

The contralateral impairment of the orienting ocular-following reflex after lesions of the lateral suprasylvian cortex in cats

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Abstract. The cortex of the middle suprasylvian sulcus was removed unilaterally in cats with brain stem transected at the pretrigeminal level. The vertical following reflex was evoked by a slit of light $(1^{\circ} \times 4^{\circ})$ moving along the vertical meridian or parallel to it up to 40° in the left or right hemifield. The reflexes from the contralateral hemifield were greatly reduced. This contrasts with previous reports with perimetry test where authors made smaller lesions.

Key words: ocular-following reflex, lateral suprasylvian cortex, pretrigeminal cat, visual neglect

Spear et al. (1983) and Hardy and Stein (1988) studied the effects of lesions of the lateral suprasylvian cortex in cats using the perimetry test. In this test two alimentary conditioned reflexes are elaborated. The cats learned to fixate one stimulus (S1) at 0° central guideline and to react to a second stimulus (S2) introduced at different guidelines during fixation of the S1. Both groups of authors found no deficit in lesioned cats on simple orientation of head and eyes from S1 to S2 (Hardy and Stein found a marked contralateral neglect when the cats were required not only to orient but also to approach S2).

In the present study this problem was reinvestigated in cats with brain stem transected at the pretrigeminal level (see Żernicki 1986). Since the pretrigeminal cat does not feel sensory pain, it can be kept in a stereotaxic apparatus without anaesthesia, permitting precise visual stimulation and eye movement recording. This preparation has only the vertical following reflex since the lateral eye movements are absent. Thus, when the visual stimulus moves eccentrically in respect to the vertical meridian, this reflex is controlled completely by the lateral periphery of the retina. In the pretrigeminal cat the vertical following reflex differs only slightly from that in the intact cat (see Żernicki 1986).

Nine cats were used. Under ether anaesthesia the brain stem was transected at the pretrigeminal level (see Żernicki 1986 for methodological details). The anaesthesia was terminated just after transection. The suprasylvians lesions were made by subpial aspiration on the left side of the brain. In cats 1-5, both banks of the middle suprasylvian sulcus were removed, in cats 6 and 7, only one bank was ablated, and cats 8 and 9 served as controls (see below). For recording the vertical eye-movements, the lower margin of the right cornea was attached with a thread to a hair spring connected to a tensometric transducer (see Folga et al. 1973 and Michalski et al. 1977 for methodological details). After surgery 20 ml of warm mixture of 5% glucose and Ringer solution was administered subcutaneously. To increase resistance to habituation of the following reflex, a small dose of amphetamine (0.5 mg/kg, i.v.) was administered 1-3 times during experiments (see Żernicki 1986).

Recording started as soon after surgery as the ocular following reflex reappeared, i.e. after 0.5-2 h. The methods of visual stimulation and recording were the same as we used in a previous study devoted to the effects of different brain lesions (Żernicki 1988). During recording one eye was covered with an occluder which did not disturb eye movements. A white tangent screen was located 57 cm in front of the cat's eyes. The stimulus was a horizontal light slit (1° x 4°, 10 cd/m2) presented in dim light (0.3 cd/m2). A reference point for the stimulus position was an average position of the fixation point for the pretrigeminal cat's eye at rest: upward inclination = 13° and lateral declination = 3° (see Żernicki 1986). The slit was moved vertically at 10°/s through this fixation point, i.e., along the average position of the vertical meridian, or parallel to it along vertical lines situated 10°, 20°, 30° and 40° to the left or to the right. The slit appeared 15° above the average position of the horizontal meridian and after 3 s disappeared 15° below it.

During recording, the position of the right eye was monitored on a polygraph. Testing consisted of 2-3 sessions. The intersessional intervals lasted 30-60 min. A session lasted about 20 min. In the first part of a session the right eye was stimulated and in the second part the left eye. The slit was presented 20 times for each eye. The intertrial intervals were about 30 s. First the slit moved along the vertical meridian and then alternatively on the left and on the right from the furthest position on the periphery (40°) back towards the vertical meridian. At each position two trials were given. The amplitude of each following reflex was measured. It was arbitrarily accepted as a distance between the lowest and the highest position of the eye during 3 s of slit movement.

The cats were sacrificed with an overdose of Nembutal. The brains were fixed in formalin, embedded in paraffin, sectioned at 10 µm and stained with Nissl and Klüver-Barrera techniques. Reconstruction of the lesions was made for all preparations. Extent of lesions was determined by

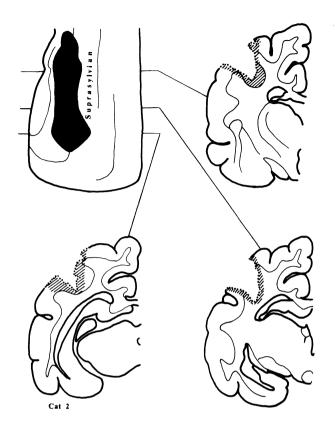


Fig. 1. A reconstruction of a typical lesion (cat 2). Dotted lines indicate extent of the lesion and hatching the area of degeneration of fibres and loss of cells. The upper left diagram shows a dorsal view of the posterior part of the left hemisphere.

comparison with the maps of Palmer et al. (1978) and it is shown in Fig.1 and Table I. In all cases the crown of the suprasylvian and ectosylvian cortex, adjacent to the middle suprasylvian sulcus, was also removed. In the control cats 8 and 9 this adjacent crown cortex was only removed.

Mean size of reflexes from the left hemifield varied from 3.0° to 20.5° in different cats. In two cases there were also marked differences between sessions: in cat 4 the mean size of reflexes varied from 4.5° to 17.6° and in cat 7 from 2.2° to 4.2° . The mean size of reflexes and the differences in their size between cats and sessions were similar to those described in non-ablated pretrigeminal cats (Żernicki 1986, 1988).

In cats 1-5 with lesions of both banks of the suprasylvian sulcus the following reflexes from the

TABLE I

Summary of data		
Cat	Lesion ^a	Diminution ratio ^b
1	PMLS+PLLS+AMLS+ALLS	0.24
2	PMLS+PLLS+AMLS+ALLS	0.28
3	PMLS+PLLS+AMLS+ALLS	0.16
4	PMLS+PLLS	0.02
5	PMLS+PLLS	0.28
6	PMLS+AMLS	0.70
7	PLLS+ALLS	0.54
8	Control	1.12
9	Control	1.32

^aPMLS, posteromedial lateral suprasylvian area; PLLS, posterolateral lateral suprasylvian area; AMLS, anteromedial lateral suprasylvian area; ALLS, anterolateral lateral suprasylvian area. ^bThe mean amplitude of reflexes evoked at 10°, 20°, 30° and 40° from the right hemifield to that from the left hemifield.

right hemifield were poor or absent at all eccentricities (Fig. 2, Table I). The diminution effect was found in all experimental sessions. In cats 6 and 7 with only medial or lateral lesions, respectively, the contralateral neglect was less extensive. In cats 8 and 9 no neglect was found.

Our results clearly show that the orienting ocular reflex is severely impaired contralaterally to lesions of the lateral suprasylvian cortex. This result is consistent with single unit data showing marked involvement of the lateral suprasylvian during the ocular fixation reflex (Yin and Greenwood 1992).

The difference between our results and those of Spear et al. (1983) and Hardy and Stein (1988) might be due to differences in lesions and testing. (1) Spear et al. (1983) ablated only the medial wall of the suprasylvian sulcus (our cat 6 with such lesion showed only mild impairment) and lesioned their cats bilaterally. (2) Hardy and Stein (1988) produced relatively small lesions, PMLS or PLLS area was usually lesioned. (3) In the perimetry test the cats were tested 1-2 weeks after the surgery. (4)

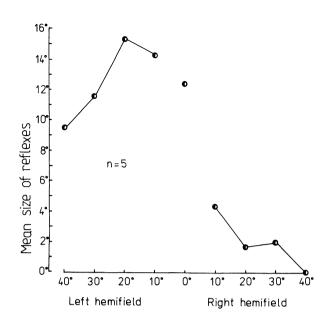


Fig. 2. Mean amplitude of following reflexes in cats 1-5, with ablation of both banks of the left middle suprasylvian sulcus.

In this test there is a competition between two conditioned reactions.

Our lesions included partly area 7p (Olson and Lawler 1987), area 21a and ectosylvian gyrus. However, the control cats 8 and 9 showed that this impairment was probably insignificant. Some increase of reflexes from the contralateral hemifield in cat 9 remains unexplained. Nevertheless, further investigations are necessary to know whether or not complete removal of these areas would produce a neglect. Krüger et al. (1993) reported that both area 7 and lateral suprasylvian cortex have overlapping functions and Toga et al. (1979) found that the posterior ectosylvian gyrus is involved in visual behaviour.

The deficit described here was similar to that found previously after unilateral ablation of the superior colliculus in pretrigeminal cats (Żernicki 1988). The contralateral neglect after ablation of the superior colliculus in cats was also found by Sprague and Meikle (1965) using the perimetry test. We know that deep laminae neurones of the superior colliculus receive a marked input from the posterior aspect of the lateral suprasylvian cortex

(Kawamura et al. 1978, Baleydier et al. 1983, Segal and Beckstead 1984, Berson 1985, Harting et al. 1992) and depend on it for their normal excitability and receptive field properties (Ogasawara et al. 1984). Thus, both collicular and suprasylvian lesions affected presumably one system.

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