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THE ELECTRICAL RESPONSES OF MAMMALIAN CEREBRAL CORTEX

By B. G. CRAGG

From the Anatomy Department, University College, London

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The potential difference between an electrode on the surface of a cortical area and an electrode on a distant indifferent tissue changes in a characteristic way after the stimulation of a tract of axons leading into the cortical area. A large number of studies during the last twenty years has established that in the visual, auditory and somatic-sensory areas the first change at the cortical electrode is of positive polarity and 5–10 msec duration and the second of negative polarity and 10–100 msec duration. This primary pattern of response is often followed by a variable number of diphasic waves of potential change, each lasting about 100 msec. The relation of the primary response to the action-potentials of single neurones has been reviewed by Eccles (1951) and there is little doubt that the two waves of the primary response represent the integrated synaptic and after-potentials of the cortical neurones first stimulated by the afferent impulses. Few studies have as yet been made of the change in this pattern of response at different depths in the cortex, though Burns & Grafstein (1952) have reported marked changes with depth in the response of cortex to direct electrical stimulation of its surface. A reversal of the polarity of the response occurs in the region of the cell bodies whose dendrites are responsible for the potential changes recorded at the surface.

The present paper describes recordings from a microelectrode at different depths in each of the three cortical areas mentioned above after the stimulation of the appropriate afferent tract. In addition to monopolar recordings, voltage gradients have been measured at different depths in the radial and tangential directions by measuring the voltage difference between pairs of microelectrodes set 200 μ apart. Marked changes with depth have been found in the electrical records and these changes can be correlated with the histological structure. The primary response waves are negative and then positive among the deep lying cell bodies, and positive and then negative among the superficial dendrites of these neurones. This result is consistent with the

interpretation of Eccles (1951) and similar to the results of Burns & Grafstein (1952).

The one exception to the pattern of response described above is that in the visual area three brief spikes are recorded after the stimulation of the optic nerve and before the two typical waves of the primary response. These spikes were first detected in monopolar recordings by Bishop & O'Leary (1938) and were shown to be extracortical in origin by Chang & Kaada (1950). By the use of tangential pairs of microelectrodes, it has been possible to associate the last of these spikes definitely with the arrival in the visual cortex of the afferent impulses in the radiation axons from the lateral geniculate body. The two earlier spikes coincide in time with potential changes in the lateral geniculate body reported by P. O. Bishop (1953) and are presumably recorded in the cortex after electrotonic spread. It can be shown that these two earlier spikes set up negligible voltage gradients in the cortex, compared with the gradients accompanying the last of the spikes and the two waves of the primary response.

It has been mentioned that the two waves of the primary response are often followed by longer diphasic waves, which presumably represent the integrated activity of large numbers of cortical neurones, as the synchronization caused by the initial stimulus is lost. In order to study the patterns of neuronal response during these later waves, microelectrode recordings have been made from single cortical neurones. The recordings consist of patterns of spikes each of about 1 msec duration. These spikes are presumably part of the extracellular action potential of the cortical neurones but no synaptic potentials have yet been detected, and it has not yet been possible to make intracellular recordings. The spikes are recordable from only a small proportion of the cortical neurones within the area responding to the stimulation and are characterized by a fairly constant latency after the stimulus, though the number of spikes occurring in a given burst is variable from one stimulation to the next.

METHODS

Electrodes

For recording from single cortical neurones glass pore microelectrodes have been used, filled with 0·9% NaCl, as described by Ling (1948), Burns & Grafstein (1952) and others. At a tip diameter of 1–2 μ, some of these electrodes succeed in penetrating the pia without being broken. The electrodes were held in an oil-operated micro-manipulator similar to that demonstrated by Matthews (1952).

For recording the integrated response of cortex at different depths steel microelectrodes made as described by Grundfest, Sengstaken, Oettinger & Gurry (1950) are more convenient than glass electrodes and can be mounted in pairs for recordings of voltage gradients. Steel needles were reduced electrolytically to a shaft diameter of about 20 μ, which tapered down to a tip of about 1 μ diameter. These needles were insulated in 'Synobel Insulating Varnish' (made by I.C.I.) by dipping in tip first, and baking till brown. After three to four coats of varnish the needles had a resistance of more than 10^9 Ω in mammalian saline (0·9% NaCl). The tip of the needle was then

removed with scissors under a dissecting microscope to give a bare end of about 5μ diameter and about 10 KΩ resistance (measured in mammalian saline at 100 c/s).

Voltage gradients were measured with pairs of these steel microelectrodes mounted 200μ apart under a microscope. A smaller separation than this often gave inconveniently small voltage differences. A photomicrograph of a radial and a tangential pair of these electrodes has been published by Cragg, Evans & Hamlyn (1954), together with a photomicrograph of a Golgi-Cox preparation showing a typical track made by a radial pair of electrodes.

The sciatic nerve was stimulated by short silver wire electrodes mounted in a small 'Perspex' holder, which insulated them from their surroundings except for the nerve trunk, and which could be sewn on to the underlying muscle so that the wound could be closed up. The optic nerve was stimulated by a steel needle electrode thrust into the nerve trunk. Two concentric steel tubes carried the earth and the indifferent stimulus connexion and made contact with the tissues in the orbit. All electrodes were insulated except where they were intended to make contact and all points of contact with the tissues were platinized, as this was found to make the stimulus artifact easier to control. The auditory system was stimulated with a small earphone held in a clamp at the external auditory meatus. The reproducibility of the electrical recordings, depth for depth, as the electrode entered and withdrew was considered to be a better test of the validity of the result than the use of a monitoring surface electrode.

Surgical preparation

Pentobarbitone was used as the anaesthetic in all the experiments to be described, including the preparations in which the brain stem was transected at collicular level. The trachea was cannulated and the animal's head held in a Palmer Czermack-type holder, or a Horsley-Clarke machine. After reflecting the temporal muscles the cortex was exposed widely and kept irrigated with warm mammalian saline. The sciatic nerve was exposed at the level of the knee, and the stimulating electrodes sewn in. The optic nerve was exposed by tying the optic stalk and removing the eye-ball. Haemorrhage from the bone was controlled with bone wax, all muscles were cut with diathermy and bleeding from the dura or in the orbit was controlled with muscle grafts. Rabbits were used in most of the experiments to be described because the pia is not so difficult to penetrate as in the cat. Some cats were used for brain-stem section, and for depth surveys of the electrical responses since it was thought that the greater stratification in the cortex of the cat (the presence for instance of a clearly defined stria of Gennari) might be associated with a greater change in the electrical records with depth.

Electronic apparatus

The amplifiers used were of the type described by Bishop & Harris (1950) and the electrodes were always connected to deflect the trace upwards in the photographs for a negative change at the active electrode. When a radial pair of the electrodes was used, the lower electrode deflected the trace upwards when it became negative to the upper one. The rejection ratio of in-phase to out-of-phase signals was at least 1000:1. The stimulator and time base were of the type described by Attree (1949, 1950), and a radio-frequency transformer was used to isolate the stimulus output from earth (Schmitt & Dubbert, 1949). The input signal to the amplifiers was applied to the grids of a balanced pair of cathode followers (Bishop, 1949). The time and voltage calibration is shown on the records by pairs of arrows whose lengths are equivalent to the times and voltages shown against them.

RESULTS

The somatic-sensory area

A primary response was recorded within a region of 2–3 mm diameter in this area after stimulating the sciatic nerve at the knee. This response is illustrated in Fig. 1, which shows a depth survey made by withdrawing a focal micro-electrode from a depth of 3 mm in the centre of the area giving the largest

surface response. It is seen that the response is largest at the surface where the first wave is of positive polarity. This response declines in amplitude to a small value at 0·75 mm below the pia and a reversed response begins to appear at 1·25 mm below the pia, reaching a maximum amplitude at a depth of about 2·25 mm. The time course of the response does not vary appreciably from the surface to the white matter. The reversed response deep in the cortex does not reach as great an amplitude as the surface response.

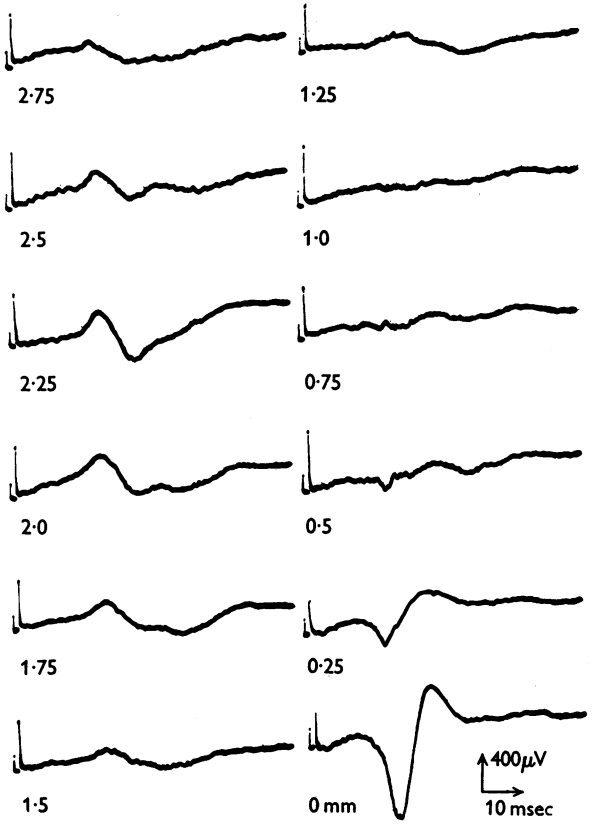

Fig. 1. Monopolar recordings at different depths in the somatic-sensory cortex of a rabbit after stimulating the contralateral sciatic nerve. The depth in mm below the pia is shown against each record.

Radial voltage gradients (before and after the local application of 1% strychnine sulphate) recorded in another animal in the same circumstances are shown in Fig. 2. The voltage gradient declines in the first millimetre in the same way as the voltage gradients implied by the monopolar records in Fig. 1, and only the time course is altered by the strychnine. No appreciable tangential voltage gradients were detected with tangential pairs of microelectrodes.

The variation of this electrical response with depth is consistent with one of the obvious features of the histological structure of cortex, for pyramidal cells lying at many different depths send apical dendrites up to ramify profusely at the surface of the cortex. The concentration of dendritic surface area in the upper part of the cortex corresponds to the large positive to negative response. The cell bodies of the pyramidal neurones are distributed throughout the depth of the cortex, and this is consistent with the smaller amplitude of the deep reversed response.

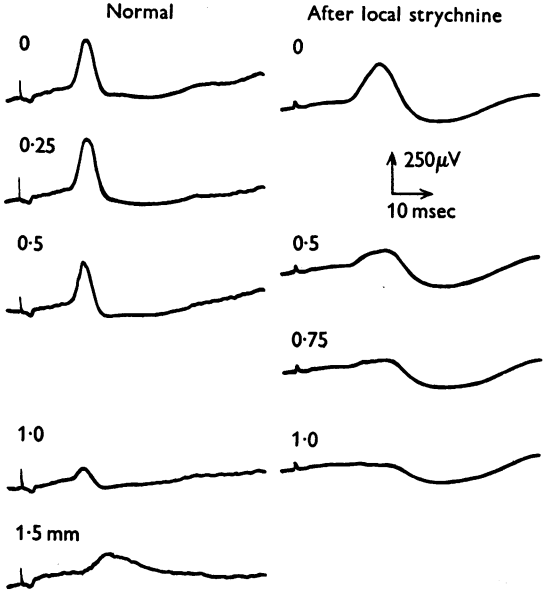

Fig. 2. Radial voltage gradients at different depths in the somatic-sensory cortex of a rabbit after stimulating the contralateral sciatic nerve. The right-hand column is of the same derivation as the left, after the local application of 1 % strychnine sulphate solution to the surface of the cortex.

The auditory area

Fig. 3 shows records of the radial voltage gradients occurring in this area at different depths. The stimulation consisted of a tone of 2500 c/s applied to the contralateral ear during the time indicated by the arrow marked 'stimulus' in Fig. 3. A primary response was recorded within a region of 1–2 mm diameter in the auditory area after this stimulation, and the records were obtained from the centre of the region giving the largest surface response. It will be noted that between 0·4 and 2 mm below the pia there is a radial voltage gradient of similar time course to that found in the somatic-sensory area, which declines in amplitude with depth in the cortex and reverses at a depth of 2·2 mm when the upper electrode of the pair would be among

the depolarized neurones deep in the cortex, and the lower electrode in the white matter. The only additional feature in this area is that between the pia and a depth of 0·3 mm, a radial voltage gradient is found of opposite polarity to the gradient just below 0·3 mm. This result would be consistent with the stimulation of a layer of cell bodies lying just below the pia, or with the presence of a feltwork of tangential fibres above the main ramifications of the apical dendrites of the pyramidal neurones deeper in the cortex. Such a layer of fibres has been described by Cajal (1911, p. 621), and if it were

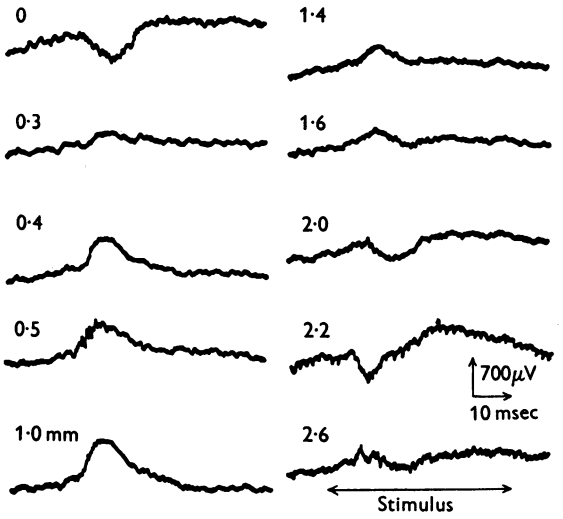

Fig. 3. Radial voltage gradients at different depths in the auditory cortex of a cat evoked by a 2500 c/s tone applied to the contralateral ear during the period marked by the arrow 'stimulus'.

unstimulated during the primary response of the neurones below, there would be a voltage gradient between the as yet unstimulated fibres above and the positive dendrites below, similar to that recorded.

The visual area

The optic nerve was stimulated in the orbit and a primary pattern of response obtained throughout the several square centimetres of the contralateral visual area. Fig. 4 shows a depth survey of the response recorded from a monopolar microelectrode as it was withdrawn vertically from the occipital lobe near the mid-line. The persistence of the response below 2 mm in these records was probably due to the proximity of tip of the electrode to the deeper cortical neurones on the medial surface of the hemisphere since in recordings from more lateral positions the response was small below 2 mm. The records show a decline in amplitude of the surface positive-to-negative response in the first millimetre of cortex, similar to the decline in the somatic-

sensory area. Below 1 mm there is a reversal of the response, and at 1·7 mm the amplitude is as great as the surface response, in contrast to the smaller reversed response found in the somatic-sensory area. It is possible that the difference between the two areas is due to the presence of the large Minot cells deep in the visual cortex. These large cells would presumably be large producers of extracellular current and they show a strong tendency to lie in a band deep in the cortex (e.g. Cajal, 1911, fig. 388). No such concentration of large cell bodies has been described in the somatic-sensory area.

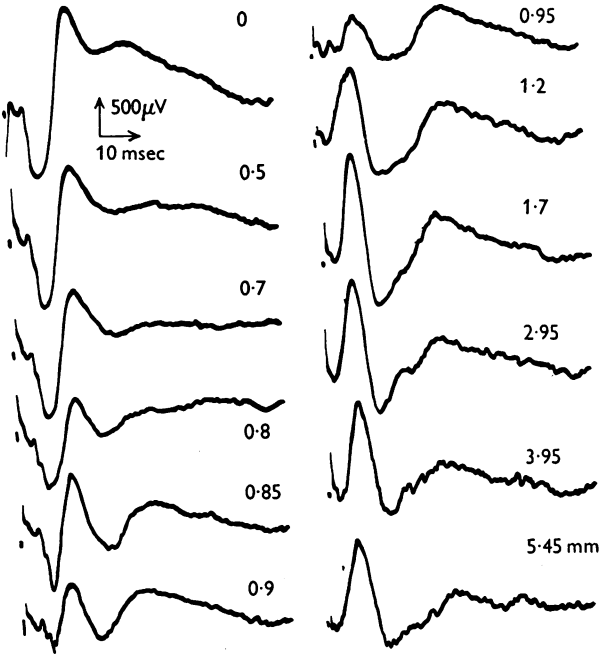

Fig. 4

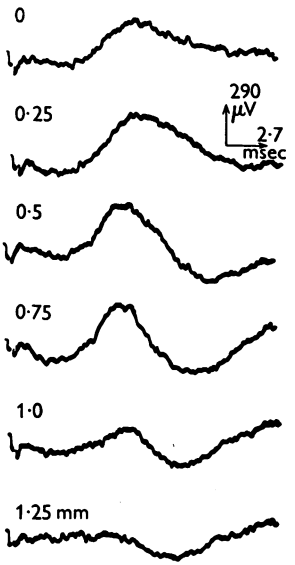

Fig. 5

Fig. 4. Monopolar recordings at different depths in the visual cortex of a rabbit after stimulation of the contralateral optic nerve.

Fig. 5. Radial voltage gradients at different depths in the visual cortex of a rabbit after the stimulation of the contralateral optic nerve.

The radial voltage gradients illustrated in Fig. 5 show a decline in amplitude in the first millimetre of cortex, similar to that found in the somatic-sensory area and consistent with that decline in the monopolar recordings. It will be noted that no preceding spikes appear in these radial voltage gradient recordings similar to those that may be seen in monopolar recordings.

Tangential voltage gradients are illustrated in Fig. 6. The outstanding feature in these recordings is the increase in the amplitude of the preceding spike with depth in the cortex. This spike occurs 2·4 msec after the stimulus,

and corresponds in time with the last of the three spikes seen in monopolar recordings (e.g. Chang & Kaada, 1950). The two earlier spikes can only just be seen in the records of the tangential voltage gradient, and this is consistent with the evidence of their extracortical origin presented by Chang & Kaada (1950). The latency of the first two spikes reported by these authors coincides with potential changes in the lateral geniculate body after stimulating the optic nerve reported by P. O. Bishop (1953). The large amplitude of the third

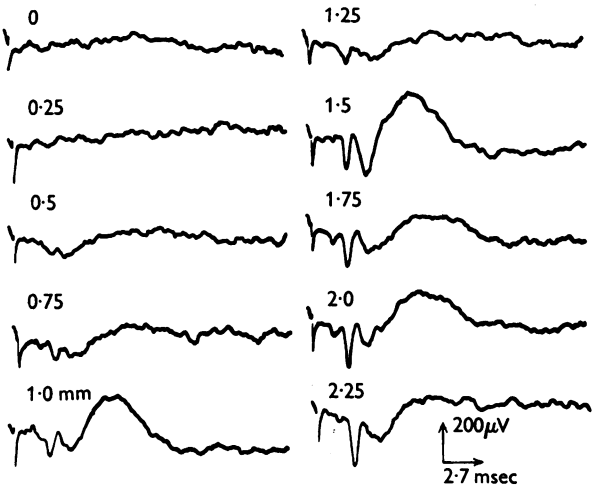

Fig. 6. Tangential voltage gradients at different depths in the visual cortex of a cat after the stimulation of the contralateral optic nerve.

spike in tangential gradient recordings is consistent with Cajal's (1911, p. 614) description of the optic afferent fibres turning tangentially as they enter the cortex. It follows that the first two spikes found in monopolar recordings are due to electronic spread of current from the synaptic and spike potentials in the underlying lateral geniculate body and that the third spike represents the arrival of the afferent impulses in the radiation axons in the cortex. The third spike is followed, in tangential gradient recordings, by irregular longer waves which may be due to a flow of current between the cell bodies and their long basal dendrites (e.g. Cajal, 1911, fig. 388) during the synaptic potential of the cortical neurones stimulated by the afferent impulses.

Recordings from single neurones

Glass microelectrodes of 1–2 μ tip diameter record patterns of spikes in some cortical loci after the stimulation of an afferent nerve. It is of interest that these fine electrodes record the two waves of the primary response of the cortex as well, implying that the integration of the responses of single neurones which these waves represent takes place in the tissue, and not merely at the

surface of large electrodes. Studies of the patterns of response of single neurones have been published recently by Jung, Baumgarten & Baumgartner (1952) and Baumgarten & Jung (1952) and the present report is confined to one aspect of the patterns of response: the tendency of the *number* of spikes occurring in a burst after stimulation to vary more than the *timing* of the burst.

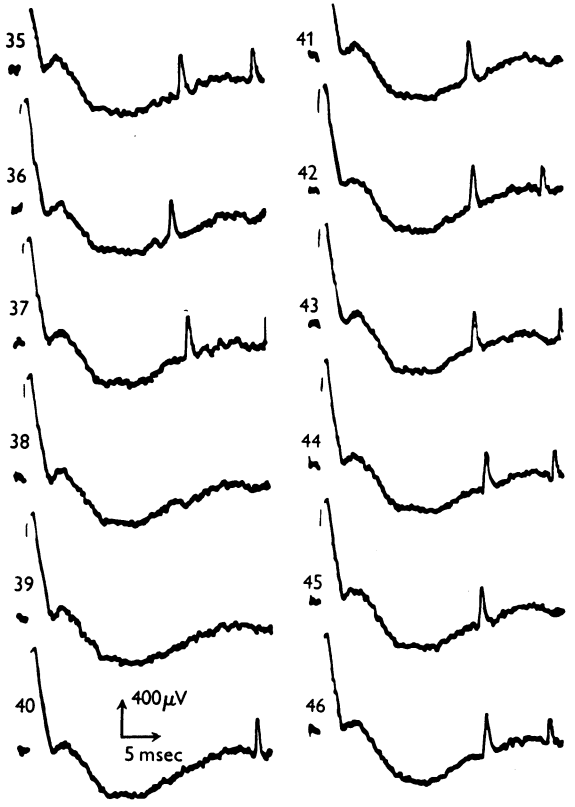

Fig. 7. Twelve consecutive records from a glass microelectrode in the visual cortex of a cat after the stimulation of the optic radiation.

Fig. 7 shows twelve consecutive records from a microelectrode in the visual cortex of a cat after stimulating the optic radiation just below the cortex. The brain-stem of the cat had been transected under pentobarbitone anaesthesia 8 hr previously, so that the preparation must have been practically unanaesthetized at the time of recording. The first of the spikes occurs about 20 msec after the stimulation, and is of 1 msec duration, and $\frac{1}{2}$ mV amplitude. There is no sign of a synaptic potential but if the ratio of the amplitudes of the spike and the synaptic potential were 10 : 1 as found by Brock, Coombs & Eccles (1952) a synaptic potential would be hardly detectable in these records.

Fig. 8 shows a further eleven consecutive records from the same locus as the records of Fig. 7 but recorded on a slower time base to show later spikes. The variability in the number of spikes, and the relative constancy of the times of occurrence of the first spikes, is perhaps the most marked feature of these records.

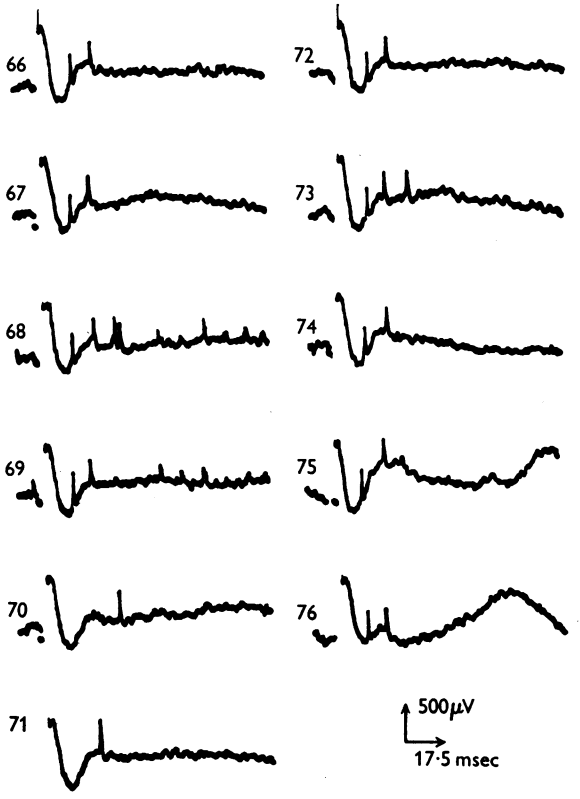

Fig. 8. Eleven further consecutive records from the same locus as in Fig. 7 but recorded on a slower time base.

Fig. 9 shows two series of six recordings from two different loci in the visual cortex of an anaesthetized rabbit after the stimulation of the optic nerve. In the left-hand column the spikes occur in pairs or not at all, and in the right-hand column the spikes are grouped about the positive wave in the middle of the records. There is a marked contrast between the constancy of the integrated response waves in the first part of the records and the irregularity in the spikes.

Fig. 10 is a series of nine consecutive recordings from a locus in the somatic-sensory cortex of an anaesthetized cat. This locus was giving spikes spontaneously, usually in threes, and although stimulation of the sciatic nerve

evoked the usual waves of response in this area (seen at the beginning of each record), no spikes could be evoked in this locus. The rate of stimulation (about 1 shock per second) was set nearly at a submultiple of the rate of occurrence of the spikes (about 10 bursts per second) so that the spikes occurred at various phases of the integrated response to the stimulation and it is seen that the two kinds of recording occur quite independently.

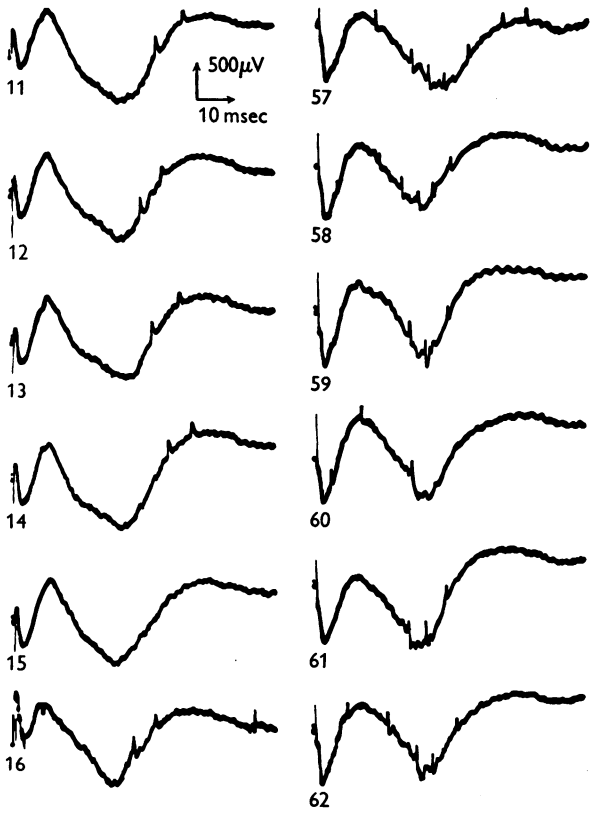

Fig. 9. Two sets of six consecutive records from a glass microelectrode in the visual cortex of a rabbit after the stimulation of the contralateral optic nerve. The two columns are from different loci.

A feature common to all microelectrode recordings is the comparative rarity of loci giving spikes. When an electrode has safely penetrated the pia and has recorded spikes at one locus it may be screwed up and down to locate other loci also giving spikes in response to the same repeated stimulation. All loci of recording give the integrated waves of response but very few give spikes, in contrast to the separation of cortical neurones which is only some 20–25μ from centre to centre (Sholl, 1953).

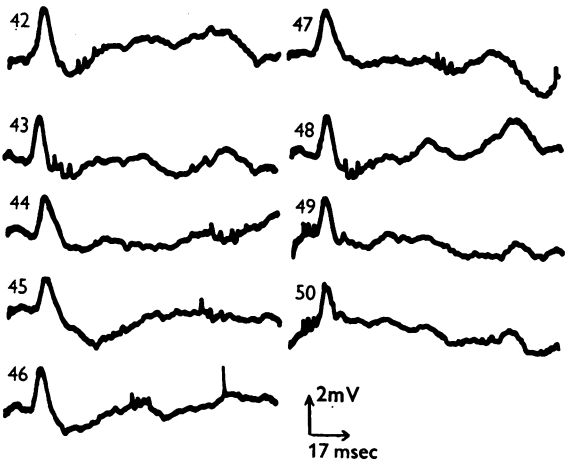

Fig. 10. Nine consecutive records from a glass microelectrode in the somatic-sensory cortex of a cat after stimulating the contralateral sciatic nerve. Spikes occur spontaneously, often in threes, and appear to be unaffected by the evoked response at the left-hand end of each record.

DISCUSSION

The changes with depth in the two waves of the primary response of the cortex to the stimulation of an afferent nerve are consistent with the interpretation given by Eccles (1951). The afferent impulses enter the cortex from beneath, and excite the cortical neurones. Some of these neurones are pyramidal cells, and the flow of current between the cell bodies and the apical dendrites during the upward spreading depolarization caused by the afferent impulses causes the potential of the upper part of the cortex to change with the same time constants as the deeper lying cell bodies but with the opposite polarity. The radial voltage gradient recorded in the upper half of the cortex during the period of the synaptic potential (the first wave of the primary response) is deep-negative to superficial-positive, and therefore consistent with an upward spreading depolarization of the cortical neurones. A useful check of this interpretation is that radial voltage gradients of the opposite polarity have been recorded with the same technique in the chicken's optic tectum (Cragg, Evans & Hamlyn, 1954) in which the afferent fibres penetrate the tissue from above. The optic nerve fibres spread out over the surface of the tectum and then turn down towards the deeper lying neurones and correspondingly a downward wave of depolarization is detected in the electrical records.

The explanation of this result that the deeper part of the cortex has a response of the same polarity as the cell bodies, while the superficial part has the polarity of the dendrites is equivocal. If there were just one layer of cell bodies deep in the cortex with apical dendrites ascending to the surface,

the result would be explained unambiguously. In fact there are cell bodies and dendrites at all depths and the result could be obtained by two different mechanisms. In the first place, only the neurones at certain depths might respond to the stimulation. This interpretation seems to be implicit in the discussion of Burns & Grafstein (1952) and might imply that the neurones at certain depths had a higher ratio of excitatory to inhibitory afferent endings than the neurones above or below them. The second possibility is that since, according to the hypothesis, the dendrites and cell bodies have potential changes of the opposite polarity, while depolarization is spreading from one to the other, the potential recorded at any given depth is related to the difference between the dendrite surface area and the cell-body surface area at that depth. If this were so, the deep and superficial peak responses would correspond to the statistical predominance of cell body or apical dendrite surfaces at certain depths and not to the location of particular neurones. In this connexion it has already been mentioned that the difference between the deep responses in the visual and somatic-sensory areas may be due to the presence in the former of the band of large Minot cells, while in the latter the cell-body surface area is more evenly distributed in depth.

It will have been noted that the integrated response of cortex does not include a spike potential, even when recorded from a fine microelectrode, although the individual neurones may have spikes in their action potentials. According to Brock *et al.* (1952) the spike of spinal motoneurones has a duration of 1 msec and an amplitude of nearly 100 mV, while the synaptic potential has a time constant for decay of 3 msec and a peak amplitude of 10 mV. These measurements imply that comparable amounts of current flow during the spike and the synaptic potential, so that the spike should appear in the integrated record unless the attenuation during electrotonic spread is much greater for the spike than for the synaptic potential. The large area of membranes with time constants of the order 3 msec might well cause such a differential attenuation. Another possibility is that only a small proportion of the cortical neurones reach the spike threshold during the depolarization of the integrated response. This would certainly be consistent with the rarity of loci in cortex that give spikes under the conditions of extracellular recording described in this paper, but the converse does not necessarily follow because the technique may not be adequate to record spikes from small neurones; the few loci giving spikes may be the sites of especially large cell bodies with a large extracellular current.

The marked variability in the number of spikes occurring from one stimulation to the next in corresponding bursts could be caused by much smaller variations in the level of depolarization. Thus Barron & Matthews (1938) showed that the rate of firing of spinal motoneurones in the frog (as indicated by the impulses recorded in single efferent axons) could be controlled in the

range of 5–70 impulses per second by changes in small depolarizing currents of the order 1 μA. Within a certain range, the rate of firing changed more rapidly than the applied depolarizing current. A general hypothesis which accounts for the variability in the number of spikes in a burst and the relative constancy of the timing of the first spike in the burst has been discussed by Cragg & Temperley (1954).

SUMMARY

1. In the somatic-sensory, visual and auditory areas the response to a volley of afferent impulses consists first of two waves, called the primary response. These waves are the integrated synaptic and after-potentials of the cortical neurones first stimulated by the afferent impulses. When recorded from the surface the first of these waves is of positive polarity and the second of negative polarity.

2. In each of these three cortical areas this primary response reverses in polarity in the lower half of the cortex. In the visual area the reversed response reaches as great an amplitude as the surface response but in the somatic-sensory area the deep reversed response is always smaller in amplitude than the surface response. In the auditory area, a small secondary reversal can be detected in the first 0·3 mm below the pia.

3. The change with depth of the primary response is consistent with Eccles' (1951) interpretation, though it is uncertain whether the deep and superficial peak amplitudes of response are related to the presence at these depths of particular neurones or of merely a peak in the difference between cell body and dendrite surface areas.

4. In the visual area tangential voltage gradients occur as the afferent impulses enter the cortex in the tangentially-curving axons, but the two previous spikes seen in monopolar recordings do not set up appreciable tangential or radial voltage gradients and are due to electrotonic spread of current from the synaptic and spike potentials of the underlying lateral geniculate body.

5. Spikes can be recorded with microelectrodes from cortical loci but they are sparse in comparison with the density of cortical neurones. Different loci exhibit different patterns of spikes in response to stimulation and, at any one locus, the number of spikes in a burst tends to be more variable from one stimulation to the next than does the timing of the first spikes in a given burst. The significance of these patterns of spikes is discussed.

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