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THE ORIENTING OCULAR-FOLLOWING REFLEX IN PRETRIGEMINAL CATS WITH LESIONS OF VISUAL AND OCULOMOTOR SYSTEMS

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Abstract. The brain stem was transected in cats at the pretrigeminal level. Additional lesions were placed in 17 cats, whereas 10 served as controls without further manipulation. All received a small dose of amphetamine. The vertical following reflex was evoked by a slit of light or a black bar ($1^\circ \times 4^\circ$). The stimuli moved along the vertical meridian or parall to it up to 40° in the left or right hemifield. A unilateral removal of the superior colliculus produced a loss of reflexes evoked from the contralateral hemifield. In contrast, after unilateral ablation of the visual cortex only in one of 4 cats was the reflex from the contralateral hemifield smaller than ipsilaterally; and after unilateral ablation of the frontal oculomotor cortex, no hemifield asymmetry of these reflexes was found in any cat. The reflexes also survived bilateral ablation of the visual cortex or the frontal oculomotor cortex. After transection of the corpus callosum the reflexes were virtually normal. The data confirm that in the cat the orienting fixation reflex is mediated by the superior colliculus. On the other hand, this reflex appears to be largely independent of the cerebral cortex.

INTRODUCTION

The fixation reflex is a conspicuous representative of ocular targeting reflexes, which bring about an optimum perception of visual stimuli (16). This reflex consists of three characteristic stages: a saccadic movement towards the object, maintenance of the fixation, and a return movement.

In our laboratory the ocular fixation reflex is investigated in cats with brain stem transected at the pretrigeminal level (see 27). The pretrigeminal cat is convenient for this purpose for several reasons. Since it does not feel pain (excepting possibly that produced by direct stimulation of certain prosencephalic elements), it can be kept in a stereotaxic apparatus without anesthesia, easily permiting precise visual stimulation and recording of eye movements. In addition, since the input of sensory information to the cerebrum is drastically reduced, the influence of accidental stimuli on the fixation reflex is eliminated, and thus the preparation's eyes are usually in the position of rest. However, in the pretrigeminal cat, only the vertical fixation reflex is available; the lateral eye movements are absent, since their center is located behind the transection.

We usually investigate the orienting fixation reflex which is evoked by the so-called neutral stimuli (see 28). In the pretrigeminal cat this vertical orienting fixation reflex differs only slightly from that in the intact cat (29). It is somewhat less precise, presumably due to the lack of proprioceptive information from the extraocular muscles and the separation from the eye movement related neurons of the pontine reticular formation and the flocculus. In addition, its size varies markedly in different acute preparations, since some of them remain in a state of low responsivity (see 27).

In previous studies (10, 12) we investigated the effects of bilateral visual and oculomotor central ablations. One-two weeks after an ablation, the pretrigeminal transection was done and the fixation reflex tested. In cats with superior colliculi removed the reflex was abolished. In cats with visual cortex (areas 17, 18 and 19) ablated the reflex was moderately diminished and habituated very rapidly. On the contrary, in cats with damaged frontal oculomotor cortex, the reflex was enhanced (the stage of maintenance of fixation was prolonged) and it was very resistant to habituation.

In the present study the effects of unilateral lesions were mainly investigated. Moreover, the procedure differed in several respects. First, the lesions were produced after the pretrigeminal transection. Since they were directly followed by testing, their effect was revealed before any compensatory processes might occur; although lesions made soon after the transection may unspecifically affect the responsiveness of such preparations (see 27). Second, the reflex was evoked by stimuli moving slowly and with a constant speed in the visual field. Thus the "following" fixation reflex was investigated, in which the stage of maintenance of fixation consists of a pursuit movement. Third, the reflexes evoked from the peripheral retina were also studied (see 19).

Fourth, the preparations were given a small dose of amphetamine to increase the resistance of the following reflex to habituation (12) and to counteract any state of low responsiveness.

METHODS

Reliable information was obtained on 27 cats. Under ether anesthesia the brain stem was transected at the pretrigeminal level (see 27 for details). Anatomical verification showed that the transection was complete in all cases. The anesthesia was terminated just after the transection. To enlarge the visual field the upper eyelids and the nictitating membranes were removed. For recording the vertical eye-movements with a tensometric technique (13), the lower margin of the right cornea was attached with a thread to a hair spring connected to a tensometric transducer.

The experimental procedure in different groups of cats was as follows. Ten preparations served as further non-operated controls. In 4 cats the superior colliculus was removed on the left side (tectal group). In 4 cats the visual cortex was removed on the left side and subsequently in 3 of them on the right side (occipital group). In 5 cats the frontal oculomotor cortex was removed first on the left side and then on the right side (frontal group). In 4 remaining cats the corpus callosum was transected (callosal group). The lesion in tectal and callosal cats and the left lesion in occipital cats was made immediately after the pretrigeminal transection. In frontal cats the control recording was done before the left ablation; thus each subject served as its own control.

Recording started as soon after any surgery as the ocular following reflex reappeared, i.e. usually after 0.5-2 h. The methods of visual stimulation and recording were similar to those used previously (19). During recording one eye was covered with an occluder which did not disturb eye movements. To make the visual axis approximately horizontal at rest, the Horsley-Clarke horizontal of the stereotaxic apparatus was tilted down by 13°. Visual stimuli were displayed on a white tangent screen located 57 cm in front of the cat's eyes. The main stimulus was a light slit (1° × 4°, 10 cd/m^2) presented in dim light (0.3 cd/m^2). The additional stimulus was a three-dimensional black bar (1° × 1° × 4°, 0.3 cd/m^2) presented against a lighter background (3 cd/m^2). Both stimuli were oriented horizontally. The slit was presented automatically, whereas the bar, connected with a long white stick, was moved by an experimenter standing on the left of the screen. In some poorly reactive cats (3 tectal cats and 3 occipital cats after the second ablation) a larger bar (2° × 8°) was used. 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 27). The stimuli moved vertically at 10°/s through this fixation point, i.e., along the average position of the vertical meridian, or parall 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, or vice versa. The movement of the bar was larger and always downward: it appeared above the visual field and disappeared below it.

The spatial relationship between the stimulus position and the eye position was established in each cat. Before recordings the fixation reflex was evoked by a stimulus located in the average resting position of the eye (a black bar oriented horizontally was moved horizontally by hand) and this point was marked on the recordings at the 0° eye position.

During recording, the position of the right eye was monitored on a polygraph. Testing consisted of 1-5 sessions. To allow the spontaneous recovery of the following reflex, the intersessional intervals lasted 30-60 min. A session lasted about 30 min. In the first part of a session the right eye was stimulated and in the second the left eye. First the following reflex was evoked by the slit which was presented ten times. The intertrial intervals were about 30 s. In the first trial the slit moved along the vertical meridian and then alternatively on the left and on the right from the furthest periphery (40°) back towards the vertical meridian. Thus, the comparison of the first and the tenth trial was an indicator of the habituation of the following reflex. Then the bar was presented in the same sequence. The analysis time used in recordings was suited rather to the following movements, so the measurement of the saccadic movements was less precise.

After surgery 20 ml of warm mixture of 5% glucose and Ringer solution, 50 : 50, was administered subcutaneously. A small dose of amphetamine (0.5 mg/kg, i.v.) was administered 1-3 times at different stages of the experiment. In some cats, amphetamine evoked spontaneous eye movements but they disappeared during the following reflex. The cats were sacrificed with an overdose of Nembutal. The brains were embedded in paraffin, sectioned at 10 μm and stained with Nissl technique.

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 and during 4 s from the beginning of the reflex to the bar. This was usually the amplitude of the following movement. Only when the saccadic movement to the stimulus was very large and the following movement small, the amplitude represented the magnitude of the sacccadic movement. The following movement sometimes continued after the disappearance of the stimulus (usually during a fraction of a second); this "after-following" up to 1 s was included to the amplitude of the reflex.

RESULTS

Control group

In confirmation of the previous study (19), the vertical following reflex with both its saccadic and pursuit components was evoked by stimuli presented within the whole tested area extending 80° horizontally (Fig. 1 and control data in Fig. 3). However, at the periphery of retina the amplitude of the reflexes was moderately decreased.

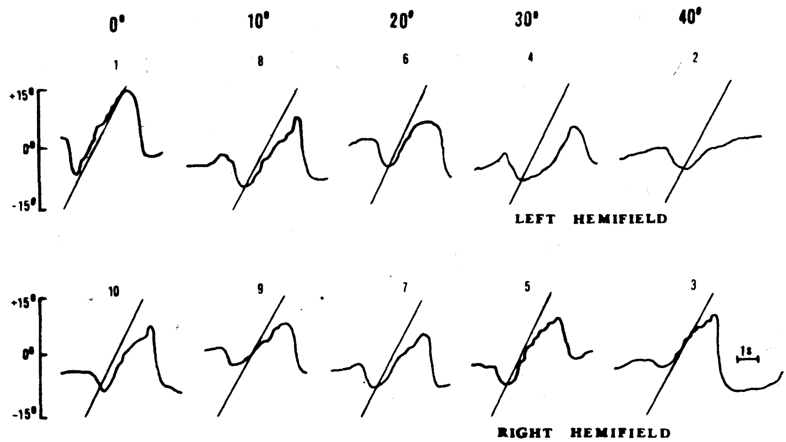

Fig. 1. Ocular following reflexes to slit moving upwards at different distances from the vertical meridian during a representative session in a control preparation (cat 41). Movement of slit indicated by fine line. Small numbers indicate order of stimuli. Ordinate: position of slit and inclination of eye. Right eye stimulated and left occluded.

Stimulation of the left and right hemifields was evenly effective in all cats. Stimulation of the temporal and nasal retina was also evenly effective, but at the temporal 40° the stimuli were sometimes less effective, as clearly seen in Fig. 1. Such diminution of the reflex was particularly marked for the bar during stimulation of the right eye (left hemifield); when its white connecting arm (certainly contributing somewhat to the reflex) was presumably not seen by the cat.

The reflexes to the bar were on the average stronger than to the slit.

The size of the following movements was on the average about 50% of the size of the slit movement and somewhat less than 50% of the size of the bar movement in the visual field.

The size and shape of the reflexes showed marked individual variation and varied also in a given preparation and even in a given session (Fig. 1). Some reflexes were inadequate. The following movements were occasionally interrupted by small corrective saccades and sometimes continued for a fraction of a second after disappearance of the stimulus.

Although the preparations received amphetamine, the reflexes nevertheless habituated somewhat as a session and an experiment proceeded. In consequence, the stimulation of the left eye (used in the second part of the sessions) was less effective.

Tectal group

In all four cats the left colliculus was completely removed except a lateral remnant in cat 21. In cat 27 (shown in Fig. 2) the lesion was limited to the superior colliculus, whereas in cats 11 and 21 the anterior part of the left inferior colliculus was also removed and in cat 34 the left pretectum and underlying structures were damaged.

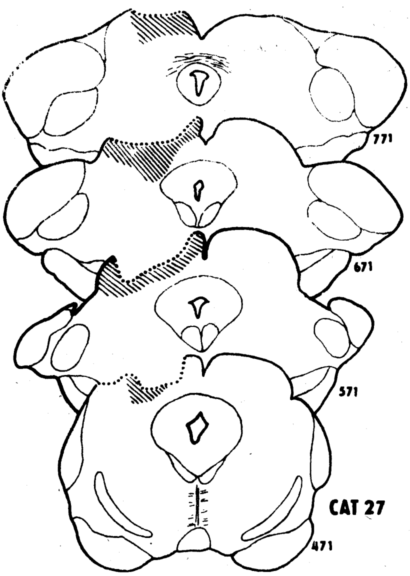

Fig. 2. Representative tectal lesion (cat 27). Dotted lines indicate extent of lesion, and hatching the area of degeneration of fibers and loss of cells.

Since the preparations were poorly reactive, in three of them (cat 11, cat 21 and cat 34) the larger (2° × 8°) bar was used. The results were similar for all cats. The following reflex virtually could not be evoked from the right hemifield (Fig. 3). Abortive responses were obtained to

$1^\circ \times 4^\circ$ bar at the sites 10° and 20° in cat 27 and to $2^\circ \times 8^\circ$ bar at the site 10° in cat 21, but they might be partially produced by the stick's white arm moving in the left hemifield.

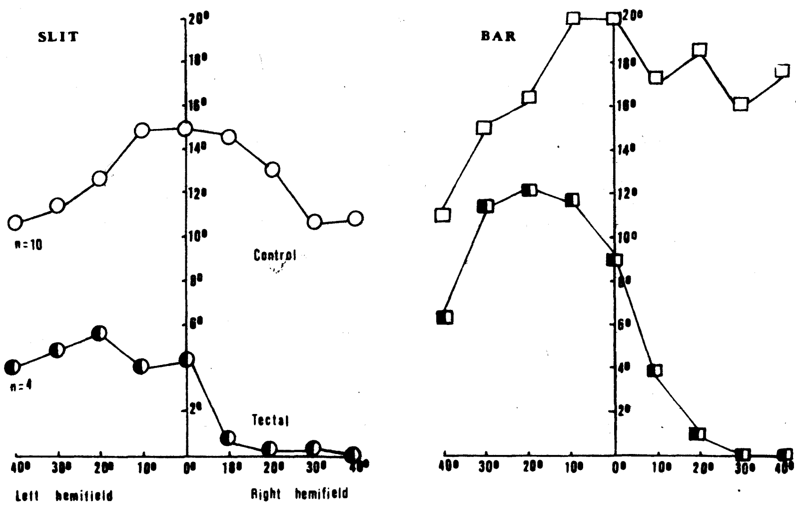

Fig. 3. Comparison of mean amplitude of following reflexes to slit (circles) and bar (squares) in control and tectal group. Superior colliculus removed on left. In three tectal preparations the larger ($2^\circ \times 8^\circ$) bar was used.

The reflexes evoked from the vertical meridian and from the left hemifield were small in all preparations (Fig. 3). However, they had both saccadic and pursuit components and their general course seemed to be normal, i.e. typical for otherwise intact pretrigeminal preparations.

Occipital group

The first, left ablation was performed in four preparations and the subsequent right in three of them. All lesions were similar and included visual areas 17, 18 and 19 with exception of the lower part of the area 19 on the medial side of the hemispheres (Fig. 4).

After the left ablation good reflexes could be evoked from the whole visual field in all cats. In only one preparation (cat 13) were the reflexes from the contralateral hemifield smaller. As compared with the control group the reflexes were on the average diminished by about 20% (Fig. 5).

After the subsequent right ablation the size of the reflexes varied. In cat 23 the reflexes remained good, whereas in cat 9 and cat 19 they were absent. However, in these cats satisfactory reflexes could be evoked by the $2^\circ \times 8^\circ$ bar.

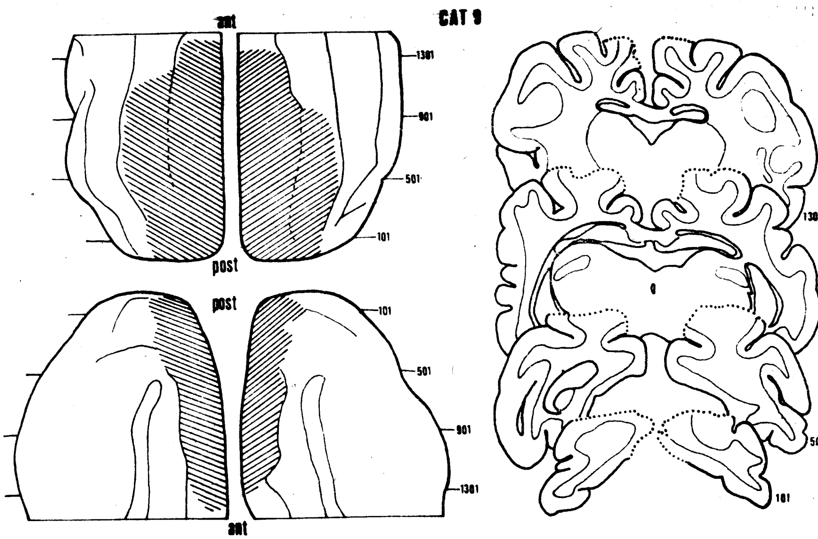

Fig. 4. Representative occipital lesion (cat 9). Hatching indicates the damaged cortex and dotted lines the extent of lesion.

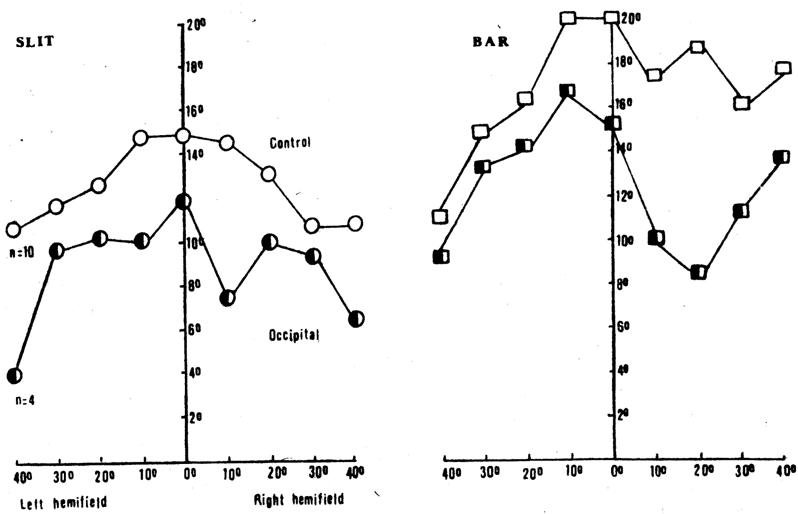

Fig. 5. Comparison of mean amplitude of ocular following reflexes to slit (circles) and bar (squares) in control group and occipital group ablated on left side.

Frontal group

In all five cats the frontal oculomotor cortex was removed first on the left side and then on the right side. The extent of the oculomotor area was estimated on the basis of the electrostimulation maps described by Dreher et al. (11) in the pretrigeminal cat, and by Schlag and Schlag-Rey (24) in intact anesthetized cats, and Guitton and Mandl (14) in intact, awake cats. Each removal included the anterior sigmoid gyrus on the lateral and medial aspects of the hemisphere and the bottom and banks of the presylvian sulcus (Fig. 6). However, the posterior part of the

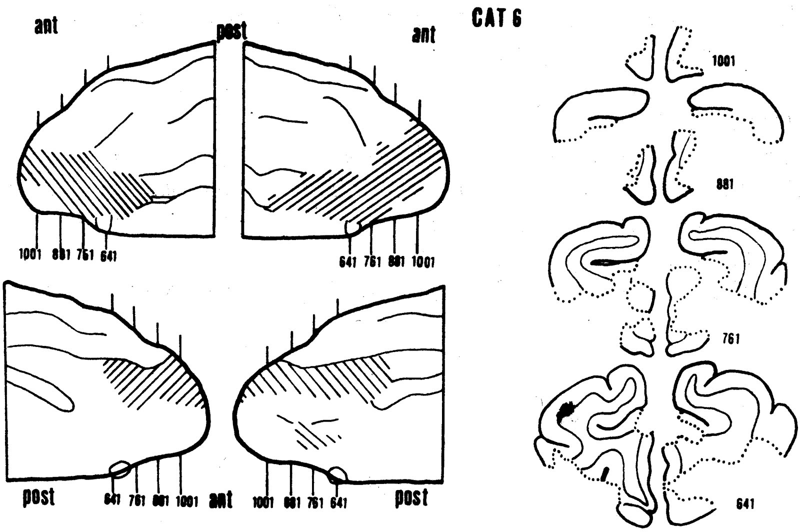

Fig. 6, Representative frontal lesion (cat 6). Hatching indicates damaged cortex and dotted lines the extent of lesion.

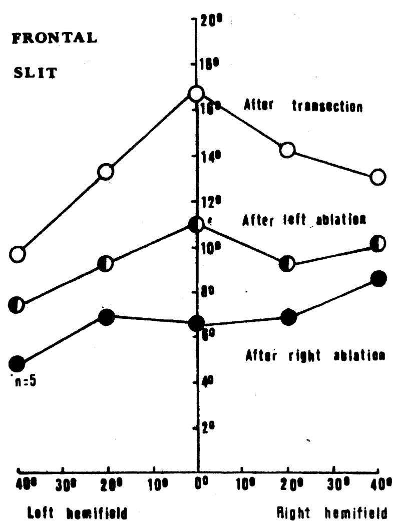

Fig. 7. Comparison of mean amplitude of following reflexes after pretrigeminal transection, after subsequent ablation on left side and after subsequent ablation on right side in frontal group. Right eye stimulated with slit.

presylvian oculomotor cortex was left in the first operation in three cases (cats 2, 3 and 7) and in the second operation in two cases (cats 2 and 7), and the posterior part of the medial oculomotor cortex was left in both operations in cat 2.

The experimental procedure in this group was different in some details: control recording was done before the first cortical lesion, only the right eye was stimulated, only the slit stimulus was used, and the sites of 10° and 30° eccentricity were usually not stimulated.

The control (preablation) data were similar to those of the control group (see Figs. 7 and 5).

After the left ablation no hemifield asymmetry was found in any cat (Fig. 7). The reflexes were greatly diminished in one case (cat 3), became moderately smaller in two cases (cats 5 and 6), remained unchanged in cat 7, and were increased in cat 2.

After the subsequent right ablation the reflexes were poor in three

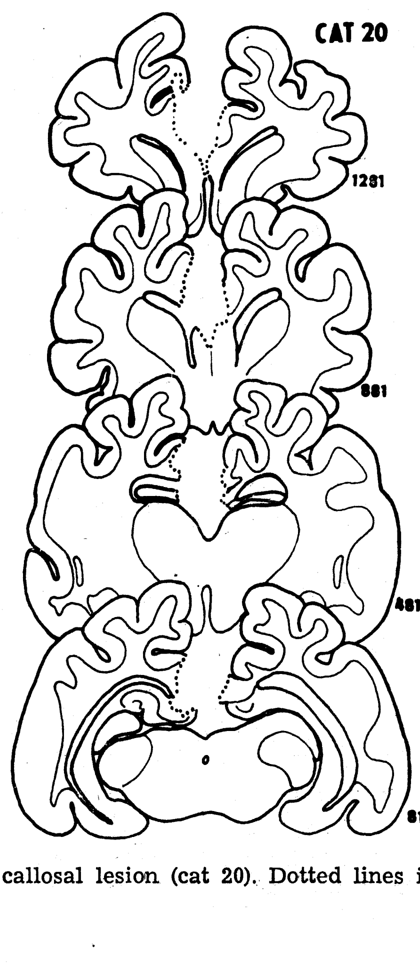

Fig. 8. Representative callosal lesion (cat 20). Dotted lines indicate extent of lesion.

cases, whereas they remained good in two cases (cats 2 and 7). Because of this great individual variability, the mean data presented in Fig. 7 are not conclusive.

Callosal group

In all four preparations the section of the corpus callosum was complete (Fig. 8).

In three cats no asymmetry of reflexes was observed, whereas in cat 20 (shown in Fig. 8) the reflexes from the right hemifield were clearly impaired: the reflexes to the slit were virtually absent and to the bar were small. In addition in one preparation (cat 15) the reflexes to the slit from the whole field were diminished. In the remaining preparations both stimuli were normally effective. The mean data for the group are shown in Fig. 9.

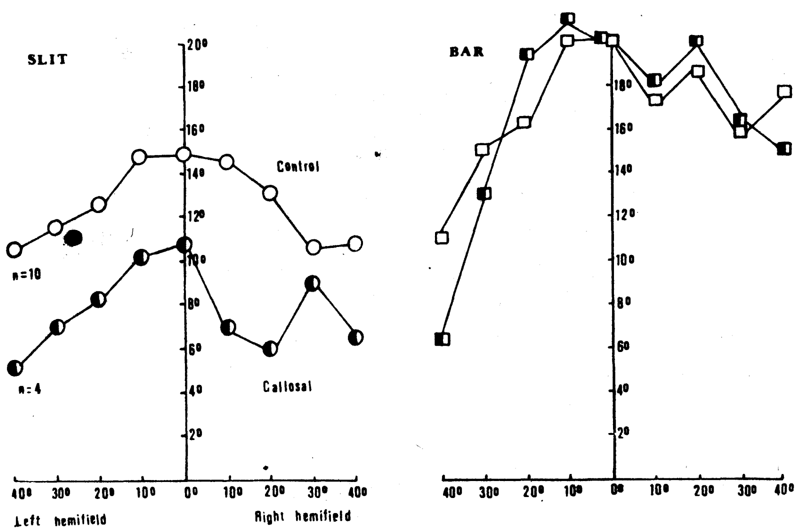

Fig. 9. Comparison of mean amplitude of ocular following reflexes to slit (circles) and bar (squares) in control and callosal group.

DISCUSSION

Contralateral impairment of the reflex

The unilateral removal of the *superior colliculus* was followed by a virtual loss of the orienting following reflex evoked from the contralateral hemifield. This result is consistent with observations of Sprague and Meikle (25) on unilaterally ablated cats as well as with the effects of bilateral collicular ablations (10, 25). Dreher et al. and Sprague and Meikle showed that the effect is not limited to the orienting reflex, but the fixation reflex to any object is impaired. Moreover, it is probable that in the collicular cat, ocular convergence and accommodation reflexes are also impaired. Thus, the visual targeting reflex (see 16, 28) would be impaired as a whole, the symptom usually referred as visual neglect (see 21). In two preparations abortive reflexes could be evoked to the stronger stimulus (stick) moved close to the vertical meridian. This result is also consistent with observations of Sprague and Meikle: some of their unilaterally ablated cats reacted to objects presented contralaterally close (10°-20°) to the vertical meridian. Sprague and Meikle observed their collicular cats chronically. The deficit was somewhat decreased during the first several weeks, but no improvement was found in the further survival up to about one year. Altogether one can thus conclude that in the collicular cat the contralateral deficit in the fixation reflex appears immediately after surgery, is severe (particularly for the peripheral retina), and is compensated only partially. Visual neglect was found also in collicular monkeys (1, 23) and rats and hamsters (for refs. see 7), and was reported also as severe, increasing with the eccentricity of the stimulus, and long-lasting.

Interestingly, in this study the total contralateral absence of the following reflex was found only in cats with lesions extending beyond the superior colliculus and penetrating the inferior colliculus or the pretectum. Dreher, Marchiafava and Żernicki (unpubl. data) made a similar observation in their bilaterally ablated cats: when the ablation was limited to the superior colliculi, the application of amphetamine (used in all cats in the present study) improved the fixation reflex, whereas such improvement was not observed when the lesion involved the posterior part of the pretectal area.

The mechanism of impairment of the fixation reflex in the collicular cat is complex. The impairment of vision is certainly not a critical factor. Collicular cats can avoid obstacles (10) and have visual placing reflexes (10, 25). Zabłocka et al. (26) found that, in cats, object discrimination is easily reacquired after bilateral removal of the superior colliculus-pretectum (the deficit was comparable to that after ablation of the visual cortex). Berlucchi et al. (3) found that split-brain cats with unilateral ablation of the superior colliculus-pretectum do not even require any retraining in a visual discrimination task. Visual discrimination learning is also relatively normal in collicular rats and hamsters (for refs. see 7). Moreover, Albano et al. (1) found that in the unilateral collicular monkeys, the deficit in stimulus detection not requiring eye movement lasts clearly for a shorter time than that in the orienting fixation reflex. On the basis of data on rodents Dean and Redgrave (8, 9) suggest that an essential function of the colliculi is to make the decision of responding to transient stimuli in the periphery of the field.

In the previous study (10) the bilateral ablation of the *visual cortex* produced only a moderate decrease of the orienting fixation reflex but it became much less resistant to habituation. In the present study, except in one preparation, the contralateral impairment of the following reflex was hardly seen. Moreover, the reflex did not habituate promptly, the obvious result of the amphetamine application. Altogether the results show that the visual cortex is usually not a critical structure for the orienting fixation reflex.

The lack of a contralateral impairment of the following reflex in the *frontal* preparations was rather unexpected, since after destruction of the frontal eye field visual neglect is observed in monkeys and man (for refs. see 5, 21, 22). Using the perimetric technique, Latto and Cowey (18) found that in monkeys the neglect grows progressively worse toward the periphery of the contralateral field. The contralateral visual neglect was also found in rats after lesions of the dorsal prefrontal cortex (for refs. see 7, 22). Moreover, in cats Orem et al. (20) observed contralateral visual neglect after thalamic intralaminar lesions. However, in all these studies the neglect was moderate and disappeared during a few weeks.

Two factors can be responsible for this difference. First, the animals neglect a contralaterally presented stimulus more readily when their attention is already engaged on another stimulus (see 21). Such stimulus is often used as the centrally positioned spot for background fixation. In contrast, in the present study the slit and bar were used when the cat's eyes were in the state of rest. Second, in the present study the amphetamine might prevent to some extent the unilateral impairment. Recently, Corvin et al. (4) reported a pharmacological therapeutic effect: administration of apomorphine diminished the contralateral neglect in rats with a dorsomedial prefrontal lesion. Another therapy has been described by Crowne and Pathria (6): postoperative visual deprivation prevented the appearance of the neglect in rats. Thus, the frontal contralateral neglect is not only relatively short-lasting but also easily affected by various experimental procedures.

The impairment of the following reflex from the right hemifield in one *callosal* cat is puzzling. Possibly during surgery the left hemisphere was significantly damaged without visible histological changes. One can also speculate that the left hemisphere had been affected during the earlier life of the cat outside of the laboratory and the right hemisphere compensated the deficit. It is known (22) that in monkeys as well as in rats after recovery from unilateral frontal lesions contralateral neglect is reproduced by sectioning the corpus callosum.

Size of the reflex

Any surgery on the isolated cerebrum of the pretrigeminal cat can decrease its responsiveness nonspecifically and even induce a comatose state (see 27). This factor was presumably responsible for the poor responsiveness of some occipital and frontal preparations. However, it seems unlikely that this would be the only reason for poor ipsilateral responsiveness affecting *all* tectal cats, although they received relatively severe surgery and the lesions might directly affect the activating structures of the brain stem. Interestingly, in the study of Albano et al. (1) the collicular monkeys also showed as light deficit in the ipsilateral hemifield. The investigation of the reflex in pretrigeminal cats with unilateral collicular ablation made prior to the transection might help in understanding this problem.

In the previous studies (10, 12) the fixation reflex was clearly increased after bilateral ablation of the cat's frontal oculomotor cortex or the prefrontal cortex, the effect considered as a hypernormality of an orienting reflex in the frontal cat. In this study the increased reflexes were observed only in one unilaterally ablated preparation. The oculomotor ablation was presently larger (in the previous study the presylvian sulcus was not involved); however, this probably can not explain the difference in results, since Jeannerod et al. (15) reported hypernormality of the ocular following reflex in cats with a large lesion (bilateral frontal lobectomy). Therefore, it may be concluded that the hypernormality of the fixation reflex usually appears only some days or weeks after the frontal ablation. An additional study in cats with the unilateral ablation made prior to the transection would be important in this respect. The hypernormality of the fixation reflex is probably due to a sensitization of structures deafferented by frontal ablation, presumably superior colliculi. Such sensitization after cortical ablation may be expected. For example, Żernicki and Santibañez (30) found in dogs that after ablation of the cortical taste area (anterior composite gyrus), the salivary reflexes were diminished for weeks and then were markedly hypernormal for weeks or months.

The results in the callosal group are roughly consistent with the unpublished results obtained in our laboratory by E. Czihak. She used essentially the same method of investigation of the following reflex but the bar stimulus was not applied. In one of their preparations, the slit was normally effective, whereas in the remaining two its effectiveness was somewhat lowered. Altogether the results show that in the pretrigeminal cat the additional extensive deafferentiation of the hemisphere by sectioning the corpus callosum does not markedly affect orienting reactivity. This result is consistent with Berlucchi's finding (2) that the isolated hemisphere can show good EEG activity.

The difference in effectiveness of slit and bar stimuli needs comment. In our previous study (19) both these stimuli were presented automatically and their movements were equal; then the stick was somewhat less effective than the slit, presumably because of its lower contrast. In the present study, on the contrary, the bar was more effective. This was presumably produced by three factors: The bar had larger movement than the slit, it was presented by hand, and the movement of its white connecting arm contributed somewhat to the reflex.

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