CORTICAL RESPONSE TO INTERMITTENT STIMULATION WITH COLORED LIGHT IN THE CAT

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It has been shown by previous investigators that the wave-length of the photic stimulus might be an important variable in the production of photic activation of the electroencephalogram. Halstead, Knox, Woolf and Walker (13) found that on unanesthetized monkeys, the blue region of the spectrum was considerably more effective in photic driving than the red region, while Carterette and Symmes (7) reported that red light was more potent in the production of epileptiform waves in photogenic epilepsy than green, blue and white lights.

The question as to whether or not the wave-length has a specific effect on the electrical activity of the cortex, is of great importance not only for its diagnostic application, but also for the central mechanism of color vision. We attempted therefore to make a systematic investigation on this problem, using spectral lights of various wave-lengths.

METHOD

Experiments were carried out on 10 adult cats. The cat was anesthetized with oltopan-sodium administered intravenously (30 mg. per kg. body weight) and in addition with urethane administered intraperitoneally (0.8 g. per kg. body weight). After the scalp had been reflected, the animal was attached to an animal board in a darkened, electrically shielded room, and placed before an aperture in one side of the room in such a manner that flashes of light introduced through the aperture gave an equal illumination to both eyes.

White light from a tungsten source of known energy distribution was interrupted at various frequencies by means of an episcotister which was interposed in front of the entrance slit of a spectroscope. The episcotister was driven by a motor. Its revolving rate was controlled by a rheostat and measured exactly by means of an electric tachometer. The light-dark ratio was always 1:1.

For recording evoked potentials, Dawson’s superimposition method (8) was employed which was suitable for statistical evaluation of the result. Such statistical treatment seemed to be absolutely necessary, because cortical evoked potentials showed considerable variability depending upon the spontaneous activity of the cortex. The horizontal sweep of a cathode ray oscillograph was made

Received for publication May 5, 1953.

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to synchronize with the rhythm of intermittent stimulation so as to superimpose cortical responses to a number of successive flashes. The photoelectric device shown in fig. 1 mediated the synchronization. Except for a transitory phase immediately after the onset of photic stimulation, a standing image of response was established on the screen of the cathode ray oscillograph. All the records shown below were taken at such stationary stages.

RESULTS

1. The effect of the wave-length

Records A and B of fig. 2 were obtained from the surface of the striate cortex, on which one thread electrode was placed, and the other on the skull at a distance of 5 mm. from the former. The downward direction corresponds to the positivity of the electrode on the surface of the cortex. The rate of flicker was 10 cps. for records A, but varied for B. In all records in A, two conspicuous positive deflections are seen, of which the first is the on-response, and the second the off-response. Each positive deflection seems to be preceded by a small negative swing.

We had expected that some effect of the wave-length might manifest itself in wave form of evoked potentials, but in reality, no pattern characteristic of the wave-length could be found in the experiments carried out with spectral lights. The amplitude of potentials, however, was altered in a characteristic
CORTICAL RESPONSE TO COLORED LIGHT

FIG. 2 (left). A: effect of wave-length at a constant frequency of 10 cps. B: effect of flicker frequency. Downward direction corresponds to positivity of the electrode on the cortical surface relative to that placed on the skull.

FIG. 3 (upper). Continuous and broken curves refer to the amplitude of first positive deflection and that of the second respectively. In amplitude is included the breadth of each record. Horizontal chain line represents the breadth of control record so that it represents zero-line of amplitude.

manner as the wave-length was systematically varied. In fig. 3 the amplitudes of positive deflections of records A in fig. 2 are plotted as ordinates against wave-lengths as abscissas. The amplitude was so measured that the breadth of each record was included in the measured amplitude. Therefore, the breadth of the control record which is represented by a horizontal chain line serves as the zero-line. There seems to be no essential difference between the on- and the off-responses (compare the continuous curve with the broken). As can be seen in this figure, the amplitude has a maximum at about 500-520 m\(\mu\). Thus, the spectral distribution shows a close resemblance to the scotopic luminosity curve. Although the maximum of our curves is shifted toward the long wave-length as compared with the maximum of the scotopic visibility curve, this may be due to the situation that the spectrum used in our experiment was not an equal-energy spectrum.

In general, blue light is more effective than red light. This finding is in line with the result of animal experiments by Halstead, Knox, Woolf and Walker, but in disagreement with the results of photic activation of seizure waves in epileptic patients (7, 9). It is, however, to be noted that in the human ex-
experiments, the effectiveness of colored lights was determined with the appearance of epileptiform waves as an index, while the index used in the animal experiments was the so-called driving effect, that is, enhancement of synchronized cortical activity. These two phenomena seem to have some aspects in common such as enhancement of synchronous discharges of cortical neurons and to have some resemblance to each other, but it is not self-evident that they are based on the same mechanism.

Bickford, Sem-Jacobsen, White and Daly (5) proposed a hypothesis that the pathway of the photoconvulsive response may be a diffuse thalamocortical system such as the reticular system, while the photic driving is mediated by the normal visual pathway. This hypothesis receives support from the fact that in photic activation, epileptiform waves appear more prominently in the frontal region than in the occipital, while in the photic driving effect, conspicuous responses are restricted to the visual cortex, as will be mentioned later. The difference in effective wave-length mentioned above also suggests that the two phenomena are based on different mechanisms.

Judging from the spectral distribution of amplitude, the system involved may be regarded as the scotopic mechanism rather than the photopic. In our experiments, the eyes were dark-adapted prior to every measurement. Spectral lights used were not sufficiently strong. These experimental conditions may have been responsible for the scotopic character of the cortical responses obtained. So we attempted to carry out experiments with a steady background illumination, but evoked potentials obtained under this condition were so small in amplitude that no systematic survey of the effect in question could be done. Then we abandoned the use of spectral lights and employed strong colored lights produced by means of filters. The range of transmission, tested spectroscopically with the light-adapted eye, was 620–740 mµ for the red filter, 490–550 mµ for the green filter and 410–490 mµ for the blue filter. These colored lights were so strong that the retina exposed to these lights was sure to become light-adapted in a few seconds.

In fact, some difference in wave form was found among records of cortical responses to these colored lights. Some examples are shown in fig. 4. The record for green light shows a large on-response and a much smaller off-response, while the two kinds of response are not so strikingly different in amplitude from each other in the records for red and blue lights. The latency of the first response is much shorter in the record for green light than in those for red and blue lights. The question is, however, if these differences were caused by the differences in spectral constitution of these colored lights. As the filter-lights used in this experiment were not equated for luminosity, the differences observed above may be due to the differences in luminosity.

In the following experiment the effect of the intensity of light was systematically studied. The result is shown in fig. 4. The top record on the left was obtained with strong white light. This record shows all characteristics of the record for green light in more exaggerated form. The remarkable difference in amplitude between the on- and the off-response and the short latency seem to be characteristic of high luminosity. It deserves attention that at a certain
intensity of white light, a record showing a pattern closely similar to those for red and blue lights was obtained. This finding indicates that the differences among the records for various colored lights were chiefly determined by the differences in intensity. Thus our attempts to find any specific effect of the wave-length have been unsuccessful.

2. The effect of flicker frequency

In another series of experiments the frequency of intermittent stimulation was varied from 4 to 40 cps. An example is shown in B of fig. 2. At lower frequencies, two responses can be seen in each record. As the frequency was raised, the off-response became smaller in amplitude and disappeared at a certain frequency between 10 and 15 cps. Thus only one response per flash appeared at higher frequencies. The responses seen in the records at 15 and 17 cps. are sure to be an on-response, because the beginning of the responses falls within the preceding half-period or light-phase of each cycle.

The critical frequency at which the off-response disappeared seemed to depend upon intensities and other unknown factors.

One may be tempted to interpret the disappearance of the off-response at higher frequencies in terms of refractoriness left behind by the preceding on-response. In such an interpretation, one presupposes that the on- and the off-response involve one and the same group of neurons. There is, however, no experimental evidence for this conception. Far from it, there are some facts suggesting that the on- and the off-response are two independent phenomena. For example, the time course of adaptation is different in such a manner that the off-response declines more rapidly than the on-response during exposure to intermittent photic stimulation. In consequence, two responses per flash appear at the onset of stimulation, but only one response to each flash at later stages.
of stimulation when the frequency is around the critical range for the disappearance of the off-response. They seem to differ from each other also in the property of recruitment; at a certain stage of anesthesia it was found that the on-response which had been silent for a number of flashes began to appear and increased gradually in amplitude to attain a constant level, while the off-response showed itself from the very beginning of stimulation. These findings indicate that the two phenomena develop independently.

The critical flicker frequency at the cortical level has been studied by a number of investigators (24, 4, 15, 2). In our experiment the critical fusion frequency lay between 25 and 35, although it was very difficult to determine the critical frequency precisely with our method. This value of critical frequency is near the value obtained by Walker et al. from the monkey's cortex (24) and falls within the range at which Brecher (6) found intermittent light to fuse for monkeys.

Bartley (3) found that apparent brightness of intermittent light was maximal at a certain definite frequency between 8 and 10 cps. In connection with this finding is noteworthy the fact that the amplitude of cortical responses was maximal at about 10 cps. This optimal frequency seemed to depend little upon the intensity and wave-length of the photic stimulus used. Whether this effect represents the physiological basis of the Bartley effect must await further investigation, because it is possible that the coincidence of the optimal frequencies in both cases is a mere chance.

3. Localization of cortical responses

Much work has been done on the localization of cortical response to photic stimulation (23, 19, 10, 11, 17). In the experiment by Gerard, Marshall and Saul

![Control](image-url)

**Fig. 5.** Localization of responses recorded with bipolar lead. Responses can be seen only in occipital region.
(10), a very large cortical area of the cat yielded responses, best in the occipital, falling off slowly anteriorly, more rapidly, but detectable well into the frontal region. Talbot (23) and Marshall, Talbot and Ades (19) observed that the response appeared over more restricted areas, i.e. the striate and extrastriate areas.

In our experiment, the most marked response was seen over the dorsal surface just forward of the apex of the tentorium. When bipolar lead at an interelectrode-distance of 5 mm. was used, cortical responses were restricted to the striate and extra-striate areas in agreement with the result of the experiment by Talbot et al. (fig. 5), but responses were detectable over very wide areas, when one reference electrode was fixed on the skull and the other was placed at various parts of the lateral surface of the exposed hemisphere (fig. 6). They appeared in the ectosylvian gyrus and the sylvian gyrus which are considered to be auditory areas. They were detectable even in the frontal region, as in the experiment by Gerard et al. These potential variations detectable outside the visual cortex did not seem to be physical artifacts, because there was a certain systematic phase difference between records obtained from any two neighboring areas. This finding suggests that excitation spreads from the visual cortex into neighboring cortical areas through some intracortical pathways.

DISCUSSION

Attempts to find any specific effect of the wave-length upon cortical responses to photic stimulation have been unsuccessful. This cannot be due to
unfavorable adaptation states of the eye, because we are sure that the eye was
in a light-adapted state at least in the experiments carried out with strong
colored lights. It may be supposed that lack of color-receptive mechanisms in
the cat's eye would be a possible cause for the scotopic character of the cortical
response, but such a possibility was ruled out by the experiment of Granit (12)
and by that of Motokawa, Iwama and Ebe (20). Granit measured the sensitivity
of retinal elements to spectral lights and could characterize each element by
its own spectral distribution of sensitivity. Motokawa et al. measured the
electrical excitability of the retina after a brief illumination of the retina with
spectral light and found that color-effects manifest themselves in the time course
of electrical excitability. In both cases spike-discharges of retinal elements were
taken as index. However, spike potentials as such showed no special pattern
characteristic of the wave-length.

Many attempts have been made to find any feature characteristic of the
wave-length in the electroretinogram, but unsuccessful in most cases. Adrian
(1) showed that ERG consists of two components which are supposed to be the
rod- and the cone-process respectively. Motokawa and Mita (21) showed that
the curve representing the amplitude of the b wave plotted against the wave-
length has a maximum shifted toward the long wave-length in moderate light
adaptation as compared with the scotopic visibility curve, and stated that a
minor fraction of the b wave may be due to cones. Karpe and Tansley (16),
Riggs, Berry and Wayner (22) brought forward more evidence that the b wave
of the human ERG is chiefly determined by rods. At any rate, there is little
doubt that rods play a predominant role over cones in electrical manifestations
of the retina, and this may be an important factor responsible for the scotopic
character of cortical responses observed above.

In the experiment by Granit, the color-effects were disclosed by a certain
special means of analysis such as selective preadaptation. Similarly in the ex-
periment by Motokawa et al. retinal processes were analyzed by taking advantage
of the time constants in excitability. It should be remembered that electrical
responses were used as an index of analysis in these experiments. It seems,
therefore, difficult to give any clue to the central mechanism of color vision, so
long as our study is confined to the recording and inspection of electrical re-
sponses of the cortex. We are looking forward to the appearance of some new
means of analysis of visual cortical responses.

SUMMARY

The effects of spectral lights of various wave-lengths upon the electrical
activity of the cat's cortex were investigated. The light was interrupted at
various frequencies by means of an episcotister driven by a motor. The hori-
Zontal sweep of a cathode ray oscillograph was made to synchronize with the
rhythm of stimulation, so that a standing image of responses was established
on the screen.

1. At lower frequencies of flicker, evoked potentials consisted of on- and off-
responses. The latter, however, disappeared above a certain frequency between
10 and 15 cps. The critical fusion frequency seemed to lie between 25 and 35 cps.
2. No pattern characteristic of the wave-length could be found. However, the amplitude of response was altered in a characteristic manner as the wave-length was systematically varied. The spectral distribution of amplitude was found closely similar to the scotopic luminosity curve.

3. When strong colored lights were used, some difference in wave form could be found, but it was shown that the difference was chiefly due to the difference in luminosity.

4. Responses obtained with bipolar lead were restricted to the striate and extra-striate areas. When monopolar lead was used, responses appeared over much wider regions, including the so-called auditory areas. A systematic phase difference was seen between records obtained from two neighboring areas, and this fact suggests that excitation spreads from the visual cortex into surrounding areas through some intracortical pathways.

REFERENCES