VISUALLY EVOKED POTENTIALS TO PATTERN STIMULI IN CORTEX OF BINOCULARLY DEPRIVED CATS

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Abstract. Visually evoked potentials (VEPs) were compared in 7 normally reared cats (N cats) and 9 cats deprived of pattern vision during postnatal period. In 4 deprived cats (D cats) recording was done immediately after deprivation period which lasted from 6 to 24 months. In 5 cats (DE cats) 6 months of deprivation was followed by 4–18 months of visual experience. Two stimuli were used: a large stationary stimulus (a 30 × 30° grating pattern illuminated by flash) and a small moving stimulus (a smaller grating pattern was located in different parts of visual field and illuminated by a moving 1 × 4° light slit). The VEPs were recorded in the marginal, suprasylvian, ectosylvian and sigmoid gyri. As compared with N cats, in D cats the VEPs in all cortical areas were of simpler form, more variable and of greater amplitude. Moreover, in contrast to N cats, in D cats the VEPs were of similar amplitude when evoked from the contra or homolateral visual field. However, results in DE cats showed that these changes are largely reversible.

INTRODUCTION

It is reasonable to assume that in cats visually deprived from birth the responses to visual stimuli are abnormal not only in the visual cortex and subcortical visual structures but also in non-visual cortical areas. The visual input received by non-visual cortex from both the
deprived visual cortex and the deprived superior colliculus-pretectum is certainly abnormal. First, these structures themselves respond abnormally to visual stimuli. Second, in the period of deprivation no associations develop between visual stimuli and stimuli of other modalities (auditory, kinesthetic etc), i.e. between visual and non-visual structures. In other words, in deprived cats the projection from visual to non-visual structures is not shaped by visual experience.

Only few papers have been devoted to that problem. The authors compared visually evoked potentials (VEPs) in visual and non-visual cortex. In binocularly deprived cats, the VEPs were recorded under chloralose anesthesia by Siegel et al. (16). As compared with normally reared controls, in the motor cortex of deprived cats the VEPs were reduced in amplitude. Moreover, in the suprasylvian and marginal gyri the VEPs did not change their latency and amplitude when patterns containing different amounts of contour were presented. Sherrer and Fourment (14) recorded the VEPs in binocularly deprived rabbits. As compared with controls, in deprived rabbits the VEPs in the somatosensory and motor cortex had shorter latency and were larger in amplitude (the results conflicting with that found by Siegel et al.). Moreover, the VEPs were very sensitive to the rate of stimulation; they decreased with repeated flash stimulation at intervals shorter than 2 s.

In monocularly deprived cats the VEPs were studied by Glass (4, 5). The recordings were done under light chloralose anesthesia or in non anesthetized cats located in a restraint box. As compared with the good eye, stimulation of the deprived eye evoked smaller VEPs and activated less number of single-units in the anterior sigmoid gyrus (premotor cortex). The late components of VEPs were reduced also in the middle suprasylvian and marginal gyri. In the anterior sigmoid and suprasylvian gyri (but not in the marginal gyrus) the VEPs became normal following 12 months of reversing the eye closure. Glass et al. (6) found also the reduction of VEPs from the deprived eye in the precentral cortex of human patients.

This study is devoted to a further analysis of VEPs in non-visual cortex of binocularly deprived cats. Our experimental procedure was as follows (a) Recordings were done after transection of the brainstem at the pretrigeminal level (23). Thus during recording we did not use narcosis which affects considerably the VEPs in non-visual cortex (5). Moreover, in the acute stage the isolated cerebrum of the pretrigeminal cat is not only continuously awake but also its level of alertness changes infrequently. Finally, non-visual stimuli do not act on the isolated cerebrum of the pretrigeminal cat (olfactory stimuli were eliminated by tracheotomy). (b) The VEPs were recorded simultaneously from several
cortical areas: visual cortex, suprasylvian associative cortex, auditory cortex and somatosensory cortex. (c) In addition to a large visual pattern-stimulus, a small stimulus was used and was located in different parts of the visual field. (d) The VEPs were studied immediately after deprivation period or following several months of postdeprivational experience.

A part of this study has been reported in abstract form (9 and 19).

MATERIAL

Sixteen cats were used. Seven were introduced into the laboratory at the age of about 1 year and were considered normally reared controls (N cats). The other nine were born in the laboratory and were deprived of patterned visual experience by means of white double linen hoods fitted on their heads before eyelid opening. Further details of our deprivation technique are described elsewhere (11).

In four deprived cats the hood was taken off just before recording (D cats). This was at the age of 26 months (cat D1), 14 months (cat D2), 13 months (cat D3) and 6 months (cat D4). The remaining five cats had been deprived during the first 6 months life (DE cats), and the recording was done after subsequent visual experience lasting 4 months (cat DE1), 7 months (cat DE2), 8 months (cat DE3), 14 months (cat DE4) and 18 months (cat DE5). During the postdeprivational period, cats DE2, DE3 and DE5 were given visual discrimination training for 2, 4 and 8 months, respectively. Thus in both D and DE groups the lower cat number indicates the presumed larger VEP abnormality.

METHODS

The brainstem of cats was transected at the pretrigeminal level under ether anesthesia (23). Just after transection the anesthesia was discontinued. The preparations were paralyzed by Flaxedil (60 mg/h). The upper and the third eyelids were removed, the pupils were dilated by 1% astropine, and contact lenses with artificial pupils of 5 mm placed over the corneas. Large craniotomy was done on the left side, dura mater removed, and four silver ball electrodes were located over marginal, middle-suprasylvian, middle-ectosylvian and posterior sigmoid gyri (Fig. 1). The position of the marginal electrode was at A4 but in four cats (N1, N2, D2, DE2) at P4. A reference electrode was located under the skin of the neck. Twenty milliliters of isotonic glucose solution was given subcutaneously. The cortex was moistened with warm Ringer solution each 15 min. The body temperature was maintained at 38°C.
The EEG activity was continuously monitored from each cortical point. During VEP recording one eye of the cat was occluded. To make the visual axis approximately horizontal, the Horsley–Clarke horizontal of the stereotaxic apparatus was tilted down by 13°. Experiments were done in darkness and visual stimuli were displayed on a dark tangent screen located 57 cm in front of the cat’s eyes.

Fig. 1. The recorded points in the cortex.

The experiment consisted of two parts. During one part a large stationary stimulus was used. A $30 \times 30^\circ$ vertical white-black grating pattern (stripe width 1°) was illuminated by a pair of flashes from OTE Biomedica SL–16 photic stimulator (intensity setting 1; energy of single

Fig. 2. The moving stimulus. Since the experiment was in darkness, the cat could see the white stripes only when illuminated by the moving slit.
flash about 0.5 J.) with the lamp placed just behind and above the cat. The light was diffused and reduced 5 times by a plexiglas plate placed in front of the lamp. Duration of a flash was 10 μs, interval between flashes of a pair 0.5 s, and intervals between pairs of flashes were 10 s.

In another part a small moving stimulus was used. A 30 × 30° white-black grating pattern (horizontal 3° stripes were of 1° width) was illuminated by a moving downward horizontal light slit (1 × 4°, 10 cd/m²) (Fig. 2). The grating was located (and the slit moved) along the average position of the vertical meridian (see ref. 11), or parallel to it along vertical line situated 20° to the right or to the left. The speed of the slit was 60°/s. It appeared 15° above the average position of the horizontal meridian and after 0.5 s disappeared 15° below it. Intervals between slit presentation were 10 s.

Thirty two VEPs were averaged at least two times for each eye and each position of the moving stimulus by ANOPs 101 digital analyzer and recorded on XY plotter. Statistical significance of the results was assessed by mixed-design analysis of variance and by the Duncan tests.

RESULTS

VEPs to the pair of patterned flashes

N group. In the marginal gyrus the VEP was complex and could be divided in three parts (a) the initial group of alternating P₁N₁P₂N₂P₃N₃ fast waves during the first 130 ms, (b) unstable waves of both polarities and of great individual variability appearing in the following 120 ms, which could not be easily identified and thus were not evaluated, (c) a late negative wave variable in peak latency (from 250 to 360 ms) (Fig. 3). Although the amplitude of VEP was somewhat smaller in P4 than in A4, the VEP patterns were roughly similar in both points. In the suprasylvian gyrus a slow NP complex of VEP was found (Fig. 4). In the ectosylvian gyrus the VEP consisted in a P₁NP₂ complex (Fig. 5). Control recordings with covered flash-lamp showed that the responses were not due to a microphonic effect. In the sigmoid gyrus the VEPs were unstable and individually variable, and only a slow PN complex could be detected from the background activity (Fig. 6).

Since the waves distinguished in N cats could not be usually identified in D cats and DE cats (see below), the peak to peak amplitude (i.e., difference between the highest positive and the lowest negative peaks) measured during 500 ms from the stimulus onset was evaluated. For the statistical analysis the data from A4 and P4 points of the marginal gyrus were combined. The VEP amplitude was largest in the marginal gyrus (P < 0.01) and smallest in the sigmoid gyrus (P < 0.05, Fig. 7).
In the suprasylvian, ectosylvian and sigmoid gyri the VEP to the second flash of a pair was smaller ($P < 0.05$; Figs. 4-6). No significant differences were found in any cortical area between the first and the second VEP averaging and the right and left eye stimulation.

**D group.** As compared with N cats, the VEPs in D group differed in several respects. The changes were most pronounced in the marginal gyrus and surprisingly were similar in all recorded areas.
Fig. 4. Visually evoked potentials to the pair of patterned flashes in the suprasylvian gyrus. Cats same as in Fig. 3. For explanations see Fig. 3.

Fig. 5. Visually evoked potentials to the pair of patterned flashes in the ectosylvian gyrus. Cats same as in Fig. 3. For explanations see Fig. 3.
1. The VEPs had a different shape: the component waves were less numerous (except the suprasylvian gyrus) and were slower (Figs. 3–6). These differences were particularly evident in the initial complex of VEPs in the marginal gyrus (Fig. 3).

![Graphs showing VEPs](image)

Fig. 6. Visually evoked potentials to the pair of patterned flashes in the sigmoid gyrus. Cats same as in Fig. 3. For explanations see Fig. 3.

2. The individual variability of VEPs was greater (Figs. 3–6). The variability of VEPs in repeated averagings was distinctly greater in the marginal and suprasylvian gyri (Figs. 3 and 4).

3. The peak to peak amplitude of VEP (measured during 500 ms) was higher (Fig. 7). The difference was significant ($P < 0.01$) for the first flash of a pair except for the sigmoid gyrus.

4. The diminution of VEP to the second flash of a pair appeared in the marginal gyrus ($P < 0.01$), and moreover the diminution became more evident in the remaining gyri.

**DE group.** The features 1 and 2 of D cats were also present in DE cats, but strongly attenuated (Figs. 3–6). The peak to peak amplitude of VEPs was similar to that in the N group (Fig. 7). The second flash of
a pair was significantly smaller only in the ectosylvian ($P < 0.01$) and suprasylvian ($P < 0.05$) gyri. In general, the VEPs were closer to those in N cats than to those in D cats. This was particularly true for cats DE3, DE4 and DE5, who had longer visual experience.

**Fig. 7.** Mean peak to peak amplitude of VEPs to the first flash of a pair in normally reared and deprived cats.

**VEPs to the moving slit**

*N group.* The moving stimulus evoked clear-cut “on” VEPs in marginal, ectosylvian and suprasylvian gyri (Figs. 8–10). The “off” responses were less distinct, and were not analyzed statistically. In the sigmoid gyrus clear responses were seen infrequently and they were not evaluated. At A4 point of the marginal gyrus each illuminated white stripe evoked the response (Fig. 8). As for flash stimuli, the greatest VEPs were in the marginal gyrus (Fig. 11). However, the difference was significant ($P < 0.05$) only between the marginal and ectosylvian gyrus.

The amplitude of VEPs was smaller when the stimulus was presented in the left (homolateral to the recorded hemisphere) visual field as compared to stimulation of the right (contralateral) field or the vertical meridian (Figs. 8–11). The difference was significant for the suprasylvian ($P < 0.01$) and ectosylvian gyrus ($P < 0.05$). The VEPs from the left eye were somewhat smaller as compared with those from the right eye, but the difference was not significant.

**D group.** The moving stimulus evoked “on” and “off” VEPs at all areas except the sigmoid gyrus (Figs. 8–11). Two differences were noted as compared to N cats.
1. The amplitude of "on" VEPs was greater (Figs. 8–11). However, the difference was significant only for the suprasylvian gyrus ($P < 0.01$).

2. The VEPs were particularly increased to stimulation of the left (homolateral) visual field. In consequence they became even somewhat greater than those to stimulation of the right field or vertical meridian (Fig. 11).

Fig. 8. Visually evoked potentials to the moving stimulus in the marginal gyrus of the representative cats. The responses were recorded at A4 point in all cats. First averaged (32 repetitions) VEPs to the stimulus presented in the right (contralateral to the recorded side) or left (homolateral) field are shown. Heavy lines at the bottom indicate duration of stimulus. Negativity upward.

**DE group.** Similarly as with the flash stimulus, the amplitude of VEPs became similar to that observed in N group (Figs. 8–11). The VEPs to stimulation of the left field became again somewhat smaller as compared to those from the right field or vertical meridian (Fig. 11). However, the differences were not significant.

**EEG activity**

The EEG activity was similar in N, D, and DE cats. The EEG patterns consisted of high-voltage activity mixed in different proportions with low-voltage activity (see 23). Fully developed spindles were frequently
Fig. 9. Visually evoked potentials to the moving stimulus in the suprasylvian gyrus. Cats same as in Fig. 8. For explanations see Fig. 8.

Fig. 10. Visually evoked potentials to the moving stimulus in the ectosylvian gyrus. Cats same as in Fig. 8. For explanations see Fig. 8.
observed in suprasylvian, marginal and sigmoid gyri. A given pattern of EEG activity was usually observed continuously for several hours. The normal EEG activity has been previously reported in visually deprived cats (1).

![Graph showing mean amplitude of P1N1 components of “on” VEPs to the moving stimulus presented in the contralateral (C) or homolateral (H) visual field in normally reared and deprived cats.]

**DISCUSSION**

Although the abnormalities of VEPs in D cats were most clearly seen in the marginal gyrus and were less pronounced in the sigmoid gyrus, they were virtually present in all recorded cortical areas. The similarity of the VEP pathology in the visual and non-visual cortex leads to two conclusions concerning the role of various factors in shaping the VEPs in the non-visual cortex of D cats: (a) The role of the input from the visual cortex was more important than that from the superior colliculus-pretectum. This conclusion is consistent with data (2, 7) indicating only moderate postdeprivational changes in single-unit responses of the superior colliculus. On the other hand, as shown by the effects of cortical and subcortical lesions of the visual system on the visual discrimination learning, in deprived cats the function of the visual cortex is partially taken over by the superior colliculus-pretectum (22). To solve the share of those two inputs further experiments on deprived cats are needed, in which one of them would be eliminated. (b) The role of the VEP abnormality itself in the visual structures was greater than the lack of development of associations between the visual structures and non-visual cortex.
In general terms the VEPs in both visual and non-visual cortex were abnormal in five respects: their form was simpler, they showed greater variability, their amplitude was higher, they were more reduced to the second flash of a pair, and their amplitude was similar when evoked from the homo- or contralateral visual field, i.e. when mediated or not mediated by the corpus callosum.

Simplicity and variability of VEPs in non-visual cortex of deprived subjects have not been previously reported. However, as shown by figures in Glass' report (4), the reduction of VEP late components from the deprived eye in the suprasylvian and marginal gyri of monocularly deprived cats made the VEP shape considerably simpler. In the visual cortex the VEPs of abnormal shape were reported by Snyder and Shapley (18) in binocularly or monocularly deprived cats, and great variability of VEPs was shown by Fox et al. (3) in binocularly deprived dogs.

The increase of VEPs in non-visual cortex is consistent with mentioned Sherrer and Fourment's data (14) but not with Siegel et al. (16) and Glass (4–6) findings. Several factors may be responsible for this inconsistency (a) at least in our cats the VEP amplitude in the sigmoid gyrus showed great individual variability (the increase was not significant statistically), (b) the position of the electrode in the sensory-motor area varied in different studies, (c) as shown by Glass (5) the level of narcosis affects considerably the VEPs in the motor cortex. On the other hand, in the visual cortex a clear increase of VEPs was found by Siegel et al. (16) and Lindsley at al. (12) in binocularly deprived cats and monkeys, respectively. One can conclude that in unanesthetized cortex of the binocularly deprived cats the VEP amplitude is increased at least in the marginal, suprasylvian and ectosylvian gyri. This VEP increase is consistent with the hypothesis that inhibitory processes are impaired in deprived cats (see refs. 13, 17).

The more reduction of VEPs to the second flash of a pair is consistent with the mentioned observation of Sherrer and Fourment (14) that in binocularly deprived rabbits the VEPs in the somatosensory and motor cortex were decreased with frequent flash stimulation. In the visual cortex the reduction of VEPs with high rate of visual stimulations was observed in binocularly deprived cats by Baxter (1) and in monocularly deprived cats during stimulation of the deprived eye by Jones and Berkley (10). Altogether those results indicate a less resistance to fatigue of VEPs in visually deprived cats.

The appearance of VEPs of similar amplitude to stimulation of contra- or homolateral field in D cats was clearly produced by the larger increase of VEPs from the homolateral field which are mediated by
corpus callosum. Innocenti and Frost (8) have recently described reduction of callosal projection in the visual cortex of binocularly deprived cats, as compared with normal controls. Further investigations are necessary to relate their finding with our result.

The similarity of VEPs to stimulation of right and left hemifields deserves emphasis in light of Sherman's report (15) that in binocularly deprived cats with monocular viewing the visual fields are restricted to the homolateral field in respect to the open eye. Our present result is consistent with previous results obtained with several perimetric methods that binocularly deprived cats, when tested monocularly, have normal visual fields (11, 21).

In our DE cats the VEPs were almost normal in all cortical areas. The recovery was particularly good in DE cats with longer postdeprivation experience. That is consistent with good behavioral recovery of binocularly deprived cats (20). On the other hand, Glass (4) found in monocularly deprived cats that after several months of visual training the VEPS to stimulation of previously deprived eye recovered in the motor and suprasylvian cortex, but not in the marginal gyrus. One can speculate that after monocular deprivation the role of the extrageniculate input is more important for the recovery of VEPs in non-visual cortex than after binocular deprivation.

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