lesions also invaded the white matter under MT. Therefore, most of the medial half of the LGN showed degeneration, indicating scotomata in the lower central visual field. On the other hand, the right hemisphere of Case 3 had incomplete MT lesions, where portions of the floor and posterior bank of STS were spared. The right LGN showed a strip of degeneration just medial to the vertical midline, indicating a small scotoma in the lower central visual field. In the left hemisphere, the whole of area MT was ablated, but the white matter underneath was also invaded, resulting in degeneration of cells in the representation of the lower central visual field of the left LGN.

3.3. Control lesions

Fig. 5 illustrates one of the PP-lesion cases (Case 5), where gray matter from the inferior parietal lobe was removed. The lesion was superficial and did not impact the optic radiation fibers, so no degeneration was seen in the LGN. On the other hand, the OR lesions were intended to transect the optic radiation fibers under MT, creating scotomata comparable to those inadvertently induced in the MT-lesion cases. In Case 8, illustrated in Fig. 5, only limited damage was done to the OR fibers. Consequentially, lateral geniculate degeneration was confined to the dorsal and anterior parts of the LGN, representing a different part of the visual field.

3.4. Behavioral results

3.4.1. Slot task

The MT-lesioned monkeys were significantly impaired on the slot task compared to their own preoperative performance levels, and compared to both groups of control monkeys. The PP- and OR-lesioned monkeys, in contrast, showed no postoperative impairments. The effects of the lesions were seen during the first and second postoperative testing periods. The results are summarized in Fig. 6A, split for Time 1 (top panel) and Time 2 (bottom panel). The figure compares the monkeys' performance levels during the ten asymptotic testing days before and after surgery (for the 1st and 2nd postoperative test phases). There was no evidence that the PP- and OR-lesioned monkeys showed any behavioral deficit in any of the three tasks. For statistical purposes they are

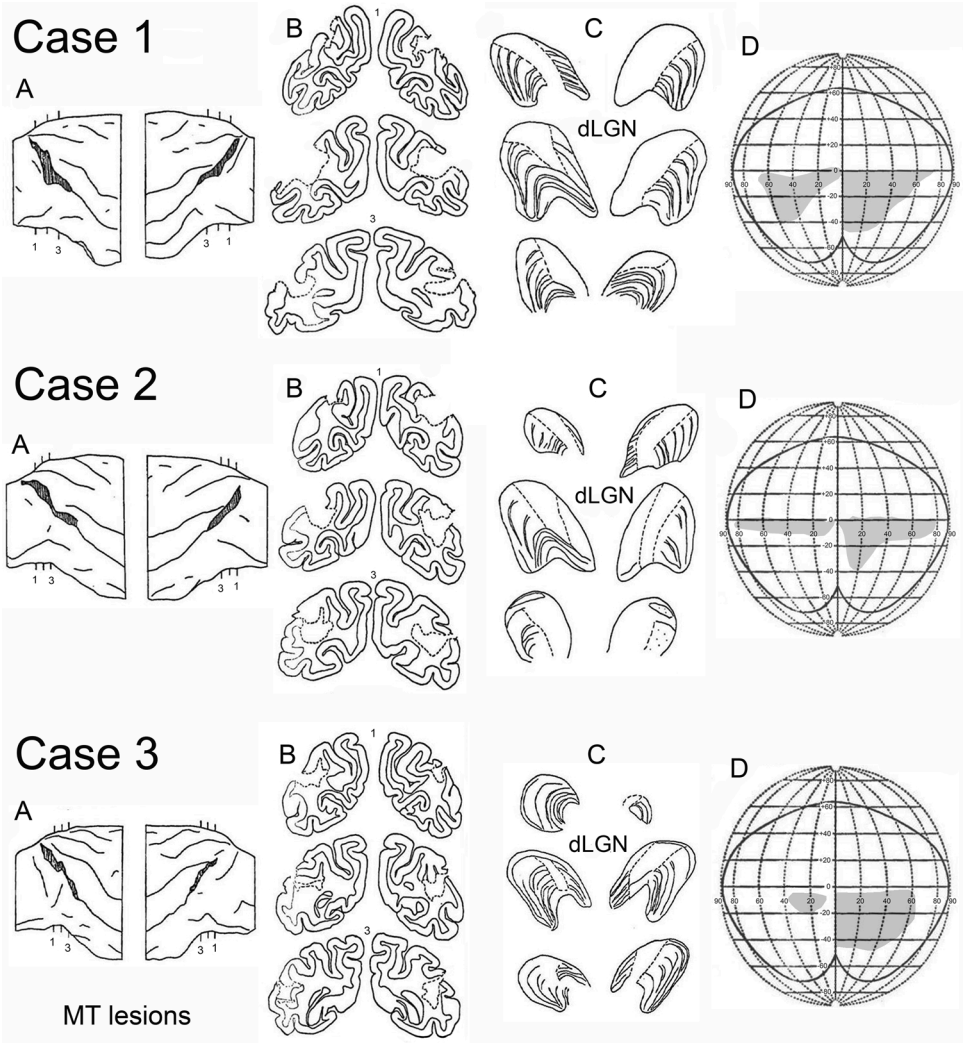

Fig. 4. The bilateral lesions of MT were mostly complete and selective. For Cases 1, 2 and 3: **(A)** Lateral reconstructions of both hemispheres of the monkey brain. The outer left and right portions of the illustration correspond to the occipital poles. The shaded portions indicate the lesions. Vertical ticks numbered 1-3 indicate the corresponding levels of the coronal sections shown in B. **(B)** The gray matter on and around the region corresponding to the MT location was ablated. **(C)** Coronal sections of the left and right lateral geniculate nuclei (LGN). White patches indicate the regions of LGN degeneration, which enabled us to predict the corresponding scotoma region on the visual field, shown in (**D**) in gray.

thereby treated together as one group of control animals on this and on all the other tasks.

Time 1. During the preoperative training period, the MT-, PP-, and OR-lesioned monkeys did not differ in the time it took them to reach for the pellet once the opaque door of the WGTA was opened. The first postoperative retention testing period showed that the MT-lesioned monkeys were impaired relative to their own preoperative performance (Mann-Whitney *U* Test, one tailed, $U = 1$, $p < 0.05$), and relative to the control monkeys' first postoperative performance ($U = 2$, $p < 0.05$). During the second retention test, however, the MT-lesioned monkeys did not show a response time that was significantly different from the preoperative period, indicating that some or complete behavioral recovery due to the lesions were taking place.

Before surgery, the mean Time 1 values for all the monkeys was 1.41 s (range 1.16–1.73 sec). During the first postoperative testing period, the mean Time 1 value· was 2.37 s (range 1.48–3.43 sec) for the MT-lesioned monkeys, and 1.66 s (range 1.22–1.70 sec) for the control monkeys. During the final retention testing, Time 1 averaged 1.79 s (range 1.40–2.45 sec) for the MT-lesioned monkeys, and 1.36 s (range 1.26–1.53 sec) for the controls.

Time 2. No statistical difference for Time 2 was observed during the preoperative training period between the groups. Postoperatively, the MT-lesioned monkeys were much slower to retrieve pellets from the slots, relative to their preoperative performance levels ($U = 0$, $p < 0.05$). Although they showed some improvement by the second postoperative test, these animals remained somewhat impaired ($U = 2$, $p = 0.057$). The PP- and OR-lesioned monkeys retrieved pellets from the slots just as well after surgery as they had done before surgery.

Before surgery, the mean Time 2 value for all the monkeys was 1.46 s (range 1.12–2.64 sec). After surgery, the MT-lesioned animals took an average of 3.34 s (range 2.24–4.70 sec) to retrieve the pellet from the slot during the first retention testing period, and 2.21 s (range 1.84–2.71 sec) during the second testing period. For the control monkeys alone, the mean Time 2 value was 1.44 s (range 0.94–2.17 sec) during the first postoperative testing period, and 1.21 s (range 1. 06−1.37 sec) during the second postoperative testing period, indicating no substantial difference relative to preoperative levels.

It is important to mention that during the first postoperative retention test, the MT-lesioned monkeys were unable to perform the task at all during 2–6 days. It was necessary to shape the response by placing bits of paper under the pellet, making it easier to grasp. Throughout postoperative testing, the MT-lesioned animals had difficulty orienting their hands and frequently placed their fingers in the distracting slots. On the other hand, the PP- and OR-lesioned monkeys had no difficulty retrieving the pellets.

3.5. Barrier task

The barrier task was only implemented postoperatively. Training on the barrier task was carried out daily until the animals performed consistently on each part of the task (i.e., until they showed no improvement with practice for ten consecutive days). During this

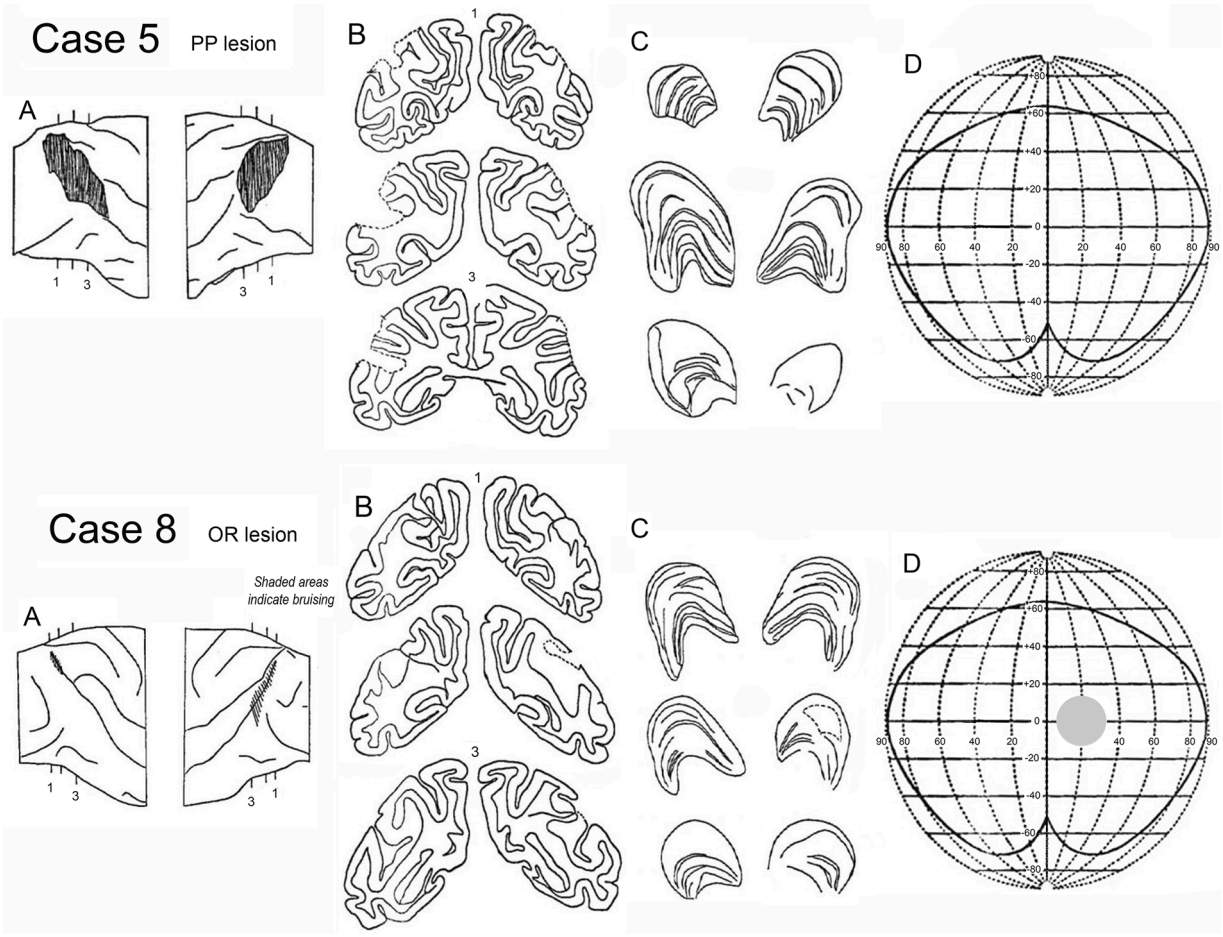

Fig. 5. Representative cases illustrating the bilateral lesion of the posterior parietal (PP) cortex and optical radiation (OR), which together composed the control group. This figure follows the same convention as Fig. 4, but now illustrating a case of PP lesion (Case 5) and OR lesion (Case 8). In Case 8, the shaded portions shown on the lateral reconstructions indicate bruise around the region where the superior temporal sulcus was opened (observed postmortem).

training period, before the animals reached asymptotic levels of performance, data showed some striking distinctions between the MT-lesioned and control animals. These distinctions appeared only when the reward had to be retrieved from the slotted disc behind a black barrier (i.e., with no visual input). Fig. 7 illustrates Time 2 values, which accounts for the amount of time the monkeys spent trying to grasp the pellet in the slot from behind the barrier. The panels compare retrieval times for clear vs. black barriers across cases for the initial training phase. Note that the PP-lesioned monkeys start-off substantially worse than MT- and OR-lesioned monkeys, but only for the black-barrier condition. For the clear barrier condition, the control group performs slightly (but consistently) better than the MT-lesioned monkeys from the very beginning of the training. (Case 9 seems to be an outliner, which performs poorly for both clear and black barriers). A possible interpretation is that lesions of the posterior parietal cortex (used here as a control) impaired the animal's ability to use somatosensory cues to correctly position the fingers on the oriented slot and solve the task.

Fig. 8 compares the mean responses for Time 2 during the last 10 asymptotic days (i.e., the final segment of the curves shown in Fig. 7). Data for Time 1 is not shown since no significant differences between groups were observed for any of the four conditions. Details for individual conditions are given below.

Plain surface. After initial training, the animals could easily grasp a banana pellet or peanut lying atop a plain surface, regardless whether the barrier was clear or opaque. No significant differences between groups were seen on this part of the task. The mean Time 1 values were 1.25 s (range 1.16–1.36 sec) for MT-lesioned monkeys reaching behind the clear barrier, and 1.22 s (range 0.91–1.51 sec) for MT-lesioned monkeys reaching behind the black barrier. For the control monkeys, the mean Time l values were 1.00 s (range 0.53–1.59 sec) for reaching around the clear barrier, and 1.00 s (range 0.83–1.35 sec) for reaching around the black barrier. The values were also homogeneous across cases and conditions for the Time 2 measure. The MT-lesioned monkeys took an average of 0.85 s (range 0.67–1.09 sec) to retrieve the pellet from behind the clear barrier, and 1.02 s (range 0.65–1.25 sec) to retrieve it from behind the black barrier. The mean Time 2 value for PP- and OR-lesioned monkeys retrieving pellets behind the clear barrier was 0.74 s (range 0.62−0.90 sec), and for retrieving pellets from behind the black barrier was 0.92 s (range 0.80–1.16 sec).

Slotted disc. As with the plain surface, there was no significant difference between groups on the Time 1 measure. The mean Time 1 value for MT-lesioned monkeys retrieving pellets in the slot behind the clear barrier was 1.41 s (range 1.19–1.51 sec) and behind the black barrier was 1.48 s (range 1.12–1.78 sec). The mean Time 1 value for PP- and OR-lesioned monkeys was 1.09 s (range 0.67–1.62 sec) for reaching behind the clear barrier, and 1.10 s (range 0.90–1.54 sec) for reaching behind the black barrier.

Contrary to the plain surface, some clear differences could be observed for the time needed to grasp the pellet from the oriented slot (i.e., Time 2). Fig. 8 (bottom panel) shows the mean values of the 10 asymptotic days for the clear vs. black barrier conditions. The MT-lesioned monkeys were expected to retrieve the pellet more quickly from behind the clear barrier than from behind the black barrier. Curiously, these animals took just as long to retrieve the pellet in both

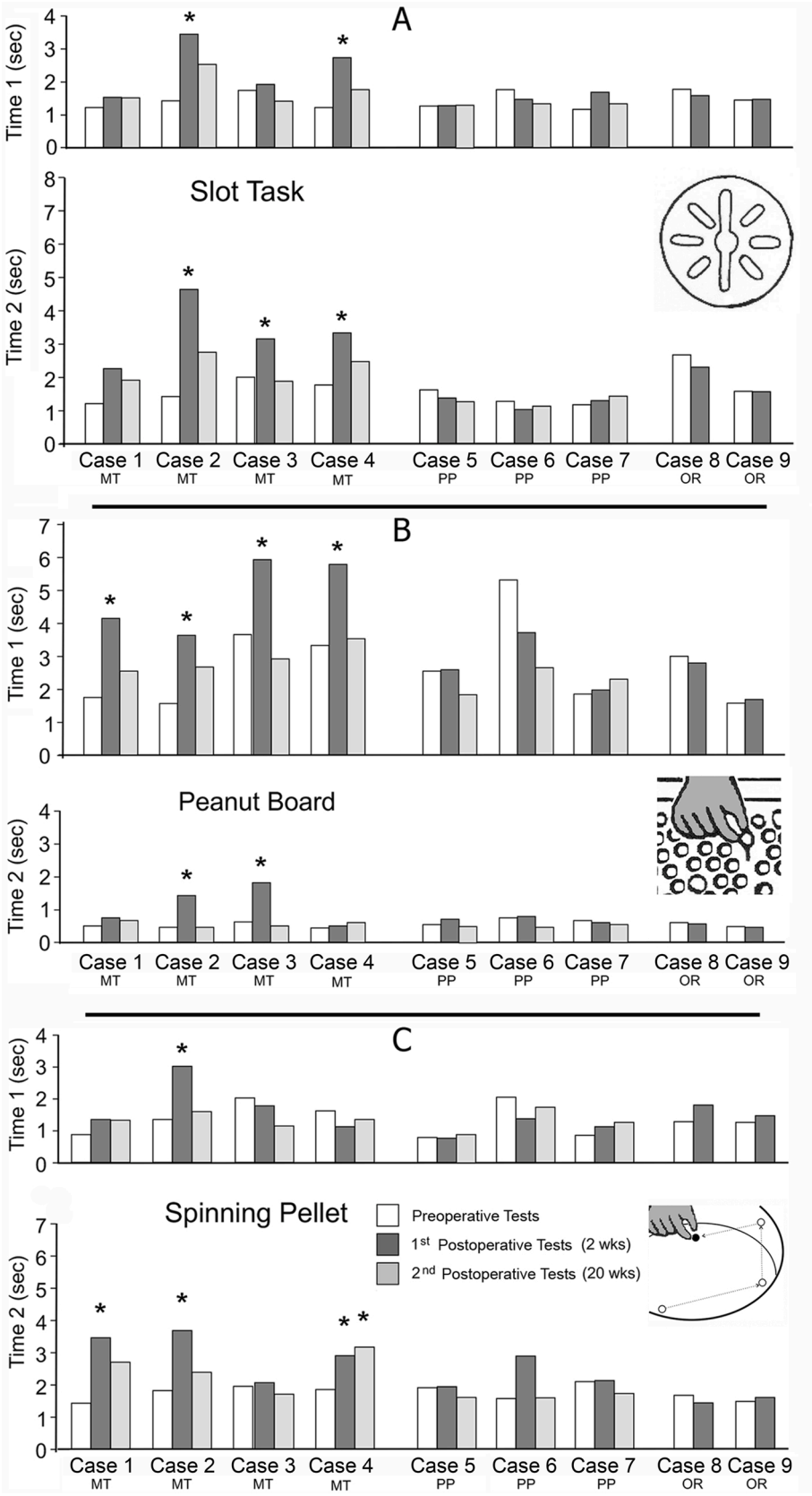

Fig. 6. MT-lesion monkeys showed behavioral deficits that involved several aspects of visual perception and visuomotor integration. *Time 1* and *Time 2* values (averaged during the last 10 days of asymptotic performance) are shown for the oriented slot task (**A**), peanut board task (**B**) and spinning pellet task (**C**). Data is for three periods: preoperative test (white bars), 1st postoperative test (2 weeks after lesion, dark gray bars) and 2nd postoperative test (20 weeks after lesion, light gray bars). All cases (Cases 1 to 9) are illustrated. Asterisks denote statistical differences with $p < 0.05$. Note that significant behavioral differences are mainly restricted to the MT-lesion monkeys during the 1st postoperative testing period.

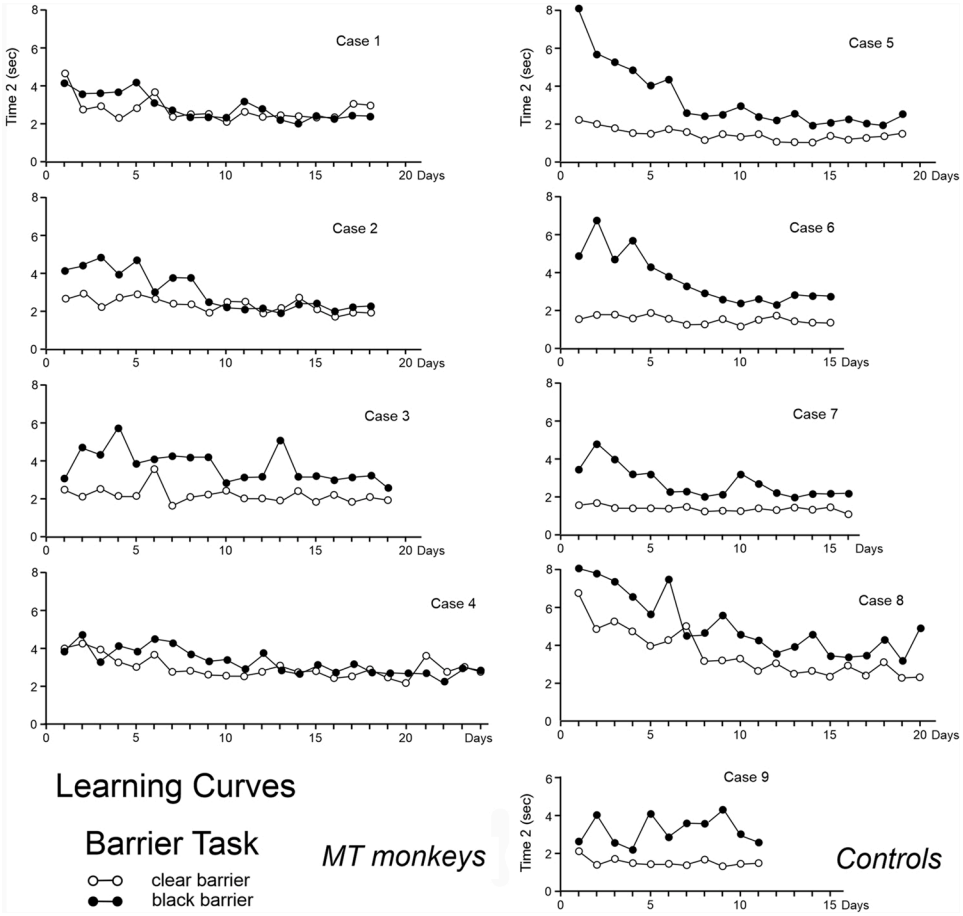

Fig. 7. Posterior parietal lesions (but not MT lesions) induced behavioral deficits when somatosensory cues were required to solve the oriented slot task. Learning curves of *Time 2* values for all cases are plotted as a function of training day for the barrier task: clear barrier (circles), and black barrier (filled dots). The barrier task was only implemented postoperatively, and consisted of either a clear barrier (i.e., visual and somatosensory cues available to solve the task) or a black barrier (only somatosensory cues available to solve the task). Note that all monkeys (with the exception of Case 8) learned very quickly to solve the task when visual cues were available (clear barrier condition). However, when the monkeys were required to solve the task using somatosensory cues alone (dark barrier condition), PP-lesioned monkeys performed comparatively worse during the initial training phase. However, these animals gradually improved, reaching a behavioral performance similar to the rest of the cases after approximately 10 days of training.

conditions. As a matter of fact, when using a black barrier, no differences in retrieval time (i.e., Time 2) were found for the MT-, PP-, and OR-lesioned monkeys. The significant difference was only revealed when comparing clear vs. black barrier for the control group (Fig. 8, bottom panel). It took the monkeys significantly longer to retrieve the pellet from behind the black barrier than to retrieve it from behind the clear barrier ($U = 3$, $p < 0.05$). These results have to be interpreted in light of the fact that we do not have a preoperative baseline to use as comparison. We can assume that retrieving the reward from the slot behind a black barrier is behaviorally more challenging than its retrieval from behind the clear barrier. Therefore, it also fair to expect a higher mean Time 2 value for the former compared to the latter. Following this logic, we would expect significant differences for clear vs. dark barrier in all cases. However, they were only observed for the control cases, and not for the MT-lesioned monkeys. One plausible explanation is that the MT-lesioned monkeys are visually impaired, implying that clear or dark barrier is irrelevant to the task, and no difference in Time 2 values is expected. The MT monkeys took an average (mean Time 2) of 2.48 s (range 2.14–2.84 sec) to retrieve pellets from the slot behind the clear barrier, and 2.79 s (range 2.40–3.30 sec) to retrieve them from behind the black barrier. The mean Time 2 values were 1.74 s (range 1.61–2.85 sec) for control monkeys reaching behind the clear barrier, and 2.98 s (range 2.23–4.13 sec) for control monkeys retrieving pellets behind the black barrier.

3.6. Peanut board

The MT-lesioned monkeys were impaired on this task relative to their preoperative levels of performance and relative to the PP- and OR-lesioned monkeys. The control monkeys showed no postoperative impairments. Fig. 6B illustrates the monkeys' performance levels during the asymptotic testing days before and after surgery.

Time 1. The MT-, PP-, and OR-lesioned monkeys did not differ on this measure during the preoperative training period. After receiving their lesions, however, the MT-lesioned monkeys were significantly slower to perform the visual search and reach for the pellet after the WGTA door was opened. The first postoperative retention period showed that the MT animals were impaired relative to their own preoperative performance ($U = 1$, $p < 0.05$), and relative to the control monkeys' first postoperative performance level ($U = 1$, $p < 0.05$). By the second postoperative testing period, the MT-lesioned monkeys partially recovered to pre-lesion performance levels (Case 3 seemed to have recovered completely).

During the preoperative testing period, the mean Time 1 value for all 9 monkeys was 2.73 s (range 1.60–5.38 sec). During the first postoperative test, the mean Time 1 value for the MT-lesioned monkeys was 4.91 s (range 3.71–5.99 sec), and for the control monkeys was 2.66 s (range 1.87–3.81 sec). The average Time 1 value for the MT-lesioned monkeys was 2.97 s (range 2.61–3.63 sec) during the second postoperative testing period, while the control animals averaged 2.38 s (range 1.94–2.74 sec) on this measure.

Time 2. The MT-, PP-, and OR-lesioned animals did not differ on Time 2 values during preoperative training. The nine monkeys' mean Time 2 was 0.57 s (range 0.42−0.72 sec). Postoperatively, two of the four MT-lesioned cases (Cases 2 and 3) took significantly longer to make the visually guided hand movement to retrieve a peanut than they did before surgery ($U = 1$, $p < 0.05$). This effect was seen only during the first postoperative test. The MT-lesioned monkeys took a mean of 1.18 s (range 0.57–1.85 sec) to grasp the peanut, while the PP and OR animals took 0.60 s (range 0.33−0.75 sec). Twenty weeks after surgery they

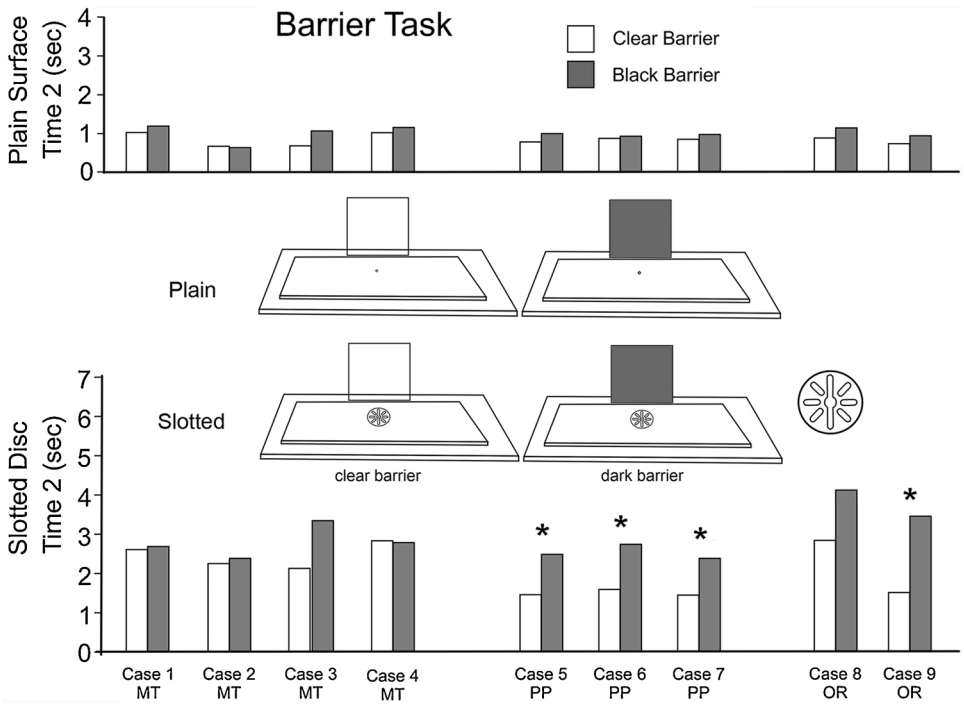

Fig. 8. MT lesions removed the ability of monkeys to use visual cues to solve the oriented slot task. Average *Time 2* values (mean of the last ten asymptotic days shown in Fig. 7) are plotted for each case when performing the barrier task to retrieve the banana pellet from a plain surface (top panel), or from an oriented slot (bottom panel). Data is also split for the clear barrier (white bars) vs. black barrier (dark bars) conditions. The task was quickly performed when reward was placed on an easily-accessible plain surface (top panel). However, reward retrieval from an oriented slot made the task slightly more challenging when visual cues were available (bottom panel, white bars), and markedly more challenging when only somatosensory cues were available to the monkey (bottom panel, dark bars). Indeed, this led these corresponding two sets of *Time 2* values to be significantly different from each other for the control cases (asterisks denote statistical differences with $p < 0.05$). However, MT lesions seems to have removed the ability of monkeys to use visual cues to solve the task. Consequentially, mean *Time 2* values for MT-lesion monkeys were equivalent (i.e., not statistically different) regardless of whether the barrier was clear or black. An alternative explanation is that MT-lesions induced a general abnormality in hand shaping and grasping. In this case, visual deficit played little or no role, and the motor difficulty of retrieving the food pellets from the slot (clear or black barrier alike) was the single main factor increasing *Time 2* values (see Figs. 9 and 10).

showed no impairment relative to their preoperative performances, during which the Time 2 values for MT-lesioned monkeys averaged 0.52 (range 0.50−0.52 sec), while the control monkeys' averaged 0.55 s (range 0.49−0.60 sec). The PP- and OR-lesioned monkeys showed no impairment on this task in either the 1st or 2nd postoperative tests.

Throughout each testing period, the monkeys reached swiftly and accurately for the free peanut once they spotted it. Although the MT monkeys took longer to locate the free peanut during the 1st postoperative test, they continued to reach accurately. Very rarely did a monkey touch the background peanuts glued to the board.

3.7. Spinning pellet

Performance on the spinning pellet task had limited diagnostic power over MT lesions. Despite the fact that we did observed significant behavioral deficits associated with MT lesion (when compared to preoperative performance), these effects did not extend to all monkeys, the corresponding average effect was not statistically different from control, and one control case (Case 6) exhibited a considerable deficit for the same task. Fig. 6C illustrates these results (see below for details).

Time 1. Average performance during Time 1 for control vs. MT-lesioned monkeys did not differ significantly from each other, either before or after lesion. Additionally, the MT monkeys as a group performed no worse after receiving their lesions, despite the fact that one single case (Case 2) did for the 1st postoperative testing. During the 10 asymptotic days before surgery, the mean Time 1 value for all the monkeys was 1.33 s (range 0.83–2.04 sec). During the first postoperative testing period, the mean Time 1 value was 1.76 s (range 1.05–2.96 sec) for the MT-lesion monkeys, and 1.19 s (range 0.73–1.75 sec) for the control monkeys. The mean Time 1 values during the second postoperative test were 1.29 s (range 1.09–1.51 sec) for the MT-lesion animals, and 1.27 s (range 0.82–1.13 sec) for the control animals.

Time 2. All groups behaved homogeneously during the preoperative period regarding the Time 2 measure. The mean Time 2 value for all the monkeys was 1.71 s (range 1.38–2.05 sec). For the 1st postoperative test, MT-lesion monkeys (as a group) showed a significant behavioral impairment compared to the preoperative stage ($U = 0$, $p < 0.04$). The trend continued until the 2nd postoperative test, but without statistical significance ($U = 3$, $p = 0.056$). However, it was not possible to attribute the behavioral deficits during the 1st postoperative test to MT lesions, since there was no significant difference between the MT-lesion group and the control group. The same was true for the 2nd postoperative test. The mean Time 2 value for the MT-lesion monkeys was 2.93 s (range 1.95–3.59 sec) during the first postoperative test, and 2.40 s (range 1.57–3.13 sec) during the second postoperative testing period. The control monkeys averaged 2.01 s (range 1.56–2.8 sec) during the first postoperative test, and 1.66 s (range 1.54–1.89 sec) during the second.

Postoperatively, the MT-lesion monkeys and one of the control monkeys (Case 6) seemed hesitant to put their hands in the spinning bowl. When they eventually did so, they would often cup their hand against the side of the bowl and hold it there until the pellet chanced to roll in. This behavior was documented on videotape.

3.8. Videotape results

Analysis of the videotape records obtained in this experiment was never completed. Therefore, we presented here only a partial result.

Videotape records revealed that normal monkeys and the monkeys with PP and OR lesions generally grasped pellets and peanuts between the tips of their fingers (Fig. 9, right). The MT-lesion monkeys, in contrast, grasped the pellets and peanuts between the fingers and palm of their hand (Fig. 9, left). The impression of the observers was that the MT-lesion monkeys, unable to grasp in the typical way, tried to maximize the amount of skin surface that might encounter the pellet as they reached for it.

Fig. 10A presents the observer's evaluations of monkeys picking up

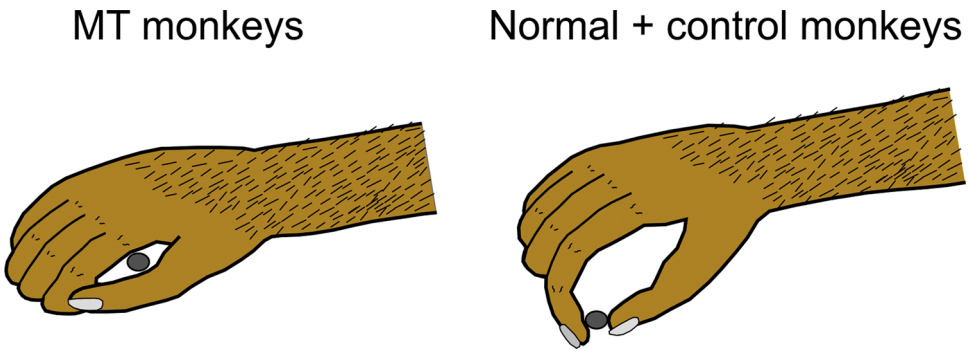

Fig. 9. Hand grasping posture was abnormal in MT-lesion monkeys during reward retrieval. Normal and control monkeys grasp the food pellet using the tips of their fingers. However, MT-lesion monkeys lose this fine ability and otherwise grasped the pellet with their whole hand.

pellets from a plain surface. Three of the four MT-lesion monkeys used the finger-to-palm hand posture on 100 % of the trials, and the fourth MT monkey used it on 75 % of the trials. The control and normal monkeys always grasped the pellets with the tips of their fingers. The evaluations of the two observers were identical (r = 1.00).

Videotapes of the monkeys picking peanuts from pins on the peanut board (Fig. 10B) revealed that the MT-lesion monkeys used a finger-to-palm hand posture to grasp the peanut on at least 75 % of the trials, while the control and normal monkeys used it on less than 20 % of the trials. Agreement between the observers was fairly good (r = 0.87).

Videotapes of monkeys performing the Barrier Task (Fig10C and D for the 2- and 20-week testing periods, respectively) showed that when

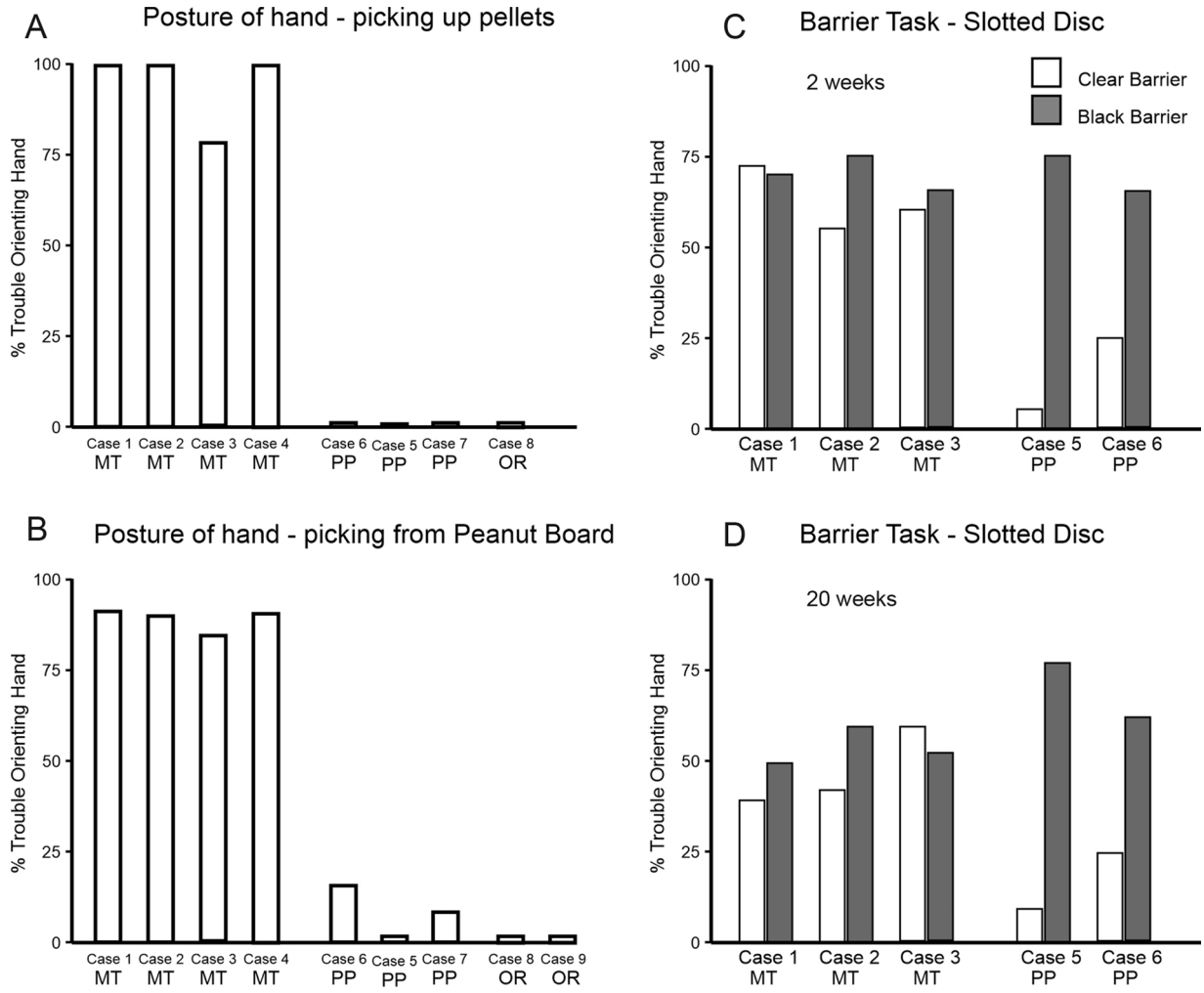

Fig. 10. Hand posture during grasping in MT-lesion monkeys was consistently abnormal. PP-lesioned monkeys also showed compromised hand shaping when required to rely exclusively on somatosensory cues. MT-lesion monkeys nearly always showed trouble orienting their hands to pick up a food pellet, either from a plane surface (**A**) or from a peanut board (**B**), as compared to monkeys with lesions in the posterior parietal cortex or optical radiation. Data presented in (**C**) and (**D**), corresponding to the 1st and 2nd postoperative testing periods of the barrier task (slotted disc), are complementary to those presented in Fig. 8 (bottom panel). MT-lesion monkeys showed just as much trouble in the clear vs. black barrier conditions. There was some behavioral improvement with time (D), but the deficit persists after 20 weeks of surgery. Data was acquired through analysis of videotapes and analyzed independently by two researchers.

they reached behind the black barrier to retrieve a pellet from the slot, all the monkeys had trouble orienting their hands correctly on at least 60 % of the trials, and placed their fingers in the distracting slots on more than half the trials. The MT-lesion monkeys had similar difficulties even when reaching behind the clear barrier. In contrast, the control animals performed much better when they had visual cues available, which meant placing their fingers in the wrong slots and orienting their hands incorrectly on less than 25 % of the trials. Agreement between observers was very good (r = 0. 92).

When the videotapes were analyzed to determine whether the monkeys looked at their hands while they grasped the pellet or peanut, no distinction emerged between groups of animals. Indeed, the monkeys very seldom looked at their hands while they reached for the peanut or pellet. The observers' impression was that the animals localized the target and then raised their eyes while they extended their hands (as if, it seemed, to look for any potential outside threat).

Observation of the tapes indicated that on the slot task the MT-lesion monkeys placed their fingers in the distracting slots and had difficulty orienting their hands correctly more often than did the normal and control monkeys. Presumably, the increased Time 2 values for MT-lesion monkeys performing the slot task reflected this. Finally, observation of the tapes indicated that when retrieving pellets from the spinning bowl, the MT-lesion monkeys and Case 6 (PP-lesion) just cupped their hands against the side of the bowl and waited for the spinning pellet to roll in.

3.9. Pattern discriminations

The number of days to criterion are presented in Table 2. There was no significant difference between groups on these tasks. The number of days it took for the monkeys to learn to discriminate between white and black squares, and between horizontal and vertical lines was variable within the MT- and PP-lesion groups. Neither group was significantly impaired relative to the other. Comparing errors to criterion and days to criterion, no difference between groups were observed.

4. Discussion

Macaque monkeys with bilateral lesions of area MT were tested on a number of tasks designed to reveal deficits in visuomotor functions. MT lesions impaired the monkeys' ability to grasp a small food pellet out of a narrow, oriented slot, to search, detect and grasp a loose peanut mounted on a background of fixed peanuts, and to retrieve an erratically moving pellet from a spinning bowl. These results suggest that area MT is part of a network involved in visuomotor functions, which likely includes areas in the parietal region to which MT is strongly interconnected.

Petrides and Iversen (1978, 1979) found that monkeys with lesions of the banks of the STS were impaired on a task which required them to respond to a visual and auditory compound cue but to withhold responses to visual or auditory stimuli presented alone. These monkeys were also impaired on a task that required them to unstring a ring-shaped sweet from a bent wire. They were not impaired, however, on tasks that required them to use visual-spatial cues to find a hidden peanut. The major difficulty in interpreting these results is that their STS lesions largely spared visual area MT. MT was completely intact in the two monkeys who showed the greatest deficits (ST1 and ST2), and the floor of STS was spared in the other three. These lesions probably ablated the superior temporal polysensory area (Bruce et al., 1981).

Wilson et al. (1977, 1979) made lesions in the posterior bank of the STS in three macaques and studied the animals' performance on a series of visual discrimination tasks, including some that required shifts in gaze. These animals were not impaired in making color or form discriminations, and performed well on problems that required maintaining fixation. However, they performed poorly on problems that required them to shift their gaze. These lesions partially spared MT in all the animals. Although the lesions destroyed the posterior bank of STS, they generally spared the floor and they were too ventral to destroy all of MT.

In our study, the results of the Slot Task indicated that the MT-lesion monkeys were impaired relative to the control monkeys immediately after the lesions, but recovered to some extent twenty weeks later. The MT animals took longer to perform the visually guided hand movements; the longer Time 2 values reflected the fact that the MT-lesion monkeys placed their fingers in the distracting slots and had trouble orienting their hands correctly more often than did the control monkeys.

On the Barrier Task, PP-lesioned monkeys performed just as poorly as MT-lesion monkeys when visual information was unavailable, and the MT-lesion monkeys performed no better when visual cues were available. Furthermore, the PP-lesioned monkeys required more practice than did the MT monkeys before they were able to retrieve the pellets from behind the black barrier. The MT-lesion monkeys, in contrast, learned quickly to retrieve the food pellet using tactile cues alone. These results indicated that monkeys with MT lesions were impaired in using visual cues to retrieve the pellets from the slot.

Monkeys with MT lesions took much longer to locate the free nut on the peanut board, while the control monkeys did not. The increased Time 1 values for the MT-lesion animals indicated that they spent more time scanning the array of peanuts trying to find the free peanut sticking out. The MT-lesion monkeys may have been impaired on this measure for a number of reasons. Two possibilities are that they may have taken longer to scan the peanut board and localize the free peanut because their visual search strategies were disrupted, or because of impairments in making depth discriminations to identify the peanut sticking out on a pin. Although all the monkeys reached accurately for the free peanut, three of the four MT-lesion monkeys took longer to make the visually guided hand movement to grasp it. By the final postoperative testing period, the Time 2 values practically decreased to preoperative levels.

The results of the Spinning Pellet Task were not as clear as the results of the other tasks. Three of the MT-lesion monkeys took longer to retrieve the spinning pellet (Time 2), but so did one control (PP-lesion) monkey.

The impairments seen in the MT-lesion monkeys were mostly short lasting. Some of the cases remained impaired on the Slot, Barrier, Peanut Board, and Spinning Pellet tasks twenty weeks after surgery, although they did show some improvement, which may have been due to practice or to partial recovery of function. For the Slot Task and Peanut Board Task, all cases showed no statistically significant impairment relative to controls 20 weeks after MT ablation for both Time 1 and 2. On the other hand, for the Spinning Pellet Task one subject (Case 4) showed no sign of recovery after the same period, which was surprising since its MT lesion was intended to be as extensive and complete as the other cases. One specific monkey with MT-lesion (Case 3) showed complete recovery on all the tasks by the end of the second postoperative testing period. On the other hand, area MT was not completely ablated in this animal.

Although the effects of the lesions were reflected in the time it took the animals to respond once the door of the WGTA was opened (Time 1)

Table 2
Pattern Discrimination Tasks. The animals were trained to discriminate ▫ vs ■ and ▬ vs ‖. The table shows the number of days to achieve criterion and the number of errors to criterion.

Pattern Discrimination Task			
Days and Errors to Criterion			
	Lesion	▫ vs ■ Days/Error	▬ vs ‖ Days/Error
Case 1	MT	0/0	2/26
Case 2	MT	0/0	2/74
Case 3	MT	0/0	11/502
Case 4	MT	1/14	6/204
Case 5	PP	0/0	11/347
Case 6	PP	0/0	5/150
Case 7	PP	0/0	1/28

and the time it took them to perform the manipulations to retrieve the pellet (Time 2), these measures did not specify the nature of the behavioral changes caused by the lesions. Several training sessions were recorded on videotape, allowing analysis of the strategies used by the monkeys to retrieve the pellets and peanuts. The videotape records revealed that although the MT-lesion monkeys reached accurately for peanuts and pellets, they had difficulty coordinating their finger movements. They grasped pellets and peanuts with the whole hand rather than with their fingertips, and on the slot task they frequently inserted their fingers into the distracting slots. These results may reflect a visual impairment or a visuomotor impairment. The MT monkeys, rather than using visual cues effectively, may instead have used tactile cues to retrieve the rewards, maximizing the amount of skin surface that might come into contact with the pellet or peanut. The MT monkeys quickly learned to retrieve pellets from behind the black barrier; perhaps they were more practiced than the control animals at retrieving pellets without visual guidance. Alternatively, MT lesions may produce visuomotor impairments in monkeys.

MT is one source of visual input to cortical areas involved in relating visual stimuli to bodily movement. It seems to be a sensory link in a system joining sensory input to action. It would be of interest to see whether lesions of other cortical areas known to be involved in visuomotor function produce effects similar to lesions of MT. It is known that lesions of the posterior parietal cortex in man and monkey impair spatial orientation, visuo-constructive skills, visually guided reaching and locomotion, and produced various neglect and inattention symptoms (Hécaen and Albert, 1978; Bates and Ettlinger, 1960). Patients suffering from optic ataxia syndrome after posterior parietal lesions have deficits in both reaching and grasping movements (Perenin and Vighetto, 1988). In monkeys, these effects are only seen in animals with large lesions of the parietal lobe; the PP lesions in this experiment were too small to produce the classical effects. Indeed, our rational was to produce PP control lesions that were comparable in size to the lesions in MT. Moreover, our PP lesions were restricted to cortical tissue located on the surface of the brain, and did not damage regions located inside the intraparietal sulcus, such as the lateral intraparietal area (LIP), as exemplified in Fig. 5A. Haaxma and Kuypers (1974) have studied the effects of disrupting the connections between visual and motor cortex on the visually guided hand and finger movements of monkeys. Transections of the white matter under the inferior parietal lobule impaired the monkeys' ability to retrieve a food pellet from a narrow slot, although the animals were still able to discriminate patterns. Mountcastle et al. (1975) have suggested that the posterior parietal cortex performs "command functions for operation within extrapersonal space".

The visual areas MT and PO (V6) belong to the dorsal stream of visual information processing. The dorsal visual stream carries information to the PP, which contains many areas related to the representation of space, spatial awareness, perceptual decision-making, learning and motor planning. Areas of the intraparietal sulcus have been shown to be associated with specific behaviors: lateral intraparietal area (LIP) and ventral intraparietal area (VIP) are involved in visual attention and saccadic eye movements; VIP and medial intraparietal area (MIP) are involved in visual control of reaching and pointing; and the anterior intraparietal area (AIP) is related to visual control of grasping and manipulating hand movements (Andersen, 1989; Colby and Duhamel, 1991; Duhamel et al., 1992; Colby et al., 1993; Sakata et al., 1995; Rizzolatti et al., 1998; Colby and Goldberg, 1999; Murata et al., 2000).

Studies of V2, V4, TEO, MT and PO connectivity in monkeys have revealed that areas V2, V4 and TEO show a complimentary pattern of connectivity with the intraparietal sulcus as compared to areas PO and MT, suggesting that the ventral and dorsal streams of visual information processing remain segregated within this region. The differential connectivity between intraparietal sulcus and areas PO and MT also corroborate the notion that the dorsal stream can be further sub-divided into dorsolateral and dorsomedial components (Colby et al., 1988; Gattass et al., 1990; Webster et al., 1994; Gattass et al., 1997; Nascimento-Silva et al., 2003; Ungerleider et al., 2008; Mariani et al., 2019). However, these areas are richly interconnected and V6A, an area involved in visuomotor integration, for example, receives projections both from PO (V6) and MT (Shipp et al., 1998; Rosa and Tweedale, 2001).

The act of prehension involves reaching and grasping actions. The medial subdivision of the dorsal visual stream has been traditionally related to reaching, decoding reach endpoints and trajectories, while the lateral subdivision is mainly concerned with grasping movements (Sakata et al., 1995; Jeannerod et al., 1995; Cohen and Andersen, 2002; Mulliken et al., 2008). However, recent work has also related the dorsomedial stream with encoding grasping and have linked the dorsolateral network to reach actions challenging this view of a strict separation of reach and grasp representations (Galletti et al., 2003; Lehmann and Scherberger, 2013; Breveglieri et al., 2019).

The data of Saito et al. (1986) suggest that the dorsolateral stream of visual information processing, as described by Nascimento-Silva et al. (2003), can be hierarchically organized. In the context where cells or discrete circuits in one specific area exhibit different response properties corresponding to the different stages of neuronal processing, we hypothesize that MT participates as an integral component responsible for building up this network. One evidence for this is the similarity of hand posture related to MT lesions and hand posture related to the injection of muscimol in area 2, a high target of this network (Hikosaka et al., 1985). Uka and DeAngelis (2003, 2004, 2006) showed that area MT plays important roles in depth perception, suggesting that absolute disparity signals are emphasized in the dorsal stream to compute the location of objects in 3D space.

Unfortunately, all the MT lesions in this experiment included damage to the optic radiation fibers running underneath STS, resulting in scotomata in the lower central visual field. These blind spots might account for the impairments seen in the MT monkeys. The OR lesions were intended to transect the white matter underneath STS while sparing MT cortex. However, the histology results from one of the OR monkeys indicate that this goal was not attained. Regarding the second OR-lesion case (Case 9), this monkey was not euthanized. Therefore, we were not able to access the level of damage to the optic radiation fibers under MT and the corresponding degeneration in the LGN. The results of the MT lesions in this experiment are thereby confounded by scotomata produced by optic radiation damage. It may not be possible to completely remove MT by aspiration without damaging the white matter underneath it. Therefore, it would be desirable in future experiments to train on these tasks monkeys with scotomata produced by OR lesions or by lesions of striate cortex in the representation of the lower central visual field.

In addition to the information from V1 via MT, the dorsal stream of primates receives information from the retina and from the superior colliculus via the pulvinar nucleus projections to the MT complex (MT, FST, and MST). The strength and role of these connections have not yet been established (Gattass et al., 2018; Kaas and Baldwin, 2019). Lesions to the optic radiation or to V1 impact vision in primates. However, patients with V1 lesions retain their ability to detect, localize, and track objects, a phenomenon called blindsight (Stoerig and Cowey, 1997). This may occur in adult monkeys and humans as a result of new or indirect inputs from the pulvinar. Recent works have shown that functions associated with the dorsal stream are preserved when V1 lesions occur early in postnatal life (Bourne and Rosa, 2006; Warner et al., 2015; Mundinano et al., 2018, 2019). Mundinano et al. (2018) provided evidence that eliminating transient retino–pulvinar input to MT in early life disrupts the development of multiple dorsal stream areas, leading to a sustained defect in visually guided actions.

The effects of MT lesions indicate that this region is important to visual and/or visuomotor function, although the specific effects of these lesions on behavior are yet to be determined in greater detail. The MT monkeys were impaired on tasks that were rather complex in nature. It will be desirable in future experiments to break down the components of

each task in order to determine just how MT lesions disrupt behavior.

5. Conclusion

Macaque monkeys with selective lesions of area MT were tested on a number of tasks designed to reveal visuomotor deficits. MT lesions impaired the monkeys' ability to pick a small food pellet out of a narrow slot, to detect and grasp a loose peanut mounted on a background of fixed peanuts, and to retrieve an erratically moving pellet from a spinning bowl. They also show an abnormal hand posture that maximizes the skin surface to retrieve the target. They grasped pellets and peanuts with the whole hand rather than with their fingertips. These results suggest that area MT participates in a cortical network involved in visuomotor functions.

In memoriam of Charles Gordon Gross

Charles Gordon Gross made fundamental contributions to the visual perception and memory and to the cortical organization of primates. He has revolutionized our understanding of sensory processing and pattern recognition. His boundless enthusiasm, superb scientific expertise and rigorous application of behavioral and electrophysiological techniques has greatly influenced the field of cognitive neuroscience research. His contribution to this paper was fundamental.

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Appendix A. The Peer Review Overview and Supplementary data

The Peer Review Overview and Supplementary data associated with this article can be found in the online version, at doi: https://doi.org/10.1016/j.pneurobio.2020.101931.

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