On the Flash Light Response Activities in the Visual Cortex of Unanesthetized Cats

Noriyoshi HIROTA*

The 2nd Department of Physiology, Nagasaki University
School of Medicine, Nagasaki, Japan.

Received for publication, March 5, 1965

Single and rhythmic flash light average responses in the visual cortex (lateral gyrus) of immobilized cats by administration of Flaxedil were observed in their time- (Fig. 2C & 3), spatio-temporal- (Fig. 4) and frequency-patterns (Fig. 5B & C).

Four positive negative diphasic average deflections were capable of tracing from a variety of portions in the lateral gyrus, each of which was able to designate, for convenience sake, P1, N1, P2, N2, P3, N3, P4 and N4 respectively (Fig. 3). Their average peak latencies were 21.6, 45.0, 63.4, 78.5, 106.9, 117.3, 154.9 and 178.3 msec respectively, so that P1 and N1 responses were the well-known primary responses. The most conspicuous responses were evoked from the mid lateral gyrus, wherein the early components P1, N1 and P2 due to contralateral stimulus were larger than those evoked by ipsilateral one, but N2 was ipsilaterally dominant. Later components of ipsi- and contralateral responses than N2 were not the same each other in their patterns. Though binocular responses were more prominent than both of ipsi- and contralateral monocular ones, occlusive binocular interaction was revealed in the positive components P1, P2 and P3, whereas facilitatory interaction in the negative components N1, N2 and N3. It was verified in the spatio-temporal average response patterns that primary positive P1 response was unable to observe in the anterior lateral gyrus, but the secondary positive P2 response, which was distinctly and ipsilaterally dominant, was suggested to be an irradiation of P2 in the mid lateral gyrus, in addition, that negative components, N1, N2 and N3 were augmented by binocular stimulation irradiating beyond the extent of responses due to the monocular stimuli to both of anterior and posterior directions.

This research has been made possible through the support and sponsorship (DA-92-S57-FEC-37212) of the U. S. Department of Army, Far East Research Office.

* 広田和子
Though, many reports have published on the evoked cerebral potentials of cat elicited by a flash light stimulus, they contributed chiefly to individualization of primary response components with shorter latencies, whereas few have been elucidated the late responses\(^3,4,8,32\). Recently, it was demonstrated by Sato\(^{16,17,18,19,20,21,22}\), Satô et al.\(^{27,28}\), Mimura\(^{13}\), Ozaki et al.\(^{14}\), Teramoto\(^{30}\), Kitajima\(^{12}\) that the average response time-patterns, i.e. crosscorrelograms of the stimulation and masspotential of various brain sites, and their frequency-patterns (frequency spectra) have an equivalent or broader physiological significance to the excitability cycle of the brain site neighbouring the lead electrode(s). Therefore, observations on the average masspotential responses elicited by mono- and binocular flash light stimuli in the posterior sigmoid gyrus and various portions in the lateral gyrus of unanesthetized cat were performed to elucidate the time-, spatio-temporal- and frequency-patterns of the primary and late responses in relation to binocular interaction.

**METHODS**

Under ether anesthesia, adult cats weighing 2.5-4 kg were mounted on the Johnson type stereotaxic instrument after a tracheal canula was fixed for artificial respiration, then the scalp was opened minimal necessarily to place the silver ball tipped monopolar electrodes on the dura or pia covering the posterior sigmoid and lateral gyri. Reference silver wire electrode was inserted into neck muscle of the animal in a dim-lit electromagnetically shielded room. After the scalp was opened, artificial respiration with oxygen to blow away ether was carried out throughout the experiment and Flaxedil was administrated to immobilize the unanesthetized animal in a rate of 15 mg/kg per an hour through a continuous injector (KN, Natsume Seisakusho), so that fluctuations in the animal conditions were capable of avoiding.

Single or repetitive flash light stimulations were delivered by the photic stimulator (PS-101, San’ei-Sokki Co.). The flash emitted from the strobo flash valve (FT-100, Mazda) was of about 6000°K daylight, 1 Watt per second energy and about 100µsec duration. In front of the flash valve, a frosted glass plate, a shutter with a round iris and a cotton white curtain were placed, through which the beam of the flash light was diffused. The both pupils of the cat were dilated by atropine and placed at the distance of 62 cm from the surface of the strobo flash valve. One of the eyes was covered carefully by a piece of dick and black woolen cloth when a monocular stimulation was delivered.

The intensity of the flash stimulus was delivered through an iris of 50, 100 or 150 mm diameters. Relative intensity of them in logarithmic
scale were 2.1, 2.6 and 2.8 db respectively if the intensity through the iris of 5 mm diameter was taken as 0 db. The bio-information processings in our laboratory for obtaining the average response time-patterns and their frequency-patterns are illustrated in Fig. 1. Masspotentials (EEGs and evoked potentials) and stimulation signal were recorded on magnetic tapes through 8-channel polygraph (RM-150, Nihon-Kohden Co.) and 8-channel data recorder (SPRA-48, Shiroymadenshi Co.) monitoring by ink records through the polygraph. The average response time-patterns were obtained by a simplified method (Sato et al. 196123', 196224') from ink records, through the Pulse Signal Multipurpose Correlator (UCA-26, Sony Co.)26) or the Digital Computer For Data Processing (ATAC-401, Nihon Kohden Co.) from magnetic tape records. The frequency spectra of these average response time-patterns were recorded by the Instant Short Range Spectrum Analyser (ESA-2, Sony Co)33). Not only the average responses in a variety of portions of the posterior sigmoid and lateral gyri respectively, but spatio-temporal response patterns15) were obtained to map equipotential lines on such a plane that the post stimulation time and the above various portions were taken as abscissa and ordinate respectively were also obtained,
Fig. 2. Ink records of brain masspotentials with stimulation signal and average responses obtained by ATAC.
A: control record without flash light stimulation. B: an example of records during 2 per sec flash light stimulation through an iris with its diameter of 100 mm (relative intensity 2.6 db). C: average response time-patterns obtained by 30 summations. PS: posterior sigmoid gyrus. GL: lateral geniculate body. CM: N. centre médian. L: lateral gyrus. Sig: signal of the stimulation. I·EYE, r·EYE & l·r·EYE: left (contra), right (ipsilateral) monocular and binocular stimulations respectively.
RESULTS

1. Temporal patterns of the average responses in the posterior sigmoid and lateral gyri.

By delivering the flash light stimulus at an interval of about 500, 350 or 100 msec, not only the well-known primary positive negative diphasic response with lesser peak latency than 50 msec in average but the late responses with longer peak latencies were capable of obtaining by applying ATAC, UCA and/or the simplified average response analysis\textsuperscript{23,24}. Two examples traced by ATAC and UCA were illustrated in Fig. 2C and Fig. 5A respectively. In the former four positive (downward) and negative (upward) deflections were able to recognize most distinctly at the mid lateral gyrus (Lead L\textsubscript{3}), around which the primary visual area will be located. In the latter, three or two positive and negative ones were observed distinctly in the visual

---

Fig. 3. Combined records of the average response time-patterns.
A: responses elicited by contralateral (left) (hatched lines connecting white circles) and ipsilateral (right) monocular (solid lines connecting black circles) flash light stimulus delivered at the time origin (arrows pointing upward). B: response due to the binocular stimulus (solid lines) and algebraic summations of ipsi- and contralateral responses (hatched lines connecting crosses "+").
cortex (Fig. 5 A, Lead 2, 3, 1 and 4), since the rhythmic flash stimuli were delivered in this instance at the interval of 100 msec. The portion of maximum response was located more posterior than the former example. This difference may be caused by the higher frequency and weaker strength of the stimulation. The first, second, third and fourth positive deflections were designated, for convenience sake, P₁, P₂, P₃ and P₄ respectively, and those of the negative ones nominated for N₁, N₂, N₃ and N₄ respectively (see Fig. 3). Their average peak latencies in five experiments are indicated in Table 1.

Table 1.

<table>
<thead>
<tr>
<th>Cat No</th>
<th>P₁</th>
<th>N₁</th>
<th>P₂</th>
<th>N₂</th>
<th>P₃</th>
<th>N₃</th>
<th>P₄</th>
<th>N₄</th>
</tr>
</thead>
<tbody>
<tr>
<td># 41</td>
<td>24.6</td>
<td>41.4</td>
<td>63.1</td>
<td>81.1</td>
<td>100.2</td>
<td>117.3</td>
<td>145.8</td>
<td>178.3</td>
</tr>
<tr>
<td># 35</td>
<td>18.7</td>
<td>51.1</td>
<td>64.0</td>
<td>77.8</td>
<td>94.0</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td># 37</td>
<td>29.0</td>
<td>54.4</td>
<td>66.6</td>
<td>80.0</td>
<td>110.5</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td># 58</td>
<td>20.0</td>
<td>38.0</td>
<td>-</td>
<td>75.0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td># 58</td>
<td>23.0</td>
<td>40.0</td>
<td>60.0</td>
<td>-</td>
<td>123.0</td>
<td>-</td>
<td>163.0</td>
<td>-</td>
</tr>
</tbody>
</table>

Average 21.6 45.0 63.4 78.5 106.9 117.3 154.9 178.3

Here the flash light stimulation of 10 and 7.7 per sec were delivered respectively to the cat # 35 and # 37, so that N₃ and more late responses were unable to recognize. It would be obvious from the results in Table 1 that the responses P₁ and N₁ are the well-known primary diphasic response and other responses would be the late secondary ones. Though the primary positive response P₁ with its peak latency of 20 –30 msec was not brought out in response to ipsi-, contralateral monocular and binocular stimuli at the anterior portion of the mid lateral gyrus (Lead L₄) and the posterior sigmoid gyrus (Lead PS) (see Fig. 2 C), more late positive and/or negative responses were exhibited. This evidence in the anterior portion of the mid lateral gyrus would suggest one of the properties in the secondary visual area.

2. Average response elicited by mono- and binocular flash light stimulus.

The average response curves brought out by ipsi- and contralateral monocular flash stimuli in Fig. 2 C were combined to compare easier the both responses, as illustrated in Fig. 3 A. It was revealed in this combined records that the P₁, N₁ and N₂ responses at the mid
Fig. 4. Spatio-temporal average responses mapped out equipotential lines. 
lateral gyrus (L3) were elicited more prominently by the contralateral (left) monocular stimulus than those by the ipsilateral (right) monocular one, whereas more late N2, P3 and P4 responses due to the ipsilateral stimulus were more enhanced. Similar tendency on the P1, N1 and P2 responses was also observed in the posterior portion of the lateral gyrus (Lead L2).

It was found by comparing the average response elicited by binocular stimulus at the mid lateral gyrus (L3) with those of the algebraic summation of the average response due to ipsi- and contralateral monocular stimuli (Fig. 3B) that the positive responses P1, P2 and P3 were smaller than those of the latter, whereas negative responses N1, N2 and N3 in the former were higher than those of the latter. Therefore, occlusive and facilitatory binocular interactions were suggested respectively in the positive and negative responses at the cerebral primary visual area. However, the responses P1, N1 and P2 due to binocular stimulus at the posterior mid lateral gyrus were the same as those of algebraic summations. Hence, no binocular interaction was observed at this portion. More late responses N2, P3 and N3 at this portion were, on the contrary, the same binocular interactions as those at the mid lateral gyrus (L3) were observed. In the dorso-lateral gyrus (Lead L1), the primary P1 and N1 responses due to binocular stimulus were the same in their amplitudes of the algebraic summation to suggest no binocular interaction, whereas P2 and N2 responses of the former were more prominent than the latter to suggest facilitatory binocular interaction.


The spatio-temporal response patterns mapped out equipotential lines of the average response, which were derived from the data in Fig. 2C and Fig. 3, are illustrated in Fig. 4. The time origin of the abscissa is the time point of the flash light stimulus delivery.

It was verified in Fig. 4 that the primary responses P1 and N1 were elicited more prominent by the contralateral monocular flash light stimulus than the ipsilateral one around the mid lateral gyrus (L3), and the second positive response P2 was also the same. On the contrary, the late response N2 elicited by the ipsilateral stimulus was rather more considerable. In addition, the second surface positive response P2 was induced by the same stimulus relatively higher in the anterior portion of the lateral gyrus (L3) and the posterior sigmoid gyrus (PS).

It was also verified that the binocular flash stimulus drove not only more regular and remarkable evoked potential of the primary (P1, N1) and more late responses (P3, N2, P3, N3, P4 and N4). They extended to both of anterior and posterior directions to indicate the irradiation of
Fig. 5. Crosscorrelograms of flash light stimulation and masspotentials and their frequency spectra. A: crosscorrelograms of 10 per sec flash light stimulation and masspotentials in a variety of somatosensory and visual cortex. B: frequency spectra of the crosscorrelograms. C: peak heights of the response in the frequency spectra in relation to the locations of leading electrodes. 1, r and 1·r: response peak heights due to left (contra-), right (ipsilateral) and binocular stimulations. 1 + r: summations of peak heights due to both monocular stimulations. White circles in the bottom are the summation of the peak at the stimulating frequency only. At each location, peak of the (first) high harmonic frequency was placed on the head of the peak at the stimulating frequency.
4. Average response frequency patterns.

When the stimulation to evoke masspotential is delivered rhythmically, wave like evoked potentials of the stimulating frequency and/or its high harmonic frequency are driven, as illustrated an example in Fig. 5A and B. In the frequency spectra of the rhythmic average response, average intensities of the response activities are indicated by the height of the peak at the stimulating frequency and its high harmonic frequency. Summation of these peak heights, therefore, express the total activity evoked by the rhythmic stimulation. When the response activities at a variety of the portions in the lateral gyrus and posterior sigmoid gyrus were arranged in spatial order, two groups of response activities were revealed, one was in the visual area (Lead 1, 2, 3 and 4) and other one was in the somatosenory area (Lead 6 and 7).

DISCUSSION

Forbes and Morison (1939) studied on the cerebral evoked potential with long latency brought out by a stimulus to sciatic nerve of cat under deep barbital anesthesia and discriminated from the primary response to designate the "secondary response". Thereafter, many investigators have tried to individualize wave components in the evoked potentials of short latencies due to visual stimulation or stimulation to the optic pathway and few have been elucidated the late responses, on which there are some discrepancies in their opinions. Tores and Warner (1962) described two types of the late responses designated Type I and II in unanesthetized and immobilized cat with Flaxedil, i.e. the late response preceded by the primary response (Type I) and that without preceding the primary response (Type II). And they reported the primary response was exhibited with its latency of 25.6 msec and the late response of Type I and II were elicited with their latencies of 58.4 and 79.2 msec respectively. However, they did not analyse precisely the wave form of these evoked potentials, since they observed the potentials by superimposition of 10 – 15 sweeps of the cathode ray oscilloscope. On the contrary, average response time-pattern derived from the summation of the masspotential under the basic principle of the average response analysis (Sato et al. 1961, 1962, Sato 1964) by means of the digital computer (ATAC 401) or the pulse signal multipurpose correlator (UCA-26) traced a regular wave form composed of four pairs of positive and negative diphasic deflections, which were able to designate P1, N1, P2, N2, P3, N3, P4 and N4 respectively. They
were most prominent by contra-, ipsilateral monocular and binocular flash light stimulations in the mid lateral gyrus (Fig. 2C, Lead L_3). This evidence coincided with the results obtained by Doty (1958)\textsuperscript{9}). Here, P_1 and N_1 are the well-known primary response and P_2 and N_2 yielded in the primary visual area, which will be located around the positions of the lead electrodes L_3, L_2 and L_1 in Fig. 2C, coincided with the type I late response by Torres and Warner, whereas those elicited in the anterior portion of the mid lateral gyrus (Fig. 2C, L_4) will be corresponded to the Type II response, since P_2 and N_2 responses at this portion did not preceded by P_1 and N_1 responses. However, it was revealed by obtaining the spatio-temporal average response pattern that these Type II late responses were spatial extention of P_2 and N_2 followed by the primary response elicited in the primary visual area (mid lateral gyrus L_3). Buser and Borenstein (1957)\textsuperscript{8}) reported that the secondary association responses localized to the surface of the association cortex seemed to occur independently from those of the primary projection cortex. These responses would also be corresponded to the P_2 and N_2 responses in the anterior mid lateral gyrus (Lead L_4), which was verified an extension of those in the mid lateral gyrus. Though Brazier (1963)\textsuperscript{9}) demonstrated such a temporal variety of the late responses in the specific visual projection cortex of unanesthetized cat that they began to fail on stimulus repetition, different patterns of the late response in various portions in the visual cortex (L_1, L_2 and L_3 in Fig. 2C) revealed their spatial variety.

As already Burns (1960)\textsuperscript{7}), Auerbach (1961)\textsuperscript{10}), etc. demonstrated, the average responses elicited by the binocular stimulation were larger than those by contra- and ipsilateral monocular stimulations. Though the primary (P_1 and N_1) and relatively fast response P_2 were elicited larger by contralateral monocular stimulation than those by ipsilateral one, as hitherto pointed out (Burns\textsuperscript{7}, Auerbach\textsuperscript{10}, etc.), the reverse was the case of N_2 response. However, it was suggested in the evidences in Fig. 5B and C that the above contralateral dominant activity will not always the case. There seemed to be some contradiction to the report that 33 % of the optic nerve fibers were uncrossed and the rest were crossed\textsuperscript{2} and more cerebral neurons were discharged by contralateral stimulus\textsuperscript{7,11}). However, there are such possibilities that all optic fibers would be not necessarily contribute to enhance the masspotential response and this response is not necessarily to keep pace with unit discharges. Though Auerbach\textsuperscript{10}) demonstrated that the primary response due to binocular stimulus is the same in its magnitude as the algebraic summation of those elicited by crossed and uncrossed responses, the binocular P_1, P_2 and P_3 responses in the mid lateral gyrus (Fig. 3B, L_3) were lower than the respective algebraic summations, i.e. occlusive binocular interaction was observed, wheres the binocular responses N_1,
N₂ and N₃ were facilitatory binocular interaction. Interactions in the average masspotential responses have already demonstrated by paired stimulation of the flash light and cutaneous electric shock stimulations (Teramoto 1964), by those of the flash light and click stimulations (Brazier 1961) and even some such evidences were demonstrated by Sato et al. 1957, 1960, 1961, Sato 1964, Sonoda, Kitajima that alpha blocking phenomenon in the spontaneous EEG caused by a rhythmic flash stimulation is capable of considering as the interaction of the flash and natural afferent inflows to induce spontaneous alpha wave. In addition, interactions in the unit discharges of visual cortex were also reported (Burns, Hubel, etc.). These interactions including binocular ones will have important unknown physiological significances for man and animal life.

ACKNOWLEDGMENT

The author wishes to express his cordial thanks to Prof. Kensuke Sato for his kind guidance, encouragement and help for preparing this manuscript. Thanks are due also to the staffs of the 2nd Dept. of Physiology.

REFERENCES


19) Sato, K.: On the role of thalamic nuclei and reticular formation upon the generation of the electroencephalogram and myotonogram. I (1963) and II (1964), Nagasaki.


