

Electrical Activity of the Cerebral Cortex as Compared to the Action Potential of Excised Nerve.

GEORGE H. BISHOP AND S. HOWARD BARTLEY.*

From the Department of Ophthalmology, Washington University, and the Laboratory of Applied Physiology, Oscar Johnson Institute, St. Louis.

As Bartley and Newman have shown, there can be recorded from the cerebral cortex, over considerable of its surface, a continuous and extremely complicated series of electrical oscillations. The record as it appears on the cathode ray oscillograph, with adequate sensitivity to show its complexity, is far too intricate for any such casual analysis into specific waves as is possible in nerve trunks.

That this activity consists of a complication of more simple elements is indicated by the following experiments: If in the rabbit's or dog's cortex shallow cuts (1 mm. deep) are made near a recording electrode (an indifferent electrode being located on the bone of the skull), the form of the record changes, becoming simpler. Cutting off the blood supply from an area causes its activity to cease in 5 to 10 minutes, without any obvious simplification. Ether anesthesia may cause marked simplification of the record at a stage shortly before all activity ceases. The simplest large waves have a duration of 30 to 100 sigma, but in the complex picture there appear to be some as short as 10 sigma. The amplitude of individual waves of the normal record may be as much as $\frac{1}{2}$ mv., increasing upon stimulation of the animal to several times this. No oscillations can be found even at a sensitivity of $\frac{1}{2}$ meter per mv., that have as short a duration as nerve-fiber action potentials. The long refractory period, low frequency, long duration and suppression by anesthesia at a concentration that does not affect nerve fibers indicate that nerve cells spontaneously active in the cortex are involved, and suggest that the potentials themselves may be cell potentials rather than nerve-fiber potentials. Further, responses to direct electrical stimuli are too long in duration for nerve-fiber potentials, and are of the order of duration of the spontaneous waves.

It therefore seemed of interest to determine what the action potential of a simple bundle of nerve fibers would look like when recorded from the surface of the cortex or from beneath the surface. A rabbit vagus nerve $\frac{1}{2}$ mm. in diameter was laid across the cortex, stimulated at one end and explored with a lead electrode. When

* Fellow, National Research Council.

the test electrode just touched the surface of the vagus the amplitude was 6% of that recorded when the vagus was lifted off the cortex. Laid in a slit of the cortex the amplitude was slightly less: it was 3% when embedded 1 mm. deep in the cortex, and not over 1% when threaded through the ventricle of the brain. It follows that if all the fibers in the cortex within 1 mm. of the test electrode were active at once, their summed potentials would be shunted by the rest of the brain tissue to not over 2 or 3% of what their value would be if insulated, and the record of fibers further away than this would soon become vanishingly small. Furthermore, to produce waves 30 to 100 sigma long these fibers would have to respond one after another or else repetitively, and in so complicated a record as the cortex gives, obviously not all are responding in any one wave.

Computing on this basis, it appears that to give a record as great as the largest of the waves recorded from the cortex after stimulation, for instance of the optic nerve, would require fibers whose activity equaled that of all the myelinated fibers of nearly one thousand vagus nerves, to be collected within recording range of the test electrode, for example, 2 mm. If each responded 3 times at, for example, 20-sigma intervals this number could be correspondingly less. Or, if each fiber in the cortex gave one potential equal to a 15-mu myelinated axon from the bullfrog's skin nerve, 250,000 such potentials would be required to form 1 cortical wave. The cross section of this bundle would be 44 sq. mm. if packed close, or over 7 mm. in diameter. Since the rabbit cortex is only 3 mm. thick, and contains many neuroglia and nerve cells as well as fibers, this would demand that some of these fibers entering into the record be over 5 mm. distant from the electrode, and at this distance they would not affect the record appreciably.

It thus appears either that the axons of the brain have a much larger potential than elsewhere, or else the record is due to nerve *cells*, having a higher and more protracted potential than nerve fibers give. On the other hand, it would be impossible at any sensitivity that is available at present (1,000 meters per volt) to detect less than five 15-mu fibers responding in a volley, even if immediately under the test electrode, and more would be required if their potentials were out of phase or their position further from the lead. This would have to be observed superposed upon an already very complicated record, whose waves at this sensitivity would, some of them, be one meter high. It is, therefore, presumable that the finer details of cortical activity are still escaping our notice.