PHYSIOLOGY

Evoked Potentials of Visual Structures in Response to Flash during Horizontal Saccades in Cats with Transection of Either Intertectal Commissure or Half of Midbrain Tegmentum

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Evoked potentials of the optic tract, superior colliculi, lateral geniculate body, pulvinar, and visual cortex (field 17) in intact cats and in cats with transection across either superior colliculi (intertectal) commissure or half of midbrain tegmentum were recorded during gaze holding and horizontal saccades in response to short flash stimulation against homogeneous background. Statistical analysis showed that transection of intertectal commissure leads to pronounced decrement of evoked potential suppression only in superior colliculi. In cats with tegmental transection, decrement of suppression was observed in the pulvinar evoked potentials. In other structures the character of changes in evoked potentials during gaze holding and saccades were similar for intact cats and those with transection of either type.

Key Words: *saccadic suppression; efferent copy; external orbital muscle proprioception; intertectal commissure; midbrain tegmentum*

In addition to retinal mechanisms of visual suppression during eye movements, the extraretinal influences (the efferent copy and proprioceptive input from external orbital muscles) also contribute to suppression of visual perception, preventing transmission and procession of specific visual signals in the major subdivisions of visual analyzer [1,7,9,11,12].

It is assumed that the efferent copy of the oculomotor command during saccade is generated in the paramedian reticular formation of the brain stem, i.e., at the emergence of the latter in front of the oculomotor nuclei of the premotor center [6]. Further pathways conveying influences of the extraretinal mechanisms of visual suppression were studied scarcely. The present work is devoted to this problem.

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MATERIALS AND METHODS

Experiments were performed on 18 cats: 12 control, 3 with commissure transected under Nembutal anesthesia (35 mg/kg) between superior colliculi, and 3 with transection of half of midbrain tegmentum. Nichrome wire electrodes 0.2 mm in diameter and spherical silver electrodes 1 mm in diameter were implanted according to stereotaxic atlas coordinates [8] into the following visual structures: optic tract, superior colliculi, pulvinar, lateral geniculate body, visual cortex field 17, and into the orbital paries for electrooculogram recording. Alert cats, with the head rigidly and painlessly fixed, were trained to perform voluntary centrifugal saccades. Evoked potentials (EP) and electrooculograms were recorded with a UBF4-03 amplifiers (band pass filter 150 Hz, time constants 0.05 and 2.2 sec) and stored and processed by an M6000 computer.

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The diffuse, total, and binocular photostimulation during gaze holding (GH) and saccadic eye movements (SEM) was performed by an FS-2 photostimulator (flash duration 50 μsec, flash intensity 0.3 J) actuated by an M6000 computer. A short flash applied against homogeneous visual background (10-20 lx) eliminated blurring of the retinal image during SEM and made it possible to examine only the extraretinal mechanisms of visual suppression. The procedure is described in detail elsewhere [1]. The neurosurgical transections were performed by Prof. N. N. Lyubimov. The results were statistically analyzed using Student's *t* test.

RESULTS

No significant difference ($p>0.01$) was found in both experimental groups between EP recorded in optic tract during SEM and GH in a homogeneous visual field (Figs. 1-3, Table 1). Thus, the afferent traffic from optic tract to the higher subdivisions is virtually identical during SEM and GH. Variations in EP may therefore be attributed entirely to the extraretinal influences.

In superior colliculi of control cats much stronger EP inhibition took place during SEM than during GH. Inhibition of EP was less pronounced in the pulvinar—dorsolateral thalamic nucleus complex. In predators these structures are known to be the tectorecipient stage of the "second" visual system. Thus, examination of EP in this complex during SEM elucidates its relation to visual suppression. Changes of EP in lateral geniculate bodies and visual cortex (field 17) during SEM and GH were insignificant (Fig. 1).

The cats of the second group had a transection through commissures of superior and inferior colliculi, and also through the dorsal cerebral commissure down to Sylvian aqueduct. This transection partially disconnected the midbrain structures, but did not strongly affect the conducting pathways passing via both hemispheres to the oculomotor nuclei. Therefore, the horizontal saccades did not disappear

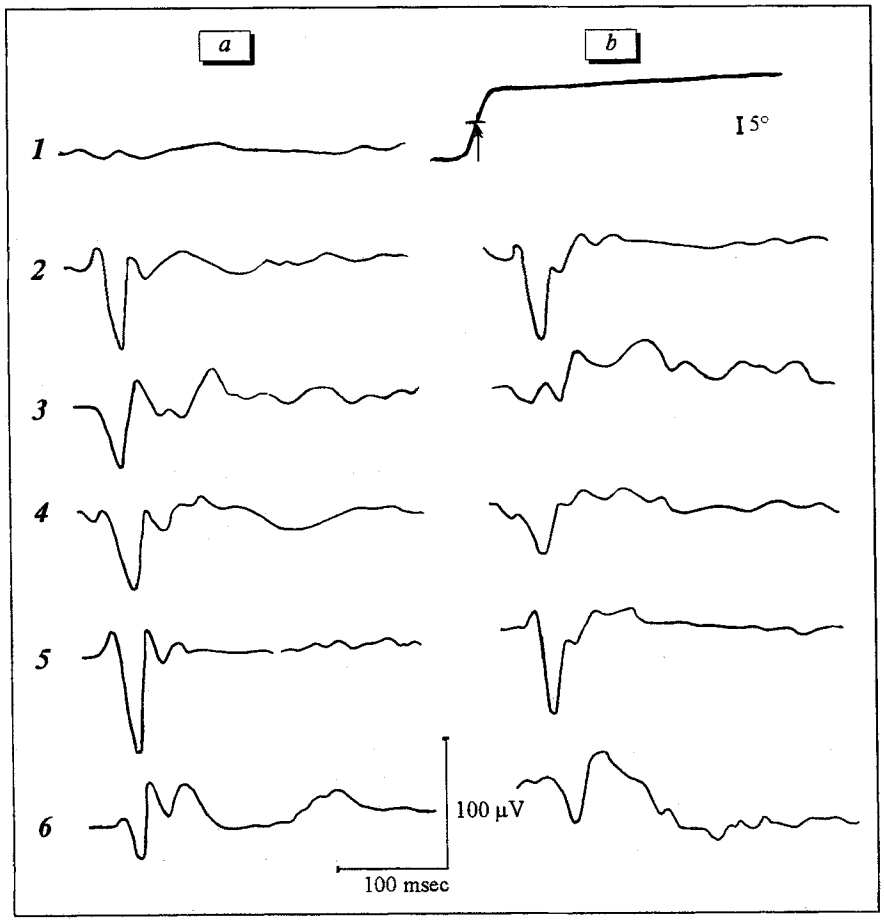

Fig. 1. Averaged evoked potentials (25 stimuli) recorded from visual structures of control cat in response to a short flash during *a*) gaze holding and *b*) horizontal saccades at phase 20°. Here and in Figs. 2 and 3: *1*) electrooculogram; 2) optic tract; 3) superior colliculi; *4*) lateral geniculate body; *5*) pulvinar; *6*) visual cortex (field 17). Origins of the curves coincide with the moment of stimulation. During saccades, stimuli were delivered at phase 10°. A homogeneous visual background. Light adaptation: 10 lx. Amplifier time constant: 2.2 sec. Positivity: downwards.

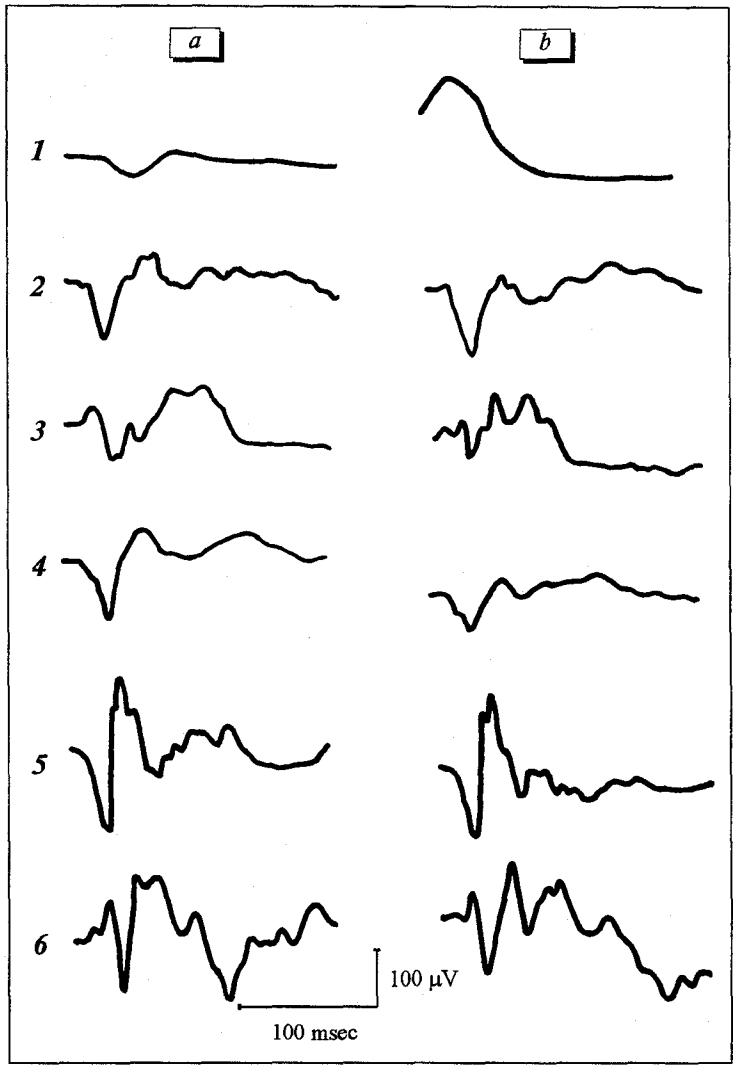

Fig. 2. Averaged evoked potentials recorded from brain structures in response to a short flash during *a*) gaze holding and *b*) horizontal saccades in cats with transection across intratectal commissure. Amplifier time constant: 0.05 sec.

in the cats of this group. At the same time, this transection eliminated, as expected, a part of the pathways conveying the extraretinal influences.

The most prominent effect of the transection was a marked decrement of EP suppression in most recording points in superior colliculi (Fig. 2). Presumably, the decrement is related to elimination of inhibitory influence, which in intact animals is conveyed to this region from another colliculus [10].

Residual inhibition found in this study can be produced by the efferent copy and proprioception in the side ipsilateral to the points of EP recording. It can also result from operation of additional pathways, which produce the inhibitory foci by-passing the commissural pathways between the colliculi via midbrain reticular formation [2]. These connections are probably the channels for extraretinal influences. These influences are not limited to the level of contralateral colliculus: the following unilateral transection of midbrain tegmentum showed that they spread further in the direction of pulvinar—dorsolateral thalamic nucleus.

Some observations showed that EP during SEM were identical in both sides of superior colliculi. Moreover, in some points these EP were even incremented in comparison with EP during GH, and in about a quarter of the recording points EP were suppressed to the same extent as in the control cats. These data reveal a tendency of EP equalizing in both sides of superior colliculi in the transected cats in comparison with the control ones.

Statistical analysis showed that amplitudes of the first and second EP components in superior colliculi were significantly smaller during SEM than during GH ($p<0.01$, Table 1). In other structures changes in EP were similar to those in intact cats.

In the third group of cats the transection was made on the left half of midbrain tegmentum at the level of its conversion into diencephalon. This transection caused visual deafferentation of the left colliculus of superior colliculi and eliminated its influence on the ipsilateral thalamic nuclei. The horizontal saccades were maintained.

EP analysis showed that qualitative changes took place mostly in both pulvinaria. EP suppression decreased markedly during SEM in comparison with that during GH, which may result from interruption of the extraretinal pathways from superior colliculi to the pulvinar—dorsolateral thalamic nucleus complex, although it did not disappear entirely (Fig. 3). Presumably, the latter relates to the slight effect of extraretinal influences conveyed into this region via the intrathalamic commissure.

EP in superior colliculi during SEM were suppressed in comparison with EP during GH, and this effect was similar to that in the control cats. In comparison to the control group, there were no marked changes in EP recorded in another structures (Fig. 3, Table 1).

In a number of works it was shown that the extraretinal influences can be conveyed to the frontal, parietal, and visual cortex areas [3-5]. New data obtained in this work by elimination of the above-mentioned pathways show that these influences (efferent copy and orbital muscle proprioception), which perform visual suppression, are conveyed to the higher sub-

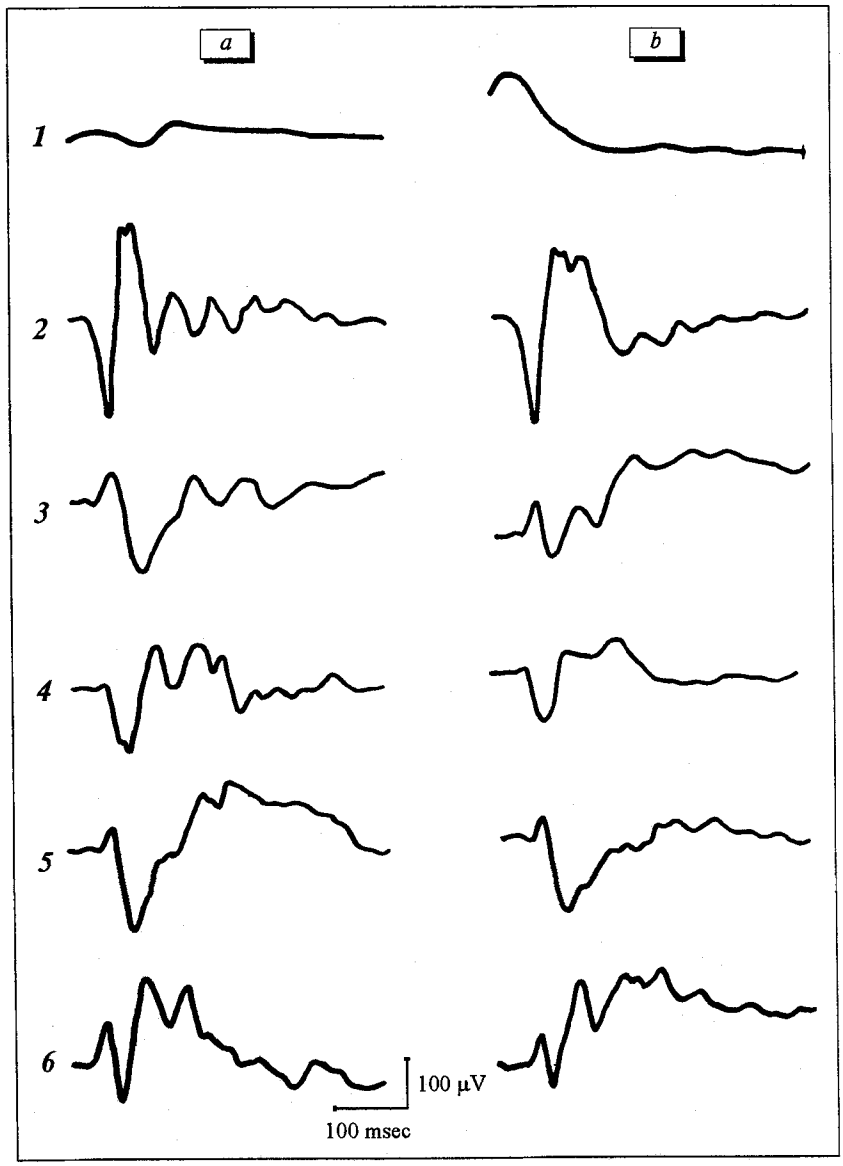

Fig. 3. Averaged evoked potentials (25 stimuli) recorded from visual structures in response to a short flash during *a*) gaze holding and *b*) horizontal saccades to the right direction in cats with transection across left half of midbrain tegmentum. Amplifier time constant: 0.05 sec.

TABLE 1. Amplitude of EP Components during Gaze Holding and Saccades in Cats with Transection Across Superior Colliculi (Intratectal) Commissure or Half of Midbrain Tegmentum, μV (*M±m*)

Brain structure	EP component	Transection of superior colliculi commissure		Transection of half of midbrain tegmentum	
		gaze holding	saccade	gaze holding	saccade
Optic tract	Positive	59.5±6.1	49.5±5.9	73.2±4.2	75.6±3.5
	Negative	55.5±5.1	41.0±6.6	77.8±3.3	69.0±4.2
Superior colliculi	Positive	33.9±2.9	30.0±3.5	31.8±1.3	13.6±2.5*
	Negative	43.8±1.9	39.0±2.5	54.5±1.5	18.2±2.9*
Pulvinar	Positive	66.9±4.4	33.6±2.3*	58.7±1.5	50.3±3.0*
	Negative	70.2±3.6	27.0±3.9*	70.8±1.4	59.5±3.5*
Lateral geniculate body	Positive	67.6±3.3	60.4±3.7	105±1.8	101±2.9
	Negative	94.2±3.8	81.6±4.4	147±2.1	140±2.7
Visual cortex (field 17)	Positive	63.2±1.6	59.6±2.2	85.1±1.7	80.6±3.0
	Negative	69.2±2.1	65.6±1.9	110±1.9	113±2.7

Note. Saccade at phase 20°, stimuli were delivered at phase 10°. Differences between EP during gaze holding and saccades are significant (*$p<0.01$).

divisions mainly via the structures of superior colliculi and pulvinar—dorsolateral thalamic nucleus complex.

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