

## AFFERENT DISCHARGES TO THE CEREBRAL CORTEX FROM PERIPHERAL SENSE ORGANS

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IN a recent paper by Adrian & Moruzzi [1939] the electrical activity of the motor area of the brain was correlated with the discharge of impulses in the pyramidal tract. It was found that there was in general a close agreement between the larger potential waves of the cortex and the groups of impulses in the pyramidal discharge, and from this various conclusions could be drawn as to the activity of the cortical nerve cells. For further progress it seemed essential to have a survey of the sensory area made from the same point of view. A great deal is already known about the electrical activity of the various regions of the cortex which receive messages from the sense organs: the reactions of the visual area have been analysed in detail by Bartley & Bishop [1933], those of the auditory area in the cat by Bremer [1938] and of the sensory area in the monkey by Marshall, Woolsey & Bard [Bard, 1938], and general surveys have been made by Kornmüller [1937], by Gerard, Marshall & Saul [1936] and Derbyshire, Rempel, Forbes & Lambert [1936]. Much of the present work has merely confirmed what has been done already, but the recording of nerve impulses as well as cortical potentials can add some details to the picture of events taking place in the brain, and in existing circumstances it seemed advisable to publish what had been done. The greater part was written before the appearance of two important papers by Marshall [1941] and Marshall, Woolsey & Bard [1941] covering the same field. This must excuse the absence of detailed reference to the many points of agreement and to the few discrepancies between the present results and theirs. It is scarcely necessary to point out how much the present work is indebted to their earlier paper which showed the precise localization of electrical reactions in the sensory area.

## METHOD

An essential feature of the method has been the use of a loud-speaker and amplifier system giving a faithful reproduction over a wide range of frequencies. The electrical changes in the cortex include both the very brief axon potentials due to impulses in nerve fibres and the much slower waves which are the characteristic product of the cortex. An optical system making a photographic record can be adapted to show one or the other but can rarely do justice to both simultaneously, whereas with a good loud-speaker it is easy to detect both impulses and waves.

Another essential in the study of cortical activity is the use of a variety of anaesthetics and of animals, for otherwise there is a grave danger of generalizing from results peculiar to one kind of brain or to one anaesthetic. The anaesthetics used have been dial and nembutal, urethane, chloralose, chloroform and ether, and ether alone and occasionally morphia. The animals have been rabbits, cats, dogs and monkeys, though the great majority of the experiments have been on cats. For the rest the technique has differed very little from that used for the motor area by Adrian & Moruzzi. One or more cortical electrodes have been held by a vulcanite support fixed to the skull. They have been either cotton-wool tufts for surface recording or else fine enamelled silver wires thrust into the cortex. An indifferent, earthed electrode is connected with the skin of the neck. Photographic records have been made with one or two Matthews oscillographs and a small cathode-ray oscillograph was used for visual observation at high speeds. Stimulation of the skin receptors was carried out by hand, a small camel-hair brush being used to move individual hairs. Pressure receptors were stimulated by weights placed on the foot. The period of stimulation was marked approximately by a hand-operated signal: the exact moment of contact was sometimes marked by arranging for it to produce an artefact in the oscillograph record.

## RESULTS

*Topography of somatic receiving area*

In the following account the term somatic receiving area will be used to imply that area of the cortex which receives the afferent impulses relayed from tactile and other receptors of the body and limbs. The terms 'sensory area' or 'somaesthetic area' are often used in this sense, but as they sometimes bear a different meaning it seemed better to avoid them for the present.

By exploring the surface of the cortex with an electrode system leading to an amplifier and loud-speaker the regions which receive the afferent fibres can be mapped out with great ease. If the cortical electrode makes contact with any part of the receiving area a touch on the corresponding part of the body will give an outburst of impulses clearly audible as a brushing or hissing sound, and unless the activity of the cortical cells is greatly depressed there will be also one or more potential waves audible as a dull thud or rumbling. In light anaesthesia these may be obscured by continued trains of waves, and there may be repeated impulse discharges which make it difficult to be sure of the primary effect. It is best,

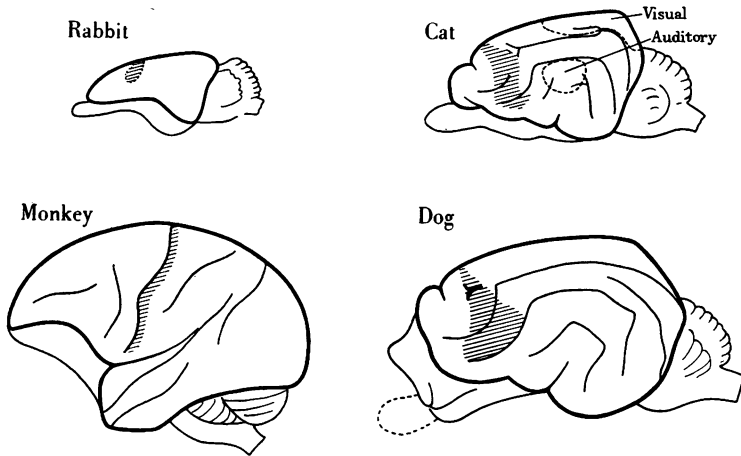


Fig. 1. Position and relative size of the area receiving afferent impulses from somatic receptors in the rabbit, cat, dog and monkey. The auditory and visual receiving areas are also shown for the cat's brain.

therefore, to restrict the degree of cortical activity by moderately deep anaesthesia, preferably with chloralose or one of the barbiturates, since these have little effect on the afferent pathways.

The position and relative size of the somatic receiving area in the rabbit, cat, dog and monkey are given in Fig. 1. The areas are those receiving impulses set up by mechanical stimulation, for touch, pressure and movement are the only stimuli which give a well-marked discharge to the cortex. It will be seen that there is a reasonable agreement with the areas determined from histological evidence, i.e. from the distribution of afferent projection fibres and from the cell structure of the cortex. Thus the areas for the cat and dog given in Fig. 1 coincide very closely with those shown by Campbell [1905]. The extent of the area is not affected by the depth of anaesthesia, except that there are marginal regions where

the discharge is only just audible under good conditions and becomes inaudible under bad. Again, there seems to be no essential difference between the area over which afferent impulses are heard and that giving the slower cortical wave response. The latter has been used by Marshall *et al.* to map out the area in the monkey, and the map given in Figs. 1 and 5 is in general agreement with theirs.

The cortical representation of different parts of the body is shown for the various animals in Figs. 2-5. The maps refer to particular animals though they were chosen to show the typical arrangement. The chief variation is in the extent to which the less important parts of the body (trunk, proximal part of limbs, etc.) are represented, but this does not affect the position of the main areas. In the rabbit (Fig. 2) it is often difficult to detect the arrival of afferent impulses in the cortex, for the potentials are never as large as in the cat, dog or monkey. Sometimes the

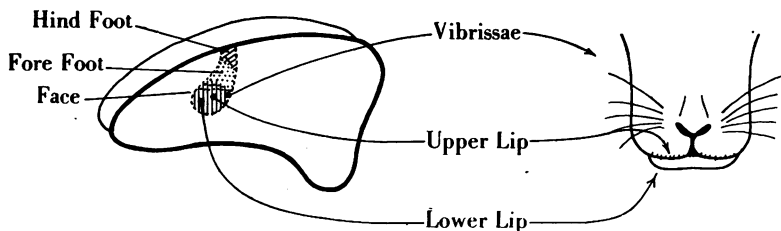


Fig. 2. Representation of different regions in the cortex of the rabbit.

only afferent effect which can be heard distinctly is the potential wave produced by touching the lips. In most animals impulse potentials and cortical waves can also be recorded from the vibrissae and usually from the fore- and hindfeet as well, but discharges from the limbs and trunk have never been identified. It will be seen that the localization follows the usual plan with the head ventral to the limbs, though the mouth-parts are represented in more detail than the rest of the body.

In the cat the most remarkable point is the double representation of the digits, impulses from the claws and ventral side of the toes appearing in a second area lying posterior to the face area and extending back into the ectosylvian gyrus (Fig. 3). The area for the claws of the hindfoot is small and easily overlooked; in a few animals it has never been found, but when present it is always caudal to that for the forefoot. No similar arrangement has been found in the dog or monkey, and it has been pointed out [Adrian, 1940] that its presence in the cat may be related to the special importance of the claws in the Felidae or may be concerned with the special mechanism for sheathing and unsheathing them. Certainly

stimulation of the area electrically or by strychnine produces well-marked flexion of the digits and protrusion of the claws provided that the motor cortex is intact and the anaesthesia not too deep.

Marshall *et al.* [1941] describe three distinct points in the cat's cortex which give a wave response when the dorsal surface of the forefoot is touched. Their 'point 1' lies within the anterior digit region shown in Fig. 3 and their 'point 3' within the posterior digit region, but their point 2 lies outside the digit regions as found in the present experiments and seems rather to fall within or near the region connected with the skin on the dorsal aspects of the wrist and forearm.

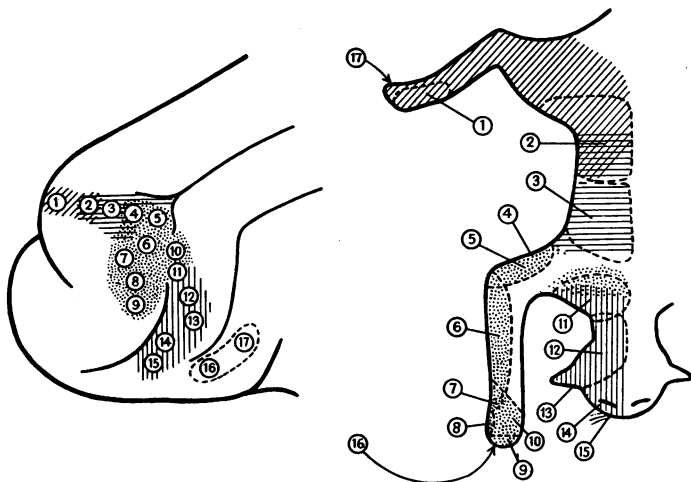


Fig. 3. Somatic receiving area in cat (exp. 10). The shaded regions show the fields for hind-limb, trunk, forelimb and head and the numbers indicate the particular areas sending impulses to different points on the cortex. The posterior digit and claw region (nos. 16, 17) is marked by a dotted line.

The discrepancy is more than a matter of anatomical detail, for Marshall *et al.* have previously found that some of the touch receptors on the monkey's hand are also represented, or give maximal potential waves, at three separate points on the cortex. Thus the existence of a triple representation in the cat would suggest some general principle of cortical arrangement. In the present experiments the double representation of the digits has seemed to be peculiar to the one species, and even there it has been very doubtful whether a single receptor sends impulses to more than one region in the cortex. The posterior region in the cat's cortex gives a response when the toe pads and the hairs round them are touched, particularly the pads on the thenar side of the foot. The anterior region responds to touching the hairs on the dorsal aspect of the digits, particularly those on the hypothenar side. Impulses reach both regions when the claws are tapped, but both toe pads, hairs and joints may then be stimulated. Elsewhere on the limbs and face a single group of hairs has not been found to send an afferent discharge to two separated points on the cat's cortex or to produce cortical waves at two points. In a few animals where the circulation in the cortex was poor there have been small inactive patches within the receiving area, so that a stimulus which was not sharply restricted would give potential waves on either side of the inactive region. But Marshall *et al.* have been at pains to confine

their stimuli to receptors in one region. The failure to confirm their finding may be due to the difference in the method of recording the cortical response, but it is difficult to see what particular factor can be responsible.

These results apply only to the cat's brain. In the dog and monkey no posterior digit region was found to correspond with that in the cat, but apart from this no detailed search was made for a double or triple representation in the cortex.

In the dog the arrangement resembles that in the cat except that the posterior claw area is absent and that the region giving impulses from the vibrissae and lips is particularly large. The localization of different parts within the face area is shown in Fig. 4. In both cat and dog certain parts of the body surface have never been found to send discharges to the exposed surface of the cortex, and with certain other parts the representation has varied from one animal to another. The mesial surface of the

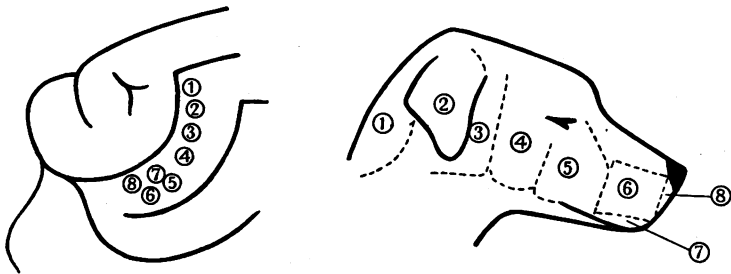


Fig. 4. Receiving area for the face in a dog. Numbers show cortical points connected with various parts of the face.

foreleg is in the former category and the trunk in the latter. It is, of course, unlikely that the mesial surface of the limbs would have much importance for the cerebrum, since they can have little contact with the outside world, but the buried area of the cortex in the coronal sulcus has not been thoroughly explored and it is possible that the missing parts are represented there though no discharges from them have been detected. It should be pointed out that the representation of the hindlimb and tail has not been worked out in any detail. Discharges from the anal region and the thigh were found on the mesial surface of the hemisphere in three cats and in the only dog in which the mesial surface was exposed.

Only two monkeys (*Rhesus*) have been investigated owing to difficulties of supply. Both gave results agreeing with Bard's map [Bard, 1938]. The receiving area did not extend forward on to the pre-central gyrus: it lay within the central fissure and over a strip about 3 mm. wide on the exposed surface of the post-central gyrus (Fig. 5). As in the cat and dog there was no evidence of bilateral representation even for the face. It is true that in light anaesthesia a sudden stimulus to

any part of the body may start a period of activity in the receiving areas of either hemisphere, but the characteristic afferent discharge is only obtained from the opposite side; and in deep anaesthesia an ipsilateral stimulus never gives any response, except on the trunk where the receptive skin field overlaps the mid-line by 1-2 cm. In all the animals there is some overlapping in the distribution of the afferent fibres leading from different parts of the body. In the monkey, for instance, from one spot on the cortex an afferent discharge may be obtained in response to

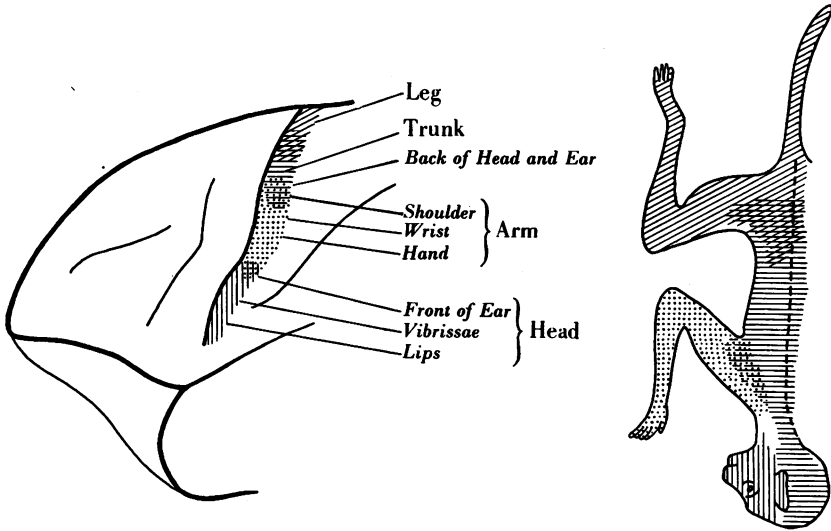


Fig. 5. Receiving area in a monkey (*Rhesus*). The trunk region includes the back of the neck and head [Marshall *et al.*].

tactile stimulation of points on a fairly large area of the abdomen and front of the thigh. And conversely, movement of a single hair will give a discharge audible over an area 1-2 mm. diameter on the cortex.

In the monkey the arrangement of the receiving area in a long, narrow strip emphasizes the serial representation of different parts of the body. But, as Bard points out, there is a marked departure from the segmental plan in that the cortical area for the back of the head adjoins that for the trunk, lying between it and the arm area. Since the back of the head is supplied by the upper cervical nerves we might expect that the points on the cortex connected with it would come between those for the face and those for the arm. It will be seen, however (Fig. 5), that the arm area intervenes between that for the face and that for the occiput, so that afferent impulses from the front and from the back of the ear arrive in the cortex at points separated by nearly 2 cm.

In the cat the segmental plan is followed more faithfully in that the neck and back of the head send impulses to the region adjoining the face area (Fig. 3), and the forelimb area intervenes between the area for the neck and that for the trunk. On the other hand, in the

cat and in the dog the area for the forefoot extends forward out of the regular line so that part of it adjoins the area for the vibrissae and snout. In the cat there is also the additional claw area which does not fit into any segmental plan.

The maps of the receiving area shown in Figs. 1-5, like those already published by Marshall *et al.* seem to represent a fixed anatomical arrangement of fibre tracts, for in animals of the same species there is very little variation in the general position and extent of the area, and in a given animal the area remains fixed in spite of great changes in blood supply, depth of anaesthesia, etc. It is not surprising that the arrangement of the afferent fibres should vary to some extent from one species to another and should not be strictly segmental, for the neopallium is not part of the primitive segmental nervous system and has developed differently in animals of different structure and habits. In each species the receiving area of the cortex is mainly concerned with those parts of the body surface which are most closely related to the outside world. In the rabbit the mouth-parts are the most important; in the cat the predatory claws have a region to themselves, and the dorsal and lateral aspects of the forelimb and trunk supply an area larger than that for the face; in the dog the face and mouth-parts are again more important though the limbs and trunk are better represented than in the rabbit.

The fixed distribution of fibres to the receiving area contrasts with the great variability in the distribution of activity in the cortex after the primary afferent discharge has reached it. A later section will deal with this activity, which may vary from a single localized wave to a prolonged rhythmic oscillation over the greater part of the hemisphere. Meanwhile the afferent discharge itself has to be discussed.

## EFFECTS OF STIMULATION

### *Part 1. The afferent discharge to the cortex*

With an electrode on the surface of the cortex the general character of the discharge can be made out although it is not possible to distinguish individual axon potentials. The movement of a few hairs will give an audible response, but the maximum effect is obtained by a light tap with the finger on the face or forefoot of the animal: a large number of tactile receptors are then stimulated simultaneously and the discharge is audible over a wide area. From many points on the surface of the body it is not possible to elicit more than a brief afferent volley. There are some regions, however, notably within the snout and forefoot areas, from which a more sustained impulse noise can always be produced by a continued (pressure) stimulus. With dial, urethane or chloralose the depth of anaesthesia



seems to make very little difference to this afferent discharge. With chloroform and ether there is more effect on the afferent pathways, and the discharge may fail entirely in moderately deep anaesthesia.

More detailed information is obtained by recording with a wire electrode from individual afferent units. An enamelled silver wire of gauge 44 or 46 (s.w.g.) was generally used, though a thicker wire sometimes gave good results. The wire is fixed to a rod sliding through a ball-and-socket joint so that it can be pushed gradually into the cortex; it is advanced until the sound of the impulse discharge breaks up into a succession of loud clicks, and further manipulation may then bring out a single series of brief potentials, alike in size and duration, and so presumably due to a single unit. In the cat such discharges are to be found at various depths from the surface, ranging from 1 to 5 mm. or more.

Axon potentials detected in this way are not all derived from afferent fibres, for if the electrode leads from the deeper layers of the grey matter some of them may be coming from cells in the cortex. But in an animal under dial it is easy to distinguish the afferent discharge, for the impulses which arise from the cortex bear a much less direct relation to sensory stimuli and often occur quite independently of stimulation. They are also much more dependent on the condition of the cortex, for they are abolished by cooling it, treating it with novocain or depriving it of blood by occluding the carotids, and they become grouped into high-frequency outbursts under the influence of strychnine. None of these procedures has much effect on the primary afferent discharge, and this is directly related to the sensory stimulation of a particular part of the body surface. In animals under chloralose or chloroform the distinction between afferent and efferent effects cannot be made out so clearly, but there is no indication that the afferent discharge differs in any important respect from that under dial.

*The discharge due to pressure.* The most straightforward results are those obtained by stimulating the pressure receptors, for the discharge lasts long enough to allow measurements of impulse frequency and regularity. The number of afferent fibres involved is also not as great as with tactile stimuli, and it is therefore easier to record from single units.

Typical records of the afferent discharge to the cortex are given in Figs. 6 and 7. In both the stimulus was pressure applied to the forefoot. Fig. 6 shows the gradual decline in the frequency with a constant stimulus and Fig. 7 shows the gradual increase when the pressure is slowly increased. In these records the general appearance of the discharge which reaches the cortex differs very little from that of the discharge

which leaves the receptor and travels up the afferent nerve fibre. It is true that the impulses reaching the cortex are not as regularly spaced as in the familiar stretch receptor records, and it is often difficult to obtain a wide range of frequencies to graded pressure. For this the character of

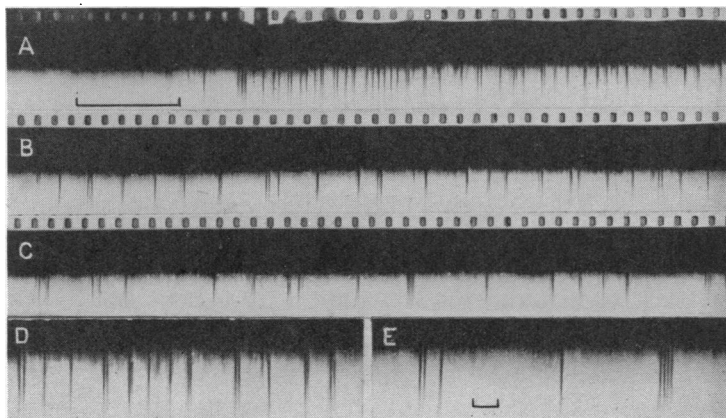


Fig. 6. Afferent impulses reaching the cortex as a result of pressure on the forefoot. Cat under dial. Single unit discharges recorded with wire electrode in the cortex. Record A shows onset of stimulation (white line above). B was made after 35 sec. stimulation and C after 60 sec. D and E are portions of A and C on a large scale to show the high frequency groups. Time shown by black line, in A 0.1 sec., in E 0.01 sec.

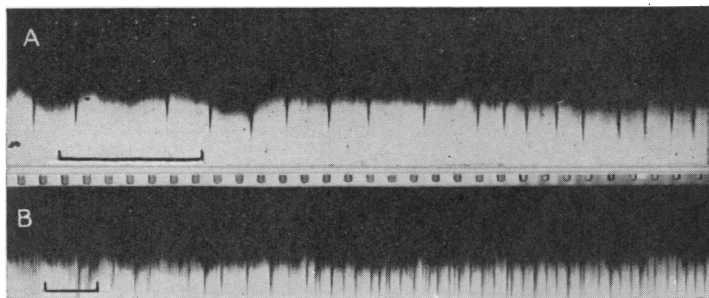


Fig. 7. Single unit discharge showing the effect of gradually increasing pressure. Records from two cats, both under dial, with wire electrode in cortex. The frequency rises to 60 a second in both. Black line gives 0.1 sec. in this and all following records.

the receptor may be partly responsible, for the impulses set up by pressure are seldom as regularly spaced as those from muscle spindles [Adrian & Zotterman, 1927], there is often a more rapid adaptation and it is more difficult to vary the frequency. In one respect, however, the discharge in the cortex may show an important difference: in Fig. 6 it will be seen

that many of the impulses come in groups of two or three very closely spaced with longer intervals between the groups. This kind of grouping is not always present—it is absent in the records in Fig. 7, but it has been found before in the fibres of the pyramidal tract [Adrian & Moruzzi, 1939] and seems to be a characteristic nerve cell reaction, each wave of activity lasting long enough to set up a repetitive discharge in the axon. The tendency for nerve cells to give high-frequency repetitive discharges is greatly increased by convulsive drugs, facilitation by electric stimuli, etc. In this case therefore it may depend on some abnormal state of the thalamic cells, and it is not certain that the kind of grouping shown in

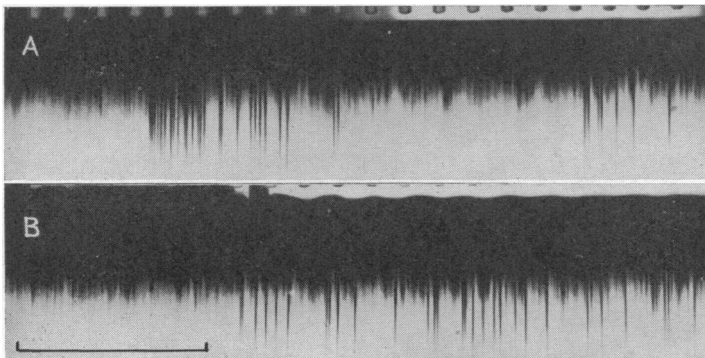


Fig. 8. Afferent impulses due to movement of vibrissae of snout. Cat under ether. In record A the hair is moved quickly up and down. In B it is moved down more slowly.

Fig. 6 would appear in the afferent discharge of a normal, unanaesthetized brain. All that can be said is that in animals under dial or chloralose brief multiple outbursts of this sort are common enough.

In records where such outbursts occur the frequency of the impulses can scarcely be compared with that in a discharge in which the impulses are evenly spaced, but apart from the outbursts the maximum frequency is considerably lower than in a peripheral nerve fibre, rarely exceeding 100 a second except for very short initial periods. With steady pressure the frequency has remained well above resting level for as long as 120 sec. The rate of decline varies greatly however. In some preparations prolonged search fails to detect any units in which the discharge persists for more than a few seconds. In others, in equally deep anaesthesia, there are many units giving a lengthy and well-graded discharge. The difference probably depends on the extent to which the thalamic part of the afferent pathway has been affected by the anaesthetic.

Pressure is the only form of stimulus which has given sustained discharges to the cortex. The receptors are to be found mainly in the pads of the forefoot and at the sides of the toe joints (a region where there are many Paccinian corpuscles). Stretching a muscle of the forelimb, though causing prolonged activity in the peripheral nerve, has never given more than a brief discharge to the cortex. Holding one of the large vibrissae of the face in a bent position has sometimes given a discharge lasting 5 sec., though movement of the ordinary hairs gives only a very brief effect. Fig. 8 B shows an afferent discharge in the face area produced by bending one of the vibrissae slowly; in Fig. 8 A a rapid up-and-down movement gives two brief outbursts at much higher frequency.

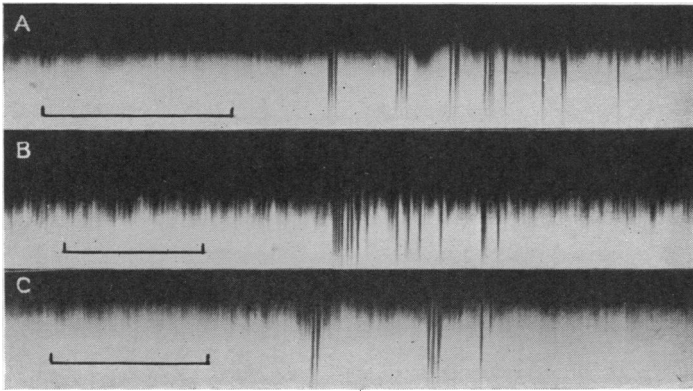


Fig. 9. Afferent impulses due to touch. A, cat under dial, touching dorsal surface of forefoot. B, cat under ether, touching hairs below eye. C, cat under chloralose, touching wrist.

*The discharge due to touch.* In the cat's cortex afferent discharges in response to thermal stimuli and to pain have not been detected: apart from the pressure receptors the tactile organs of the skin and hairs are the main source of the messages which reach the cortex, and discharges due to touch can be obtained from every part of the receiving area. When a wire electrode is used it is often difficult to be sure how many units are concerned, since the discharges are too brief to allow the sequence of impulses to be analysed, but in Fig. 9 A, B and C the larger spikes are all alike and so are probably derived from a single source.

As with the pressure response the tactile discharge to the cortex does not differ greatly from that in the peripheral nerve fibre, for in the latter the impulses are often spaced at intervals of only a few milliseconds and the whole discharge may be very brief. In most of the fibres to the cortex

it is very brief indeed (0.05 sec. or less) when the foot is tapped, and if it lasts longer there is a tendency for the impulses to appear in several high-frequency groups rather than in a continuous series. This may be seen in Fig. 9. The grouping recalls that found in the pressure discharge though it may be due merely to a similar grouping in the peripheral nerve fibre or to several discharges converging on to one thalamic neurone and reaching their maximum at slightly different times. The amount of convergence is considerable, for in the cat one afferent unit in the cortex may be activated by touching any group of hairs within an area 7 cm. square on the back. On the forefoot the convergence, in terms of skin area, is much less: in one unit, for instance, impulses could only be produced by touching the hairs covering an area 3 mm. square between the toes.

*The afferent (thalamic) after-discharge.* In the cat, dog and monkey if the anaesthetic is not too deep a discharge from the touch receptors to the cortex is often followed by a characteristic after-discharge. This consists of a succession of short volleys of impulses occurring at a frequency of between 10 and 20 a sec. and producing an oscillating noise in the loud-speaker. The after-discharge has been found with dial, chloroform and ether or morphia but not with chloralose and rarely with nembutal. The extent to which it is separated into distinct volleys varies considerably but seems to be greatest under moderately deep dial. It is most prolonged when the afferent pathway has been at rest for some time and is then made to transmit a considerable volley from the receptors. It is brief or entirely absent if the primary afferent discharge itself lasts more than a second or two. The duration of the after-discharge also varies with the depth of anaesthesia as well as with the magnitude of the afferent volley. The frequency of the outbursts changes very little, though the rhythm is slower in deep anaesthesia.

It is easier to study the after-discharge by listening to it than by making photographic records, for in these the impulse volleys become confused with the slower cortical waves and with impulses in cortical neurones. A wire electrode in the superficial layers of the grey matter (less than 2 mm. deep) will usually avoid the latter but will rarely show individual impulses of the after-discharge. The records in Fig. 10 give a good idea of the effect though the frequency is on the low side as the anaesthesia was deep.

The volleying character of the after-discharge shows that it is made up of synchronous or nearly synchronous outbursts from a collection of neurones which have been activated by the primary afferent volley. It is true that a single volley of impulses reaching the cortex may start a

period of rhythmic activity in the cells there, and the impulses coming from these cells would then be heard as an after-effect of the afferent volley. But there is no doubt that a rhythmic after-discharge can also arise in the afferent pathways before the cortex is reached, for in many preparations the repeated volleys can be detected in the exposed white matter and they remain audible in the cortex after the cells there have been put out of action by novocain or occlusion of the carotids. The effect does not develop below the thalamic level, for the sensory pathways can be tapped by a wire electrode at the level of the pons and there is then no trace of an after-discharge. It must therefore be due to thalamic neurones discharging more or less in unison as a sequel to the primary volley.

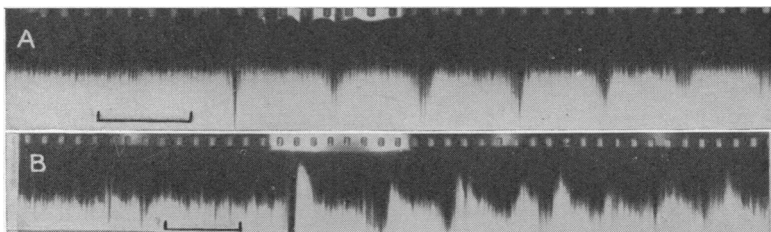


Fig. 10. Afferent (thalamic) after-discharge. Both records from cats under dial with wire electrode in the cortex. Stimulation by single touch to the forefoot. The primary afferent volley is followed by a series of volleys at intervals of 0.1 sec. or less.

The neurones concerned seem to be on or close to the direct pathway from the sense organs to the cortex, for the primary discharge and the after-discharge have the same distribution in the receiving area. The neurones must also be capable of reacting with one another, for otherwise the impulses would not be so well grouped. There is also some evidence that they may discharge spontaneously; for in light dial anaesthesia oscillating discharges are often heard from time to time in the receiving area, apparently in the afferent fibres and in the absence of deliberate stimulation. It is true that the general level of excitation in the thalamus may need a constant stream of impulses from the receptors to maintain it, but it is not at all unlikely that the thalamic cells which are normally set into rhythmical activity by an afferent volley should tend to discharge in the same way from time to time although no volley reaches them. They would then be displaying their affinity with the cells of the cortex which tends also to give rhythmic groups of waves under dial. The rhythm of the corresponding thalamic activity is somewhat faster

(15 a sec. as against 10 a sec.), but the character of the discharge certainly suggests that the same kind of mechanism is concerned in both cases.

In light anaesthesia in addition to rapidly oscillating discharges there is often a continued noise of impulses in the whole of the somatic receiving area. The noise is not as loud as that due to a tactile volley, but it seems to be caused by persistent discharge from the thalamus, for a wire electrode in the white matter will pick up continued trains of impulses at 10–25 a second. It is uncertain whether they correspond to particular afferent signals from the periphery, for it is usually impossible to find particular sense organs which will control them. They may represent a generalized excitation from the proprioceptors, since they can sometimes be modified temporarily by altering the position of the limb, although not by manipulation of particular muscles. The effect is present, though less distinct, in deep anaesthesia, for the noise derived from the receiving area still differs from that of neighbouring regions in having more high-frequency components.

#### *Part 2. The effect of the afferent discharge on the cortex*

*The afferent cortical wave.* When the foot or the face is touched, the afferent volley may influence the electrical activity of the cortex in a variety of ways, but almost invariably it will set up a brief potential wave in the somatic receiving area with its first phase surface positive. This initial wave has often been described and many of its properties are known. It occurs in the auditory area [Bremer, 1938; Bremer & Dow, 1939] and visual area [Bartley & Bishop, 1933] as well as in the somatic receiving area [Bartley & Heinbecker, 1938], and is produced by an electric stimulus to a nerve trunk [Forbes & Morison, 1939] as well as by a touch to a few hairs [Bard, 1938]. Examples of the initial wave in the different areas are given in Fig. 11. Prolonged stimulation by pressure or by rubbing the skin may give an initial wave if the afferent discharge has an abrupt onset, and during a sustained discharge there may be small, irregular oscillations which have some of the properties of the initial wave, but the analysis of these later events is more difficult and the characteristic response needs an abrupt stimulus to evoke it.

The most significant feature of the initial wave is that it is very closely related to the afferent discharge, so closely that it may be called the afferent cortical wave. As far as can be gathered by combining oscillograph and loud-speaker observations it has the same localized distribution within the receiving area as the afferent impulses, and

though it is reduced by failure of blood supply, deep chloroform anaesthesia, etc., it can nearly always be detected as long as the impulses are still audible. In light anaesthesia it may be hard to distinguish against a background of continued potential change, and the initial positive phase may be greatly cut down by the early development of a change in the opposite sense (surface negative). For this reason the wave is usually more obvious in deep anaesthesia with dial, nembutal or chloralose where the negative swing develops later or not at all. Sometimes there is a genuine increase in the positive phase as anaesthesia deepens, and there are considerable variations in the relative prominence of the afferent

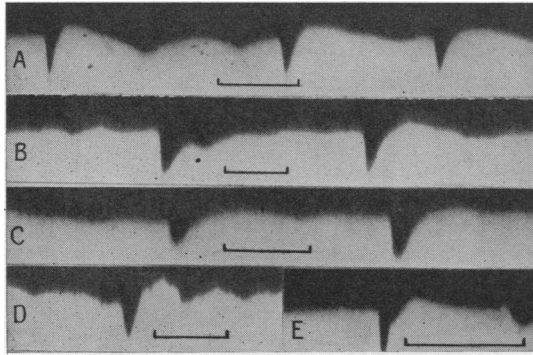


Fig. 11. Afferent waves recorded from the surface of the cortex. Downward movement indicates a positive potential at the cortical electrode in this and all subsequent records. A. Cat. Touches to forefoot. B. Rabbit. Touches to upper lip. C. Cat. Record from dorsal surface of medulla showing similar afferent wave in dorsal columns produced by touching foot. D. Cat. Record from visual area, showing similar wave produced by illuminating the eye. E. Cat. Auditory area. Afferent wave response to a click.

wave and afferent impulse noise in different animals. But in spite of this the wave appears as a relatively stable event depending mainly on the size of the afferent volley and not much on the state of the cortex.

In very deep anaesthesia the wave is monophasic or nearly so, with a potential (from a tap on the foot) of 0.1–0.5 mV. and a duration of 0.01–0.03 sec. In lighter anaesthesia with chloralose the positive phase is still large but it is followed by a lengthy negative phase. The whole wave complex then seems to be due to the brief afferent effect with a slower activity developing soon after it has begun and leading to a superimposed potential change which is mainly surface negative. This slower and later activity cannot be made to repeat itself at such short intervals as the afferent wave, so that if the touch is repeated 5–10 times a second



the negative phase disappears (Fig. 12). With dial in moderate doses a negative phase appears earlier, lasts for a shorter time and is less affected by rapid stimulation. Cutting down the blood supply to the cortex causes a much greater reduction of the later (negative) than of the initial (positive) activity, though the difference is not so great with dial as with chloralose. Convulsant drugs, on the other hand, cause a greater increase in the later activity than in the initial wave.

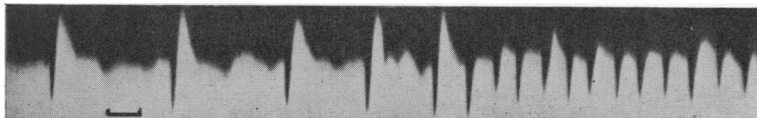


Fig. 12. Afferent waves in a cat under chloralose produced by repeated touches to forefoot, showing diphasic response changing to monophasic when the frequency of stimulation is increased to 10 a second. Downward movement (first phase of the response) indicates a positive potential at the cortical electrode.

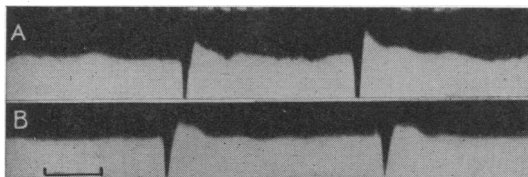


Fig. 13. Afferent waves recorded from the surface of the cortex (record A) and from the exposed white matter after removal of the cortex (record B). Cat under dial. Stimulation by touching foot.

The later activity will be considered more fully in the next section. Its much greater dependence on the state of the cortex suggests that it is due to neurones whose cell bodies are in the grey matter and are separated by one or more synapses from the afferent fibres. The appearance of an efferent impulse discharge in association with the negative wave supports this view (cf. p. 177). On the other hand, the initial surface positive wave seems to be due entirely to potential changes taking place in the afferent fibres. Its sign is compatible with an activity travelling from the deeper parts towards the surface of the cortex, but the best evidence of its origin was supplied by Forbes & Morison [1939] when they showed that a similar wave could be recorded from the underlying white matter by a needle electrode. As the waves which they described were evoked by electrical stimulation of a nerve trunk it seemed advisable to confirm the result with tactile stimulation. It is illustrated in Fig. 13 which gives the response to touching the foot in a cat deeply anaesthetized with dial.

The upper record is from the surface of the cortex. The whole of the grey matter of the motor area and somatic receiving area was then cut away: the exposed white matter was explored with the electrode until a point was found where the tactile discharge was again audible and the lower record was made from this point. It shows a potential wave scarcely distinguishable from that in the upper record, and as the lower record was made after destruction of the cortex we may reasonably conclude that the waves in the upper record were not the product of cortical neurones.

Evidence of this kind has led to a general agreement that the initial positive wave must be due to potential gradients in afferent fibres from the thalamus. The magnitude of the potential change at the surface of the cortex seems difficult to explain on the assumption that the wave represents no more than the summed action potentials in the afferent volley, but these might well be reinforced by changes of longer duration, e.g. after-potentials or depolarizations spreading from the nerve cells of the thalamus. The relatively constant time relations of the afferent wave are explained by the constant time relations of the afferent discharge from the receptors when the hairs are touched. This can be seen in a record from the medulla (Fig. 11 C). The potential wave there differs very little from that in the cortex except when the latter is cut short by an early negative swing. Both medullary and cortical waves can be given a slower rise and longer duration by manipulating the stimulus, but the range of variation is small, as the discharge must be abrupt if it is to give an adequate effect.

*Cortical activity following the afferent wave.* The events which succeed the afferent wave depend so much on the nature as well as on the depth of the anaesthetic that they are best described under separate headings for chloralose, dial and chloroform and ether. The main distinction is that chloralose slows down the activity of the cortical cells so that spontaneous waves occur at relatively long intervals, but it does not interfere with conduction from the afferent fibres provided that the cortical neurones have time to recover. With dial an afferent discharge may have much less effect, but in medium doses there may be considerable spontaneous activity in the cortex. Chloroform and ether are less selective and have more effect on the afferent pathways. In light dosage they seem to cause little slowing or interference with conduction, and their chief effect on the cortex is to promote a rapid synchronous activity of the nerve cells.

(1) *Chloralose. The efferent wave.* With chloralose and in the absence of deliberate stimulation the receiving area shows no more than two or

three potential waves every second. They are usually monophasic and surface negative with a maximum potential of as much as 2 mV. and a duration of 0.2–0.08 sec. (Fig. 14). The sign of the potential wave implies an activity developing near the surface of the cortex, or travelling away from the surface towards the interior. In agreement with this a wire electrode in the deeper layers of the cortex will often pick up an outburst of impulses corresponding to each of these waves, and in the motor area, where similar waves occur, each one is associated with a discharge in the fibres of the pyramidal tract [Adrian & Moruzzi, 1939]. Thus the waves mark recurring periods of activity involving the larger pyramidal cells.

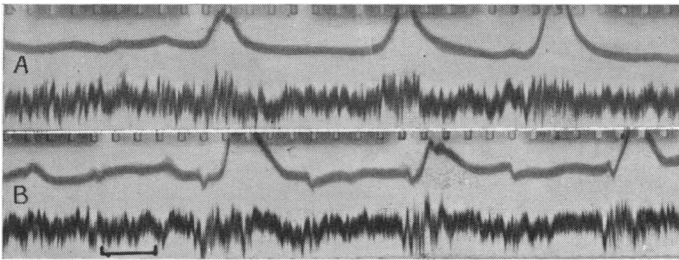


Fig. 14. Potential waves in chloralose anaesthesia occurring spontaneously (record A) or induced by tactile stimulation (record B). The upper tracing in both records is from the surface of the receiving area for the forefoot. The lower tracing is from a wire electrode in the pyramidal decussation. In A the three surface negative (efferent) waves are each accompanied by a pyramidal discharge. In B a pyramidal discharge occurs when the afferent (surface positive) wave is followed by an efferent wave.

With tactile stimulation repeated at short intervals the occasional negative waves are replaced by a succession of diphasic waves of the type already shown in Fig. 12. The first phase is then positive and coincides with the afferent volley to the cortex whilst the larger negative phase seems to be the equivalent of the spontaneous waves and like them is associated with an efferent discharge from the cortical cells (Fig. 14B). A cortical response of this sort may be regarded as a combination of the afferent wave with an 'efferent wave' which marks the successful excitation of the cortex and the discharge of impulses from the deeper cell layers. The efferent wave seems to have an initial positive component which sums with that of the afferent wave, but like the spontaneous activity it is mainly surface negative. The negative phase is certainly associated with the discharge of impulses by the cells, for if the stimuli are repeated at shorter and shorter intervals the negative phase and the efferent discharge are lost together and return together when the interval

is prolonged (Fig. 15). On the other hand, the negativity of the cortical surface greatly outlasts the discharge of impulses, so that much of the wave may be thought of as an after-potential. This may be seen when the potential wave in the motor area is compared with the discharge in the pyramidal fibres.



Fig. 15. Cat under chloralose. Upper tracing from surface of receiving area for forefoot, lower from wire electrode in pyramidal decussation. Four afferent waves (surface-positive) are evoked by touching the foot: the last two are at longer intervals and each gives rise to an efferent wave and a pyramidal discharge.

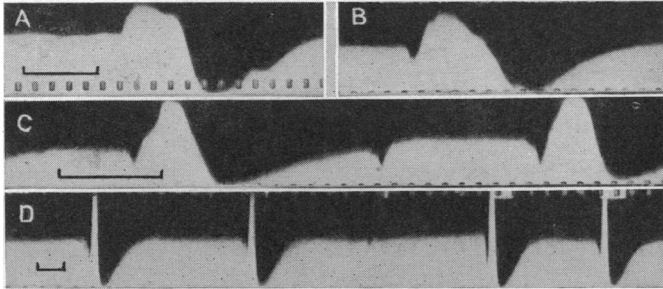


Fig. 16. Potential waves from the surface of the receiving area after local treatment with convulsant drugs. A. Cat under chloralose. Picrotoxin on cortex. Spontaneous wave with first phase surface-negative. B. Same animal. Compound wave evoked by touching the foot. First phase surface-positive. C. Cat under chloralose. Strychnine (0.5%) on cortex. Three touches to foot giving positive waves, the first and last followed by large negative waves. D. Cat under dial. Strychnine (0.5%) on cortex. Five touches to foot. The third gives only an afferent wave; the others give a complex response with a larger positive phase as well as the following negative phase.

*Convulsant drugs.* The same sequence of events is shown even more clearly after some part of the receiving area of the cortex has been treated locally with a convulsant drug like strychnine or picrotoxin. The anaesthetic in use is then immaterial, for with convulsant drugs the cortical neurones become readily accessible to the afferent discharge and give very large potentials, though they need a long time to recover between one excitation and the next. The efferent discharge can also be recognized easily when the effect is well established, for it is the characteristic high-frequency outburst described by Adrian & Moruzzi.

In the absence of intentional stimulation the area treated with the drug shows occasional waves which are initially surface negative (Fig. 16 A), as with chloralose. The chief difference is that the waves are much larger (up to 5 mV.) and are usually diphasic and the intervals between them are longer (2-10 sec.) with a steadier base-line. At each wave an outburst of impulses at a very high frequency can be detected in the deeper layers of the cortex and in the white matter. The discharge begins as the cortical potential starts to change but ends some time before the wave is over. With tactile stimulation there is again a close parallel with the response in chloralose, for if the touches are spaced 1 sec. or more apart each will produce the compound afferent-efferent response, beginning with a small surface-positive phase which is followed by a large negative one (Fig. 16 B). With a wire electrode it is often possible to hear both the initial afferent discharge and the high-frequency outburst from the cortex which follows it. With frequent stimulation or restricted blood supply the afferent discharge and the afferent wave can be made to appear without the efferent effect (Fig. 16 C).

It will be noticed that in the records in Fig. 16 D the initial positive phase of the response is larger when the efferent effect occurs than when the wave represents the afferent process alone. Apparently when the convulsive response is started by an afferent volley (though not when it occurs spontaneously) it begins with a surface-positive change which adds itself to that of the afferent wave. It is sometimes possible to detect the beginning of this second positive component, but more often all that can be seen is that the initial wave is much larger when the full response occurs. A similar increase produced by strychnine in the positive as well as in the later negative components has been found also with electrical stimulation of the optic nerve [Bartley, O'Leary & Bishop, 1937] and of somatic afferent nerves and of the fibres of the corpus callosum [Curtis, 1940].

(2) *Dial.* Under dial (or nembutal) there is a general tendency for the potential waves of the cortex to occur in groups with frequencies between 6 and 12 a second [cf. Bremer, 1935, 1936 and Derbyshire *et al.* 1936]. With light or medium dosage there is usually a continuous succession of waves over most of the cortex at a frequency which remains steady for considerable periods at about 10 a second or falls every few seconds to about half this rate. In deeper anaesthesia the slower waves drop out leaving the more rapid groups separated by periods of inactivity, or rather by periods in which the only sign of activity is a very small rapid oscillation.

With anaesthesia of medium depth whenever the large waves are not confluent it can be seen that the great majority of them make the cortical electrode negative to the indifferent, and when the waves are recorded in the motor area it is found that each is associated with a discharge of

impulses in the pyramidal tract [Adrian & Moruzzi, 1939]. Thus the groups of negative waves under dial resemble the occasional waves under chloralose and indicate an activity spreading inwards from the surface and giving an efferent discharge. But there is the difference that under chloralose the electrical activity of a given point in the receiving area can be entirely controlled by stimulation of the appropriate receptors, for with a series of touches the occasional waves are replaced by a series of the complex afferent-efferent responses. With dial, however, the afferent volley rarely produces such a comprehensive effect. It is true that the initial wave is usually diphasic, with the first, positive phase cut short by a brief negative phase (cf. Fig. 17 B), and as the latter is absent in deep anaesthesia it probably indicates an excitation spreading to certain elements in the cortex. But this excitation, if it occurs, is often quite

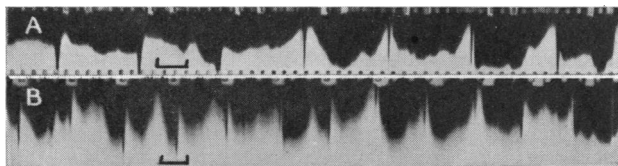


Fig. 17. Waves from the receiving area in cats under dial during repeated tactile stimulation. The brief afferent waves (initially positive) are superimposed on the slower negative waves of the spontaneous rhythm.

unable to influence the rest of the cortical mechanism in its neighbourhood, for the usual rhythmic waves may continue unchanged during the stimulation as though the afferent volleys had never arrived. The diphasic wave due to each volley is then superimposed on the slower and larger rhythm (cf. Fig. 17).

The dissociation of the cortex from the afferent pathways is not always so complete and in fact all degrees may be found, a common result of the volley being a tendency to a local increase in cortical activity rather than a specific and immediate excitation. Thus a tap on the foot may start a group of waves or may interrupt the rhythm, continued pressure may raise the frequency for as long as it is applied, and repeated tactile volleys usually succeed after a time in imposing their rhythm on the cortex (Fig. 18). These facilitating effects are more prominent when the cortex itself is less active; but there is very seldom the complete control of cortical activity in the receiving area which is found with chloralose or with convulsant drugs. Indeed in many preparations the tactile volley and the subsequent volleys of the thalamic after-discharge can be heard

as one series of oscillations and the groups of cortical waves as another series quite independent of the first. In some records it is even possible to distinguish the two as a series of positive and of negative waves, though they are often too close together for their sign to be recognizable.

The difference between the action of dial and chloralose is no doubt largely a matter of the range over which the afferent volley can effect the neurones of the cortex. In Fig. 17 (dial) neurones which are so situated in relation to the electrodes that they can influence the potential record are not affected by the afferent volley. In Fig. 12 (chloralose) all these neurones are affected by it. Theoretically some of them might be a long way from the

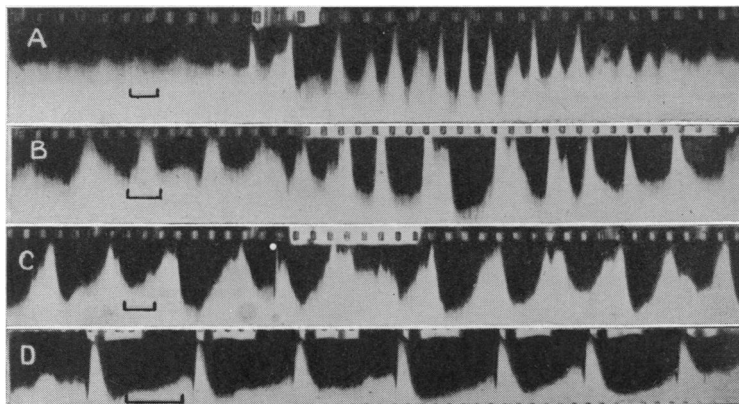


Fig. 18. Modification of cortical rhythms by afferent discharges in cats under dial. All records from the forefoot area. A. A single touch produces a train of waves at 10 a second. B. Pressure on the foot increases the size and frequency of the waves. C. A touch disturbs the rhythm momentarily (note diphasic afferent wave, marked by white dot above). D. Repeated touches impose their own rhythm on the cortical waves.

cortical electrode, for with monopolar recording a large group of neurones anywhere in the brain might produce a potential change. Actually the neurones responsible for the waves in Figs. 12 and 17 are not likely to be more than a few millimetres from the cortical electrode, for a local application of novocain will abolish the waves and local strychnine will replace them by waves of the large convulsive type. In fact the structures responsible for both the surface positive and the surface negative waves are probably very close together.

A dissociation at the level of the cortex was recognized by Bremer [1938] as a characteristic effect of dial and other anaesthetics of the barbituric series. In deep anaesthesia when there are long inactive periods between the groups of waves the dissociation is much less evident. The afferent volley has no longer to compete with the pacemaker which determines the spontaneous cortical waves and touches at suitable intervals will always start a period of rhythmic activity. It should be pointed out, however, that in deep anaesthesia the waves which follow

an afferent volley may not indicate any activity on the part of the neurones of the cortex. In Fig. 19, for instance, the record is from the cortex, but the primary afferent wave is no longer cut short by a negative phase as it would be in lighter anaesthesia, and all the succeeding waves are, like it, surface positive. In all probability therefore there is no excitation of the cortex at all, and the waves which follow the primary volley are all afferent effects due to the rhythmic volleys of the thalamic after-discharge. Similar trains of waves following the afferent response can be recorded from the cut surface of the white matter after removal of the cortex (Fig. 19 B), and nothing more seems to have been added by the presence of the grey matter in the record shown in Fig. 19 A.

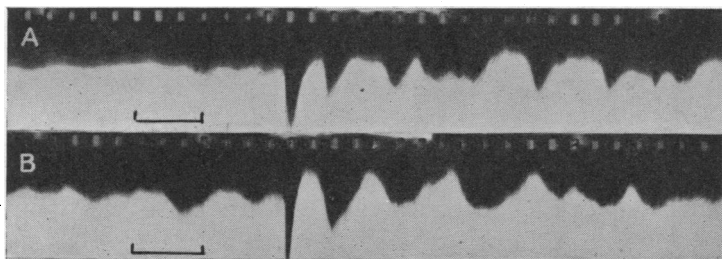


Fig. 19. Afferent wave and thalamic after-discharge recorded from the surface of the cortex (record A) and from the white matter after removal of the cortex (record B). Cat under dial. All waves are surface positive and, though recorded from the cortex in record A, are not due to cortical neurones.

In preparations like this, when the thalamus still responds rhythmically but the receiving area of the cortex seems to have become quite inactive, it is interesting to find that the waves which occur in groups from time to time in other regions of the cortex are also mainly surface positive and may therefore be of deep (i.e. thalamic) origin. In deep barbituric anaesthesia the cortical waves are abolished by cutting the thalamo-cortical fibres [Lewy & Gammon, 1940], and this result would be bound to follow if the waves merely represent discharges from the thalamus. In many regions, however, the waves are not accompanied by the noise of an impulse discharge, and there is sometimes a change from surface positive to surface negative during a series of waves without any interruption of the rhythm. This suggests a system of waves spreading laterally in the cortex from an origin which shifts in relation to the cortical electrode: but whatever its explanation it shows that the sign alone is not a certain indication that a wave is of thalamic or of cortical origin.



(3) *Chloroform and ether.* As Bremer [1937] has pointed out, these anaesthetics differ from dial and chloralose in that their effect on the central nervous system is more widespread. With either of them all signs of an afferent discharge to the receiving area may be suppressed at a stage of anaesthesia which still allows some cortical activity. In light anaesthesia, however, there is nothing to distinguish the afferent discharge due to touch or pressure from that under dial or chloralose, except that there is a more persistent impulse noise apart from stimulation and that the rhythm of the thalamic after-discharge is somewhat faster if it can be distinguished at all.

In light anaesthesia the characteristic activity of the cortex is a continuous series of potential oscillations with a frequency of 30–60 a second,

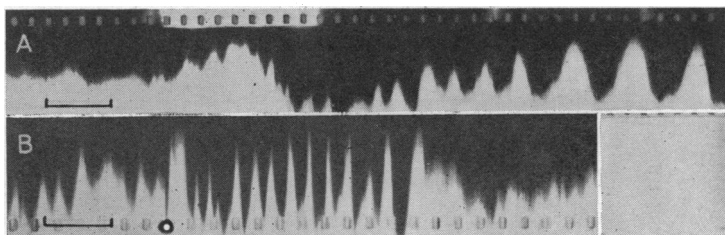


Fig. 20. Potential waves in the receiving area in cats under chloroform and ether. A. Cat under light ether, record from face area, stimulation by touching one of the vibrissae. Note decreasing frequency and increasing size of waves following stimulation. B. Cat under chloroform and ether. Response to touching forefoot. The afferent wave is marked by a white dot.

but there may be periods when the rhythm is lower and the waves larger and periods of very little electrical activity. Renewal of the anaesthetic after a period of withdrawal often leads to an increase of the rhythm up to 50 a second or more, owing possibly to stimulation of sense organs or to a direct effect on the cortex, and sometimes a single touch or noise causes a change from a slow to a rapid rhythm over a large part of the hemisphere.

In the appropriate region of the receiving area, if afferent impulses are able to reach it, the rhythm responds immediately to any sudden change in the discharge. A touch gives the usual afferent wave, diphasic and followed by rapid oscillations lasting for 1/10–1/2 sec. (Fig. 20). Pressure gives more regular waves with frequencies as high as 90 a second and a potential swing of 0.5 mV. or more. The depth of anaesthesia has little effect on the initial frequency but decides the rate of decline when the stimulus is kept constant. With gradually increasing pressure the fre-

quency can sometimes be made to rise gradually from the resting to the stimulated value (e.g. from 10 to 60 a second); in fact the cortical waves can be made to vary over the same frequency range as the impulses in the afferent fibres.

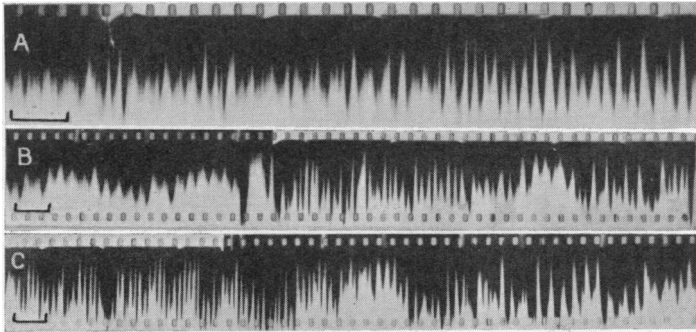


Fig. 21. Records from the receiving area in cats under chloroform and ether, showing the increase in frequency of the waves during stimulation. A. Gradually increasing pressure to forefoot. B. Another animal, pressure suddenly applied causes waves at 60 a second. C. Same animal as B. End of a pressure stimulation showing fall in frequency from 60 to 25 a second.

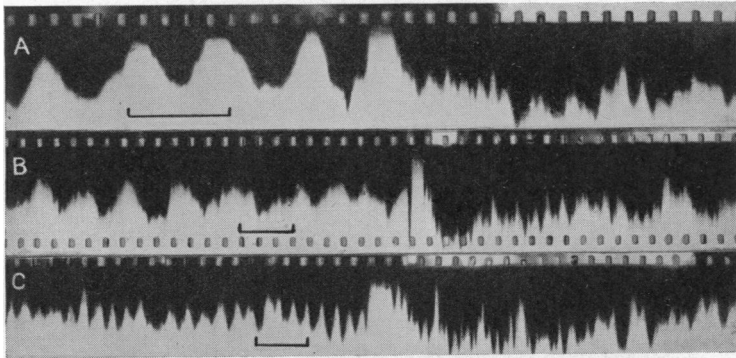


Fig. 22. Potential waves under chloroform and ether showing breakdown of regular rhythms by an afferent discharge. Records from three cats from the forefoot area of the cortex. Stimulation by pressure to the forefoot. Resting rhythm at about 10 a second in A and B, 40 a second in C.

Records illustrating the rise and fall in frequency on stimulation are given in Figs. 21 and 22. Some of them show also what happens when the synchronization is not maintained. In Fig. 22 A, for instance, there are regular waves at 10 a second before, but only an irregular and much smaller oscillation during the period of stimulation. In Fig. 21 A there

were regular waves during stimulation but not in the period before or after.

When there are regular waves during stimulation their frequency seems to run more or less parallel with that of the impulses in the afferent units. But there is clearly a pooling of excitation from many fibres and an interaction of the excited neurones rather than a direct transmission from afferent fibre to cortical nerve cell. In the absence of stimulation, for instance, the cortex often shows a rapid rhythm (25 a second) superimposed on a slow (5 a second) or recurring at regular intervals, but no corresponding rhythm has been found in the resting afferent discharge. Again, during continued stimulation there is a far greater synchronization in the cortical than in the afferent neurones, for

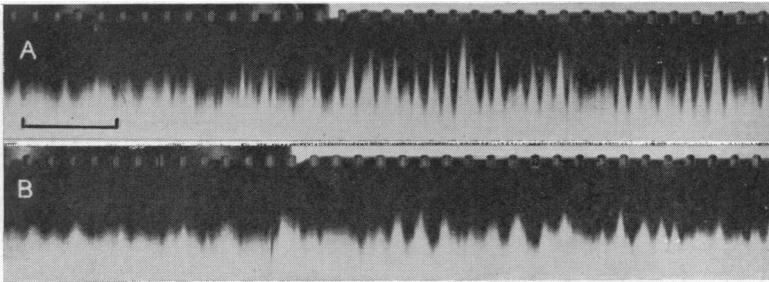


Fig. 23. Potential waves evoked by pressure to A, contralateral, and B, ipsilateral forefoot in a cat under light chloroform and ether.

very regular waves are evoked by a discharge which is heard as a non-rhythmic noise, and if a touch produces a grouped after-discharge from the thalamus the frequency of the volleys in it may differ considerably from that of the cortical waves which occur at the same time.

*Excitation in other regions.* Under light anaesthesia with chloroform or ether a touch, besides causing the localized excitation of a particular part of the receiving area, may produce a widespread increase of activity in other parts of the cortex. Thus the frequency of the waves in the fore-foot area of the right hemisphere may be increased by touching the right foot as well as the left, though the increase is not so great (Fig. 23). Similarly, the movement of one of the vibrissae of the face may increase the frequency in the foot area of either hemisphere. These secondary effects are most clearly seen when the cortex, though lightly anaesthetized, has passed into a period of relative inactivity: from this it can be roused, not only in the somatic receiving area but in regions farther back, and not only by tactile stimuli but by visual and auditory as well. In fact it

may become necessary to blindfold the eyes and avoid any noise when the effects of a touch are to be investigated.

In light anaesthesia a touch, sound or change of illumination may raise the level of activity in the cortex generally, but it is only in the appropriate receiving area, somatic, auditory or visual, that the noise of an afferent volley can be heard. Elsewhere there is sometimes an increase in the fainter rushing sound which forms a background to the thud of the cortical waves, but in parts of the supra-sylvian and marginal gyri there is rarely anything to suggest an increased afferent discharge. It does not follow that the increased cortical activity is not then due to impulses from the thalamus, for there is no reason to think that all impulses from the thalamus would be equally audible at the surface of the cortex. But the excitation of remote areas clearly depends on a mechanism which differs considerably from that responsible for the localized afferent discharges to the various receiving areas. The nature of this mechanism is beyond the scope of the present paper. There is evidently a clue to it in the work of Forbes & Morison on the widespread secondary cortical response which follows electrical stimulation of a nerve trunk, and the various possibilities are discussed in their papers.

#### DISCUSSION

As regards the afferent pathway the most striking result which has appeared in this work has been the fidelity with which the message from the receptors is handed on to the cerebral cortex. This applies only to the receptors for touch, pressure and hair movement, but when these are stimulated the noise of the discharge which reaches the cortex is not obviously different from what it would be in the peripheral nerves. With more exact recording certain differences are found; the impulses reaching the cortex may come in groups of two or three very close together and there may be a more rapid decline in frequency than there is likely to be in the discharge from the sense organ. With ether and chloroform the pathway may become completely blocked, but dial or chloralose seldom produce complete failure in spite of the synaptic regions which the signals must pass.

The phenomenon of masking found by Marshall *et al.* [1941] shows that there is a convergence of pathways on the way up to the cortex, and this has been confirmed. When a wire electrode leads from a single afferent unit it is often found that receptors over a considerable area can produce a discharge in it; and it is probable though not certain that a restricted stimulus may activate a number of afferent units. Thus the

connexion between the tactile receptors and the cortex is like that between the rods and cones of the retina and the fibres of the optic nerve, securing much convergence but allowing a spread of excitation in synaptic areas instead of limiting the signals to fixed and insulated pathways.

Such an arrangement might be expected to display inhibitory as well as excitatory effects, but so far no clear evidence of inhibition has appeared. The anaesthetic may be responsible for this, for the inhibition which Barron & Matthews [1935] have found in the spinal pathways was greatly reduced by anaesthetics. In light anaesthesia, however, provided that the pathway is unoccupied and has had time to recover, a touch on the face or the forelimb is signalled to the corresponding region of the cortex and the signal is not greatly changed en route.

But the primary signal is usually accompanied or followed by additional signals which it has aroused in its passage through the thalamus, and these are subject to much more variation. They are shown by the widespread activity which appears if the anaesthesia is light and the stimulus intense, and by the rhythmic after-discharge which follows the afferent volley. The mechanism of the widespread effect has not been investigated: that of the rhythmic after-discharge is made somewhat clearer by the proof that it can occur after removal of the cortex. Evidently it does not necessarily depend on a circulation of impulses from thalamus to cortex and back, and the thalamus must have its own mechanism for producing the after-discharge whether the cortex is there or not. The mechanism need not involve any special nerve-cell organization, for the same kind of reaction is found in other collections of excitable cells of quite different origin. In two papers by Eccles & Magladery [1937] on smooth muscle there are many records from the nictitating membrane showing a rhythmical after-effect essentially similar to that of the thalamus. The time scale is, of course, different, but as in the thalamus a single stimulus sets up an immediate response and this is followed by a series of waves due to the synchronous activity of many units and repeated at intervals which tend to settle down to a standard value. Evidently the smooth muscle fibres and the neurones of the thalamus have common properties which give them the same tendency to discharge in a synchronized rhythm.

The tendency can be seen in the cortical nerve cells as well as in those of the thalamus, for a single electrical stimulus to the cortex or an afferent volley (without an after-discharge) may set up repeated cortical waves. But the cortical neurones are more unstable than the thalamic and may continue their rhythmic activity for long periods. In the

thalamic neurones on the afferent pathway there are occasional rhythmic discharges in the absence of a deliberate stimulus and sometimes with chloroform or ether the neurones are in continued activity. But as a rule under dial an afferent volley is needed to set them off and their discharge seldom lasts for more than a second, whereas the neurones of the cortex maintain their rhythm for hours on end.

The thalamic after-discharge is sometimes non-rhythmic, and the primary discharge during continued stimulation by pressure or rubbing the skin seldom shows any dominant rhythm. Thus the thalamic neurones are associated in a way which makes for synchronous activity only when there are no local inequalities to prevent it, for local inequalities are more likely to be present during the actual transmission of a message than in the period of raised excitability which follows. The cortical neurones show

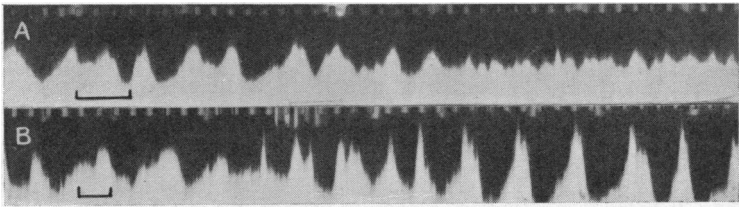


Fig. 24. A. Abolition of large waves by an afferent discharge in a cat under light dial anaesthesia. B. Increase in waves produced by an afferent discharge under deeper dial anaesthesia.

an association of the same kind. It is well illustrated by the records in Fig. 24 made from two cats, one lightly, the other deeply anaesthetized with dial. The potential waves are recorded from the forefoot area of the cortex and midway through each record a steady pressure is applied to the foot. In the lightly anaesthetized brain the synchronous beat is broken up into rapid, irregular wavelets, for in the light anaesthesia the impulses in the afferent discharge can exercise a more direct effect on the different neurones of the cortex. Deeper anaesthesia prevents this direct transmission but a general facilitation can still occur. The result is that the waves increase in size and frequency and their synchronization is not disturbed (Fig. 24 B).

The way in which the anaesthetized brain will react to an afferent discharge will vary according to the relative degree to which the anaesthetic has affected cortex or thalamus, excitability or rate of recovery, direct transmission or indirect facilitation, etc. In different animals there are considerable variations although every care may have been taken to

give the anaesthetic in the same way. In the unanaesthetized brain this particular difficulty would be avoided, but the afferent signals will arrive in an area in which the conditions vary from moment to moment owing to the continued rhythmic activity and vary over longer periods owing to the changing frequency of the waves. We need to know much more of the origin of these continued rhythms and of the factors which determine the general level of activity in the unanaesthetized brain. But the present study shows how profoundly the reactions of the brain are modified when spontaneous changes are reduced or absent. Under chloralose, for instance, the cortex is reduced to the level of a simple reflex mechanism. Spontaneous waves occur at a very low frequency but direct synaptic transmission is still possible, with the result that a signal arriving by the afferent pathway is passed at once to the motor area and down the pyramidal tract to the spinal motor neurones. Thus a tap on the foot causes a twitch of the leg by a reflex arc which includes the cerebrum. At each relay station the signal is reconstituted by fresh neurones but the alterations which occur in the cortex are of the same order as those on the way in or out.

Cerebral reflex arcs of the same sort can be produced by treating the surface of the cortex locally with strychnine, though in this case the signal is amplified on the way. The cortex can give such an immediate and direct response because it is doing so little on its own account. As soon as the effect of the drug and the anaesthetic passes off the grey matter will regain its normal instability and tendency to continued discharge, the motor neurones will be exposed to a changing pattern of excitations and inhibitions and direct reflexes will cease.

#### CONCLUSIONS

The area of the cerebral cortex which receives afferent signals from the somatic sense organs has been surveyed by recording the impulse discharges in afferent fibres as well as the potential waves in the grey matter. To avoid confusion the area is spoken of as the somatic receiving area. A variety of anaesthetics has been used.

1. The area receiving the primary afferent discharges from the thalamus agrees with the 'sensory area' determined histologically and with the area determined by recording cortical potential waves in deep anaesthesia. The representation of different parts of the body surface shows the same stability as that found by Marshall *et al.* using the potential wave method.

2. The receiving area of the cortex is concerned with those parts of the body surface which are most closely related to the outside world. In the rabbit the mouth parts are most important, in the cat the claws and the dorsal and lateral aspects of the forelimb, the face area is large in the dog, and the hand and face in the monkey.

3. In the cat the digits are represented in two regions separated by the area for the face, but this appears to be an arrangement peculiar to one species and the triple representation suggested by the results of Marshall *et al.* has not been found.

4. Brief afferent volleys are sent to the cortex when the hairs are touched and more sustained discharges can be produced by pressure. With a wire electrode penetrating the grey matter impulses in single conducting units can be recorded. The pressure discharge in a single unit may last for a minute or more and the frequency shows some grading according to the intensity of the stimulus. The impulses often appear in groups of two or three very closely spaced as in the discharges in the pyramidal tract.

5. The afferent volley produced by a touch is often followed by a rhythmic after-discharge from the thalamus. This has the same distribution to the cortex as the primary discharge. It consists of a series of short volleys at a frequency between 10 and 20 a second. It can be detected in the afferent fibres after destruction of the cortex and is therefore not dependent on a circuit from thalamus to cortex and back.

6. The arrival of an afferent volley produces a potential wave in the cortex with its first phase surface positive. This wave is due, as others have shown, to potential gradients in the afferent fibres and not to an activity in the cortical neurones.

7. In chloralose anaesthesia the afferent cortical wave is followed by an efferent wave which is mainly surface negative and is associated with a discharge of impulses from the cortical neurones. When convulsant drugs are applied locally to the receiving area there is a similar afferent-efferent response to a touch, though the efferent component is much larger. The efferent response is abolished by restricting the blood supply to the cortex, etc.

8. With dial or nembutal anaesthesia in medium dosage there is more activity in the cortex apart from stimulation and afferent discharges may have very little effect on this activity. The dissociation of the cortex from the afferent fibres is less marked when the cortex is less active and repeated tactile volleys usually succeed in imposing their rhythm on the cortical neurones.



9. In very deep dial or nembutal anaesthesia although the cortical neurones have become quite inactive afferent effects can still occur and rhythmic after-discharges from the thalamus will produce groups of surface positive cortical waves.

10. In deep anaesthesia with chloroform and ether afferent discharges may fail to reach the cortex. In lighter anaesthesia there are rapid potential oscillations which are increased in frequency by an afferent discharge. The cortical neurones are often well synchronized and may become more or less so during afferent excitation.

11. In light ether anaesthesia a touch may produce widespread activity in other parts of the cortex, though the rise of frequency is not as great as in the appropriate part of the receiving area. Auditory and visual stimulation may also produce a generalized increase in activity.

12. It appears that signals from tactile receptors are handed on to the cortex without much alteration, but that they are accompanied by additional signals from the thalamus which are much more variable.

13. The thalamic neurones resemble those of the cortex in their tendency to rhythmic discharge though they are more stable and less inclined to spontaneous activity. When the rhythmic activity of the brain is depressed (as in chloralose anaesthesia) it may react as though it were a simple reflex mechanism.

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