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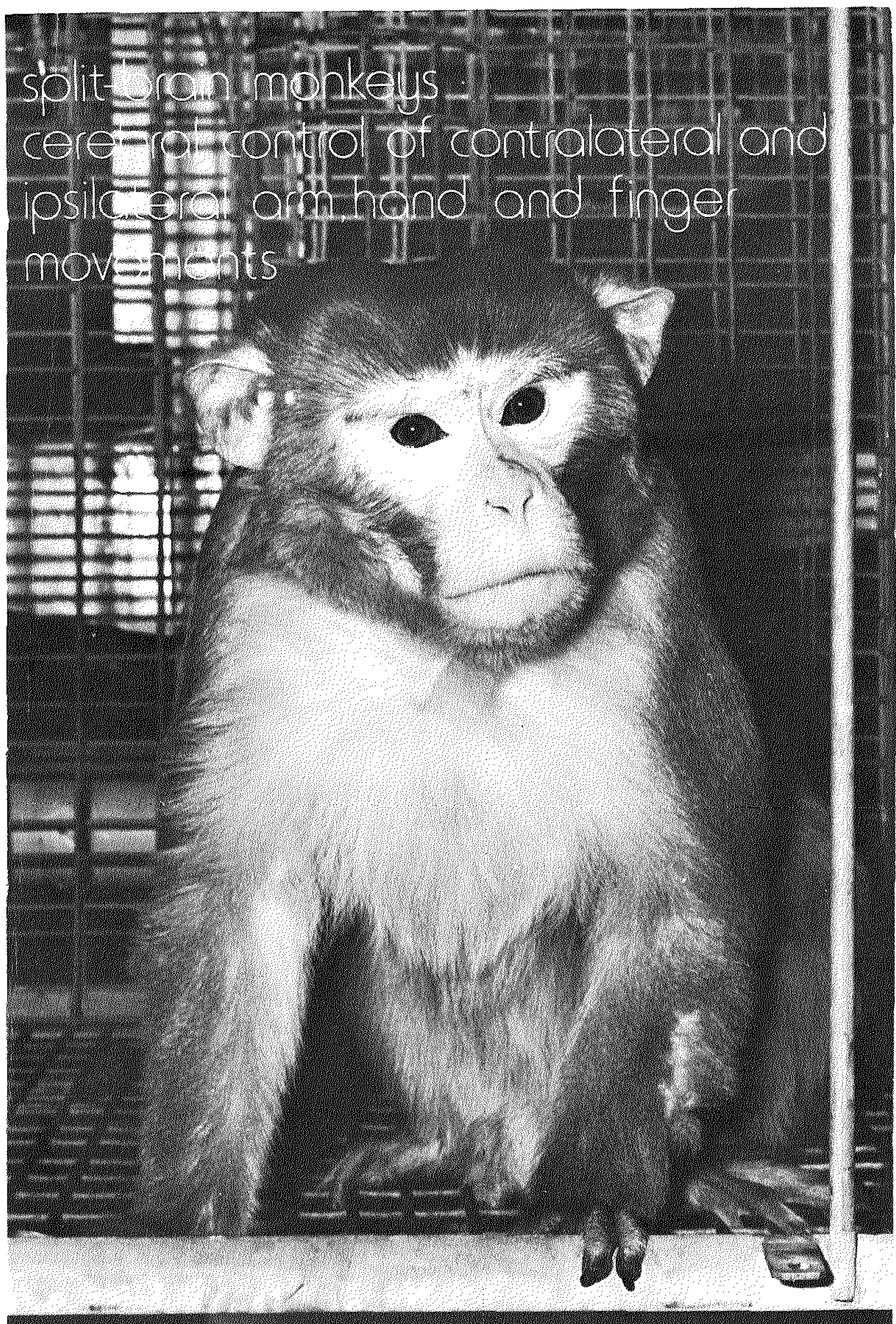
cerebral control of contralateral and ipsilateral arm, hand and finger movements



SPLIT-BRAIN MONKEYS:
CEREBRAL CONTROL OF CONTRALATERAL AND IPSILATERAL ARM, HAND AND FINGER MOVEMENTS

proefschrift

ter verkrijging van de graad van doctor in de geneeskunde
aan de Erasmus Universiteit te Rotterdam
op gezag van de rector magnificus
prof.dr P.W.Klein
en volgens besluit van het college van dekanen.
de openbare verdediging zal plaatsvinden
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door

Jacoba Brinkman

geboren te Schiedam

Promotor : Prof.Dr H.G.J.M.Kuypers
Coreferenten: Prof.Dr M.W.van Hof
Dr C.B.Trevarthen

To all primates
—human or simian—
who contributed

CONTENTS

Simiarum quoque genera hominis figurae proxima caudis inter se distinguntur; mira sollertia.

Nam simiarum genera perfectam hominis imitationem continent facie, naribus, auribus, palpebris,.....
solae quadrupedum habent et crura et brachia in contrarium similiter flexa, in manibus ungues, digitos longioremque medium......
Pollex quoque iis et articuli ut homini.

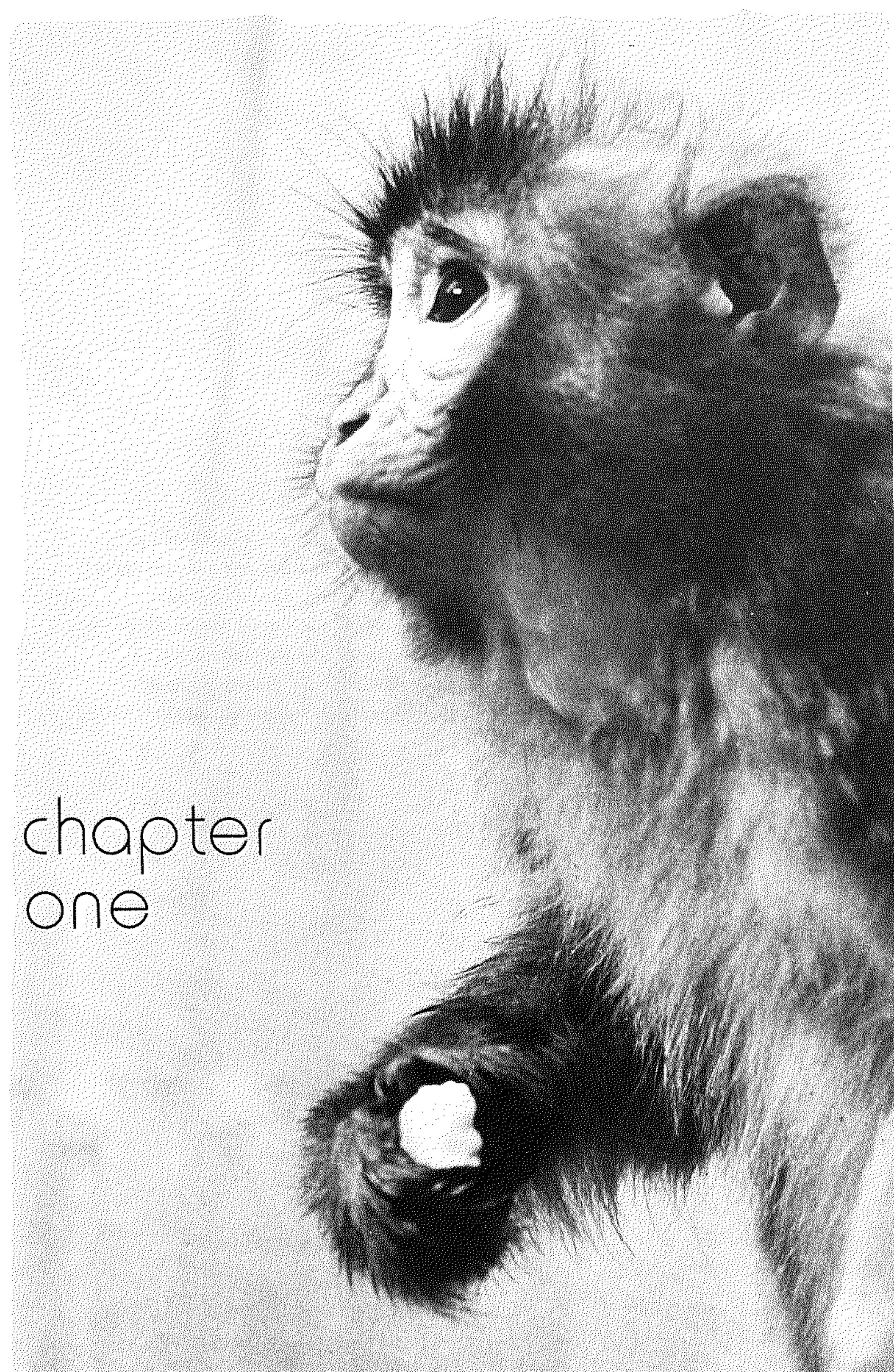
Gaius Plinius Secundus :
"Naturalis Historia"
Liber VII, LXXX
Liber XI, XCIX

The kinds of monkey which are closest to man are distinguished from each other by the tails.
They are marvellously cunning.

In fact the monkey tribes have a perfect imitation of a human being in their face, nostrils, ears and eye-lashes,......and they alone of the four-footed animals have arms and legs bending similarly, in opposite directions, and nails on their hands, and a longer middle finger....
They also have a thumb, and knuckles like man.

Introduction

In the present study, an investigation has been made of the visuomotor control exerted by one half of the brain over each of the two upper extremities in the rhesus monkey.
The hypothesis that one half of the brain can steer movements of each of the two extremities relatively independent from the other half has been tested and an attempt has been made to define more precisely which pathways in the central nervous system are involved in this control.
These studies have been done in the 'split-brain' monkey, i.e. an animal in which both halves of the forebrain have been surgically separated.



chapter one

In order to better understand the effects of brain bisection, this chapter first gives a short account of the anatomy and physiology of the interhemispheric connections of the brain. Secondly some experiments in 'split-brain' cats, monkeys and humans concerning the functions of the interhemispheric pathways and the functional capacities of the isolated brain halves will be reviewed. Special attention will be paid to interhemispheric differences and to studies dealing with motor control.

Chapter I: The interhemispheric pathways. Some effects of brain bisection in animals and man.

The cerebral hemispheres are interconnected with one another through two major commissural systems: a) the *corpus callosum*, a thick band of nerve fibers which is found in the median fissure between the two hemispheres, and b) the *anterior commissure*, a much smaller band of fibers which crosses the midline through the lamina terminalis at the rostral border of the third ventricle. In the diencephalon, the small *habenular commissure* is found interconnecting the habenular nuclei of the posterior thalamus, and the tiny *supraoptic* and *suprachiasmatic commissures* in the hypothalamus. In the midbrain roof, the *posterior commissure* interconnecting the pretectal areas and the *commissures of the superior and inferior colliculi* are found. In the diencephalon of the cat and monkey diffuse commissural systems also exist in the *massa intermedia thalami*. A distinct commissure between the complexes of somato-sensory nuclei on both sides running in the massa intermedia has been described and called the *interthalamic commissure*[108]. In man, the massa intermedia is either absent or small[236].

Anatomically the fiber connections through the corpus callosum and anterior commissure have been studied either by removing part of the cerebral cortex in one hemisphere and mapping the areas showing degeneration in the other one, or by transecting the commissures partially or totally and studying the ensuing degeneration in either hemisphere. These studies have indicated the following arrangement: In both cat and monkey, most cortical areas receive commissural fibers through the corpus callosum. However, almost no such fibers terminate in the primary visual cortex (area 17)[65,198,312,313,314] or the primary auditory cortex[216]. In the monkey, the areas representing the hand and foot in the precentral gyrus (the primary motor cortex[309])and the postcentral gyrus (the primary somato-sensory cortex[309]) remain free of callosal connections. This is also found for the hand and foot representation areas of the secundary motor and somato-sensory cortices[129,130,218,219]. The rostral part of the temporal lobe, i.e. its frontal pole and the anterior parts of the superior, middle and inferior temporal gyri also receive no callosal afferents. These areas, however, are interconnected through the anterior commissure[9,216,300,314]. Fibers from different cortical areas cross the midline in different parts of the corpus callosum. Fibers from the occipital and posterior temporal lobe run in the most caudal part of the callosum, the splenium[198,314] while fibers from the parietal and precentral areas are found in its central part[217]. Fibers from the prefrontal cortex travel in the most rostral part of the callosum, its genu[217].

Physiological data obtained with the evoked response technique in cats, monkeys and chimpanzee confirm the anatomical findings on the distribution of the corpus callosum and anterior commissure[19,68,69,87 180,278,301] and like the anatomical studies stress the fact that most callosal connections are homotopical, i.e. interconnecting opposite areas of cortex on both sides but that heterotopical connections interconnecting different cortical areas are by no means uncommon[2,16,42 43,59,152,153,278].

The anatomical and physiological findings on the distribution of the callosal connections may be summarized as follows:
Fibers in the corpus callosum interconnect areas in the pre- and postcentral gyri in the two hemispheres of the monkey which are involved in axial and proximal motor and sensory processes and which are preferentially concerned with midline structures[88,126,130]. This is also found for the visual modality: commissural fibers preferentially interconnect the areas which represent the vertical meridian of the visual field[70,302,303]. Microphysiological studies on fibers of the splenium of the corpus callosum (which part interconnects the visual cortex on both sides) reveal that these fibers are derived from cells which can be excited only by stimuli presented in the midline of the visual field[27,125].

In view of the findings described above, it is surprising that after surgical transection of the corpus callosum and anterior commissure few if any disturbances of every day behavior have been reported. In monkeys, a slowness of movements has been noted[119,133,169] and also the occurrence of bilaterally symmetrical motor responses i.e. in reaching out for food which is normally done with one extremity only [133,161,287,288]. In order to demonstrate some of the functions of the corpus callosum and anterior commissure and the effects of transecting these connections more refined experiments are required in which input is lateralized to one hemisphere and in which the functional capacities of that hemisphere can be tested separately. A number of these studies with special reference to monkey and man will be reviewed.

Split-brain is a term coined by Sperry[260] to describe an animal in which the corpus callosum and the anterior commissure as well as the optic chiasm have been transected. The optic chiasm contains the fibers from the nasal retina of each eye crossing to the opposite hemisphere. After transection of these fibers, only ipsilateral visual input from the temporal retina into each hemisphere is available to the animal (Fig. 1-1). In this preparation, visual discriminations learned through one eye by one hemisphere do not transfer to the other eye and the other hemisphere i.e. when a cat with one eye closed has learned to respond to one of a pair of visual stimuli, e.g. a circle and a cross, as positive, and subsequently the other eye is opened and the first eye closed, and the animal tested for retention of the solution to the problem, the cat shows no signs of knowing this task and has to be trained again to criterium which may take as many trials for this hemisphere to learn the task as for the first[195,266].
When only the optic chiasm has been cut, leaving the corpus callosum and anterior commissure intact and the cat is trained in the same way, the hemisphere tested second shows almost perfect retention of the solution to the problem learned by the first hemisphere, indicative of transfer of visual information through the intact commissures[199].
The same results have been described for split-brain monkeys and chimpanzees[32,33,50,75,77,90,92,95,116,196,199,259,260].
The interhemispheric connections thus seem to play an essential role in the transfer of information related to visual pattern discrimination learning. This transfer is critically dependent on the splenium of the corpus callosum (which interconnects the occipital lobes) and the anterior commissure (which interconnects the inferotemporal cortex an area which has been shown to be involved in the elaboration of visual pattern discrimination[190,191]). This absence of visual transfer after section of the optic chiasm, anterior commissure and corpus cal-

losum is not found for simpler visual discrimination tasks such as the detection of differences in flicker frequency, color and perhaps brightness. Succesfull transfer of this kind of information in the absence of the forebrain commissures is dependent on the midbrain commissures i.e. the posterior commissure and the commissure of the superior colliculus, in cat, monkey and chimpanzee[34,182,183,224,285,294]1)

In order to study the role of brainstem mechanisms in visual discrimination a technique has been developed by which each hemisphere of a split-brain animal receives a different input at the same time. This is done by projecting stimuli with differently polarized light to animals wearing different polaroid filters on each eye[284]. These studies have indicated that a split-brain monkey can not only learn different visual discriminations, or even conflicting problems with each hemisphere, but also it is capable of comparing some features of stimuli projected to each brainhalf and choose one of the two, e.g. the larger of a pair of circles[285,286,288;cf 90,265].

On the basis of these experiments, Trevarthen[288] has postulated the existence of two modes of processing visual information in the central nervous system, 'focal' and 'ambient' vision.

Fig. 1-1. Diagram showing lateralization of visual input in the split-brain monkey. The anterior commissure (ac) and the corpus callosum (cc) have been cut. When the fibers crossing in the optic chiasm are also sectioned, lateralization of visual input can be achieved by simply closing one eye. Note that because of section of the fibers from the nasal retina (hatched) only information presented to the temporal retina (black) is perceived and transmitted to the lateral geniculate body (lgb) and visual cortex and to the brainstem visual centers.

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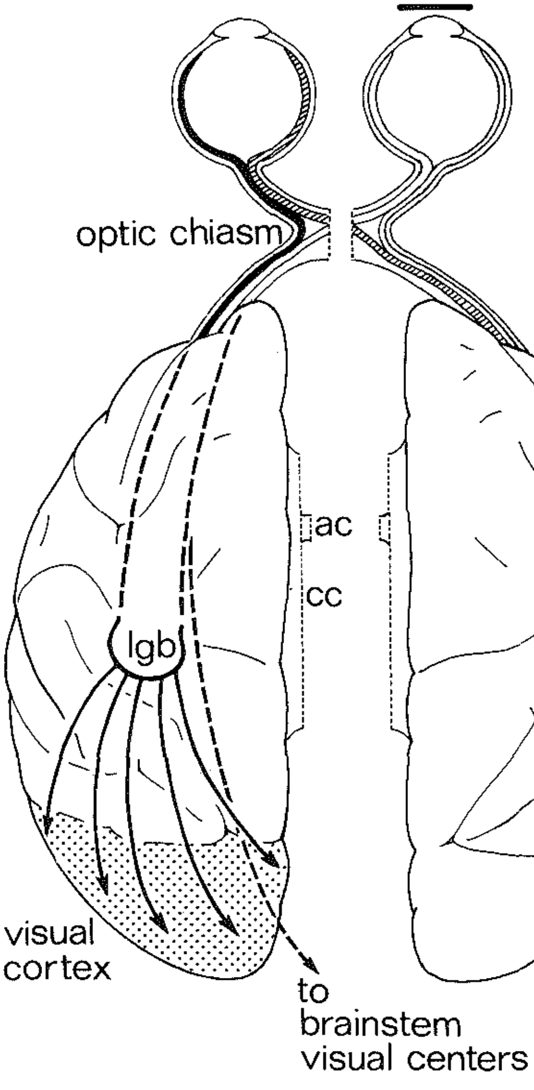
1) In this respect it is of interest to note that monkeys with bilateral removal of the cortical visual areas (17 totally and most of 18 and 19) can be retrained in or taught to discriminate differences in brightness, color and even some form[223,224,247,248]. Lesions in the socalled accessory optic system[105] in the brainstem disrupted this performance[220,221,225].

Focal vision is subserved by the cerebral cortex and is applied to one place in the behavioral space and a specific kind of object. This examining and identifying kind of vision is used in refined discriminatory acts, and is especially developed in the higher primates including man. *Ambient* vision is subserved by brainstem circuits and is used to define the animal's place in its behavioral space i.e. the space around its body in which it may act by postural adjustments,



such as orientation of the head or body, or by locomotion[288]. The same distinction of mechanisms of vision is found in experiments with split brain man when tested with lateralized stimuli and monitoring of head and eye movements. As in the split-brain monkey, stimuli presented separately to each of the two hemispheres could be cross-integrated[289-292]. In the split-brain monkey, only the cortical mechanism of focal vision which would be especially involved in the execution of refined motor acts on one particular site in the behavioral space would be completely lateralized. More gross motor acts in the entire behavioral space may also be steered using the subcortical mechanism of ambient vision which is not lateralized and involves structures on both sides of the brainstem (Fig. 9 in ref.292).

Thus, transfer of visual information may or may not occur depending on the type of stimuli to be discriminated. However, transfer may or may not be present also depending on the type of motor response the animal is required to make. This is demonstrated by the fact that split-brain monkeys show no sign of transfer when taught a visual discrimination in a go-no go test situation in which the animal has to respond by pressing a panel which displays the positive stimulus but has to withhold a response when different stimuli are shown. However, a split-brain monkey taught a delayed response task through one eye and with one hand, shows transfer of the task when tested through the other eye[310,311]. It has been pointed out that this kind of test involves a major component of orientation[135,268,270,271] which could be governed by brainstem mechanisms.

In the *tactile modality* differences in the amount of transfer may likewise be related to the type of input and perhaps also to the motor acts the animal has to perform during the discrimination task[109]. Normal, intact monkeys may fail to transfer difficult discriminations learned with one hand to the other untrained hand unless the monkey has been given some preliminary experience with simple tactile discriminations prior to its being tested for recall of the difficult task[250,251]. A normal monkey may even learn conflicting tactile discriminations with each hand without showing signs of emotional disturbance[199].

Section of the corpus callosum and anterior commissure prior to training interferes with transfer. Some authors claim that no transfer occurs at all in the split-brain animal, and that the learning curves for the second hand or paw are almost identical to those obtained for the first hand[78,199,201]. Others observe only a deficit of transfer [109,233,259] or even complete transfer[83,84].

These conflicting data have been interpreted as being caused by a discrepancy in distribution of somato-sensory afferents of the proximal parts of the extremity as opposed to its more distal parts[158]. The proximal parts tend to have a more bilateral cortical representation than the distal parts[98,100,101] and consequently, a tactile discrimination which involves the participation of proximal body structures will provide information to both hemispheres and will be 'transferred' in spite of the commissurotomy.

One experiment which has some relation to the foregoing problems was done by Butler and Francis[51]. Their animals were *intact* baboons which had to learn shape or size discriminations using the fingers of one hand with the arm immobilized, restrained at elbow and wrist. When tested with the second hand, this hand did not show signs of transfer. The authors stress the fact that their task may involve joint receptors more than is the case with other tactile discriminations, and joint sensation is known to project mainly contralaterally[194]. In this experiment, a task learned with the distal part of the extremity does not transfer which would seem to support the theory described earlier. Another factor of importance with respect to possible transfer of tactile discriminations in split-brain animals are somato-sensory pathways projecting also to the ipsilateral hemisphere. An indication for the existence of such pathways is the fact that after ablation of the sensorimotor and posterior parietal cortex of one hemisphere somatosensory loss as indicated by an impairment on discriminations of shape and roughness has been described[250,251] ipsilaterally.

As is the case in the visual system, some somato-sensory information may be integrated at subcortical levels[20,21,22] as has been shown physiologically in the cat. In the monkey, this mechanism seems to pertain to discriminations of roughness or size. The massa intermedia thalami (in which fibers are found interconnecting the ventrobasal complex, the main sensory nucleus of the thalamus[108]) seems to play a role in this transfer and to a lesser extent also the posterior commissure which interconnects the pretectal areas of the midbrain[171].

The overall conclusion that can be drawn from the experiments described above is that intermanual transfer and integration of tactile cues are dependent on the forebrain commissures but some qualifications are required. The cortical representation areas of the most distal parts of the limbs are acallosal. Since commissurotomy affects at least some forms of tactile discriminations other cortical areas which are interconnected through the callosum may function as a relay for interhemispheric transmission. In the cat, the secundary somatosensry cortex is of importance[278].

More data are needed to fully assess the function of the interhemispheric commissures in the transmission of somato-sensory information and the role played by the various ascending pathways in the registration of different sensations since an animal can adopt various strategies to solve tactile problems depending on the type of information received[295].

The experiments described above may be summarized as follows: the interhemispheric connections are critically involved in the transfer of visual discrimination learning for which the splenium of the corpus callosum and the anterior commissure seem to be most important. Transfer of more elementary visual cues such as flicker frequency, color and perhaps brightness, is adequately subserved by the posterior commissure and the commissure of the superior colliculus or by other brainstem pathways. The corpus callosum, especially its central parts, is involved in the interhemispheric transfer of some kinds of tactile information although some transfer may also occur through the massa intermedia and the posterior commissure.

So far only cat and monkey data have been presented. However, there are now a number of studies on the effects of brain bisection in man. This operation is performed for the treatment of severe convulsive disorders not controlled by medication.

Early studies of these patients failed to reveal any severe deficits [3,4,5,6,7,8,257,317]. Deficits reported in still earlier studies[10,11, 71,166,237,275] were considered as having been caused by extracallosal damage. Even as recently as 1956[44] there was no substantial change in this rather negative view of callosal function. However, incited by the animal experiments of Myers and Sperry, a whole new series of investigations after the results of callosal section or destruction in man was started. A case with partial infarction of the callosum was described which showed definite deficits when properly tested[104]. The full 'disconnection syndrome' of the corpus callosum occurs only in surgical cases. Tests with a series of such patients have been done mostly by Dr Sperry's group. These experiments have given much insight in the role of the interhemispheric connections in man and provided some answers to questions concerning the capacities of one hemisphere, how independent are the two hemispheres when separated and wether the hemispheres differ in their ways of handling information[67,82,99,120, 164,209,262,263,264].

In the patients, the corpus callosum with the underlying hippocampal commissure, the anterior commissure and the massa intermedia, when present, were transected. As was found in the animal experiments, the behavioral symptoms produced by this operation are surprisingly inconspicuous in every day life but some deficits have been noted, e.g. conflicting responses of the two hands (such as one opening a drawer, the other closing it), the 'diagnostic dyspraxia' of Akelaitis[317] and 'complementary dyspraxia'[36,38,102] i.e. one hand may not be able to perform a task the other can do well (e.g.,writing is normal for the right hand but illegible with the left;however, the left is superior to the right in copying block designs). With special testing techniques, more subtle deficits are revealed.
The optic chiasm has not been divided;however, lateralization of visual stimuli is achieved by asking the patient to fixate on a point and stimuli are flashed to the right or the left of the fixation point for a period too brief for the eyes to make a saccadic movement towards the stimulus thus confining the information to the left or the right hemisphere respectively (Fig. 1-2).
As has been found in the animal experiments, the patient is unable to match an object seen in one visual field with one in the other i.e. visual transfer does not take place. Likewise, objects held in one hand by a blindfolded patient cannot be selected from an array of different objects with the other hand, or be drawn with this hand.

Substances smelled through the right nostril are not identified through the left and vice versa[112].

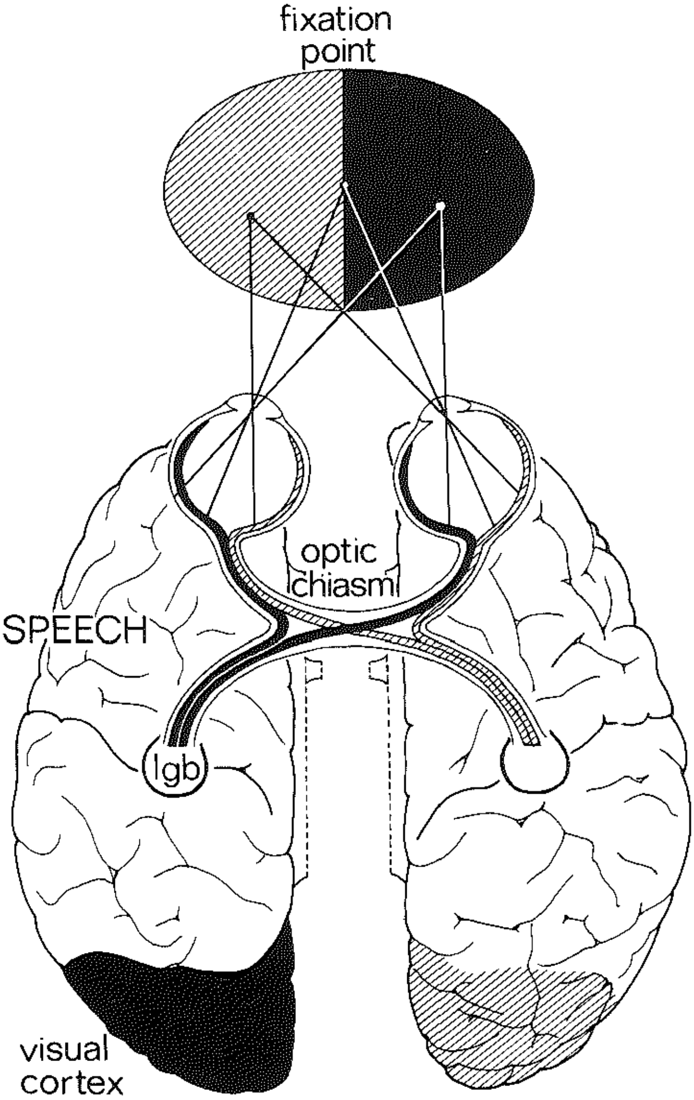
A striking group of disabilities appears on the left side of the patient because speech in the majority of human beings is lateralized in only one hemisphere, the left. This group of deficits is not paralleled in animal experiments. Verbal commands are carried out correctly by the right hand but not by the left. The blindfolded patient can name objects placed in his right hand but not in his left. Writing is normal with the right, illegible with the left hand. Reading in the right visual field projecting to the left hemisphere is normal but the patient seems unable to read in the left visual field.[101]. This implies that for proper testing of the capacities of the right, socalled 'minor' hemisphere a non-verbal mode of response is required. When this is taken into account, a number of differences between the two hemispheres become evident which in part had already been known from patients with unilateral brain damage.

Despite the deceptive normality of the commissurotomized patient a long series of studies indicates that the two hemispheres function relatively independently and to a certain extent even have a mind of their own[101,102,163,165,188,206,207,208,210,261,264]. These studies seem to point to a different mode of processing information for each of the two hemispheres:The left hemisphere does essentially all the talking, reading, writing and calculation in right-handed subjects and analyzes stimuli presented to it on the basis of their separate

Fig. 1-2. Diagram showing lateralization of visual input in the human split-brain patient. Only the anterior commissure (ac) and the corpus callosum (cc) are transected. The optic chiasm is left intact. Note that the right halves of the retina (hatched) project to the right visual cortex, and the left halves (black) to the left hemisphere. The patient is asked to fixate on a point. Stimuli flashed to the left of the fixation point are perceived only by the right halves of the retina and thus by the right hemisphere only, and stimuli flashed to the right are likewise perceived only by the left hemisphere.

In most humans, verbal abilities are lateralized in the left hemisphere. Modified after Gazzaniga[96].

features, and often does this latter work with a running verbal commentary. The right hemisphere remains essentially mute, agraphic and alexic and is capable of only very simple calculation, but is superior to the left hemisphere in the appreciation of spatial relationships and recognition of stimuli on the basis of their overall appearance using simple visualization rather than analyzing the separate features of the stimuli.



Therefore the right hemisphere has been called a "Gestalt" specialist [36,38,164,189,208,261].

The findings in human split-brain patients may be summarized as follows. A lack of interhemispheric transfer of visual and tactile stimuli is present in man like it is in the split-brain animal; moreover, a number of specific deficits exists in man because of the lateralization of linguistic ability in one hemisphere and spatial ability in the other.
The left, verbal brain appears to be superior and dominant for verbal communication, linguistic and numerical processing, sequential and analytical thinking, for conceptual recording and for directing motor capacities in general. The right hemisphere is found to be superior for perceptual recognition of faces, of non-descript figures as whole patterns and for dealing with spatial and part-whole relationships, for non-verbal thinking and direct perceptual transformation, and for skilled use of the left hand in drawing and use of objects[263].
At the same time the minor hemisphere in situations in which it is in equal and free competition with the major hemisphere - where the sensory input is equated and the subject is free to use either hand - is quite capable of capturing and controlling the motor system[165] although normally the dominant left hemisphere seems to be in control.
These last data are of importance for the study reported on here on the motor control in the split-brain monkey. They may be taken to imply that motor control may be different depending on wether it is being exerted by one hemisphere or the other, provided that in monkey as in man a kind of hemispheric specialization exists.
In this respect it is important to know wether a) the monkey shows hand preference, b) there is evidence of hemispheric specialization in this animal and wether c) there is a relation between one specialized hemisphere and hand preference as is found in man.
Hand preference in monkeys is the subject of a number of studies[61,66,81,139,160,187,296,297]. Most authors agree that monkeys do show hand preference which is more pronounced in trained animals and may be influenced by situational factors. Although the advantages of having an asymmetrical brain have been stressed[64,163,164] not until recently have studies been done investigating the existence of hemispheric

specialization in subhuman species:the hemispheres were considered to be equal. This notion was based mainly on data obtained with simple tasks which resulted in almost identical learning curves for each of the two hemispheres of a split-brain animal[78,183,199,269]. Using visual discrimination tasks, Robinson and Voneida[240] have demonstrated differences in cognitive capacity between the hemispheres of split-brain cats. Evidence for some kind of difference between hemispheres has now been found for a number of species:mice[63],rats[242] and even birds[213]. Only a few studies have been done in the monkey.

There are some indications of a left-right difference in visual learning[50,74,91,117] or in visual versus tactile learning[89]. In the baboon, a difference in motor performance has been found[52,290].

If the same parameters of hemispheric specialization are applied to the monkey which are valid in man, then one the basis of these few studies it may be tentatively suggested that in the monkey we find the reverse of man:The left hemisphere seems to be more involved in the appreciation of spatial aspects[117,318] while perhaps the right is more concerned with visual discrimination (analysis of features??)[91]. In the baboon, this seems to be the reverse:as in man, the right hemisphere is said to be more involved in spatial aspects of behavior[52] and the left in visual discrimination[286].

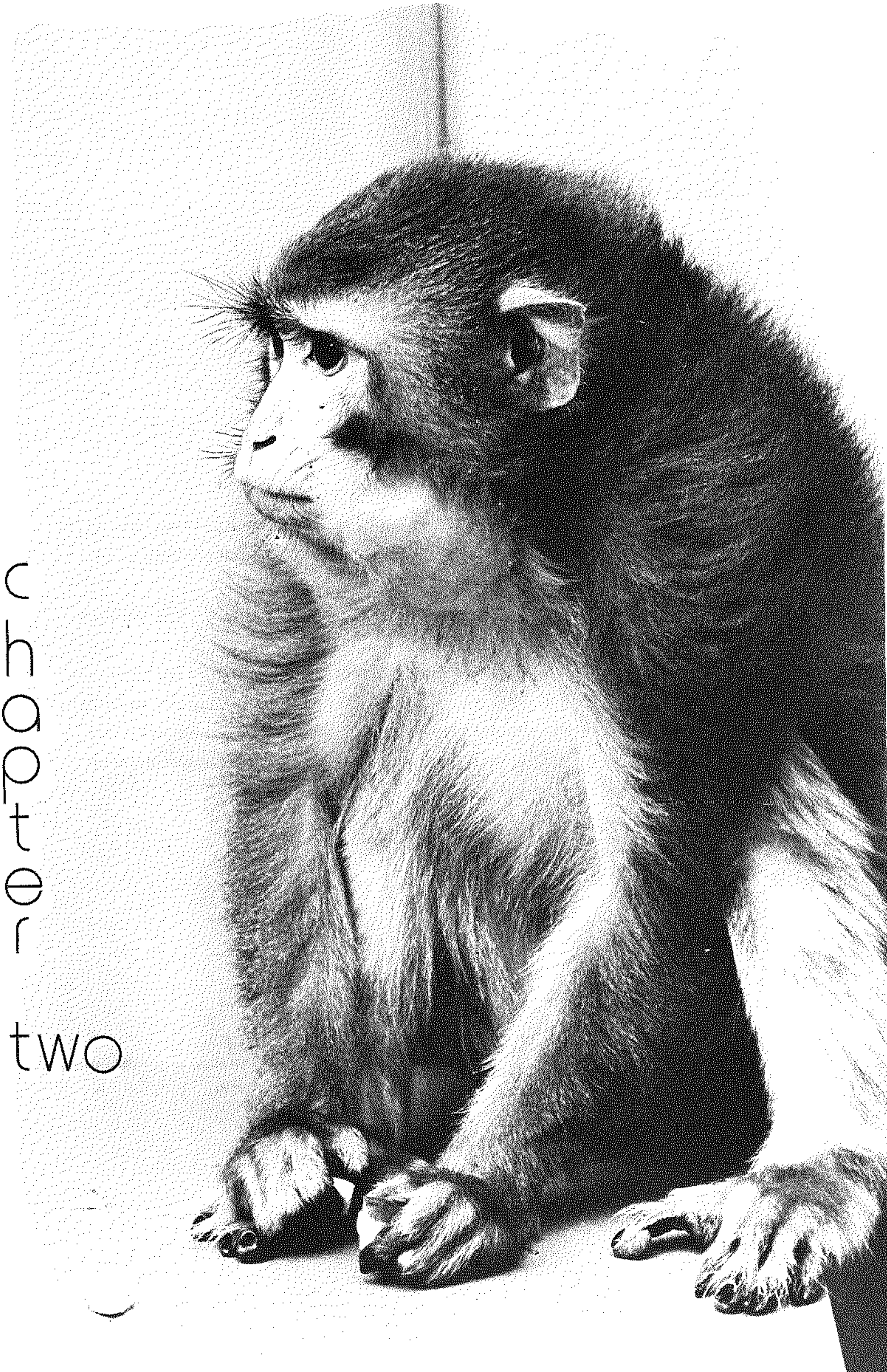
However, direct comparison with man may not be possible nor desirable. Monkeys have no speech, and bilateral lesions of the monkey homologue of the human cortical speech area does not affect the animal's vocalization[274]. No conclusive evidence has been found for a link between one particular hemisphere and hand preference in the cat[298] or the monkey[162].

In a recent study in the monkey the existence of a strong hand preference was denied[26]. Instead it was suggested that hand preference was dependent on the type of motor skill required for the task and that an animal would use one hand for one kind of motor act and the other for another one. This would correspond with man and indicate a difference in motor capacity between the two hemispheres in the monkey as has been found in the baboon also[290] and is relevant for the present study which investigates the motor control exerted by one half of the brain over each of the two upper extremities in the split-brain monkey.

The nature of this control is subject to controversy in the literature. In most of the experiments visual input is restricted to one hemisphere by closing one eye and the animal then has to respond with the arm contralateral or ipsilateral to the open eye. This response may consist of simple food retrieval, or pressing a panel displaying a certain stimulus during a visual discrimination task.
No deficits in visuomotor control are found for the contralateral extremity but opinions differ with respect to the ipsilateral one.
Some authors reported poor control over this extremity, at least initially[76,90,94,132,169,211,212,288] while others observed that the contralateral and ipsilateral extremities were equally proficient in reaching, visual pursuit and grasping[33,39,50,92,115,202].
However, in only few of these studies[173,260,288] has the fact been mentioned that the capacity of the brain to steer movements of body and limbs depends on the descending pathways from the cerebral cortex and brainstem to the spinal cord.
In order to come to a meaningfull concept of the nature of the motor control of one half of the brain over the contralateral and ipsilateral extremities, the anatomical and functional organization of these pathways has to be taken into account.

The present study was initiated to test the validity of the concept of motor control in the monkey first put forward by Kuypers[144,145], a concept which was based on the anatomical organization of the descending pathways to the spinal cord.
In the next chapter, a short review will be given of the anatomical organization of the descending pathways from the brainstem and cerebral cortex to the spinal cord, and of the functional implications of this organization.

chapter two



In this chapter, the anatomy of the descending pathways from the brain stem and cerebral cortex to the spinal cord will be described with special reference to the monkey.
Some experiments concerning the functional capacities of the various pathways will be discussed.
On the basis of these findings the hypothesis is put forward that one half of the brain has full control over arm, hand and finger movements of the contralateral extremity by way of the descending connections but controls mainly proximal movements and synergistic movements of the whole limb ipsilaterally.

Chapter II: Descending pathways to the spinal cord in the monkey. Anatomical and functional considerations.

In order to understand the function of the various fiber systems descending from the brain to the spinal cord, it should be realized that the motor capacities of these pathways are ultimately determined not by their areas of origin (e.g., the cerebral cortex or the reticular formation) but by their modes of termination in the spinal cord i.e. by the interneurons and motoneurons upon which those fiber systems converge[144,145,146].

The spinal gray matter may be subdivided into the dorsal horn with its nucleus proprius and the substantia gelatinosa (Rexed's[239] laminae I-V in the cat) and the ventral horn with the lateral and medial motoneuronal cell groups (lamina IX) and the intermediate zone (laminae VI -VIII) which contains the bulk of the interneurons to the motoneurons (Fig.2-1 B).

In the cat[215,227] and the rhesus monkey[148] the fibers descending from the brainstem to the spinal cord terminate mainly in the intermediate zone. On the basis of their modes of distribution within the spinal gray they may be subdivided into two groups:

a) a ventromedial group of brainstem pathways which descends in the core of the brainstem and in the ventral and ventromedial funiculi of the spinal cord and which terminates in the ventromedial parts of the intermediate zone, and

b) a lateral brainstem pathway which descends laterally in the brainstem and in the dorsolateral funiculus of the spinal cord and which terminates in the dorsolateral part of the intermediate zone.

The *ventromedial brainstem pathways* to one side of the spinal cord are derived from various cell groups: the ipsilateral interstitial nucleus of Cajal, the deep layers of the contralateral superior colliculus, the ipsilateral and contralateral medial vestibular nuclei, the ipsilateral lateral vestibular nucleus and the ipsilateral pontine and medullary reticular formation[80,148,215,227,277]. The mesencephalic reticular formation does not distribute fibers to the spinal cord[214] [280] but it is extensively interconnected with the pontine and medullary reticular formation and therefore can be considered to be also a part of the ventromedial system[145]. The nuclei from which the ventromedial pathways originate are also extensively interconnected, and some have projections to eye muscle nuclei[12,46,47,54,131,150,168,174,175,181,205,226,234,245,276,277]. Fibers from these cell groups traverse the medial parts of the brainstem and descend in the ventral and ventrolateral funiculi of the spinal cord and terminate in the ventromedial parts of the intermediate zone, to some extent bilaterally (the ventral part of lamina VII, and lamina VIII, Fig.2-1 A).

The *lateral brainstem pathway* contains fibers derived mainly from the magnocellular red nucleus[56,62,145,149,184,215] which decussate in the mesencephalon. The pathway descends laterally in the brainstem just ventral to the spinal trigeminal complex into the lateral funi-

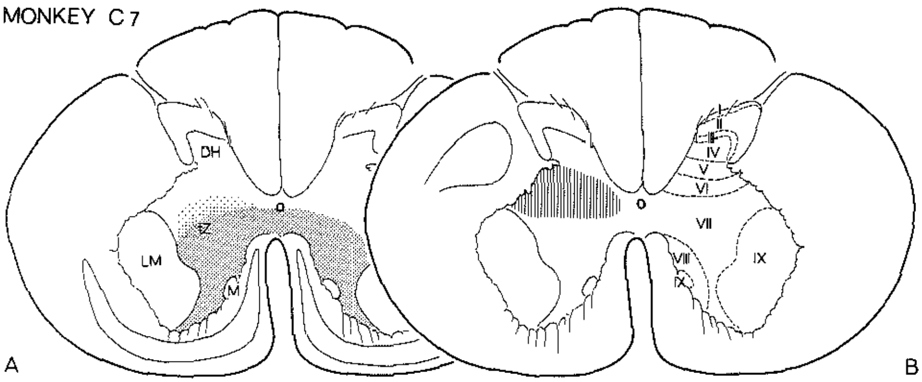


Fig. 2-1. Semidiagrammatic representation of the termination of the descending brainstem pathways in the spinal cord of the monkey.
A. The ventromedial group of brainstem pathways descends in the ventral and ventromedial funiculi and terminates in the ventromedial part of the intermediate zone (IZ) to some extent bilaterally (⁚⁚⁚⁚⁚).
B, left side. The lateral brainstem pathway descends in the lateral funiculus and terminates in the dorsolateral part of the intermediate zone unilaterally (||||||||).
No terminations are found anatomically in either the lateral (LM) or the medial (M) motoneuronal cell groups. After Kuypers et al.[148]
B, right side. Rexed's[239] laminae as defined in the cat are here indicated for the monkey.
DH, dorsal horn.

culus of the spinal cord and terminates in the dorsolateral part of th the intermediate zone (the lateral parts of laminae V and VI, and the dorsolateral part of lamina VII),unilaterally (Fig.2-1 B).

The differential relationship between the two groups of descending brainstem pathways and the motoneurons of different groups of muscles may be clarified by determining more precisely the fiber connections of the interneurons in the different parts of the intermediate zone upon which those pathways converge.

Cells in the spinal intermediate zone send their axons into the funiculi[178,246] in which they ascend or descend before re-entering the gray matter. Most of these *propriospinal* connections are short and travel only over a distance of a few spinal segments;however, long propriospinal systems interconnecting the enlargements have been demonstrated[45,106].

Studies in the cat have shown that cells in the ventromedial parts of the intermediate zone send their axons into both the ipsilateral and the contralateral ventromedial funiculi. Cells in the central intermediate zone send their fibers into the ipsilateral ventral and ventrolateral funiculi[177,192,273] (Fig. 2-2 A).

Cells in the dorsolateral part of the intermediate zone project into the ipsilateral dorsolateral funiculus[136,177,192,273] (Fig.2-2 A). This is in agreement with some physiological findings[29,138].

In the cat, the short propriospinal fibers which travel over a distance of only a few segments in the ventral and lateral funiculi show a contrast in their distribution within the gray matter. This difference is especially prominent in the enlargements[243,273].

Fibers from the ventromedial and ventral funiculi are distributed to the ventromedial part of the intermediate zone, to some extent bilaterally, and to the ipsilateral medial motoneuronal cell group and the ventral parts of the lateral motoneuronal cell group. The long proprio spinal fibers which run in the ventrolateral funiculus[186] show a similar distribution pattern[45] (Fig. 2-2 B,left side).

Fibers in the lateral funiculus project to the ipsilateral dorsolateral part of the intermediate zone and the dorsal part of the ipsilateral lateral motoneuronal cell group[243,273] (Fig. 2-2 B,left side).

So far, no anatomical data are available concerning the organi-

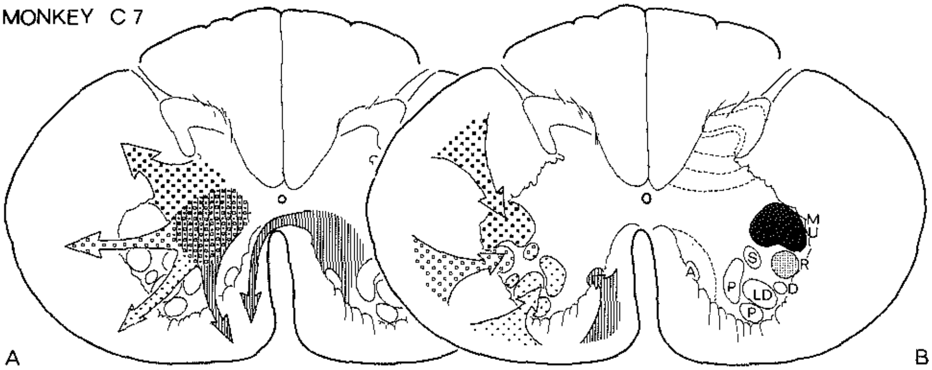


Fig. 2-2. Semidiagrammatic representation of the origin and distribution of short propriospinal connections. Drawn for the monkey, based on findings in the cat[192,243,273].

A. Cells in the dorsolateral part of the intermediate zone send their axons into the lateral funiculus (■ ■ ■), while cells in the ventromedial part send fibers to the ventromedial funiculus (|||||||||). Cells in the central parts send their axons into the ventrolateral (□ □ □) and ventral (● ● ●) funiculi. Note that the ventromedial funiculus (|||||||||) also contains fibers from cells in the contralateral ventromedial intermediate zone (|||||||||).

B,left side. Fibers running in the lateral funiculus are preferentially distributed to the dorsolateral part of the lateral motoneuronal cell group (■ ■ ■),while fibers in the ventrolateral and ventral funiculi terminate more ventrally in this group (□ □ □ ,● ● ●). Fibers from the ventromedial funiculus are directed to the medial motoneuronal cell group (|||||||||).

B,right side. Somatotopic organization of the motoneuronal cell groups in the C 7 segment of the monkey[45,238,267].

A,axial muscles along the vertebral column;LD,latissimus dorsi;MU, median and ulnar nerves;P,pectoral muscles;R,radial nerve;S,suprascapular nerve.

Motoneurons of physiological flexors (black) are situated more dorsally than those of physiological extensors (stippled).

zation of the short propriospinal connections in the monkey although some of the long systems show a mode of termination in the intermediate zone which is similar to that found in the cat[45]. For this reason, fig. 2-2, which shows the cat data on the organization of the short propriospinal systems transposed upon a cross-section of the monkey spinal cord, must be regarded as hypothetical until more data are known for this animal.

The *motoneuronal cellgroups* are somatotopically organized[45,172,238,241,256,267,272]. The motoneurons of the medial group send their axons to axial muscles along the vertebral column. Cells in the ventral part of the lateral motoneuronal cell group innervate the muscles of the hip and shoulder girdle and those of the more proximal parts of the extremity (e.g., in fig.2-2 B, at the level of the C 7 segment in the monkey, motoneurons innervating the pectoral muscles, latissimus dorsi, deltoid and some of the scapular muscles are found in this part of the cell group). The dorsal ans dorsolateral parts of the lateral group which are most prominent in the enlargements and most developed in the higher primates, contain the motoneurons of the intrinsic muscles of the limbs and the distal extremity muscles, i.e. those of hand and fingers (fig.2-2 B, median, ulnar and radial nerves). Moreover, motoneurons of physiological flexors (fig. 2-2 B, median and ulnar nerves) are found dorsal to those of physiological extensors (fig. 2-2 B, radial nerve).

The anatomical data may be summarized as follows:
The *ventromedial brainstem pathways* terminate in the ventromedial parts of the spinal intermediate zone among interneurons which are preferentially connected with motoneurons of axial muscles and of girdle and proximal extremity muscles.
The *lateral brainstem pathway* terminates in the dorsolateral part of the intermediate zone among interneurons which are preferentially connected with motoneurons of muscles intrinsic to the limb and distal extremity muscles.
Taken together the data presented above suggest that the ventromedial brainstem pathways would be especially concerned with the steering of body and integrated limb-body movements and with maintaining posture. In contrast, the lateral brainstem pathway would be more involved in guiding movements of a single limb, in particular its more distal parts

Numerous physiological data provide support for a distinction between the two groups of brainstem pathways.

In the cat, fibers from the medullary reticular formation and from the lateral vestibular nucleus influence interneurons located mainly in the ventromedial part of the intermediate zone[80]. Interneurons in the dorsolateral part of the intermediate zone are facilitated by the rubrospinal tract[23,29,137,138,293].

Fibers from the lateral vestibular nucleus facilitate extensor motoneurons and inhibit those of flexor muscles[113,170,305,307],while the rubrospinal tract facilitates especially flexor motoneurons through interneurons in the dorsolateral part of the intermediate zone[124,137,293]. The lateral vestibulospinal tract also plays an important role in proximal reflex movements[179]. The medial vestibulospinal tract has an inhibitory action upon neck motoneurons[306] and possibly also upon back motoneurons[308]. Tectospinal fibers influence the motoneurons of several neck muscles[14]. Fibers from the mesencephalic tegmentum via a polysynaptic pathway exert an influence upon proximal extremity muscles[15]. Long propriospinal pathways in the ventrolateral funiculus activate proximal extremity muscles and play an important role in the regulation of locomotion[186]. Pathways in the dorsolateral funiculus to the dorsolateral part of the intermediate zone are especially involved in distal reflex movements and facilitate motoneurons of distal extremity muscles[18,79,123,124,235].

Recently, monosynaptic connections of vestibulospinal and reticulo spinal fibers with motoneurons of proximal extremity muscles have been demonstrated physiologically in the monkey[252,253,255]. In contrast, rubrospinal fibers were found to influence monosynaptically motoneurons of distal extremity muscles[254]. 1)

The physiological data as the anatomical evidence suggest that the ventromedial brainstem pathway is primarily involved in guiding

1) No such monosynaptic connections have been demonstrated anatomically. This would suggest that these connections are either limited in number, or the synapses are located on motoneuronal dendrites which extend into the intermediate zone beyond the limits of the motoneuronal cell group proper.

axial and proximal extremity movements, while the lateral brainstem pathway is especially concerned with distal movements of the limb.

The *corticospinal fibers* in the monkey are distributed to the same area of the intermediate zone as are the brainstem pathways. Fibers from one cerebral hemisphere terminate in the dorsolateral part of the intermediate zone (the lateral parts of laminae V and VI, and the dorsolateral part of lamina VII) contrlaterally but in the ventromedial part of the intermediate zone (the major part of lamina VII) both contralaterally and ipsilaterally (Fig. 2-3).

In addition, fibers are distributed to the nucleus proprius of the dorsal horn contralaterally and a substantial amount of fibers terminates in the contralateral motoneuronal cell group among motoneurons of distal extremity muscles[142,145,167].

The fibers to the dorsal horn are derived from the postcentral gyrus [142,167] and are involved in the modulation of sensory transmission[1,13, 85,193] while those to the intermediate zone are derived from the precentral gyrus and would especially influence motoneurons[142,145,167, 228]. The fibers to the motoneuronalcell group are also derived from

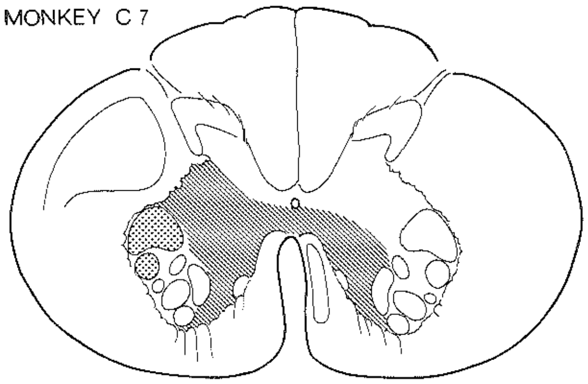


Fig. 2-3. Semidiagrammatic representation of the termination of the precentral component of the corticospinal tract in the monkey. Fibers from the precentral motor area are distributed to the dorsolateral part of the intermediate zone unilaterally but to its ventromedial part bilaterally ( ).

In addition, fibers are distributed to motoneurons of distal extremity muscles ( ). Based on data from Kuypers and Brinkman[147].

the precentral gyrus, especially its caudal part[17,147] (Fig.2-3) and make direct monosynaptic connections with motoneurons of distal extremity muscles[17,28,60,229,231].
Thus the corticospinal tract on the basis of its termination area within the spinal gray encompasses not only the medial and lateral components of the brainstem pathways -which would steer whole body and integrated limb-body movements, and movements of the individual extremity, especially its distal parts, respectively- but also a third group of fibers terminating directly upon motoneurons of distal extremity muscles which would be of special importance for the execution of discrete movements of the most distal part of the extremity.

This notion is corroborated by the fact that such direct corticomotoneuronal fibers are found in increasing numbers in monkey, baboon, chimpanzee and man[142,145,228,249], species which show a similar in increase in manipulative dexterity.
No such fibers are present in the rat[48,110], opossum[176], cat[215], dog[53] or tree shrew (*Tupaia glis*)[127] animals which do not manipulate things. Nor are they present in great abundance in prosimian primates like the slow lori (*Nycticebus coucang*)[41] or the potto (*Periodicticus potto*)[127],which animals use their hand as a whole in prehension[30,31], or even in a New World simian like the squirrel monkey (*Saimiri sciureus*)[118], a species which also does not display discrete movements in its hand and fingers but rather uses it as a whole, although some finer movements have been observed in this animal e.g. in grooming[31].
In contrast to these animals, the raccoon (*Procyon lotor*) a carnivore which displays a great variety of manipulatory movements when handling its food does show a substantial amount of terminal degeneration in the lateral motoneuronal cell group after a lesion of the motor cortex[53,228]. The data presented above thus suggest that the direct corticomotoneuronal connections are of primary importance for the execution of fine fractionated movements of hand and fingers[230]. Several anatomical and behavioral experiments further support this notion.

In the infant rhesus monkey, no degeneration pattern similar to that found in the adult animal among motoneurons of distal extremity muscles can be demonstrated after a precentral lesion until the monkey is about 8 months of age[143]. It seems that the direct connections are only gradually established during the first six months of postnatal life[73,143]. Infant monkeys do not show discrete hand or finger movements but rather use the hand as a whole.1) Fractionation of distal movements as exemplified by the execution of relatively independent finger movements only gradually develops;moreover, this development is dependent on the corticospinal tract[154].

Functional organization of the descending pathways in the monkey. Lawrence and Kuypers[155,156] have investigated the role of the corticospinal and descending brainstem pathways in motor behavior in the monkey by means of selectively interrupting these tracts either alone or in combination.

In a first series of monkeys the corticospinal (pyramidal) tracts were sectioned bilaterally. After a suitable recovery period, these animals were still capable of a wide range of movements:they could sit, walk, run and climb, and used their hands to pick up food morsels. However, when presented with a small piece of food in a small well, they showed a persistent motor deficit. An intact monkey will use its index finger to pry the piece of food out of the well, keeping the other fingers flexed and out of the way, and pick up the piece between index finger and thumb.2) Pyramidotomized monkeys lacked this ability and used their hand as a whole, closing all fingers in concert. This lack of relatively independent finger movements persisted throughout the animals' survival periods which lasted up to 12 months. It is another indication of the importance of the corticospinal tract for the execution of highly fractionated movements[155].

In a second experiment,the role of the descending brainstem pathways

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1) For this reason, learning experiments in baby rhesus can only be done when using a maze i.e. a whole body response to show the appropr appropriate response to a discrimination task since the adult test design requires more elaborate motor performance[315].

2) This opposition of thumb and index finger has been called *precision grip*, as opposed to *palmar* or *power grip*, a prehensile movement of the whole hand[203].

in the regulation of movements has been investigated.
In a number of monkeys, first the pyramidal tracts were sectioned bilaterally thus eliminating the direct corticospinal influence. Subsequently, in some of these animals the ventromedial brainstem pathways were interrupted by making a transverse cut in the core of the lower brainstem. Postoperatively, the animals showed a striking picture:they could not right themselves, sit up, or walk. Even when they eventually regained the ability to sit up, they frequently toppled over or when trying to walk, ended up in the wrong corner. They were unable to extend their arms and reach for food. However, when strapped into a monkey chair with the body properly supported, they would take food when it was brought close to their hands, using their hands in much the same way as an otherwise intact pyramidotomized monkey. Interruption of the ventromedial brainstem pathways thus seems to affect preferentially the axial and proximal extremity musculature, and leave more distal extremity movements relatively undisturbed.
A strikingly contrasting picture was observed when in pyramidotomized animals the lateral brainstem pathway was severed. Immediately after the operation these monkeys could right themselves, walk, run and climb. They could also reach out for food, fully extending their arm. However, they were unable to close their fingers around the food and pick it up. Instead, they made sweeping movements of the arm trying to catch the food between the extended inert fingers of the affected hand. These findings suggest that the lateral brainstem pathway is primarily involved in the guidance of the more distal parts of the extremity[156].

From these functional findings it may be concluded that the *ventromedial brainstem pathways* are particularly concerned with the regulation of whole body and integrated limb-body movements, and of synergistic movements of the whole limb, and with maintaining posture. The *lateral brainstem pathway* adds further resolution and provides the capacity for individual movements of the extremity in particular its distal parts. The *corticospinal tract* further amplifies these controls and, probably by way of its direct connections to motoneurons, provides the capacity for a high degree of fractionation of movements, such as relatively independent movemenst of the fingers.

In the present study the validity of these conclusions has been examined *without* interruption of the descending pathways i.e. by investigating the motor control exerted from one half of the brain over the movements of the ipsilateral as compared to those of the contralateral extremity. This was prompted by the fact that the contralateral and ipsilateral fiber connections from one half of the brain to the spinal cord are directed to different portions of the spinal gray matter (Fig. 2-4).

The fibers from one half of the brainstem and from one cerebral hemisphere maintain direct connections to both the dorsolateral and the ventromedial parts of the intermediate zone contralaterally, but mainly to the ventromedial part ipsilaterally[148,215]. Cortical fibers also terminate directly on motoneurons of distal extremity muscles contralaterally[17,142,145,167,229]. Indirect connections from each hemisphere to the spinal intermediate zone also exist, which are established by way of the descending brainstem pathways. These indirect connections follow roughly the same pattern as the direct ones, since each hemisphere is connected to cells of origin of the lateral brainstem pathway ipsilaterally, but to those of the ventromedial brainstem pathways bilaterally[149] (Fig. 2-4).

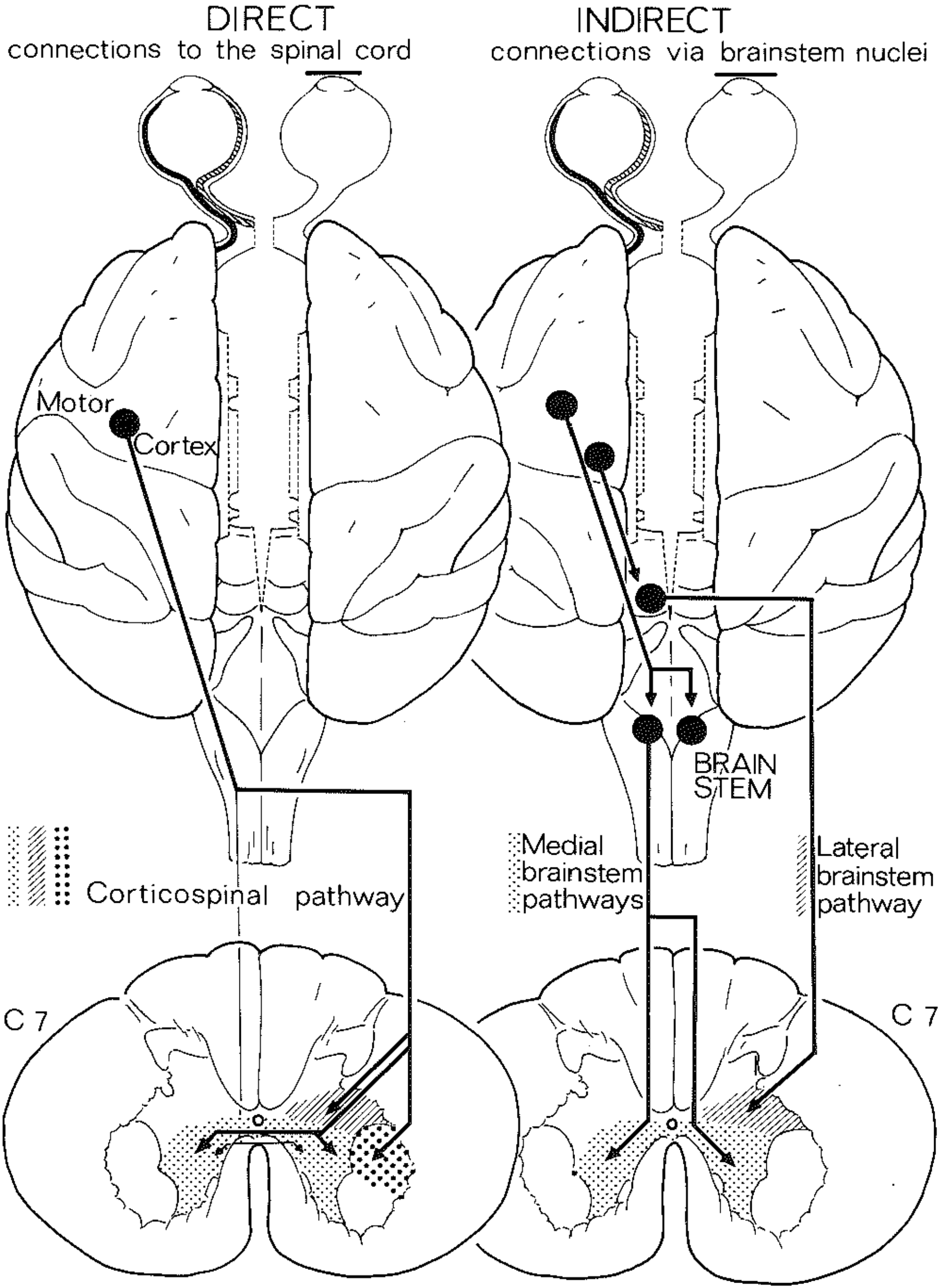
One half of the brain is therefore connected to both the ventromedial and the dorsolateral parts of the intermediate zone and to motoneurons of distal extremity muscles contralaterally but only to the ventromedial part of the intermediate zone ipsilaterally (Fig. 2-4).

In the light of the findings of Lawrence and Kuypers[155,156] this implies that each half of the brain has full control over arm, hand and finger movements contralaterally but controls mainly arm movements ipsilaterally.

This hypothesis has been tested in split-brain monkeys. In such animals the visual input was restricted to one half of the brain by covering one eye. The visuomotor control exerted by the seeing half of the brain over the contralateral and ipsilateral arm and hand was compared by studying the visually guided movements of the respective extremities in reaching out and picking up pieces of food.

To minimize tactile guidance of hand and fingers in retrieving the food pellets, a specially designed test board was used on which the food was visible but not palpable. An attempt was made also to assess the role of the descending motor pathways from the non-seeing hemisphere in guiding movements of the arm ipsilateral to the open eye by studying the movements of split-brain monkeys with unilateral pericentral and frontal cortical ablations. Some data on the role of the indirect connections to the spinal cord were obtained in split-brain monkeys after either a bilateral pyramidotomy or a bilateral precentral cortical ablation.

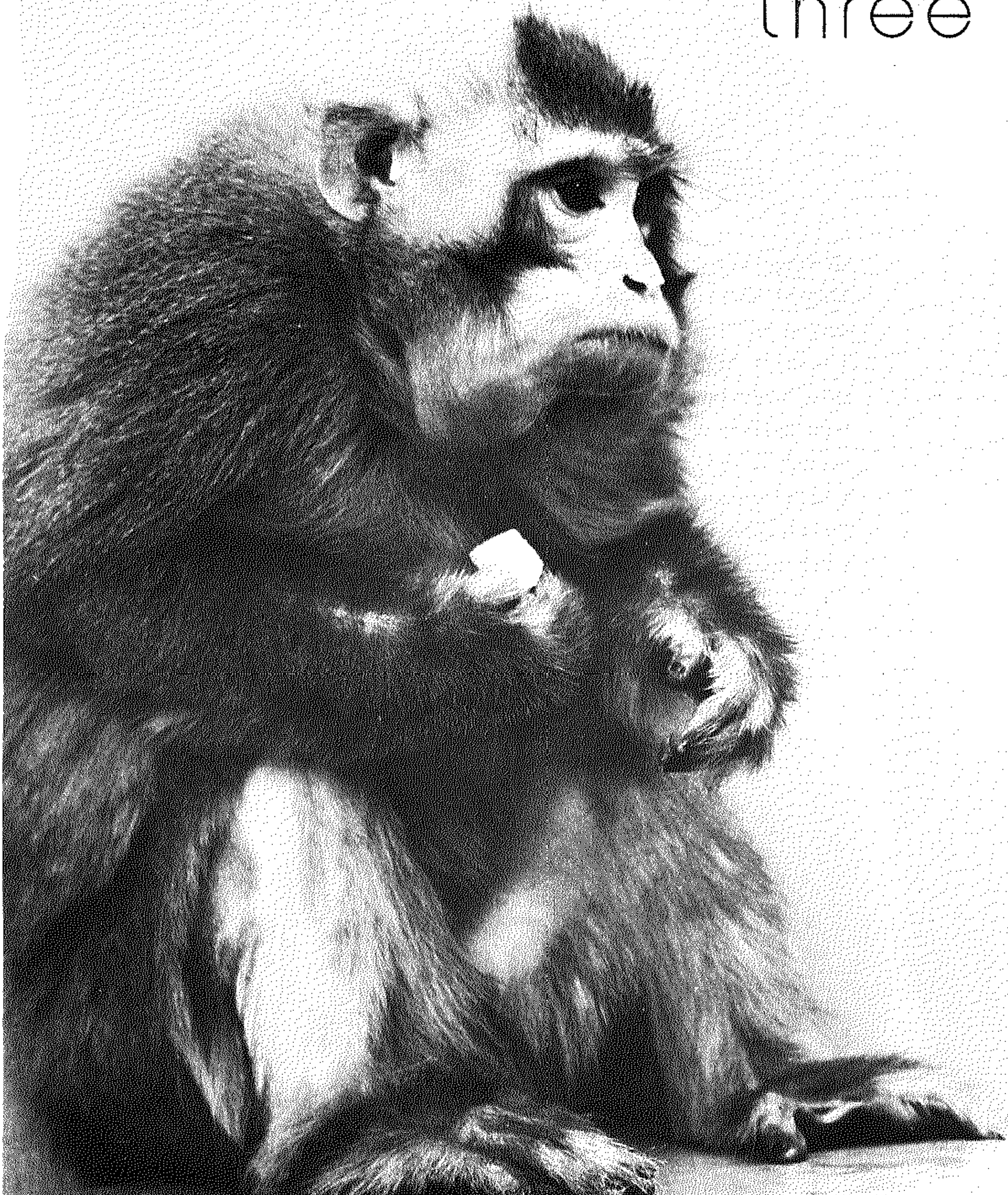
Fig. 2-4. Diagrams of the descending connections from the cerebral cortex and the brainstem to the spinal cord in the monkey. Note that one half of the brain is connected directly and indirectly to the dorsolateral part (hatched) and the ventromedial part (stippled) of the intermediate zone and to motoneurons of distal extremity muscles (dots)contralaterally but mainly to the ventromedial part of the intermediate zone ipsilaterally.



Corticospinal (pyramidal) tract

Descending brainstem pathways

chapter three



An inventory is given of the monkeys used in this study and of the kind of operations they received. The use of general hypothermia during split-brain surgery is discussed.
A special test board is described for assessing the visual control of relatively independent finger movements in the monkey. On this board, food pellets are visible but not palpable and the animal is thus forced to rely mainly on vision to retrieve the food.
A brief account of the testing procedure is given .
The histological techniques used to verify the extent of surgery are given at the end of this chapter.

Chapter III: Monkeys, materials and methods.

16 Rhesus monkeys (*Macaca mulatta*) were used in this study, 15 males and 1 female. All were juvenile or adolescent animals except for one adult male (case 15). One Java monkey (*Macaca irus*), an adult male (case 6) was also used. The animals were housed individually. Water was provided *ad lib.* During testing periods, the animals were kept on a reduced food ration schedule.

In most of these monkeys the optic chiasm, corpus callosum, and the anterior, habenular, posterior and tectal commissures as well as the massa intermedia thalami -which in monkey in contrast to man is a structure of substantial size- have been transected in the midline. In most of the animals the commissures were cut in a single operation while in some others it was done in several steps (Fig.3-1). In three animals the posterior part of the corpus callosum, the splenium, was left intact. In two of these animals, the splenium was cut in a second operation.

Split-brain surgery was performed using a dorsal approach [185,262] A right frontoparietal parasagittal boneflap was turned extending from the orbital ridge rostrally to a point about 2 cms rostral to the lambdoid fissure caudally. The bone overlying the superior sagittal sinus was carefully removed with the aid of a rongeur to avoid exces bleeding. The dura was then incised and turned aside over the midline. If possible, the large bridging veins to the sinus were left intact. The hemispheres were gently separated by means of a special retractor, the corpus callosum was visualized with the aid of a binocular operating microscope and split in the midline using gentle suction and fine glass pipettes. The anterior commissure was identified and cut and the anterior part of the third ventricle entered to find the optic chiasm. This structure was also transected. In most animals, the massa intermedia of the thalamus was subsequently split;the entrance to the aquaduct was visualized and the habenular, posterior and tectal commissures cut. The hippocampal commissure which cannot be clearly distinguished from the overlying corpus callosum was transected in all animals. After the operation the dura was closed with interrupted silk stitches the bone flap was returned and the muscle and skin closed in anatomical

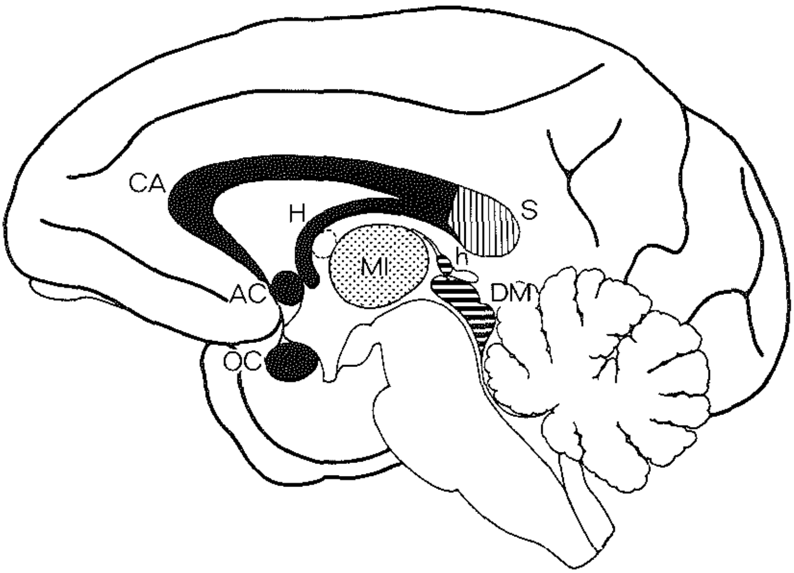


Fig. 3-1. Medial aspect of a monkey brain showing the various structures sectioned together or in combinations.
AC:anterior commissure;CA:corpus callosum;DM:dorsal mesencephalic (posterior and collicular) commissures;H:hippocampal commissure;h: habenular commissure;MI:massa intermedia thalami;OC:optic chiasm; S:splenium of corpus callosum.

layers. Antibiotics were routinely given postoperatively;the animals also received 10 mgs/kgm body weight of pentobarbital IM twice a day to prevent convulsions and 0.04 mgs/kgm body weight of dexamethason IM twice a day to prevent cerebral edema. These drugs were given for 5 days after which period the doses were gradually diminished.

Two animals (cases 1 and 2) were operated under nembutal anesthesia and urea was used to reduce the brain volume. In order to prevent the excessive postoperative edema, all subsequent operations were performed under general hypothermia[35,40,157].

For this procedure, the animal was pre-anesthetized with intravenous Penthotal®,intubated, paralyzed with Flaxedil®and artificially respirated using an infant respirator with a mixture of oxygen, nitrous oxide and metoxyflurane (Penthrane®). The superficial femoral artery was canulated to measure blood pressure directly and a thermocouple was placed in the esophagus. Respiratory CO_2 and the electrocardiogram were monitored throughout the operation.

The animal was cooled by placing plastic bags containing ice cubes on its body. The bags were removed at a central temperature of about 29.5 centigrades. Usually, the animal's temperature would then drop another centigrade and stabilize itself at about 28 centigrades. Lower temperatures are not advisable[157]. After the operation the animal was slowly rewarmed using a homeothermic blanket wrapped around its body. The blanket's temperature never exceded 40 centigrades. If necessary, small doses of aramin were given intravenously to maintain adequate blood pressure (about 90 mms Hg). Spontaneous breathing would usually return 4-6 hours after the administration of Flaxedil; if not, small quantities of atropin and neostigmin were given intravenously.

The animal was returned to its home cage when its temperature had reached a level of approximately 34 centigrades and when it was breathing regularly and making spontaneous righting movements.

Using this procedure signs of elevated intracranial pressure caused by postoperative edema were minimal or even absent (cases 1 and 2 which had been operated under nembutal anesthesia with urea as a means of reducing the brain volume, temporarily stopped eating and became less active on the 3rd to 5th postoperative days). Moreover, the rate of cerebral metabolism is greatly reduced with lower temperatures and light pressure on the hemispheric tissue i.e. when spreading the hemispheres to reach the corpus callosum is tolerated for longer periods without causing ischemia.

Behavioral testing was usually started two weeks after the split-brain operation. Most animals had been observed preoperatively in their home cages or when sitting in an examining chair. Special attention was paid to their motor performance and their possible hand preferences in order to be able to optimally evaluate their postoperative performance.

Closure of one eye was achieved by simply taping the eye shut. This method was preferred to the use of opaque occluders or black contact lenses since it proved to be easier this way to switch eyes frequently without much discomfort or excitement for the animal.

At first, all four possible eye-hand combinations (contralateral combinations: left eye-right hand, and right eye-left hand, as well as ipsilateral combinations: left eye-left hand, and right eye-right hand) were studied in simple food retrieving tasks like taking food from a table-top, forceps or the experimenter's hand.

In order to minimize tactile guidance of movements, especially of the ipsilateral eye-hand combinations, a specially designed test board was used in further assessing the animal's visuomotor capacities. On this board, the food was visible but not palpable and it thus forced the animal to rely mainly on vision to retrieve the food. The board was painted black to provide contrast with the light colored food pellets and contained randomly distributed food wells which would just accomodate a food pellet. Towards each well, two or three radially oriented grooves, 5 mms wide, were cut through which the monkey's

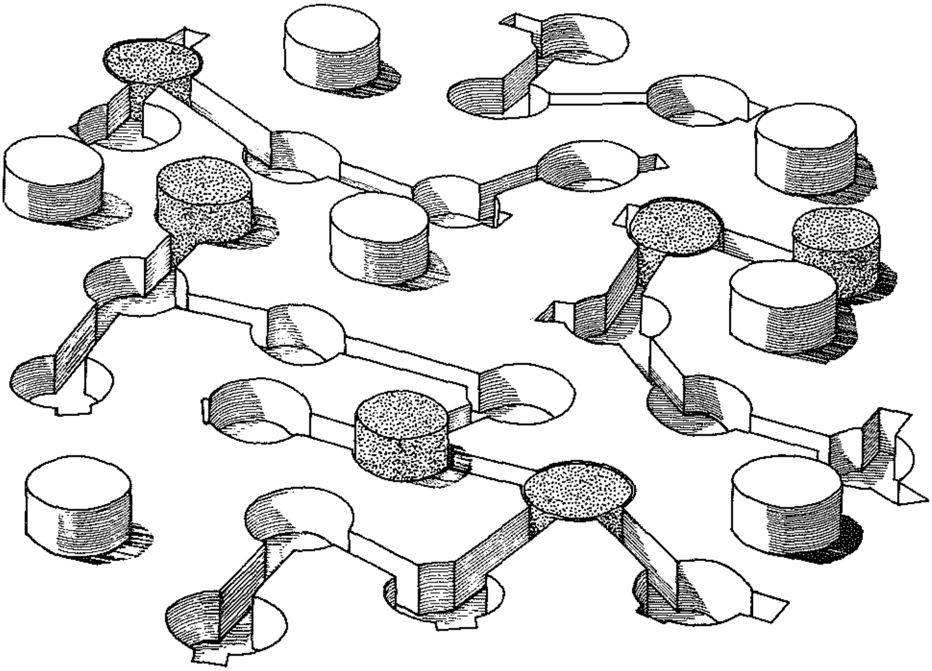


Fig. 3-2. Diagram of the test board. Large and small pellets (stippled) are shown. Note that the small pellets are flush with the board's surface and presumably are hard to detect using tactile guidance;note also knobs used as false tactile cues when large pellets are used.

individual fingers could dislodge the pellet (Fig. 3-2). Either small or large pellets were placed into the wells, one at each trial. The surface of the small pellets was flush with the board's surface and these pellets were very hard to detect without the aid of vision for a blindfolded human subject. To provide false tactile cues when large pellets were used, knobs were affixed to the board's surface between the wells.

The animal with one eye closed and both arms restrained was presented with a food pellet on the board. Subsequently, one arm was released and the animal had to try and retrieve the food. In order to further eliminate tactile cues given to the extremity by restraining it, in later test sessions food pellets were placed under a lid covering the board's surface, and the extremity which was tested remained free. The lid could be pulled aside to disclose the site of the pellet to the animal which would then reach out with the unrestrained limb.

The split-brain monkeys were studied for periods ranging from 2½ to 12 months. Subsequently, in seven animals (cases 3-8,and case 14) unilateral pericentral and frontal cortical ablations were made using subpial suction. These animals were studied on simple food retrieving tasks and on the board for periods ranging from 3-5 months.

In one animal (case 1) a unilateral lesion was made in the right ventral quadrant of the spinal cord at the C 2 level. After recovery from this operation the right pyramidal tract was sectioned using a parapharyngeal approach[155].

In two other split-brain animals (cases 2 and 15) the pyramidal tracts were sectioned bilaterally.

In two split-brain monkeys (cases 16 and 17) bilateral lesions were made in the precentral gyrus. The lesions included the leg and hand areas[309] and part of the rostrally adjoining frontal areas but spared the supplementary motor cortex on both sides as well as the face areas bilaterally.

In some animals an attempt was made to interrupt selectively the rubrospinal tract in the medulla oblongata using either an electrode to make the lesion or a small knife.

The various operations and the interval between them or the sur-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vival time, as well as the structures spared or damaged during the surgery are listed in Tables IV-I, IV-II and VI-I in the text.

The movements of the animals were recorded on film. To analyze fast movements, slow motion pictures (60 frames/sec.) were taken.

Histology.- Cases 15,16 and 17 are still alive and kept for further study. Upon completion of the experiments, the rest of the animals were deeply anesthetized with nembutal and perfused through the heart with saline followed by 10% formalin. The brains were taken out and embedded in celloidin or gelatin-albumen[258] for frozen sections and cut at a thickness of 40 u in the stereotaxic plane. Every 5th or 10th section was stained with cresylviolet or Luxol Fast Blue[134]. At the level of the optic chiasm and the tectum every section was examined. The cortical lesions were reconstructed on glass slides in order to assess their exact extent. The split-brain surgery was complete in all animals. In two animals (cases 1 and 4) the commissure of the inferior colliculus had remained intact and in one animal (case 7) a small portion of the massa intermedia had remained uncut.

In most animals, there was slight admage to the right cingulate gyrus, and one fornix had been partially or totally transected. In cases 1 and 2 which had been operated with the use of urea, one cingulate gyrus had been completely destroyed.

Fig. 3-3 shows the histology of one of the animals (case 7)

Fig. 3-3. Photomicrographs of three brain sections of case 7 showing the transection of the corpus callosum (cc), anterior commissure (ac), optic chiasm (oc), massa intermedia (mi), hippocampal commissure (h) and the commissure of the superior colliculus (sc). Luxol Fast Blue.

chapter four

In this chapter, the data obtained in this study on the nature of the visuomotor control exerted by one half of the brain over each of the two upper extremities in the split-brain monkey are presented.

The deficit in this control pertains mainly to the distal parts of the ipsilateral extremity.

The results thus seem to confirm the hypothesis that each half of the brain can steer arm, hand and finger movements contralaterally but mainly arm movements ipsilaterally.

Evidence is presented that the ipsilateral deficit is not due to the restriction of the visual fields in these monkeys.

Chapter IV: Cerebral control of contralateral and ipsilateral arm, hand and finger movements in the split-brain monkey.

Eleven rhesus monkeys were used for this part of the study. In all animals, the corpus callosum, optic chiasm and the anterior, hippo campal and habenular commissures as well as the massa intermedia and the dorsal mesencephalic commissures had been transected. In most of the animals this operation was done in one session but in some cases (7,8 and 9) it was done in several steps. This type of operation will be referred to as *complete commissurotomy*.
The animals are listed in Table IV-1. This table also indicates the time the animals have been studied after completion of the surgery, as well as the structures which were inadvertently spared or damaged.

Immediately after the operation and the recovery from anesthesia, the animals sat up, walked and climbed without signs of motor disturbance. The only abnormality observed was a tendency for bimanual behavior when the animals were approached with food:the two arms would reach out simultaneously for the food and show mirror motor responses (Fig. 4-1,cf 161,287,288). This behavior usually disappeared after a few days and the animals again reached out with one arm only, usually the arm preferred for this task before the operation. Conflict between the two arms was sometimes evident when the animal tried to take food from one hand into the other (most of the time the preferred) hand. This would then result in a brief tug of war (cf 287,288) between the hands, one trying to get the food, the other holding on to it. This struggle would immediately cease when the animal paid visual attention to what it was doing.1)
Other signs after complete commissurotomy were a pronounced dilatation of the pupils and extreme retraction of the upper eye-lids due to section of the posterior commissure (cf 55,222).
All these signs tended to diminish with time. After some time, the

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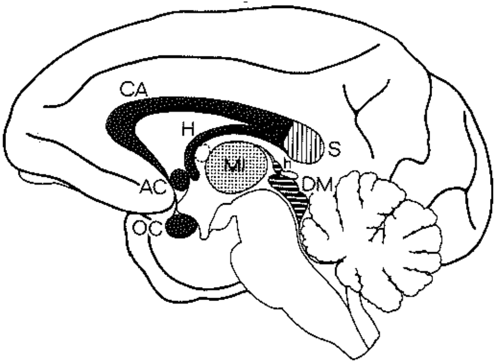
1) This only gave rise to difficulties on one occasion when an animal was returned to its home cage after testing and got its hands caught in one another behind its back. The monkey was unable to release the grip of either hand and had to be helped out by the experimenter.

TABLE IV-I. ANIMALS WITH COMPLETE COMMISSUROTOMY.
EXTENT OF THE TRANSECTION OF THE COMMISSURES AND
ADDITIONAL DAMAGE



CASE NO.	OPERATION				SURVIVAL /INTERVAL	STRUCTURES SPARED	STRUCTURES DAMAGED
1	●	◍	◌	⊜	4 months	Part commissure inferior colliculus	Left cing. gyrus Left fornix
2	●	◍	◌	⊜	4 months	–	Right cing.gyrus Right fornix
3	●	◍	◌	⊜	10 months	–	Right fornix
4	●	◍	◌	⊜	10 months	Part commissure inferior colliculus	–
5	●	◍	◌	⊜	12 months	–	Right fornix
6	●	◍	◌	⊜	10 months	–	Dorsal mesenc. tegm.;Ri.nucl.III
7·	●	◍	◌	⊜	1½ months	Part anterior massa intermed.	Right fornix
8·	●	◍	◌	⊜	2½ months	–	Local infarct ri. superior frontal + cing gyri
9·	●	◍	◌	⊜	6 months	–	Right fornix
10	●	◍	◌	⊜	4 months	–	Left fornix
11	●	◍	◌	⊜	4 months	–	Left fornix

In cases 7,8 and 9 marked with a dot the commissures were interrupted in steps. The survival periods are listed. AC,anterior commissure;CA, corpus callosum;DM,dorsal mesencephalic commissures;H,hippocampal commissure;h,habenular commissure;MI,massa intermedia;OC,optic chiasm; S,splenium of corpus callosum.

split-brain animals on casual observation could no longer clearly be distinguished from normal ones.

Behavioral testing was usually started two weeks after surgery, or even as soon as one week for the animals operated serially. The monkey was strapped into an examining chair which more or less immobilized its body but allowed free movements of the extremities. The animal was first tested with both eyes open. Subsequently, either one eye was closed and the various eye-hand combinations tested. Upon completion of this test, the animal was presented with food pellets in the special test board (see chapter III) with both eyes open and then with either eye closed.

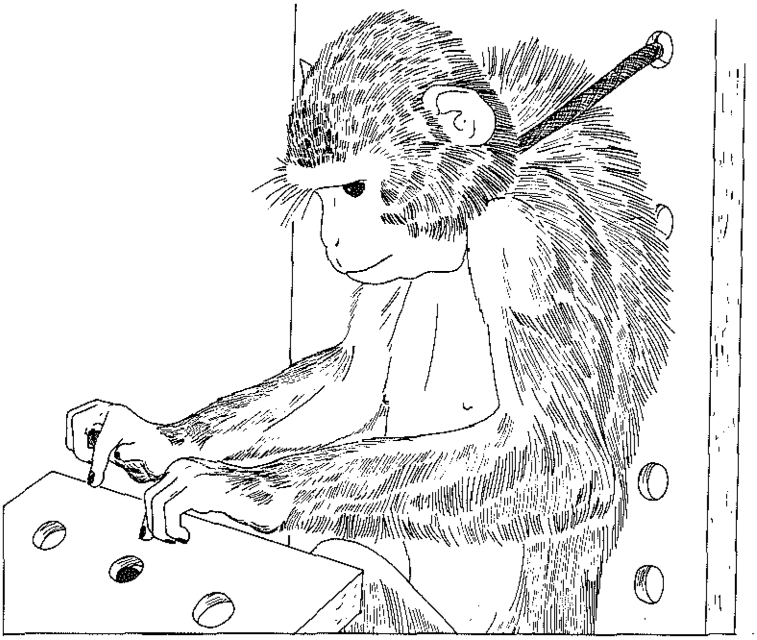


Fig. 4-1. Drawing from a film showing mirror motor responses in a split-brain monkey (case 4) reaching for a small food morsel (indicated in black) in a tray. Note bilateral extension of the index finger while the other fingers are kept flexed (precision grip posture).

a) *Retrieval of food pellets from forceps or from the examiner's hand.* When the animal with both eyes open was presented with small food pellets while one of its arms was restrained, the free arm and hand reached out and swiftly retrieved the pellet. When the pellet was presented in a forceps the monkey's hand in reaching was held slightly dorsiflexed with the thumb and fingers semiflexed.
With one eye closed and the food presented in the nasal,'seeing',half of the visual field, the motor performance of the extremity contralateral or ipsilateral to the open eye did not differ significantly although the animal when left the choice would consistently prefer the contralateral eye-hand combination. Both eye-hand combinations swiftly retrieved the pellet and displayed discrete movements of hand and fin-

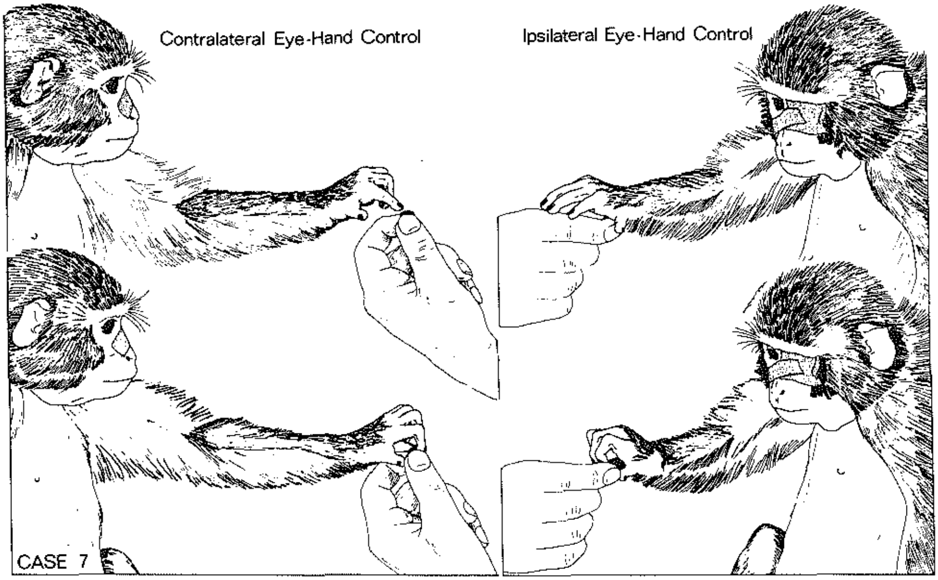


Fig. 4-2. Drawings from a film showing a split-brain monkey (case 7) retrieving a food morsel (black) from between the examiner's fingers with the contralateral hand and the ipsilateral one respectively. The contralateral hand in reaching assumes the precision grip posture (upper drawing,left) and seizes the pellet with the index finger and thumb. The ipsilateral hand in reaching does not assume this precision grip posture. The hand only assumes this posture after first having made contact with the pellet and the examiner's fingers.

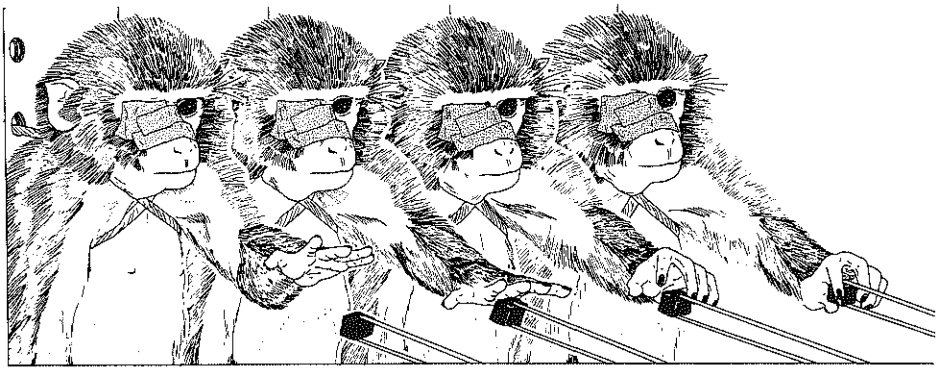


Fig. 4-3. Drawings from a film showing a split-brain monkey (case 9) reaching for food in a forceps with the left arm under guidance of the ipsilateral eye. Again, only after the hand has made contact with the food (second figure from the left) do discrete movements of hand and fingers occur (third and fourth figures from the left).

gers although sometimes the impression was gained that the ipsilateral hand in approaching the target showed more extension in wrist and fingers. Differences between the contralateral and ipsilateral hands were more pronounced when the monkey had to retrieve the food from the examiner's hand. The contralateral hand and fingers in reaching assumed the precision grip posture with the index finger and thumb extended and the other fingers kept flexed and out of the way (Fig. 4-2,upper left drawing). In contrast, the ipsilateral hand and fingers in reaching never assumed this posture;the thumb and fingers were all held in approximately the same way varying between animals from semi-flexion to full extension. As soon as the ipsilateral hand and fingers had touched the target they assumed the precision grip posture. Later the index finger and the thumb made a few exploratory movements along the tips of the examiner's fingers and then retrieved the pellet (Fig. 4-2,right half). Analysis of the films showed the same sequence of movements of the ipsilateral hand and fingers when food was presented in a forceps. The thumb and index finger retrieved the pellet after having made some exploratory movements along the tip of the forceps and the pellet (Fig. 4-3).

These differences between the movements of the contralateral and ipsilateral hand and fingers were observed in all animals of this group regardless of which of the two eyes had been closed.

The exploratory movements of the ipsilateral hand and fingers suggested that this hand in retrieving the pellets relies to a much greater extent on somato-sensory information than its contralateral counterpart. In addition, the relatively independent movements executed by the ipsilateral hand and fingers in seizing the pellet seemed to be elicited by somato-sensory information derived from the hand and fingers touching the food.

In this respect it is of importance to realize that in the split-brain monkey tactile information derived from the ipsilateral hand can freely recruit the full motor control from the non-seeing half of the brain over this hand, since the somato-sensory pathways which decussate in the spinal cord and the lower brainstem remain undamaged by the operation. This implies that in order to demonstrate the possible limitations of the motor control exerted from the seeing half of the brain over the ipsilateral hand, it is necessary to minimize tactile information to this hand. This was achieved by using the specially designed test board (see chapter III,Fig. 3-2).

b) *Retrieval of food pellets from the test board.*

When the animal with both eyes open was presented with a small food pellet in a food well, either arm brought the hand and fingers to the proper place on the board and the hand and fingers in reaching assumed the precision grip posture. When the hand had reached the board, the index finger was placed into one of the grooves leading to the food well and dislodged the pellet with the aid of the thumb. When one When one eye was taped shut and the pellet presented in the seeing half of the visual field, the contralateral hand and fingers removed it from the well in the way described above (Fig. 4-4,left column). However, the ipsilateral hand and fingers behaved quite differently. The arm brought the hand to the proper place on the board although the reaching movement seemed slightly less accurate than that of the contralateral arm. The way in which the ipsilateral hand and fingers were held in reaching for the food differed between animals and in several differed between the two hands, ranging from full extension of thumb and fingers to slight extension of the thumb combined with semiflexion of the fingers. The ipsilateral hand and fingers while reaching for the food never assumed the precision grip posture. This posture occured only after they had made contact with the board. Despite the appearance of the precision grip posture, however, the index finger was not placed into one of the grooves leading to the pellet and did not dislodge it from the well. Instead the ipsilateral hand and fingers began to explore the board's surface as if blind (Fig. 4-4,right). This behavior seemed not to be under strict visual guidance in contrast to the movements of the contralateral hand and fingers to which the animal seemed to be closely attending. During the exploratory movements of the ipsilateral hand and fingers the animal may not even be looking at what it is doing at all. Sometimes, the ipsilateral hand and fingers wandered into the blind visual field during the exploration. The animal then seemed to reorient itself towards the site of the pellet, the hand was brought back to the proper place and a new sequence of exploratory behavior would follow. Yet, this exploratory activity virtually never led to the retrieval of the small pellet and the hand was ultimately withdrawn from the board.

These differences in the behavior of the contralateral and ipsilateral arm, hand and fingers in retrieving small food pellets from the board were present in all animals and persisted throughout the survival periods ranging from four to twelve months.

c) *Retrieval of large pellets from the board.*

The animal with one eye closed was also presented with a *large* pellet in the board which protruded above the board's surface. Both the contralateral and the ipsilateral hand and fingers were brought to the food morsel and removed it from the board by means of relatively independent hand and finger movements. However, the relatively independent hand and finger movemnts of the ipsilateral extremity again only occurred after they had made contact with the pellet or the board.

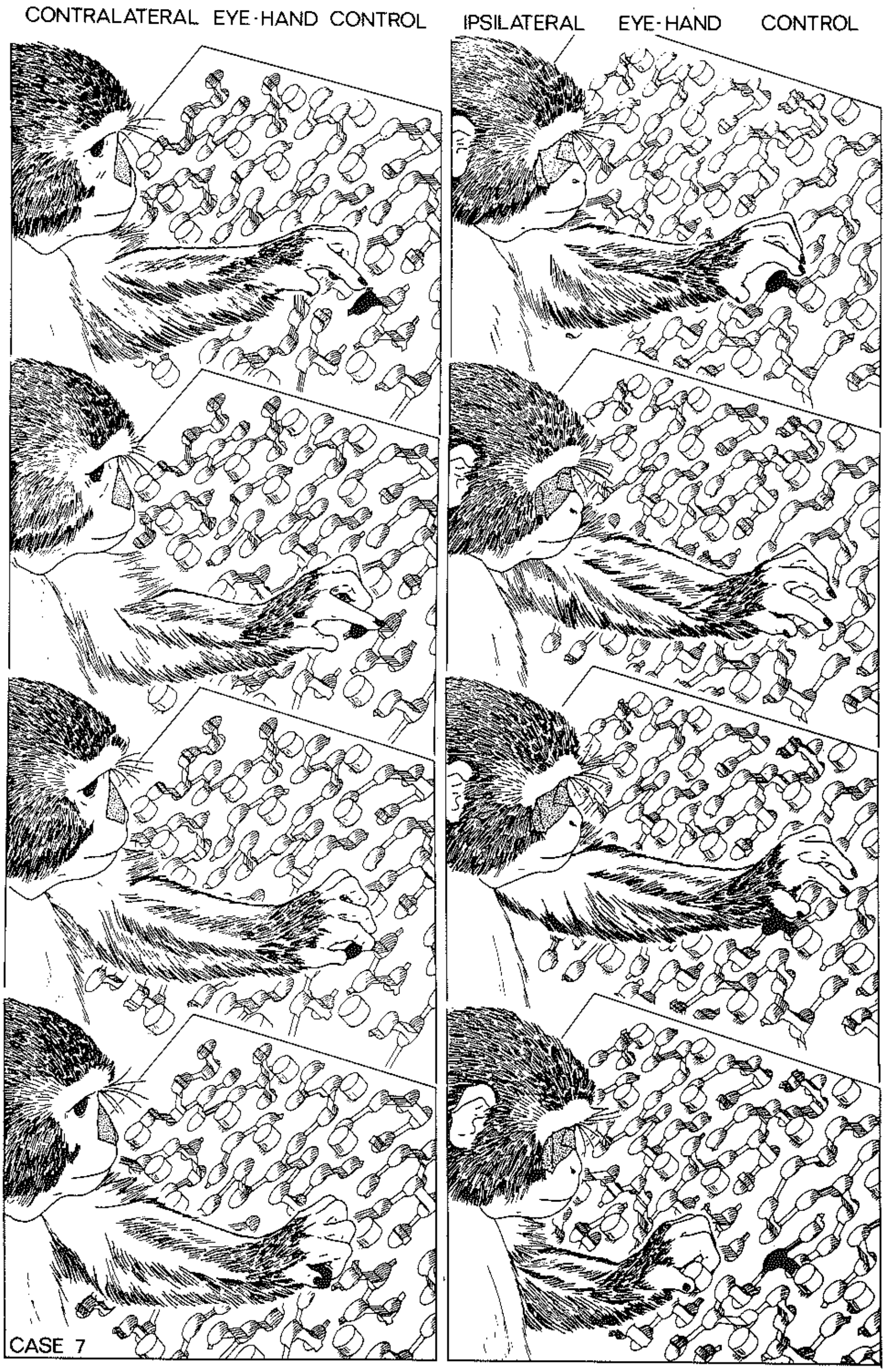
d) *Retrieval of pellets from the test board without vision.*

It has been suggested above that the behavior of the ipsilateral hand and fingers when the animal was presented with a small pellet in the test board looked as if the animal was blind[1] and it was unable to take out small pellets which were flush with the board's surface. Larger pellets protruding above the board's surface were removed from the board by the ipsilateral hand by means of relatively independent hand and finger movements which were presumably guided by the non-seeing hemisphere on the basis of somato-sensory information.

In order to assess the importance of vision in retrieving the small and large food pellets respectively, the animal was presented with a great many small and large pellets in the test board when blind folded. When one arm was released, it immediately brought the hand to the board. The hand and fingers then began to explore the board's surface and retrieved many of the larger pellets but seldom if ever retrieved any of the smaller ones which were flush with the board's surface and, without vision, apparently remained undetected.

[1] That the animal is in fact not blind but knows where the food is on the board, is proved by releasing the contralateral arm which will immediately reach out and retrieve the pellet, sometimes even pushing the ipsilateral hand out of the way. The animal can also bring the ipsilateral hand back to the target. Sometimes, however, the animal seems to have to reorient itself when doing this which suggests that it may temporarily 'loose sight' of the pellet.

Fig. 4-4. Drawings from a film showing the hand and finger movemnts of a split-brain monkey with a complete commissurotomy (case 7), taking a small food pellet (shown in black) from the test board under guidance of either eye.
Under guidance of the contralateral eye (left column) the hand and fingers in reaching out assume the precision grip posture (top drawing) and the index finger and thumb dislodge the pellet from the well.
Under guidance of the ipsilateral eye (right column) the hand and fingers do not assume the precision grip posture until the hand has touched the board. The hand is brought to the proper place but the pellet is not taken from the well. Instead, the hand and fingers explore the board's surface as if blind.


CONTRALATERAL EYE-HAND CONTROL

IPSILATERAL EYE-HAND CONTROL

The findings described above seem to confirm the hypothesis that one half of the brain by way of its descending connections can steer arm, hand and finger movements contralaterally but mainly arm movements ipsilaterally.

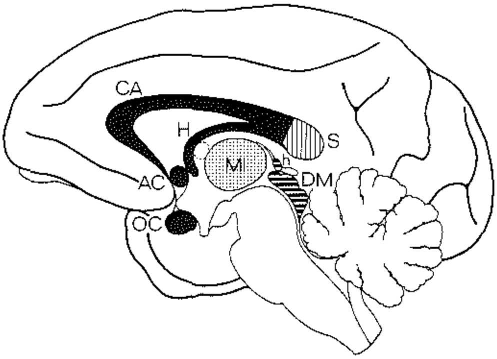
However, if the finger movements of the contralateral hand when dislodging a pellet from the well are as closely visually guided as they seem to be, the deficit observed in the ipsilateral hand and fingers may not be a motor deficit but rather be caused by the restriction of the visual field of the animal both because of chiasm section and of taping one eye shut. The ipsilateral arm reaches out from the blind half of the visual field into the seeing half. Due to the animal's restricted vision the hand may thus cover the target and hide it from view. In contrast, when the arm is guided by the contralateral eye it reaches out in the seeing half of the visual field.The target can be seen by the animal at all stages of the reaching movement and unless the hand is fully extended when it reaches the board it tends not to obscure the target.

In the split-brain monkey with the splenium of the corpus callosum intact and one eye closed both hemispheres receive visual information. In this way not only the motor apparatus of the seeing hemisphere but also that of the non-seeing hemisphere may be recruited for the execution of a visuomotor task.

If in such an animal the hand and fingers ipsilateral to the open eye would receive adequate motor control from the non-seeing hemisphere to execute the relatively independent finger movements necessary to dislodge a small pellet from a well this would support the interpretation of the findings in monkeys with a complete commissurotomy, in which the visual input is restricted to one hemisphere only, that the limitation of movements of the ipsilateral hand and fingers is due to a lack of visuomotor control rather than due to a restriction of the visual field.

For this reason, three split-brain monkeys were prepared (cases 11,12 and 13) in which the optic chiasm, anterior commissure and the anterior two-thirds of the corpus callosum had been transected. In case 12 the anterior massa intermedia had to be cut and in case 11, the entire massa intermedia as well as the habenular and dorsal mesencephalic

TABLE IV-II. SPLENIUM INTACT ANIMALS.
EXTENT OF THE TRANSECTION OF THE COMMISSURES AND
ADDITIONAL DAMAGE.



CASE NO.	NO. and TYPE OPERATIONS	SURVIVAL /INTERVAL	STRUCTURES SPARED	STRUCTURES DAMAGED
11	1st ● ◌ ⊜	2 months	—	Left fornix
	2nd ◍	4 months		
12	1st ●	2½months	—	—
	2nd ◍	5 months		
13	●	3 months	—	Ant.part massa Left fornix

The survival periods and the intervals between operations are listed. AC,anterior commissure;CA,corpus callosum;DM,dorsal mesencephalic commissures;H,hippocampal commissure;h,habenular commissure;MI,massa intermedia;OC,optic chiasm;S,splenium of corpus callosum.

commissures had been transected (See Table IV-II). In all three monkeys the splenium of the corpus callosum was left intact. Thus visual information from one eye was available to both hemispheres, to one directly through the ipsilateral retinal projections from the open eye and to the other indirectly through the splenium.

In these monkeys with only a partial commissurotomy the behavior of the contralateral and ipsilateral hands in retrieving food pellets was very similar, in contrast to the findings in monkeys with a complete commissurotomy.

a) *Retrieval of pellets from forceps.*
When these animals with one eye covered were presented with a pellet in a forceps, the two hands retrieved the food in virtually the same

fashion. Either hand reached quickly for the pellet and the index finger and thumd of either hand swiftly removed it from the forceps. In addition, the ipsilateral index finger and thumb generally retrieved the pellet directly, i.e. without the exploratory movements observed in the animals with a complete commissurotomy.

b) *Retrieval of pellets from the test board.*
When the monkeys with one eye closed were presented with a small pellet in the test board, the contralateral hand and fingers behaved in the usual manner and the index finger was placed into one of the grooves and with the aid of the thumb swiftly dislodged the pellet from the well. The ipsilateral hand and fingers also reached accurately for the food and after a few trials, the index finger was also placed into one of the grooves leading to the pellet and with the aid of the thumb swiftly dislodged it from the well (Fig. 4-5).

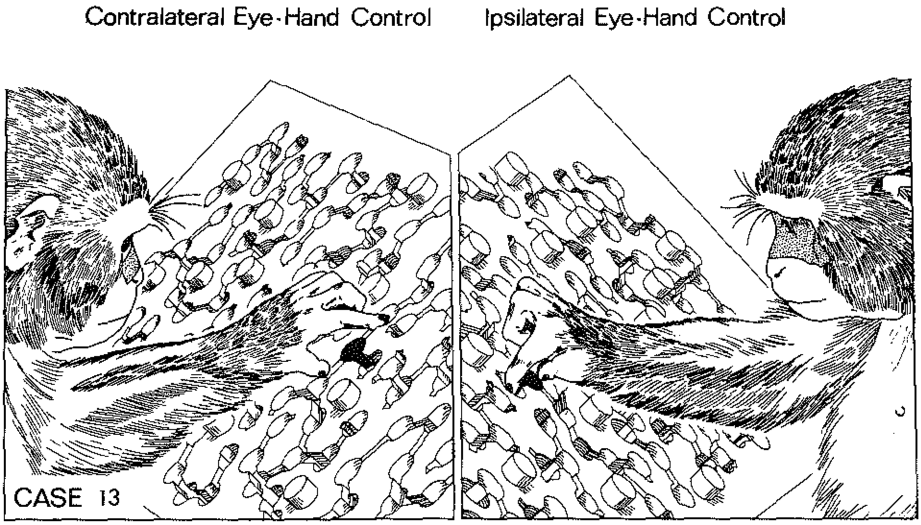


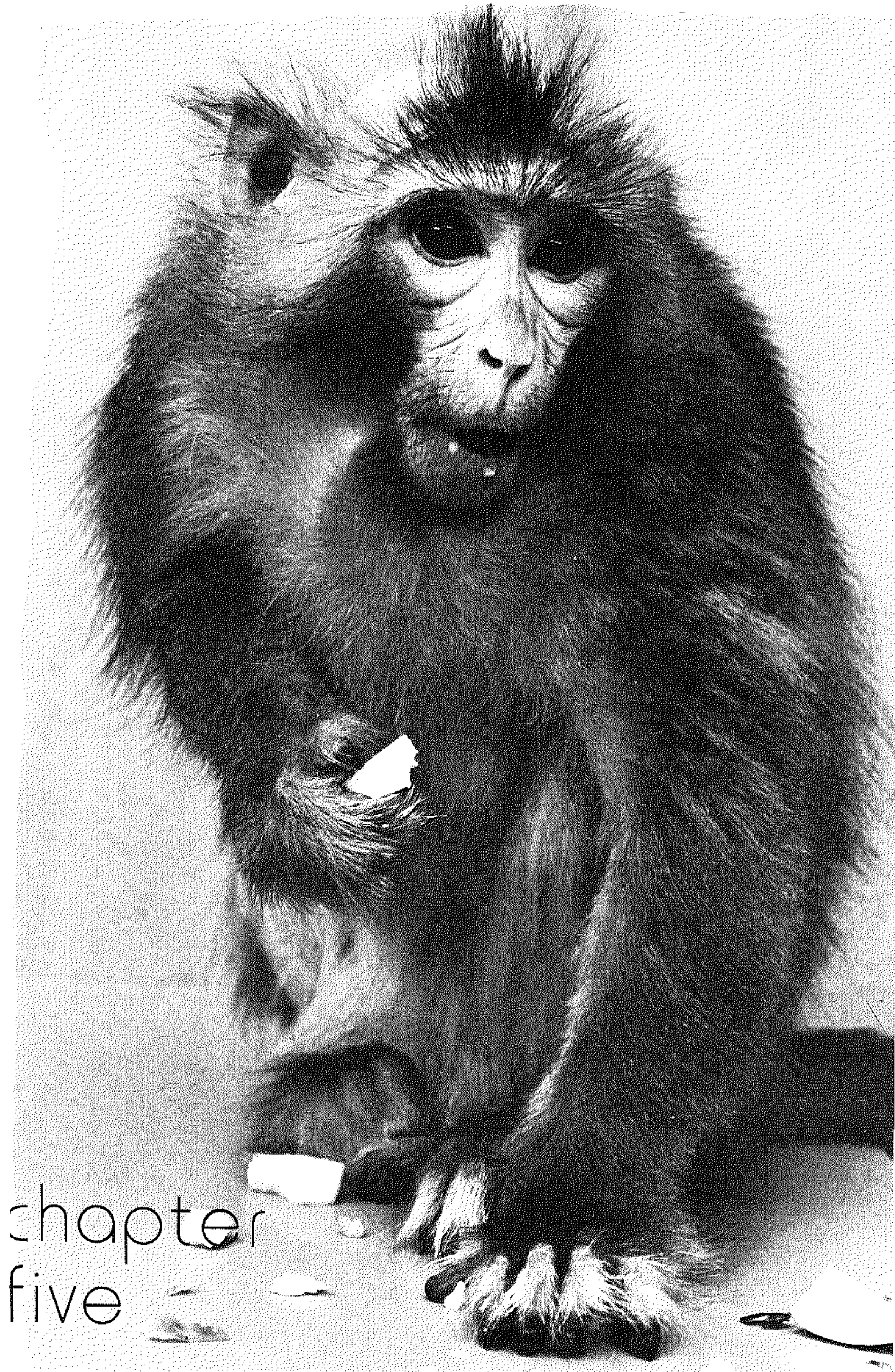
Fig. 4-5. Drawings from a film of a split-brain monkey with a partial telencephalic commissurotomy leaving the splenium of the corpus callosum intact (case 13). Note that the contralateral hand and fingers (left) as well as the ipsilateral ones (right) are about to dislodge a small pellet (shown in black) from the well. Additional transection of the spenium abolished this capacity in the ipsilateral hand and fingers (cf cases 11 and 12).

However, some subtle differences still could be noticed between the behavior of the two hands. For example, the contralateral index finger in dislodging the pellet was generally placed directly into a proper groove while the ipsilateral index finger frequently reached the proper groove indirectly, i.e. after first having been placed immediately adjacent to the well.

After completion of testing, one animal (case 13) was sacrificed In the two other monkeys (cases 11 and 12) the section of the corpus callosum was completed in a second operation and the splenium cut. After this second operation, the visually guided movements of the ipsilateral hand and fingers described above disappeared and a permanent deficit was present similar to that observed in animals with a complete commissurotomy. This deficit thus was also present in the animal with only the optic chiasm, corpus callosum and anterior commissure cut (case 12) sparing the massa intermedia and the dorsal mesencephalic commissures.

These findings in splenium intact split-brain monkeys indicate that the deficit in visuomotor control exerted from one half of the brain over the hand and fingers of the ipsilateral extremity in a monkey with a complete commissurotomy is due to a lack of visuomotor control rather than due to the restriction of the visual fields.

chapter five



In this chapter the ipsilateral eye-arm control is further investigated. The 'cross-cuing' theory put forward by Gazzaniga[93] claims that movements of the extremity ipsilateral to the open eye are brought about by the non-seeing hemisphere on the basis of somato-sensory information about the position of head and eyes which is relayed ('cross-cued') to this hemisphere, and that ipsilateral connections from the seeing half of the brain are not essential for these movements A reinvestigation of this theory was thought warranted taking into account the organization of the descending pathways.

The findings indicate that one half of the brain can steer proximal movements of the ipsilateral arm in the absence of the bulk of the descending pathways from the other hemisphere;although they do not prove conclusively that cross-cuing does not exist, the data from the present study suggest it may not be necessary to postulate such a mechanism for the guidance of ipsilateral movements.

Chapter V: Ipsilateral eye-arm control. Visuomotor coordination in in split-brain monkeys with unilateral cortical ablations.

It has been proposed that in the split-brain monkey with one eye closed the ipsilateral response is dependent on the non-seeing hemisphere[93] and not on the ipsilateral connections from the seeing hemisphere. The mechanism by which the blind hemisphere would be informed about the location of the target has been called 'cross-cuing'. Sensory information derived from the orientation of head and eyes towards the target would be transmitted ('cross-cued') to the non-seeing hemisphere. On the basis of this information, it would guide the extremity ipsilateral to the open eye (of which the main motor centers are situated in the non-seeing hemisphere) towards the target.
However, according to the hypothesis on the organization of the motor system outlined in the foregoing chapters and based on several anatomical and functional findings, postulation of such a 'cross-cuing' strategy to account for ipsilateral movements is not necessary: ipsilateral movements could well be subserved by the ipsilateral connections from the seeing half of the brain (See Fig. 2-4).

In a first experiment, the role of the ipsilateral connections from the seeing half of the brain in guiding proximal movements was studied in one split-brain animal (case 1) after unilateral transection of the ventral quadrant of the spinal cord at the level of the second cervical segment. This operation intended to interrupt the uncrossed fibers of the pyramidal tract in the ventromedial funiculus as well as fibers from the ventromedial group of brainstem pathways

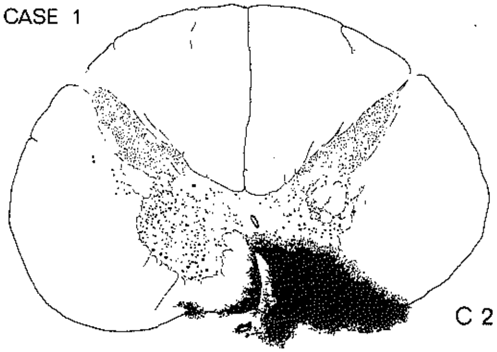


Fig. 5-1. Lesion of the right ventral funiculus in case 1 at the level of the second cervical segment.

running in the ventral and ventrolateral funiculi of the spinal cord (Fig. 5-1). The animal was tested using the arm ipsilateral to the lesion under guidance of the ipsilateral eye in retrieving food pellets from a forceps and from the test board.

At the first postoperative session when presented with food in a forceps, the animal tried to reach out;however, the movements of the extremity were grossly impaired. The animal made sweeping movements in the direction of the pellet which seemed to come mainly from the shoulder and it did not succeed in hitting the food or grasping it. The same deficit was observed when food was presented on the test board:the arm was flung onto the board's surface and made broad sweeping movements over it. Hardly any tactile exploration was seen.

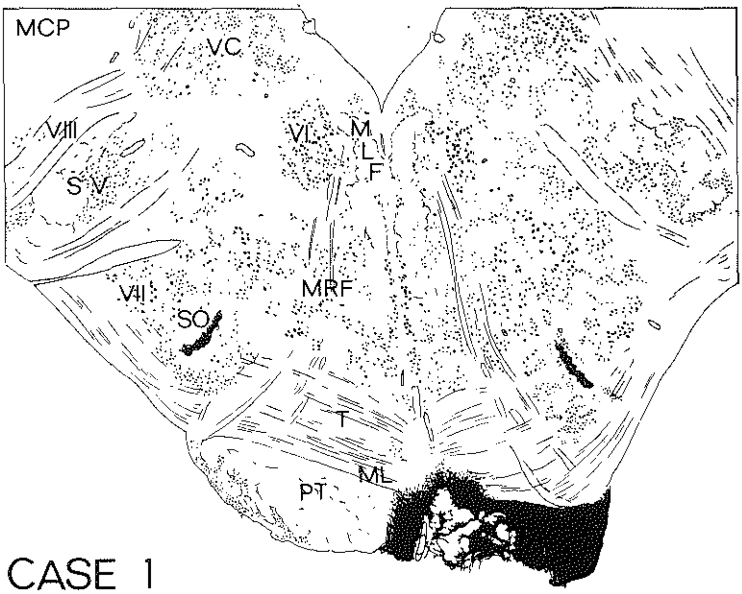


Fig. 5-2. Lesion of the right pyramidal tract in case 1. Note that the lesion has invaded the overlying medial lemniscus (ML) and has damaged the medial part of the contralateral pyramidal tract (PT).
MCP,medial cerebellar peduncle;MLF,medial longitudinal fasciculus;MRF, medial reticular formation;SO,superior olivary complex;S V,spinal trigeminal complex;T,trapezoid body;VC,vestibular complex.
VI,nucleus of abducens nerve;VII,nucleus of facial nerve;
VIII,vestibular nerve.

This motor disturbance, however, quickly disappeared with prolonged testing and after two weeks practice, almost no impairment could be detected. It was assumed that the ipsilateral motor deficit was compensated for by the fibers from the crossed lateral corticospinal tract from the seeing hemisphere which crossed back to the ipsilateral side at spinal cord levels caudal to the lesion, or by contralateral fibers from the ventromedial brainstem pathways likewise recrossing at spinal levels (cf 204). A third explanation, that the lesion in this animal may not have involved all of the ventromedial system since it spared the ventrolateral funiculus was provided only much later at autopsy (Fig. 5-1). Therefore this experimental approach was given up in favor of the following one in which the possibility of the monkey using the descending pathways from the non-seeing hemisphere was largely eliminated.

In one animal (case 1) the direct corticospinal pathway from one hemisphere was interrupted by unilateral section of the pyramidal tract at the medullary level (Fig. 5-2) and the movements of the monkey when reaching for food with the affected extremity under guidance of the ipsilateral eye studied. The lesion involved the entire tract on one side and encroached slightly on the medial part of the other one. The ipsilateral medial lemniscus which is situated immediately above the pyramidal tract had been damaged.

After the operation the animal at first refused to use the affected arm. After some time, however, and with intensive training with frequent rewards the monkey started to use the arm and finally would take food with it. Individual movements of the fingers were permanently abolished. Misreaching indicative of medial lemniscal damage was present throughout the survival period of 15 months.

At this stage of training, visual input was restricted to the intact hemisphere (i.e. the hemisphere with the intact pyramidal tract) and the reaching movements of the ipsilateral arm (i.e. contralateral to the transected pyramidal tract) were studied. The food pellets were presented in a forceps since due to its neurological deficiencies the ipsilateral hand had difficulty retrieving pellets from the test board.

When the animal was presented with a food pellet in a forceps, it reached out with the affected extremity despite the neurological deficits of this arm due to the pyramidal lesion. This reaching movement was sometimes ataxic but seemed to be initiated from the seeing hemisphere. After a number of trials the animal would occasionally succeed in bringing the ipsilateral hand directly onto the target (Fig. 5-3) [1] and grasp it, using the whole hand closing all fingers in concert (cf 155). This closing of the fingers again seemed to occur only after the hand had made contact with the food similar to the normal split-brain monkey when tested with the ipsilateral eye-hand combination.

These data suggest that the seeing hemisphere can guide proximal movements of the ipsilateral arm in the absence of the direct corticospinal connections from the non-seeing hemisphere.

This experiment was extended to include both the direct and the indirect connections from the non-seeing hemisphere. In the rhesus monkey, these connections are derived mainly from the precentral gyrus and the rostrally adjoining frontal areas[149].

In seven split-brain monkeys with a complete commissurotomy

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1) For more detailed information on the kind of ipsilateral movements in this animal, the Appendix contains plates showing the complete sequences of the ipsilateral movements in this and other animals described in this chapter.

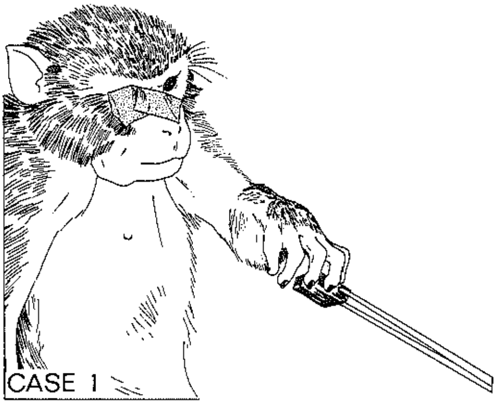


Fig. 5-3. Drawing from a film showing a split-brain monkey (case 1) reaching for food with the left arm under guidance of the ipsilateral eye after destruction of the right pyramidal tract. Note adequate reaching movement of the arm in the absence of the corticospinal tract from the non-seeing hemisphere.

(cases 3,4,5,6,7,8 and 14) the precentral gyrus together with varying portions of the adjoining frontal and postcentral areas were therefore ablated unilaterally and the movements of the animals studied using various eye-hand combinations.

The animals can be divided into three groups on the basis of the extent of the cortical ablations. Representative lesions for each group are shown in Fig. 5-4.

In the first group (cases 6,7 and 8) the lesion involved mainly the precentral gyrus. In cases 6 and 7, the precentral gyrus was ablated and part of the rostrally adjoining areas and part of the cortex wihtin the concavity of the arcuate sulcus together with the rostral

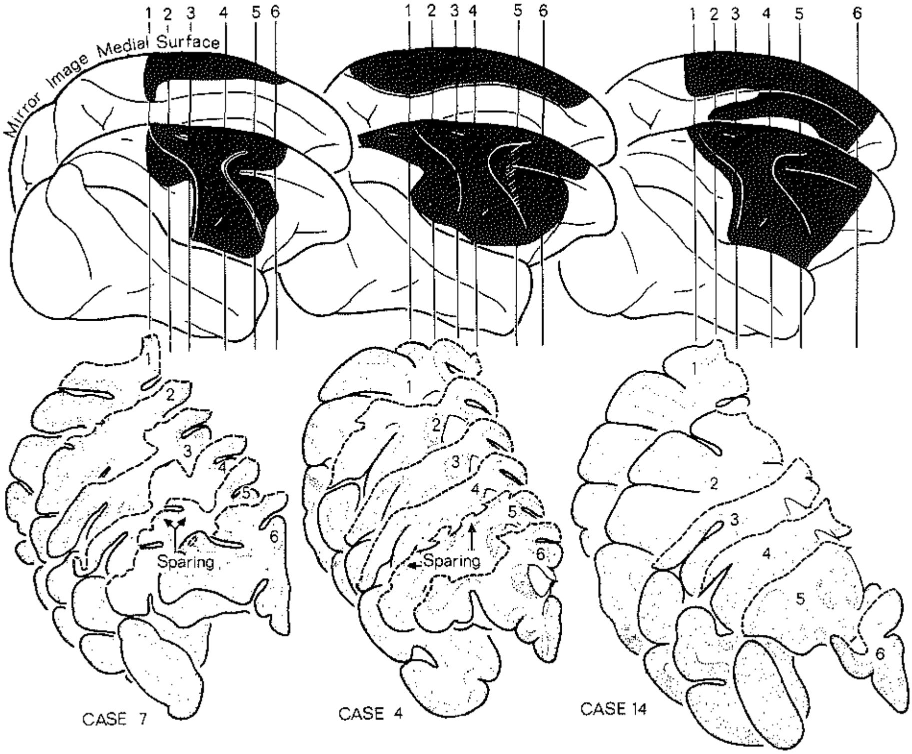


Fig. 5-4. Scheme of the unilateral cortical ablations of cases 7,4 and 14. The movements of the affected arm under guidance of the intact half of the brain are shown in Figs. 5-5, 5-6 and 5-7. Numbers in the upper row of drawings refer to the sections drawn below.

part of the postcentral gyrus and the entire postcentral hand area as well as part of the cortex on the medial side of the hemisphere rostral to the central sulcus (Fig. 5-4,case 7). In case 8, the entire primary and supplementary motor areas[309] were taken out leaving the postcentral gyrus intact.

In the second group (cases 3 and 4) much more extensive lesions were made. The entire precentral gyrus and the bulk of the frontal areas above and below the arcuate sulcus and within its concavity were destroyed as well as the entire postcentral gyrus and the convexity of the superior parietal lobule. On the medial side of the hemisphere the lesion involved the upper bank of the cingulate sulcus rostral to the central sulcus (i.e., including the supplementary motor cortex) in case 3. In case 4, a small strip of cortex in the upper bank had been left intact (Fig. 5-4,case 4). In both cases some cortex had been spared in the depth of the arcuate sulcus. In case 3, a small strip of the rostral bank had been left intact, in case 4, of the caudal bank.

In the third group (cases 5 and 14) most of the cortex on the lateral convexity of the hemisphere and on the medial surface rostral to the central sulcus had been ablated as well as the rostral part of the postcentral gyrus. In case 5, the entire superior frontal and cingulate gyri had been removed;in case 14, part of the upper bank of the cingulate sulcus had been spared. In both animals, all cortex in the depth of the arcuate sulcus had been completely removed (Fig. 5-4).

All four possible eye-hand combinations were tested in these monkeys. The neurologically affected arm contralateral to the lesioned hemisphere was tested on a simple food retrieving task only. The pellets were presented in a forceps since the hand due to its neurological deficits had difficulty retrieving pellets from the board. The normal arm was tested on the board.

a) *Normal hemisphere-paretic arm: ipsilateral eye-hand combination.* The visual input was restricted to the intact hemisphere and the reaching movements of the ipsilateral arm, i.e. contralateral to the lesioned hemisphere, were studied.

In all the animals the paretic arm under guidance of the ipsilateral eye reached out and tried to retrieve the food pellet. The behavior of the paretic arm and hand differed between the animals.

In cases 6 and 7, in which the lesion involved mainly the precentral gyrus and a part of the rostrally adjoining frontal areas the extended arm brought the hand from above on to the food (Fig. 5-5, left side) and the hand after having made contact retrieved it from the forceps by closing all fingers together. In case 8 the paretic arm was never fully extended but was kept in a permanent flexed posture despite extensive training. However, the animal would make a reaching movement and would succeed in bringing the hand onto the food (See Appendix, Plate 2-B).

The animals from the second and third group (cases 3 and 4, and 5 and 14, respectively) with more extensive lesions also reached for the food with the paretic arm despite the fact that the arm and hand

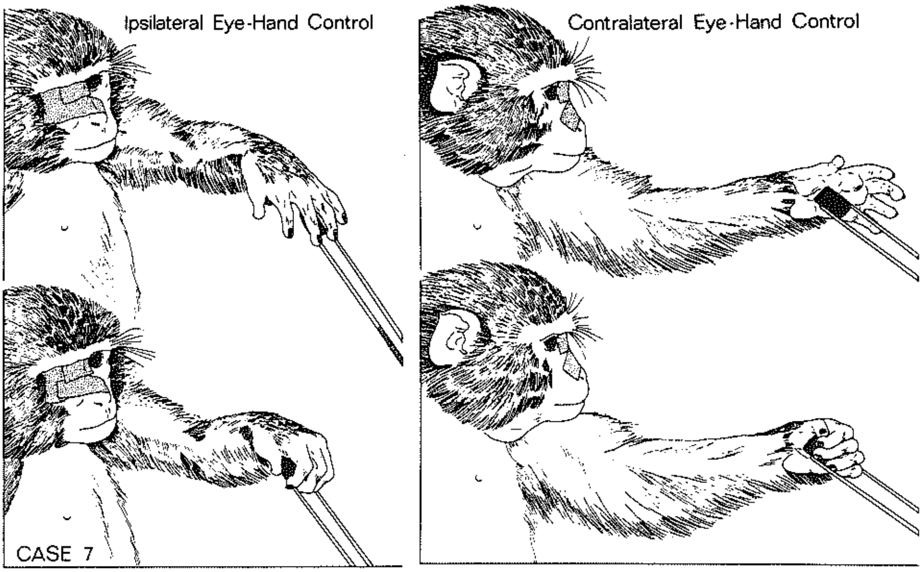


Fig. 5-5. Drawings from a film of a split-brain monkey (case 7) with a complete commissurotomy retrieving a food pellet from forceps with the left hand after destruction of the right precentral gyrus (cf Fig.5-4) Under guidance of the ipsilateral eye (left) the arm brings the hand onto the food and the hand after having made contact with the food retrieves it from the forceps. Under guidance of the contralateral eye (right) the arm brings the hand close to the food and the hand seizes it without prior contact with the food.

showed a much greater defect in movements than in cases 6 and 7. For example in the two animals with the most extensive destruction of the frontal lobe including the upper bank of the cingulate sulcus (cases 3 and 5) the affected arm in reaching for the food was never fully extended and the hand was held flexed at the wrist with the fingers either semiflexed or extended (Appendix,Plates 3-B and 4-B, cf 281,282 283). In case 4, in which the upper bank of the cingulate sulcus had been spared the arm in reaching for the food was fully extended but the hand after having made contact with the food generally did not grasp it, a defect probably resulting from the extensive lesion of the postcentral gyrus. Moreover, in the animals with this extensive ablation of the postcentral gyrus also apronounced ataxia was present which did interfere with their accuracy of reaching so that they would not always hit the target (Fig. 5-6 and Appendix,Plate 3-B). In the animals with only partial ablation of the postcentral gyrus mild ataxia was present initially but would disappear after a couple of weeks. Case 14 with ablation of almost all of the frontal cortex on the lateral and medial surfaces of the hemisphere rostral to the central sulcus as well as of the rostral part of the postcentral gyrus but with sparing of the upper bank of the cingulate sulcus likewise reached out with a fully extended arm (Fig. 5-7 and Appendix,Plate 4-B)

These findings in the animals with unilateral cortical lesions show that the visually guided reaching movements of the arm ipsilateral to the open eye do occur after destruction of the pre- and postcentral motor and sensory areas and in the absence of the bulk of the

CASE 4

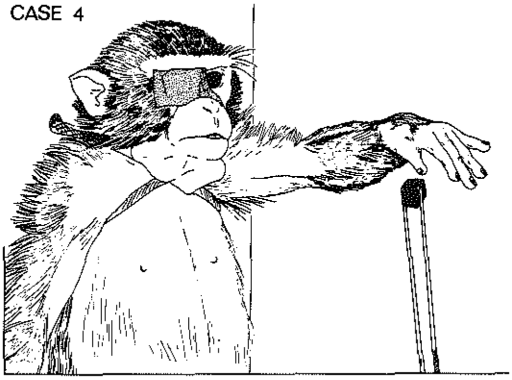


Fig. 5-6. Drawing from a film of a split-brain monkey (case 4) with a complete commissurotomy reaching for food with the left arm under guidance of the ipsilateral eye after destruction of the right fronto-parietal cortex (cf Fig. 5-4,case 4).

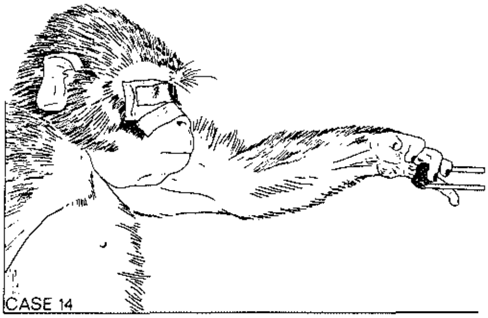


Fig. 5-7. Drawing from a film of a split-brain monkey (case 14) with a complete commissurotomy reaching for food with the left arm under guidance of the ipsilateral eye after destruction of the right frontal cortex (cf Fig. 5-4).

descending direct and indirect connections from the frontal and postcentral areas of the non-seeing hemisphere to the spinal intermediate zone and motoneurons.

b) *Lesioned hemisphere-paretic arm: contralateral eye-hand combination.* In the animals with cortical lesions attention was paid also to the movements of the paretic arm reaching for food under guidance of the contralateral eye. After a recovery period of three months, the paretic arm and hand were found to be more agile in retrieving food when guided through the contralateral eye and thus by the damaged hemisphere than when guided through the ipsilateral eye and the intact hemisphere. This was most pronounced in cases 6 and 7 in which mainly the precentral gyrus and part of the rostrally adjoining frontal areas had been destroyed. The paretic arm guided by the ipsilateral intact hemisphere tended to place the hand onto the food from above (Fig. 5-5 left side). In contrast the arm when guided by the contralateral damaged hemisphere brought the hand directly onto the food and the hand often retrieved the food from the side (Fig. 5-5,right side). Further, the hand and fingers when brought to the food under guidance of the ipsilateral intact hemisphere either remained immobile or the hand gradually opened while the arm was extended. In both instances, however, the closing movements of the hand and fingers in prehending the food tended to occur only after the hand and fingers had made contact with the food (Fig. 5-5,left side). In contrast, when guided by the contralateral damaged hemisphere the hand and fingers seized the food directly by opening and closing the hand without the necessity of prior contact as in the case of the ipsilateral hand. These movements were generally executed on an extended arm and occurred independently,

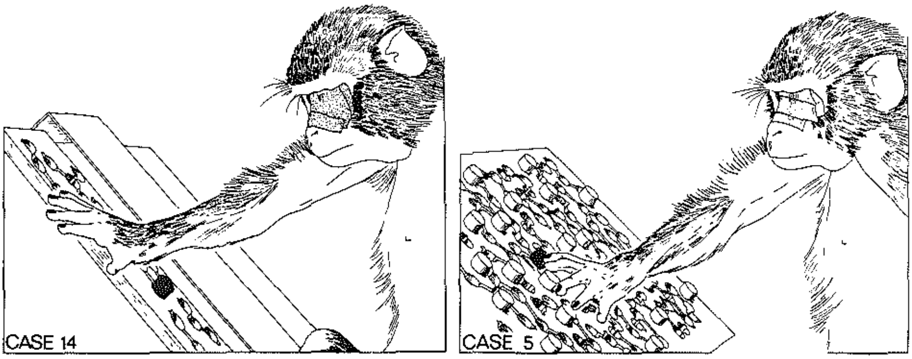


Fig. 5-8. Drawings from films of two split-brain monkeys with a complete commissurotomy (cases 14 and 5) reaching for food (shown in black) on the board with the right arm under guidance of the ipsilateral eye after a right frontal cortical lesion (cf Fig. 5-4). Note severe misreaching in both animals with this eye-hand combination.

i.e. without being accompanied by gross movements of shoulder and elbow (Fig. 5-5, right side).

In the other animals with cortical lesions somewhat similar differences seemed to occur. However, these differences were difficult to demonstrate since in three of the animals the paretic arm and hand were generally held flexed at the elbow and wrist.

c) *Normal hemisphere-normal arm: contralateral eye-hand combination.* The behavior of the normal arm and hand when guided through the contra lateral eye and thus by the intact hemisphere was not altered by the cortical lesion in the opposite hemisphere.

d) *Lesioned hemisphere-normal arm: ipsilateral eye-hand combination.* In this eye hand combination visual input was restricted to the

Table V-I. Under guidance of the ipsilateral eye and the intact hemisphere, the paretic arm is used in adequate reaching movements. Movements of the whole hand and closing of the fingers in concert is seen when this arm is guided by the contralateral eye and the lesioned hemisphere. Under guidance of the ipsilateral eye and the lesioned hemisphere the normal arm shows defective reaching movements.

Only when the entire postcentral gyrus is added to the lesion indicated (hatched) does misreaching of the paretic arm occur ipsilaterally.

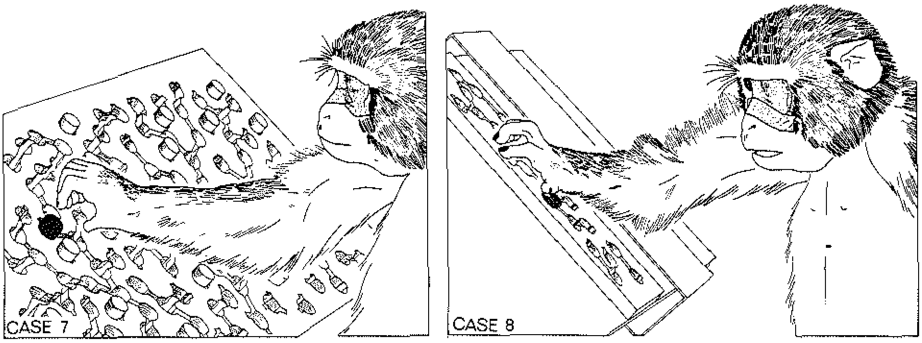
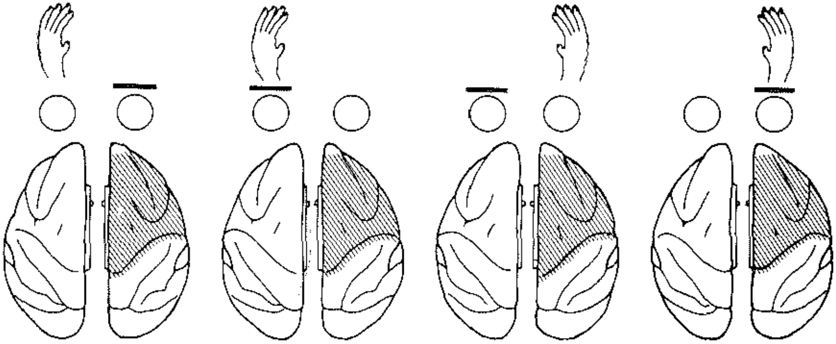


Fig. 5-9. Drawings from films of two split-brain monkeys with a complete commissurotomy (cases 7 and 8) reaching for food (shown in black) on the board with the right arm under guidance of the ipsilateral eye after destruction of the right precentral motor areas (cf Fig 5-4). Note only slight misreaching with this eye-hand combination.

lesioned hemisphere and the reaching movements of the ipsilateral arm, i.e. contralateral to the intact hemisphere were studied when the monkey was reaching for food in a forceps or on the test board.
All seven animals showed misreaching. This deficit was most pronounced in the animals with the most extensive lesions and was much smaller in

TABLE V-I. VISUOMOTOR COORDINATION AFTER UNILATERAL CORTICAL LESIONS.



	PARETIC ARM		NORMAL ARM	
	ipsilateral	contralateral	ipsilateral	contralateral
arm	+	+	−	+
hand	−	+	±	+
fingers	−	−	−	+

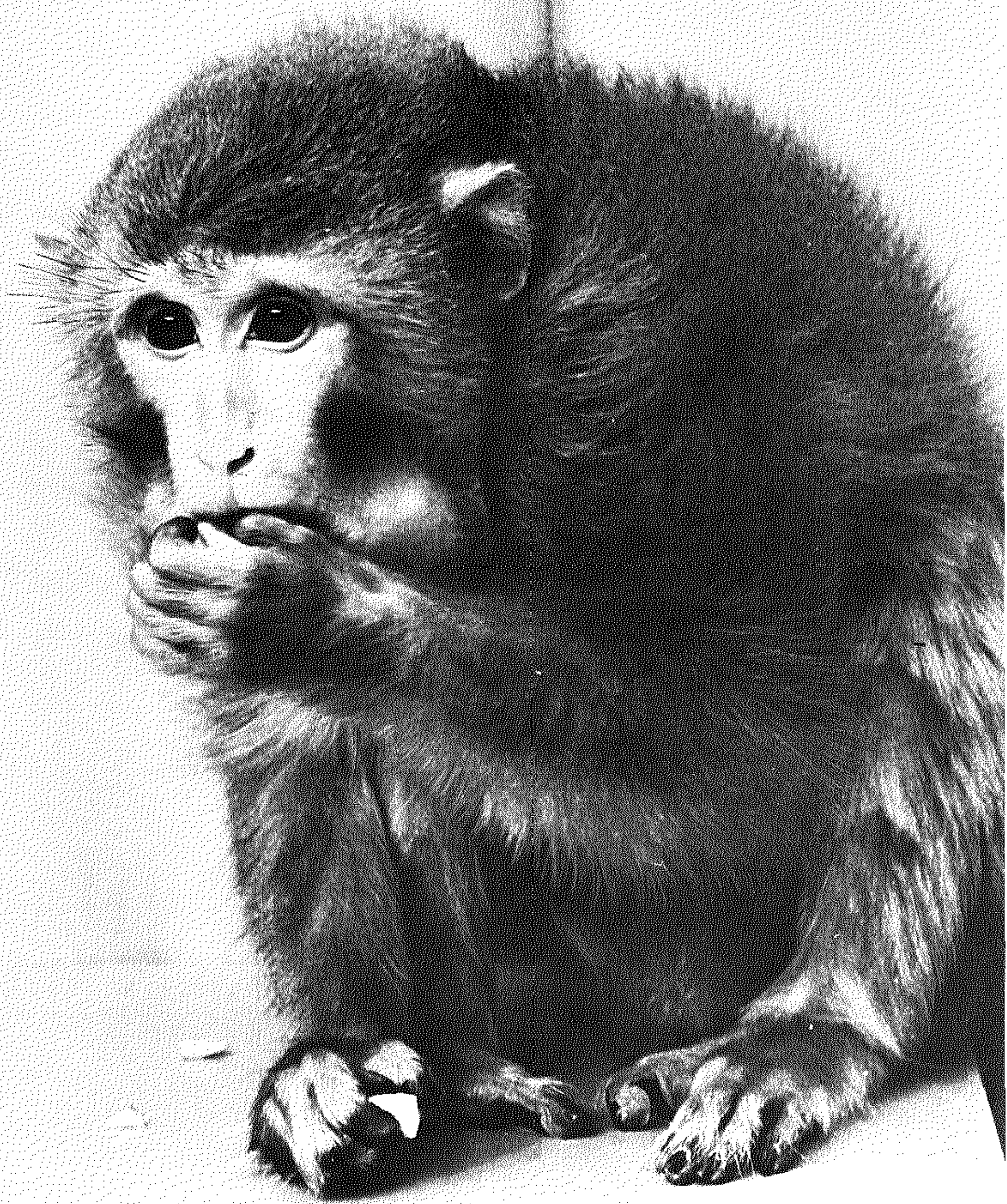
cases 6,7 and 8 with mainly precentral cortical ablations.

When presented with food in a forceps monkeys 3,4,5 and 14 showed gross incoordination of movements. They were unable to bring their hand directly onto the food and instead made anumber of sweeping movements until they hit the food or gave up altogether.

The same deficit was seen when these animals tried to retrieve large pellets from the test board:they misreached severely (fig. 5-8). Animals 6,7 and 8 with smaller lesions also showed this deficit but were less impaired. However, comparison with their preoperative performance likewise showed a drop in reaching accuracy (Fig. 5-9).

The findings obtained in the animals are summarized in Table V-I.

chapter six



In several split-brain monkeys with a complete commissurotomy, the two hands when reaching for food on the board under guidance of the ipsilateral eye assumed a different posture. In general, the hand which was preferred in reaching with both eyes open tended to be kept more flexed than the other. The relationship between hand preference and this flexed posture was verified in two animals which were tested for hand preference before and after split-brain surgery.

Animals in which only the telencephalic commissures (corpus callosum and anterior commissure) had been transected were compared with the complete commissurotomy group. In the former group, the ipsilateral hand posture was reminiscent of the precision grip posture;flexion of the fingers was present in both hands when used ipsilaterally in these monkeys, and subsequent completion of the commissurotomy did not significantly alter this posture in most of the animals.

Evidence is presented that the flexed posture of the ipsilateral hand may be subserved by the rubrospinal tract.

Chapter VI: Ipsilateral eye-hand control. Effects of serial commissurotomy, and of lesions of the lateral brainstem pathway.

So far, the study has been concerned mainly with the cerebral control of ipsilateral *arm* movements. However, when in the animals with a complete commissurotomy were tested on the board, in several animals a difference existed in ipsilateral hand posture which suggested a possible difference in ipsilateral eye-*hand* control also. In such an animal, one hand when used ipsilaterally tended to be kept more flexed than the other when reaching for food on the board (Fig. 6-1). In general, the hand which was preferred in reaching with both eyes open tended to be held more flexed than the other.

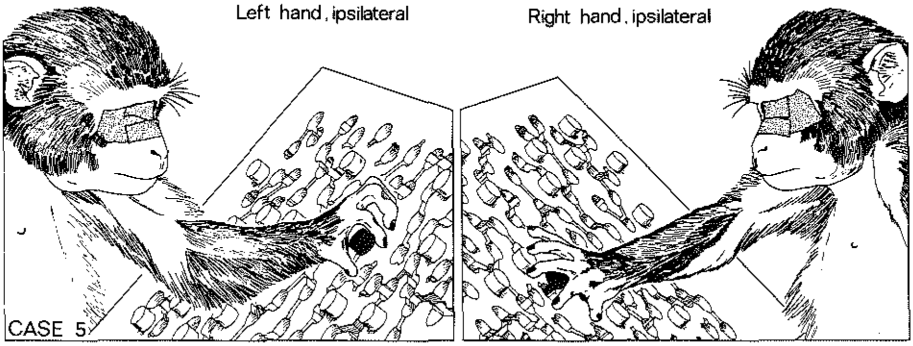


Fig. 6-1. Drawings from a film showing a split-brain monkey (case 5) with a complete commissurotomy in one session. Note the difference in posture of the two hands when reaching for food on the board under guidance of the ipsilateral eye. This animal normally preferred its left arm for reaching with both eyes open.

The relationship between hand preference and ipsilateral hand posture was investigated in two animals (cases 10 and 11). The monkeys were tested for hand preference before and after split-brain surgery using a simple reaching test and a test intended to require a more refined motor action. The first test consisted of three food wells 15 cms apart which were randomly baited. The second test was derived from the test board and consisted of a small disk with one central food well which accomodated a small pellet. Two grooves gave access to the food well through which the individual fingers could dislodge the pellet. The position of the grooves could be varied by rotating the disk[144]. The disk was presented randomly at three different sites 15 cms apart and the position of the grooves was changed randomly. The animals received 30 trials on the first test for 5 consecutive days and 20 trials on the second one for 10 consecutive days. Both monkeys used their left hand to retrieve the food in both test situations in more than 90% of the trials. This preference for the left hand was not altered by the split-brain surgery (cf 161). In case 11, the corpus callosum had been transected in two steps. However, this did not affect the results.

When these animals with a complete commissurotomy were presented with a pellet in the board using the preferred hand under guidance of the ipsilateral eye the animals tended to keep the fingers of this hand flexed and the thumb semiflexed or extended when reaching out. In contrast, the other, non-preferred hand when used ipsilaterally tended to be much more extended and the fingers were extended and abducted.

This difference in posture of the ipsilateral hands observed in most animals with a complete commissurotomy (cases 1,2,3,5,6,10 and 11) was not seen in two animals in which only the telencephalic commissures had been transected (cases 8 and 12). In these animals the fingers and thumb of the ipsilateral hand were held in a way reminiscent of the precision grip posture, i.e. the hand was held dorsiflexed and the lateral fingers rather flexed while the index finger was held semiflexed and the thumb slightly extended. In addition, the index finger was more frequently placed accurately on the pellet than occurred in the animals with a complete commissurotomy (Fig. 6-2).

The difference between the two ipsilateral hands in the animals with a telencephalic commissurotomy was far less pronounced than in the monkeys with a complete commissurotomy. In general, the index finger of the preferred hand was slightly less flexed than the other fingers thus giving the impression of the precision grip posture while the fingers of the non-preferred hand were all kept equally flexed.

This suggested that the intact massa intermedia and the dorsal mesencephalic commissures, alone or together, might help to induce this

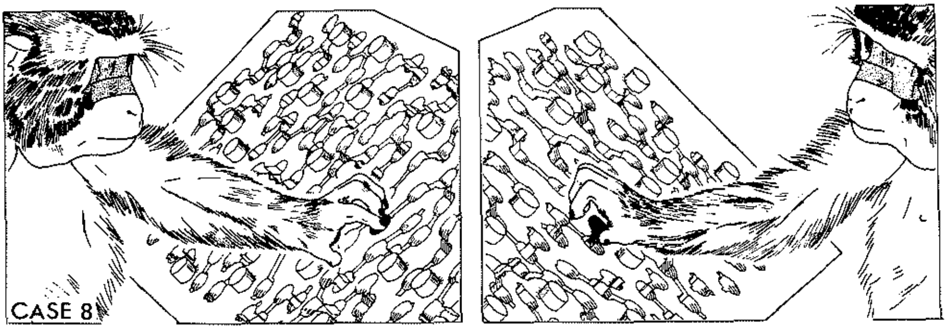


Fig. 6-2. Drawings from a film showing a split-brain monkey (case 8) with a telencephalic commissurotomy. Note the similarity in hand posture when reaching for food on the board under guidance of the ipsilateral eye.

elaborate posture of the ipsilateral hand and might contribute to its apparent accuracy in reaching.

Therefore the posture of the ipsilateral hands was studied in five animals in which these commissures had been transected serially.

The animals and the sequence of their operations are listed in Table I.

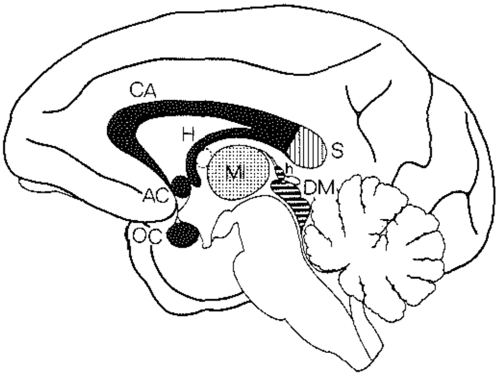
To prevent possible tactile guidance of the posture of the ipsilateral hand induced by the restraining between trials of the extremity the test board covered by the lid was used throughout and the arm was left free (See chapter III).

In the two animals with a telencephalic commissurotomy (cases 8 and 12) the massa intermedia and the dorsal mesencephalic commissures were left intact. In one of these animals (case 12) the corpus callosum had been transected in two steps.

Retrieval of pellets from the board.- In these monkeys the contra lateral arm, hand and fingers retrieved a small pellet in the usual fashion. The ipsilateral hand and fingers, however, behaved in much the same way as in the animals with a complete commissurotomy and consistently failed to retrieve a small pellet from a well. In case 8, additional section of the dorsal mesencephalic commissures did not alter the posture of the ipsilateral hands.

In animals following a commissurotomy which spared either the dorsal mesencephalic commissures (case 7) or the massa intermedia (cases 9

TABLE VI-1.- ANIMALS WITH COMMISSUROTOMIES DONE IN SEVERAL STEPS. EXTENT AND ORDER OF THE TRANSECTION OF THE COMMISSURES.



CASE NO.	NO. and TYPE OPERATIONS					SURVIVAL /INTERVAL
7	1st	●	▥	░		3 months
	2nd				▤	1 months
8	1st	●	▥			2½months
	2nd				▤	2 months
	3rd			░		2½months
9	1st	●	▥		▤	4 months
	2nd			░		6 months
12	1st	●				2½months
	2nd		▥			5 months
14	1st	●				? months
	2nd		▥		▤	9 months

The survival periods and the intervals between operations are listed. AC,anterior commissure;CA,corpus callosum;DM,dorsal mesencephalic commissures;H,hippocampal commissure;h,habenular commissure;MI,massa intermedia thalami;S,splenium of corpus callosum.

and 14) the posture of the ipsilateral hand and fingers in reaching for the food also resembled the precision grip posture. Completion of the commissurotomy by transection of the dorsal mesencephalic commissures (case 7) or the massa intermedia (cases 8 and 9) only transiently abolished this phenomenon in one animal (case 8) but hardly altered it in the others (cases 7 and 9).

The lateral brainstem pathway of which the main constituent are fibers derived from the magnocellular red nucleus has been shown to be involved in the control of distal extremity muscles[156]. Therefore in three split-brain monkeys (cases 9,10 and 11) an attempt was made to interrupt the rubrospinal tract unilaterally at the medullary level.

In two animals (cases 9 and 10) this was done by introducing an electrode into the medulla oblongata through the area postrema at an angle of 45 degrees with the midsagittal plane. The electrode was advanced until it met the resistance of the outer pial lining of the brainstem, was withdrawn about 1 mm and current was passed to make a small electrolytic lesion.

In case 11, a cut was made laterally in the brainstem with the aid of a small knife (3 mms long and 1 mm wide).

The animals were tested using the hand ipsilateral to the lesion under guidance of the ipsilateral eye in retrieving pellets from the board.

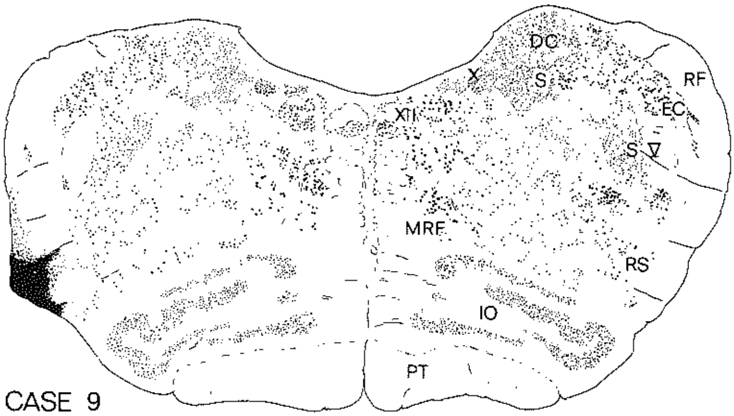


Fig. 6-3. Lesion (black) of the area of the left rubrospinal tract in the medulla oblongata of case 9. The lesion included approximately 60% of the rubrospinal fibers as judged from the cell loss in the corresponding magnocellular red nucleus.

DC,dorsal column nuclei;EC,external cuneate nucleus;MRF,medial reticular formation;IO,inferior olive;PT,pyramidal tract;RF,restiform body; RS,rubrospinal tract;S,solitary tract and nucleus;S V,spinal trigeminal complex;X,motor nucleus of vagus;XII,hypoglossal nucleus.

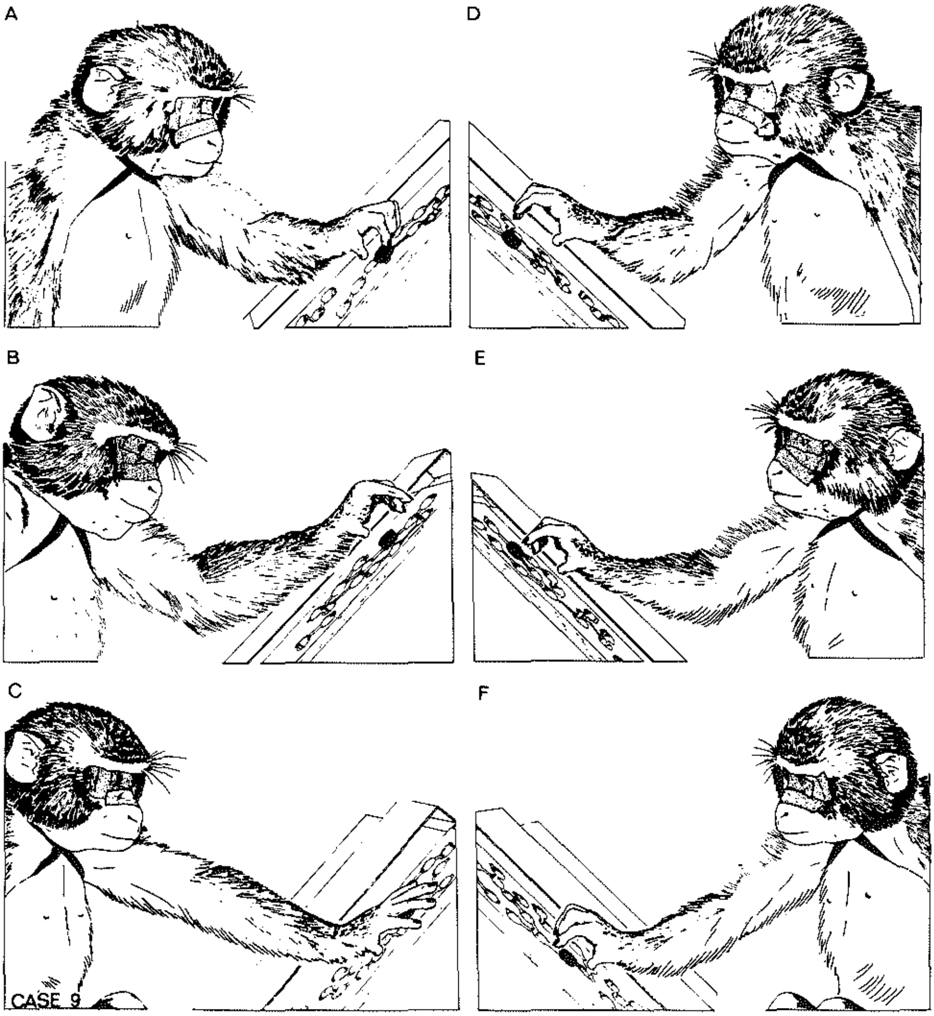
In case 10, the lesion was found to occupy the area just dorsal to that of the rubrospinal tract and had destroyed the spinal trigeminal complex and part of the adjoining lateral reticular formation at that level. No changes in the posture of the hand ipsilateral to the lesion when guided by the ipsilateral eye were found.
In case 11, the lesion was more extensive and involved most of the inferior cerebellar peduncle, the external cuneate nucleus, spinal trigeminal complex and the lateral reticular formation at that level.
No retrograde changes or cell loss was found in the contralateral red nucleus of this animal and no change of posture of the hand ipsilateral to the lesion when guided by the ipsilateral eye was detected.

In case 9, however, a small lesion was found in the area of the rubrospinal tract and approximately 60% of the magnocellular elements of the contralateral red nucleus had disappeared (Fig. 6-3). In this animal, a striking difference occurred in the posture of the hand ipsilateral to the lesion before and after the operation. Before the operation, the animal kept the fingers of this hand flexed with the thumb semiflexed or extended when reaching for food under guidance of the ipsilateral eye. Slight extension of the index finger reminiscent of that seen in the precision grip posture was often present. After the rubrospinal lesion this flexion of the fingers had disappeared and now the animal reached out with an extended hand with the fingers abducted, which posture resembled that of the non-preferred hand of an animal with a complete commissurotomy in one session (Fig. 6-4). This difference in ipsilateral hand posture before and after the rubrospinal lesion could already be seen when the animal was awaiting

Fig. 6-4. Drawings from films showing a split-brain monkey (case 9) reaching for food with the ipsilateral hands after transection of the telencephalic and dorsal mesencephalic commissures (A and D), after additional transection of the massa intermedia (B and E), and after a lesion of the left rubrospinal tract (C and F). Note that the elaborate posture of the ipsilateral hands is not affected by completion of the commissurotomy (A and D,and B and E,respectively) but that after a lesion of the rubrospinal tract, this flexed posture changes into extension (C). See also Appendix,Plate 5.

a run on the test board. Before the operation, the hand was held close to the animal's body, the fingers were flexed and the thumb flexed against the side of the hand. Postoperatively, the hand hung down from the wrist with extended fingers, and remained inert (Appendix,Plate 5)

The data from this last animal suggest that the rubrospinal tract may be of importance for the control of posture of the hand ipsilateral to the open eye. The pathways involved in this control are not clear, but it seems possible for a monkey to spontaneously find this route. This is suggested by the findings in case 10 with a complete



commissurotomy in one session. This monkey showed a clear difference in posture of the ipsilateral hands for three weeks of testing, and then from one test session to the other showed the improvement in the 'shaping' of the non-preferred ipsilateral hand like that found in the serially operated animals. The commissurotomy was verified to be complete in this animal.

chapter seven

The role of the indirect connections to the spinal cord in the control of movements was investigated in split-brain monkeys in which the direct corticospinal connections had been interrupted either by means of bilateral section of the pyramidal tracts or bilateral ablation of a major part of their precentral areas of origin. In these animals visual input was restricted to one half of the brain and the motor performance of the extremity contralateral and ipsilateral to the open eye was studied.

The findings, although preliminary, suggest that a difference exists in this indirect control between the contralateral and ipsilateral extremity. This difference parallelled that seen in the previous experiments using split-brain monkeys which were otherwise intact.

Under guidance of the contralateral eye, both visually guided proximal and distal movements seem possible but under guidance of the ipsilateral eye mainly visually guided proximal extremity movements and synergistic movements of the whole limb are observed.

Chapter VII: Role of the indirect corticospinal connections in motor control. Effects of bilateral pyramidotomy and of bilateral precentral cortical ablations.

An attempt has been made to assess the capacity of one hemisphere in guiding movements of the contralateral and ipsilateral extremities by way of its *indirect* connections to the spinal cord, i.e. established via the descending brainstem pathways. This investigation was prompted by the fact that the connections from one half of the brainstem to either side of the spinal cord terminate in different parts of the intermediate zone (Fig.2-4). The lateral brainstem pathway from one side of the brainstem terminates in the contralateral dorsolateral part of the intermediate zone. The ventromedial group of brainstem pathways from one side of the brainstem terminates mainly in the ventromedial part of the intermediate zone to some extent bilaterally. The cortical projection from one hemisphere to the cells of origin of the brainstem pathways are distributed as follows:cortical fibers to the cells of origin of the lateral brainstem pathway are distributed ipsilaterally but to the cells of origin of the ventromedial group bilaterally. Thus one hemisphere is connected indirectly with the dorsolateral part of the spinal intermediate zone *contralaterally* but with the ventromedial parts *bilaterally*. Anatomically, no indications have been found of direct terminations of brainstem pathways on spinal motoneurons although they have been demonstrated physiologically. Functional studies on the behavioral effects of interrupting the two groups of brainstem pathways have shown that interruption of the lateral brainstem pathway preferentially affects distal extremity movements while transection of the ventromedial pathways affects preferentially proximal movements of the limbs and integrated movements of body and limbs such as righting, walking and climbing.

It was therefore assumed that one hemisphere by way of its indirect connections to the spinal cord would be able to steer both proximal and distal extremity movements contralaterally but mainly proximal movements ipsilaterally. This hypothesis was tested in split-brain monkeys in which the direct corticospinal connections had been largely eliminated either by means of bilateral section of the pyramidal tracts or by means of bilateral ablation of a major part of their cortical area of origin. Four animals have been used.

In two split-brain monkeys (cases 2 and 15) the pyramidal tracts were sectioned bilaterally. In case 2 the commissurotomy preceded the pyramidotomy while in case 15 the pyramidotomy was performed first.

In two other monkeys with a complete commissurotomy (cases 16 and 17) ablation of the precentral motor areas was performed sparing, however, the precentral face area bilaterally. In this operation care was taken not to remove the entire supplementary motor areas or to damage the postcentral gyri. Rostrally the lesion involved part of the area above the arcuate sulcus and its posterior bank.
Both these animals required intensive postoperative care and training. Case 17 was tube-fed for three months before it could feed itself and chew its food. Both animals initially had difficulty in righting themselves, walking and climbing but this handicap disappeared with time. Twelve months after the operation they both ran, walked and climbed well. In the first two postoperative months they did not take food into their hands but this altered with training.

Cases 15,16 and 17 are still alive and kept for further study while case 2 was sacrificed 15 months after pyramidotomy. The lesion of the pyramidal tracts in this monkey was complete but it damaged the medial lemnisci substantially. Case 15 with a bilateral pyramidotomy has survived its lesion for over four years. In this monkey no relatively independent finger movements indicative of sparing of pyramidal fibers is present and signs of lemniscal damage such as misreaching or a flexed posture of the limbs are not observed. In the split-brain animals with bilateral precentral ablations likewise no individual finger movements were found. In one animal (case 17) slight flexion of the extremities is present and may reflect damage to the postcentral gyri or the supplementary motor areas.

In all four monkeys visual input was restricted to one half of the brain by taping one eye shut and their movements were studied when retrieving food pellets from a forceps or from a specially designed test board with the contralateral or the ipsilateral extremity.

A. *Retrieval of food pellets from forceps.*- All animals were able to reach out and grasp food presented in a forceps with either hand although case 17 had difficulty even with this simple task. However, in some of the animals the movements of the arm and hand when guided by the contralateral eye differed from those guided by the ipsilateral eye.

In case 15 with a *bilateral pyramidotomy* the reaching movements of the contralateral and ipsilateral arm did not differ significantly and consisted of an extension movement which brought the hand onto the food. It was noticed, however, that the contralateral hand sometimes showed movements of all fingers in concert before the hand had made contact with the food (Fig. 7-1 and Appendix,Plate 6).

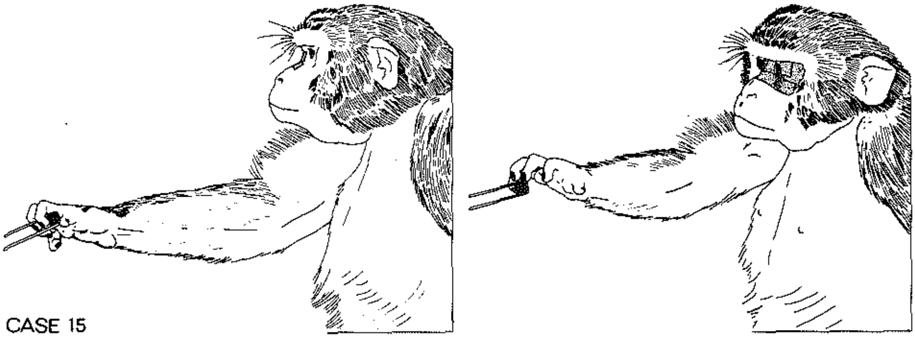


Fig. 7-1. Drawings from a film showing a split-brain monkey with a bilateral pyramidotomy (case 15) reaching for food in a forceps with the right hand under guidance of the contralateral eye (left) and the ipsi lateral eye (right). The reaching movements of both eye-hand combinations do not differ significantly;however,active movements of all fingers in concert prior to touching the food was seen only in the con tralateral combination. See also Appendix,Plate 6.

In case 2 with a bilateral pyramidotomy and lemniscal damage the movements of the arm ipsilateral to the open eye consisted of a strong ele vation of the arm from the shoulder with flexion at elbow, wrist and fingers. This flexion persisted throughout the movement and hardly any extension was seen in the hand as it was brought onto the target. When the arm was used contralaterally no elevation was seen at the shoulder

flexion was far less pronounced and movements of the whole hand were present before it had touched the food.
The reaching movements of the contralateral and ipsilateral arm in case 16 with a *bilateral precentral cortical ablation* strikingly resembled those of the paretic arm in animals with a unilateral precentral ablation (cases 6 and 7,Fig.5-5) under guidance of the contralateral and the ipsilateral eye respectively. The ipsilateral hand in case 16 was also brought onto the food from above and the hand remained inert or gradually opened during the extension of the arm.

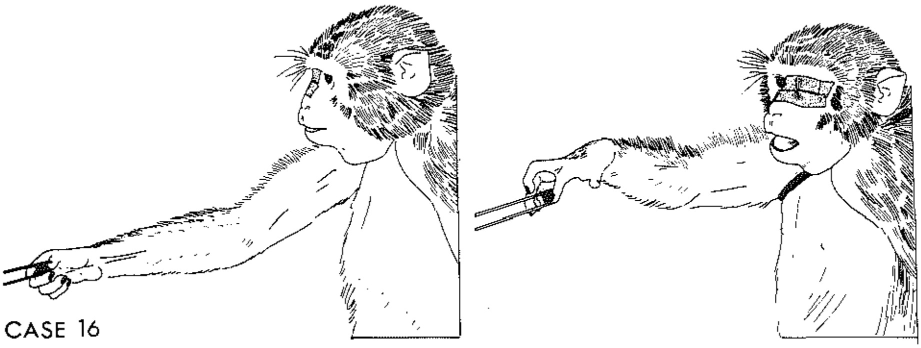


Fig. 7-2. Drawings from a film showing a split-brain monkey with a bilateral precentral cortical ablation (case 16) reaching for food in a forceps with the right arm under guidance of the contralateral eye (left) and the ipsilateral eye (right). The contralateral arm brings the hand to the food from the side and the fingers close actively around it. The ipsilateral arm brings the hand onto the target from above and the hand retrieves the food only after having made contact with it. Note awkward posture of the ipsilateral hand at the moment it touches the food. See also Appendix,Plate 7.

Flexion of the fingers in concert occurred only after the hand had made contact with the food. The contralateral hand approached the food from the side and movements of all fingers in concert were seen as the hand approached the food. Closing of the hand and fingers seemed to occur without prior contact (Fig.7-2 and Appendix,Plate 7).
A somewhat similar difference was seen in the other monkey with a bilateral cortical lesion (case 17) but the difference was less clearcut

due to this animal's more pronounced neurological deficits. In both eye-hand combinations some flexion persisted in the elbows and the movements of the hand had less well recovered .

Due to the lack of relatively independent finger movements in these four animals the test board developed for the otherwise intact split-brain monkeys could not be used. Therefore a new board was designed (Fig.7-3). This board contains food wells in an hexagonal array and has knobs, 8 mms high, affixed to its surface in the center of a hexagon formed by six food wells. The space between knobs is 6 cms. Additional knobs could be placed into empty wells in order to modify the array and to diminish space. A large pellet was placed into one of the wells with its upper surface flush with those of the knobs. It was anticipated that an animal which is able to close its fingers in concert would be capable of retrieving pellets from this board while a hand which lacked such control would have difficulty in achieving this.

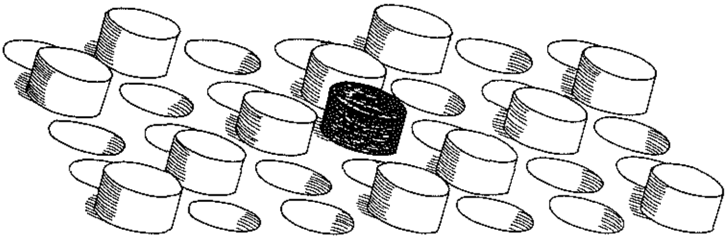


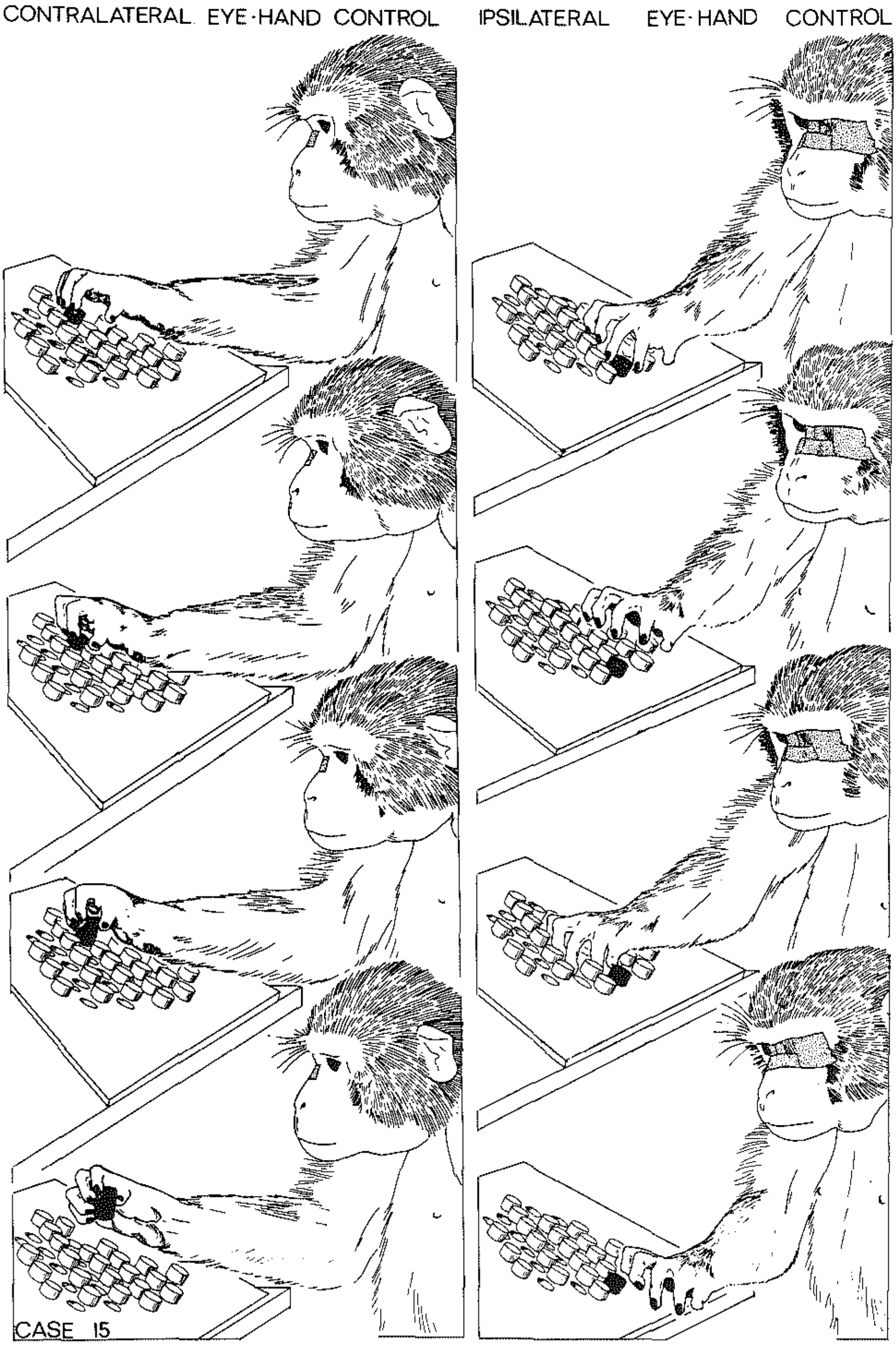
Fig. 7-3. Scheme of test board used for split-brain monkeys with bilateral pyramidotomy or bilateral precentral cortical ablations. Knobs are affixed to the board's surface in the center of a hexagon formed by six food wells. A large pellet (indicated in black) is placed into a well with its upper surface flush with those of the knobs and is difficult to detect on the basis of somatosensory cues.

B. *Retrieval of food pellets from the test board.*- Monkey 15 with a *bilateral pyramidotomy* readily performed this task with both eyes open. The animal reached out with the hand slightly dorsiflexed and the fingers flexed. The hand was brought onto the target and the fingers closed around the pellet which was dislodged from the well by means of small flexion-extension movements of the wrist accompanied with flexion-extension movements of the fingers. The same behavior was observed when one eye was closed and the arm and hand were guided by the contralateral eye (Fig.7-4,left column). However, when the same extremity was guided by the ipsilateral eye a difference occurred. The animal reached out but this reaching movement in a number of trials did not bring the hand onto the target but missed it. The posture of the hand was also different;the fingers were abducted and semiflexed or extended. When the hand had touched the board the animal sometimes started a sequence of blind groping movements over the board's surface closing the fingers around knobs and pulling them. Sometimes the hand wandered into the blind half of the visual field. These movements were reminiscent of the exploratory movements of the ipsilateral hand of an otherwise intact split-brain monkey,although they were much cruder (Fig.7-4,right column). The ipsilateral hand never dislodged a pellet from the board. After a few unsuccessfull trials with the ipsilateral extremity the monkey became extremely reluctant to even reach out despite frequent rewarding.

The other animal with a bilateral pyramidotomy,case 2,has never been tested on this board.

A difference in visuomotor performance between the animal with bilateral pyramidotomy (case 15) and the best of the two animals with a *bilateral precentral cortical ablation* (case 16) was noticed. The deficits in case 16 were more pronounced. When presented with a pellet in the board with both eyes open the animal reached out but the fingers were rather extended and almost no dorsiflexion occurred at

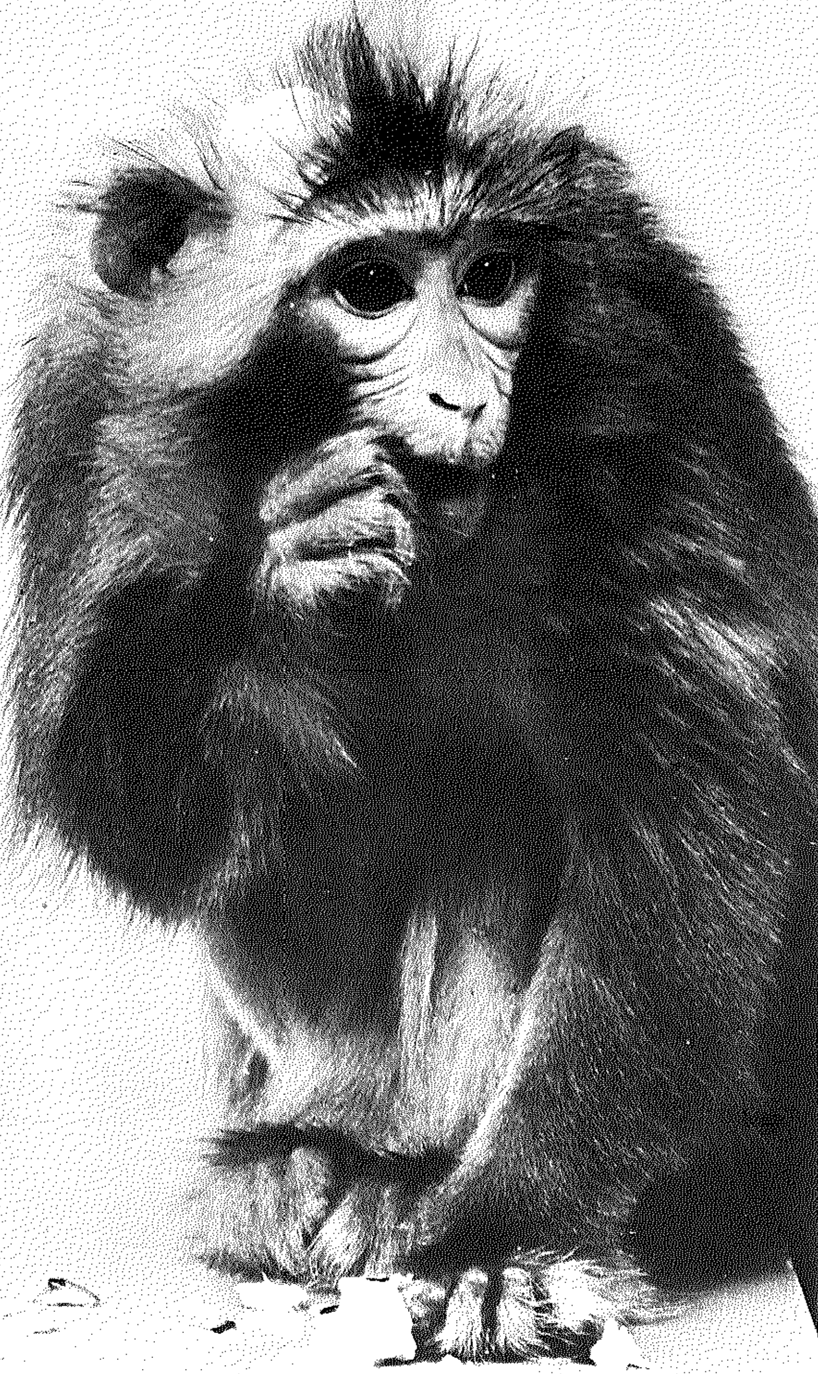
Fig. 7-4. Drawings from a film showing a split-brain monkey with a bilateral pyramidotomy (case 15) taking food from the test board with the right hand under guidance of the contralateral eye (left column) and the ipsilateral eye (right column). The contralateral hand is brought to the target and dislodges the pellet (black) by means of flexion-extension movements of wrist and fingers. The ipsilateral hand is brought to the proper place but the hand does not dislodge the pellet. Instead, the animal makes a few groping movements over the board's surface and soon gives up.


CONTRALATERAL EYE-HAND CONTROL
IPSILATERAL EYE-HAND CONTROL
CASE 15

the wrist. Moreover, the animal did not always succeed in dislodging the pellet. This failure seemed to be caused mainly by a lack of flexion-extension movements of the fingers around the pellet and by a lack of dorsiflexion at the wrist necessary to lift the food out of the well. The same deficit was observed in the contralateral eye-hand combination. When using the ipsilateral eye-hand combination in a number of trials the hand was brought onto the food in the same way as when the animal was reaching for food in a forceps. The ipsilateral hand never dislodged a pellet from the board and exploratory movements never occurred. The tendency to refuse working with an ipsilateral eye hand combination as observed in case 15 was also found in this monkey. Case 17 has never been tested on the board.

The data form this study, although preliminary, suggest that the motor control exerted by one hemisphere by way of its indirect connections to the spinal cord is different for each of the two upper extremities.
In the split-brain monkey with a bilateral pyramidotomy a variety of proximal movements of the extremity as well as distal movements of the whole hand and of all the fingers in concert seem possible under guidance of the contralateral eye. In contrast, under guidance of the ipsilateral eye mainly proximal extremity movements are observed and movements of the hand do not seem to be present except to a minimal degree in combination with movements of the whole limb.
A somewhat similar difference was observed in split-brain monkeys with bilateral precentral cortical ablations but the motor performance of these animals was inferior to that of the pyramidotomized monkeys, especially in the ipsilateral eye-hand combination.

chapter eight



The present study was undertaken to test further the ideas of Lawrence and Kuypers (1968) that the ventromedial brainstem pathways to the ventromedial parts of the spinal intermediate zone mainly steer body and integrated limb-body movements while the lateral brainstem pathway to the dorsolateral part of the intermediate zone provides the capacity for individual movements of the limbs in particular their distal part. The cortical fibers to both the ventromedial and the dorsolateral parts of the intermediate zone and to motoneurons of distal extremity muscles further amplify these controls and provide the capacity for a high degree of fractionation of movements as exemplified by relatively independent hand and finger movements.
The present results in split-brain monkeys are in keeping with this concept.
The striking agreement of these findings with observations in human patients makes it likely that hte foregoing concept on the functional organization of the motor pathways in the monkey also applies to man.

Chapter VIII: Discussion of the results.

The present findings in split-brain monkeys with a complete commissurotomy led to the following conclusions.

For the retrieval of small food pellets from the test board visual guidance is necessary. Under guidance of the nasal, seeing half of the visual field of one eye both the contralateral and the ipsilateral hand can be brought to the proper place by means of a proximal arm movement but the reaching movement of the ipsilateral arm seems slightly less accurate than that of the contralateral one. Furthermore, the contralateral hand and fingers can execute the relatively independent movements necessary for the retrieval of small pellets from the wells, in contrast to the ipsilateral hand and fingers which do not execute such movements; instead, they begin to explore the board's surface tactually, as if blind, in the same way as blindfolded animals.

The same behavior is observed when only the optic chiasm and the telencephalic commissures (corpus callosum and anterior commissure) were transected (cases 8 and 12).

From these findings it was inferred that the seeing hemisphere does not provide the ipsilateral hand and fingers with the motor control necessary to execute relatively independent hand and finger movements. This inference is only valid if the failure of the ipsilateral hand and fingers to execute such movements was not due to the reaching hand obscuring the view of the target because of the restriction of the animal's visual field. In the animals with a partial commissurotomy sparing the splenium of the corpus callosum and thus allowing transfer of visual information to the non-seeing hemisphere (cases 11,12 and 13) the ipsilateral hand and fingers did retrieve the small pellets from the wells by means of relatively independent hand and finger movements despite the fact that the hand in reaching also tended to obscure the target. This additional finding indicated that the failure of the ipsilateral hand to retrieve the small pellets after complete commissurotomy must have been caused by the inability of the seeing hemisphere to provide the ipsilateral extremity with the distal motor control needed for the execution of relatively independent hand and finger movements.

These data support the hypothesis based on anatomical and functional findings that each half of the brain has full control over arm, hand and finger movements contralaterally but mainly controls arm movements ipsilaterally. This is further strenghthened by the fact that in split-brain monkeys with unilateral cortical lesions the paretic arm when guided by the ipsilateral intact hemisphere can still execute adequate reaching movements independent of the precentral and postcentral motor and sensory areas of the non-seeing hemisphere. These findings suggest that descending connections from the seeing hemisphere are of importance for the execution of proximal movements of the ipsilateral arm. This notion is further corroborated by the fact that when in these animals the normal arm is guided by the ipsilateral lesioned hemisphere a deficit in reaching is found despite the fact that the main afferent and efferent pathways of this extremity are intact. This again indicates that the visuomotor control by one hemisphere is exerted over both the contralateral and ipsilateral extremity and not just over the contralateral one.
The conclusions presented above will be discussed in more detail in the following paragraphs.

a) *Contralateral and ipsilateral motor control in the split-brain monkey.*

The present findings concerning the differences in motor control exerted by the seeing half of the brain over the ipsilateral and contralateral arm, hand and fingers are in striking agreement with the findings in human patients in whom either the corpus callosum had been transected[102,264] or brain damage had disconnected the hemispheres[103 104]. For example, when pictures of hand postures are flashed to one hemisphere of a split-brain patient and the patient has to copy these postures with either the hand contralateral or ipsilateral to the hemisphere stimulated, the contralateral hand and fingers have no difficulty in copying any of the postures shown. In contrast, the ipsilateral hand and fingers are capable only of extending or flexing all fingers together and are unable to copy any more refined postures such as extending the index and little fingers, keeping the others flexed[102,264].

However, in contrast to the findings in human patients, in the split-brain monkey and chimpanzee the differences in motor control exerted by one hemisphere over the contralateral and ipsilateral arm, and hand have been subject to controversy.
Some authors stated that at least initially, ipsilateral eye-hand control is poor[24,76,91,94,132,169,211,212,284,287,288] while others observed that the contralateral and ipsilateral eye-hand combinations are equally proficient in reaching, visual pursuit and grasping[33,39,50,92,115,202]. The present findings may help to resolve this controversy, first by emphasizing that the limitations of the control over the ipsilateral extremity mainly pertains to relatively independent hand and finger movements. This aspect has been briefly mentioned by other authors[97,173] and is supported by the findings in human patients[102,264]. The controversy may further be resolved by the demonstration that the limitation of the motor control exerted by the seeing half of the brain over the ipsilateral hand is easily masked by relatively independent hand and finger movements which are guided not by visual but by tactile information presumably through the non-seeing hemisphere[1)].
All authors who observed no difference between contralateral and ipsilateral visuomotor control in the split-brain monkey have used simple reaching tasks in which the animals might freely use tactile cues. The same tasks were also used by those authors who noticed initial deficits in the control of the ipsilateral hand such as a 'fanning' of the fingers[91,169] and inspection of the extended hand and fingers[169]. Inspection of hand and fingers is also found in the baby monkey[121,122] and in the human infant[291] and has been regarded as a step towards

1) In the test used in the present study a defect in visual perception after the first reaching movement of the ipsilateral arm due to a shift of visual 'attending' to the non-seeing hemisphere is not ruled out. This shift may manifest itself by the exploratory movements of the ipsilateral hand into the blind half of the visual field. By reorienting towards the pellet which results in bringing the hand back to the proper place visual attention may be shifted back to the seeing hemisphere.

linking the direction of regard with that of reaching[232]. However, others have found that in the human infant the inspection behavior is competitive with reaching and is probably concerned with the first step in the development of individual control of the fingers for fine manipulation and direct guidance of them in relation to details of form perceived[291]. This notion may apply to both the baby monkey in which the capacity for individual movements of the fingers also develops only gradually[143,154] and to the ipsilateral hand in the split-brain monkey which hand lacks the direct corticospinal connections to motoneurons of distal extremity muscles presumably necessary for the execution of such movements.
The impression of some authors[90,91,132,169] that the deficit seen in the ipsilateral hand is transient may be caused by the animal's learning to use tactile cues more quickly and efficiently so that deficits may only be observed by close inspection or by analysis of slow motion pictures.

Only two authors reported severe deficits in ipsilateral motor performance in the split-brain monkey. Pronounced loss of motor abilities was described by Downer[76]. In his experiments one eye of a split-brain animal was sutured closed for a long time. Deficits in ipsilateral motor control were found especially when the first eye was opened and the second eye closed. However, this experiment has been criticized on the basis of creating an attentional bias for visual stimuli in one half of the brain because of the prolonged closure of one eye[169] which may be comparable to sectioning of the optic tract, an operation known to affect the visual cortex[244].
Keating[132] has also described deficits of both proximal and distal movements of the ipsilateral extremity when the animal had to retrieve food in a "formal test situation". The test apparatus consisted of an array of bins of varying size, the smallest requiring the use of an individual finger to retrieve the bait. The animal's arm was left free or restrained at the elbow or at the elbow and wrist. A deficit in distal movements was noticed as well as a deficit of more proximal movements which manifested itself as misreaching around the baited bin. However, "the animals often showed very little misreaching on informal tasks such as picking food off a platform or the observer's fingers".

Thus Keating's findings in this respect are similar to those of the present study which used an 'informal task' on which the animals showed little if any misreaching. However, the deficit in distal movements of the ipsilateral extremity which deficit became apparent when the test board was used, presisted throughout the survival period of the various monkeys which lasted up to 12 months.
Keating's animals all compensated for the misreaching with training and in most of them, the distal deficits also disappeared. This finding was interpreted to indicate that "the seeing half of the brain can by itself guide either limb by access to motor systems of homolateral origin". However, no ipsilateral projections to motoneurons of distal extremity muscles have been demonstrated which could account for the recovery of distal movements of the limb. A more likely explanation would be that the animals had learned how to use optimally the tactile cues provided by the test apparatus in order to retrieve the bait after the hand was brought to the target.

In summary, the differences between the findings of the present study and of those cited above concerning the motor control in the otherwise intact split-brain monkey may be explained by two factors:
a) the deficit in motor control exerted by one hemisphere over the ipsilateral extremity pertains mainly to its distal parts and affects mostly the relatively independent movements of the fingers.
b) this deficit is easily masked by hand and finger movements which are guided not by visual but by tactile information presumably through the non-seeing hemisphere.

b) *Contralateral and ipsilateral motor control in the splenium-intact split-brain monkey.*

However, the possibility exists that the deficit found in this study may have been caused by the fact that the ipsilateral hand in reaching tends to obscure the target from view because of the monkey's limited visual field. Thus the animal may not have been provided with the visual information necessary for the execution of the relatively independent hand and finger movements needed to retrieve a small pellet from the well. In split-brain monkeys with a partial commissurotomy sparing the splenium of the callosum, the ipsilateral hand and fingers were able to retrieve the pellets from the board by means of relatively independent finger movements. This indicates that the deficit observed in the ipsilateral hand of monkeys with a complete commissurotomy is due to a limitation of the visuomotor control exerted by the seeing hemisphere rather than due to the restriction of the visual field in these animals.

The almost equally proficient visually guided motor performance of the contralateral and ipsilateral extremity in splenium intact animals has also been found by other experimenters[90,212]. A transient drop in ipsilateral performance after subsequent section of the splenium (cf case 11 and 12) has been reported[90].

The present findings in splenium-intact split-brain monkeys are in good agreement with findings in human patients with only partial section of the corpus callosum[111]. These patients have no difficulty in copying any hand posture flashed to one hemisphere with either hand. The minor differences found in the motor control of one half of the brain in a splenium-intact monkey over the ipsilateral extremity as compared to the contralateral one may be a reflection of the well-documented phenomenon that intrahemispheric connections are more efficient than are interhemispheric connections in a number of tasks[25,50,95,140,141,159,195].

c) *Contralateral and ipsilateral motor control in split-brain monkeys with unilateral cortical ablations.*

The hypothesis that one hemisphere has full control over arm, hand and finger movements contralaterally but controls mainly arm movements and synergistic movements of the whole limb ipsilaterally has been confirmed further in split-brain monkeys with unilateral cortical ablations. In such animals the paretic arm when guided by the ipsilateral intact hemisphere can still execute adequate reaching movements despite interruption of the descending pathways from the non-seeing hemisphere. These observations are in conflict with those of Gazzaniga[93] who in a similar experiment observed that "the ability to use the affected hand and arm purposefully never returned" and that "an attempt by these animals to use the paralysed hand with either or both eyes open completely failed". As a consequence, "the integrity of the contralateral motor cortex is imperative for good ipsilateral eye-hand movements since the intact hemisphere could not effect any kind of purposeful control over the ipsilateral paralysed arm". The present findings indicate that the use of an extremity when guided by the ipsilateral eye is greatly facilitated by the presence of the precentral and postcentral motor and sensory areas on the convexity of the contra lateral hemisphere but that these areas are not critical for an adequate control of the reaching movements of the extremity ipsilateral to the open eye. This conclusion is supported also by findings in human patients with a complete hemispherectomy[151,279,299,304]. Gazzaniga's conclusions to the contrary stem probably from the fact that in all his cases the fronto-parietal lesions additionally destroyed the banks of the rostral part of the cingulate sulcus. The present observations as well as previous reports[281,282,283] indicate that such additional lesions result in a flexion posture of the extremity which severely restricts its reaching movements. Gazzaniga also mentions that the motor performance of the normal arm when guided by the ipsilateral, lesioned hemisphere was not affected although "when food was presented on a moving stick, reaching accuracy broke down". In contrast with these observations all the monkeys with unilateral cortical lesions used in the present study with vision restricted to the lesioned hemisphere showed reaching deficits of the normal arm. This deficit was only slight in animals with lesions involving mainly the precentral motor areas (cases 6,7 and 8) but was severe in monkeys with large fronto-parietal ablations comparable to those of Gazzaniga (cases 3,4,5 and 14). These findings may also be taken to support the notion that one hemisphere normally also exerts some control over the ipsilateral extremity.

On the basis of the findings described above, Gazzaniga has postulated that the motor control of the ipsilateral arm is based on 'cross-cuing' strategies i.e. its accurate motor response is brought about by the non-seeing hemisphere which is informed about the location of the target by means of the somato-sensory information derived from the orienting response of neck, head and eyes and it is not dependent on ipsilateral connections from the seeing hemisphere.

The present findings indicate that if such cross-cuing strategies are employed they are subject to the following restrictions. The cross-cued information can be used by the non-seeing hemisphere only in respect to arm movements, not in respect to relatively independent hand and finger movements. Further, neither the processing of cross-cued information by the non-seeing hemisphere, nor its control of reaching movements of the extremity ipsilateral to the open eye depend critically on the precentral and postcentral motor and sensory areas of this hemisphere together with the convexity of the superior parietal lobule and a major portion of the frontal areas above and below the arcuate sulcus and within its concavity. Within the framework of these restrictions the non-seeing hemisphere may control the movements of the extremity ipsilateral to the open eye.

However, if cross-cuing strategies are employed it becomes hard to understand why in the animals with unilateral cortical lesions the normal arm when guided by the ipsilateral lesioned hemisphere showed gross motor impairment while the ascending and descending connections to and from the non-seeing hemisphere are intact. However this would be explained if the ipsilateral pathways from the seeing hemisphere normally play a role in the guidance of the ipsilateral arm. This notion is supported by some older observations[49,107]. The same mechanism has been postulated to explain associative movements in hemiplegic man[316] and it has been known for a long time that in hemiplegic patients proximal movements may recover to a surprising extent,but distal movements are far more seriously affected[319].

According to Gazzaniga[97,98] the poor performance of the ipsilateral eye-hand combination with either the head or the eyes fixed cannot be predicted on the basis of the functional organization of the descending pathways described earlier (chapter II). It should be realized however, that the ipsilateral response is at least partially governed by the descending brainstem pathways since it persists after bilateral pyramidotomy or bilateral cortical ablation. Among these pathways, the ventromedial brainstem system probably plays a major role in this respect since it has a strong ipsilateral distribution in the spinal cord[148] and particularly governs integrated limb-body movements and complex movements of the limbs[156]. The fact that this system also governs head movements[156] and maintains profuse connections with structures governing eye movements[12,54,168,181,204,245,276] might provide an explanation for the deterioration of the ipsilateral

response with the head fixed[97]. Gazzaniga's experiments with split-brain monkeys with the head fixed have been criticized because fixation of the head would interfere with basic postural mechanisms[72]. These animals were not permanently impaired when using the ipsilateral eye-hand combination and with training regained their proficiency in reaching. Gazzaniga explains this by assuming that although the head is fixed, the eyes can still cross-cue information about the location of the target to the non-seeing hemisphere. In an experiment with human split-brain patients in whom the head and eyes were fixed deterioration of the ipsilateral response was also found[98]. However, the motor response required of the ipsilateral hand in this study was pressing a small lever, a task which seems to require the kind of refined motor action which the ipsilateral hand and fingers cannot perform in the split-brain patient[102,264] and Gazzaniga's conclusion in favor of cross-cuing seems therefore not wholly valid.
The present findings although based on a "simple connectionist's view" [93,99] suggest that the seeing half of the brain also plays a major role role in the guidance of the ipsilateral extremity and by way of its descending connections can bring about the adequate reaching movements of this arm.

When studying the motor performance of split-brain monkeys with unilateral cortical ablations two other interesting findings were obtained. In these monkeys the capacity to execute relatively independent finger movements had been abolished contralaterally but the paretic extremity could still execute some individual movements of the hand when guided by the contralateral, damaged half of the brain. These individual movements of the hand were probably steered by the lateral brainstem pathway (cf 156) the bulk of which originates in the magnocellular portion of the red nucleus[149] and terminates in the contralateral half of the spinal cord[148]. This magnocellular portion of the red nucleus receives cortical projections from the ipsilateral precentral gyrus[149] which was destroyed in these animals. The persistent capacity of these monkeys to make some visually guided movements of the contralateral hand under control of the damaged half of the brain therefore shows that in the absence of the cortical projections to the magnocellular red nucleus the visual centers still possess other routes of access to the ipsilateral cells of origin of the lateral brainstem pathway. A second additional finding in these monkeys with cortical lesions was the important role of the cortex in the rostral upper bank of the cingulate sulcus, the supplementary motor cortex[309] in respect to reaching movements. In all animals in which the entire supplementary motor cortex had been included in the lesion, the paretic arm developed a flexion posture with adduction in the shoulder, flexion of the elbow and wrist and flexion or extension of the fingers (cf 281,282,283). When only part of the supplementary motor area was spared this flexion posture did not develop and the animals were capable of full extension of the affected arm.

d) *Contralateral and ipsilateral motor control in split-brain monkeys with telencephalic and serial complete commissurotomies.*

The findings in the split-brain animals with only a telencephalic commissurotomy (cases 8 and 12) suggested that although the ipsilateral extremity lacks the visuomotor control for the execution of relatively independent finger movements some form of control of whole hand movements was present. In these animals each hand when reaching out for food on the board assumed a posture reminiscent of the precision grip posture seen in the contralateral hand, keeping the fingers flexed but the index finger semiflexed and the thumb semiflexed or extended. In contrast, animals with a complete commissurotomy showed a different posture in each hand when reaching for food under guidance of the ipsilateral eye. In general, the hand which the animal prefered in reaching with both eyes open tended to be kept more flexed than the other. Completion of the commissurotomy in the former group of animals did not abolish the elaborate posture of the ipsilateral hands. This probably results from the fact that operations done in several steps do not necessarily produce the same effect as that same operation done in one session[86].

In the split-brain patient an asymmetry is also found in the motor control exerted by each hemisphere over the ipsilateral hand[102,264]. The control of the minor hemisphere over the right (preferred) hand is inferior to that of the dominant left hemisphere over the left hand. In the split-brain monkey this difference in ipsilateral control of each of the two hemispheres thus seems to be the reverse of man, and the hand which is normally preferred seems to receive more motor control than the other hand. However, while in man there are strong indications for the existence of hemispheric specialization and hand preference linked to one particular hemisphere, evidence for hemispheric differentiation in the monkey is scanty and evidence for a link between one specialized hemisphere and the preferred hand in this animal is virtually non-existent. In a recent investigation, Beck and Barton[26] have investigated the existence of hand preference in ten monkeys using a variety of tasks which included one or more sequential motor acts in order to retrieve the bait. "Incentive retrieval (picking up the raisin using the precision grip) tended to be performed with the left hand whereas acts not directly involved in the picking up of the reward tended to be performed with the right hand" using more the palmar or power grip[203]. A difference in motor 'sophistication' was also found in the baboon for each hand and was reflected in a difference in manipulative strategies[290]. The difference found in our experiments in the ipsilateral motor control exerted by each half of the brain may also be caused by a hemispheric difference.

e) *Effects of a lesion of the lateral brainstem pathway on ipsilateral eye-hand control.*

The results in case 9 with a partial lesion of the rubrospinal tract suggest that elements of the lateral brainstem pathway may be involved in bringing about the elaborate posture of the ipsilateral hand since in this animal the flexion of the fingers of the hand ipsilateral to the lesion when guided by the ipsilateral eye disappeared after the rubrospinal lesion and changed into extension. The effect persisted until the animal was sacrificed 3 months later although the lesion was only partial as could be judged from the cell loss in the corresponding red nucleus. It is not clear, however, how a monkey can normally recruit these rubrospinal elements for the red nucleus which sends its fibers to the extremity ipsilateral to the open eye is situated in the contralateral, non-seeing half of the brain. To the experimenter's knowledge no anatomical or physiological data exist which could help to explain the findings in case 9.

f) *Contralateral and ipsilateral motor control in split-brain monkeys with bilateral pyramidotomy or bilateral precentral cortical lesion lesions.*

The data obtained on the visuomotor control in split-brain monkeys with either a bilateral pyramidotomy or bilateral precentral cortical ablation (cases 2 and 15,and 16 and 17,respectively) must be considered as preliminary. The evidence so far suggest that in these animals also a difference exists in the control exerted by one hemisphere via its indirect pathways to the spinal cord over the movements of the contralateral and ipsilateral extremities. This difference parallels that found in otherwise intact split-brain monkeys and seems again to pertain mostly to the more distal part of the extremity.
The animals with a bilateral pyramidotomy performed better than those with bilateral precentral cortical ablations. This has also been found in rats[57,58] and has been described in human patients[128].
This may be explained by the fact that after bilateral pyramidotomy, the cortical projections to the cells of origin of the descending brainstem pathways are still intact while in animals with cortical lesions cells of origin of as well the pyramidal tract as cells projecting to the brainstem nuclei are destroyed.

Conclusion. The present study was undertaken to test further the ideas of Lawrence and Kuypers[155,156] that the ventromedial brainstem pathways to the ventromedial part of the intermediate zone mainly steer body and integrated limb-body movements while the lateral brainstem pathway to the dorsolateral part of the intermediate zone provides the capacity for individual movements of the limbs in particular their distal parts. The cortical fibers to both the ventromedial and dorsolateral parts of the intermediate zone and to motoneurons of distal extremity muscles further amplify these controls and provide the capacity for a high degree of fractionation of movements as exemplified by relatively independent finger movement. The present results in split-brain monkeys are in keeping with this concept. The striking agreement of these findings with observations in human patients[102,103,104,264,279,299,304] makes it likely that the foregoing concept of the functional organization of the motor pathways in the monkey also applies to man.

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SUMMARY

1.- In the present study an investigation has been made of the motor control exerted by one half of the brain over each of the two upper extremities in the rhesus monkey. The hypothesis based on anatomical and functional findings that one half of the brain can steer movements of each of the two extremities has been tested in split-brain monkeys and an attempt has been made to define more precisely which pathways in the nervous system are involved in this control.

2.- A short account has been given of the anatomy and physiology of the interhemispheric connections of the brain. Some experiments in split-brain cats, monkeys and humans concerning the functions of these connections have been briefly reviewed.

3.- The anatomical organization of the descending pathways from the brainstem and cerebral cortex and some experiments concerning the functional capacities of these pathways have been described. On the basis of these data the hypothesis has been put forward that one half of the brain by way of its descending connections to the spinal cord has full control over arm, hand and finger movements contralaterally but controls mainly proximal movements and synergistic movements of the whole limb ipsilaterally.

4.- Investigations of the visuomotor control in split-brain monkeys in which one eye was taped shut,thus confining the visual input to one hemisphere, confirmed this hypothesis. Each half of the brain was found to be able to steer arm, hand and finger movements contralaterally but mainly arm movements ipsilaterally. The limitations in visuomotor control over the ipsilateral extremity pertain mainly to its distal parts. However, the ipsilateral hand tended to cover the target and hide it from view. Thus the limitation of the movements of this hand might have been caused by the fact that the seeing hemisphere did not receive adequate visual information. Studies of the visuomotor control of split-brain monkeys in which the splenium of the corpus callosum had been left intact and in which both hemispheres received visual information revealed no deficit in the visuomotor control of the extremity ipsilateral to the open eye. These findings indicate that the deficit observed in monkeys with a complete commissurotomy was due to a lack of visuomotor control rather than due to lack of visual information since in the former group of animals the non-seeing hemisphere on the basis of the same visual information seemed to provide the hand and fingers ipsilateral to the open eye with adequate motor control.

5.- In split-brain monkeys with unilateral pericentral and frontal cortical ablations the motor control of the intact hemisphere over the ipsilateral extremity has been studied. The animals with vision restricted to the intact hemisphere were still able to make adequate reaching movements with the ipsilateral extremity despite its neurological deficits,i.e. in the absence of the descending pathways from the non-seeing, lesioned hemisphere. These data suggest that each hemisphere by way of its descending connections may control not only movements of the contralateral extremity but also plays a role in steering movements of the ipsilateral one. This is in agreement with anatomical and functional data on the organization of the motor system in the monkey and also with data obtained in human patients but is in conflict with the 'cross-cuing' theory put forward in the literature The possible reasons for the difference in results from the present study as compared to those of other studies have been discussed.

6.- The posture of the ipsilateral hands in split-brain monkeys with only a telencephalic commissurotomy has been compared with that of monkeys with additional section of the diencephalic and dorsal mesencephalic commissures. The differences found between the two groups suggested a role for the diencephalic and/or dorsal mesencephalic commissures in the control of posture of the ipsilateral hands. However, sequential transection of these commissures in several animals produced different results.

7.- A possible difference between hemispheres in directing motor behavior as reflected in the differences in hand posture in monkeys with a complete commissurotomy has been investigated. This difference in the animals studied tended to be correlated with the animals'preference for the use of one hand over that of the other with both eyes open.

8.- Data obtained in split-brain monkeys after unilateral lesions in the medulla oblongata suggest that the rubrospinal tract may be involved in the control of posture of the ipsilateral hand.

9.- The visuomotor control exerted by one hemisphere via its indirect connections to the spinal cord, i.e. by way of the descending brainstem pathways has also been investigated in split-brain monkeys.
The contralateral and ipsilateral eye-hand control has been studied in after bilateral pyramidotomy and bilateral precentral cortical ablation respectively. The findings obtained in these animals suggest that the indirect control by one hemisphere over each of the two upper extremities differed. This difference parallelled that found in otherwise intact split-brain monkeys and seemed again to pertain mostly to the control of distal extremity movements.

10.- The present study has been undertaken to test further the ideas of Lawrence and Kuypers (1968) that the ventromedial brainstem system to the ventromedial parts of the spinal intermediate zone mainly steers body and integrated limb-body movements while the lateral brain stem pathway to the dorsolateral part of the intermediate zone provides the capacity for individual movements of the limb in particular its distal parts. The cortical fibers to both the ventromedial and dorsolateral parts of the intermediate zone and to motoneurons of distal extremity muscles further amplify these controls and provide the capacity for a high degree of fractionation of movements as exemplified by relatively independent hand and finger movements.
The present results in split-brain monkeys are in keeping with this concept. The striking agreement of these findings with those in human patients make it likely that the foregoing concept of the functional organization of the motor pathways in the rhesus monkey also applies to man.

SAMENVATTING

1.- In deze studie is de besturing door één helft van de hersenen van bewegingen van de contralaterale en ipsilaterale arm, hand en vingers onderzocht bij de rhesus aap. De hypothese gebaseerd op gegevens uit anatomische en functionele onderzoekingen dat één hersenhelft bewegingen van zowel de contralaterale als de ipsilaterale extremiteit kan besturen onafhankelijk van de andere helft is getest en gepoogd is de banen binnen het zenuwstelsel die betrokken zijn bij deze besturing nader te bepalen. Dit onderzoek is gedaan bij 'split-brain' rhesus apen, dat wil zeggen in dieren waarbij de beide hemisferen van de grote hersenen chirurgisch van elkaar zijn gescheiden.

2.- De anatomie en fysiologie van de interhemisferische verbindingen en experimenten bij split-brain katten, apen en mensen betreffende de functies van deze verbindingen zijn in het kort besproken.

3.- De anatomische organisatie van de descenderende banen uit de hersenstam en hersenschors en enkele experimenten betreffende de functie van deze banen in de besturing van bewegingen zijn beschreven.
Op grond van deze gegevens kan gesteld worden dat één helft van de hersenen via de verbindingen daarvan met het ruggemerg arm, hand en vinger bewegingen kan besturen van de contralaterale extremiteit, maar voornamelijk proximale bewegingen en synergistische bewegingen van de gehele extremiteit ipsilateraal.

4.- Deze hypothese werd bevestigd door de resultaten van het onderzoek naar de visuele besturing van bewegingen van split-brain apen, waarin door een oog dicht te plakken visuele informatie kan worden beperkt tot één hersenhelft. Wanneer deze dieren met één oog gesloten stukjes voer moesten halen uit een daarvoor speciaal ontworpen test bord bleek de ziende hemisfeer in staat arm, hand en individuele vinger bewegingen te besturen van de contralaterale extremiteit, maar voornamelijk arm bewegingen van de ipsilaterale extremiteit. De beperking van visueel geleide bewegingen ipsilateraal heeft dus vooral betrekking op de meer distale delen van de extremiteit.

Deze beperking kan echter ook veroorzaakt zijn door het feit dat de ziende hemisfeer niet genoeg visuele informatie krijgt omdat door de verkleining van het gezichtsveld van deze dieren ten gevolge van de doorsnijding van het chiasma opticum èn het sluiten van een oog, de ipsilaterale hand het voer kan bedekken en dus het dier het gezicht daarop ontnemen. In split-brain apen waarbij het splenium van het corpus callosum intact is gebleven ontvangen beide hemisferen dezelfde visuele informatie. In deze dieren was er geen stoornis in de visueel geleide hand en vinger bewegingen van de ipsilaterale extremiteit aan de zijde van het open oog.Dit is een belangrijke aanwijzing dat het gebrek aan visueel geleide hand en vinger bewegingen van de ipsilaterale extremiteit bij dieren met een volledige commissurotomie niet veroorzaakt wordt door de beperking van het gezichtsveld maar veeleer het gevolg is van het ontbreken van adequate verbindingen uit de ziende hemisfeer.

5.- De besturing van bewegingen van split-brain apen met unilaterale pericentrale en frontale corticale lesies is eveneens bestudeerd. Wanneer alleen de intacte hemisfeer visuele informatie ontvangt, zijn deze dieren in staat tot het maken van adequate reikbewegingen met de paretische ipsilaterale arm ondanks het feit dat de descenderende banen naar deze arm vanuit de niet-ziende hemisfeer zijn onderbroken. Deze resultaten zijn een aanwijzing dat een hemisfeer niet alleen betrokken is bij de besturing van bewegingen van de contralaterale extremiteit maar ook bij die van de ipsilaterale. Dit stemt goed overeen met de gegevens over de anatomie en de functie van het motorische systeem bij de aap, en ook met gegevens verkregen bij de mens, maar zijn in tegenspraak met de 'cross-cuing' theorie die in de literatuur beschreven is. De mogelijke redenen voor de verschillende resultaten van deze studie en die van andere zijn bediscussiëerd.

6.- De houding van de ipsilaterale hand bij split-brain apen met slechts een telencephale commissurotomie is vergeleken met die van dieren waarbij ook de diencephale en dorsale mesencephale commissuren waren doorsneden. Het verschil tussen deze twee groepen suggereerde dat de diencephale en/of de mesencephale commissuren een rol zouden spelen bij het besturen van de houding van de ipsilaterale hand. Split brain operaties die deze commissuren stap voor stap onderbraken gaven echter resultaten die verschilden van die bij dieren waarbij alle commissuren in één operatie waren doorsneden.

7.- Een verschil in houding van de ipsilaterale handen in een aantal dieren suggereerde dat er een verschil bestond tussen de hemisferen betreffende hun capaciteit voor het besturen van bewegingen. Dit verschil scheen gecorreleerd te zijn met de natuurlijke hand preferentie van een dier.

8.- Gegevens verkregen uit split-brain apen met unilaterale lesies in de medulla oblongata suggereren dat de tractus rubrospinalis is betrokken bij het besturen van de ipsilaterale hand houding.

9.- De visuele besturing van bewegingen via de indirecte verbindingen van een hemisfeer met het ruggemerg dat wil zeggen via de hersenstam banen is ook bestudeerd bij split-brain apen. De besturing van de contralaterale en ipsilaterale bewegingen werd bestudeerd in deze dieren na een dubbelzijdige onderbreking van de pyramidebaan of na het aanbrengen van een dubbelzijdige lesie in de precentrale motorische cortex. De gegevens tonen aan dat er een verschil bestaat in de indirecte besturing door één hemisfeer van bewegingen van de contralaterale en ipsilaterale extremiteit. Dit verschil is van dezelfde aard als dat gevonden bij normale split-brain apen en heeft vooral betrekking op de besturing van distale bewegingen.

10.- Deze studie had tot doel de hypothese van Lawrence en Kuypers (1968) betreffende de organisatie van het motorische systeem bij de aap verder te onderzoeken. Volgens deze hypothese is het ventromediale hersenstam systeem naar het ventromediale deel van de intermediaire zone van het ruggemerg vooral betrokken bij de besturing van bewegingen van het lichaam en bewegingen van lichaam en extremiteiten gezamenlijk, terwijl de laterale hersenstambaan naar het dorsolaterale deel van de intermediaire zone vooral individuele bewegingen van de extremiteit bestuurt en in het bijzonder van de meer distale delen daarvan. De vezels van de hersenschors die zowel naar het ventromediale als het dorsolaterale deel van de intermediaire zone gaan en ook naar motoneuronen van de distale extremiteits-spieren vergroten de mogelijke besturing van bewegingen nog aanzienlijk en maken zeer fijne gefractioneerde bewegingen zoals bij voorbeeld relatief onafhankelijke bewegingen van de individuele vingers.

De resultaten verkregen in dit onderzoek bij split-brain apen zijn in overeenstemming met deze theorie.

De grote overeenstemming tussen deze resultaten en die verkregen bij de mens maken het aannemelijk dat het bovenomschreven concept betreffende de organizatie van het motorische systeem bij de aap ook van toepassing is op de mens.

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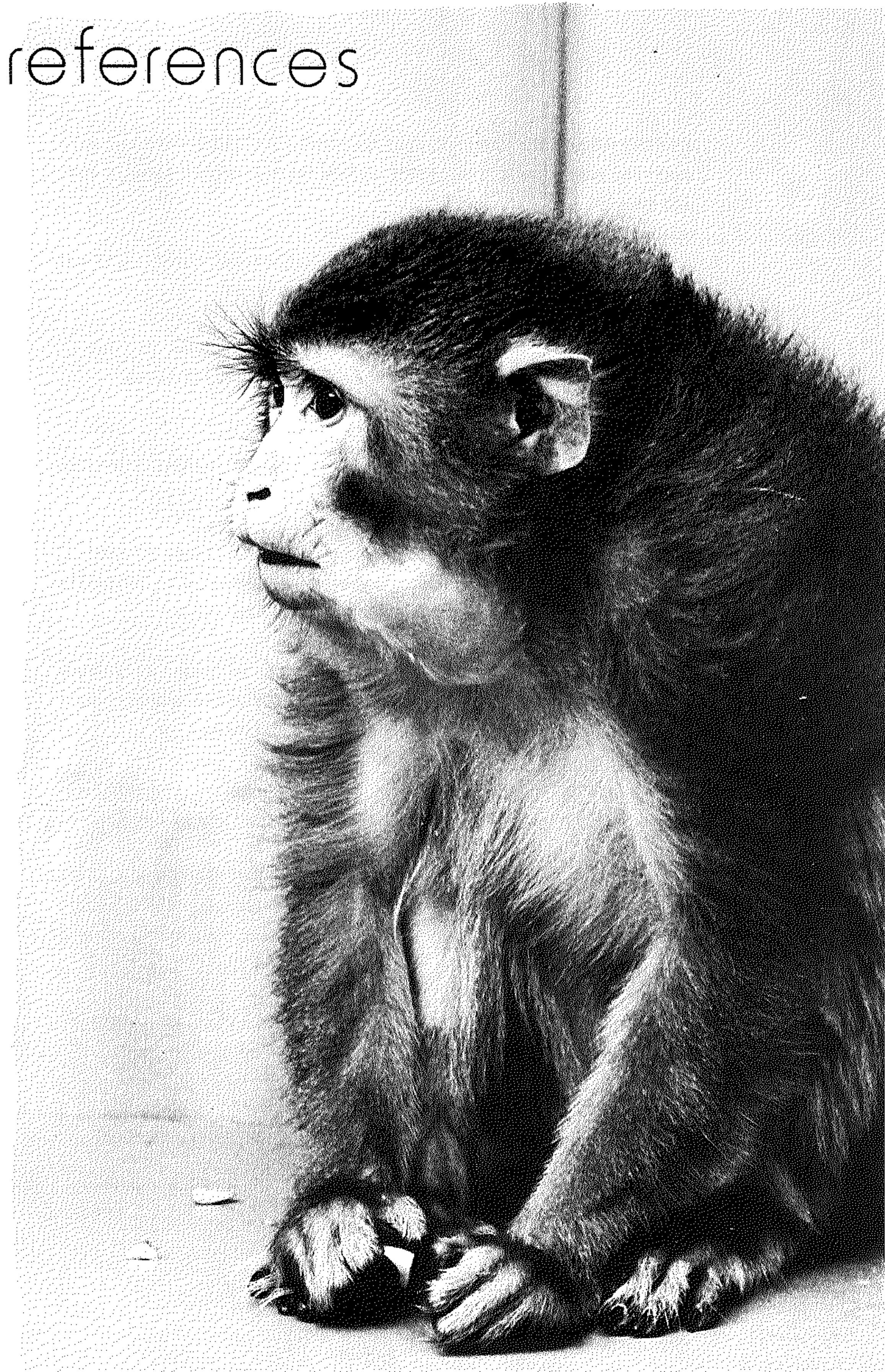

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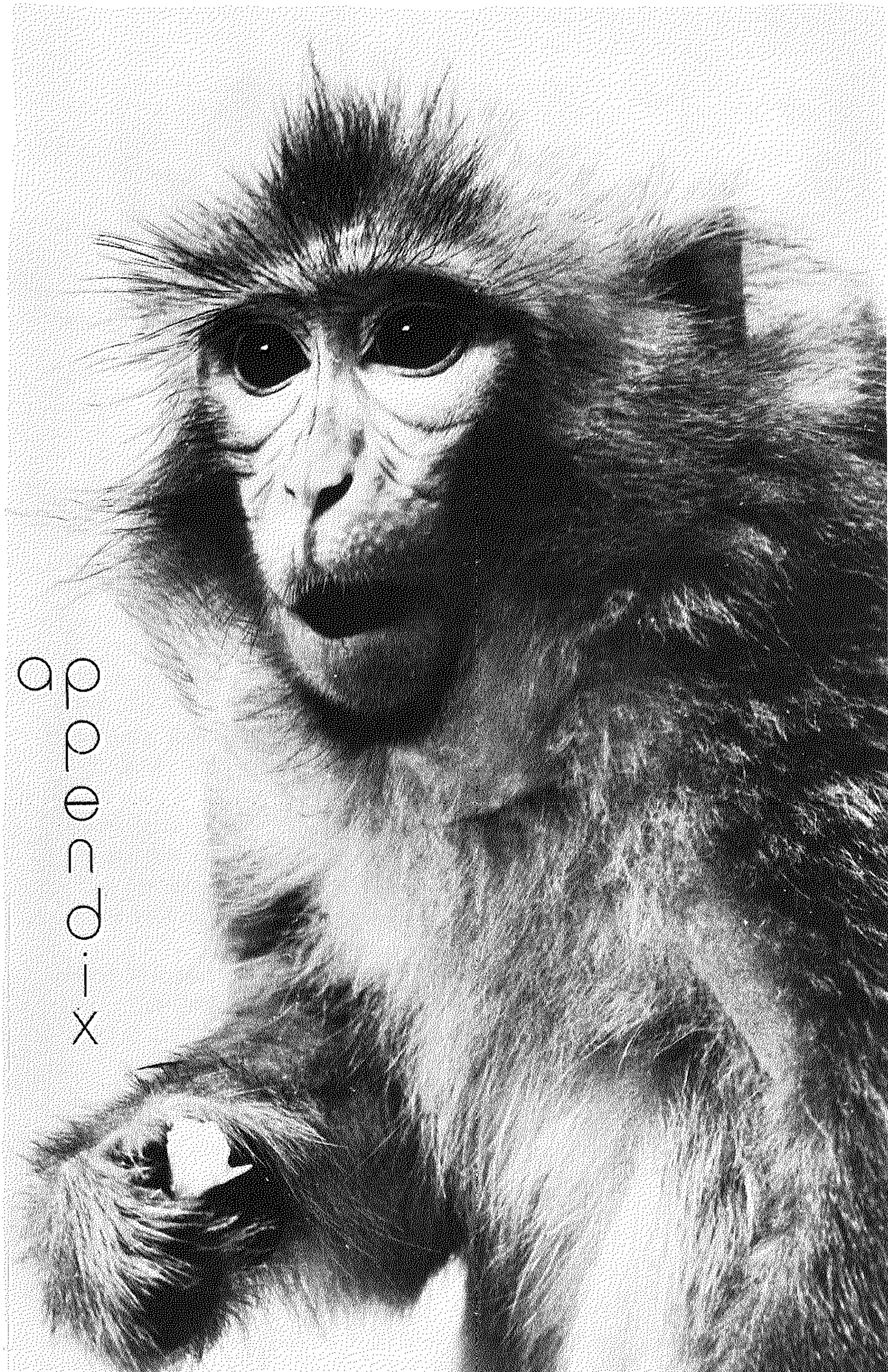
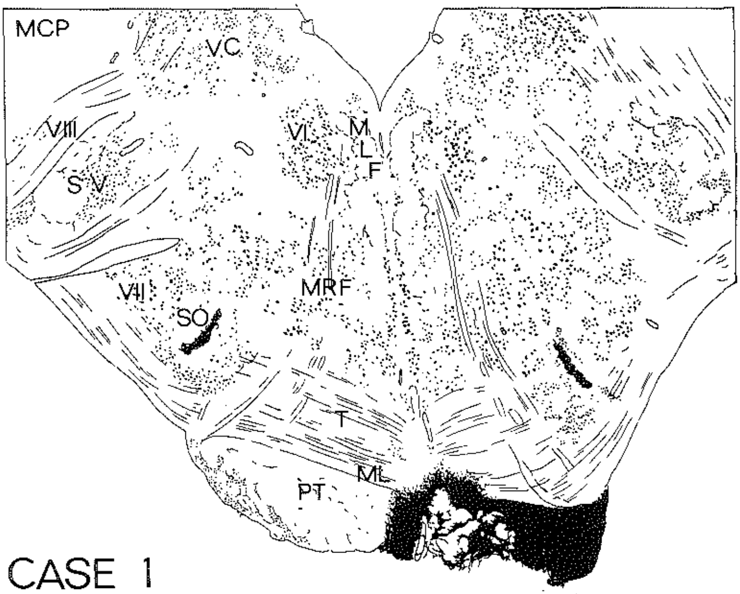
appendix

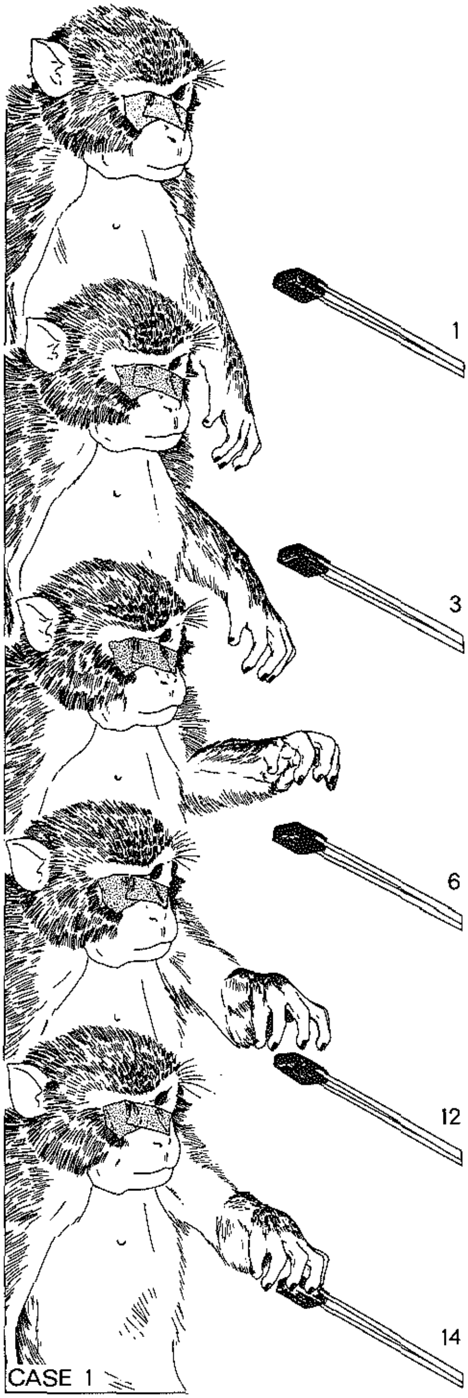




CASE 1

Plate 1-A. Lesion of the right pyramidal tract (shown in black) in a split-brain monkey with a complete commissurotomy (case 1). Note that the lesion has invaded the overlying medial lemniscus (ML) and has damaged the medial part of the contralateral pyramidal tract (PT). MCP,medial cerebellar peduncle;MLF,medial longitudinal fasciculus;MRF, medial reticular formation;SO,superior olivary complex;S V,spinal trigeminal complex;T,trapezoid body;VC,vestibular complex. VI,nucleus of abducens nerve;VII,nucleus of facial nerve;VIII,vestibular nerve.

Plate 1-B. Drawings from a film showing this monkey reaching for food in a forceps with the affected arm under guidance of the ipsilateral eye. Note the adequate reaching movement of this arm despite the fact that the pyramidal tract from the non-seeing hemisphere to this arm has been cut.
The numbers in this and subsequent plates refer to the number of frames after frame no 1 on which the movement could first be detected.
The films were taken at a speed of 24 frames/second.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CASE 1

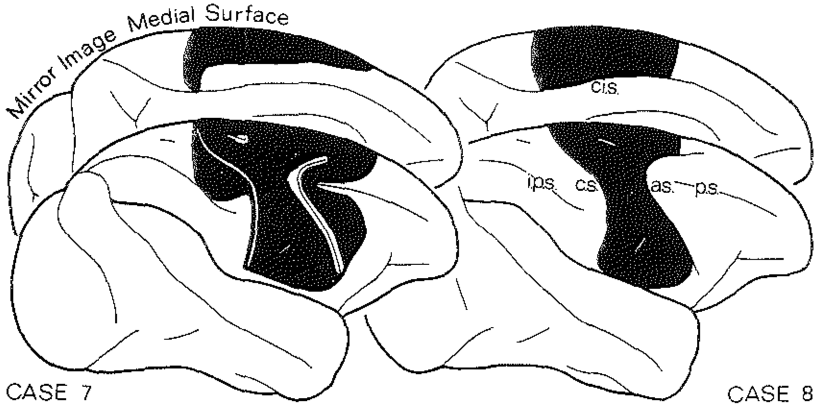
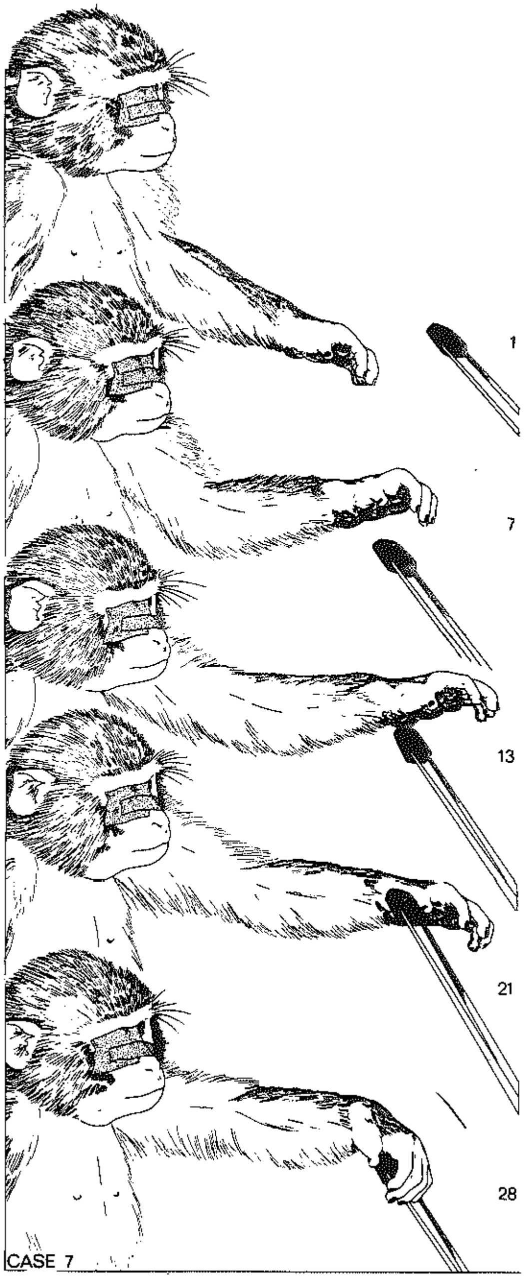
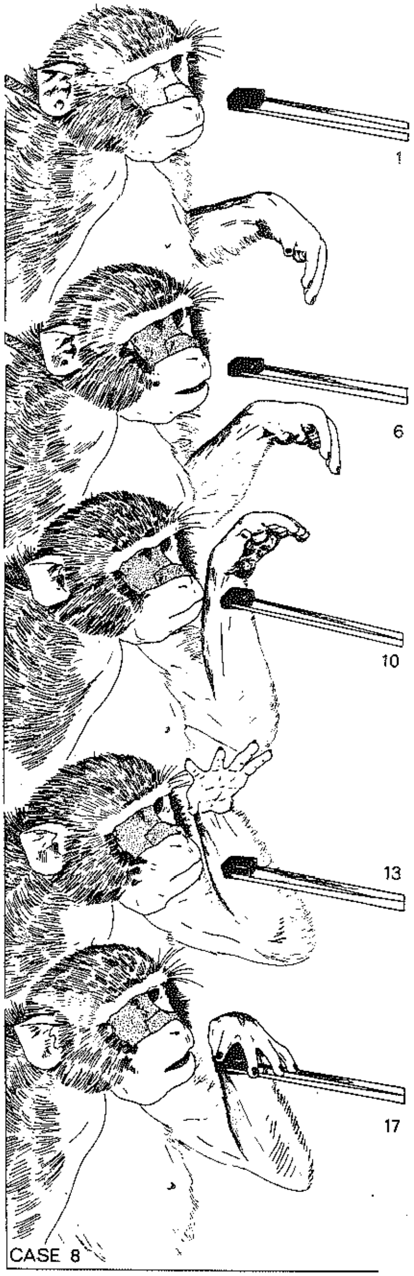


Plate 2-A. Diagrams of unilateral precentral cortical ablations in two split-brain monkeys with a complete commissurotomy (cases 7 and 8). In case 7 (left) the lesion also involves the rostral part of the post central gyrus and the somato-sensory hand area and part of the cortex above and within the concavity of the arcuate sulcus. The cortex in the banks of the arcuate sulcus has been spared. In case 8 (right) the entire precentral gyrus has been removed. The lesion was extended rostrally to include the posterior bank of the arcuate sulcus. Note sparing of the upper bank of the cingulate sulcus on the medial surface of the hemisphere in case 7 as compared to case 8 in which this area had been completely removed.
a.s.,arcuate sulcus;c.s.,central sulcus;ci.s.,cingulate sulcus;i.p.s., interparietal sulcus;p.s.,principal sulcus.

Plate 2-B. Drawings from films showing these monkeys reaching for food with the affected arm under guidance of the ipsilateral intact hemisphere. The hand was brought onto the food from above and seized it only after having made contact with it.
Note strong flexion of the arm in case 8 with ablation of the entire supplementary motor area in the upper bank of the cingulate sulcus as compared to the full extension of the arm in case 7 in which part of this area had been spared;note also the difference in posture at the start of the movement.



CASE 7



CASE 8

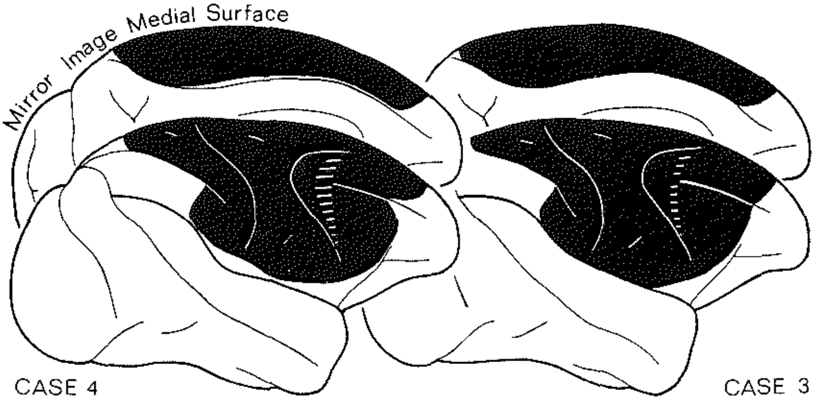


Plate 3-A. Diagrams of unilateral pericentral lesions involving the pre- and postcentral gyri and the lateral convexity of the superior parietal lobule as well as most of the cortex of the arcuate area in two split-brain monkeys with a complete commissurotomy (cases 4 and 3) In both cases some cortex in the depth of the arcuate sulcus had been spared. Note slight sparing of the supplementary motor area in the upper bank of the cingulate sulcus in case 4 whereas in case 3 this area has been completely removed.

Plate 3-B. Drawings from films showing these monkeys reaching for food with the paretic arm under guidance of the ipsilateral intact hemisphere. Ataxia presumably because of the ablation of the entire postcentral gyrus is present in both animals and was not corrected. Note full extension of the arm in case 4 with sparing of the supplementary motor cortex and the strong flexion of the arm in case 3 in which this area had been removed completely, and the different postures of the arm in these two animals at the beginning of the movement.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CASE 4
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CASE 3

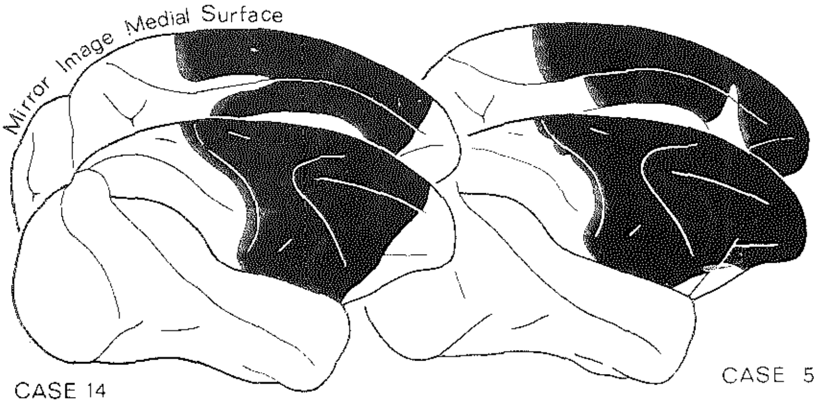
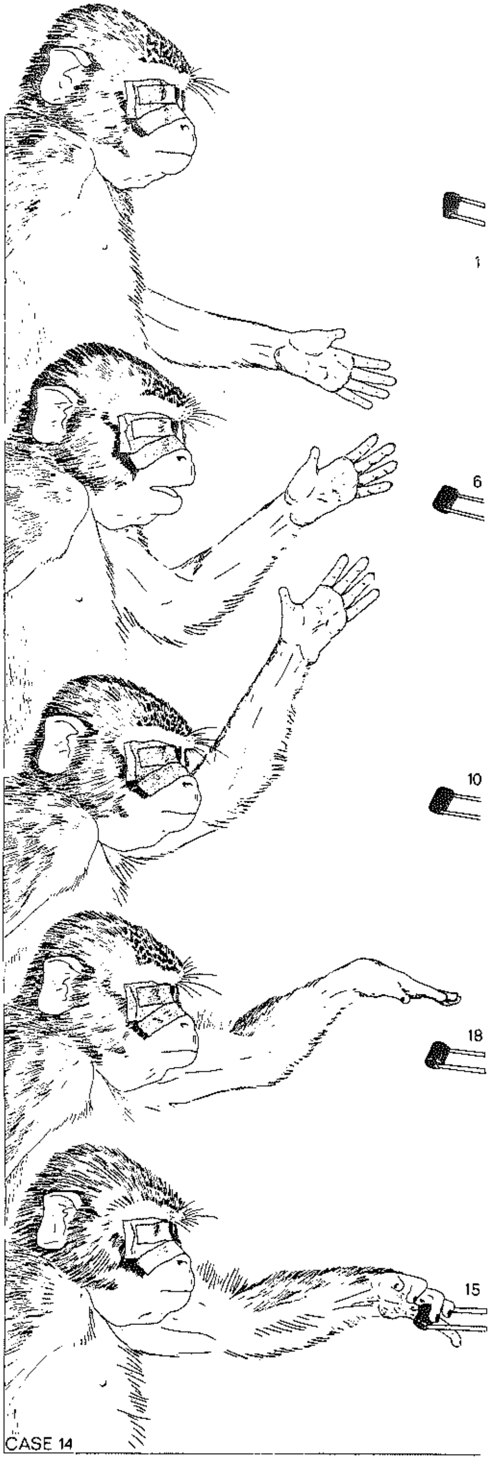


Plate 4-A. Diagrams of the unilateral frontal cortical lesions in two split-brain monkeys with a complete commissurotomy (cases 14 and 5). In both animals the lesion involved the entire precentral gyrus and the rostral part of the postcentral gyrus as well as the entire arcuate area and most of the cortex on the medial side of the hemisphere rostral to the central sulcus. Note again sparing of the supplementary motor area in case 14 as compared to case 5.

Plate 4-B. Drawings from a film showing these animals reaching for food with the paretic arm under guidance of the ipsilateral intact hemisphere. Both monkeys bring the hand onto the food from above with elevation of the arm from the shoulder which is especially pronounced in case 14 (left). Note again the full extension of the arm in the animal with sparing of the supplementary motor area (case 14). Note also the difference in the posture of arm and hand in these animals at the beginning of the movement.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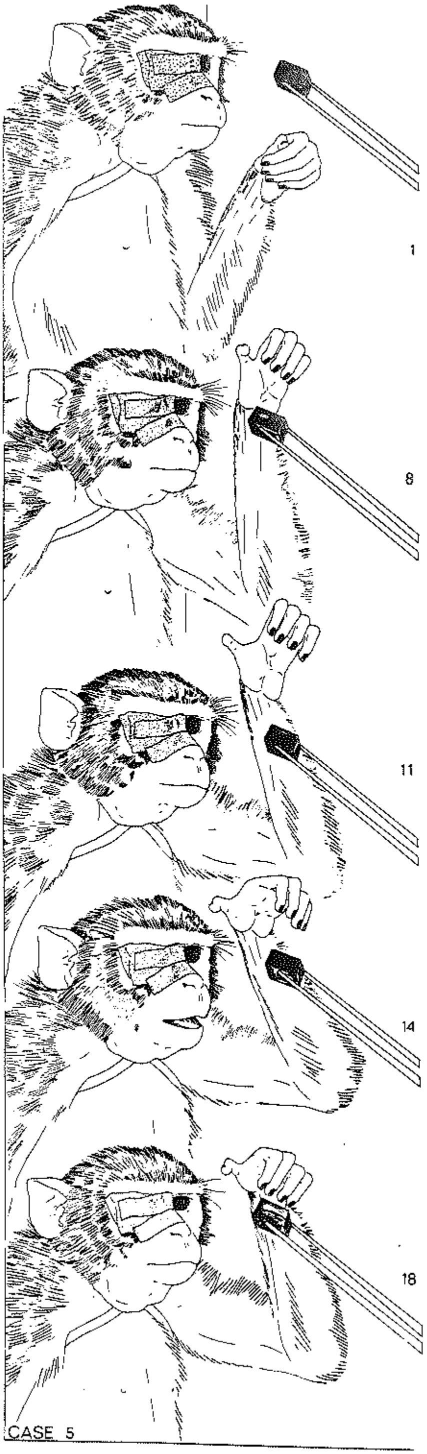
CASE 14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CASE 5

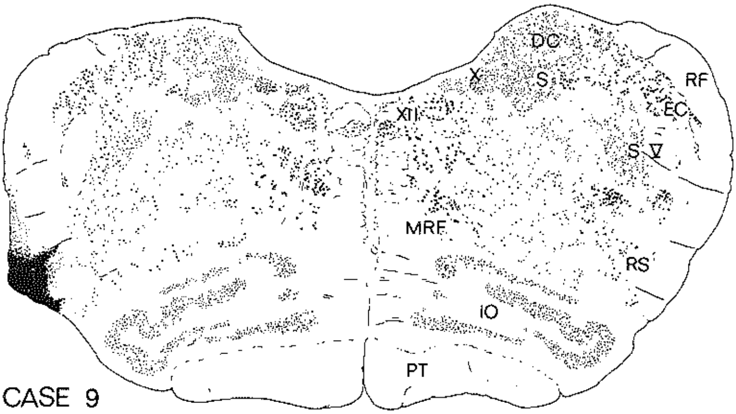
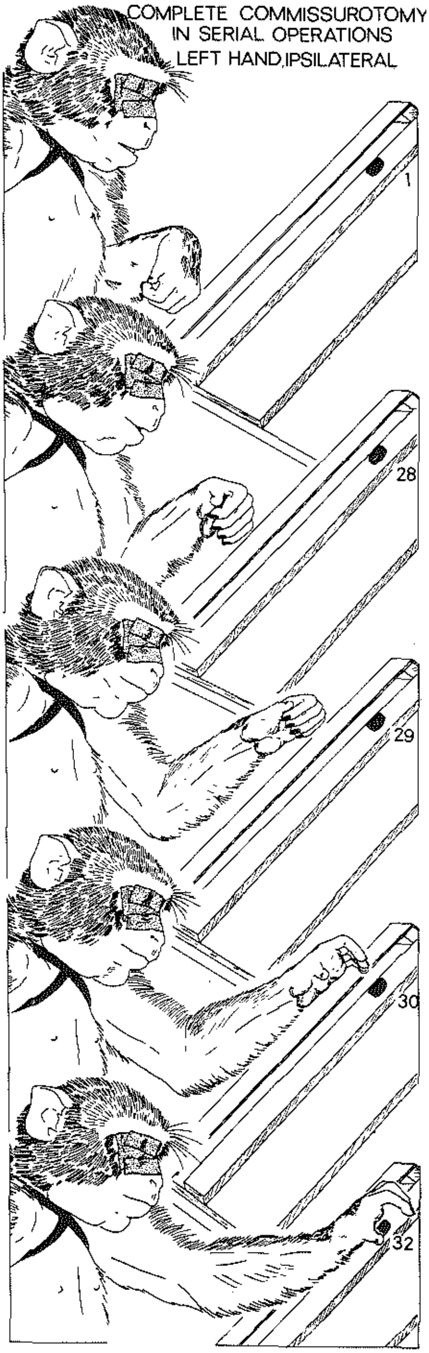


Plate 5-A. Semidiagrammatic representation of a lesion of the left rubrospinal tract (black) in the medulla oblongata of a split-brain monkey with a complete commissurotomy in serial operations (case 9). The lesion included approximately 60% of the rubrospinal fibers as judged from the cell loss in the corresponding magnocellular red nucleus.

DC,dorsal column nuclei;EC,external cuneate nucleus;MRF,medial reticular formation;IO,inferior olive;PT,pyramidal tract;RF,restiform body;RS,rubrospinal tract;S,solitary tract and nucleus;S V,spinal trigeminal complex;X,motor nucleus of vagus nerve;XII,hypoglossal nucleus.

Plate 5-B. Drawings from films showing this animal reaching for a large pellet on the board with the left arm under guidance of the left eye before (left) and after (right) a lesion of the left rubrospinal tract. Note the elaborate posture resembling that of the precision grip posture on the left. In this trial the animal spotted the bait, started a slight reaching movement which was arrested for about 1 second and then swiftly reached out anf retrieved the pellet. After the lesion, the flexed posture of the hand had changed into extension and the reaching movements were slower.

Note also the difference in hand posture at the start of the movement.


COMPLETE COMMISSUROTOMY
IN SERIAL OPERATIONS
LEFT HAND, IPSILATERAL
1
28
29
30
32

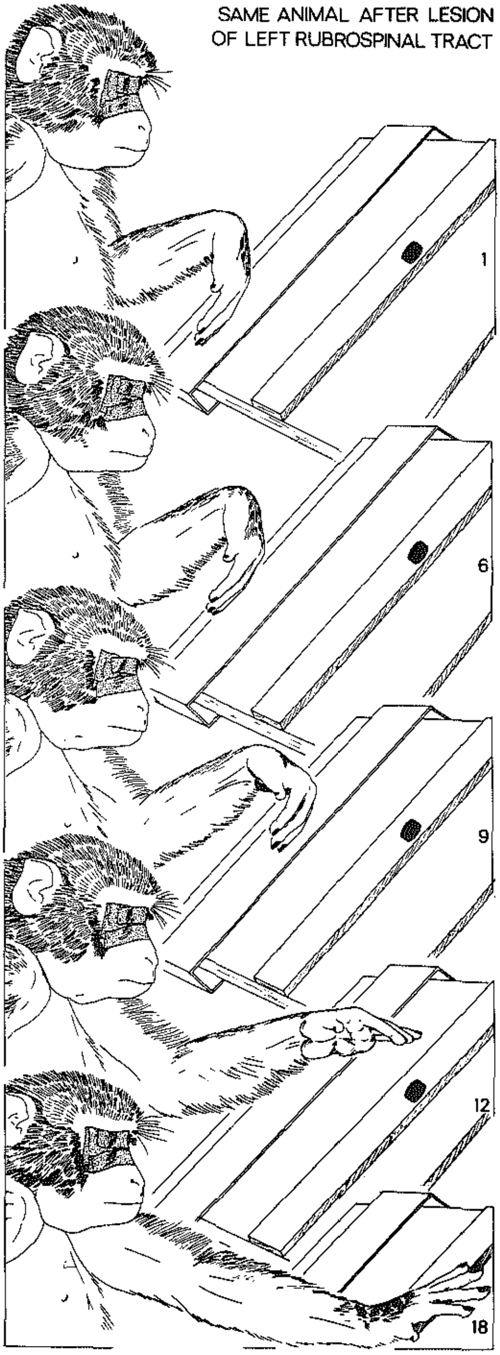
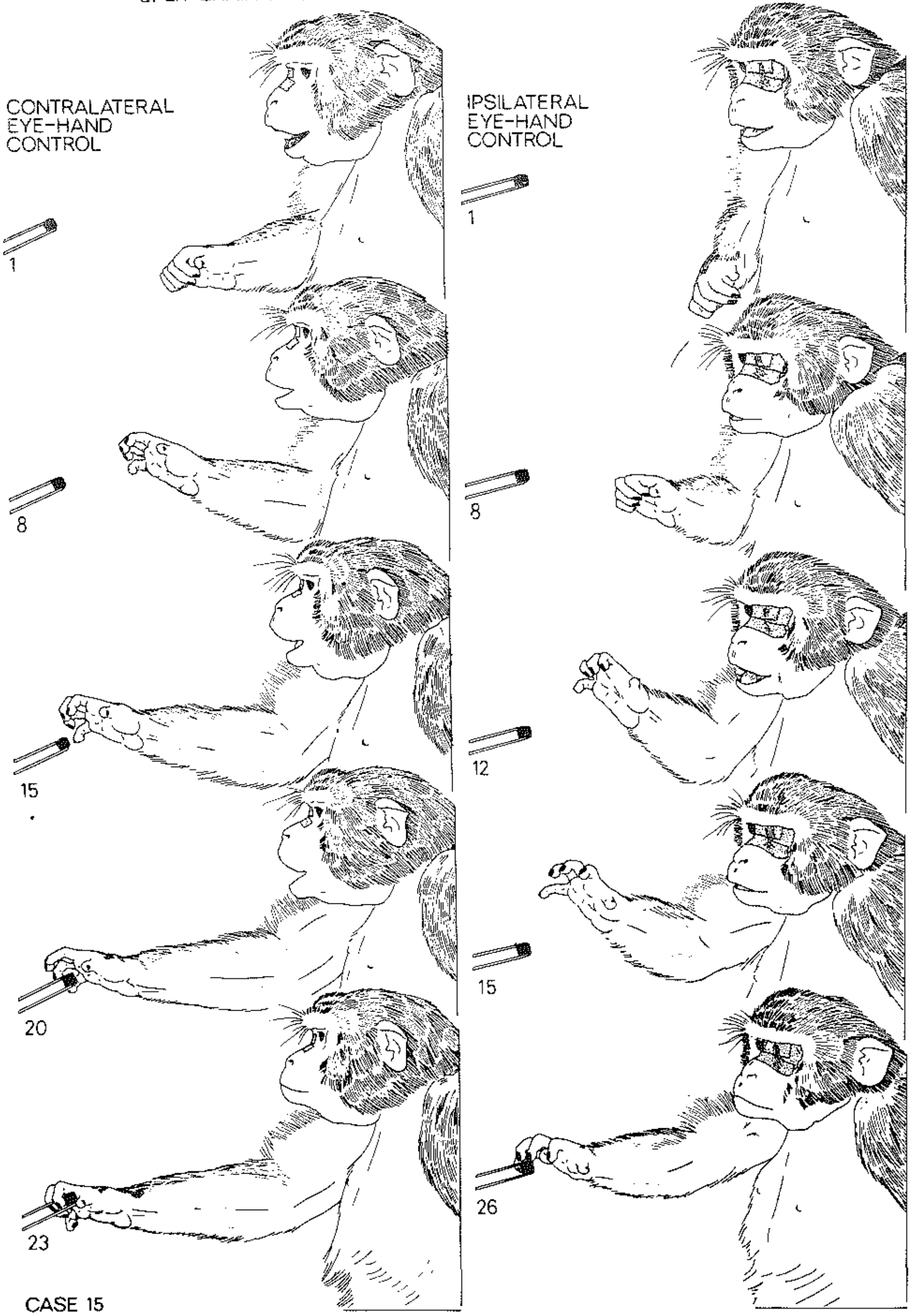

SAME ANIMAL AFTER LESION
OF LEFT RUBROSPINAL TRACT
1
6
9
12
18

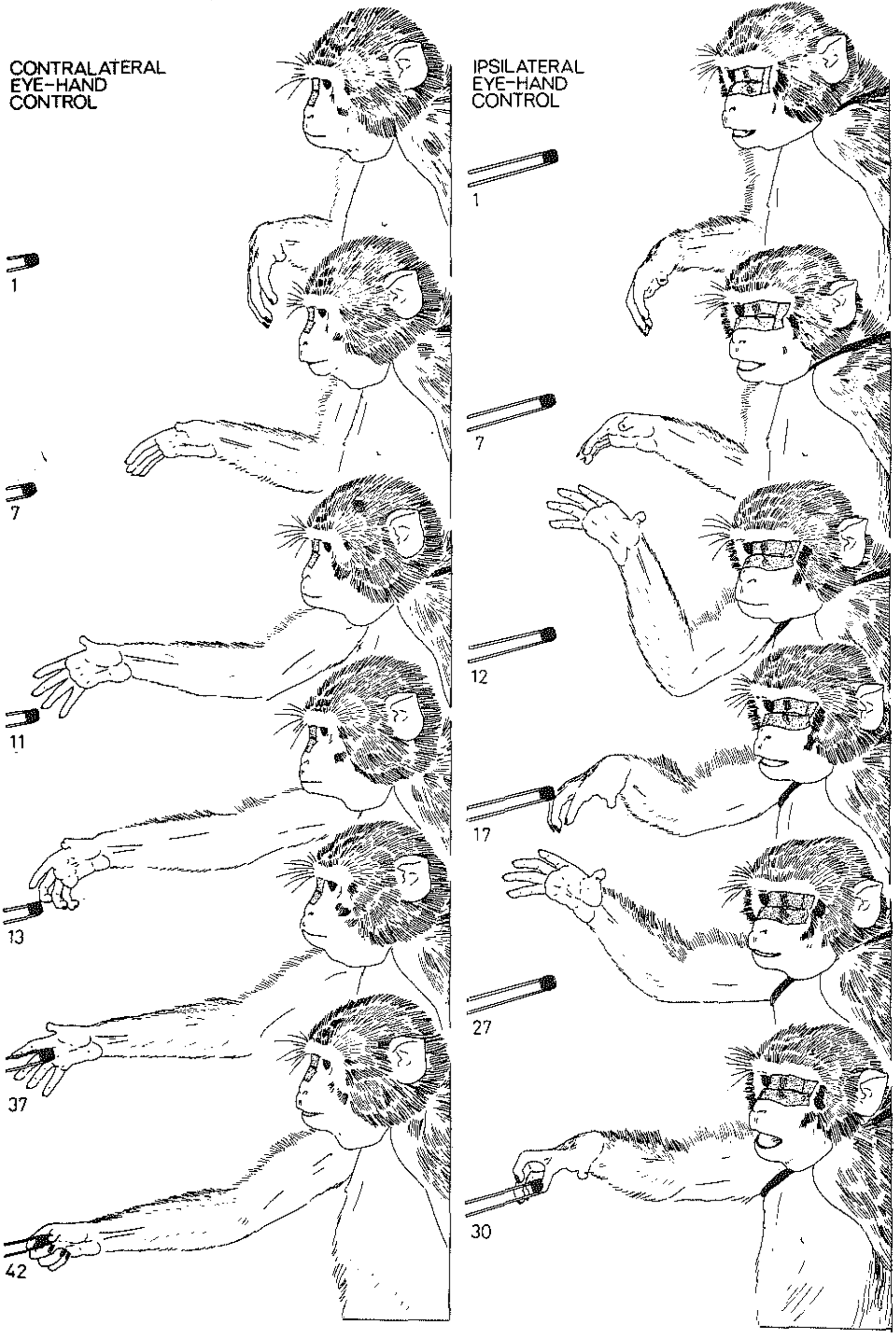
Plate 6. Drawings from a film showing a split-brain monkey with a bilateral pyramidotomy (case 15) reaching for food in a forceps with the right hand under guidance of the contralateral (left column) and the ipsilateral eye (right column).
The reaching movements do not differ significantly between the two eye-hand combinations, The contralateral hand seizes the food by opening and closing all the fingers in concert on a stable arm without prior contact.
The ipsilateral hand and fingers only retrieve the food after touching and no independent hand movements are present although some extension occurs during reaching.

Plate 7. Drawings from a film showing a split-brain monkey with a bilateral precentral cortical ablation (case 16) reaching for food in a forceps with the right arm under guidance of the contralateral (left column) and the ipsilateral eye (right column).
The contralateral arm brings the hand to the food from the side. Active closing of the hand prior to contact with the pellet can be seen in frames 11 and 13 where the food is purposely held just out of reach. When approached with the food, the fingers extend and close around the pellet (37 and 42).
The ipsilateral arm brings the hand onto the food from above. The animal just misses the target (17) but corrects its error (27,30). Note the awkward posture of the hand in 30, and compare this sequence with the ipsilateral motor control of the animal with a unilateral precentral ablation (Plate 2-B, left column).

SPLIT-BRAIN MONKEY AFTER BILATERAL PYRAMIDOTOMY



SPLIT-BRAIN MONKEY AFTER BILATERAL MOTOR CORTEX LESION



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J.BRINKMAN and H.G.J.M.KUYPERS (1972). Split-brain monkeys:Cerebral control of ipsilateral and contralateral arm, hand and finger movements.
Science 176,536-539.

J.BRINKMAN and H.G.J.M.KUYPERS (1973). Cerebral control of contralateral and ipsilateral arm, hand and finger movements in the split-brain rhesus monkey.
Brain 96,653-674.

CURRICULUM VITAE

Schrijfster van dit proefschrift, geboren 31 december 1947, behaalde in 1966 het diploma Gymnasium-B aan het Groen van Prinsterer Lyceum te Vlaardingen. In hetzelfde jaar legde zij met goed gevolg het staatsexamen Gymnasium-A af. In september dat jaar begon zij haar studie aan de toenmalige Medische Faculteit Rotterdam. In 1969 werd het kandidaatsexamen afgelegd. In het kader van het zog. keuzepracticum was zij gedurende 8 maanden werkzaam op het laboratorium voor neuroanatomie van de afdeling Anatomie in een project betreffende de distributie van corticopsinale vezels bij de rhesus aap. Hierna koos zij voor een doctoraal vrije studierichting met als hoofdvak neuroanatomie en als bijvakken neurofysiologie en neurochemie. Onderzoek werd verricht naar de projecties naar de kern van de nervus phrenicus in het ruggemerg van de kat, en naar de distributie van lange opstijgende propriospinale verbindingen en de relatie daarvan tot motoneuronen in het ruggemerg van de kat en rhesus aap. In 1971 was zij gedurende 8 maanden betrokken bij het neurochemisch onderzoek op de afdeling Chemische Pathologie. In het kader van een student-assistentschap werd van 1969-1971 geassisteerd bij het practicum neuroanatomie. In februari 1972 werd het doctoraal examen cum laude afgelegd. Sinds die tijd is zij werkzaam als wetenschappelijk medewerkster op de afdeling Anatomie waar zij betrokken is bij het onderwijs in de neuroanatomie en de anatomie van hoofd en hals en waar het onderzoek beschreven in dit proefschrift is verricht.