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PROJECTION FROM LOW-THRESHOLD MUSCLE AFFERENTS OF HAND AND FOREARM TO AREA 3a OF BABOON'S CORTEX

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SUMMARY

1. The precentral and postcentral banks of the Rolandic fissure of the arm area of the baboon's cortex have been probed to their depths with extracellular micro-electrodes under nitrous oxide and oxygen anaesthesia, supplemented by minimal intravenous pentobarbitone or chloralose.

2. Afferent volleys were sent in from the deep (motor) radial nerve and the deep palmar (motor) branch of the ulnar nerve. Their entry into the central nervous system was timed at the dorsal root entry zone. The nerves were stimulated in continuity and the effects of stimuli below threshold for the motor axons were investigated.

3. Area 3a, in the depths of the postcentral bank, which is cytoarchitectonically transitional between areas 3 and 4, is the receiving area for afferent impulses from muscle.

4. Evoked potential waves and unitary discharges began 4 msec, and the majority of units discharged between 5 and 10 msec, after the afferent volley reached the dorsal root entry zone.

5. Similar responses were elicited by a brief pull (70 μ in 1 msec) or brief vibration (50 μ at 250–400 Hz) applied to the tendons of m. extensor digitorum communis.

6. No potential waves were evoked in area 4, even in the depths adjacent to area 3a, by muscle afferent volleys.

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INTRODUCTION

In monkeys rewarded for making a prescribed displacement of the wrist, the output of force is increased if the displacement is resisted by an external load (Evarts, 1967). If the brain recruits α and γ motoneurones together (Granit's '$\alpha\gamma$ linkage'), resisting the movement should cause increased signalling from the muscle spindles (Matthews, 1964; cf. Corda, Eklund & Euler, 1965). The increased input from the primary endings would monosynaptically depolarize the α motoneurones and tend to increase the output of force. But this may not be the whole explanation, for Evarts (1967) found that the discharges of 'related' pyramidal-tract neurones were also increased. In view of this increase, and since the pyramidal corticomotoneuronal (CM) projection to the baboon's hand contributes, on average, more monosynaptic excitation than the input from the spindle primaries (Clough, Kernell & Phillips, 1968), it has been suggested (Phillips, 1969) that the CM projection may form the efferent limb of a trans-cortical servo loop. If this were so, the simplest afferent limb would be provided by a three-neurone pathway from the spindles to the pyramidal neurones.

Albe-Fessard & Liebeskind (1966) have reviewed earlier evidence that volleys in muscle nerves could evoke activity in the monkey's cortex, and their own experiments have provided abundant evidence of acceleration of the discharges of precentral neurones by stretch of denuded muscles or by localized pressure on their bellies. Graded electrical stimulation of muscle nerves evoked cortical potentials at 1·35 thresholds, supporting the belief that the spindle input was responsible (Albe-Fessard, Liebeskind & Mallart, 1964). After a critical degree of curarization, which blocked skeletomotor but not fusimotor end-plates, stimulation of fusimotor axons in lumbosacral ventral roots caused discharges in dorsal roots: under similar conditions four precentral neurones in the knee-flexion area were activated (Albe-Fessard, Lamarre & Pimpaneau, 1966). The cells in the foregoing experiments were not identified by antidromic pyramidal stimulation, and the experimental design did not permit the critical measurements of latency that would be needed to establish the 'directness' of the afferent pathway.

Computer-averaged potentials from pre- and postcentral gyri, evoked by stimuli to the hamstring nerve, showed latencies of 10–12 msec (Albe-Fessard, Liebeskind & Lamarre, 1965, Fig. 2). These evoked responses were rather similar in configuration from pre- and postcentral cortex, which suggests the possibility that the focus of activity was located in the depth of the Rolandic fissure.

In the cat, the cortical receiving area for the spindle input, as deter-

mined electrophysiologically (Oscarsson & Rosén, 1963, 1966; Landgren & Silfvenius, 1969), does not correspond to area 4, but to area 3a as determined cytoarchitectonically (Hassler & Muhs-Clement, 1964). In the monkey area 3a lies in the depth of the Rolandic fissure (Roberts & Akert, 1963; Powell & Mountcastle, 1959*a*). Powell & Mountcastle (1959*b*) recorded their 'impression that this region of transition between the koniocortex of the postcentral gyrus and the motor cortex of the precentral does in fact receive a heavy projection from deep tissues. The data are so far too meagre to prove this statement'. On the basis of its afferent connexions from cortex and ventrobasal thalamus, and by analogy with the cat, Jones & Powell (1969) concluded of the monkey: 'It therefore seems possible that area 3a may be a specific cortical projection area in SI for Group I muscle afferents'.

We have now recorded evoked potentials and unitary activities at short latency from area 3a for the baboon's forearm and hand in response to minimal afferent volleys in the deep radial and deep ulnar nerves, and to brief stretch or vibration of m. extensor digitorum communis. No such early responses could be recorded from area 4 (Phillips, Powell & Wiesendanger, 1970). The more delayed, less tightly coupled responses of antidromically identified pyramidal neurones will be described in a later paper by M. Wiesendanger.

METHODS

Twenty-two baboons of both sexes, weighing 3·8–5·5 kg, were anaesthetized and maintained in good condition for as long as necessary (up to 30 hr) by the methods described by Clough *et al.* (1968). During surgery anaesthesia was maintained with 50–70 % nitrous oxide, the initial intraperitoneal dose of pentobarbitone (20 mg/kg) being supplemented as necessary by smaller doses intravenously. This regime was maintained throughout the earlier experiments. In later experiments, the pentobarbitone was replaced, during the period of recording, by small intravenous doses of chloralose (about 20 mg/kg), given at intervals of 1–2 hr. Bipolar cuff electrodes were fitted to nerves of the left arm and the skin closed over them. In the first experiments, the median and ulnar nerves were stimulated in continuity at the wrist and the radial nerve at the elbow. In later experiments, the sheath of the radial nerve was opened and the superficial (cutaneous) radial nerve was separated from the motor branches; these were stimulated in continuity, and the superficial radial stimulated separately. The deep branch of the ulnar nerve was stimulated in continuity in the palm of the hand, distal to the branch to palmaris brevis. In some experiments the palmar cutaneous branches were also stimulated. The laminae of C1–C7 vertebrae were removed bilaterally, or of C3–7 unilaterally or bilaterally, and the dura opened to expose the left dorsal roots. The strength of stimuli to the muscle afferents in the motor nerves could thus be both monitored by their relation to the electrical threshold for the motor axons in the nerve (detected by visible and palpable twitches) and by the threshold and amplitude of the Group I volley recorded triphasically from the dorsal roots. The dorsolateral column was also exposed for antidromic stimulation of the corticospinal tract by a focal cathode resting on the surface. The term 'Group I' is used to refer to the fastest, lowest threshold axons conducting impulses from the

muscle nerves into the dorsal roots and dorsal columns. In the baboon, these axons conduct much more slowly than the corresponding axons in the cat (Clough *et al.* 1968; Eccles, Phillips & Wu Chien-ping 1968). Mean conduction velocity in the present experiments was 74 m/sec (range 66–84 m/sec).

In three experiments the primary endings of the muscle spindles of extensor digitorum communis (EDC) were selectively stimulated by small brief stretches, 70 μ in < 1 msec (Lundberg & Winsbury, 1960) or brief periods of vibration, 50 μ at 250–400 Hz (Brown, Engberg & Matthews, 1967) applied to all its tendons. The ulnar and median nerves were cut in the axilla; the deep radial was fitted with stimulating electrodes in continuity; the branch to EDC was not isolated. The muscle was prepared and the limb fixed as described by Eccles *et al.* (1968). It was usually held at a length half way between minimum and maximum physiological length. The mechanical stimuli were delivered by a Goodman vibration generator Type V 47 whose moving element was attached to a flanged 4 BA nylon nut, lashed direct to the tendons by stout thread passing through holes drilled in the flange, by a threaded tensile aluminium rod weighing (with lock nuts) 2·4 g (weight of moving system of vibrator 6·5 g). The vibration generator was driven by a DC power amplifier designed and made by Mr W. J. Bannister. For the brief stretches, the movement of the aluminium rod was limited by stops separated by 70 μ. A 1·0 msec rectangular current pulse of 0·8 A, locked to the oscilloscope time base, began to move the rod after 0·2 msec latency and the 70 μ stop was reached 1·05 msec from the start of the pulse. The curve of velocity was plotted initially, and checked between experiments, by bolting the vibrator to a heavy compound measuring table (divisions 10 μ) and allowing it to pull the edge of the terminal nylon nut against the free end of an isometric strain gauge myograph, first 'isometrically' and then with free travel over measured distances. The curve was unaffected by loading the movement with a 100 *g* spring. For vibration the stops were removed and the travel at different sinusoidal frequencies was measured with a microscope with micrometer eyepiece, as the elongation of bright spots reflected from the aluminium rod (Matthews, 1966). Loading the system with a 100 *g* spring displaced it 250 μ from its resting position but did not alter the amplitude of vibration.

The right mid-Rolandic region was exposed with a 30 mm trephine and a circle of dura was excised; prior drainage of c.s.f. from the spinal opening prevented bulging of the brain. The meningeal arteries were sealed by temporary clamping of their bleeding points in the elevated dural edge. The cortex was protected by a curved Perspex window which fitted the trephine opening, or by Ringer-or-paraffin-soaked cotton balls.

The head was held in a Horsley–Clarke holder, which could be positioned independently below the micro-drive whose axis remained always vertical. In order to insert the micro-electrodes at an angle approximately normal to the surface of the arm areas of the right postcentral and precentral gyri, the horizontal Horsley–Clarke plane was first tilted about 30° (actually 31°) to the left (left ear below right), and then rotated about 10° (actually 9°) muzzle downward about the interaural axis. The angle between the axis of penetration and the Horsley–Clarke coordinates was thus standardized for the whole series of experiments. The trunk was suspended in a sling, so that the cervical spine was approximately vertical, the thoracic and lumbar spine approximately horizontal.

Micropipettes with shafts 15 mm × 50 μ, nearly coaxial with the axis of the micro-drive and absolutely parallel with that axis, and tapering evenly over the terminal 1 mm, were essential for these experiments. They were formed in the Schuster micro-forge. Pipettes tapering down to 3–8 μ were filled with 4 M-NaCl, or 2 M-NaCl saturated with Fast Green (Thomas & Wilson, 1965), or with silver wire which just

protruded from the tip, for recording evoked potentials. For recording from single units we preferred pipettes tapering to 1–2 μ filled with 2 M potassium citrate (3–10 MΩ). All these pipettes could usually penetrate the pia-arachnoid without need for prior incision, and crossed the depths of the Rolandic fissure without breakage or distortion. Arterial pulsation of the brain was always formidable, and never completely controlled. It was reduced by drainage of c.s.f. from the spinal opening, and by coating of cortex with 4 % agar or by pressure with a celluloid plate. Respiratory pulsation gave no difficulty and pneumothorax was not needed. The microelectrode was connected to a cathode follower, whose output was led to a Tektronix Type 122 Pre-amplifier and Type 502A Oscilloscope. Two such oscilloscopes could be photographed simultaneously and provided three other channels for the dorsal root volleys (via a second Type 122 Pre-amplifier), for the signals of stimuli and for d.c. recording from the cathode follower. Responses of single units were sometimes stored on tape for subsequent analysis. A reciprocal time-interval display unit (Kay, 1965) was also available for continuous recording of the frequency of discharge of single units.

Localization of recording sites. Three methods were used for the correlation of the sites of recording of wave and unit responses with the cytoarchitectural subdivisions of the pre- and postcentral gyri.

1. The first was essentially the same as that used in an earlier study of the olfactory bulb (Phillips, Powell & Shepherd, 1963). During the experiment a photograph of the exposed area of the cortex was taken through a dissecting microscope, and a print was made before the first electrode penetration. The precise site of insertion of each of the micropipettes in relation to adjoining vessels was marked on the photograph at the time of penetration. At the end of the penetration, when the tip of the micropipette was at a depth of 9·1 mm in the brain, the shaft of the micropipette was cut across, either flush with the surface of the brain or a few mm above it. The number of micropipettes left in the brain varied, in different experiments, from one to fourteen. At the end of the experiment two guide pipettes were inserted, in a parasagittal plane and with the same orientation as the recording pipettes, into the brain near the medial edge of the bone opening; one was in the precentral gyrus and the other in the postcentral. The brain was removed and fixed by immersion in 10 % formalin. The next day a block of the pre- and postcentral gyri containing the electrodes was cut out. This block was then cut, under a dissecting microscope, with a razor blade along the guide pipettes and Indian ink deposited along their tracks; all the pipettes which had been cut above the surface of the brain were then removed, but those cut flush with the surface were left within the brain. The block was immersed in 70 % alcohol and 2 % acetic acid for a few days before being embedded in paraffin wax; serial sections were cut at 25 μ in the sagittal plane parallel to the tracks of the guide pipettes. All the sections were mounted and stained with thionine. All the tracks in which electrodes had been left were readily found, and it was possible to identify individual tracks from their position on the photographs in relation to blood vessels and the central sulcus. Depending upon the accuracy of alignment of the block for cutting, either most of the length of the track appeared on one or two sections (Pl. 2) or portions of the track were found on adjoining sections (Text-fig. 1; Pl. 1). When only portions of a track were present they were traced on succeeding sections both up to the surface and to its deepest point. In the sections of those blocks in which the micropipettes were left in the brain during the processing for histology, portions, of varying length, of the pipette were found on adjacent sections. The example shown in Pl. 2*A* shows the greatest length of pipette found on one section, but there were several in which there was approximately half of this length. The degree of shrinkage due to fixation and histological processing was estimated by measuring the depth of the deepest point of each track from the

surface of the brain and comparing this figure with the known depth of 9·1 mm to which all micropipettes were inserted during the experiment.

2. Micropipettes filled with fast green dye were used, and at the site of recording of either the maximum wave response or of unit responses to nerve stimulation a small amount of dye was iontopheretically ejected by passing 12 μA for 5 min; in one case the dye was deposited at the maximum depth of penetration. The relevant sections were intensively searched for green spots independently by two of the authors and approximately half of them were found. In some sections small tracks of gliosis could be seen passing from the spot. There are two reasons why the spots are hard to find. First, the cortex is a densely cellular structure and the green spot is not readily seen amongst the cells; this explanation is supported by the fact that the green spot deposited at the maximum depth of penetration was readily found in the white matter deep to the cortex of area 3a (Text-fig. 2*b*). Secondly, in some cases the dye was ejected several hours before the end of the experiment, and during this time diffusion of the dye could have occurred – evidence of such diffusion was actually seen in certain sections.

3. With silver-filled micropipettes a small lesion was produced at the site of recording by passing 25 μA for 25 sec. These lesions were approximately 0·3 mm in diameter and were easily found (Pl. 3).

The depths of the green spots and of the lesions on the sections, methods 2 and 3, were compared with the *in vivo* micrometer readings at which the dye was deposited or the current passed. Comparison of the results obtained by the three methods in several experiments gave a mean value of shrinkage of 20 %.

Outline drawings of sections were made to show each track. These were drawn with a projector at a magnification of 12·5 × and the boundaries of the architectonic subdivisions marked in after examination under the microscope. The architectonic areas through which the track passed were noted, and the site of the response was found from a correlation with the micrometer reading.

In addition to the tracks which were identified by an electrode being left *in situ* during fixation, numerous other electrode tracks were seen in the sections as narrow bands of gliosis similar to those seen in the experiments of Powell & Mountcastle (1959*b*).

In five experiments the dorsal or lateral columns of white matter of the spinal cord were sectioned in the cervical region in order to investigate the spinal pathway taken by impulses passing from low threshold muscle afferents to the cerebral cortex. At the end of these experiments the cervical region of the spinal cord was removed, fixed in 10 % formalin and embedded in paraffin wax. The cord was cut transversely at 25 μm and the sections stained with thionine to show the extent of the lesion.

RESULTS

Correlation of recording sites with cytoarchitecture

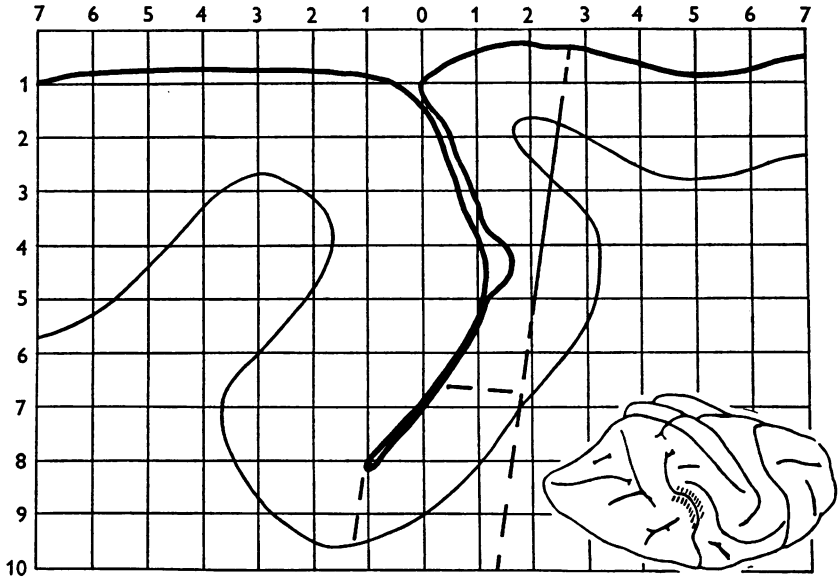
The cytoarchitecture of the pre- and postcentral gyri was examined only over the medio-lateral extent containing the representation of the upper limb, but over this part both the structure and limits of the subdivisions of the somatic sensory cortex were found to be essentially the same as that of the macaque monkey (Powell & Mountcastle, 1959*a*; Roberts & Akert, 1963). A full description need not, therefore, be given, and for further details reference should be made to these papers; the

boundaries of the cytoarchitectural subdivisions in the present material are closely similar to those shown by Powell & Mountcastle (1959*a*, Figs. 4 and 5). Area 3a is a region of transition between somatic sensory cortex proper, in area 3b, and the motor cortex of area 4. It is perhaps relatively slightly greater in extent in the baboon as compared with the monkey, and occupies approximately the deepest third of the posterior wall of the central sulcus together with most of the bottom of this sulcus. Its posterior or superior limit is between 5 and 6 mm from the surface of the brain and its greatest depth is at about 9 mm (Text-fig. 1; Pl. 1).

The boundary between 3b and 3a is not sharp, but is marked by several features (Pl. 1). There is a gradual diminution in the density of neurones in layers III and IV as one passes from area 3b to area 3a, so that these layers become lighter, and the fusion of layers II, III and IV which is characteristic of area 3b is lost. As Roberts & Akert (1963) noted, layer III becomes gradually thicker and layer IV correspondingly thinner. In layer III the cells increase in size, especially in its deeper part, and here and occasionally in layer V quite large pyramidal cells are seen. This change in size of the neurones and increasing pyramidalization becomes more marked anteriorly as one passes from area 3a towards area 4. The prominence of layer V in area 3b as a clear band is lost in 3a. The cortex of area 3a is of the same total thickness as that in area 3b, but there is a sudden, marked increase in its thickness at its junction with area 4, and this together with the increased pyramidalization characteristic of area 4 makes the anterior boundary of 3a sharper than the posterior limit. This subdivision is thus a region of transition from konio sensory cortex to that of agranular motor cortex and shows features of both, but is more 'sensory' posteriorly and 'motor' anteriorly.

The location *in vivo* of the buried cortex that responds to afferent volleys in deep radial and ulnar nerves was very difficult in the absence of prior knowledge of its position in relation to surface landmarks. First we standardized the angle of insertion of all micropipettes with respect to the Horsley–Clarke planes (see Methods). We then had to discover, by systematic probing, (1) the anteroposterior and medial extent of the area through which the pipettes must pass in order to reach this buried cortex, and (2) its minimum and maximum depth below the surface. The plan of experiment changed, therefore, as experience accumulated. In the first experiments, up to 15 micropipettes, orientated at the standard angle, were inserted in a two-dimensional grid which extended pre- and postcentrally as well as medio-laterally. The third dimension was added by recording, in every track, from sites separated by not less than 0·5 mm in depth; and all pipettes were driven in to a depth of 9·1 mm. The basic three-dimensional grid could therefore include as many as 270 points. The response of

each of these points had to be tested to volleys in three or four nerves (superficial radial, deep radial, deep ulnar, whole median at wrist). When a response was obtained, from any site, the threshold for the appropriate nerve had to be found and the grain of the grid had to be made finer by testing sites less than 0·5 mm apart in depth. This experience led to the construction of Text-fig. 1, which shows a parasagittal section of a representative arm area, superimposed upon a 1 mm grid orientated perpendicularly to the cortical surface, and which also shows the inclination of all

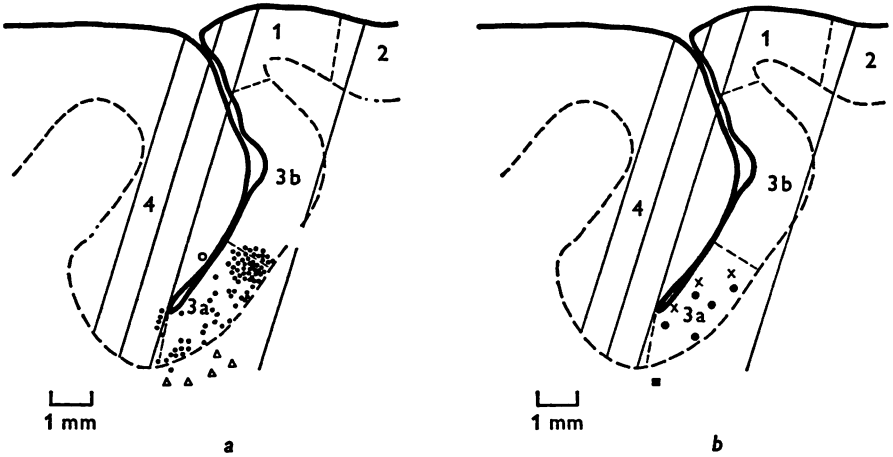


Text-fig. 1. Outline of parasagittal section through pre- and postcentral gyri of arm area of a representative baboon's brain, superimposed on a 1 mm grid. Area 3a enclosed by dashed lines (see also Text-fig. 2). Sloping line shows a single micro-electrode track: continuous line appeared in this section, interrupted line plotted from adjacent sections. For use of this diagram see text.

Inset: dorsolateral aspect of R. hemisphere of baboon, viewed from above, to show orientation of section. Pre- and postcentral arm area hatched.

the microelectrode tracks. Once this diagram was available, we were always able to enter area 3a by inserting a pipette 1·5 mm behind the Rolandic vein, and did not need to waste time exploring at depths less than 4·5 mm. The degree of forward bending of the Rolandic fissure was occasionally less than in the typical geometry of Text-fig. 1, and could not, of course, be known at the time of experiment. In such a case the pipette would need to be inserted nearer to the Rolandic vein, and the responses would be encountered at a depth greater than 'normal'.

Eighty electrode tracks from eighteen experiments, six green spots and three lesions were found. All but one of the slow wave and unit responses to stimulation of group I muscle afferents were found, from a correlation of the micrometer readings with the histology, to lie either within area 3a or at the boundaries of this area with 3b or 4 (Text-fig. 2*a*). The only exception was in area 4 about 1 mm superficial (or anterior) to 3a, and it is considered that this one discrepancy was due to an error in the depth



Text-fig. 2*a*. Composite diagram of histologically verified recording sites (filled circles) from which wave and unitary responses were evoked in the whole series of experiments by volleys in deep radial nerve or in deep palmar branch of ulnar nerve. They are superimposed on a single diagram: the location of each point in relation to the cytoarchitectonics and lamination of areas 3b, 3a and 4 was verified for each experiment.

Open circle: the only response 'typical' for area 3a that was found in area 4 in the whole series of experiments.

Triangles: spike responses to volleys in superficial radial nerve, recorded from fibres in subcortical white matter.

Oblique lines: tracks from which no evoked responses were recorded (areas 2 and 4).

b. As in *a*; points, additional to those in *a*, marked by Fast Green spots (filled circles, filled square) or by small electrolytic lesions (crosses).

measurement. All the green spots and the lesions which were made at the site of recordings were well within area 3a (Text-fig. 2*b*), and the green spot deposited at the maximum depth of a penetration was in the white matter immediately deep to the cortex of 3a. Text-fig. 2*a* and *b* were made by transposing the actual sites of recording on the outline drawings of individual experiments to the same *relative* position, in relation both to the cytoarchitectonic boundaries of 3a and to the *laminar* depth within the cortex, on the standard Figure. It will be seen that the majority of the responses were recorded in the posterior part of 3a, close to its junction

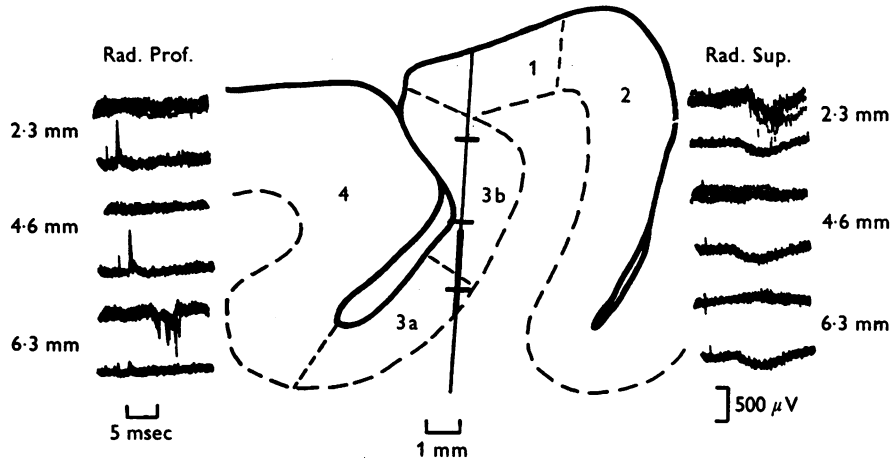
with 3b. This clustering implies that, as the histological structure suggests, this part of 3a is more 'sensory' than that placed more anteriorly. It was not due to any bias in the number of electrode penetrations traversing this part as examination of the position of all tracks shows that all parts of 3a were traversed with about equal frequency.

The medio-lateral extent of the part of area 3a that is activated by muscle afferent volleys in distal ulnar and deep radial nerves is restricted, and very easy to miss. Once it had been located by systematic grid-making in the early experiments, however, it could be reached fairly quickly by reference to the position of the responses evoked in area 1 of the post-central gyrus by stimulation of ulnar and median nerves at wrist, with stimuli well above threshold for their motor axons (Pl. 4, UM) and by stimulation of the superficial radial nerve (Pl. 4, R); and also by reference to the position of the lowest-threshold precentral focus for flick movements of thumb-index in response to single surface-anodal pulses (Pl. 4). Some or all of these areas were mapped with a unifocal ball-pointed, spring-mounted electrode at the outset of each experiment. In the later experiments, in which the deep palmar branch of the ulnar nerve was stimulated in isolation from cutaneous branches, two landmarks only, the lowest-threshold motor focus and the superficial radial focus, were sufficient to guide us into the depths. The medio-lateral extents of the buried receiving areas for the deep ulnar and deep radial nerves are shown for a single brain in Pl. 4. The topography in the three other brains that were investigated in such detail was similar. In the centre of each buried area, the evoked potentials were 'pure ulnar' or 'pure radial'. The boundaries between the areas were fairly sharp, but the degree of overlap would have been difficult to map accurately, because, as can easily be seen in Pl. 4, the pial vessels limited the points at which micropipettes could be inserted. At the point marked by the 'fused' ur in Pl. 4, a potential wave was evoked in response to an ulnar or a radial volley. Pl. 4 shows, characteristically, that the buried (muscle afferent) sites lie to the medial side of the postcentral sites for maximal cutaneous response, and medial to the lowest-threshold precentral focus for flick movement of thumb-index.

Of the eighty identified tracks, thirteen passed through the cortex of area 4 in the anterior wall of the central sulcus and on the exposed surface of the precentral gyrus. Ten of these tracks passed just in front of area 3a at the bottom of the sulcus. It is noteworthy that none of these penetrations, which were all made under nitrous oxide and pentobarbitone anaesthesia, yielded any responses to weak stimulation of muscle nerves. These penetrations traversed most of the antero-posterior extent and laminar depth of area 4 (Text-fig. 2). Strong stimulation of muscle nerves, or stimulation of cutaneous nerves, often produced small and late responses.

Field potentials evoked in area 3a by weak stimulation of deep radial and deep ulnar nerves

Text-fig. 3 illustrates a micro-electrode track passing through areas 1, 3b and 3a of the right arm area and thence into white matter. At depth 2·3 mm, when the tip of the micropipette had just entered area 3b, stimulation of the left (contralateral) superficial radial nerve evoked a negative-going wave with amplitude about 0·5 mV and associated with small spikes.



Text-fig. 3. Parasagittal section (orientation as in Text-fig. 1), showing track of NaCl-filled micropipette. Potentials evoked by single volleys in deep radial nerve (Rad. Prof., left of Figure) and superficial radial nerve (Rad. Sup., right of Figure) were recorded at depths noted at side of records and marked on micro-electrode track.

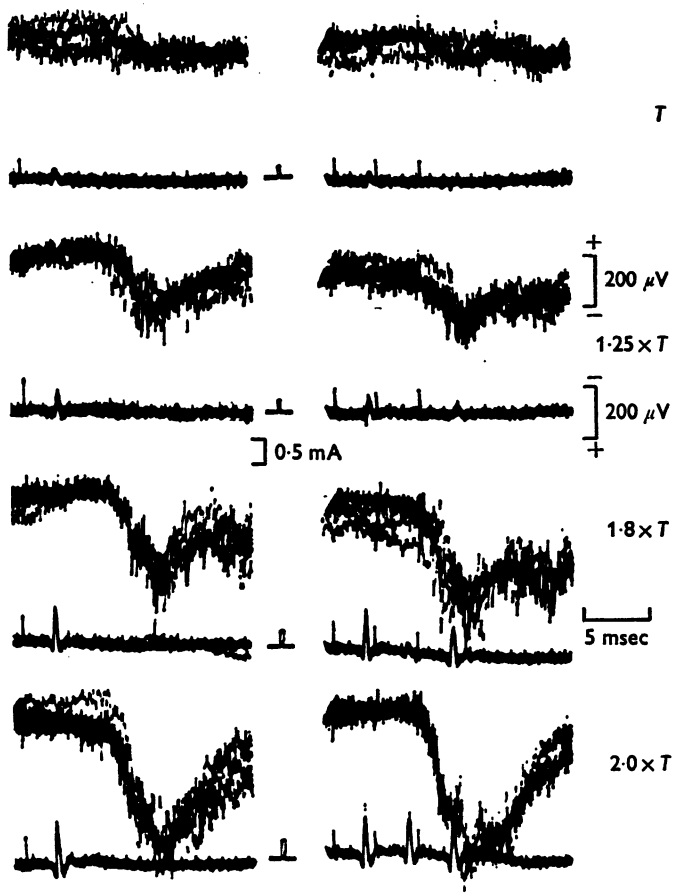
In this and remaining Figures, micro-electrode recordings appear as upper traces of each pair; dorsal root entry-zone records as lower traces. All traces are of five or more superimposed sweeps. Negative deflexion *downwards* in micro-electrode recordings; *upwards* in dorsal root-dorsal column recordings.

This response was not recordable at greater depths (4·6 and 6·3 mm). At 2·3 and 4·6 mm, both in area 3b, stimulation in continuity of the left deep radial nerve at a strength above threshold for its motor axons (eliciting a twitch in dorsiflexors of wrist and fingers), and maximal for the Group I volley, evoked no response. At 6·3 mm, in area 3a, a weaker stimulus, just supraliminal for the Group I volley (bottom record on left) but below threshold for the motor axons, evoked a negative-going wave and spikes.

In some experiments we found that cutaneous volleys again elicited responses when the micro-electrode had passed beyond area 3a into the white matter (Text-fig. 2*a*, open triangles). Such responses were spikes,

and were presumably recorded from axons entering the white core of the postcentral gyrus *en route* for areas 3b and 1.

Responses in area 3a were generally obtained with the smallest volley that could be detected at the dorsal root entry zone at C5–7, elicited by stimuli below threshold for the motor axons of deep radial or deep ulnar nerve. Text-fig. 4 shows that the amplitude of the negative wave increased concomitantly with that of the Group I volley as stimulus strength was increased to twice-threshold. In several experiments, further increase in



Text-fig. 4. Potentials evoked in area 3a by volleys in deep radial nerve, recorded at depth 6·8 mm with NaCl-filled micropipette.

Left column: single volleys.

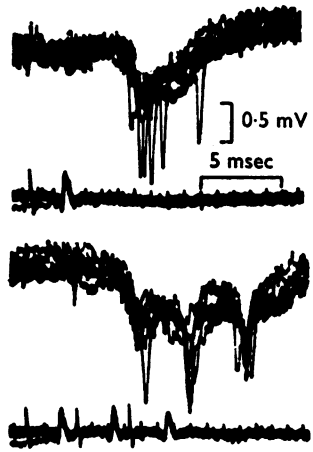
Right column: three volleys at 330 Hz.

Strength of stimulation increasing from above downwards, expressed in multiples of threshold for dorsal root spike (noted at right of Figure).

Records of stimulating current pulses, and calibration 0·5 mA, in vertical mid line of Figure.

stimulus strength did not increase the amplitude of the initial peak of the negative wave, but did prolong its decay. It is possible that such prolongation was due to the addition of Group II impulses to the incoming volley, but we could not confidently identify a Group II component in our triphasic records.

Latency of response was measured from the time of entry of the Group I impulses into the cord (signalled by the negative peak of the triphasically recorded Group I spike) to the start of the negative-going cortical potential (Text-figs. 3–6). The range was similar for deep radial and deep ulnar



Text-fig. 5. Responses recorded from area 3a with fine micropipette (potassium citrate) at depth 5·9 mm to deep radial volleys; stimuli below threshold for motor axons.

Upper pair: single volleys.

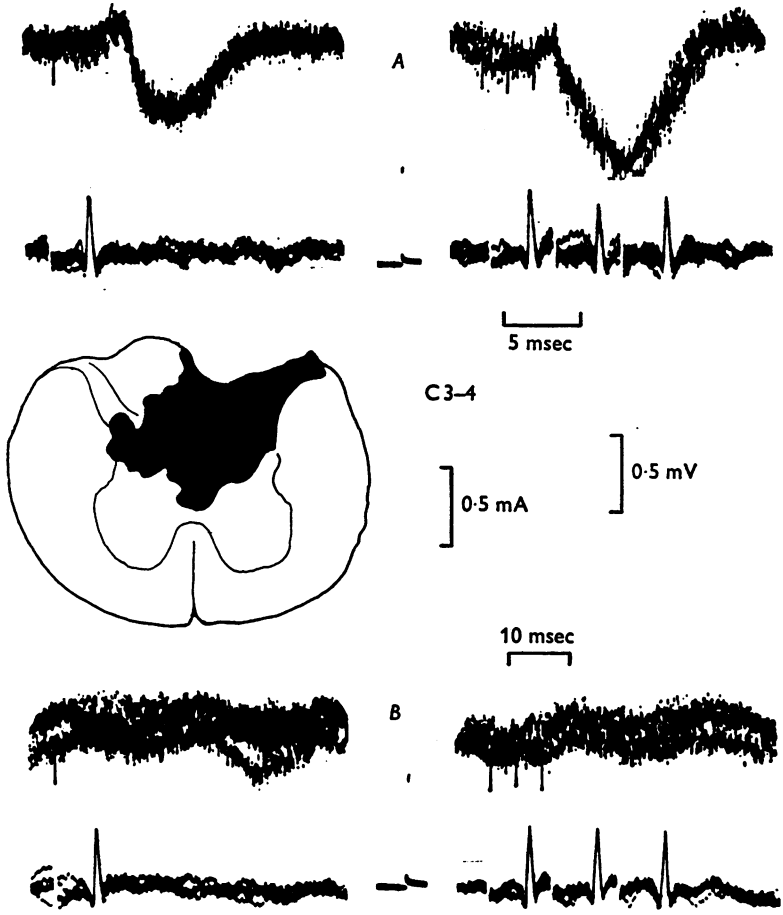
Lower pair: three volleys at 330 Hz.

A wave follows each dorsal root spike at latency 4·0 msec, with high probability of spike discharge on each wave.

nerves: 3·8–5·2 msec (mean 4·2 msec). Transmission across the first-second and second-third order synapses were secure. At optimal recording sites the negative-going deflexion was steep and spikes were superimposed on top of the wave. A brief train of volleys (3 at 330 Hz) frequently elicited three distinct waves, with high probability of spike discharge on top of each wave (Text-fig. 5).

The spinal pathway from the low threshold muscle afferents to area 3a was investigated in five acute experiments. Lesions of the dorsolateral funiculus at C3–4, ipsilateral to the stimulated nerves, did not appreciably change the evoked potential (two experiments). Lesions of the dorsal columns (which were found to be complete in one only out of four experiments), however, completely abolished the cortical responses to area 3a

(Text-fig. 6). The micro-electrode remained *in situ*, and no recovery was observed when the recording was repeated one hour later. The general state of the animal, as judged by the blood pressure, was not changed by these lesions. The responsiveness of the cortex to an afferent volley, set up by a focal stimulating cathode applied to the dorsal column rostral to the lesion, was undiminished.



Text-fig. 6. Acute section of left dorsal columns abolished response evoked in area 3a of right post-central gyrus, recorded at depth 5·8 mm with NaCl micropipette, by single and repetitive (330 Hz) deep radial volleys. Traced section of cord shows lesion complete on left, partial on right, at C3–4 level.

Responses of single neurones in area 3a to electrical stimulation of muscle afferents

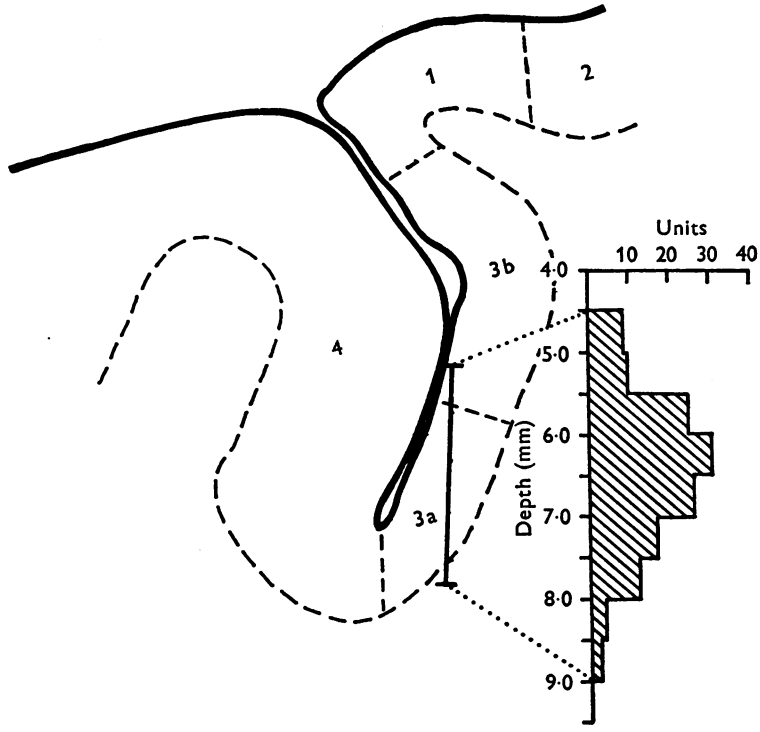
Once the receiving area for one of the muscle nerves had been localized at the beginning of the experiment the coarse-tipped micropipette which was used to record the evoked potential was broken off and left *in situ*. Fine citrate-filled microelectrodes were then used to record the activity of single neurones. Many tracks were made in the immediate vicinity of the marking track. Although precautions were taken to reduce the heavy cardiovascular pulsations (see Methods) it was still difficult to record from neurones for any length of time. Extracellular recording was often frustrated by pulsatile impalement and destruction of these small cells. The largest cells of area 3a are much smaller than the largest pyramidal cells of area 4.

A total of 143 units were collected within area 3a and were analysed with respect to their responses to stimulation of low threshold muscle afferents. Ninety-two neurones were within the receiving area for the deep radial nerve, forty neurones in the area for the deep ulnar nerve. The median nerve (mixed, mostly cutaneous at this level) was stimulated at the wrist in one experiment and six neurones were recorded in the median receiving area. Five single-unit responses were definitely from fibres at the bottom of area 3a (Text-fig. 2*a*). The depth distribution of the neurones is shown in Text-fig. 7. It has to be kept in mind that the outline and the dimensions of the pre- and postcentral gyrus is idealized in this Figure; in some preparations the fissure was more curved in cross-section; in others, less so. This explains why some units were recorded relatively near the surface (4·0–4·5 mm) and some unusually deep (8·5–9·0 mm).

Most units were picked up by probing area 3a while single brief pulses were being applied at 1/sec to the uncut muscle nerves. The intensity was first kept above threshold for a muscle twitch; when a unit was isolated the intensity was then reduced and the threshold determined. The cells tested in this way responded to nerve stimuli which were below or just above motor axon threshold, and were always too weak to elicit a maximal Group I spike.

The majority of the cells responded at a latency longer than the initial deflexion of the field potential. The latencies to deep radial and deep ulnar nerve stimulation, which were measured from the negative peak of the Group I spike at the cord level, had a similar distribution and the modal value was 6–7 msec for both (Text-fig. 8). Typically, the latency to a single shock was remarkably constant from stimulus to stimulus as seen in the superimposed records of Text-fig. 9*a–d*. Repetitive stimulation at 330 Hz did not enhance the probability of firing to the first volley, but each sub-

sequent volley was followed by a high probability of firing. The records did not reveal an incoming thalamo-cortical volley which would allow a statement about the synaptic connexion with lower order neurones. The short latency for the majority of neurones and the security of transmission, however, strongly suggests a monosynaptic pathway from the thalamus to the neurones of area 3a.

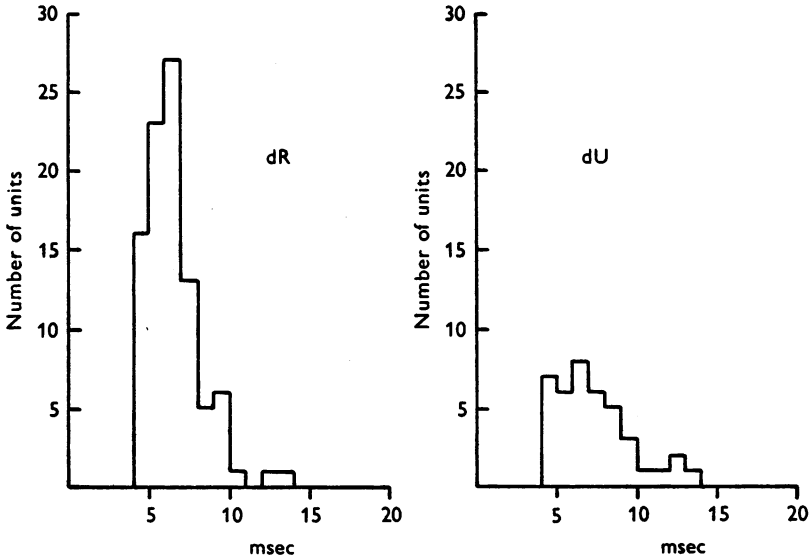


Text-fig. 7. Distribution in depth (microdrive readings) of 138 units in the whole series of experiments, transferred to the outline of Text-fig. 1. See text.

Within the deep radial receiving area seventy cells, all reacting to weak stimulation of the nerve, were tested for convergence with the deep ulnar nerve. It was found that the deep ulnar nerve was effective in only nine of these neurones; five of these were excited by a train stimulus only. Convergence was also exceptional for neurones recorded within the deep ulnar receiving area: of thirty-one units tested twenty-eight showed no convergence, and only three units reacted to both nerves. Discharges occurring at much longer latencies (about 60 msec) to strong stimuli producing vigorous muscle twitches were probably responses to the movement and are not included (in one experiment, the late responses disappeared when

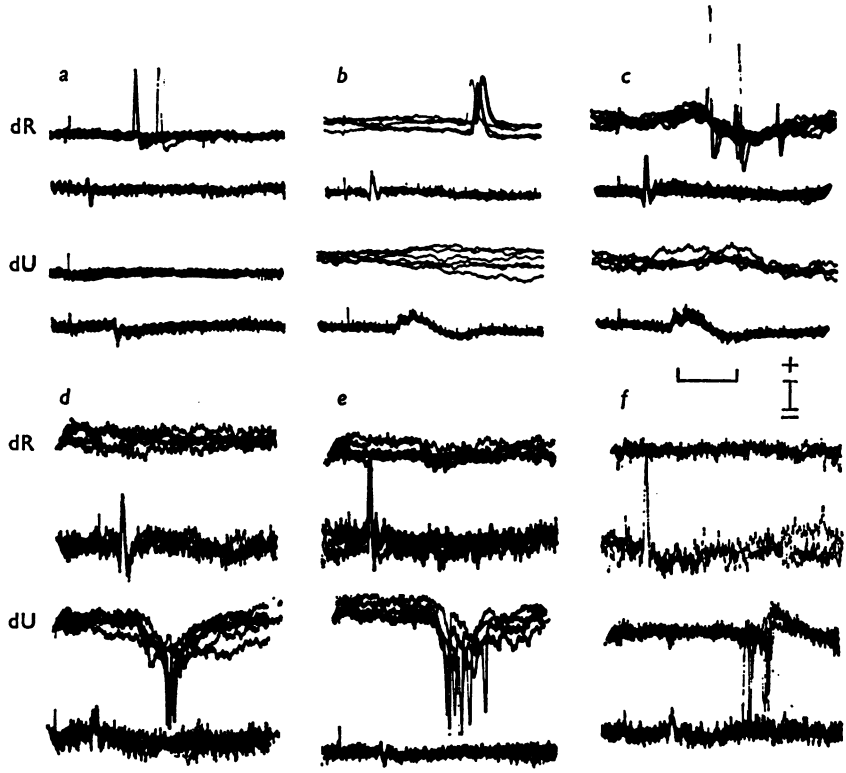
the nerve was cut distal to the stimulating electrodes). The seventy neurones reacting to the deep radial nerve were also tested for convergence from the superficial radial nerve. Only nine of these cells were excited by strong stimuli, the latencies to the cutaneous volley being always longer (mean difference 4 msec).

When neurones in area 3a were penetrated by the micro-electrode, this resulted in injury discharges and rapid deterioration of the cell. The few intracellular records made from cells in which a membrane potential of 30–40 mV was maintained for long enough to allow any investigation are



Text-fig. 8. Latencies of response of units in area 3a, excited by single volleys in deep radial nerve (dR, ninety-three units) and deep palmar branch of ulnar nerve (dU, forty units), measured from time of arrival of volley at dorsal root entry zone.

illustrated in Text-fig. 10. In one of these neurones a large EPSP was recorded but the spike mechanism had already deteriorated (Text-fig. 10*a*). The onset of the EPSP to a weak deep radial nerve stimulus corresponded to the latency of the field potential. The duration of the EPSP was 25 msec. An IPSP was recorded in one neurone; the latency measured from the Group I spike was remarkably short (6 msec) and the duration was about 40 msec (Text-fig. 10*c*).



Text-fig. 9. To show lack of convergence from deep radial and deep ulnar volleys on to six 3a cells (*a–f*) from six preparations.

Cells *a* (depth 8·8 mm), *b* (5·7 mm) and *c* (6·1 mm) responded to deep radial volleys (dR) evoked by stimuli below threshold for motor axons, but not to deep ulnar volleys (dU) set up by stimuli strong enough to evoke cord dorsum potential (lower records).

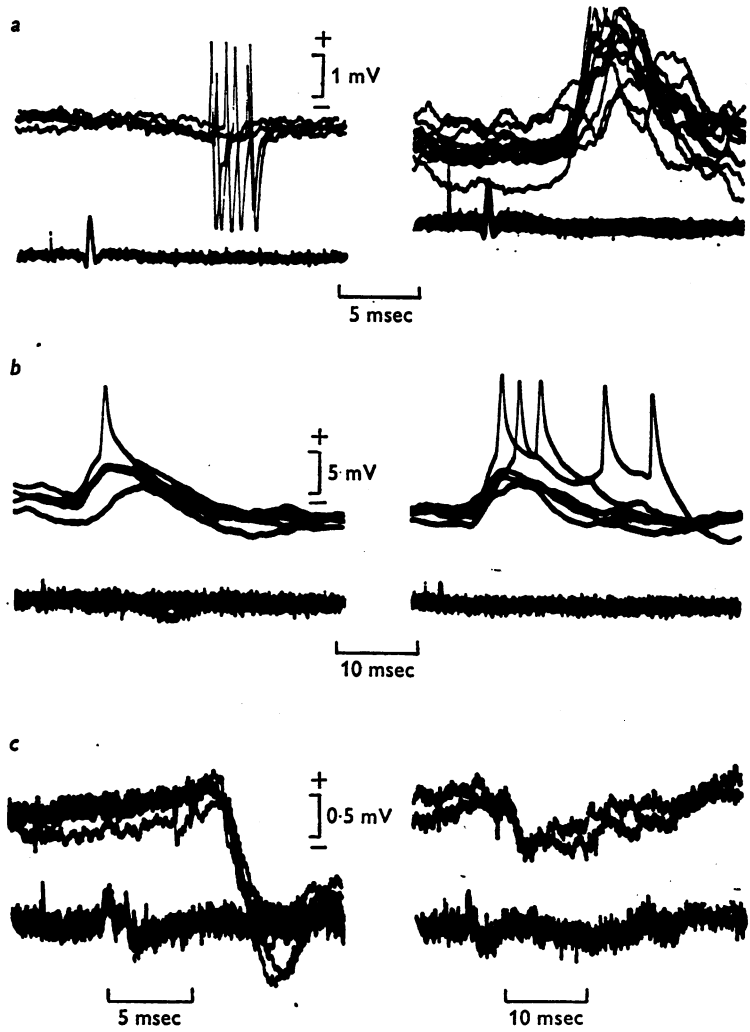
Cells *d* (7·4 mm), *e* (6·0 mm) and *f* (5·3 mm) responded to deep ulnar volleys (dU: stimuli below motor axons threshold), but not to deep radial volleys (dR: stimuli maximal for Group I dorsal root spike).

Calibrations: time: 5 msec for all records; voltage: vertical bar represents 1 mV for *a* and *b*, 0·5 mV for *c*, 0·2 mV for *d–f*.

Responses of units in area 3a to brief stretch or vibration of extensor digitorum communis

Although weak electrical stimulation of muscle nerves is generally accepted as a reliable method of generating an input corresponding exclusively to that from a single receptive field, that of the primary endings of the muscle spindles, we wished to strengthen our evidence by applying selective adequate stimulation to extensor digitorum communis, a muscle which is preferentially accessible to the cortex (Phillips, 1969):

rapid brief stretches (70 μ in 1 msec: cf. Lundberg & Winsbury, 1960) or brief high-frequency longitudinal vibration of its tendons (50 μ at 400 Hz for 15–20 msec: cf. Brown *et al.* 1967). We applied these stimuli in three preparations, and evoked field potentials in nine tracks in area 3a, in spite



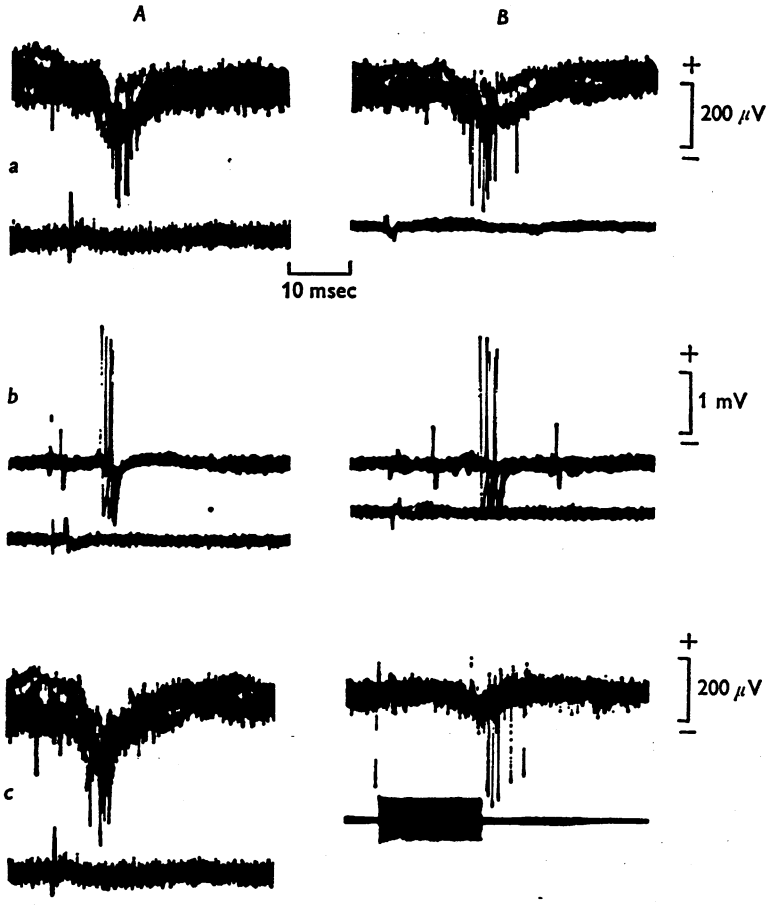
Text-fig. 10. Intracellular recording from three cells in area 3a in three preparations. Potassium citrate micro-electrodes.

a. Cell at depth 6·9 mm. Responses to deep radial volley. Extracellular recordings of impulses (left) followed by penetration (right). Membrane potential 40 mV: EPSP only, no impulses after penetration.

b. Cell at depth 5·5 mm. Deep radial volleys evoke EPSP. Background injury discharges.

c. Cell at depth 7·3 mm. Deep ulnar volleys evoked IPSP.

of the narrowing of the receptive field to one only of the muscles supplied by the deep radial nerve. Of twelve units tested for their response to the brief stretch, five were excited (e.g. Text-fig. 11*B*, *a*, *b*), and three out of six units responded to vibration (e.g. Text-fig. 11*B*, *c*). These units were also activated by stimulation of the deep radial nerve below threshold for



Text-fig. 11. Responses of three cells in area 3a of the same preparation to weak electrical stimuli to deep radial nerve (*A*) and to brief stretch (70 μ in 1 msec) or vibration (50 μ, 400 Hz for 16 msec) of tendons of extensor digitorum communis (*B*). Muscle length intermediate between minimum and maximum physiological length. Cells encountered in three separate tracks.

Upper records: cell at depth 6·5 mm.

Middle records: cell at depth 6·3 mm.

Lower records: cell at depth 6·0 mm.

At least five sweeps superimposed in each series. Vibrator not time-locked to sweep, hence solid black, not sine wave, in bottom rt. record.

its motor axons (Text-fig. 11*A*, *a*, *b*, *c*). We cannot exclude the possibility that these responses were due to mechanical stimulation of Pacinian corpuscles in the distribution of the deep radial nerve, or to electrical stimulation of their axons. Pacinian corpuscles supplied by the ulnar and median nerves were denervated by section of those nerves in the axilla.

'Spontaneous' activity of neurones in area 3a and responses to natural stimulation

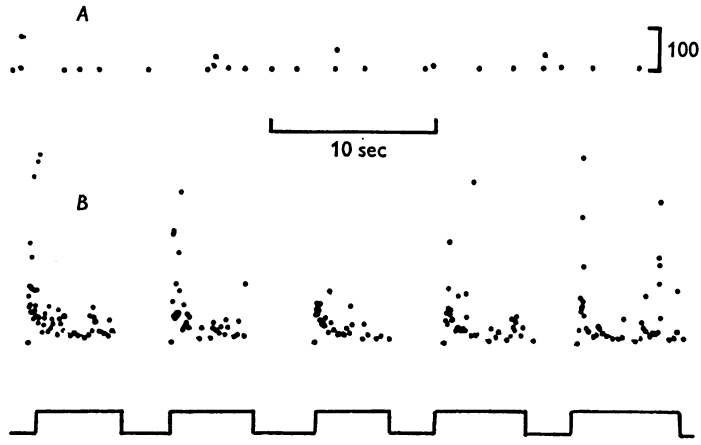
Most of the neurones in area 3a exhibited 'spontaneous' activity (seventy-nine out of eighty-eight neurones observed over prolonged periods). It varied from a few occasional spikes (mostly grouped discharges) to profuse activity. To inspection the spike trains seemed irregular. The interval distribution was computed for seven cells; in six of them the distribution had a large peak for the short intervals and a long 'tail' for long intervals. One neurone only showed periods of fairly regular spontaneous activity and the interval distribution was near to symmetric with a mode around 100 msec.

Twenty-four neurones were excited by passive movements of the wrist or fingers and it was found that brisk ('dynamic') movements were the only effective stimuli. It was rarely possible to specify the most adequate manipulation or the preferred direction of the movement. The following ('dynamic') manoeuvres accelerated the discharge of neurones: wrist movements in any direction (five), flexion of wrist (one), ulnar abduction of the hand (two), metacarpo-phalangeal flexion of fingers (four), movements of thumb and index finger in any direction (one), abduction of thumb (one), flexion of the fourth and fifth finger (two), repeated light tapping of index (two), tapping on localized region of hypothenar or interossei (three), light tapping over wrist joint (one), light tapping of thumb (one). The ineffectiveness of gentle stroking of the skin was in striking contrast to the behaviour of many cells in the superficial cutaneous projection zones. Text-fig. 12 shows an example of a spontaneously active neurone which was activated by ulnar abduction of the hand and inhibited by radial abduction of the hand.

Do neurones of area 3a project into the lateral corticospinal tract?

We were interested to see whether neurones of arm area 3a contribute to the lateral corticospinal tract, which makes monosynaptic connexions with the motoneurones of the extrinsic and intrinsic muscles of the hand. Antidromic corticospinal volleys were set up by a focal stimulating cathode applied to the dorsolateral funiculus at about C3. The strength of these stimuli was adjusted to evoke a maximal antidromic potential recorded

unifocally at the surface of the precentral gyrus. They were adequate to excite antidromically many neurones of the precentral gyrus: the criteria were the ability of these neurones to follow frequencies higher than 100/sec, and fixed latencies of response. None of the neurones of area 3a, however, could be identified as a corticospinal neurone. Of thirty neurones thus



Text-fig. 12. Effect of adequate stimulation on 'spontaneous' firing of unit in area 3a (depth 6·5 mm).

A. Background impulse activity (displayed as 'instantaneous frequency').

B. Effect of brisk passive ulnar deviation of the hand (roughly indicated by upward deflection of lower line). Unit silenced by radial deviation.

Cell responded to electrically evoked volleys set up in ulnar nerve at wrist, but not to deep radial volleys.

tested, the majority would respond to these stimuli, but with variable latencies of more than 4 msec, and could not be driven by high frequency stimulation.

DISCUSSION

Because of the position of area 3a in the Primate brain, far from the surface and deep in the posterior wall of the central sulcus, it is necessary to discuss briefly the validity of the conclusion, drawn from the correlation of the physiological and histological observations, that responses to stimulation of lowest-threshold muscle afferents are restricted to this region of cytoarchitectural transition between the somatic sensory and motor areas. The lines of evidence in support of this conclusion are several: all but one of the responses were found to be either within this area or close to its anterior or posterior boundary; the correlation made in those experiments in which a correction had to be made for shrinkage was confirmed directly in the brains in which a green spot had been deposited or in which

a lesion had been produced: all the spots and lesions were clearly within this area; in repeated traverses through the adjacent architectonic subdivisions of the pre- and postcentral gyri no responses to muscle nerve stimulation were found, although responses to stimulation of superficial nerves were recorded in areas 1 and 3b. There is little question about the identification of area 3a as a separate subdivision on the basis of its morphological features, as most workers who have studied this region are agreed about its structure and position (e.g. Brodmann, 1905, in cercopithecus; Bonin & Bailey, 1947; Powell & Mountcastle, 1959*a*, and Roberts & Akert, 1963, in macaca; and Hassler & Muhs-Clement, 1964, in cat). Cytoarchitecturally it is a region of transition between the cortex of the somatic sensory and motor areas, but it appears to have essentially the same pattern of anatomical connexions as the other subdivisions of the somatic sensory cortex.

Our direct correlation of the electrophysiological and histological findings in the same experimental brains confirms the earlier suggestions of Oscarsson & Rosén (1966), Jones & Powell (1968) and Landgren & Silfvenius (1968, 1969). A comparison of the area of cortical responses to stimulation of group I muscle afferents of the forelimb of the cat with the cytoarchitectural maps of the sensori-motor region of Hassler & Muhs-Clement (1964) suggested to Oscarsson & Rosén (1966) that the projection area corresponded to field 3a, as the maximal response was always found in this area. From a study of the anatomical connexions of the somatic sensory cortex in the cat Jones & Powell (1968) concluded that area 3a is an integral part of the somatic sensory cortex, and they suggested that a projection from muscle afferents of the hind limb might be found in that part of 3a which is on the medial surface of the hemisphere in the vicinity of the representation of the apical hind limb. Such a projection from the muscle afferents of the cat's hind limb has been shown by Landgren & Silfvenius (1968, 1969).

The present experiments extend the previous physiological observations to the Primate, and it is of interest that they are in accord with certain observations in the monkey mentioned by Powell & Mountcastle (1959*b*). These workers found that in area 3a, in contrast to 3b, there was a marked increase in the number of units responding to stimulation of deep tissues; no attempt was made to identify the peripheral receptors whose stimulation gave rise to these responses, but it was suggested that area 3a receives a heavy projection from deep tissues.

The conclusion that area 3a is the specific cortical projection area for group I muscle afferents is further evidence for the functional significance of the subdivisions of the sensory areas made on the basis of their cytoarchitecture. In their combined anatomical and physiological investigation

of the auditory region of the cortex of the cat Rose & Woolsey (1949) first showed the significance of such a correlation of structure and function, and subsequent studies on the somatic (Powell & Mountcastle, 1959*b*) and visual areas (Hubel & Wiesel, 1965) have confirmed the importance of this concept. The present findings also extend the earlier correlations, which have been made on the architectonic subdivisions *within* a sensory area, to the 'regions of transition between cortical areas which are clearly different from one another' (Powell & Mountcastle, 1959*a*). The finding that the projection area for muscle afferents is at the anterior margin of the somatic sensory area whereas that for joints and other deep tissues is predominantly near its posterior boundary, and separated by the tactile receiving area, is rather unexpected. By itself it might be taken to confirm the suggestion of a close association of the muscle afferent information with the motor cortex (Oscarsson & Rosén, 1963, 1966) (see below). There is certain evidence to indicate that, in addition to its specific relationship to muscle afferents, area 3a may differ from the other subdivisions of the sensori-motor region in its efferent connexions, as it appears to be the main, if not the sole, origin of cortical fibres to the dorsal column nuclei in the cat (Gordon & Miller, 1969).

In the cat, the available evidence is that area 3a has reciprocal and well-organized connexions with area 4, but this evidence is not completely conclusive (Jones & Powell, 1968) as the lesions in that study were not strictly confined to area 3a. It would be valuable to establish the nature of such connexions in cat and primate and also their functional significance, e.g. in the processing and feedback of information about movements (cf. Oscarsson & Rosén, 1963, 1966) to the pyramidal neurones which form the output from area 4.

The possibility raised in the Introduction, of a dense three-neurone pathway leading from spindle primaries to the baboon's motor hand area, and forming the afferent limb of a transcortical feed-back loop (Phillips, 1969), can now be ruled out. There were never any early responses in area 4 to weak muscle-nerve stimulation, under the same conditions, and in the same preparations, in which such responses were unequivocally demonstrated in the adjacent area 3a. Such lack of response to afferent volleys from the deep branch of the ulnar nerve has been confirmed in parts of area 4 from which motor units of intrinsic hand muscles could be excited at lowest threshold by Asanuma & Sakata's (1967) technique of intracortical microstimulation (P. Andersen & C. G. Phillips, unpublished observations). These ulnar stimuli, which were shown by electromyography to be subliminal for the motor axons, evoked excellent responses in area 3a. The conclusion that there is no pathway from spindle primaries to area 4 comparable to that coming direct from the thalamus to area 3a is in

accord with the available data on the thalamic connexions of these areas (Jones & Powell, 1970).

Any connexions passing from 3a to 4 are not likely to provide the final relay of a major four-neurone afferent pathway from the spindles. Strong microstimulation within area 3a, delivered through the same microelectrode at a site from which the ulnar-evoked response had just been recorded, failed to evoke any recordable response from a second microelectrode which had just been used for microstimulation of a low-threshold 'hand-muscle' site in area 4 (P. Andersen & C. G. Phillips, unpublished). Any functional linkage between areas 3a and 4 would appear to be more complex and subtle than a simple axonal tract, and may involve chains of interneurones, and possibly dendro-dendritic interactions, etc.

The effects on the discharges of unidentified precentral neurones of stretching muscles, or of localized probing of their bellies (Albe-Fessard & Liebeskind, 1966) were presumably due to impulses arriving over less direct pathways. Such impulses may have originated in the secondary endings of the muscle spindles, which furnish precise measurements of muscle length at any instant, as well as in the primaries which measure velocity as well as length (Matthews, 1964). There is a delayed input, and no early input, to antidromically identified corticospinal neurones in the primate (M. Wiesendanger unpublished).

Of the alternative possibilities (Phillips, 1969) to account for the acceleration of pyramidal-tract neurones when displacement of the wrist was resisted in Evarts' (1967) experiments, namely, a crude excitatory input from the muscle spindles, or an excitatory signal computed in the cerebellum (or elsewhere, ? area 3a), the first must now be considered improbable, and the second remains to be investigated.

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EXPLANATION OF PLATES

PLATE 1

Cytoarchitectonic differentiation of areas 1, 3b, 3a and 4 (see text). Parasagittal section: orientation as in Text-fig. 1. Thickness 25 μ, stained with thionine. Part of one micro-electrode track can be seen in area 3a. Magnification × 18.

PLATE 2

A. Parasagittal section, orientation as in Text-fig. 1. Thickness 25 μ, stained with thionine. Micropipette *in situ* in areas 3b and 3a: originally broken off at cortical surface, but sliced by microtome knife during sectioning. Tip depth 9·1 mm. Magnification × 15.

B. Most of a micro-electrode track appears in a single section. × 15.

PLATE 3

Parasagittal section, thickness at 25 μ, stained with thionine, orientation as in Text-fig. 1. Depth marked by a small electrolytic lesion in upper part of area 3a. Microdrive reading 6·5 mm, depth on section 5·1 mm. Magnification × 20.

PLATE 4

Map of arm area of right Rolandic cortex, showing topographical relationships of responsive loci of postcentral gyrus. Orientation as in inset of Text-fig. 1: medial edge of exposure is at bottom of map. Scale in mm.

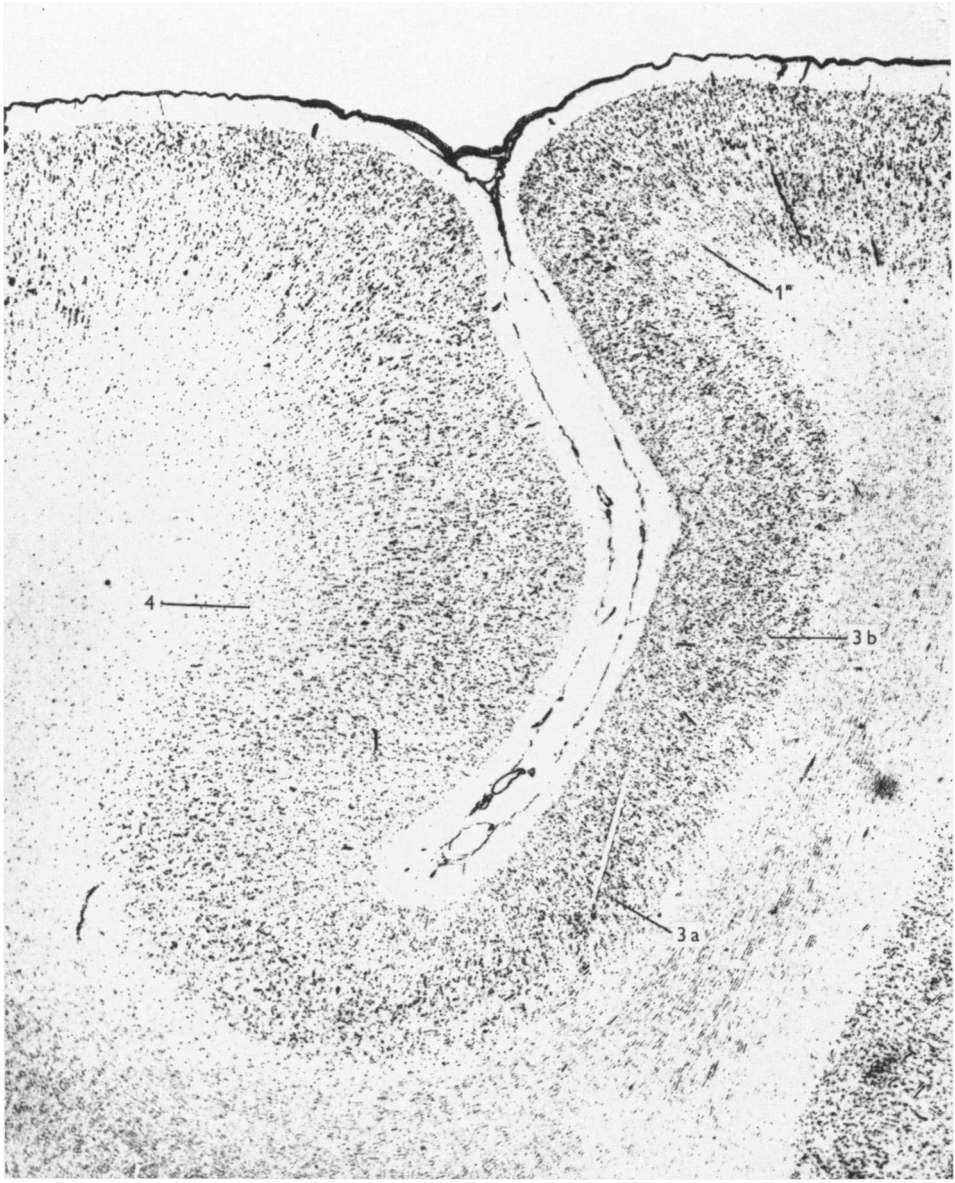
Open circles: tracks in which no responses could be recorded.

u: tracks in which waves were evoked by ulnar nerve volleys in area 3a (nerve stimulated at wrist, below threshold for motor axons).

r: tracks in which waves were evoked by deep radial volleys in area 3a. Note track indicated by 'fused' ur: here a wave was evoked in area 3a by deep radial or ulnar volley.

U, M, R: approximate areas for surface potentials evoked by ulnar volleys (from wrist: includes palmar digital nerves 4 and 5), median volleys (from wrist: includes digital nerves 1–4), and superficial radial volleys.

Dashed line encloses lowest-threshold focus of precentral gyrus for flick of left thumb (S+, 5·0 msec pulse, 1·5 mA).



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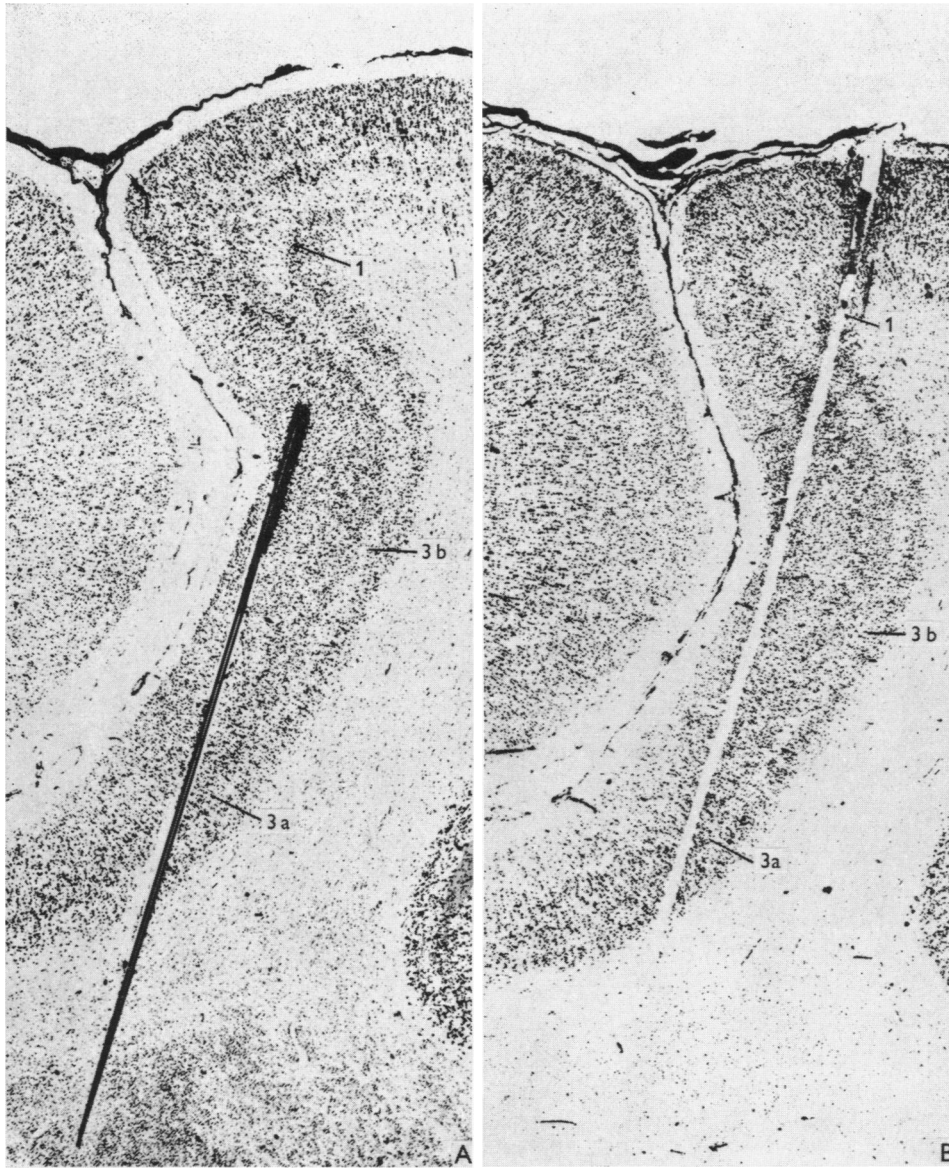

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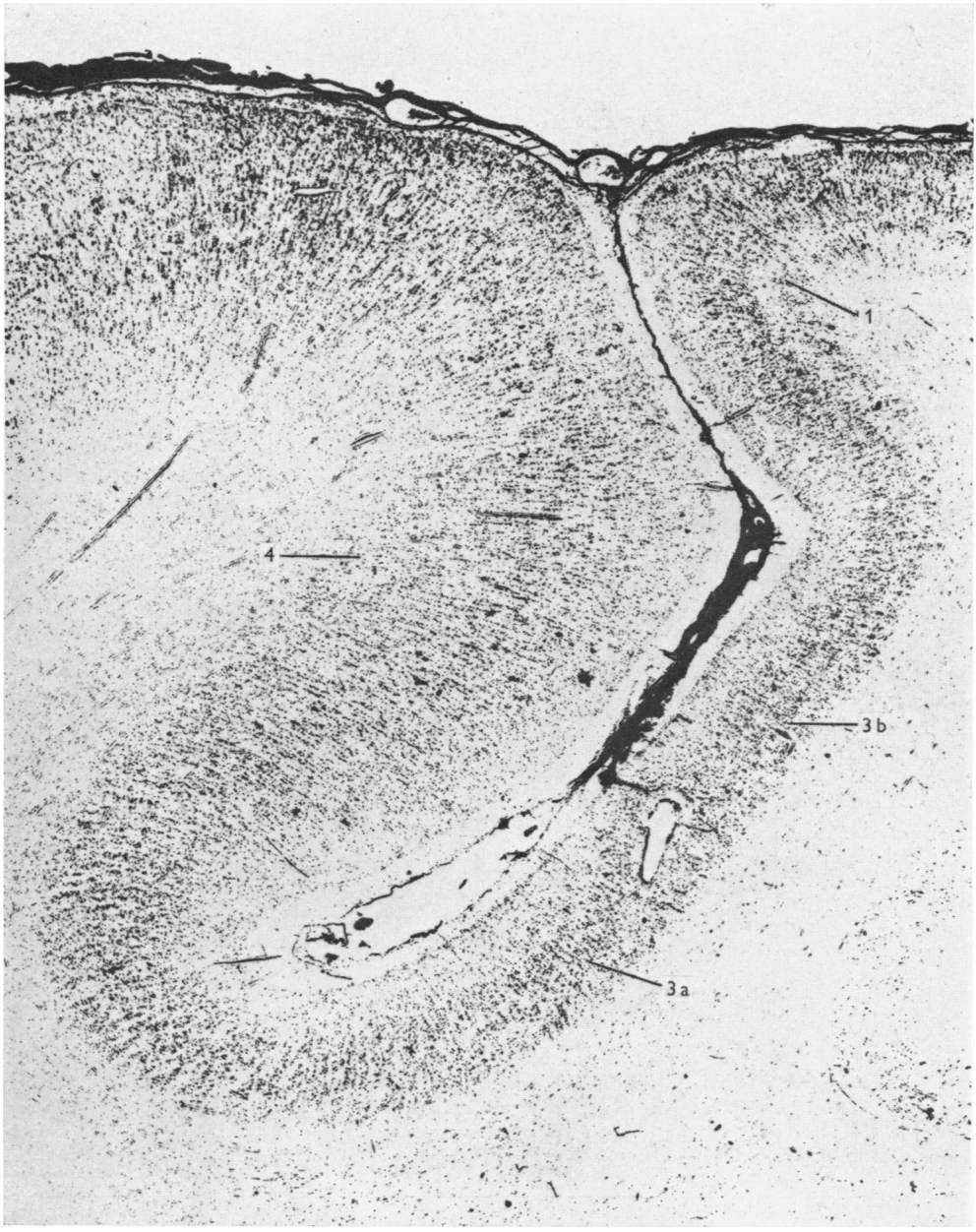

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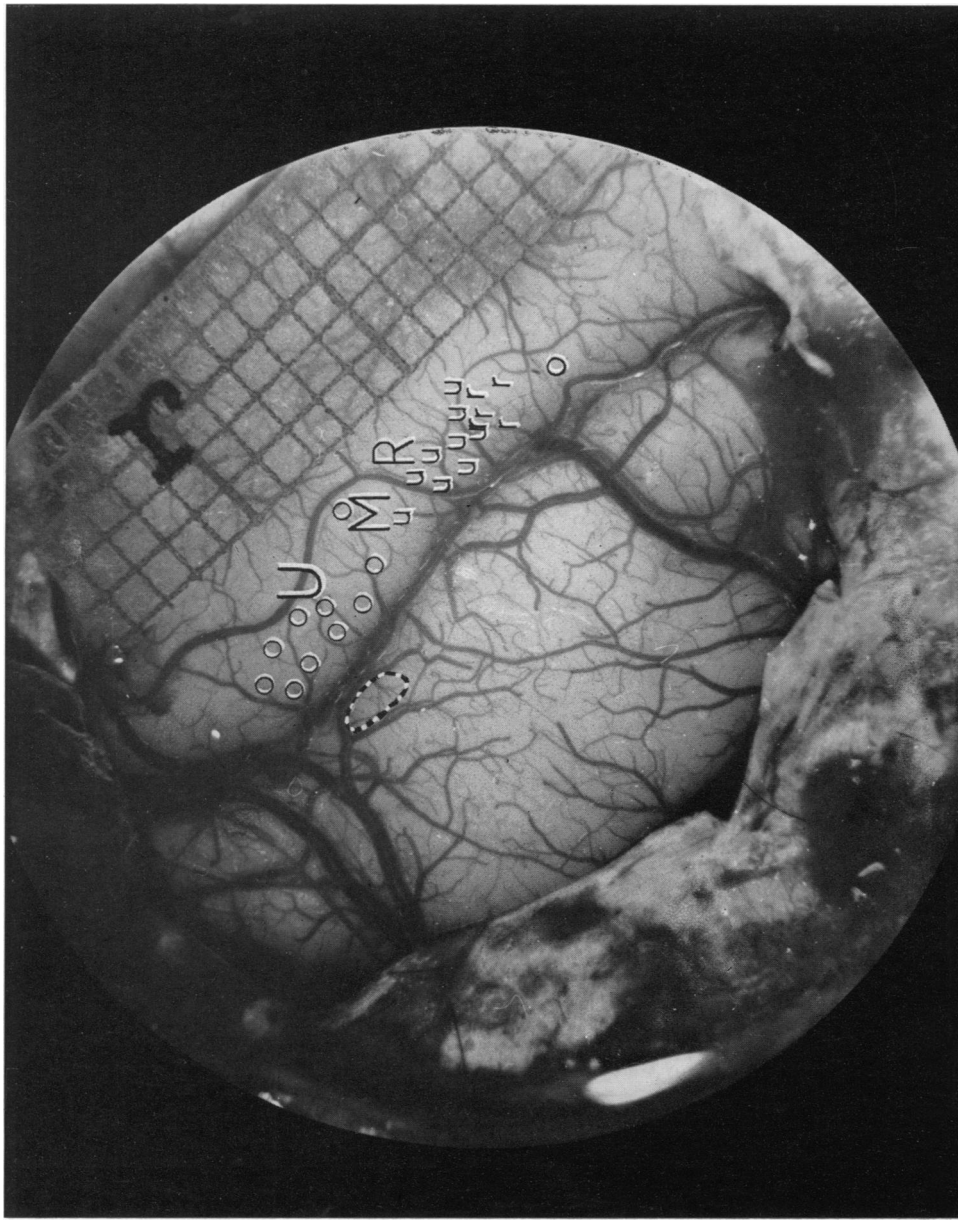

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