On the Flash Impulse Responses in the Visual System of Unanesthetized Cat as Related to the Stimulus Intensity

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Received for Publication June 1, 1966

The ERG and average evoked masspotential in the optic tract, lateral geniculate body, optic radiation and cerebral cortex (suprasylvian and lateral gyri) in response to mono- and binocular flash stimulus to atropinized eye (s), were studied in cats which were unanesthetized but immobilized by administration of Flaxedil. The size of the initial primary and later response components and the total activities in the frequency spectra of auto-correlograms of the masspotentials (power spectra of the masspotentials) were studied in relation to the stimulus intensity. As the flash stimulus was increased, reduction of the latency, increment of the size of the response and complication of the wave form were observed. An occlusive binocular interaction was seen in the responses at a variety of brain sites. This interaction in relation to the stimulus intensity was more complicated, the higher the level of the brain site was in the visual system. Not only an occlusive interaction but a facilitatory interaction was also exhibited in the visual cerebral cortex.

Reduction of the peak latency and increment of the wave size proportional to the stimulus intensity in logarithmic scale were seen in the a- and b- waves with 15–30 msec and 55–70 msec peak latency, respectively, in the ERG, as well as in the initial surface positive and negative primary components with 12–35 msec and 15–55 msec peak latency, respectively, in the above various brain sites. However, only the peak latency of the later response components, which were time-locked with the stimulus in the range of 70–120 msec, showed proportional relation to the logarithmic intensity of the stimulus. No finite tendency was brought out in either the peak latency or amplitude of the later response components of more than 120 msec peak latency in relation to the logarithmic strength of the stimulus. The total activity on logarithmic scale in the power spectra of the masspotentials were related linearly to the logarithmic intensity of the flash stimulus. The gradient of the linear relationship of the ERG was distinctly steeper than that of the cerebral visual cortex.

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Recently, the fundamental concepts in physiology concerning the intensity, time and slope factors of an effective stimulus to living organisms were reevaluated by Sato et al.\textsuperscript{(34)(36)(37)(38)(42)} and Sato et al.\textsuperscript{(46)} from the standpoint of "system analysis" (Trimmer)\textsuperscript{(54)}. It was demonstrated that the extended property of the excitability, designated as the "activity" or "transforming action", of a physiological element or system can be given quantitatively by the size of its response and the intensity of an arbitrary superthreshold stimulus which is delivered. The size of this response can be determined by taking the size of the response to the threshold stimulus as unity. Here, the amount of the activity of the element or system can be given by dividing the size of the response by the stimulus intensity. As a further extension, it was inferred by the above authors (Sato et al.\textsuperscript{(46)}) that the impulse response and frequency response of a physiological system are none other than the above activity in the time and frequency domains, respectively. In the experimental situation, the human EEG activities (Sato\textsuperscript{(31)(32)(33)(35)(39)(40)(41)(42)}; Sato et al.\textsuperscript{(44)(45)(46)(47)}; Mimura\textsuperscript{(27)}; Mimura et al.\textsuperscript{(29)}; Ozaki et al.\textsuperscript{(30)}; Sato and Kitajima\textsuperscript{(43)}) and the masspotential activities of the cerebral cortex and subcortical structures of rabbit (Mimura and Sato\textsuperscript{(28)}) and cat (Teramo\textsuperscript{(53)}; Hirota\textsuperscript{(14)}) have been studied in terms of the frequency responses and average response time-pattern (crosscorrelograms between the stimulation and masspotential, and autocorrelograms of masspotential responses). Kitajima\textsuperscript{(19)}, and Sato and Kitajima\textsuperscript{(43)} have observed a typical instance where the spontaneous EEG activity of 10 cps and the driven EEG activity of the stimulating frequency along with its high harmonic due to photic flicker stimulation, which could be clearly seen in the frequency spectra of the autocorrelograms of the EEGs, were depressed and augmented, respectively, in linear relation to the logarithmic intensity of the stimulation. On other instances, augmentation of the spontaneous EEG activity and/or depression of the driven EEG activity occurred by increasing the stimulus intensity. Many reports have been made on the evoked responses or unit discharge responses in the visual system in relation to the stimulus intensity. These include the observations on the frog retina by Hartline\textsuperscript{(12)}, cat retina by Kuffler\textsuperscript{(21)}, Wohlgemuth\textsuperscript{(57)}, Brown and Wiesel\textsuperscript{(6)}, the optic tract of cat by Lennox\textsuperscript{(22)(23)}, the lateral geniculate body of cat by Erulkar and Fillenz\textsuperscript{(10)}, the visual cortex of cat by Madsen and Lennox\textsuperscript{(25)}, Van Hoff\textsuperscript{(55)}, the ERG and visual cortex of cat by Lennox and Madsen\textsuperscript{(21)}, Auerbach et al.\textsuperscript{(1)}, the visual cortex of rabbit by Bartley\textsuperscript{(2)(3)}, Mimura and Sato\textsuperscript{(28)}, and the human cortex by Ebe and Mikami\textsuperscript{(9)}, Wick et al.\textsuperscript{(56)}, Keidel\textsuperscript{(18)}. However, there is little data on cat that include the masspotential average activities at various levels of the cat visual system. In this study, therefore, attempts were made to elucidate the impulse response activities in the average masspotential in relation to the intensity of mono- and binocular flash stimulation, at various levels of the
visual system (the retina, optic tract, lateral geniculate body, optic radiation and visual cortex) in cat which were unanesthetized but immobilized by Flaxedil administration.

METHOD

Eight adult cats, weighing about 3 kg, were used in this study. Each animal was mounted under ether anesthesia on a JOHNSON'S type stereotaxic instrument after a tracheal cannula had been attached for artificial respiration with oxygen-mixed air. Then, after subcutaneous administration of 0.5% procaine to avoid pain sensation, an opening as small as possible was made in the skull for placement of silver ball tipped monopolar electrodes of 0.5 mm diameter onto the dura or pia of the cerebral cortex (lateral and suprasylvian gyri) and for insertion of steel or nicrome wire (Gauge 22 and 24) mono- and bipolar depth electrodes, insulated except at their tips, into a variety of subcortical structures (optic tract, lateral geniculate body and optic radiation).

The location of the tip of each depth electrode was ascertained by histological examination using KLÜVER-BARRERA'S staining method (1953) after completion of the experiments. Both pupils of the animal were dilated by corneal administration of 2% atropine sulphate.

After the skull was opened, inhalation of ether was ceased in place of which artificial respiration with oxygen-mixed air was continued throughout the experiment. To immobilize the animal, Flaxedil was administrated intraperitoneally through a continuous injector (KN, Natsume Seisakusho) at a rate of 15 mg/kg per hour or was injected 20 mg/kg every two or three hours intraperitoneally.

Flash stimulus of about 6000°K daylight, 1 Watt/sec, and about 100 μs duration, emitted from a strobo flash bulb (FT-100, Mazda) attached to a photic stimulator (PS-101, San'ei Sokki Co.) was used. The flash bulb was placed in a box so that the flash beam would be delivered in only the forward direction. A frosted glass plate was placed before the flash bulb, and 2 cm in front of this was set a shutter with a round iris. Further, a white cotton curtain was hung at the distance of 12 cm through which the flash was diffused. The intensity was varied by changing the diameter of the iris in eight steps; 5, 10, 15, 20, 30, 50, 100 and 150 mm, respectively. The animals were placed so that the eyes would be 50 cm away from the white curtain. One eye was covered carefully by a piece of thick, black woolen cloth when monocular flash stimulus was to be delivered. The flash which passed through the iris of various diameters were transformed to photoelectric potentials by a photoelectric cell and the relative amplitude of this potential was measured by a cathode ray oscilloscope (VC-7, Nihon Kohden Co.) attached to an amplifier (AVB-2) (SATO and KITAJIMA 1965). When the relative intensity of the flash through
the iris of 5 mm diameter was taken as 0 on a logarithmic scale, those through the iris diameter of 10, 15, 20, 30, 50, 100 and 150 mm were 0.8, 1.1, 1.4, 1.7, 2.1, 2.6 and 2.8, respectively.

The masspotentials (ERG, EEGs and evoked potentials) in the retina and various brain sites, and the signals of the flash stimuli were simultaneously recorded on 1/4 inch magnetic tape through a 8-channel polygoph (RM-150, Nihon Kohden) or a 8-channel electroencephalograph (EG-803, San’ei Sokki), and a 8-channel (SPR-48, Shiroyama Tsūshin) or a 3-channel (TPW1-3, Shiroyama Tsūshin) data recorder. Monitoring was done by inkrecords through the polygraph or electroencephalograph and sweeps of two four-beam cathode ray oscilloscopes (VC-6, Nihon Kohden). Magnetic recordings of ERG and brain masspotentials were taken by the PWM method and the flash stimulation signals by the FM method.

The average response time-patterns (crosscorrelograms between the flash stimulation and masspotentials) over a 50 sec length of the magnetic record and those by 50 summations, and the average time-patterns (autocorrelograms) of the masspotentials in a 35 sec length of the magnetic record were automatically obtained, respectively, by using a Multipurpose Pulse Signal Correlator (UCA-26, Sony Corp.), a Computer For Data Processing (ATAC-401, Nihon Kohden) or an Analogue Magnetic Correlator (CCA-22, Sony Corp.). This Multipurpose Pulse Signal Correlator had been developed originally in our laboratory (SATO et al. 1962)⁴⁸ to perform not only formal auto- (SATO et al. 1962)⁴⁸ and crosscorrelation analysis but also average response analysis (SATO et al. 1962)⁴⁸ and simplified auto- and crosscorrelation analysis (SATO 1962⁴⁸, SATO et al. 1962⁴⁸, SATO et al. 1962⁴⁸, SATO et al. 1962⁴⁸).

The frequency spectra of the above autocorrelograms were obtained by 201-ordinate harmonic analysis through the Parametron Digital Computer (MI-B, Electrical Communication Institute, Tokyo), wherein the time series sampled from the autocorrelograms were punched onto oiled paper tapes for the computer (MI-B) by 6-unit Perforator (KY-8069, Oki Electric Ind. Co., Tokyo) and the Transmitter (KC-30072, Oki Electric Ind. Co.).

RESULTS

1) General view of the flash impulse responses at various levels.

ERG. Though the ERG records led from the corneal lead were contaminated by irregular background fluctuation (Fig.1Y), clear-cut regular ERG curves were obtained by tracing the crosscorrelograms between the stimulus signals and the contaminated records through the pulse signal correlator (UCA-26) or the digital computer (ATAC-401), as illustrated in Fig. 1Z, r-ERG. Between weak to intermediate intensities, the negative a-wave of 15 – 24 msec peak latency and the
positive $b$-wave of 56–66 msec peak latency grew slowly in their amplitudes by increasing the intensity of the flash stimulus. Thereafter, intermediate to strong intensities accelerated increase occurred by increasing the stimulus.

Optic tract. In the optic tract (Fig. 1Z, r-TO), near the optic chiasm, a prominent negative shift preceded by a less prominent initial positive one with onset latency of 10–15 msec were elicited by ipsi- and contralateral monocular stimuli. This negative response was accompanied by a positive response of longer duration, upon which several wavelets were superimposed during contralateral (left) monocular stimulus. The more intense the stimulus was, the more reduced was the onset latency of the initial positive response and the more remarkable was every

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**Fig. 1** Masspotential ink records and average flash responses at a variety of levels in the visual system of unanesthetized cat.

Y : left ; control ink records without flash stimulus. Middle and Right ; ink records during flash stimuli of 1.5 per sec through iris, 20 mm and 150 mm in diameters, respectively. Time mark : 1 sec. r-SS : right suprasylvian gyrus. r-L : right lateral gyrus. r-GL(A) : A-layer of right lateral geniculate body. r-RO : right optic radiation. r-TO : right optic tract. Depth electrodes were monopolar steel wire leads. r-ERG : right electoretinogram between the cornea and apex of nose. Sig. : stimulus signals. No stimuli were delivered in the control (left) record.

Z : average flash impulse response of 50 summations at various stimulus intensities (Analysis time 500 msec). C (top line) : control without stimulus. Numerals (D-5, 10, 15,......, 150 mm) on the left ; iris diameters. 1-eye, r- and b- ; left, right monocular and binocular flash stimulus, respectively.
response component. The second positive component during contralateral and ipsilateral monocular stimuli preceded to a negative swell with a crest at about 200 msec. Some obvious differences were observed in the case of binocular stimulus. Though a negative swell was also clearly observed during weak binocular stimuli (at iris diameter of 5, 10 and 15 mm) only a slight swell was suggested during intermediate (20, 30, 50) and intense (100, 150) stimuli. The initial positive shift was more prominent than that due to monocular stimulus and two negative spiky responses, which seemed to have occurred due to the separation of the highest negative response during the monocular stimulus, were observed.

Lateral geniculate body. The depth electrodes in the lateral geniculate body (GL) were located in the A and B layers, where contralateral optic fibers terminate, and not in A1 where ipsilateral optic fibers terminate (Cohn 1956). No electrode was located in the intralaminar zone, which receives binocular optic nerve fibers (Hayhow 195813). The lateral geniculate responses depicted in Fig. 1, r-GL (A), were led from the A layer. The contralateral responses in this case were much more remarkable than the ipsilateral responses. The initial positive shift with onset latency of 10–13 msec did not appear in the latter, but were elicited in the former and binocular responses. The stronger the flash light stimulus was, the first negative hump elicited by the weakest contralateral stimulus became more pointed and higher with less peak latency which suggested a more synchronized response. The contralateral first negative response was followed by several wavelets with weak stimuli (D 5 and 10). However, with moderate and strong stimuli, the second (or third) wavelet was enhanced predominantly and the two or three wavelets that followed were depressed due to occurrence of a slow and deep positive response. In the contour of the ipsilateral response, however, only the first negative response was induced relatively regularly suggesting that no direct afferent impulses may be flowing into the A layer. A second negative response also was observed by intermediate and intense stimuli. In the situation of binocular stimuli, the negative hump which was elicited by the weakest stimulus and which was preceded by an initial positive shift, seemed to be separate into two by other stimuli and build up with increasing intensity of the stimulus.

Optic radiation. The average contralateral response in the optic radiation (r-RO), about 2 mm above the GL, was approximately similar to the contralateral r-GL response, whereas the average ipsilateral response were irregular with respect to the stimulus intensity. The obvious responses brought out by binocular stimulus were the initial positive shift and first negative swell. Both were built up with increasing stimulus intensity.

Lateral gyrus of the cerebral cortex. An initial surface positive wave
with onset latency of 11–15 msec was brought out in the average response led from the midportion of the lateral gyrus, where the maximal potential is evoked (A-region by DOTY 1958\(^3\); L\(_3\) by HIROTA 1964\(^4\)). This initial positive response was followed by a negative response. Following this response, two or three positive and negative responses were observed, as already reported by HIROTA (1964)\(^4\). The more prominent the initial positive response was, the stronger was the stimulus.

2) Binocular interactions.

Except for the responses in ERG (a- and b-waves), the shortest, intermediate and longest onset and peak latencies of the initial response were brought out in each of the more central sites rather than in the retina by binocular, contralateral and ipsilateral monocular stimuli, respectively. The response amplitude with the shortest or the longest latency was the highest or the lowest, respectively, in general. These relationships became more evident with stronger stimulus. In the late response components, however, no such consistent relation was observed. The response amplitudes of the initial and late response components in every site of the visual system (TO, GL, RO and L), except for the ERG in retinal response, were the highest with binocular stimulus and the lowest with ipsilateral monocular stimulus. An augmentative (facilitatory) or depressive (occlusive) binocular interaction will be verified if the summation of the responses to contra- and ipsilateral monocular stimuli is lower or higher than the response to the binocular stimulus (Fig. 2).

![Fig. 2 Average impulse responses elicited by mono- and binocular flash stimuli.](image)

Dotted response: algebraic summation of the responses to left (contralateral) and right (ipsilateral) monocular stimuli. Abbreviations see Fig. 1.

No binocular interaction was revealed in the ERG, since algebraic summation of the ERGs elicited by both contra-and ipsilateral monocular flash stimuli of various intensities were almost the same as that by binocular stimuli (Fig. 1, r-ERG).

No binocular interaction was verified in the initial positive response in the optic tract (TO), optic radiation close to the A layer of the
lateral geniculate or in RO(D) about 2 mm above the GL, whereas occlusive interaction was observed in many of their late response components.

The response components in the cerebral visual area (lateral gyrus, L) elicited by contralateral monocular stimulus were higher in general than those by ipsilateral monocular stimulus, while those by binocular stimulus were lower than the summation of the components except the second negative one in monocular stimuli (Fig. 2, r-L).

Though no obvious binocular interaction was brought out in the initial positive response in the lateral gyrus by strong stimulus, occlusive depression was verified by intermediate and weak stimuli. And occlusive binocular interaction was demonstrated in the first negative response to all stimuli, whereas facilitatory binocular augmentation was brought out in the second negative response by weak and intermediate stimuli but not by strong stimulus, which induced occlusive binocular depression.

3) Onset and peak latency.

An obvious a-wave in the ERG could be observed with strong stimulus and its onset and peak latencies were 8 msec and 15–24 msec, respectively. The latter was reduced in inverse proportion to the intensity of the stimulus as the intensity was increased. The peak latency of the b-wave in the ERG was 56–66 msec. As the stimulus was intensified, it lengthened at first to a maximum at an intermediate stimulus, thereafter it was reduced by further intensification of the stimulus (Fig. 3, r-ERG). However, in some instances, it was reduced linearly in inverse relation to the logarithmic strength of the stimulus. The c-wave, which is considered as originating in the cells of the pigment layer, was hardly identified, but its presence was suggested in some instances by the positive plateau with a gentle slope preceded by a negative valley. When the intensity of the flash stimulus was increased, the peak latency of the negative valley (Fig. 3, r-ERG, S) showed no change by weak or strong stimuli, but grew considerably longer by intermediate stimuli.

The onset latency of the response in the optic tract (TO) was 10–15 msec. The peak latency of the initial, second and third negative responses, i.e. those of the response components within 100 msec, were reduced with increasing stimulus intensity, whereas those of the later components produced in the range of 100–200 msec lengthened with weak to intermediate stimulus and then tended to shortened by further increase of the stimulus intensity. The peak latencies of these response components coincided with the slow negative deflection which is preceded by the b-wave in the ERG.

Not only the initial response with onset latency of 10–13 msec but the later positive and negative response components in the lateral
FLASH IMPULSE RESPONSE OF CAT BRAIN

Latercy and Peak-Latency Curves

Ly: Latency
P: Positive Wave
N: Negative Wave
p: Slow Positive Deflection
n: Slow Negative Deflection
S: Slow Negative Deflection of ERG

Fig. 3 Onset and peak latencies of the flash responses at various sites in the visual system in relation to the logarithmic intensity of the binocular stimulus.

Abscissa: latencies in msec. Ordinate: logarithmic intensity of the flash stimulus. Numerals of the ordinate are the diameter of iris, through which the flash stimulus was delivered. Ly: onset latency. P, N, p and n, respectively, are the peak latencies of the positive, negative, slow positive and slow negative responses. S: peak latency of the slow negative deflection of ERG. P1 and P2 are the first and the second positive responses. N1, N2, ..., N6 are the first, second, ..., sixth negative responses, respectively. In the optic tract (TO), no responses corresponding to the P1 and N1 responses in the lateral geniculate body (GL) were seen. Three different trends in the latencies with respect to the stimulus intensity are seen, i.e. the trend in the latencies shorter than 70-120 msec, that in the range of 170-200 msec and that in the longer latencies. Abbreviations see Fig. 1.

geniculate body (GL) elicited within 80 msec showed reduction of their peak latencies with increasing strength of the stimulus. On the contrary, components later than 80 msec peak latency showed that the later
the appearance of the response components was, the more irregular were changes in the peak latencies in relation to the stimulus intensity.

In the optic radiation (RO), the initial response was elicited with onset latency of 11–15 msec and the response components brought out within 70 msec showed reduction of their onset and peak latencies as the stimulus was increased. However, some of later components appearing within 170 msec showed reduction and others showed extension of their peak latencies with increasing stimulus intensity. The peak latency of the even later responses (n) showed irregular fluctuation in relation to the stimulus intensity.

The first, second and third positive deflections, etc., in the response of the cerebral lateral gyrus were designated, for convenience sake, P₁, P₂, P₃, etc., respectively, and those of negative ones were named N₁, N₂, N₃, etc., respectively, as done previously by Hirota (1964)¹⁴. In relation to the onset and/or peak latencies of the above components in the lateral gyrus, similar designations were given to every response component in other sites at various levels of the visual system.

The response in the lateral gyrus (L) was initiated at an onset latency of 11–15 msec, and the onset and peak latencies of the positive and negative responses produced within 120 msec were reduced in approximately proportion to the logarithmic scale of the strength of the stimulus, whereas those of later responses appearing within 170 msec were lengthened at first and thereafter reduced by increasing the stimulus intensity. More later responses showed irregular changes in their peak latencies in relation to the stimulus intensity.

In the suprasylvian gyrus (SS), the response was initiated with an onset latency of 11–21 msec. The onset latency of the initial response and the peak latencies of the later responses, which were brought out within 120 msec, became shorter in proportion to the intensity of the stimulus. More later responses showed changes resembling that in the peak latencies of the lateral gyrus.

4) **Response amplitude.**

The amplitude of the b-wave in the ERG and the trough to peak amplitude of the primary positive and negative responses, at various brain sites brought out by the strongest binocular stimulus were taken as 100 % and the relative amount of the amplitudes of not only these response but also the later responses were plotted in relation to the logarithm of the stimulus intensity (Fig. 4). The amplitude of the primary response was considerably larger than those of late response components and the gradients of the curve of the ERG and that of the primary response of the optic tract (TO) tended to increase as the stimulus was intensified, whereas those of the optic radiation (RO (D)) about 2 mm about the lateral geniculate body and the lateral gyrus (L)
Fig. 4 An example of the relative amplitudes of the various impulse response components in Fig. 2 elicited by binocular flash stimulus at various level of the visual system in relation to the intensity of the stimulus.

Abscissa: logarithmic intensity of the stimulus. Ordinate: relative trough to peak amplitude of the diphasic responses. The amplitude of the response due to the strongest stimulus (iris diameter 100 mm.) was taken as 100%.

The initial response amplitudes (a-b in r-ERG, P2-N2 in r-TO, and P1-N1 in r-RO and r-L) were strikingly higher than those of the later responses and grew up as the stimulus intensity increased, whereas the responses did not show any regular tendency.

Fig. 5 Relative amplitude of the average of the first diphasic responses in relation to the logarithmic intensity of the flash stimulus.

Abscissa: logarithmic intensity of the flash stimulus. Ordinate: relative trough to peak amplitude in the average of the initial diphasic responses (a-b in ERG, P2-N2 in TO, and P1-N1 in RO, L and SS). The response amplitude elicited by the weakest stimulus was taken as 100%. The slopes of the curves were in the order of ERG, TO, GL, RO, L and SS.

were decreased. On the contrary, the amplitude of the late response components were variable in their behaviour: some were increased by intensifying the stimulus, though their gradients were lower than that in the primary response, while others were inversely related to the stimulus intensity and the rest showed no obvious changes in relation to the stimulus intensity on logarithmic scale.

In order to draw further inferences on the differences in the primary response in a variety of brain sites, the response amplitude brought out by the weakest stimulus was taken as 100% (Fig. 5). It was found that with increasing intensity of the binocular stimulus, the amplitudes
of the $b$-wave in the ERG and the optic tract were built up exponentially in relation to the logarithmic intensity of the stimulus, though the latter gradient of build-up was lower than the former. On the other hand, the other structures (lateral geniculate body (GL), optic radiation (RO), lateral gyrus (L) and suprasylvian gyrus of cortex (SS) were built up linearly with far less gradient. These gradients were the highest in GL, followed by RO. The gradient in L was slightly lower than that in RO and was the lowest in SS.

5) Autocorrelogram and its frequency spectrum of ERG and brain masspotential.

Shown in figure 6 are the autocorrelograms of the ERG (r-ERG) and the masspotential led from the lateral gyrus (r-L) in the experiment where repetitive binocular flash stimuli were delivered about every 0.7 sec at a variety of intensities. In the former autocorrelograms, only a trace of rhythmic swells was seen about every 0.7 sec superimposed on an almost flat background pattern in the case of stimuli delivered through iris diameters of 5 and 10 mm, whereas repetitive swells clearly appeared when the stimuli were delivered through iris diameters of 30 and 100 mm. In the latter autocorrelograms, on the contrary, rhythmic swells of about every 0.7 sec were observed in all four instances. In those autocorrelograms in which repetitive rhythmic swells appeared, the first swell at the time origin ($t=0$) was considerably higher than the others, while the second and later swells were all of the same size suggesting a consistent response, as already demonstrated by SATO (1963)$^{39,40}$, and SATO and KITAJIIMA (1965)$^{43}$.

The fact that the rhythmic swells with the frequency of the repetitive rhythmic stimuli are all the same size in an autocorrelogram suggests the disappearance of irregular background potentials by the autocorrelation procedure. The more intense the repetitive flashing light stimuli, the higher were the rhythmic swells of ERG and lateral gyrus (r-L). All peaks at the stimulation frequency (approximately 1.5 cps) and their high harmonic frequencies in the frequency spectra of the above rhythmic swells in the autocorrelograms indicate the
amount of activity in response to the experimental repetitive stimuli, as demonstrated in the appendix. On the other hand, the peaks at a frequency (0.4cps) lower than the stimulation frequency do not indicate the response activity to the experimental stimulation but suggest the background activity and/or some other activity derived from harmonic analysis of a limited portion of the autocorrelogram. The height of the peaks brought out by the repetitive stimuli shows, therefore, the total activity of the response (see Appendix). The total activity of the ERG was built up exponentially, whereas that of the lateral gyrus grew approximately in proportion to the logarithm of the stimulus intensity.

Both of these total activities on logarithmic scale were linear in relation to the logarithmic intensity of the stimulation. The slope of the line for the ERG was considerably higher than that of the lateral gyrus.

DISCUSSION

The impulse responses at various levels in the visual system, except the retinal impulse responses (ERG), seemed to show regular changes in the initial short latency responses, according to the intensity of the flash stimuli, but not in the later response components with longer peak latencies. The initial response in the ERG, which is well known as the a-wave, was too feeble in this study for the quantitative determination of its amplitude in response to various grades of stimulus intensity. Therefore, in order to quantify the retinal impulse activity, attention was paid to the far more prominent b-wave. As the b-wave is associated mainly with the PII process of the ERG (Granit 1936) and said to originate in the layer of bipolar cells, which reflect a scotopic mechanism, it would be reasonable to adopt the b-wave as an indicator of the retinal activity, as Mima and Satoh (1965) have done.

The latency and wave forms of the initial positive and negative components in the average responses in the optic tract (TO), lateral geniculate body (GL), optic radiation (RO) and cerebral lateral gyrus (L) resemble in many instances those observed by Brazier (1957).

The first positive and negative deflections in the optic tract (TO), respectively, did not seem to correspond to the first positive, P1, and negative, N1, deflections in the lateral geniculate body (L), optic radiation (RO) or the lateral gyrus (L). Their latencies and some of their other properties corresponded rather to the second positive, P2, and negative, N2, deflections, respectively, so that the initial responses in the optic tract were designated as the P2 and N2 components.

Four or five multiple responses, time-locked to the flash stimulus, were distinctly exhibited within 100-150 msec after flash stimulus in the lateral gyrus. They may be identical with the six to eight multiple
responses brought out within 125 msec after flash stimulus by Steinberg (1965) through chronically implanted electrodes in the visual area of cat. Some disparity in number may possible occur from differences in the cerebral activity due to different experimental situations, individual differences, etc. Marshall et al. (1943) stated that the initial positive deflection (P1) reflects the ascending cortical process while the following negative deflection (N1) is related with activation of the association area and that the multiple responses is induced by facilitation of this initial negative one (N1). It is highly possible, at any rate, that the multiple responses in the cerebral visual area are of value in the transport of important bio-information as Hughes (1964) supposed for those responses in the visual cortex of monkey.

**Binocular interaction.**

Auerbach et al. (1961) have reported inhibitory binocular interaction in the ERG via the centrifugal optic nerve fibirs, since monocular light stimulus elicited a higher ERG than did binocular stimulus when the electrodes were placed on the cornea and nasion of cat under pentobarbital anesthesia. In the author's experiments, however, no evidence verifying the inhibitory or facilitatory interaction was obtained.

Hubel and Wiesel (1961, 1962) have demonstrated that the number of single cell impulses in the visual cortex of cat are synergetically increases and/or cancelled by binocular stimulation, whereas there is little binocular interaction upon the single cell in the lateral geniculate body. Bishop et al. (1959) have observed only delayed interactions in GL, most of which were considered as mediated by interneurons. Although no binocular interaction was demonstrated by Auerbach et al. (1961) in the primary positive evoked potential in the visual cortex of cat under pentobarbital anesthesia, Hirota (1964) observed binocular interaction upon the initial positive and later deflection in the mid-portion of the lateral gyrus of unanesthetized, immobilized cat.

In agreement with Hubel and Wiesel, no binocular interaction upon the masspotential response was seen in the initial positive component elicited by weak, intermediate and intense stimuli in the optic tract, lateral geniculate body or the optic radiation. However, an occlusive interaction was observed in the later response components, which tended to exhibit more distinct action, the weaker was the stimulus. Not only an occlusive but a facilitatory binocular interaction was also brought out in response to an intense stimulus. In addition, binocular interactions in the lateral gyrus were seen even in the initial positive deflection, wherein the occlusive and facilitatory interactions in relation to the stimulus intensity were the most intricate. These tendencies in the binocular interactions seemed to be more complicated, the higher the level was in the visual system from the retina to the visual cortex.
Latencies and amplitudes of the response components.

Three groups of response components in various sites of the visual system were found with increasing intensity of the flashing light stimulus: (i) both a reduction of the latencies and build up in the amplitudes were observed in the first group, i.e. the a- and b-waves in the ERG, and the initial positive (12–35 msec peak latency) and negative components (15–55 msec peak latency) in a variety of sites in the visual system, (ii) the second group exhibited only the reduction of the peak latency, i.e. the late responses of 70–120 msec peak latencies and (iii) the third group was the late responses with longer peak latencies than 120 msec, in which no regular trends such as noted above were seen. The characteristics of the first group have already been demonstrated by many authors (Lennox and Madsen 195524; Madsen and Lennox 195525; Auerbach et al. 196117; Brown and Wiesel 196169; etc.). However, in the average of three animals under the same experimental situation (Fig. 5), the gradient of the curve formed by the amplitudes of the b-wave in ERG against the logarithmic intensity of the flash stimulus was the steepest, followed by that of TO, third was that of GL, fourth were those of RO and L, and that of SS was the most gentle. This finding reflects the greater modification (possibly negative feedback) that occurs with increasing stimulus intensity and the higher the sites in the visual system.

In contrast to the initial response, the later response components did not show regular quantitative characteristics in relation to the intensity of the flash stimulus. However, when the total size of all response components in the frequency domain was obtained from the frequency spectrum of the autocorrelogram of the masspotential activities during stimulation, its logarithmic size was found to be linearly built-up with increasing logarithmic intensity of the flash stimulus. The fact that the slope of this linear relationship in the ERG was higher than that in the response of the lateral gyrus suggests that it has the same significance as the initial response noted above.

APPENDIX

Frequency spectra of autocorrelograms of masspotential records of ERG and various brain sites.

The irregular masspotential record led from corneal surface and/or from a variety of brain sites during repetitive or single flash stimuli is composed of evoked and irregular background potentials, wherein the former is contaminated by the latter in general. Let the size of the masspotential during stimulation, and the background and evoked potentials with respect to an arbitrary time, t, be \( y_0(t) \), \( y_0(t) \) and \( y_e(t) \),
respectively. Then, the above finding can be expressed in the first step by the following relation:

\[ y_{o1}(t) = y_0(t) + y_1(t), \]

as this has previously been pointed out by Sato et al. (1961)\(^{46}\)\(^{47}\), Sato (1964)\(^{12}\) and Sato and Kitajima (1965)\(^{43}\) in the EEG. Further, let the autocorrelation function of \( y_{o1}(t) \), \( y_0(t) \) and \( y_1(t) \) and the crosscorrelation function between \( y_1(t) \) and \( y_0(t) \) with respect to the time delay, \( \tau \), in an appropriate length of time, \( T \), be \( \varphi_{o1,o1}(\tau) \), \( \varphi_{00}(\tau) \), \( \varphi_{11}(\tau) \) and \( \varphi_{10}(\tau) \), respectively. Then the first autocorrelation function of the masspotential \( y_{o1}(t) \) is the summation of the other three correlation functions (Sato and Kitajima 1965)\(^{43}\), i.e.

\[ \varphi_{o1,o1}(\tau) = \varphi_{00}(\tau) + \varphi_{11}(\tau) + \varphi_{10}(\tau) + \varphi_{10}(\tau). \]

The power spectra of \( y_{o1} \), \( y_0 \) and \( y_1 \) with respect to the angular frequency \( \omega \) are assumed to be \( Y_{o1}(\omega) \) and \( Y_1(\omega) \), respectively, and the Fourier transform of \( y_0 \) and \( y_1 \) are \( Y_0(i\omega) \) and \( Y_1(i\omega) \), respectively, where \( i^2 = -1 \). Then taking Fourier transform of the both side of the above Eq. (2), the next relations; i.e.

\[
\begin{align*}
Y_{o1}(\omega) &= Y_0(\omega) + Y_1(\omega) + I_{o1}(\omega) \\
I_{o1}(\omega) &= Y_0(i\omega) \cdot Y_1^*(i\omega) + Y_0^*(i\omega) \cdot Y_1(i\omega) \\
&= 2 \cdot Re(Y_0(i\omega)) \cdot Re(Y_1(i\omega)) + Im(Y_0(i\omega)) \cdot Im(Y_1(i\omega))
\end{align*}
\]

are easily obtained, where the starred functions are the complex conjugates of the unstarred ones, and \( Re \) and \( Im \) are, respectively, the real and imaginary parts in the enclosed complex functions in the parenthesis.

In this study, no background potential of about every 0.7 (\( \approx 1/1.5 \)) sec frequency was observed (Fig. 6, control) under the experimental situation where a single flash stimulus was delivered at about 1.5 per sec to a cat which was unanesthetized but immobilized by Flaxedil administration. Thus, the correlation between the evoked potential \( y_1(t) \) in response to the experimental stimulus and the background potential \( y_0(t) \) is negligible. Therefore, the amplitudes of the crosscorrelogram would be negligibly smaller than those of autocorrelograms of the background and evoked potentials. Thus,

\[ |\varphi_{00}(\tau) + \varphi_{11}(\tau)| \gg |\varphi_{10}(\tau) + \varphi_{10}(\tau)| \]

Consequently, Eqs. (2) and (3) may be rewritten respectively in the following simple forms,

\[
\begin{align*}
\varphi_{o1,o1}(\tau) &= \varphi_{00}(\tau) + \varphi_{11}(\tau) \\
Y_{o1}(\omega) &= Y_0(\omega) + Y_1(\omega).
\end{align*}
\]

The above Eqs. (2–1) and (3–1) indicate that the autocorrelation function of the masspotential and its Fourier transform (power spectra of the masspotential) during experimental stimulation are composed of the masspotential activities induced by natural (background) and experimental stimulations.
Further, no obvious background activities with the frequency of the experimental stimulation and its high harmonics were observed in the autocorrelogram of the control records obtained without experimental stimulation.

\[ Y_0(k\omega_e) = 0, \quad \omega_e = 2\pi f_e \quad \text{and} \quad k = 1, 2, 3, \ldots, \]

If \( f_e \) is the circular frequency of the experimental stimulation (every 0.7 sec. in this study), Eq. (3-1) is rewritten as

\[ Y_{01}(k\omega_e) = Y_1(k\omega_e). \]

Therefore, summation of \( Y_{01}(k\omega_e) \); i.e.

\[ \sum_{k=1}^{\infty} Y_{01}(k\omega_e) \]

indicates the total masspotential response activities elicited by the experimental stimulation, in which all of the initial and later response components are included.

ACKNOWLEDGMENT

This research has been made possible through the support and sponsorship (DA-92-557-FEC-37212) of the U.S. Department of Army, Far East Research Office.

The author wishes to express his cordial thanks to Prof. KENSUKE SATO for his kind guidance, encouragement and help for preparing his manuscript. Thanks are due also to the staffs of the 2nd Dept. of Physiology and also to Dr. Z. KIYASU and Dr. T. KIMURA, Electrical Communication Laboratory N. T. T. PC, Tokyo, for their invaluable help to apply the parametron digital computer (MI-B).

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FLASH IMPULSE RESPONSE OF CAT BRAIN


