Neuronal Activity in Cortical and Thalamic Networks

A study with multiple microelectrodes

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One of the major problems with which neurophysiological research has been confronted, in recent years, is the way in which the brain deals with the information that it receives over the sensory pathways. The study of this problem has been much enhanced by the development of techniques for the recording of the activity of single neurons. The use of such techniques has provided valuable information in two fields of investigation. One field, the electrophysiology of the brain cell: in this respect it has been found that electrical characteristics of cortical and thalamic neurons are very similar to those of neurons located elsewhere in the central nervous system (4, 5, 11, 16, 22). Another field, the study of the patterns of response of single brain cells to peripheral stimulation: in this respect it has been found that the latency of response, the number of spikes and the intervals between spikes generated by each individual neuron are related to the intensity, the frequency and the position of the peripheral stimulus (2, 3, 6, 7–10, 15, 17, 18, 23). Thus, cerebral neurons participate in the coding and the displaying of information upon the maps which, in the sensory receiving areas of the brain, represent the spatial, temporal, and other characteristics of events that occur in the outside world. Little is known, however, about the way in which the coded information displayed upon these maps is selected and organized in order to result in the processes which we call perception and integration. Whatever the mechanism of these processes may be, it is evident that, since it involves comparison, selection, and organization of sensory and memory data, it cannot be based on the activity of isolated neurons but it must be based on the interrelated activities of the large number of neurons which, with their connections, form the complex networks present in the brain stem and in the cortex.

It is well known that some neurons in these networks are spontaneously

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active even in the absence of incoming impulses from the periphery. When information is coming in from the outside world and impulses are conveyed to the brain stem and to the cortex over the sensory pathways, these impulses must interact with the spontaneous activity which they encounter in the cortical and subcortical networks and this raises two important questions: First, what is the nature of this spontaneous activity and how is it affected by the states of consciousness, wakefulness, and sleep? Second, what sort of interaction develops between the spontaneous activity and the "evoked" activity which is engendered by incoming information? If a study of these processes is to be attempted, it is evident that it becomes necessary to observe, simultaneously, the activity of a number of neurons in a network, rather than that of isolated neurons.

During the last 8 years methods have been developed, in this laboratory, which permit such simultaneous observation of several neurons and these methods have been applied to the study of thalamic and cortical networks. Among the structures studied more recently were the lateral geniculate body and the visual cortex of the cat and this report presents the results obtained in these investigations and considers the possible relations between the behavior of such networks and central visual mechanisms.

Two methods can be used for the simultaneous recording of the activity of several neurons. One method is based on the fact that, in a volume conductor, the amplitude of the action potential of a neuron, recorded by a microelectrode, is related to the distance between the neuron and the tip of the microelectrode (13, 21). Thus a larger microelectrode (5 to 10 μ) introduced into the brain will record the activity of several neurons whose action potentials will appear on the tracing as spikes of different amplitudes, the latter being related to the respective distances of the neurons from the tip of the microelectrode. By using several such microelectrodes cemented together, with their tips separated by distances of 25 to 160 μ, a number of neurons can be identified on the several tracings, by the amplitude and the time relations of their action potentials (25, 26). Another method is based on the use of multiple microelectrodes of small tip diameter (0.5 to 5 μ). When several microelectrodes are cemented together and introduced into the brain each tip records the activity of one single neuron, so that the total number of neurons identified on the tracings is equal to the number of microelectrodes used. The first method has the advantage of showing the activity of a larger number of neurons, the second has the advantage of providing higher accuracy in the identification of the individual activity of each neuron in the group.

By using the first method, Verzeano and Calma showed, several years ago (26), that, when the electrical activity of the brain undergoes "synchronization," the action potentials of cortical and thalamic neurons appeared to

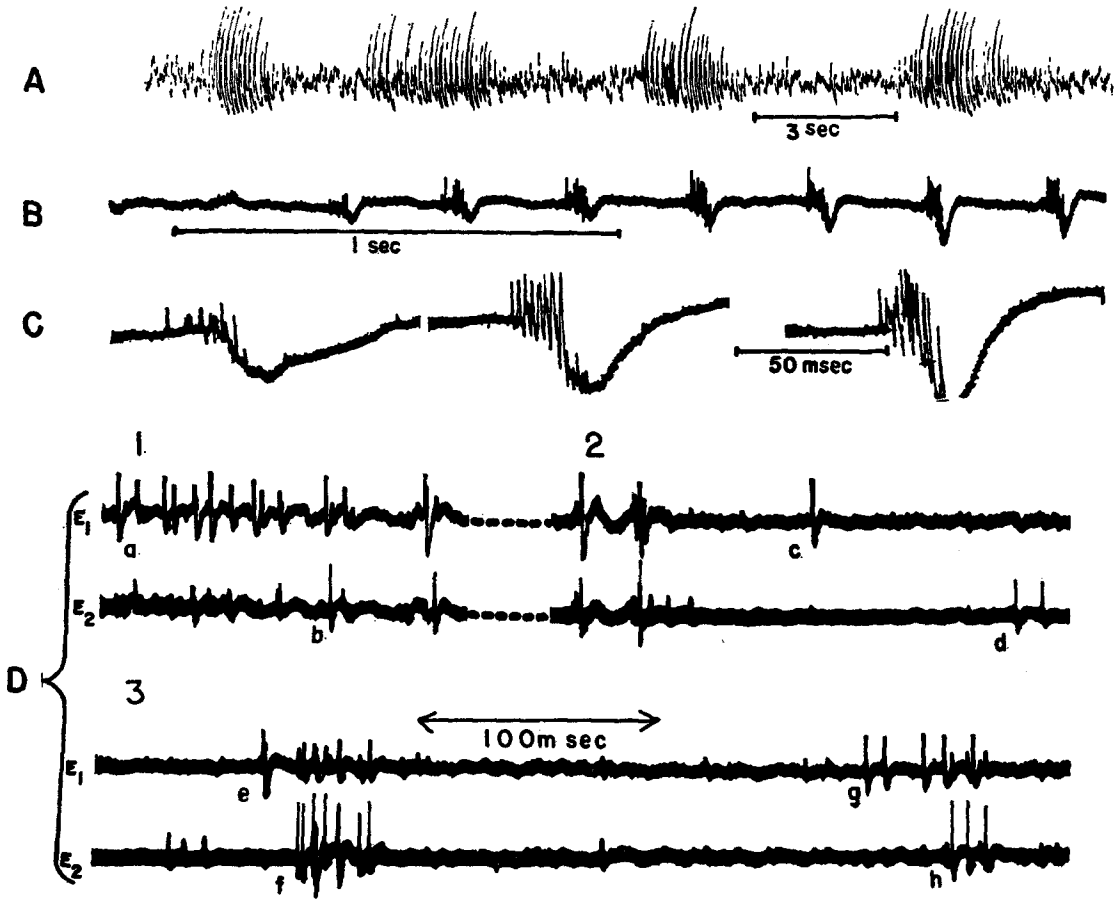

FIGURE 1. Analysis of neuronal activity with successively increasing resolutions.
A.—"Gross" waves. Periodic "spindles" of "synchronized" activity recorded with standard EEG amplifier and ink oscillograph from nucleus medialis thalami.
B.—Same activity recorded with *one* microelectrode. Amplifier time constant = 1 second. Oscilloscope tracing photographed on continually moving film at speed of 3.3 inches/second. Each gross wave of the spindle in tracing A is, now, resolved into a group of spike potentials followed by a positive wave.
C.—Same oscilloscope tracing photographed on moving film at 20 inches/second. The individual spikes in each group can be clearly seen.
D.—Similar activity studied with double microelectrodes. Recordings obtained, simultaneously, with two microelectrodes (E_1 and E_2) from gyrus cinguli of cat. Strips 1 and 2, waking state; strip 3, light sleep (nembutal 4 mg./kg.). Time elapsed between arrival of activity first at the tip of E_1, next at the tip of E_2, can be seen at *a-b*, *c-d*, *e-f*, and *g-h*. Microelectrode tips, 4 μ diameter. Distance between tips, 42 μ. Amplifier time constant, 0.002 second. Negative deflections upward, in this and all other figures.

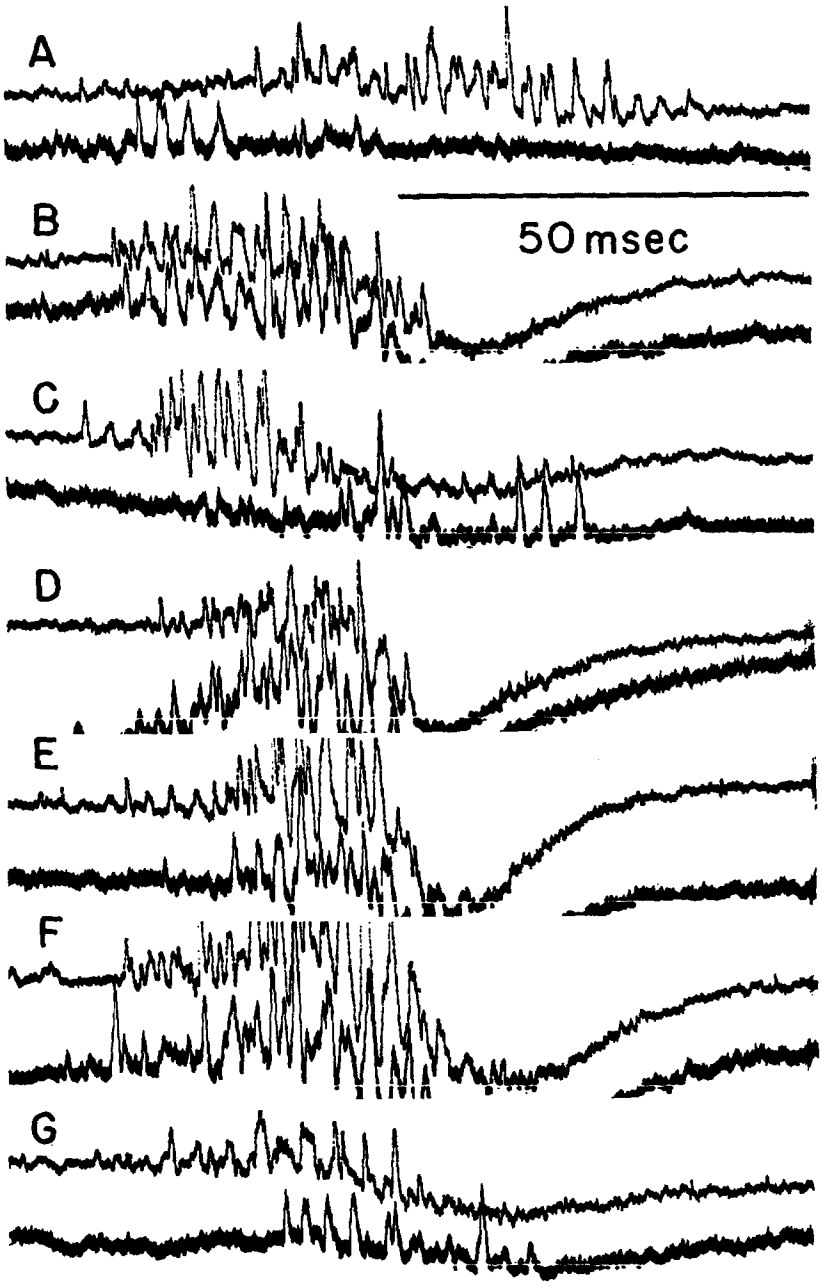

FIGURE 2

be grouped, each group corresponding to a wave of the synchronized gross record (Fig. 1). Such groups of action potentials could be recorded from the cortex, the diffusely projecting nuclei of the thalamus (26) and from the medial and lateral geniculate bodies (24). These findings were later confirmed (1, 14, 19, 20, 28) and extended to all thalamic nuclei (19) by other investigators. Because the action potentials, in each group, appeared to be progressively increasing and decreasing in amplitude from the beginning to the end of the group, they were thought to represent the activity of neurons firing in a regular sequence; *i.e.*, activity approaching, reaching, and going beyond the tip of the recording microelectrode (26). Further investigations conducted by Verzeano (25) by means of double microelectrodes strongly supported this hypothesis, suggesting, in addition, that the direction of propagation of activity changed and reversed frequently and that the velocity of propagation could be estimated (Fig. 2). By increasing the number of electrodes to three, records were obtained which definately established that such propagation of activity actually occurs. Furthermore, triple electrodes provided the means for studying these phenomena in a tridimensional system, and it was found that the direction of propagation changes continually not only within one plane but in a tridimensional pattern.

Fig. 3 gives a diagrammatic summary of these findings. A and B show the tracing (E) obtained with one microelectrode large enough to record the activity of several neurons. As neurons a to c fire in a regular sequence approaching the microelectrode, the latter records spikes of progressively increasing amplitudes; as the firing continues from d to g, going beyond the microelectrode, the latter records spikes of progressively decreasing amplitudes. C and D show the simultaneous tracings (E_1 and E_2) obtained with two such microelectrodes whose tips are separated by a distance of from 25 to 160 μ: as the activity proceeds from a to g, it reaches first electrode E_1 and later electrode E_2; the spikes corresponding to the successive neurons appear therefore, first on tracing E_1 and later on tracing E_2 showing, on each tracing, the progressive increase and decrease in amplitude characteristic of propagating activity; since the distance between the two microelectrodes is known and the time that the wave of activity takes to travel from one microelectrode

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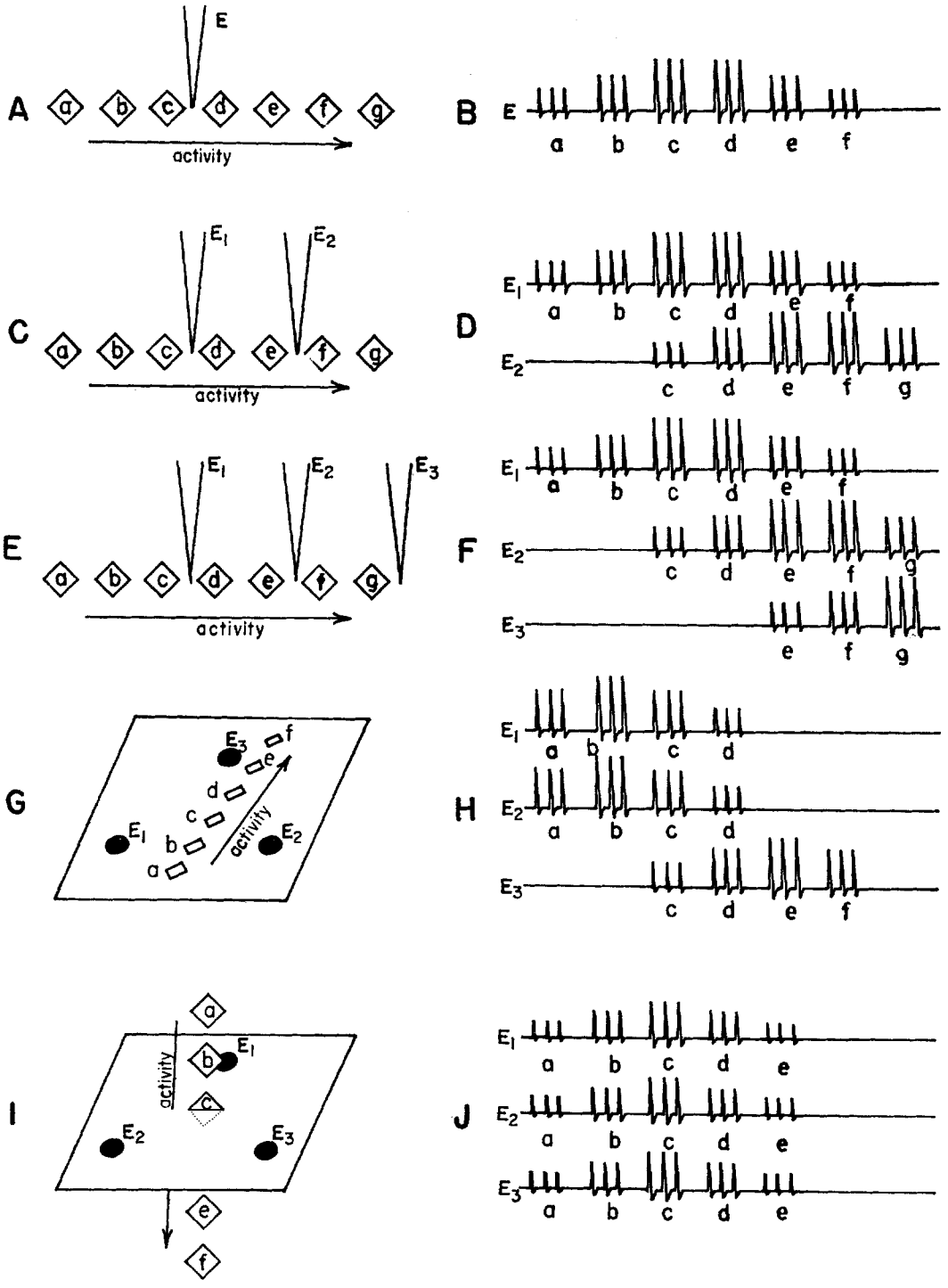
FIGURE 2. Successive groups of action potentials (from a complete "spindle" developing at 7 cycles/second) recorded from the centre median, with one pair of microelectrodes, directed mediolaterally. Tips of microelectrodes 4 μ in diameter, 30 μ apart. Upper tracing in each strip is from the lateral electrode, lower tracing from the medial electrode. Amplifier time constant, 0.2 second. The order of arrival of activity at the tips of the two microelectrodes can be seen to change and reverse from one strip to the next, indicating that the circulating activity goes back and forth, through and around the recording site. Time between strips equals approximately 0.14 or 1/7 second. Data from *Science*, 1956, **124**, 366.


A
E
a b c d e f g
activity
B
E
a b c d e f
C
E1 E2
a b c d e f g
activity
D
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E2
c d e f g
E
E1 E2 E3
a b c d e f g
activity
F
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a b c d e f
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I
a b c d e f
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activity
J
E1
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FIGURE 3

to the next can be measured on the tracings, the velocity of propagation can be estimated by dividing the distance by the time. A similar procedure is used with three or four microelectrodes whose tips are aligned along one axis, in which case the simultaneous tracings exhibit the pattern shown in E

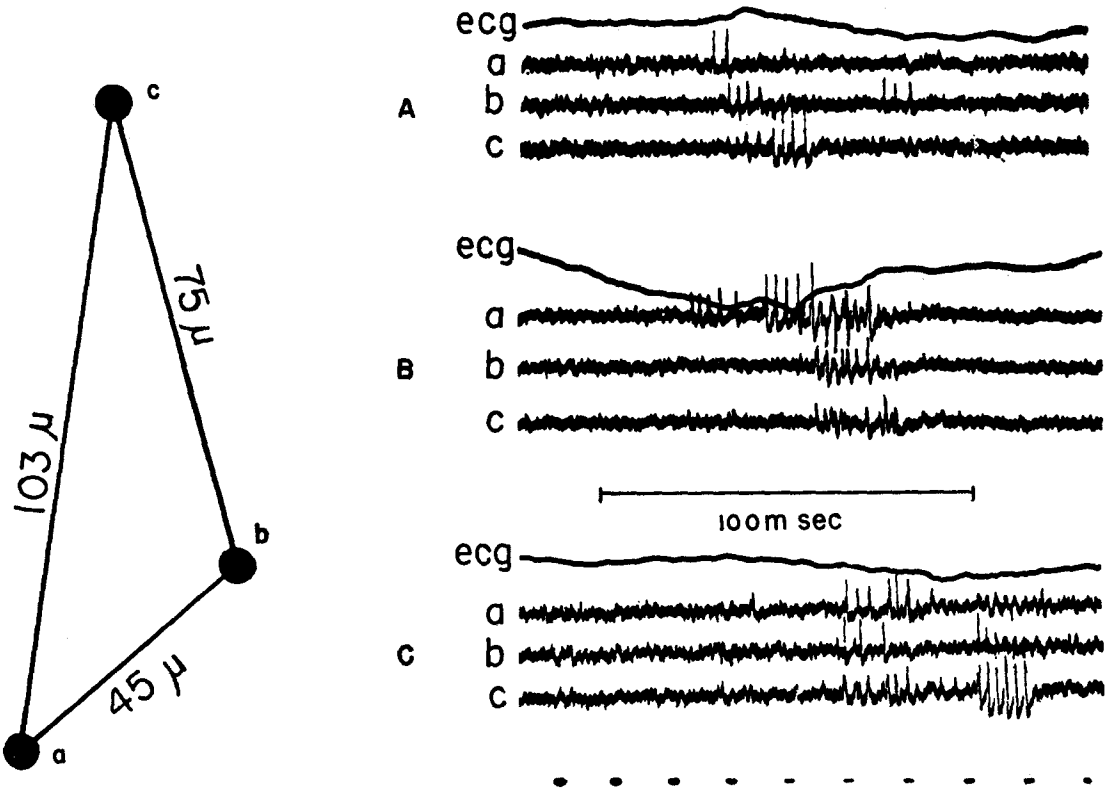

FIGURE 4. Simultaneous tracings obtained with three microelectrodes whose tips (*a*, *b*, *c*) were arranged as shown in the diagram at left; location, nucleus lateralis posterior; anesthesia, nembutal 6 mg./kg. In A, activity propagates from *a* to *b* then to *c* and back to *b*. In B, activity arrives first at *a*, then progresses towards the center of the triangle (all three microelectrodes show spikes simultaneously). In C, activity appears first, near the center of the triangle (all three microelectrodes show spikes simultaneously) then moves toward the vicinity of *c* (high spikes on tracing).

and F (E_1, E_2, E_3). When the tips of the microelectrodes are arranged in such a way that they form a triangle, as in G and I, information can be obtained on the tridimensional pattern of the propagation of activity. In G, as activity proceeds from neurons *a* to *f*, it reaches first a point equidistant from electrodes E_1 and E_2 so that the spikes on tracings E_1 and E_2 (H) appear

FIGURE 3. Diagrammatic summary of results obtained by simultaneous recording of activity of several neurons with multiple microelectrodes (see text).

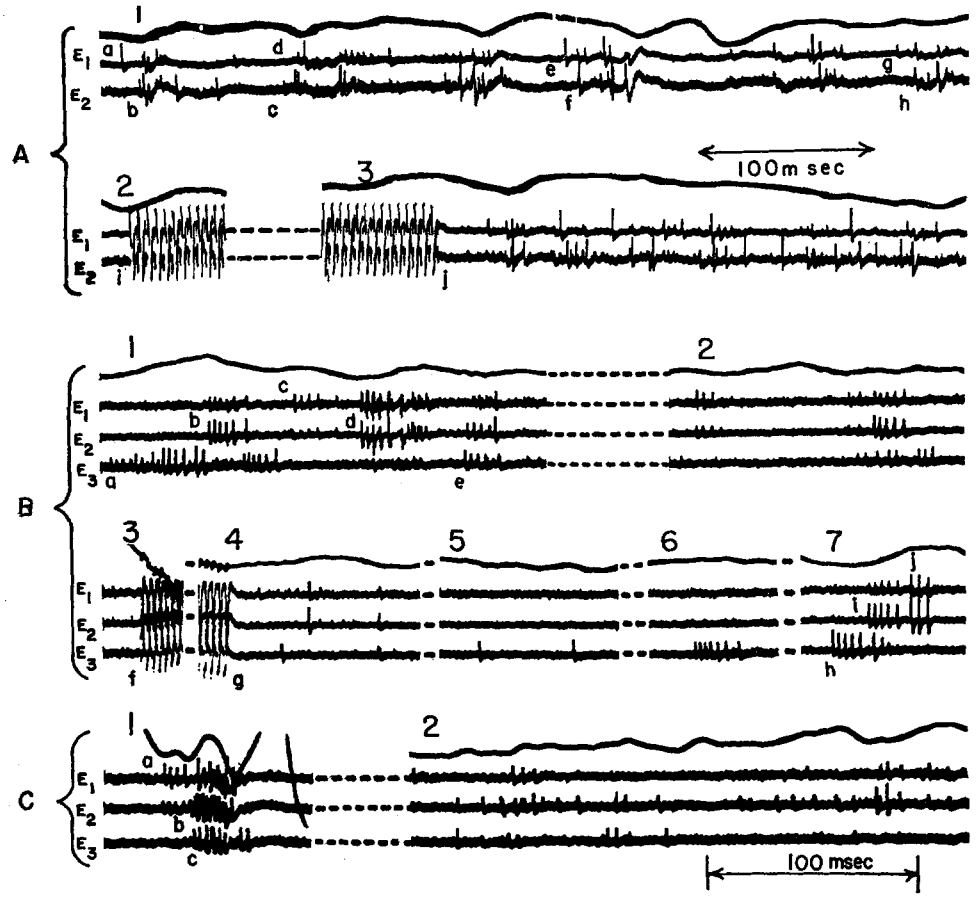

FIGURE 5. A.—Recordings obtained, simultaneously, with two microelectrodes (E_1 and E_2) from posterior sigmoid gyrus in *encéphale isolé* of cat showing the effects of high frequency stimulation of reticular formation in mid-brain. Strip 1, before stimulation; strip 2, stimulation starts at *i*; strip 3, stimulation ends at *j*.

B.—Recordings obtained, simultaneously, with three microelectrodes (E_1, E_2, and E_3), from nucleus ventralis lateralis of cat in light sleep (nembutal 7 mg./kg.), showing the effects of stimulation of reticular formation. Strips 1 and 2, before stimulation; propagation of activity along the direction $E_3E_2E_1$ can be seen at *a*, *b*, *c*. Strips 3, 4, and 5, stimulation (*f* to *g*) and its effects. Strips 6 and 7, return to original condition, 10 seconds after stimulation. Propagation of activity along direction $E_3E_2E_1$, can, again, be seen at *h*, *i*, *j*.

C.—Recordings obtained in the same experiment as in B, above, after administration of an additional dose of nembutal (7 mg./kg.). Strip 1, before stimulation; propagation of activity along the direction $E_1E_2E_3$ can be seen at *a*, *b*, *c*. Strip 2, after stimulation. Stimulation occurred during the period marked with dotted lines.

In all tracings of this figure, the dotted lines represent sections where a continuous record has been cut, and the line showing slow oscillations is the simultaneous recording of the electrocorticogram.

at the same time; as the activity, finally, approaches electrode E_3, the spikes appear on tracing E_3; in I, as the activity proceeds along an axis perpendicular to the plane determined by the tips of the microelectrodes, the spikes appear on the three tracings at the same time (J). Actual recordings of the activity of several neurons with three microelectrodes whose tips form a triangle are shown in Fig. 4.

More recently Verzeano and Negishi (28) showed that this kind of constantly circulating activity occurs both in wakefulness and in sleep but that there are, however, marked differences between the neuronal activities of the two states: in wakefulness many neurons fire independently of the periodic groups of action potentials and do not necessarily participate in the regular propagation of activity. In sleep this independent firing is silenced, the periodic groups of action potentials appear with high regularity, the repetitive firing of each neuron is enhanced and its repetition rate increased (Fig. 1). Furthermore, if the reticular formation of the mid-brain is electrically stimulated the periodic groups of action potentials are disrupted and the circulation of impulses through the network is suppressed or modified. Such effects of stimulation of the reticular formation are shown in Fig. 5. Section A shows records obtained simultaneously with two microelectrodes (E_1 and E_2; tip diameters, 4 μ; distance between tips, 140 μ) from the posterior sigmoid gyrus in an *encéphale isolé* preparation. Periodic groups of neuronal activity can be seen in strip 1 and the time relations between the appearance of activity at the tips of the two microelectrodes can be seen at *a-b*, *c-d*, *e-f*, and *g-h*. Stimulation of the reticular formation (4 volts, 200 pulses/second for 5 seconds) is started at *i* and ended at *j*. The disruption of the periodic grouping of action potentials can be seen immediately after the cessation of stimulation (strip 3). It, generally, lasts for a number of seconds after the stimulation has ceased. Section B (strip 1) shows records obtained simultaneously with three microelectrodes (E_1, E_2, and E_3; tip diameters 3, 2, and 2 μ, respectively) from an animal under light nembutal anesthesia (7 mg./kg.). The tips of the microelectrodes were located on a straight line and the distances between the tips were E_1 to E_2 = 67 μ; E_2 to E_3 = 120 μ; the records were taken from nucleus ventralis lateralis of the thalamus. The periodic grouping of action potentials as well as the appearance of activity first at the tip of E_3 and then successively at the other tips, indicating propagation, can be seen at *a*, *b*, *c*, *d*, and *e*. Stimulation of the reticular formation is started at *f* and ended at *g*. The disruption of the propagated activity can be seen in strips 4 and 5. The propagation activity reappears 10 seconds later, at *h*, *i*, *j* (strip 7). Section C shows the effects of stimulation of the reticular formation in the same preparation, after the administration of an additional 7 mg./kg. of nembutal.

These findings lead to the conclusion that there is, in the neuronal net-

works of all the thalamic nuclei and in the pyramidal layer of the cortex, a continual circulation of impulses along loops of complex geometric confirmation; that this circulation of impulses takes place at velocities from 0.5 to 8.1 mm./per second; that it is dependent upon the state of wakefulness or sleep of the animal and that it can be influenced by the reticular formation. For purpose of simplicity this type of neuronal activity will be called "circulating neuronal activity" and will be designated below as CNA. In order to determine in which way this CNA may be influenced by sensory stimulation, a series of investigations was recently conducted in which the effects of visual stimulation on the activity of cortical and thalamic networks were studied by means of simultaneous recordings with double, triple, or quadruple microelectrodes. The methods used and the results obtained in these investigations are presented below:

ANIMALS AND ANESTHESIA

Experiments were conducted in cats anesthetized with ether during a brief period, sufficient for tracheotomy and craniotomy, after which they were paralyzed with flaxedil and maintained with artificial respiration.

The microelectrodes were made of stainless steel electrolytically sharpened to diameters of 0.5 to 5 μ and covered, for insulation, with several coats of enamel. The multiple microelectrodes were made by bringing together, with micromanipulators, under a microscope, the tips of several electrodes, maintaining them at the desired distance (25 to 160 μ), and joining the stems solidly with an acrylic cement. The microelectrodes were stereotaxically introduced into the brain through small openings in the bone and dura. When cortical recordings were taken, the opening in the bone was sealed after the introduction of the electrode in order to minimize displacements due to arterial pulsation or respiration.

RECORDING DEVICES

The electrodes were connected to amplifiers especially designed for this purpose (Fig. 6) consisting of a first stage providing a very high impedance input and low grid current, followed by three fully transistorized stages with a total gain of 70 DB and a frequency response, flat within 2 DB, from 3 to 9000 cycles/second. Time constants could be varied from 0.2 to 0.001 second. The output leads of the amplifiers were connected to a multiple channel magnetic tape recorder. After each experiment the tape was "played back" into a multiple channel oscilloscope and the tracings were photographed on moving film, at speeds varying from 3 to 30 inches/second. The magnetic tape recorder limited the lower frequency response of the system to 30 cycles/second; when frequencies below this range were to be studied, the output of

the amplifier was connected directly to the oscilloscope. In some experiments, in which the study of slow potentials was particularly important, conventional amplifiers were used, with a time-constant of 1 second and the lower limit of the frequency response at 0.2 cycles/second.

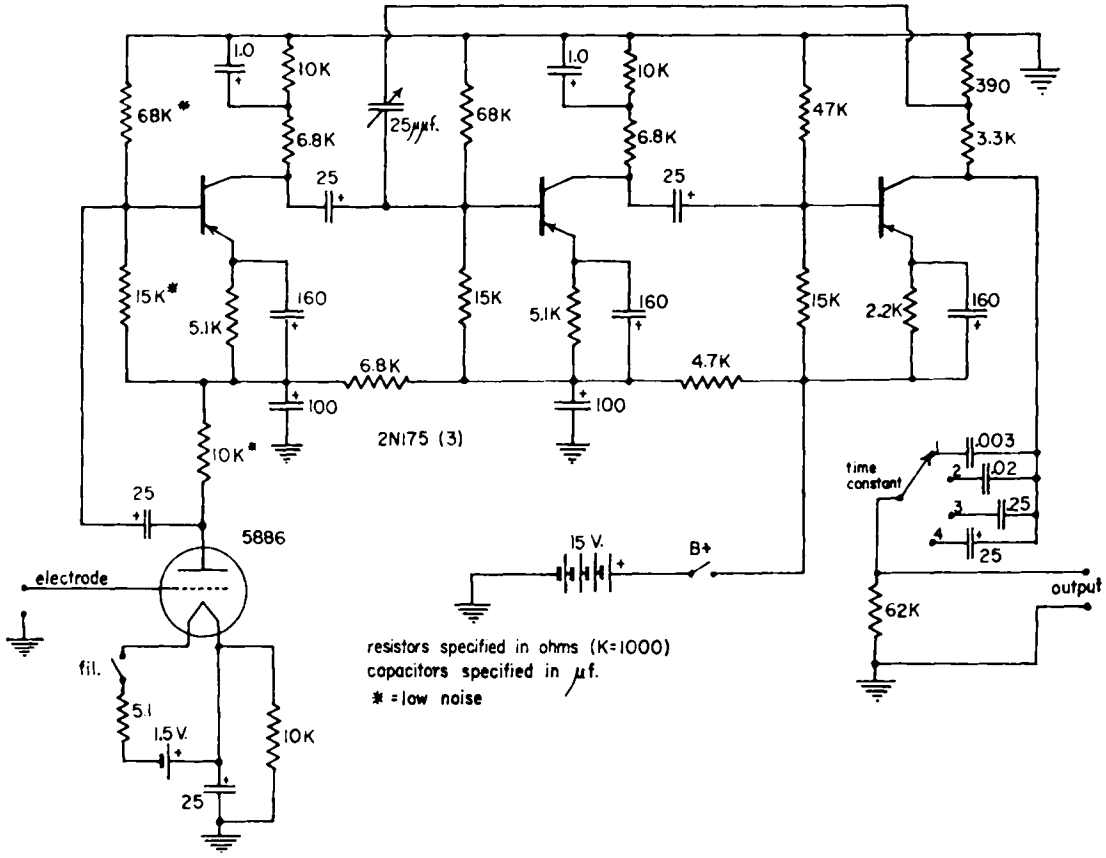

FIGURE 6. Compact transistorized amplifier used with multiple microelectrodes. 5886 = micrometer pentode used in triode connection. The tube and first transistor are enclosed in a small probe which can be mounted directly on the stereotaxic instrument.

HISTOLOGICAL CONTROL

The tissues were fixed in formaldehyde and stained according to a modified Nissl method. The tracks of the microelectrodes and their locations were identified on serial sections. (Fig. 7).

Visual stimulation was binocular. It was achieved with brief flashes of light of 2 to 3 msec. duration, produced by electrical discharges in a gas tube. The spectrum was a mixture of violet, blue, and red and the illumination was 11 lux.

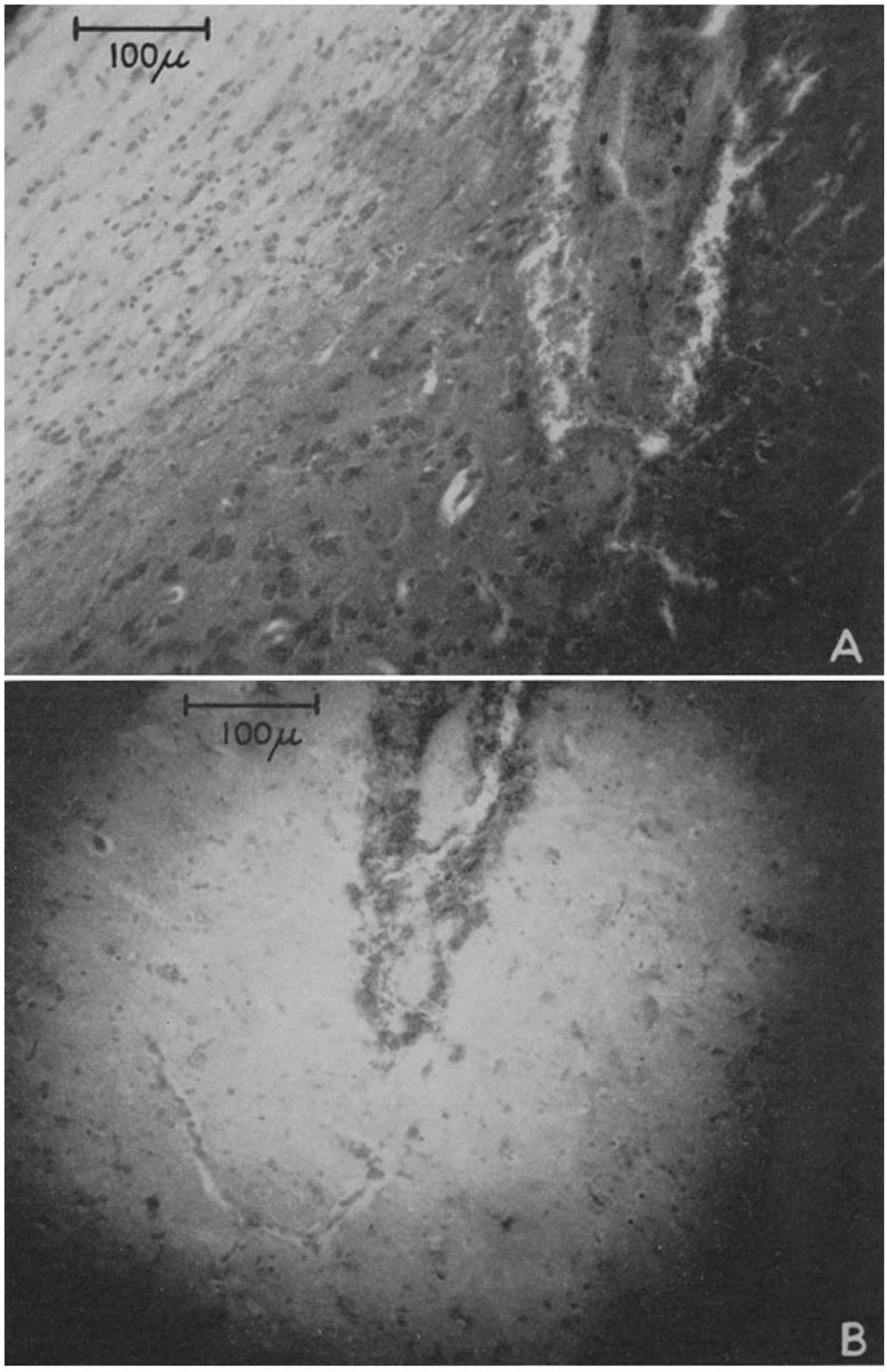

FIGURE 7. Microphotographs showing tracks of double microelectrodes. A, gyrus cinguli. B, nucleus medialis thalami.

Recordings were obtained, with multiple microelectrodes, from the lateral geniculate body pars dorsalis and from the gyrus lateralis. The CNA was studied (*a*) as it appeared spontaneously; (*b*) as it appeared in response to single flashes of light; (*c*) as it appeared in response to repetitive flashes of light (1 to 15 flashes/second). For purposes of comparison similar studies were made of the activity of the nucleus reticularis and of the gyrus cinguli. Fig. 8 shows records obtained under such conditions from the nucleus reticu-

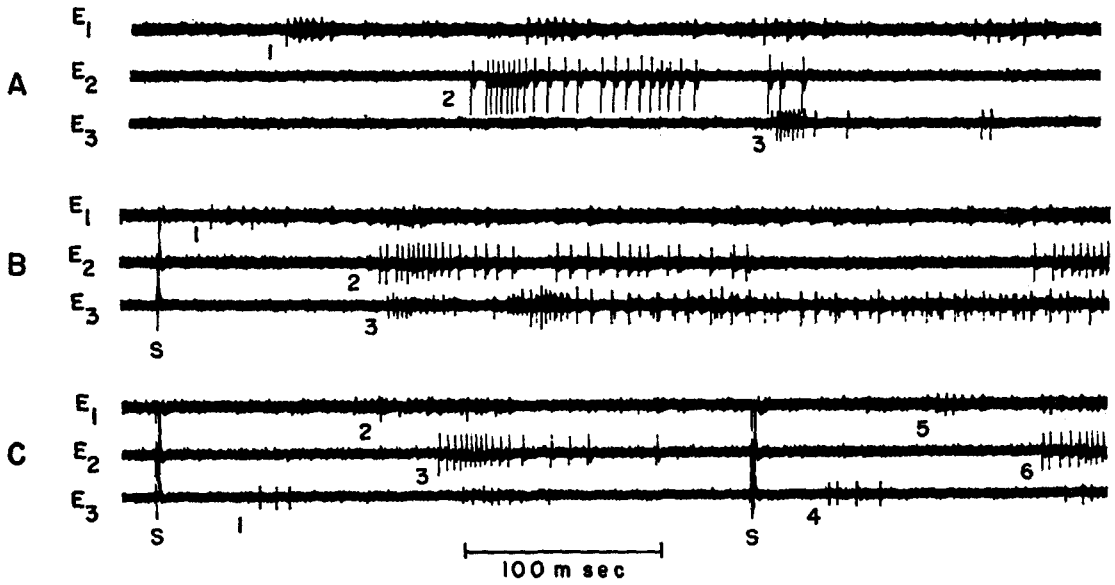

FIGURE 8. Records obtained, simultaneously, with three microelectrodes (E_1, E_2, E_3) from nucleus reticularis.
A, spontaneous activity; B, stimulation with single flash of light (S); C, stimulation with repetitive flashes (S).
1, 2, 3, etc., order in which neurons become active (see text).

laris. E_1, E_2, and E_3 represent the tracings corresponding to the three tips of a triple microelectrode, (tip diameters 4, 2, and 3 μ, respectively) aligned along a straight line, at distances E_1 to E_2 = 135 μ and E_2 to E_3 = 110 μ. In A, the activity was spontaneous and arrived first at tip E_1, next at tip E_2, and finally at tip E_3 (1, 2, 3, on the tracings) indicating propagation in the direction E_1 E_2 E_3. In B, the activity was evoked by a single flash of light (S) and appeared at the tips of the microelectrodes in the same order (E_1 E_2 E_3, at 1, 2, 3, on the tracings) although time relations between E_2 and E_3 were different from what they were in A. In C, the activity was "driven" by repetitive flashes of light (S) at a frequency of 3.2 flashes/second. In this case the CNA appeared at the tips of the microelectrodes in a different order: first at E_3, next at E_1, finally at E_2 and these time relations, between the appear-

ance of activity at the tips of the three microelectrodes, were maintained throughout the period of stimulation. The frequency of stimulation was quite critical and unless it was maintained very close to 3.2 flashes/second, "driving" did not occur.

Fig. 9 (A, B, and C) show records obtained under similar conditions, with a triple microelectrode, from the gyrus lateralis. The tips of the triple microelectrode (E_1 , E_2 , E_3 ; tip diameters, 2, 3, and 4 μ, respectively) were aligned

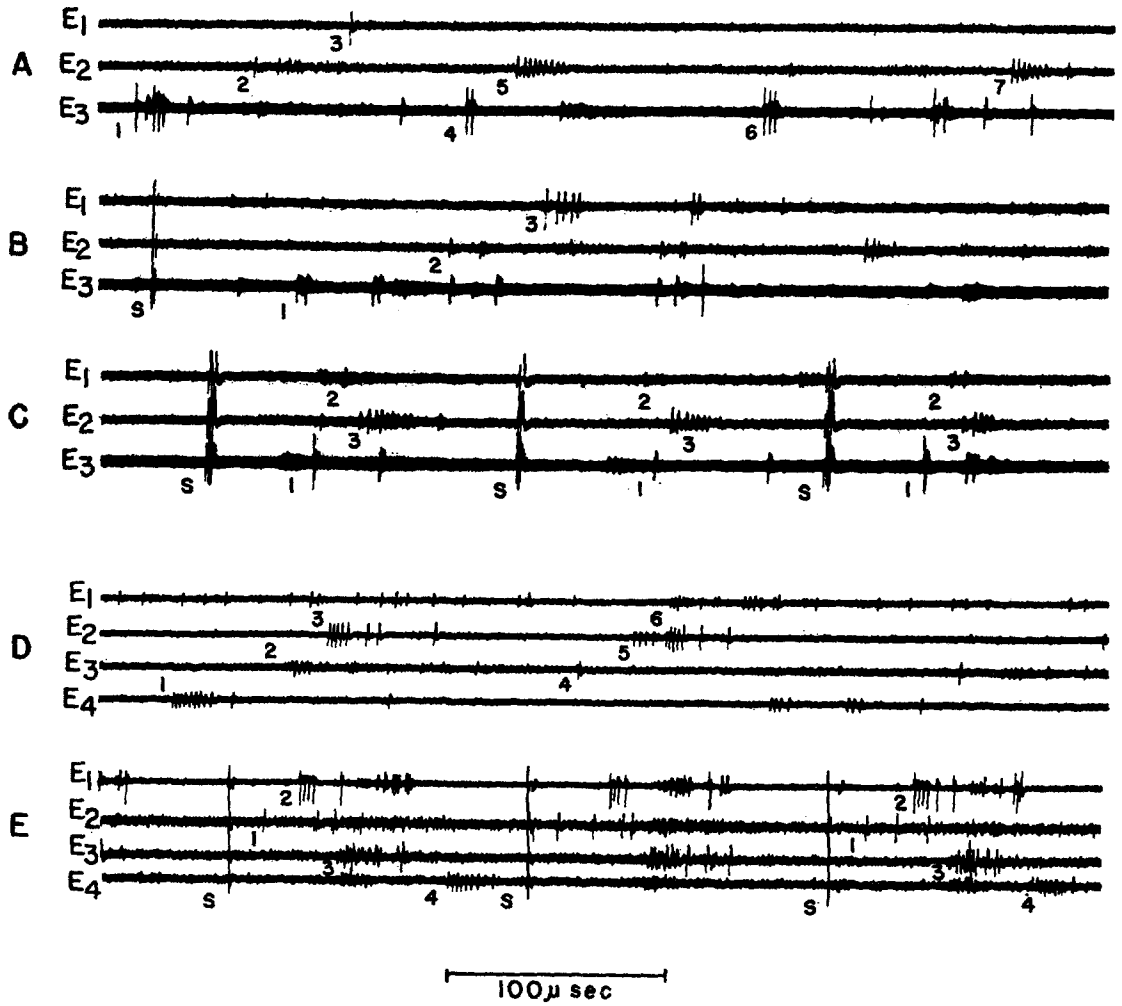

FIGURE 9. A,—B,—C.—Records obtained, simultaneously, with three microelectrodes (E_1, E_2, E_3) from the gyrus lateralis. A, spontaneous activity; B, stimulation with single flash of light (S); C, stimulation with repetivive flashes (S); D and E records obtained, simultaneously, with four microelectrodes (E_1, E_2, E_3, E_4) from the lateral geniculate body. D, spontaneous activity; E, stimulation with repetitive flashes of light (S).
1, 2, 3, 4, etc., order in which neurons become active (see text).

along a straight line, with distances E_1 to E_2 = 160 μ and E_2 to E_3 = 150 μ. In A the CNA was spontaneous and arrived first at tip E_3, next at tip E_2, finally at tip E_1 (1, 2, 3), indicating propagation in the direction $E_3 E_2 E_1$. The activity could be seen to propagate again in the same direction at 4 to 5 and 6 to 7. In B the CNA was evoked by a single flash and appeared at the tips of the microelectrodes in the same order ($E_3 E_2 E_1$ at 1, 2, 3 on the tracings). In C the CNA was "driven" by repetitive flashes of light (S) at the frequency of 7 flashes/second. In this case the CNA appeared at the tips of the microelectrodes in the order $E_3 E_1 E_2$, and these time relations were maintained throughout the period of stimulation.

Fig. 9 (D and E) shows records, obtained with a quadruple microelectrode, from the lateral geniculate body. The tips of the quadruple microelectrode (E_1, E_2, E_3, E_4 tip diameters: 5, 2, 3, 4 μ, respectively) were aligned along a straight line, with distances E_1 to E_2 = 150 μ, E_2 to E_3 = 160 μ, E_3 to E_4 = 150 μ. In D the CNA was spontaneous and appeared first at the tip of E_4, next at E_3, finally at E_2 (at 1, 2 and 3 on the tracings); the propagation, in this instance, did not reach E_1 which recorded spikes that seemed to be independent of the propagated activity; at 4, 5, and 6 the propagation occurred in the same direction, reaching the tip of E_1. In E the CNA was "driven" by repetitive flashes of light at the frequency of 8 flashes/second. In this case the CNA appeared at the tips of the microelectrodes in the order $E_2 E_1 E_3 E_4$, and these time relations were maintained during the period of stimulation. In the gyrus lateralis as well as in the lateral geniculate body the frequency of stimulation had to be maintained between 7 and 9 flashes/second in order to "drive" the neuronal activity.

In order to investigate the relations between the CNA and the activity of neurons which do not participate in it, tracings were obtained with quadruple microelectrodes (Fig. 10) in which three microelectrodes (E_2, E_3, E_4) recorded the propagated activity (1, 2, 3), while a fourth microelectrode (E_1) recorded the activity of neurons which do not participate in it. In section A, microelectrode E_1 was recording the spontaneous activity of several neurons. When propagated activity occurred (1, 2, 3) the activity recorded by E_1 disappeared (a to b on tracing E_1). In section B, microelectrode E_1 recorded the spontaneous activity of a *single* neuron; propagated activity was evoked by a single flash of light (S); when the propagated activity appeared (1, 2, 3), the activity of the neuron disappeared (a to b on tracing E_1).

It, thus, appears that, as elsewhere in the cortex and in the thalamus, spontaneously circulating neuronal activity is present in the visual cortex and in the lateral geniculate body and that it propagates at velocities of the same magnitude as that of velocities previously reported (28). In addition, it appears that the CNA can be evoked by a single visual stimulus and that it can be "driven" by repetitive stimuli.

The question arises as to what might be the nature and the role of this neuronal activity which constantly circulates through cortical and thalamic networks.

With respect to its nature an indication is given by its very close association with the "synchronization" of the "gross" electrical activity of the brain. The terms "synchronization" and "desynchronization" of the EEG have been used, at first, with the implication that "synchronization" corresponded to a state in

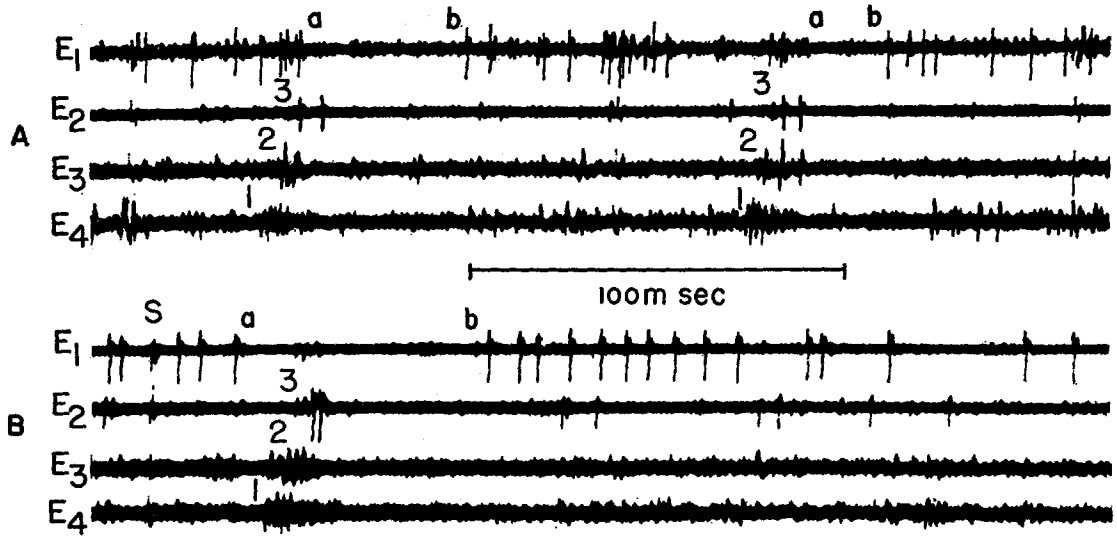

FIGURE 10. Records obtained, simultaneously, with four microelectrodes (E_1, E_2, E_3, E_4) from the lateral geniculate body. A, spontaneous activity; when propagated activity occurs (1, 2, 3), activity recorded by E_1 is inhibited (*a* to *b*). B, stimulation with single flash of light (*S*) causes propagated activity, recorded at 1, 2, 3; activity of single neuron recorded by E_1 is inhibited (*a* to *b*). Electrodes E_1, E_2, E_3, E_4 had tip diameters of 5, 2, 3, and 4 μ, respectively and the distances between tips were: E_1 to E_2 = 150 μ; E_2 to E_3 = 160 μ; E_3 to E_4 = 150 μ.

which many neurons became active simultaneously and "desynchronization" corresponded to a state in which there was no such simultaneity of action. However, Renshaw, Forbes, and Morison (17) recorded, with microelectrodes, the activity of neurons in the hippocampus and demonstrated that during "synchronization" of the EEG such simultaneous action did not, usually, take place. This was later confirmed by Li, McLennan, and Jasper and by Li (12). Recent work by Verzeano, Naquet, and King (27) and by Verzeano and Negishi (28) has provided evidence which indicates that, while such simultaneity of action does not occur, there are, nevertheless, close relations between the characteristics of the neuronal activity and the degree of "synchronization" of the gross waves: The appearance of "synchronized" gross waves in a

neuronal field corresponds to an increase in the frequency of the spikes generated by individual neurons and an enhancement of the periodic grouping of these spikes. These changes develop in conjunction with the successive passages of the CNA through the neuronal field, while an increase in the regularity of these passages accompanies any increase in the degree of "synchronization" of the gross waves. Thus, the "synchronization" of the electrical activity of the brain may be related to the CNA.

With respect to its role, the fact that the activity of some of the neurons in the network is arrested when the CNA passes in their vicinity or immediately thereafter (28), suggests that the CNA may have an inhibitory action. Recent findings indicate that this action changes in the transition from wakefulness to sleep and varies with the depth of sleep. This suggests that the CNA may be implicated in the mechanisms which are at the basis of the control of wakefulness and sleep (29).

Another finding of significance is that the CNA is influenced by impulses coming over the visual pathways. Single and repetitive stimuli give rise to patterns of temporal and spatial interaction between neurons and these patterns are reproducible: The same stimulus, if repeated at an appropriate frequency, will cause a number of neurons to fire in the same sequence, in time and in space. These close relations between some of the characteristics of the visual stimulus and the patterns of interaction developed by neurons in the networks of the lateral geniculate body and the visual cortex, suggest that such interaction may be an important factor in the cerebral processes which deal with the treatment of incoming information in the visual system.

Amplifiers were designed and constructed by Michael Kelly; anatomical materials were prepared by Esther Lu; photographic materials were prepared by W. R. Almond.

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