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EXCITABILITY CYCLE AND INTERACTION IN GENICULATE-STRIATE SYSTEM OF CAT*

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INTRODUCTION

THESE experiments were conducted on the geniculate-striate system of the cat to obtain more information concerning the excitability cycle of the neurons and the mode of interaction in this system in which the pathway is multiplied and in which partially shifted reciprocal overlap occurs extensively. Recruitment or occlusion in the overlapping synaptic connections accompanies the course of the excitability cycle and can be estimated by measuring the relative amplitudes of the conditioning and test shock postsynaptic responses. The variations in number of neurons activated represents an elementary type of interaction. Hence interaction and excitability cycle must be considered together in any observations dealing with aggregations of neurons.

The synaptic organization in the lateral geniculate of the cat involves two demonstrable types of synapses (4) One is a bouton on the perikaryon of the radiation neuron, and the other is a bouton connection with the dendritic processes of the radiation neuron. The simplified electrical records to be discussed in this paper are presented with no presumption of distinguishing the reactions of these two types of synapses.

Another qualification must also be mentioned. These data represent comparisons of action potentials recorded by a "monopolar" electrode in the lateral geniculate and another similarly connected electrode on the striate cortex. The electrodes may not be in corresponding parts of the projection pathway in any given case. However, enough experiments were done to indicate that the generalizations to be drawn in this discussion are valid.

METHODS

Cats were anesthetized with nembutal, dial, or chloralosan, usually the former. The eye was resected, and the optic nerve dissected free in the orbit. Both optic nerves were prepared in this manner for experiments on bilateral interaction. The calvarium was removed and the animal's head placed in our modification of the Horsley-Clark type of stereotaxic instrument. When surgical procedures were completed 40 cc. of 0.6 per cent saline was usually injected intraperitoneally.

The stimulus impulses (square waves) were coupled to the electrodes through shielded transformers, and applied to the optic nerve through silver wire electrodes. The cathode of

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the pair was centrally oriented. Two separate electrical units were used to generate the pulses for the stimulating shocks of the conditioning and test pair, so that all parameters of each shock could be independently adjusted. A third electrical unit was used to generate the train of shocks for the experiments on facilitation in the subnormal phase. The timing of stimuli and control of the multiple trace cathode-ray system (17) was done with a series of electronic switches (10).

Several types of "monopolar" and "bipolar" electrodes were tried from time to time. The one which we used most often was a "monopolar" electrode consisting of a short section of No. 40 stainless steel wire which had been enameled by a standard factory process. The outside diameter of the wire, including the enamel, was 75 micra. Mechanical rigidity was attained by threading the wire through a section of No. 18 stainless steel hypodermic needle tubing. The wire projected 5–10 mm. from one end of the tubing and was cemented there by a small amount of cellulose imbedding material. A composition block at the other end of the steel tube served as a support on which to anchor the electrode wire to the head amplifier leads. Our first models were sharpened on a rotary stone, but after a few trials this was discontinued and the wire merely cut cleanly with sharp scissors. This provided an electrode assembly which could be clamped in the Horsley-Clark apparatus, and from which a small amount of iron could be plated to mark positively points in the tissue, and which also approached micro dimensions. The undesirable feature of this electrode is the ever-present possibility of insulation breakdown, for which tests must be made with a resistance meter before and after each experiment. Such insulation failure is rare, but it is always possible. The remote connection was usually made at some point on the exposed skull, its position not being critical except for control of stimulus artifact. The preparation was grounded as a rule, by grounding the Horsley-Clark.

The electrode positions were checked by application of the Prussian blue reaction to sections cut by a frozen sectioning method and stained with Thionin (6). The entire process could be applied the day following the experiment if the brain had been perfused with fixative at the conclusion of the experiment. It provided precise checks of electrode position and possessed the great advantage of permitting us to keep our anatomical information up to date with current experiments. The experiments were conducted in a warm cubicle in which the air was maintained near saturation with water vapor at body temperature. The body temperature was kept between 37.0 and 38.0°C. by the application of heat or cold as required.

RESULTS

Action potential pattern. In general the records taken with "monopolar" leads in the geniculate show a triphasic record for the optic tract spike with positive phase leading. The third phase (positive) is usually not tangible, its amplitude depending on how far conduction proceeds from region of focal recording and whether or not the succeeding negative postsynaptic potential occurs early enough to mask this detail. The relative amplitude of the negative phase of the tract spike is also a function of "killed end" effects.

The negative phase following the triphasic tract sequence presumably represents radiation soma activation. A second phase (positive) of more variable dimensions is usually seen to succeed the negative soma spike. The latency differences of tract spike and soma spike, or time from peak to peak, are from 0.4 to 1.0 msec. which is within the range of bouton-soma synapsis in other systems. It is not certain at just what points latency should be measured. The first point must be somewhere from optic tract positive peak to tract negative peak, assuming the latter is not shortened by the third positive phase. Likewise, there are no certain grounds for considering the soma spike peak to be a critical time dimension for conduction across axon hillock.

The soma sequence is always somewhat longer in duration than the axon

time dimensions of the tract sequence. This general pattern is well known. There are numerous variations of pattern, descriptions of which are omitted. It should be mentioned, however, that if recording sensitivity is high and stimulus intensity moderate to high, a monopolar lead records a roughly "M" or "W" shaped complex from any point in the cerebrum. When the electrode is moved into or very near the lateral geniculate or optic tract, the amplitudes suddenly increase, and the patterns described in the previous paragraphs are seen.

However, we recorded approximately the same patterns from the entire geniculate region—for instance, an electrode in the ipsilateral segment showing about the same potential sequence as one in either of the contralateral segments with unilateral optic nerve stimulation.

Comparison of the geniculate records and cortical records indicates that the first cortical spike occurs with a time lag of 0.1–0.2 msec., a time delay compatible with the assumption that activation of the soma directly fires the radiation axon. However, several observations were made which render this simple assumption less certain. If the animal is killed by asphyxia with the electrodes in place, the first cortical spike should disappear with the geniculate soma spike. The sequence observed is that the cortical events disappear in inverse order, the last one being most susceptible, while the first and second spikes are relatively much more resistant but eventually decrease and disappear simultaneously. At this time a significant soma spike may still be present in the geniculate, which subsequently disappears and the diphasic or triphasic tract spike sequence remains. Then the tract sequence undergoes regression, apparently from central terminations since the second and third phases completely disappear first, at which time a pure monophasic positive spike is clearly seen. From this we infer that transmission across the axon hillock is more susceptible to asphyxia than the soma potential process, that the radiation-terminating elements are likewise more susceptible to asphyxia than the soma potential process, and that the tract-terminating processes are likewise more susceptible to asphyxia than are the parent fibers. The above general sequences are also seen for the case of ipsilateral optic nerve stimulation.

Excitability cycle with paired shocks. Paired shocks were applied to the contralateral optic nerve, adjusting the intensity of the conditioning shock so that the tract spikes for conditioning and test response were approximately equal. That equality of tract spike amplitudes indicates equality of number of fibers activated is open to question. Up to a separation interval of 10–12 msec. refractoriness and supernormality occur. During the supernormal phase it is probable that fiber action potential is supernormal or near resting level, so decreasing stimulus intensity to make tract test spike equal to tract conditioning spike should over-correct for decreased threshold at the stimulating electrodes and should result in fewer tract fibers firing into the geniculate. Below about 3 msec. the tract fibers are in the postconduction refractory phase, and it is necessary to increase the intensity of the test

shocks to make the tract amplitudes match. In this situation the fiber amplitudes are smaller so matching amplitudes result in activation of more fibers by the test shock. Systematic data were not obtained for intervals shorter than 2 msec. because of this factor and also because the overlap of the geniculate sequence made amplitude comparison a problem in itself.

Typical data are shown in Figure 1 for three ranges of intensity. The

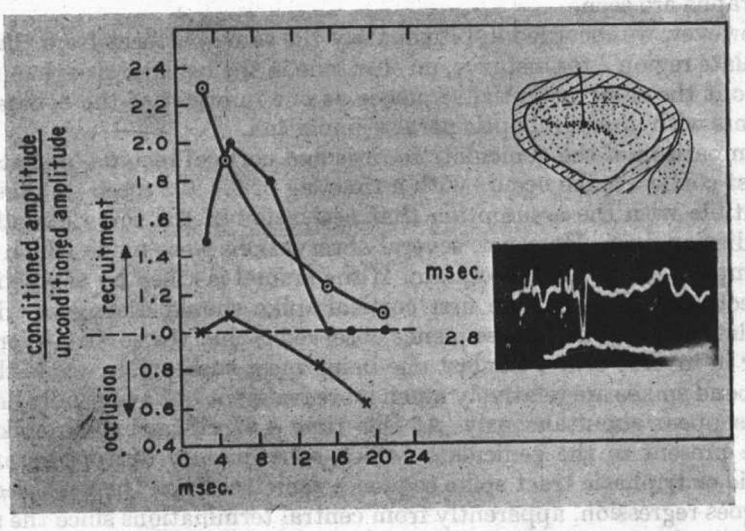

FIG. 1. Recovery cycle of lateral geniculate. Record from geniculate contralateral to optic nerve stimulated, locus of active end of electrode marked by iron deposit as shown in upper right. Sample oscillogram of a 2.8 msec. separation of stimulus pulses shown in lower right. Lower trace immediately succeeds upper trace to provide a longer time base. *Positive up*. Positive spike representing optic tract potential, succeeding negative spike representing radiation soma potential. Plots of ratios of conditioning and test soma spike response are shown at left. Ratios are ordinates and time separating shocks are abscissa. The three curves represent three shock intensities; circles—weak stimuli, dots—moderate stimuli, and crosses—strong stimuli.

actual values obtained are a function of the cycle frequency at which the paired shocks are repeated. As has been noted by others (2), if no stimulus has been applied for several seconds, and then a test pair presented, the first response is larger. If the pair is presented again within 1 or 2 seconds or less, the first reponse is smaller and the second is larger. This facilitation effect is thus a function of two variables, the shock intensity and the cycle frequency. This led us to obtain some data on recruitment in the subnormal phase.

Recruitment in subnormal phase. The stimulating and recording apparatus was arranged as described in the legend of Figure 2. In this particular experiment the conditioning train of maximal shocks was applied as 9 shocks at an equivalent frequency of 400 per sec., and (in the experiment shown) only the first three geniculate sequences show the typical postsynaptic

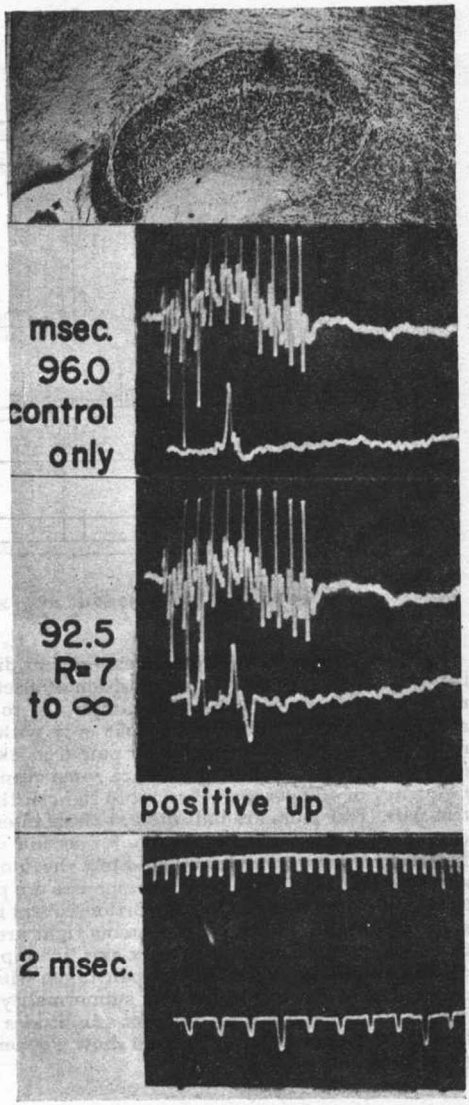

Fig. 2. Illustrating technique employed to examine recruitment in subnormal phase. Locus of electrode marked by iron deposit shown in photomicrograph at top. Stimuli applied to contralateral optic nerve in sequence shown in potential records. *Positive up*. Oscillograms are divided into three pairs. Bottom pair are time lines for the two successive sweeps, upper sweep occurring first, followed after test interval by second sweep. In topmost oscillogram is shown response to a barrage of 9 conditioning shocks at frequency of 400 per sec. Note that only first three shocks are followed by a definite soma spike (negative). Smaller slow negative wave was not always seen, and in this particular experiment, it does not show any decrease during barrage. After interval of 96 msec. (from last shock of conditioning barrage to next stimulus) the second only of test pair was presented. This record constitutes control for one shown below it. Latter record shows how soma spike is facilitated if first shock of test pair precedes second by 2 msec. Note that tract spike amplitudes of test pair are approximately equal but that the first is followed by no demonstrable soma spike. Soma spike following second shock is 7 mm. record amplitude. In this case ratio of test to conditioning response (of test pair) is very high and is indicated as 7 to ∞ because soma spike of first reaction is either absent or its amplitude is too small to record. Cycle frequency at which entire operation was automatically repeated was 1 in 4 sec.

negative spikes. In other experiments four were seen, and sometimes five. If five were present, the fifth was always of lower amplitude. No less than three postsynaptic spikes have been seen.

The paired shocks were presented at various intervals following the conditioning volley. Plots of typical data are shown in Figure 3. It is seen that recruitment is relatively high during the major subnormal phase. It is maximum for conditioning shock strengths of medium intensities, and usually parallels the degree of subnormality. This result shows that the recruitment follows directly according to magnitude of subliminal fringe. The subliminal fringe can, in effect, be made relatively large by two factors, both of which reduce dimensions of excited zone. The barbiturates prolong thalamic

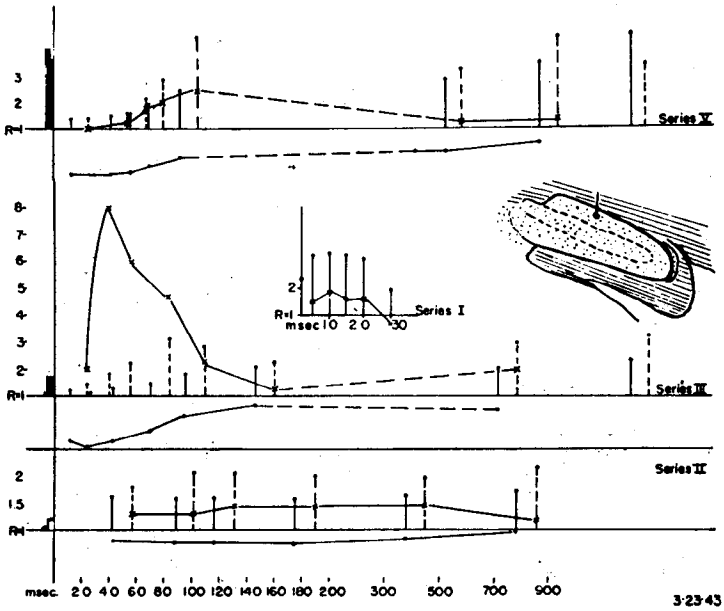

FIG. 3. Plots of data from an experiment different from that illustrated in Fig. 2. Tracing of geniculate section shows position of electrode marked by iron deposit. "R" on ordinates is ratio of test soma spike amplitude to that of conditioning soma spike. Series I: recruitment curve for paired shocks only without conditioning barrage. All other curves represent recruitment observed for paired shocks in subnormal phase. Series III: Black vertical lines to left of plot frame are soma responses to conditioning barrage delivered at frequency of 400 per sec. Abscissa to right of this indicates msec. interval to application of test pair. Test pairs are indicated at these intervals by a solid line for first shock response (soma amplitude) and dotted line for second shock response (reading from left to right). Interval between conditioning and test shock of these pairs is 14 msec. and can be read on abscissa. Ratios of these pairs of responses are plotted for the various intervals as solid vertical line above x-axis. Dotted portion covers interval for which no data was taken. Two soma amplitudes indicated at extreme right are controls for test pair alone without conditioning barrage. Solid line below x-axis line represents ratio of first response of test pair to control amplitude of first of test pair taken without conditioning barrage. This line can be considered to represent degree of subnormality. The other series represent different shock intensities as indicated by different amplitudes of soma spike responses. No great accuracy is claimed for these data. They do show a general relation of extensive recruitment in subnormal phase.

total recovery time after a series of stimuli in the primary sensory systems (7). This total recovery time becomes important for single shocks if the stimuli are repeated over any cycle frequency below about 5 seconds. Secondly, the magnitude of the subliminal fringe is likewise an inverse function of stimulus intensity because a small excited zone has a relatively larger subliminal fringe. This can be looked upon as a function analogous to specific area which increases as volume diminishes, and is descriptively similar to the classical facilitation of Sherrington. It is thus obvious that

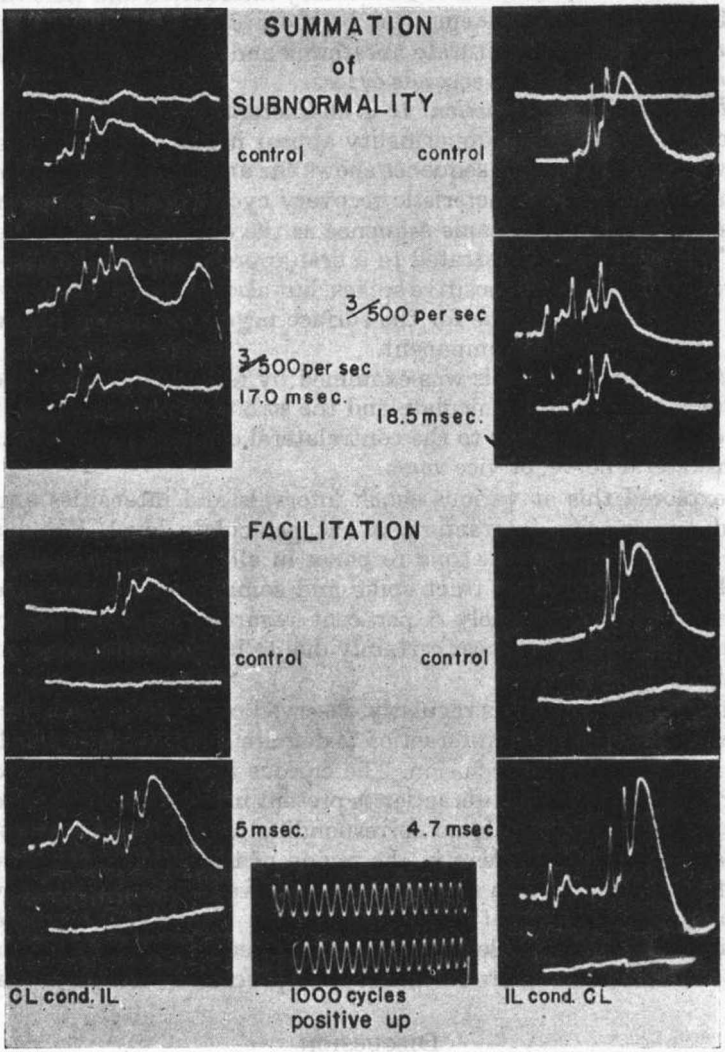

FIG. 4. Cortical reactions to conditioning and test stimuli applied to opposite optic nerves. Left column, contralateral conditioning ipsilateral. Note that amplitude of first cortical spike is decreased in subnormal phase and significantly enhanced in facilitation phase. Small deflection between stimulus artifact and first cortical spike is essentially a lead artifact and definitely represents subcortical activity. Column on right is self-explanatory. In facilitation example of ipsilateral conditioning contralateral, first cortical spike shows no significant difference in this instance. However, as noted in text, second reaction has always been observed to be decreased about 5 per cent in all components in geniculate. Fact that first cortical spike is same amplitude as control indicates general rule of bilateral interaction of all cortical spikes, apparently in absence of demonstrable geniculate bilateral interaction in direction of recruitment.

recruitment is a manifestation of elementary interaction and that the interaction between neuron systems can be more clearly seen, perhaps even exaggerated, by using barbiturate anesthesia and repeating the single shock stimuli at intervals of 1 or 2 seconds or less.

Unilateral cortical interaction. It is characteristic that the same general phases of facilitation and subnormality appear in the cortical record. Each of the events of the cortical sequence shows the amplitude changes, but each event has a different characteristic recovery cycle, and the time course of each one lengthens in the same sequence as the order of appearance of the events. This can be demonstrated to a first approximation not only for the events recorded as surface positive spikes, but also for the succeeding surface positive wave. It is also true for the surface negative wave, which we consider to be a definite fifth component.

Bilateral interaction. This was examined by recording from an electrode in various regions of the geniculate and the striate projection area and presenting conditioning shocks to the contralateral optic nerve and test shocks to the ipsilateral nerve, or vice versa.

We explored this at various shock intervals and intensities and never observed any specific interaction at the geniculate level. We did see a peculiar diminution of the second response in all components for intervals up to about 10 msec. The tract spike and soma spike were both equally diminished by approximately 5 per cent regardless of which nerve was stimulated first. This is almost certainly due to interfiber interaction in the optic chiasm and tract.

Bilateral interaction was regularly observed on the cortex. Typical data are shown in Figure 4. The interaction is definite and significant in all ways, in both recruitment and occlusion. The curious feature of these records is, however, that the cortical interaction is present in all components, including the first cortical spike, while no corresponding changes in geniculate soma spikes can be found anywhere in the region of that nucleus. This absence of demonstrable interaction at the geniculate level agrees with observations of Bishop and O'Leary, but we do not confirm their report of little or no interaction at the cortical level (2). This difference is due to the fact that these authors did not explore the interaction processes through the recovery cycle.

Discussion

The general features of our records appear to be comparable with those reported by Bishop and O'Leary (2, 3), who offer more extensive discussion of experiments in which the position of the remote electrode was given more consideration.

In all cases, relative amplitude of these records should be considered a function of relative reaction intensity as well as a function of position of the electrode, and it should be remembered that the patterns described are recorded only from within the immediate region of the structures concerned. The form of potential must be a rigorously definable physical quantity, but the biological material is not even a homogeneous medium from an electrical

point of view. It appears to be clear that the focal electrode technique provides good average pattern definition but imperfect detail when aggregations of neurons are activated. One can readily see considerable changes in pattern by manipulating any of the variables, stimulus intensity, stimulus frequency, depth of anesthesia, oxygenation of the blood, or position of the electrode. In this type of experiment some of the fibers of the optic nerve are more favorably placed in relation to the stimulating electrode than others, and the focal recording electrode is somewhere in the geniculate region. Unavoidably, any change in stimulus strength below maximal results in a change of the position of the reacting elements relative to the position of the recording electrode. We attempted, unsuccessfully, to avoid this dilemma by applying electrodes to the exposed retina, thus confining activation to a relatively few particularly located fibers. This is one of the characteristic deficiencies of this type of experiment. The difficulty is two-fold. First is the difficulty of placing the electrodes in corresponding parts of the ascending pathways so that weak reactions can be more adequately studied. Second is the difficulty of securing concrete anatomical proof that the electrodes were successfully placed in such corresponding positions. The employment of maximal stimuli does not solve this dilemma because the high potentials plus minor temporal dispersion mask the detail and only an averaged pattern appears on the oscilloscope. Passive electrotonic conduction potentials including the transneuronal type (7) must also be considered. There are other factors which undoubtedly mask detail to an unknown extent. Minor, more or less rhythmic, vascular and respiratory pulsations are of some significance in an opened skull. These disturbances are much smaller under the barbiturates than with ether and are also reduced by supporting the head above the body in a stereotaxic apparatus. These mechanical displacements can be overlooked because low grid current amplifiers reduce microphonic effects. All of these factors operate to reduce resolution of detail.

The recruitment observed is obviously a combination of long interval threshold changes and subliminal fringe effects in overlapping synaptic connections. The excitability change must be due to two overlapping processes of facilitation and subnormality which extend over appreciable intervals of time. The facilitation process leads the subnormal curve and the latter persists longer. Pitts has presented such curves for the phrenic nucleus (16). The facilitation process appears to operate on both threshold and subthreshold reactions. In the former case it is seen as the ability of the soma to show full amplitude depolarizations for three or four briefly spaced and maximal tract reactions. There is no absolute proof that each soma is firing each time, but it probably is a repetitive reaction. Some observations on the somatic sensory system of the cat (7) are pertinent on this point. A steel needle electrode in the internal capsule recorded high frequency groups of presumably single fiber activity, each group following a weak, discrete tactile stimulus. The ability of the somatic radiation neuron to transmit a group of 3 to 5 impulses at an equivalent frequency of 500 per sec. is strikingly similar to the repetitive soma negative spike picture observed in the geniculate. The apparent synapse time is also shortened in the facilita-

tion interval. After 3 to 5 depolarizations at this frequency, the reaction abruptly ceases. This presumably means that subnormality now dominates or that some extinction process now intervenes, followed by subnormality, or coincident with development of subnormality.

The subthreshold changes in the subliminal fringe result in the test shock recruiting more elements. Presumably, the time course of the subthreshold changes in excitability follow a resultant of the two processes of facilitation and subnormality.

The recruitment observed in the facilitation interval is striking because the soma cells detonated by the conditioning shock are also detonated by the test shock, and added to the latter are the cells recruited in the subliminal fringe of the first reaction. It thus follows that a group of weak stimuli produce relatively greater recruitment than a group of strong stimuli. In effect the neural mechanism amplifies weak stimuli much more than strong stimuli, and for strong stimuli temporal summation rapidly reaches a ceiling. Some of the implications of these phenomena in the essentially discontinuous visual processes have been discussed elsewhere (12).

It is highly desirable to repeat these observations with some of the typical volatile anesthetics because the frequency of spontaneous rhythms is appreciably greater, and the time scale of the subnormal phase of the recovery cycle is appreciably less than with the barbiturates (1, 5, 7, 14). We have made some observations under ether which showed the same general phenomena with a contracted time base, but we have not secured sufficent data for descriptive discussion because of various operational difficulties. The observations described here were made with several barbiturates at various levels but not, as a rule, under deep anesthesia.

The unilateral cortical interaction requires no comment except to point out the significance of summation processes as they affect the fifth event. This event is the negative wave which typically cuts into the latter part of the preceding positive wave. In moderate anesthesia it may be absent for one stimulus, but the summation of two or more stimuli in the facilitation interval clearly elicits this phase (13). The negative sign indicates that this reaction has ascended to a region closer to the electrode than the events associated with the preceding surface positive phases. Strong stimuli or light anesthesia also typically favor the appearance of this negative phase. Local application of convulsants, as previously shown (13), appear merely to enhance this negative phase and with the enhancement may be clearly demonstrated cortico-cortical projection discharges. We infer that the relatively large and definite negative phase indicates the activation of another group of neurons, probably in the plexiform layer; and with less certainty, we infer that the cortico-cortical projection processes may be coupled through the plexiform layer. The facilitation and subnormal intervals of this negative phase are essentially similar to those of the preceding phases but have a greater duration.

Under standard conditions the magnitude of succeeding cortical reactions approximately follows the reaction magnitude of the geniculate soma

potential. However, it remains to be proved that soma depolarization necessarily leads to conduction into the radiation fiber. Hence the fact that asphyxial disappearance of first cortical spike and of soma spike are often not concurrent presents no great theoretical difficulty. Furthermore, the fact that the branching terminations of the tract fibers are more sensitive to asphyxia than the parent fibers suggests that the same may be true of the dividing terminal branches of the radiation axons. This point has not been checked, and, if true, would explain the occasional failure of the first cortical spike without any postulations concerning the axon hillock. This time sequence of the asphyxial changes also suggests that the soma dendrites become inactive before the soma in asphyxia. This can conceivably be connected with failure of transmission across the hillock while a full-sized soma potential still appears. There are many such possibilities about which these experiments give no information.

The bilateral interaction data are not self-explanatory. It is conventional to infer that interaction results because the ipsilateral and contralateral neurons converge with overlapping terminal branches on some common neuron, and that the excitability cycle phenomena are qualitatively similar to that which can be observed in the linearly ascending neuron chains of the homolateral systems. On this basis we should not expect the first cortical spike to show the facilitation phase of interaction since such specific interaction has not been demonstrated in the geniculate. This reasoning implies, of course, that the soma potential is a reliable sign of radiation neuron activation. The anatomical evidence indicates that any specific connections between contralateral and ipsilateral geniculate segments are scanty or absent (15).

If we assume that present experimental evidence is correct and that completely corresponding bilateral interaction is not present in the geniculate, then the bilateral interaction observed between the first cortical spikes demands interesting revision of current conceptions of these events. The first cortical spike may not be entirely due to radiation endings. Therefore, an additional depolarization process of appreciable magnitude and fast development must be postulated. On the other hand, if the first cortical spike is due entirely to radiation fibers, then we must assume interaction between the ipsilateral and contralateral radiation endings. The interaction observed does not conform to available data on fiber interaction in nerve trunks. Hence the radiation interaction observed at the cortical level may be mediated by antidromic electrotonic mechanisms across the common neurons on which the contralateral and ipsilateral radiation endings converge.

Summary

1. The postsynaptic negative spike observed in the lateral geniculate exhibits the general properties of soma potentials.

2. The potential magnitude recorded from a group of units (geniculate or cortex) shows a summation or recruitment interval extending to 30 msec. and a subnormal phase lasting for seconds.

3. The relative recruitment is greater in the subnormal phase, and proportional to it by a function not yet defined. It is partly proportional to subliminal fringe and hence an inverse function of strength of stimulus, or of excited zone dimensions.

4. The subnormal phase in the geniculate has never been observed to develop fast enough to quench the first 3 responses occurring within the initial period of about 5 msec. This initial extinction phenomenon is not necessarily part of the conventionally defined subnormality, however.

5. It is not certain that the first cortical spike is entirely due to radiation fiber action potential.

6. Bilateral interaction occurs at cortical level for all components, but comparable interaction has not been demonstrated anywhere in the geniculate.

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REFERENCES

1. BEECHER, H. K. AND MCDONOUGH, F. K. Cortical action potentials during anesthesia. *J. Neurophysiol.*, 1939, *2:* 289–307.
2. BISHOP, G. H. AND O'LEARY, J. S. Electrical activity of the lateral geniculate of cats following optic nerve stimuli. *J. Neurophysiol.*, 1940, *3:* 308–322.
3. BISHOP, G. H. AND O'LEARY, J. S. Factors determining the form of the potential record in the vicinity of synapses of the dorsal nucleus of the lateral geniculate body. *J. cell comp. Physiol.*, 1942, *19–20:* 315–331.
4. GLEES, P. Termination of optic fibers in lateral geniculate body of the cat. *J. Anat., Lond.*, 1941, *75:* 434–440.
5. HEINBECKER, P. AND BARTLEY, S. H. Action of ether and nembutal on the nervous system. *J. Neurophysiol.*, 1940, *3:* 219–236.
6. MARSHALL, W. H. An application of the frozen sectioning technic for cutting serial sections through the brain. *Stain Technol.*, 1940, *15:* 133–138.
7. MARSHALL, W. H. Observations on subcortical somatic sensory mechanisms of cats under nembutal anesthesia. *J. Neurophysiol.*, 1941, *4:* 25–43.
8. MARSHALL, W. H. Facilitation and recruitment during the subnormal stage in the geniculate-striate system of the cat. *Proc. Amer. physiol. Soc.*, 1942, *1:* 57–58.
9. MARSHALL, W. H. AND TALBOT, S. A. Recovery cycle of the lateral geniculate of the nembutalized cat. *Amer. J. Physiol.*, 1940, *129:* 417–418.
10. MARSHALL, W. H. AND TALBOT, S. A. A multi-channel time delay unit. *Rev. sci. Instrum.*, 1940, *11:* 287–289.
11. MARSHALL, W. H. AND TALBOT, S. A. Relation of the excitability cycle of the geniculate-striate system to certain problems of monocular and binocular vision. *Amer. J. Physiol.*, 1941, *133:* 378–397.
12. MARSHALL, W. H. AND TALBOT, S. A. Recent evidence for neural mechanisms in vision leading to a general theory of sensory acuity. *Biol. Symp.*, 1942, *7:* 117–164.
13. MARSHALL, W. H., TALBOT, S. A., AND ADES, H. W. Cortical response of the anesthetized cat to gross photic and electrical afferent stimulation. *J. Neurophysiol.*, 1943, *6:* 1–14.
14. MARSHALL, W. H., WOOLSEY, C. N., AND BARD, P. Observations on cortical somatic sensory mechanisms of cat and monkey. *J. Neurophysiol.*, 1941, *4:* 1–24.
15. O'LEARY, J. S. A structural analysis of the lateral geniculate nucleus of the cat. *J. comp. Neurol.*, 1940, *73:* 405–430.
16. PITTS, R. F. The basis for repetitive activity in phrenic motoneurons. *J. Neurophysiol.*, 1943, *6:* 439–454.
17. TALBOT, S. A. Multiple sweep system for cathode ray oscillography. *Rev. sci. Instrum.*, 1940, *11:* 289–291.
18. TALBOT, S. A. AND MARSHALL, W. H. Binocular interaction and excitability cycles in cat and monkey. *Amer. J. Physiol.*, 1941, *133:* 467–468.