Visual evoked cortical response in the cat

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The cortical response of the cat to light flashes has been studied, the locus of greatest amplitude of response noted, and the conformation described. Recordings through the dura indicate that there is diminution of the response amplitude and reduction of localization caused by the dura. The effects of stimulus parameter changes, of application of strychnine locally, and of intravenous pentobarbital were noted.

Although a number of investigators have studied the cortical response to light stimulation of the cat's visual system, most of the studies have been carried out under general anesthesia. This study has been carried out in succinylcholine-immobilized cats to avoid the effects of general anesthesia upon responses evoked by light stimulation.

Methods

Approximately 40 adult cats were studied. Ether anesthesia was used to permit tracheotomy, installation of a cannula for artificial respiration, venotomy for administration of succinylcholine, resection of sacciating membranes, and craniectomy of an area sufficient for exposure of the required brain surface. The animals were given no general anesthetic following this, topical procaine being used on skin edges. The pupil was maximally dilated with 1 per cent atropine and 10 per cent Neo-Synephrine. Corneal anesthesia was obtained with topical tetracaine and the cats were secured in a stereotaxic head holder. Prior to any experimental run the animal was totally dark adapted for 30 minutes.

Light stimuli were provided by a fiber optic light guide illuminated by a General Electric DEF projection bulb. Maximum luminance of this source, measured in the plane of the entrance pupil of the cat eye, was $2 \times 10^6$ foot lamberts (human photopic evaluation). An adapting light was situated in the path of the stimulus light with a prism arrangement. The luminance of this was about $2 \times 10^4$ foot lamberts. The luminance of the light sources was measured daily and controlled by neutral density filters. Stimulus duration was controlled by an electromagnetic shutter driven by an electronic stimulator. The rise time of the light stimulus was 4 msec. The active electrode for the ERG was a platinum needle inserted in the corneal limbus. For the brain response a 1 mm. chlorided ball of silver was placed on the surface of the brain exposed by craniectomy. The indifferent electrode was placed in the ear. The opposite ear served as ground electrode. The exit end of the fiber optics was located 5 mm. from the corneal apex.

The potentials obtained were led to a Tektronix Type 122 preamplifier condenser coupled with time constants available from 1 to 0.002 second. The amplified potentials were displayed on a Tektronix Type 555 oscilloscope and photographed with a Grass recording camera. From three to five sweeps were superimposed in most recordings.

Results

The visual evoked response recorded was found to be a complex sequence of poten-
Fig. 1. Topography of responses evoked with photic stimuli. ERG (top trace) and cortical response (center trace) at the indicated sites on cat cortex. Lowest trace, light stimulus. Similar records throughout this section of report. Stimulus luminance $2 \times 10^4$ foot lamberts.

The potentials, varying with the parameters of the stimulus and state of adaptation and also with the individual animal. The initial response was composed of a relatively large slow wave upon which were superimposed smaller, shorter duration positive potentials. The initial response had a latency of 18 to 25 msec. and an amplitude of 200 to 260 mv. The duration of this segment of the response varied from 22 to 78 msec.

The short components of the response occur most prominently in large healthy animals. The narrow peaks last 4 to 7 msec. and vary from 50 to 400 mv. The two to six narrow peaks were most easily recorded from those portions of the cortex where the entire response is largest. Fig. 1 shows the general conformation as well as the distribution of the response. As can be seen, the maximum response was elicited at the junction of the middle and posterior thirds of the midline of the lateral gyrus. This localization was most constant for the well-defined elements of the responses. The distribution of the lesser components was less consistent.

The negative deflection was observed following the positive wave, and then one or two positive, later swings, sometimes separated by a definite negative wave.

The first slow positive wave and, to a somewhat lesser degree, the first negative swing are most consistent in their appearance. The later components were more variable in the course of a series of experiments upon any one animal and when the responses of one animal are compared to those of another.

Fig. 1 also shows the ERG recorded in each instance simultaneously, at the top of each frame. In the response from the area of greatest amplitude it is apparent that the cortical response begins before the b-wave of the ERG.
Fig. 2. Evoked responses in 20 different animals at same site in each. ERG and VER in each frame, except G, P, Q, S, where symmetrical leads from both hemispheres are used. Stimulus binocular. Amplification is the same except for H. Luminance and frequency of stimuli:

<table>
<thead>
<tr>
<th>Frequency</th>
<th>Luminance</th>
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<tr>
<td>A, B, C, D, +0.1 per second, $2 \times 10^3$ foot lamberts</td>
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<tr>
<td>E, F, G, H, +0.1 per second, $2 \times 10^4$ foot lamberts</td>
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<tr>
<td>I, J, K, L, M, +0.1 per second, $2 \times 10^5$ foot lamberts</td>
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<tr>
<td>N, O, P, +0.04 per second, $2 \times 10^6$ foot lamberts</td>
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<tr>
<td>Q, R, S, T, +0.01 per second, $2 \times 10^8$ foot lamberts</td>
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Fig. 3. Recording from animal in Fig. 1 prior to opening of dura. Stimulus parameters and recording conditions identical to those in Fig. 1.
Fig. 2, taken from the records of 20 individual animals under five different stimulus intensities, indicates, as much of our data do, that there is considerable variation in the response between individual animals. In any one animal, however, the response is remarkably constant and the response to binocularly presented stimuli is symmetrical between the two hemispheres.

The traces of Fig. 3 were obtained from the same animal used in Fig. 1, the electrode being placed on the dura before it was opened. This record indicates that the response thus recorded is of lesser amplitude and that the area of maximum response is not as sharply localized as that observed when the recording electrode is in contact with the brain. The reduction in amplitude is about 30 per cent.

The lesser elements of the response, particularly the late narrow peaks, were markedly attenuated.

Fig. 4 demonstrates the effect of variation in the luminance of the light stimulus. With diminishing stimulus luminance, reading downward, there was a diminution in the amplitude of the initial positive potential as well as an increased latency.

The above mentioned time relationship between ERG b-wave and occipital response is likewise most clearly apparent at an intermediate stimulus intensity—here at 200 and 2,000 foot lamberts, with the occipital response clearly preceding the b-wave.

The effect of variation in frequency of stimulus presentation is shown in Fig. 5. Since the stimulus was of constant duration (80 msec.), increased frequency necessarily induced greater light adaptation. This factor may be deduced from the reduction of the ERG amplitudes with higher frequency of stimulation. The effect upon the occipital response was also one of reduction of response amplitude, although not to the degree noted in the ERG.

Fig. 6 is a record obtained in the course of dark adaptation. The occipital response is noted to recover following light adaptation faster than the ERG.

Fig. 7 is the converse experiment, obtained by utilization of the noted levels of light adaptation. It shows similar tracings, of lower amplitude at higher levels of light adaptation, and a seeming peak of late response at an intermediate (100 foot lamberts) level of background light. A similar reduction of ERG amplitude was noted.

Fig. 8 demonstrates an often-observed clinical finding—that the response in the contralateral hemisphere of man is of greater amplitude than that of the ipsilat-
Fig. 5. Effect of stimulus frequency. Luminance $2 \times 10^4$ foot lamberts, binocular, time constant 0.2 per second.

Fig. 6. Effect of progressive dark adaptation. Stimulus $2 \times 10^3$ foot lamberts, 0.1 per second, light adaptation source $3.2 \times 10^4$ foot lamberts, for 30 seconds.
Fig. 7. Effect of light adaptation levels. Conditions same as Fig. 6.

Fig. 8. Binocular, ipsi-, and contralateral stimuli, 2 x 10^4 foot lamberts; same conditions as Fig. 6.

Fig. 9. Effect of strychnine solution placed on cortex. Stimulus luminance 2 x 10^4 foot lamberts, frequency 0.1 per second. Top trace at site of drug application; center trace contralateral hemisphere control; lowest trace stimulus.
Fig. 10. Effect of intravenous pentobarbital. Binocular stimulus $2 \times 10^6$ foot lamberts, frequency 0.1 per second. Top trace, cortex; center, ERG; bottom, stimulus. Top left record control. Nembutal (25 mg. per kilogram) injected as marked (xN) at times in minutes denoted by numbers at left of columns of records, except 50 mg. per kilogram as noted at 20 minutes. Recordings 10 and 20 seconds following conclusion of injection after each dose. Final record 10 minutes after last dose.

The ipsilateral responses are of lesser amplitude than the binocular in all elements of the response. The contralateral response is approximately equal to the binocular, except for a reduced amplitude of the second positive peak.

Fig. 9 shows the reversible effect of application of a 3 per cent solution of strychnine to the area of the cortex studied. Little change was noted in the initial positive narrow peaks or the later response. However, a 100 mv. slow negative wave was seen to develop following these initial elements, which was reversible by lavage of the brain surface. No such alteration was observed on the contralateral control hemisphere.

The effect of intravenous administration of pentobarbital is shown in Fig. 10. The earliest effect noted is a loss of the minor narrow peak components of the response, until the response (10 minutes) was reduced to a very simple form. This type of response is what has been noted in many previous reports. A commonly observed phenomenon at certain doses of the drug is seen at 20 minutes, consisting of an apparent doubling of the on-response. The great increase of ERG amplitude is also noted in this set of tracings.

Discussion

It is clear from this work, as indeed has been shown before by other techniques,12,13

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that the b-wave of the ERG does not preceed the cortical response.

The records obtained in response to varying frequency of stimulation and variation in adaptation levels may be interpreted as verifying our clinical findings, which seem to indicate that the cortical response is more indicative of the photopic function than is the ERG. This is in keeping with reports of other investigators. The initial response was composed of a positive slow wave upon which were superimposed smaller narrow peak potentials. A negative deflection was observed following the positive wave, then one or two positive later swings. The later swings may correspond to the "secondary discharge." The relationship of the late discharges to possible off-effect discharges is under investigation.

The second positive peak is more pronounced at lower levels of light adaptation than is the first. This may indicate a scotopic character for the second peak and a photopic one for the first (Fig. 8).

Differential effects upon the first and second positive peaks with contralateral and ipsilateral stimulation as compared to bilateral stimulation, as well as the observed differential effects on first and second peaks of pentobarbital and strychnine, may indicate differing physiologic natures of the two peaks.

The loss of the narrow peaks upon pentobarbital administration with consequent simplification of the response form is notable and must be taken into account in interpretation of records obtained with this and similar agents.

The similarity of effect of strychnine upon the early and late portions of the response may indicate a similar mechanism of production of both.

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REFERENCES