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DEFICIENT INFLUENCES OF PERIPHERAL STIMULI ON PRECENTRAL NEURONES IN MONKEYS WITH DORSAL COLUMN LESIONS

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SUMMARY

1. Four male monkeys (*M. fascicularis*) were trained in a movement performance task which involved pulling a horizontal lever into a target zone and then collecting, from one of a variety of positions, a small food reward. The same animals were also trained to sit quietly and accept passive manipulation and natural stimulation of the arm and hand while remaining relaxed.

2. After complete bilateral section of the cuneate fasciculi or division of a major part of these dorsal column afferents at C1–C2 or at C5 level, the animals were still able to perform movement tasks normally. Disturbance of discrimination ability was revealed after vision was occluded if the animal was required to detect differences in texture with only a small cutaneous area in contact with the object (e.g. using only the tip of the index finger). Contactual-placing reactions could be performed in the absence of vision and the movements the animal made in these reactions were well controlled and appropriately directed. Minimal disturbance of contact placing was noticed if the surface touched was on the hand or fingers or if the reaction involved crossed placing.

3. An examination of the natural discharges of 342 precentral neurones revealed that the patterns of activity exhibited in relation to complex movements were indistinguishable from patterns recorded in normal monkeys carrying out similar tasks.

4. Discharges of ninety-one of 321 precentral neurones could be produced by appropriate natural stimuli delivered within the cell's afferent input zone at the periphery. The zone from which a given cell could be influenced was usually limited and its location could be on any part of the contralateral forelimb. However, all but nine of these responses were found in animals in which a small proportion of the cuneate fibres remained intact. In an animal with histologically proven complete section of the cuneate fasciculi very few (nine of 171) precentral neurones were influenced by natural activation of peripheral receptors in the forelimb. The zones from which these few afferent inputs were found could all have been proximal to the level of the cuneate lesion.

5. The very small number of responding pre-central neurones found in an animal with complete section of the cuneate fasciculi made it likely that the dorsal columns

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provide the major pathway for effects from circumscribed peripheral receptors in the forelimb to influence precentral neurones. However, even in an animal with complete interruption of cuneate fibres, a proportion of post-central neurones could still be influenced by natural activation of peripheral receptors within restricted regions of the forelimb. Hence the 'sensory' cortex was still in receipt of afferent projections which could be revealed readily by the tests used.

6. Normal movement performance of the forelimbs, including independent finger movement, which is demonstrated after cuneate lesions is not dependent on short-latency feed-back to neurones in the *motor* cortex of precise information about joint position, muscle contractions or skin contact.

INTRODUCTION

Precentral neurones, including pyramidal tract neurones whose activity precedes and is closely related to aspects of movement performance, are influenced by natural stimuli arising from peripheral receptors (Albe-Fessard & Liebeskind, 1966; Fetz & Baker, 1969; Rosén & Asanuma, 1972; Wiesendanger, 1973; Fetz, Finocchio, Baker & Soso, 1974; Lemon & Porter, 1976; Porter, 1976). Asanuma (1975) discussed the relationship of this peripheral input to the apparent output function of the precentral cortical neurones which is detected by intracortical micro-stimulation. Lemon & Porter (1976) studied conscious monkeys trained with food rewards to accept a wide range of manipulation of the limbs. They used natural stimuli and concluded that most precentral neurones in area 4 of the cerebral cortex of the monkey could be influenced by afferent projections from limited zones in the appropriate limb. The most effective stimulus (for 71 % of the responding neurones) was joint movement, often of only a single joint in a single direction, but tapping of a muscle belly (for 16 %) and light cutaneous touches within a small receptive field (for 13 %) could cause neurones to discharge. No evidence for extensive convergence on to individual neurones of different inputs from different peripheral territories was found. In man also, natural stimulation of peripheral receptors has been shown to influence precentral neurones which discharge in close temporal relationship to voluntary movement performance (Goldring & Ratcheson, 1972).

Some of the responses to brisk stimulation of muscles or skin, even of identified pyramidal tract neurones in area 4 of monkeys, occurred with very short latencies of 6–10 msec after the peripheral stimulus (Lemon & Porter, 1976). This very brief latency, in the same range as that reported by Devanandan & Heath (1975), together with the single form of effective stimulus within a very restricted zone, suggested that the pathway for conveying influences from peripheral receptors to the motor areas of the cerebral cortex must be relatively direct and exhibit secure synaptic transmission and faithful representation of the peripheral stimulus. A candidate for such an afferent pathway in the spinal cord must be the dorsal column pathway (Mountcastle, 1961). Evidence exists to show that dorsal column section in the primate abolishes the early responses of neurones in area 3a to stimulation of group I afferents in muscle nerves (Phillips, Powell & Wiesendanger, 1971). Marsden, Merton & Morton (1973) found that, in a patient with an isolated lesion of the dorsal column, the rapid correction for an imposed disturbance of a simple flexion movement of the fingers (which could involve a 'transcortical loop') was impaired.

It was therefore of interest to examine the influences produced on pyramidal tract and other precentral neurones by natural peripheral stimuli similar to those employed by Lemon & Porter (1976) in conscious trained monkeys, but after bilateral section of dorsal column fibres travelling in the cuneate fasciculi. It became clear that monkeys need not develop serious and severe disturbances of forelimb movement performance after interruption of afferents in the cuneate fasciculi. Even though these animals demonstrated disorders of discriminative ability, particularly with their fingers, movement performances were skilfully executed in the absence of a major part of the afferent projection normally available to the motor cortex.

METHODS

Four male cynomolgus monkeys (*M. fascicularis*) were trained to pull a small horizontal lever repetitively with the right arm for food rewards. They were also trained to sit quietly and accept, without struggling, passive manipulation of all the joints of both limbs, tapping of muscles and natural stimulation of the skin (Lemon & Porter, 1976). Noxious stimuli were not used. All training employed food rewards and was continued for a period of several weeks until the animal remained relaxed and cooperative through long periods of repeated manipulation of the limbs. This relaxed state and cooperation were essential for the testing of influences of natural stimuli, and the results to be described here could not have been obtained without this prolonged preparation. The animal's motor performance and acceptance of manipulation were recorded on movie film.

At this stage, an operation was performed under general anaesthesia and with full aseptic precautions. In three animals the uppermost levels of the spinal cord were exposed through the atlanto-occipital membrane and after removing parts of the arch of the atlas vertebra. Through an incision in the dura and using a small guarded iridectomy knife the dorsal columns on both sides were divided under microscopic visual control at about C1–C2 level. Extreme care was taken to avoid damage to dorsal root filaments entering the spinal cord and to small local blood vessels. The knife-cut was extended medially and especially laterally in an effort to completely sever all dorsal column fibres in the cuneate fasciculus. The dura was closed and the wound sutured. In the fourth animal the cuneate fasciculi were sectioned at lower C5 level.

On the day following the operation the animals were replaced in the holding area where social contact with other monkeys was resumed and training in the movement task was continued. Irrespective of the level of section and in contrast to the reports of others describing the effects of dorsal column lesions in monkeys (Ferraro & Barrera, 1934; Gilman & Denny-Brown, 1966), these animals exhibited minimal ataxia of the forelimbs after recovery from the operation. They quickly demonstrated an apparently normal repertoire of movements in their free-range behaviour. Within a few days they were performing the learned movement task in a manner indistinguishable from that which had existed preoperatively. These movements were also recorded on movie film for comparison with the preoperative performance. A permanent movie record of the movement abilities of these animals is available.

The animals were retrained in the movement task and in the acceptance of manipulation for a period of about 2 weeks. Then, at a second operation under general anaesthesia and with full aseptic ritual, a specially designed headpiece was implanted on the skull giving access, through a skull defect, to the arm area of the motor cortex of three of the monkeys and the sensory cortex in one (Porter, Lewis & Linklater, 1971). Electromyographic leads were brought subcutaneously from representative flexor and extensor muscles in the right forearm to a multi-pin socket within the headpiece. Stimulating electrodes were directed stereotaxically towards the left pyramidal tract to allow subsequent identification of pyramidal tract neurones according to their responses to stimulation of axons at this level.

During two recording sessions on each day for a period of about 6–8 weeks, the activities of individual precentral neurones in the left cerebral cortex were studied using tungsten microelectrodes while the animal carried out repetitive performances of the movement task. This enabled an association to be established between a neurone's firing and an aspect of movement performance (Lemon, Hanby & Porter, 1976). The responses of each of these cells were then tested with a variety of natural stimuli delivered to the skin, joints and muscles of the right arm and hand in order to attempt to define the effective natural stimulus for causing responses in the neurone and the peripheral zone from which these responses could be obtained. In this way, for each neurone, its response to peripheral stimulation could be classified and compared with the response of the same cell during an aspect of active movement. In one animal, neurones in the post-central gyrus were examined for comparison with the observations of Dreyer, Schneider, Metz & Whitsel (1974).

At the completion of the recording period, the animal was again anaesthetized, marker electrodes were inserted stereotaxically into the brain, and the brain was perfused with fixative. Serial sections were cut and stained for identification of electrode tracks and for examination of the region of the dorsal column lesion. A tracing of a photomicrograph of the complete section of the cuneate fasciculi in Monkey 3 is shown in Fig. 1. All reconstructions of the dorsal column lesions were made after careful microscopic examination of serial sections of celloidin embedded blocks of the appropriate region of spinal cord. Since no individual 25 μm section of the spinal cord could give a representative picture of the total extent of the damage to the cuneate fasciculi or of the gliosis resulting from it, reconstruction of the full extent of the lesion was possible only by projection of a large number of sections and tracing of the damaged regions. High-power microscopy confirmed the loss of axons in the cuneate fasciculi and their replacement by glial reaction.

RESULTS

(A) *Behaviour of the monkeys following dorsal column section*

It has been stated by Gilman & Denny-Brown (1966) that high cervical dorsal column section disturbs all spatially projected movements of the forelimbs and causes particularly severe defects in contactual orientating reactions. But the four monkeys which were subjects for these experiments were not seriously handicapped even immediately after the operation to divide the cuneate fasciculi. Repeated study of the animals and careful examination of the movie film of their free-range motor performance revealed that, with vision intact, even on the first few days after the operation to divide the cuneate fasciculi, the forelimbs could be projected into space successfully, were accurately directed towards a food target or the handle of the lever, formed an appropriate grasp on the object once contact was made and performed subsequent flexion movements in a well co-ordinated manner. An exception was a monkey with a lesion which extended beyond the dorsal columns to involve the dorsal horn on both sides (Monkey 4, lesion illustrated in Fig. 5). This animal had difficulty in fine manipulations with the hand, which persisted after the lesion had been made. With retraining, performance was restored to normal levels in a few weeks for the lever-pulling task. Fine control of finger movements, particularly in the right hand during grooming and food manipulation, was never restored to normal in this monkey, however. The fingers were not used independently by this animal but spatial exploration and manipulation of surfaces to retrieve food rewards using the whole hand were well executed under visual control. Even with vision occluded, this animal, like all the others, demonstrated dexterity in tactile exploration of a surface containing gutters and raised areas which were scattered with food rewards.

The lever-pulling movement task was performed in a way indistinguishable from the normal action observed pre-operatively in all the animals. Even when vision was occluded, after a period of retraining, each animal projected his arm to the lever, located the handle even if this was purposely displaced in space, orientated and closed his hand on this appropriately and carried out the flexion task accurately to bring the handle into the target zone. Trajectories of the hand plotted using frame-by-frame analyses of the movie film, and rates of angular movement at the shoulder, elbow and wrist were not disturbed by the section of dorsal column afferents, even in the two animals in which histological controls demonstrated this to be complete for the cuneate fibres.

With vision occluded by taping 'patches' over both eyes in each of the monkeys, contactual placing could still be performed even by the animals subsequently demonstrated to have complete cuneate lesions. Small pieces of food, held in long-handled forceps, were touched against the hairs on a part of the body surface (e.g. the forearm) and then moved slightly away but still kept in the vicinity of the point contacted. The animal immediately brought his hand to the region of the food reward, located the food or the forceps, manipulated the food from the forceps and rapidly placed it in his mouth. The accuracy of projection of the hand through space to the vicinity of the surface point contacted was slightly impaired in relation to the performance of a normal animal and, if the contact of food was made with the animal's hand or fingers, it sometimes elicited no movement response. It was as if the animal sometimes failed to register brief, light cutaneous stimuli delivered to the most distal parts of the forelimbs.

The reaching and grasping movements were most accurate when the point contacted by the food in these contact-placing tests was on the same side of the body surface as the hand which was moved to it. 'Crossed' contactual reaching and grasping, directed to a point on the opposite side of the body to the moving limb, was less accurately performed. But the impairment was minimal; the animal responded to contact and the movement performance it produced was well directed and correctly executed. These responses were recorded on movie film and have been described in full (Brinkman & Porter, 1977).

Exploration of a surface to locate food rewards hidden in small 'gutters' of such a size that they admitted only the index finger (Fig. 1) was poorly performed by all these monkeys after vision was occluded. They would insert the finger tip into gutters on the board but apparently failed to recognize and retrieve raisins which were contacted by the finger. Food rewards, even similarly small items such as raisins, were readily manipulated and picked up from a flat surface, and for this motor performance in extra-personal space, independent finger movements were executed with near normal precision. The general movements of the arm, hand and fingers executed by the monkeys with cuneate lesions were indistinguishable from those carried out by normal animals. (A tendency existed for the animals to use more than one finger in opposition with the thumb rather than to employ the index and thumb alone in gripping small food rewards but independent finger movements were still possible even after complete cuneate lesions as is illustrated in Fig. 1.)

Hence the study of the behavioural performance of the monkeys after lesions of the cuneate fasciculi and in the absence of vision indicated an impairment of discriminative ability – detection with the finger tip of the difference between an empty gutter and a gutter containing a raisin. Related to this may have been a minimal impairment of contactually directed movements, particularly when the hand had to be directed to a point on the surface of the opposite side of the body or a distally located point on the wrist, hand or fingers. These results, showing a defect of discriminative ability, are consistent with those of Vierck (1973). But natural and learned movements of the forelimb projected into space, contact-directed manipulation of the hand, grasping, and flexion movements of the whole arm were performed in a manner indistinguishable from normal. Fig. 1 illustrates the nature of the independent finger movements in representative frames from movie records before and after complete interruption of the cuneate fasciculi in one of the monkeys.

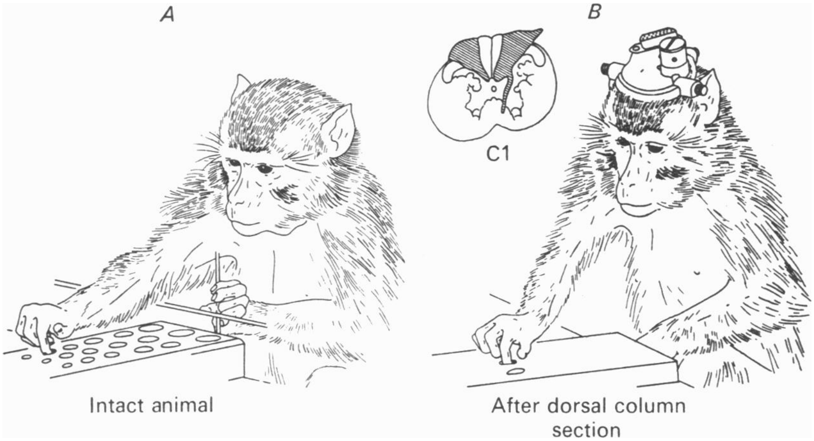

Fig. 1. Tracings made from frames of movie film to show the normal attitude of the limb and the natural movement performance of a monkey (monkey 3) before and after lesions of the cuneate fasciculi. Inset is a tracing constructed by superimposition of a number of photomicrographs of the complete lesions of the cuneate fibres in this monkey. Both before and after the lesion, the animal extended the index finger and opposed the thumb to retrieve food from a small well while keeping the other fingers flexed and out of the way.

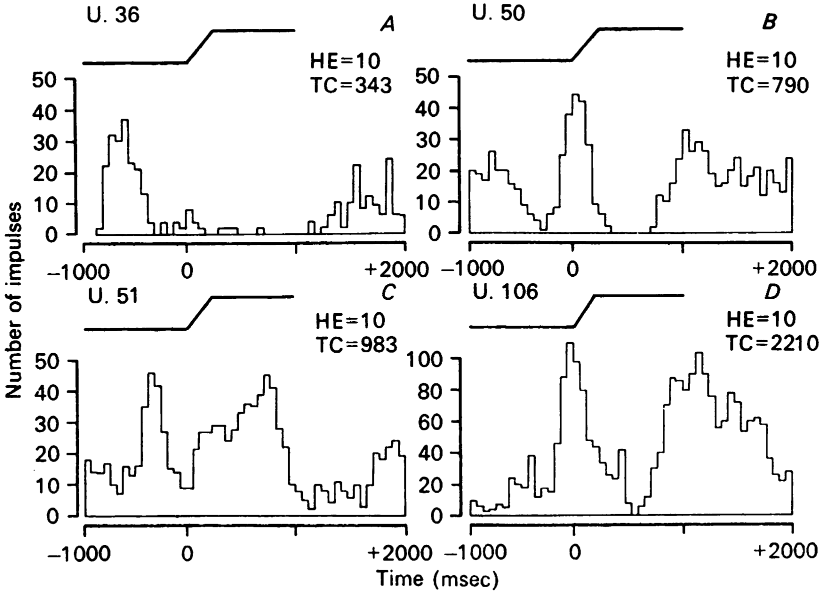

Fig. 2. For legend see facing page.

(*B*) *Afferent input to precentral neurones*

A total of 342 neurones whose natural activity was clearly related to an aspect of movement performance were examined in area 4, but only 321 were studied for long enough for a thorough and detailed examination to be made of their responses to a variety of afferent stimuli in a number of situations. These 321 will be described. Each of them was found to give a characteristic increase in discharge which was temporally associated with an aspect of the total movement performance of the animal whenever this was executed (see also Lemon *et al.* 1976). Some neurones produced bursts of firing in relation to protraction of the shoulder early in the learned movement task, others showed discharge related to extension of the elbow, extension of the fingers, grasping (the handle or the food reward), elbow flexion, wrist movements or shoulder

Fig. 2. Examples of patterns of natural activity occurring with movement performance in sample precentral neurones studied in one monkey (monkey 2) with incomplete dorsal column lesions. Each histogram is the peri-response time histogram of the discharges of a single cortical neurone examined during ten repetitions of the lever pulling and food collection movements (HE). The average duration of the lever movement is indicated by the ramp above the histogram and the total number of nerve impulses recorded during the repetitions of the movement is shown as total counts (TC).

Histogram *A* refers to a neurone whose discharges were always associated with shoulder protraction early in the performance. Subsequent elbow, wrist and hand movements associated with food collection (about 1 sec after the start of the lever movement) were not associated with discharges of the cell. This cell was not a pyramidal tract neurone but it was caused to discharge by passive extension of the fingers (category: active shoulder protraction, passive finger extension).

Histogram *B* is for a pyramidal tract neurone which discharged just before and during the movement of the lever in association with flexion of the elbow. It became silent when the animal released the lever and extended the elbow to collect the food reward (collection occurred about one second after the start of the lever movement). It then discharged again when the elbow was flexed to bring the food to the mouth. Passive flexion of the elbow was the effective natural stimulus for causing responses in this cell (category: active elbow flexion, passive elbow flexion).

Histogram *C* illustrates the responses of a pyramidal tract neurone located in a track 1 mm removed from that in which the previous unit was located. This cell always discharged during extension of the elbow, both when the arm was reached out to contact the handle on the lever and again, after completion of the pull, when the arm was extended to the food reward. Discharge was low during the flexion phase of pulling the lever and during flexion of the arm to place the food in the mouth. Food collection again occurred about 1 sec after the start of the lever movement and flexion of the elbow occurred in the next 500 msec or so. No responses of this cell to peripheral stimuli could be demonstrated even though thorough testing of the receptive zones in skin and muscle and by joint movement were carried out (category: active elbow extension, no apparent afferent input).

Histogram *D* shows the responses of a precentral neurone which was not a pyramidal tract neurone. It discharged a burst of impulses with finger flexion to perform the grasp on the lever and again to grasp the food about 1 sec after the beginning of lever movement. The cell became silent very briefly when the fingers were extended to release the lever at the end of the pull. The discharge of this cell was intense and the activity continued while the grasp (on the lever or the food) was maintained. This unit had a small cutaneous receptive field on the palm of the hand. The latency of the response to brisk stimuli applied within this receptive field was 7–10 msec, and was sometimes as short as 6 msec (category: active finger flexion, passive cutaneous field on palm).

retraction. These patterns of activity in relation to aspects of movement performance were similar to and covered the same range as patterns seen in normal monkeys. We have no way of measuring whether more or fewer cells were active for the same movement performance in the monkeys with dorsal column lesions and we have no measure of overall increases or decreases in an individual neurone's discharge in relation to the task which might have resulted from the absence of some dorsal column mediated influence (see Lewis & Porter, 1974). But the variety of patterns of discharge seen in these animals was similar to that seen in normal monkeys and the whole range of natural neuronal activity described for normal monkeys was also seen in these animals. Fig. 2 illustrates the peri-response time histograms of some representative precentral neurones during the lever-pulling movement and subsequent food retrieval about 1 sec later. This animal had some intact cuneate afferents. But similar patterns of precentral responses were seen in an animal with complete cuneate lesions (Fig. 3).

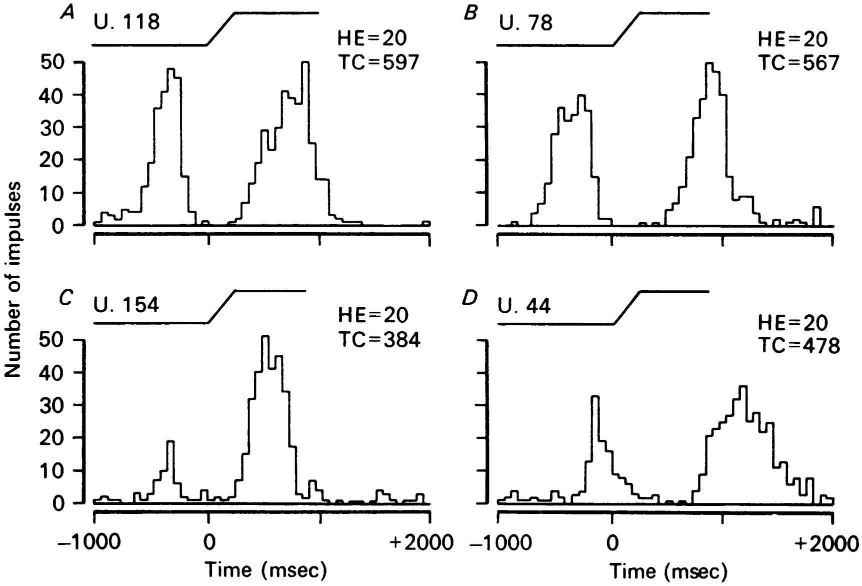

Fig. 3. Peri-response time histograms of four precentral neurones recorded in a monkey (no. 4) with complete interruption of the cuneate fasciculus on both sides. These examples, which are representative, indicate that the patterns of activity and the varieties of modulation of discharge are indistinguishable from those in a normal animal or in one with incomplete lesions of the dorsal column. Bursts of discharge accompanied characteristic movements of elbow extension (*A*), finger extension (*B*), wrist extension (*C*) and finger flexion (*D*) whenever these were performed. None of these neurones could be influenced by natural activation of peripheral receptors.

While recordings were being made from each of the 321 movement-related precentral neurones, passive movement of all the joints of the arm, muscle tapping and gentle skin stimulation with a brush or blunt probe were provided repetitively while the animal sat quietly and remained relaxed. A proportion of the precentral neurones which discharged during natural movement performance could also be influenced by these peripheral stimuli. The legend of Fig. 2 indicates the effective stimulus for each of the neurones illustrated and reveals that different precentral neurones were influenced by different peripheral stimuli. Table 1 shows the location of the peripheral zone from which each neurone could be influenced when the appropriate stimulus was provided within that zone. It is clear that, in two of the monkeys, some neurones in the precentral cortex were influenced from every region of the contralateral arm. However, histological examination of the spinal cords of each of these animals revealed some intact cuneate fibres. The distribution of 'input zones' differed in each of these two monkeys and this may have been related to the slightly different regions of the motor cortex examined, even though all the micro-electrode penetrations were made in the 'arm area'. However, the total sample studied in these monkeys was drawn from a similar region of motor cortex to the region examined in normal monkeys under the same conditions. Thus it may be useful to compare the findings in the first two experimental monkeys of Table 1 with those obtained in normal monkeys.

It appears that, in the animals with large but incomplete dorsal column lesions, a higher proportion of precentral neurones was uninfluenced by natural activation of receptors in the joints, muscles or skin of the passively manipulated limb of quiet, relaxed conscious monkeys. This observation can be accepted only tentatively because the total sample includes observations made in one animal (Monkey 2) in which many more of the neurones were studied in anterior parts of area 4 in the convexity of the precentral gyrus, a region which in normal monkeys contains a larger number of movement-related neurones without detectable afferent input from the limb (Lemon & Porter, 1976).

The effects produced in the neurones which were influenced by the natural stimuli in these two monkeys were indistinguishable from those seen in normal animals. Natural stimulation within a small and limited peripheral zone was effective. Stimuli outside this zone caused no responses. The zone for an individual neurone could be found in proximal or in distal parts of the limb. Within the zone, the most common effective stimulus was joint movement. Frequently movement of only one joint (or two or more joints of a finger or fingers) in a single direction was the effective stimulus: movement in the opposite direction had no effect (Table 2 and Fig. 7). It was the dynamic movement which influenced the precentral neurone and once the movement ceased the neurone's response generally ceased. Only a few precentral neurones continued to discharge during maintained position of a joint and this occurred when the joint was held in one extreme position.

Some neurones could be influenced by palpation (brief taps) over a small region of a muscle belly. This could be a muscle which would be stretched by the joint movement which was also effective in influencing the cell. However, a muscle input could be demonstrated for a few neurones which were not influenced by joint manipulation.

A small number of cells was discharged by gentle cutaneous stimulation within limited receptive fields usually on the hand. The sample of such neurones is too small to be compared statistically with those studied in normal animals, but the general impression was gained that cells were influenced from cutaneous fields of larger area than those most commonly found in normal monkeys (where cutaneous receptive fields tended to be confined to a single digit and to occupy an area of less than 2 cm^2).

The suggestion must be made that a tendency existed in the first two animals for stimuli to be effective in discharging precentral neurones when delivered within slightly larger peripheral territories than those found in normal monkeys. Hence, whereas a single movement at a single joint (e.g. flexion of only one inter-phalangeal joint of one finger) was by far the commonest effective stimulus in normal monkeys, movement at two or more joints (including joints in more than one digit) was

TABLE 1. Location of effective input zones

	(Normal)*	Monkey 1	Monkey 2	Monkey 3	Monkey 4
Level of lesion	(—)	C1–2	C1–2	C1–2	C5
Completeness of lesion	(—)	Incomplete: estimated 10% spared	Incomplete: estimated 15% spared	Complete:	Complete: plus damage to dorsal horns
Region studied	(Precentral 'arm' area 4)	Precentral 'arm' area 4	Precentral 'arm' area 4	Postcentral S1 areas 1, 2 and 3b	Precentral 'arm' area 4
Location of input zone					
Shoulder	(19)	1	19	4	4
Elbow	(71)	2	6	3	5
Forearm		—	5	5	—
Wrist	(61)	16	12	4	—
Hand	(14)	2	1	11	—
Fingers	(37)	7	5	9	—
Thumb	(12)	5	1	5	—
No apparent input	(43):17%	16:33%	52:51%	26:38%	162:95%
	(257)	49	101	67	171

* From Lemon & Porter (1976).

effective for a roughly equal number of cells in the animals with incomplete cuneate lesions.

When a brief tap applied over a portion of a muscle belly or a brief gentle touch applied within a small cutaneous receptive field was capable of influencing the discharge of a neurone, an estimate of the latency between application of the brief stimulus and the response of the cell could often be obtained by applying the stimulus with a blunt probe which had a sensitive mechano-electric transducer attached to its end (Lemon & Porter, 1976). Responses with very brief latencies (6–15 msec) were measured and these were within the same range as those recorded in normal monkeys. Fig. 4 illustrates the responses of an identified pyramidal tract neurone to brief taps applied within its receptive field on the palm of the hand and on the skin pads at the base of the first two digits. This cell responded regularly to these stimuli with a minimum latency of 6–8 msec after the cutaneous stimulus.

TABLE 2. Adequate stimuli for precentral neurones

(Normal)			Monkey 1	Monkey 2	Monkey 3 (post-central)	Monkey 4
(98)	(*A*)	One movement at one joint	12	17	(21)	9
(12)		More than one movement at one joint	2	5	(—)	—
(42)		Movement at two or more joints	16	16	(6)	—
(9)	(*B*)	Muscle palpation alone	—	3	(1)	—
(18)		Movement at one joint and muscle palpation	—	—	(—)	—
(8)		Movement at two or more joints and muscle palpation	2	1	(—)	—
(12)	(*C*)	Cutaneous stimulation: field $< 2\ \text{cm}^2$	—	0	(8)	—
(10)		Cutaneous stimulation: field 2–5 cm^2	1	2	(3)	—
(5)		Cutaneous stimulation: field $> 5\ \text{cm}^2$	—	5	(2)	—
(43)	(*D*)	No apparent input	16	52	(26)	162
(257)			49	101	(67)	171

The striking result indicated in Tables 1 and 2 is that, when the cuneate lesion was complete (Monkey 4 and Fig. 5), very few precentral neurones could be influenced at all by the kinds of natural stimulation of peripheral receptors which were used in these experiments. Those neurones which did respond to peripheral stimuli were only influenced by activation of receptors in the most proximal parts of the limb. The afferents from these effective zones could conceivably have been intact and could have entered the spinal cord above the C5 lesion made in this animal. The observations made in this monkey provide commanding evidence that the responses found in a smaller than normal proportion of precentral neurones in Monkeys 1 and 2 resulted from effects produced via intact afferents in the cuneate fasciculi which inadvertently escaped section at the earlier operation.

The 171 neurones recorded in Monkey 4 and referred to in Table 1 all showed pronounced modulation of their discharges in relation to movement performance. Another twenty-one neurones in the same region also exhibited bursts of activity in association with characteristic movements, but these could not be examined completely enough for their afferent input to be classified. The 171 units included representatives of all the patterns of association of neuronal discharge with movement performance that have been recorded in normal monkeys. Hence twenty-four were associated with natural, self-initiated shoulder movements (seven with protraction, ten with retraction, five with adduction and one each with abduction and rotation).

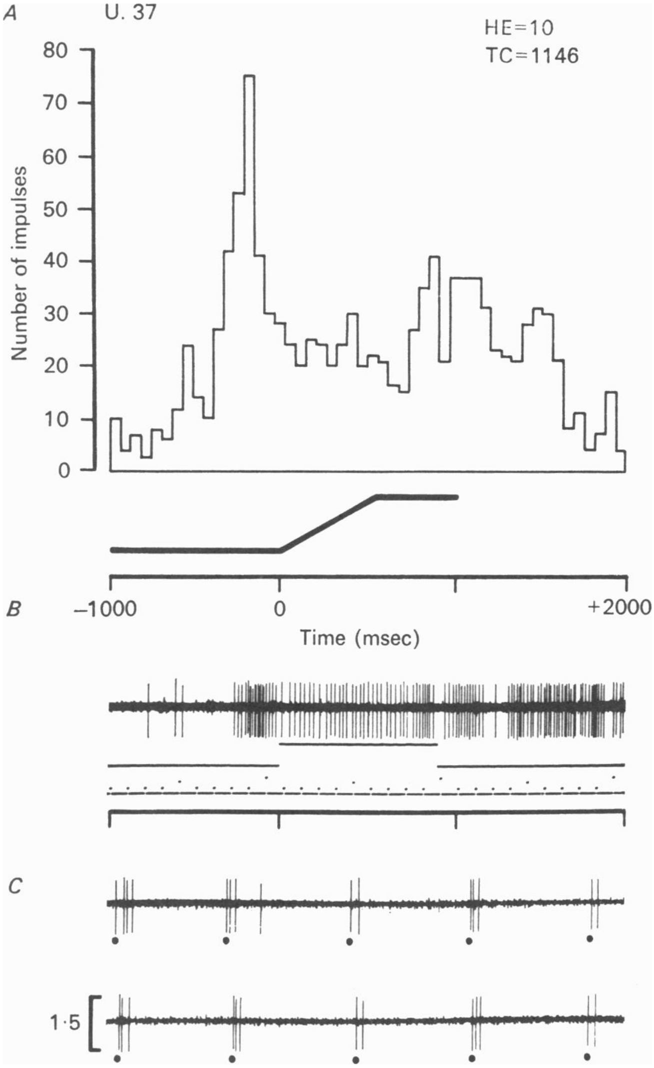

Fig. 4. For legend see facing page.

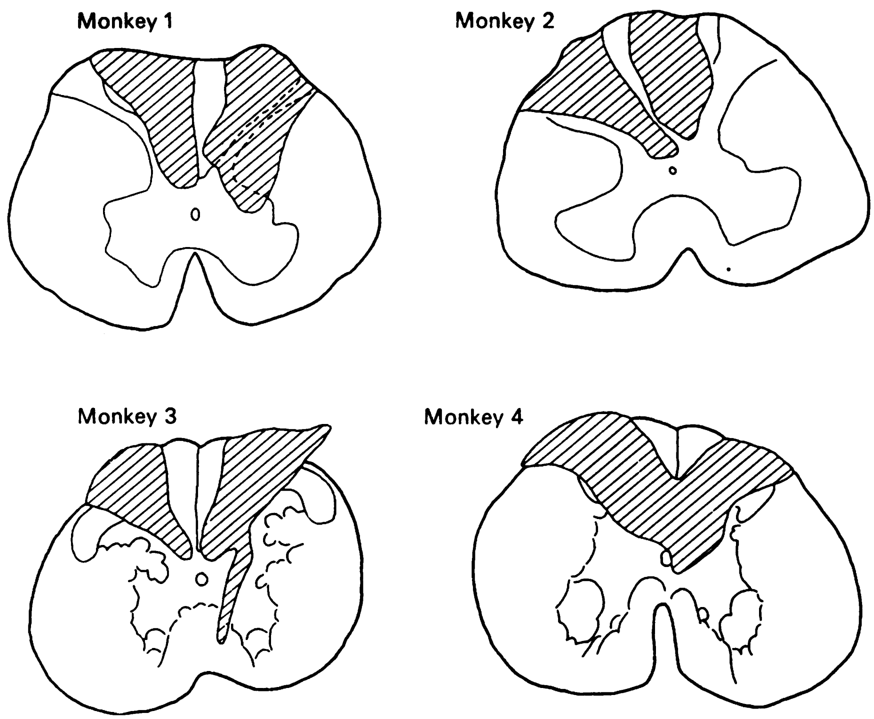

Fig. 5. Reconstructions of the lesions in the spinal cord of each of the four monkeys. These have been drawn by projection of a large number of serial sections cut through the damaged region of the spinal cord. Each section was examined with high-power microscopy to observe loss of fibres and gliosis. The diagram indicates the extent of the lesion which cannot be adequately assessed in a single section through the spinal cord.

Fig. 4. The peri-response time histogram (*A*) shows the peak of activity which occurred in this pyramidal tract neurone before each of ten movement performances to pull the lever into the target zone and then collect a food reward. The average duration of the movement of the lever is represented by the ramp below the histogram. The latency following pyramidal tract stimulation in the medulla for the discharges of this cell was 0·8 msec. Its natural activity was always associated with flexion of the fingers and a second peak of activity occurred during food collection about 1 sec after the beginning of the lever movement.

B, the responses of this cell during one performance of the movement task. The upward movement of the second trace indicates the period during which the lever was pulled away from its rest position. So the hand released the lever to reach for the food reward at a time indicated by the return downward movement of this trace.

C, the discharges produced by brisk taps applied to the palmar pad at the base of the index finger. Each time the pad was touched, the cell fired a few impulses. But, with the limb relaxed and the animal sitting quietly without moving, the neurone was otherwise silent. Tests using a mechano-electric transducer to apply the taps to this small cutaneous receptive field indicated that the first impulse in response to each mechanical stimulus occurred with a latency of 7–10 msec and very commonly with a latency of 8 msec.

Time scale for all records includes 3 sec.

A relationship to spontaneous elbow movements was seen in twenty-four cells (five were flexion-related and nineteen extension-related), and a relationship to pronation of the forearm was found for five and to supination for six neurones. The remaining associations were wrist flexion (eight cells), wrist extension (twenty-four), ulnar deviation of the wrist (two), radial deviation (seven), flexion of the fingers (sixty), extension of the fingers (thirty-two), opposition of the thumb (eight), adduction of the thumb (one) and extension of the thumb (one cell). Hence the finding of very few afferent inputs in this monkey did not relate to sampling only of neurones whose discharges were associated with proximal joint movement (Fig. 3).

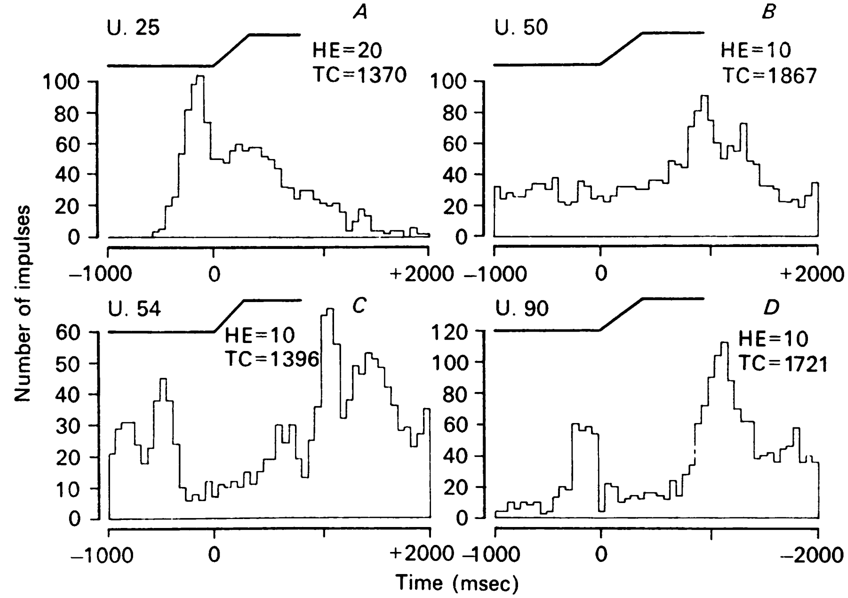

Fig. 6. For legend see facing page.

In the same animal, recordings were made from a small number of precentral neurones situated laterally within the region available for study. Of ten cells which could be examined completely and which discharged with jaw or face movements, three showed a clearly defined response to natural activation of receptors in the face.

But other regions of the cerebral hemisphere were not denied afferent input from the forelimb, even when cuneate fibres were completely severed. The findings in Monkey 3 indicated that post-central neurones were still in receipt of inputs from all regions of the forelimb. A few post-central responses to stimuli applied to the contralateral forelimb were also recorded in Monkey 4. These inputs were directed mostly to areas 1 and 2 and, although electrode penetrations were made into area 3b, very few responsive neurones were found in that cytoarchitectonic region. The inputs to areas 1 and 2, which must be conducted by pathways other than the cuneate fasciculi, could be demonstrated to come from cutaneous and from deep receptors (Table 2). In general, the findings parallel for the arm area of the somato-sensory cortex of the conscious monkey, the findings of Dreyer *et al.* (1974) for the leg area and these postcentral responses, which are independent of conduction in cuneate afferents, have been described (Brinkman & Porter, 1977).

(*C*) *Relationship of input to apparent output function*

Only the identified pyramidal tract neurones can be considered as being output cells of the precentral gyrus. The further course of their axons beyond the medullary pyramids is not known, but some could be capable of influencing motoneurones or their adjacent interneurones. Discharges of these cells before the occurrence of a particular movement response (e.g. grasping the handle or a food reward) whenever it occurred suggested a function for such output cells in influencing the performance of that movement. A range of temporal associations of discharge from the pyramidal tract neurones and movement performance was recorded, and different such neurones

Fig. 6. Patterns of activity during the lever-pulling task and subsequent movements of the right arm to collect food rewards are illustrated for four representative identified pyramidal tract neurones in one monkey (no. 1). Each histogram is constructed by summing impulse activity of a single neurone occurring with repetition of the movement performance. HE (histogram events) records the number of movement performances summed and TC (total counts) shows the total number of impulses accumulated. The average duration of the lever movement is represented, in each case, by the ramp above the histogram.

Histogram *A* shows the behaviour of a pyramidal tract neurone during grasping of the lever before the beginning of the pull movement and continuing during this movement performance. Testing the responses of this cell during food collection with the arm in a variety of different attitudes made it clear that wrist flexion was the active movement with which the characteristic discharges of this cell were associated. When the wrist was actively extended at the completion of the lever pull and the animal reached to collect food (about 1 sec after the beginning of the pull movement) there was less discharge of the cell. Passive extension of the thumb and index finger at the metacarpophalangeal joints was the effective adequate stimulus for causing this cell to respond in the absence of movement (category: active wrist flexion, passive extension of thumb and index).

Histogram *B* shows the tonic discharge of a pyramidal tract neurone which showed no clear modulation during the lever pulling task, but which increased its discharge before and during supination of the wrist after food collection and when the hand was being turned to place the food in the animal's mouth. The effective stimulus for causing this neurone to respond when the animal was still was brisk pronation of the wrist. Passive supination of the wrist caused no response (category: active supination, passive pronation).

Histogram *C* shows the activity of a pyramidal tract neurone with peaks of response during extension of the fingers immediately before grasping the lever and again just before grasping the food reward. While the fingers were flexed round the handle of the lever (before and during the pull movement) there was less activity in this cell. Discharges increased again when the fingers were extended to release the grasp on the lever and increased in a second larger burst when the hand was extended to the food reward about one second after the beginning of the lever movement. The effective adequate peripheral stimulus for this neurone was extension of the thumb and index finger at the metacarpo-phalangeal joint (category: active finger extension, passive extension of thumb and index).

Histogram *D* summarizes the discharge pattern of a pyramidal tract neurone which discharged only before and less during finger flexion. Hence it shows one burst of activity before and during grasping of the lever prior to the pull movement and a second burst during finger flexion to grasp the food reward (about 1 sec after the beginning of lever movement). The effective peripheral stimulus for causing this cell to respond was passive extension of the thumb (category: active finger flexion, passive thumb extension).

fired in association with different aspects of the complex movement (Fig. 6). Some were active in relation to shoulder or elbow movements, others to wrist or finger movements. This association could be confirmed by requiring the animal to collect food rewards from different positions with different attitudes of the forelimb (Lemon *et al.* 1976). It was then of interest to ask, for those neurones which received a peripheral input, what relationship the demonstrated input zone and its effective natural stimulus bore to the apparent output function of the cell. For a majority (roughly two thirds) the effective stimulus for activating the unit under passive conditions came from a zone which coincided with the characteristic joint movement occurring when the cell's natural discharge was associated with self-initiated movement. Thus the pyramidal tract neurone illustrated in Fig. 4 discharged

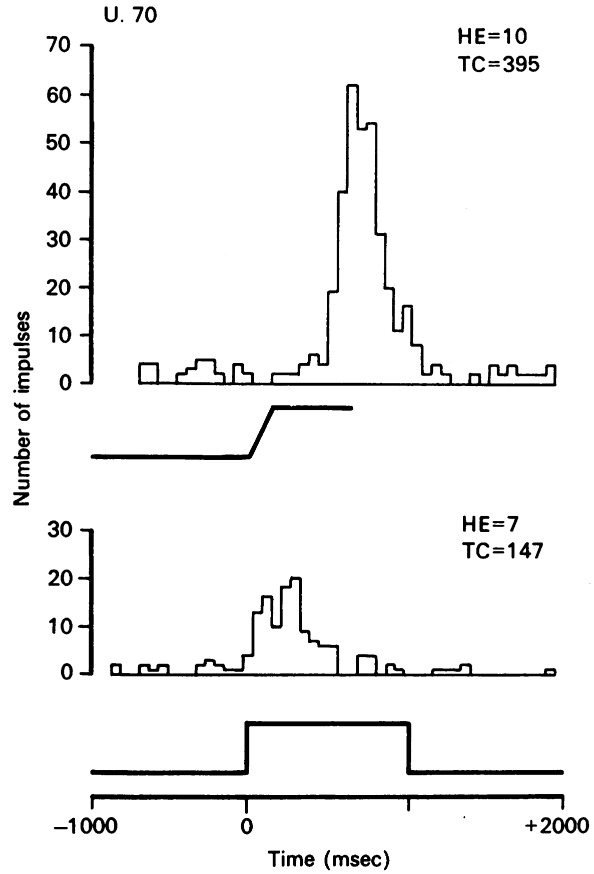

Fig. 7. The upper histogram is the peri-response time histogram of a pyramidal tract neurone which fired before and during active elbow flexion to bring a food reward, collected about 1 sec after the beginning of the ramp of lever movement, to the mouth. The smaller degree of elbow flexion associated with the earlier phase of pulling of the lever was not accompanied by significant discharge of this cell. The lower histogram indicates the influence of passive elbow flexion (performed briskly at the upward deflection of the square wave trace) and passive elbow extension (performed at the downward movement of the same trace) on the discharge of this same neurone.

regularly whenever the monkey flexed his digits in forming a grasp. The cutaneous receptive field of this unit was in the palm and at the base of two digits – a zone which would have been activated whenever a grasping movement caused successful closure of the hand over an object.

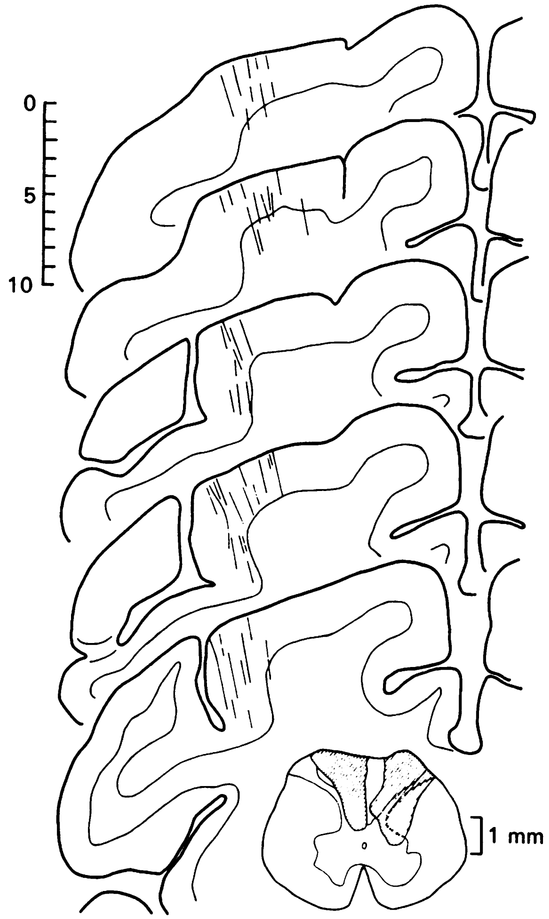

Fig. 8. Tracings of representative coronal sections through the cerebral cortex in one monkey (no. 1). These sections span an antero-posterior extent of about 3·5 mm through the arm area of the precentral gyrus and show that electrode penetrations had occurred in anterior parts of area 4 (on the convexity of the gyrus) and also in posterior regions (where some electrodes penetrated into the depths of the central sulcus).

The inset shows the extent of the lesion in the cuneate fasciculi. Projections of a number of serial sections through the damaged region were superimposed and the extent of the lesions plotted on a representative outline after microscopic examination of the region under high power. The cuneate fasciculus on the right side was almost completely interrupted.

Some of these pyramidal tract neurones whose input zones were anatomically related to the region moving during the correlated output activity of the cell were influenced by passive movements in a direction opposite to that which occurred actively during the natural discharge of the cell. Hence a pyramidal tract neurone similar to the one illustrated in Fig. 4 and discharging whenever the fingers were actively flexed was shown to be influenced by passive extension of the thumb and by extension of the metacarpo-phalangeal joints of the first two fingers. A pyramidal tract unit situated very close (within 500 μm) to the cell illustrated in Fig. 4, discharged regularly whenever the animal supinated the wrist actively. This cell was driven by passive pronation movements of the forearm and by no other peripheral stimulus (Fig. 6*B*). Roughly similar numbers of cells were affected by passive stimuli in the opposite or the same direction as those that were observed to occur during the responses of the cell accompanying self-initiated movement. Examples of these responses are shown in Figs. 6 and 7.

For approximately one third of identified pyramidal tract neurones the peripheral zone from which a natural stimulus could influence the cell was not anatomically related to the region observed to be moving when the cell's activity accompanied spontaneous movements. An example was a pyramidal tract neurone which discharged in relation to active hand movements in forming a grasp, but which was caused to respond by passive extension of the elbow and by brisk taps applied over the belly of the biceps muscle.

(*D*) *Proof of the anatomical location of the precentral neurones*

These animals were studied over long periods of time during which a very large number of electrode penetrations were made. As a consequence it was not possible to localize a given set of recordings to a particular cell in an histologically identified electrode track. But we are able to make some general comments about the locations of the responses in the precentral gyrus. The sample of precentral neurones discussed in this paper includes cells recorded in the convexity of the gyrus and also others located deeply in the buried cortex of the bank of the sulcus (Fig. 8). All the precentral neurones for which responses have been analysed were in area 4 and none was situated within area 3a, deep within the sulcus. The behaviour of neurones in the post-central gyrus (areas 3b, 1 and 2) is the subject of a separate paper (Brinkman & Porter, 1977).

DISCUSSION

It is difficult to reconcile the lack of disturbance of movement performance in these monkeys with the severe motor disability of forelimb function reported by others (Gilman & Denny-Brown, 1966; Gilman, 1975). Yet the interference with structure and the loss of afferent signals caused by section of the cuneate fasciculi must be less than those caused by division of dorsal root fibres (which cuts off all regional input to the spinal cord). Animals with complete deafferentation of the forelimbs have been shown to be capable of forelimb movement performance (Taub & Berman, 1968; Bossom, 1974). Therefore one might expect monkeys with cuneate lesions to be able to project their forelimbs into space and carry out visually-guided exploratory manipulations. Cook & Browder (1965) did report that surgical lesions of the dorsal columns produced little or no sensory or motor impairment in man. Our monkeys exhibited good motor function, including fine manipulation, even in the absence of vision, and these results are much more like those of Mettler & Liss (1959), whose monkeys with dorsal column lesions were not seriously handicapped (see also Azulay

& Schwartz, 1975). Beck (1976) also reported that squirrel monkeys with dorsal column lesions could manipulate and collect food even when this was hidden behind a partition. The monkeys he described showed no movement disability except when trying to catch pieces of food which were dropped past them. In his review, Beck (1976) points out that monkeys with complete dorsal column lesions showed disturbances of discrimination ability and of rapid, skilled movement performance. But these disorders were subtle and required refined tests to reveal them. The simplest approach to the differences between our results and those of Gilman & Denny-Brown (1966) would be to ascribe the preservation of function to the intactness of some fibres in the cuneate fasciculi of our monkeys, but we cannot conclude that this is the complete explanation, because the lesions of the cuneate fasciculi were complete in two animals and motor performance in these two animals was well controlled and skilfully executed. Our animals were studied for three to four months after damage to the cuneate fasciculi and were subjected to considerable retraining of movement performance. But, even in the first few days after operation, the only animal which showed disordered movements akin to those described by Gilman & Denny-Brown (1966) was monkey 4. It is possible that the damage to the dorsal horn in this animal caused interruption of dorsal root afferents since ataxia is common in animals with dorsal root interruption (Bossom, 1974).

Unilateral damage to the nervous system may cause more severe disturbances of function in the affected limb than bilateral damage (Gilman & Denny-Brown, 1966) and the lesions in all four monkeys described here were bilateral. The animal could not compensate for a disability in one forelimb by using only the other. We were at pains to avoid damage to dorsal root filaments or the blood supply to local regions of the spinal cord, both of which could have caused more interference with function than dorsal column section alone. Three of our lesions were made at the top of the cervical spinal cord, whereas many of the interruptions produced by Ferraro & Barrera (1934) and Gilman & Denny-Brown (1966) were made at C4–5 level in regions where local damage to other structures in the spinal cord could have directly influenced the function of the forelimbs. But, after retraining, our animal with lower cervical lesion showed motor behaviour in the natural three dimensional exploration of its environment similar to that of the other three monkeys.

Our animals were well trained and could be handled by the experimenters. They were kept in a laboratory where they interacted daily with other monkeys and with the experimenters. It was not necessary to test motor responses in defensive situations with a 'threatening object' (Gilman & Denny-Brown, 1966). Normal motor responses could be studied as the animals moved about their cages, collected food, groomed one another and took part in training of movement performance tasks. Movie film has been made of these movements and has been studied in frame-by-frame analysis to reach the conclusions reported here.

The four monkeys did demonstrate deficient capacity to discriminate the different afferent input caused by the walls of any empty groove from that caused by a raisin within the groove if only a limited surface area of contact with the tip of the index finger was permitted. We have taken this to be evidence for a significant interruption of cuneate fasciculus mediated afferent influences and a convincingly demonstrated effect on discriminative ability. Vierck (1973) found marked deficiencies in the abilities of monkeys to discriminate differences in size of disks pressed against the sole of the foot which persisted for many months after dorsal column lesions.

The animals were not required to learn any new or unaccustomed movement tasks after the dorsal columns had been cut. Those movements which they had already learned or which were part of their natural repertoire were carried out skilfully and without significant impairment even in the first few days after the operation and even in the absence of visual guidance. Other pathways (spino-thalamic, spino-cerebellar) from peripheral receptors must be competent to permit the range of sensory and motor behaviour described here.

These findings do not conflict with those of Dreyer *et al.* (1974) but may give some support to the general concept of organization of afferent projections to the cerebral cortex outlined by them. While they found that, in the monkey, the inputs to cells in central zones of the 'leg area' of somato-sensory receiving cortex, S1 (areas 1 and 3) came mainly from cutaneous receptors and via the dorsal columns, other cortical regions (e.g. area 2) received more inputs from deep receptors over ascending pathways outside the dorsal columns. Even within the central zones, they found neurones which continued to respond to peripheral stimuli following dorsal column section. We now add to their observations the finding that a majority of neurones in the core of the arm region of area 4, which have a short-latency input predominantly from 'deep' receptors, receive this input via afferents in the cuneate fasciculi. In a separate paper we have reported on the nature of the afferent projections to the 'sensory' cortex (areas 3, 1 and 2) which were shown to persist in these monkeys after lesions of the cuneate fasciculi (Brinkman & Porter, 1977).

In animals with incomplete dorsal column lesions fewer precentral cells were in receipt of these inputs from peripheral receptors than is the case in normal animals. Moreover, the cells which continued to be influenced may have been the ones which received inputs from more than one joint or from larger cutaneous fields. These influences could have been contributed by a small number of intact dorsal column afferents. In addition, Applebaum, Beall, Foreman & Willis (1975) have described spino-thalamic afferent fibres in the ventral part of the spinal cord of monkeys which respond only to one form of stimulus delivered in their peripheral territory and to stimulation only within restricted local regions. Some of these afferent fibres travelling in ventral parts of the spinal cord were signalling joint movement, muscle stretch or cutaneous stimuli. Such afferents would, of course, have remained intact in our monkeys and could have served to transmit influences to the cerebral cortex (via the thalamus).

We must conclude that the dorsal column system is the major one capable of transmitting short-latency inputs to neurones in the *motor* cortex from local peripheral territories and concerning joint movement, muscle length or tension and skin contact. But the natural pattern of behaviour of many precentral neurones in relation to forelimb movement performance appears to be relatively independent of the transmission through the cuneate fasciculi of any feed-back from peripheral receptors which could signal aspects of the movement performance. Hence 'long-loop reflexes' of the sort studied in man by Marsden *et al.* (1973) may not have a major role in control of natural self-initiated and self-paced movement performance.

Our experiments cannot provide detailed information on the receptor populations involved in influencing precentral neurones. A projection from muscle receptors to pyramidal tract neurones has been demonstrated (Albe-Fessard, Lamarre & Pimpaneau, 1966; Wiesendanger, 1973; Lucier, Ruegg & Wiesendanger, 1975; Hore, Preston, Durkovic & Cheney, 1976). Some of the responses described here and by others (Asanuma, 1973) undoubtedly arise in cutaneous receptors. But it appears likely that joint receptors, in addition to the effects of joint movement in stretching muscles, may have to be considered as significant contributors of peripheral influences to precentral neurones (Fetz & Baker, 1969). After complete lesions of the dorsal columns we have been able to produce very little evidence of short-latency responses in the motor cortex to natural activation of any of these receptors.

All the tests of responsiveness of precentral neurones to influences arising in forelimb afferents were conducted in animals trained with food rewards to sit quietly and remain relaxed during the natural activation of peripheral receptors in skin or deep tissues. Such stimuli in similarly 'passive' animals caused activation of a large majority of precentral neurones in normal animals (Lemon & Porter, 1976). Responsiveness of precentral neurones to such afferent inputs may be modified during active, 'voluntary' movements of the limb. But even under these circumstances, clear-cut responses of precentral neurones to disturbances of active movement, which could influence local receptors, are readily recorded (Evarts, 1973). However, in the present animals, with a deficient complement of cuneate fibres or complete section of the cuneate fasciculi, no short latency responses could be recorded for many of the precentral neurones. In spite of this, movement performance was well preserved and skilfully executed. And, of course, the cerebral cortex was still in receipt of precise information derived from peripheral receptors in the forelimb as demonstrated by the recorded responses of many postcentral neurones.

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