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OCULOMOTOR CORTEX LOCALIZATION IN THE UNANESTHETIZED CAT

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In recent years two of us have investigated the neural structure of the visual fixation reflex in the cat (Dreher et al. 1965, Dreher and Żernicki 1969ab). In these studies we were interested in the effects of ablation of cortical oculomotor areas. However, available data in the localization of these areas are not adequate. In anesthetized cats relatively small cortical oculomotor areas were described (Garol 1942, Shipova 1965). We know, however, that the oculomotor effects of cortical stimulation may be affected by the narcosis (Krieger et al. 1958). Small oculomotor areas were also observed by Claes (1939) in the *encéphale isolé* cats. On the contrary, some data obtained in the intact freely moving cats suggest that the cortical oculomotor areas are very large (Fangel and Kaada 1960).

The objective of this paper was to complete the data concerning the localization of the oculomotor cortex in the cat. For this purpose the pretrigeminal preparation was used (Batini el al. 1959, Żernicki 1968). A well-known drawback of this preparation is that only vertical eye movements are controlled by the isolated cerebrum. However, due to the pretrigeminal transection the pain factor is eliminated and consequently neither the narcosis nor local anesthesia necessary.

METHODS

For the main experiments 23 pretrigeminal cats were used. During stimulation sessions only 10 preparations were awake (as shown by the presence of the following eye movements to the moving objects). The lack of wakefulness in 13 animals was probably due to extensive cortex exposure (see Żernicki 1968). Additional

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experiments were performed on 4 *encéphale isolé* cats, 7 cats under chloralose anesthesia (80 mg/kg), and 4 cats under Nembutal anesthesia (40 mg/kg). In the *encéphale isolé* cats 2⁰/₀ novocaine was applied to all cut surfaces and pressure points, and 2 mg d-amphetamine sulphate was administrated intravenously every 5—6 hr. All these animals were awake during stimulation sessions.

In all preparations a large craniotomy was performed on the right side, and in some animals complemented by the removal of the right eyeball. In the pretrigeminal and *encéphale isolé* cats the craniotomy preceded the transection of the nervous axis and both were done under short-lasting anesthesia (light ether anesthesia followed by an intravenous administration of 100 mg/kg of Viadril)[2]. The stimulation of the cortex began 2—4 hr after the surgery. In some animals several stimulation sessions, with intervals ranging from 2 hr to 12 hr, were conducted (in some pretrigeminal cats the last session was performed on the second day). At the end of an experiment is some preparations (5 pretrigeminal cat, 4 cats under chloralose anesthesia and 3 cats under Nembutal anesthesia) the right hemisphere was partially removed, and the medial aspect of the left hemisphere stimulated.

During a session the exposed cortex was surrounded with a high wall of wet cotton wool and moistened with warm physiological NaCl solution every 5—10 min. In the intersessional intervals the space over the cortex was covered by placing an additional piece of wet cotton wool on the wall. In some preparations, however, the cortex was covered with warm mineral oil. With both techniques of cortex protection the effects of stimulation were the same.

The cortex was stimulated bipolarly with small silver ball electrodes, 1—3 mm apart. The stimulus was a 2—3 sec train of square wave pulses of 1 msec duration delivered at a frequency of 60/sec. The stimulating current was monitored with an oscilloscope. The effects of current lower than 1.5 ma were usually considered. Every point was stimulated a few times to establish treshold current. The intertrial intervals lasted at least 1 min. During the course of an experiment, cortical points were plotted on a drawing of the individual cat cortex. All the data were then summarized on an average cortex.

The ocular effects of stimulation were observed by two experimenters. When an animals was awake, it was placed in a small compartment to isolate it from inadvertent stimuli, and the eyes were observed through peep holes. In seven pretrigeminal cats the movement of an eyeball was recorder by a photokymograph. A band of light was reflected by a small mirror, which was attached to a light pulley pivoting above the eye and connected with the eyeball by a thread (improvement of "mirror" technique by B. Dreher and W. Kozak, unpublished).

RESULTS

Pretrigeminal cats

In all preparations three large oculomotor areas were found which will be referred to as the *occipital* area, the *occipito-parietal* area and the *frontal* area (Fig. 1). However, on the medial aspect of the hemisphere,

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[2] If the craniotomy (complemented or not by the anesthesia) is performed after the pretrigeminal transection, the mortality of preparations is increased.

and in some preparations also on the lateral aspect, the occipital and occipito-parietal areas created one oculomotor complex. It is worth noting that the unresponsive region between the occipital and occipito-parietal areas corresponds to the cortical projection of the central meridian of visual field (see Talbot and Marshall 1941). In the majority of preparations within the oculomotor areas some unresponsive points were dispersed. The frequent close vicinity of the responsive and unresponsive points suggest that under our experimental conditions the role of spreading of current was moderate. Surprisingly, the extent of the oculomotor areas and the treshold current (see below) were similar in the awake and unawake preparations.

The stimulation of all areas produced conjugate deviations of eyes but with a low current the movements were occasionally observed exclusively in the contralateral side. Stimulation of the lower part of the marginal gyrus in the occipital area evoked upward movements, while the stimulation of the upper part of the marginal gyrus in the occipital area, the marginal gyrus in the occipito-parietal area, and the splenial gyrus evoked downward movements (Fig. 1). The presence of the downward deviations from the occipital oculomotor area (to which there is projection from the upper part of the visual field, Talbot and Marshall 1941) may be due to some upward inclination of visual axis in the pretrigeminal cat during position of rest (Żernicki and Dreher 1965)[3]. The stimulation of the suprasylvian and ectosylvian gyri induced upward movements. On the other hand, the stimulation of the frontal area usually evoked downward movements. In the frontal area the movements in the vertical plane were occasionally accompanied by convergence movements. In addition, the eye deviations (particularly those from occipito-parietal and frontal areas) were frequently accompanied by a small pupillary dilatation.

The values of treshold current for eye deviations varied considerably for different stimulation points, but they were similar for downward and upward movements and the means from larger areas were also similar (Table I). The preliminary data for latent period, amplitude and speed of movements were calculated from seven cats in which the eye movements were recorded by photokymograph (Table I). Again the range of scores for the movements induced from different points was large, but the mean values for larger areas seemed to be similar with the exception that the latent period for the movements induced from the suprasylvian gyrus in the occipito-parietal area was smaller. It may be noted

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[3] Such upward inclination of visual axis is also observed in the cat under flaxedil (Bishop et al. 1962).

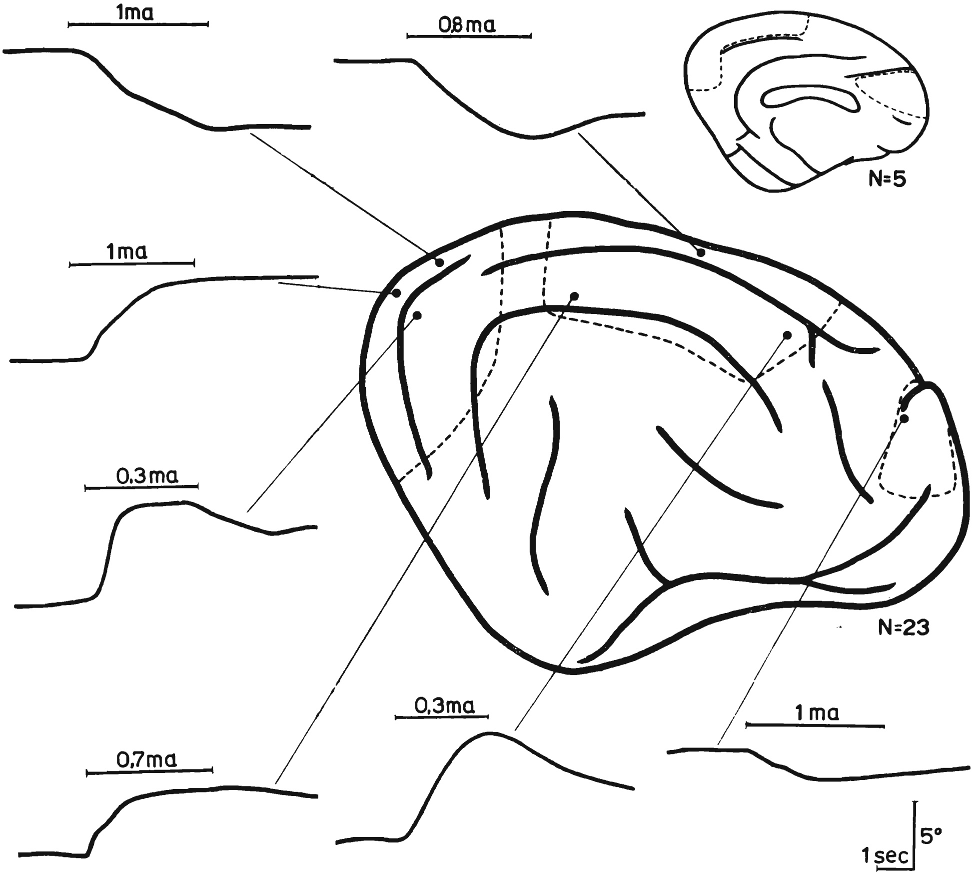

Fig. 1. Cortical oculomotor areas in the pretrigeminal cat. For the lateral aspect of the hemisphere the data from 23 cats are summarized and for the medial aspect the data from 5 cats. All illustrative records are taken from one preparation. The stimulation is marked with a heavy line

that from this area the abundant projection to the efferent layers of superior colliculi was described (Sprague 1963). In some movements quick and slow phases could be distinguished, the quick phase being usually the first one. After the stimulation (particularly of the marginal gyrus) the deviations of eyes were occasionally maintained for several seconds. When the stimulation of a given point was repeated a few times (with intervals of at least 1 min) the character of a movement was preserved.

Additional experiments

In the *encéphale isolé* cats and in the cats under chloralose anesthesia the occipital, occipito-parietal and frontal oculomotor areas were also distinguished and their extent was similar to that in the pretrigeminal

Table I

Characteristics of movements induced from the lateral aspect of the hemisphere in the pretrigeminal cat[a]

Area and gyrus	Threshold current (in ma)		Latent period (in msec)		Amplitude (in deg)		Speed (in deg/sec)	
	mean	range	mean	range	mean	range	mean	range
Occipital								
marginal	0.8	0.5—1.0	343	80—720	7.8	1.6—20.0	3.7	0.4—15.2
suprasylvian	0.8	0.3—1.0	145	20—280	6.2	0.6—15.8	6.2	0.4—33.0
Occipito-parietal								
marginal	0.9	0.5—1.0	146	20—280	9.5	1.6—18.4	4.0	0.3—28.7
suprasylvian	0.6	0.2—1.0	30	10—60	5.1	1.3—10.4	4.7	1.9—7.2
Frontal	0.9	0.6—1.0	253	80—800	5.6	0.8—11.3	3.6	0.4—12.2

[a] The data for latent period, amplitude and speed of movements are only from seven cats and have preliminary character. For these data the movements induced by a current approximately 50% higher than the treshold value were considered. When the speed of a given movement varied, several independent measurements were made.

preparations (Fig. 2). In addition, the stimulation of most cortical points induced eye movements in the vertical plane and the distribution of downward and upward movements was similar to that in the pretrigeminal cats. However, the threshold currents were somewhat higher and latent periods seemed to be longer. In the preparations under chloralose anesthesia the eye movements induced by stimulation of the anterior part of the frontal area were accompanied by movements of legs and ears, and by body jerks.

On the other hand, in the cats under Nembutal anesthesia only occipital and frontal oculomotor areas were present, and the former was present only on the lateral aspect of the hemisphere (Fig. 2). However, when with time the anesthesia was considerably lowered the occipito-parietal area could be also found. In addition, in contrast to the preparations described so far the majority of movements (about 60%) were in the horizontal plane. Most of them were conjugate, directed towards the contralateral side.

DISCUSSION

In our data the extent of the cortical oculomotor areas was similar in the awake pretrigeminal cats, unawake (but not deteriorated) pretrigeminal cats, *encéphale isolé* cats and the cats under chloralose anesthesia. This similarity suggests two conclusions: (i) The pretrigeminal transection (followed by the absence of the horizontal eye movements) does

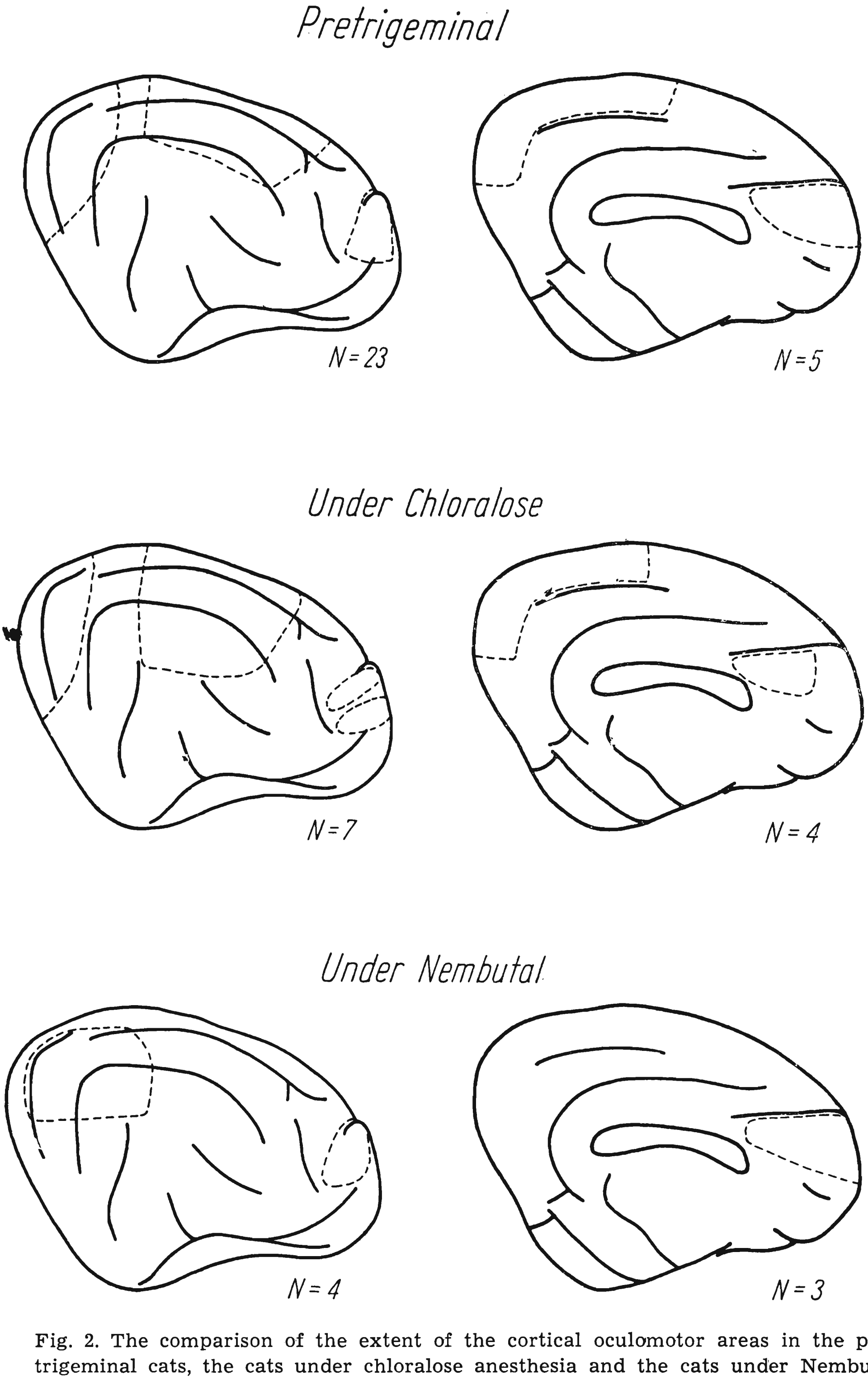

Fig. 2. The comparison of the extent of the cortical oculomotor areas in the pretrigeminal cats, the cats under chloralose anesthesia and the cats under Nembutal anesthesia

not change considerably the extent of the oculomotor areas. (ii) The lack of wakefulness does not affect considerably the oculomotor effects of cortical stimulation. Because we know that in unawake animal the fixation reflex and the "voluntary" eye movements are absent, it may be supposed that the stimulation of any part of the oculomotor cortex does not imitate the action of an external stimulus. In other words, such stimulation rather puts in operation an efferent part of the oculomotor system.

From a functional point of view the oculomotor cortex in the cat may be divided in three parts: (i) primary visual cortex, (ii) associative cortex (main part of suprasylvian gyrus) and (iii) premotor cortex (frontal area).

1. The facts that stimulation of the visual cortex induces eye movements and that the direction of such movements is related to the visual field projection are well known. There is also satisfactory evidence that the visual cortex is the link for the fixation reflex (see Dreher and Żernicki 1969b).

2. As we know, non-visual stimuli contribute in evoking eye movements. An eye movement is often initiated by a non-visual stimulus and when the image of the sound emitting object appears on the retina the fixation reflex occurs. Obviously there must be a close collaboration between the non-visual and visual stimuli in the process of eye directing toward a target. We may speculate that the associative cortex from which the eye movements are induced is involved in the mechanism of such collaboration. This hypothesis is supported by the known fact that in the suprasylvian gyrus the non-primary evoked responses to visual, auditory and somatic stimuli are present (see Buser and Bignall 1967).

3. There is some evidence that the frontal oculomotor area is important for voluntary eye movements and for inhibition of the fixation reflex (see Dreher and Żernicki 1969ab). Present data show that in the cat this area is large, overlapping with the areas for head and forelegs (see Woolsey 1958). Similar overlapping is present in the monkey (Wagman 1964) but not in man. In the freely moving cat the isolated eye movements seem to appear rarely, being usually associated with the movements of head and foreleg, and possibly this association is manifested in the premotor cortex organization.

Finally, the considerable diminution of the oculomotor cortex under Nembutal narcosis should be commented upon. We may suppose that some oculomotor responses are mediated via brain stem reticular formation, and they are lost during barbiturate anesthesia. Such a hypothesis is supported by the usual presence of the pupillary dilatation during oculomotor responses. However, in the experiments of Kaada and Johannessen (1960) and Fangel and Kaada (1960) the distribution of the points eliciting the ECoG arousal in the anesthetized cats and the "attention" behavior in awake ones was different than the distribution of the oculomotor responses in our experiments.

SUMMARY

1. In the pretrigeminal cat three large cortical oculomotor areas were described and referred to as occipital, occipito-parietal and frontal. From a functional point of view the oculomotor cortex was divided into visual, associative and premotor.

2. Additional experiments were performed in *encéphale isolé* cats, in cats under chloralose anesthesia, and in cats under Nembutal anesthesia. In the *encéphale isolé* and chloralose cats the extent of the oculomotor cortex was similar to that in the pretrigeminal cats, but in the Nembutal cats it was much smaller.

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