Abolition of Optokinetic Nystagmus in the Cat

Abstract. *Combining a behavioral and a surgical manipulation, namely complete visual deprivation with surgical section of the optic chiasm, results in the abolition of optokinetic nystagmus in the cat. This basic optomotor reflex remains relatively unaffected by either of these manipulations performed singly.*

Most movements of the eyes are made not in order to look at objects in the world, but to compensate for motion of the visual world caused by the organism's own movement (1). The visual response by which an image is stabilized on the retinas is called the optokinetic reflex and its properties are surprisingly similar in animals as diverse as crab, cat, and human (2). We have measured optokinetic responses in the cat and now report that combining two manipulations abolishes the optokinetic response to visual stimuli. Either of these manipulations alone has relatively small effects on the response. The manipulations are total visual deprivation starting near birth and surgical section of the optic chiasm, which severs direct connections from the eye to the opposite side of the brain. The results will be discussed in terms of the physiology of the nucleus of the optic tract.

We measured optokinetic responses by placing the cat in the center of a rotating striped drum which filled most of the visual field. The cat's head was fixed to a stereotaxic frame with previously implanted tubes, and eye movements were recorded through the use of a magnetic search coil technique (3). When the drum is rotated around a normal cat, a characteristic pattern of eye movement is observed. This is called optokinetic nystagmus (OKN) and has a time course resembling a sawtooth. In normal cats, the velocity of the slow phase of OKN matches the velocity of the moving stripes rather well (4). We compared optokinetic responses of (i) normal cats, (ii) dark-reared cats, (iii) normally reared cats in which the optic chiasm had been surgically sectioned, and (iv) dark-reared cats in which the chiasm has also been sectioned (5).

The binocular optokinetic responses to stripes moving with different velocities around the animals are shown in Fig. 1. The responses to movement in both directions have been combined. For normal cats, the gain indicated nearly perfect image stabilization over most of the velocity range. In both the dark-reared and the split-chiasm groups, responses were vigorous at low velocities, but stabilization became progressively worse at higher velocities. Surgical section of the optic chiasm in cats also reared in the dark caused much more severe effects

than those found with either manipulation alone. The effect of sectioning the optic chiasm is to remove retinal input to the opposite side of the brain while leaving uncrossed retinal pathways intact. Thus, the results suggest that in normal cats crossed or uncrossed visual pathways are sufficient to sustain OKN. The dark-reared cat appears to use exclusively crossed pathways for this response, thus increasing its vulnerability to optic chiasm section.

The experiments illustrated in Fig. 1 were all performed under binocular viewing conditions. Experiments with monocularly presented stimuli (Fig. 2) suggest the set of pathways illustrated in Fig. 3 as those underlying horizontal nystagmus in the cat.

Interpretation of the effects of the various surgical and deprivation conditions on monocularly elicited OKN is complicated by the finding that monocularly viewed stimuli moving medially (for example, rightward when viewed through the left eye) are more effective than are laterally directed stimuli even in normal cats (6). The preference for medially over laterally directed stimuli is reversed, however, in the animals in which the optic chiasm has been sectioned. In these animals, the response to lateral movement is reduced only marginally from normal, while that to medially directed stimuli is very weak above the lowest stimulus velocities.

Conversely, medially directed optokinetic responses are less affected than laterally directed responses in the dark-reared cat (7). While medial responses

are certainly depressed especially with high drum velocities, these animals respond only weakly to a drum moving laterally to the open eye, even at low speeds. The apparently negative gain for laterally directed stimuli and the apparent gain of greater than unity with low medially directed stimulus velocities is a consequence of a spontaneous nystagmus (slow-phase medial), which we have observed in all three dark-reared cats studied. This nystagmus is unrelated to visual stimulation, since it is observed in the dark and also when the drum is stationary. An example of the spontaneous nystagmus of a typical dark-reared cat is shown as an inset in Fig. 2. This inset also shows examples of the nystagmus evoked in response to monocular optokinetic stimulation (8).

In the dark-reared cat in which the chiasm was sectioned, combining these manipulations that affect laterally and medially directed OKN yields a complete absence of OKN in response to either direction of stimulus movement. Both the apparently negative gain for medially directed stimuli and the apparent response to laterally directed stimuli can be accounted for by a spontaneous nystagmus (slow-phase lateral in the monitored eye) observed in these animals. Allowing the animal visual exposure for as long as 10 months in a normally lit animal colony has not resulted in any recovery of optokinetic responses to stimuli moving in any direction.

We believe that our findings can be understood in terms of emerging studies implicating the nucleus of the optic tract (NOT) in the control of horizontal OKN (9). This nucleus contains binocularly driven direction-selective neurons preferring movement toward the ipsilateral hemifield; the velocity characteristics of these neurons are appropriate for the generation of OKN. Moreover, lesions

Fig. 1. Gain (eye velocity ÷ stimulus velocity) of horizontal optokinetic nystagmus (OKN), measured with both eyes open, as a function of drum speed. A gain of 1 indicates perfect following of the drum by the eyes. These data represent the means of at least two determinations of OKN slow-phase gain in both horizontal directions of movement in each of two subjects. The drum consisted of a large cardboard cylinder (diameter, 90 cm) on which high-contrast vertical black and white stripes were painted (stripe period was 20°). Background luminance was 0.1 cd/m².
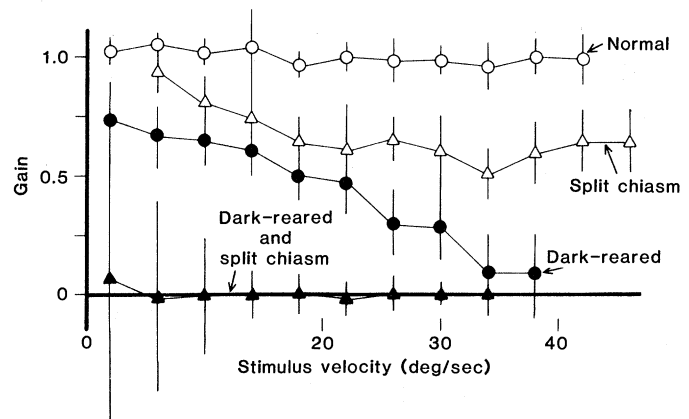
of this structure abolish horizontal OKN in rabbits, and electrical stimulation of the NOT elicits OKN with the slow phase toward the side of stimulation [that is, stimulation of the left NOT produces leftward OKN (9)].

Our manipulations do not alter the function of the NOT, but affect the access of visual input to this nucleus. The direct retinal projection to this nucleus originates primarily from the contralateral eye, while the ipsilateral eye input takes an indirect route through the visual cortex (Fig. 3) (10). After chiasm section, only the ipsilateral eye has access to the NOT, exciting only neurons that are responsive to laterally directed stimulation of that eye. By contrast, visual deprivation appears to exert its major effects on the cortex and its output pathways leaving access to NOT units only through the direct pathway from the contralateral eye (11). When the optic chiasm is sectioned in the dark-reared cat, the visual input from both retinal and cortical sources is virtually abolished by the combination of deprivation and surgery. Hence this animal lacks visual input of any kind to its optokinetic systems and exhibits a profound blindness which does not diminish over time.

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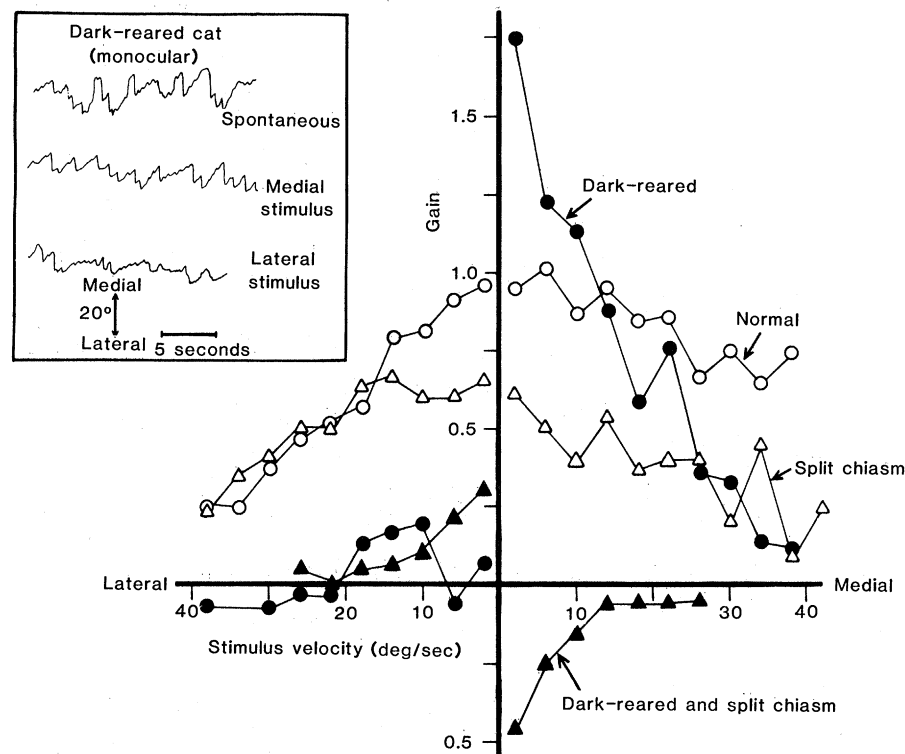*Physiology, Dalhousie University*

Fig. 2. Responses to monocularly viewed stimuli moving medially (toward the nose) or laterally. The gain of the reflex is lower for laterally directed high-velocity drum movement than for medial in the normal cat (6). (Inset) Nystagmus of the dark-reared cat under monocular viewing conditions. Another oculomotor anomaly characteristic of dark-reared cats is the low-amplitude, high-frequency pendular nystagmus (12).

Fig. 3. Visual pathways to the nucleus of the optic tract (NOT). Each eye sends a direct projection to the NOT on the other side of the brain. This projection is interrupted by chiasm section, so the NOT lacks direct contralateral eye input after surgery. In addition, both eyes project to cells in the visual cortex on both sides of the brain after a relay in the lateral geniculate nucleus. The visual cortex then projects to the NOT, providing the sole route by which stimuli viewed monocularly can influence the cells of the ipsilateral NOT. Visual deprivation appears to result in a functional loss of cortical efferent pathways to the midbrain; thus, in the dark-reared cats, stimuli presented monocularly may not influence cells of the ipsilateral NOT. This result would be consistent with the lack of response to laterally directed stimuli in these animals. When the chiasm is sectioned in cats reared in the dark, all access routes to either NOT become nonfunctional, with the result that the cats become incapable of responding to stimuli moving in either direction.
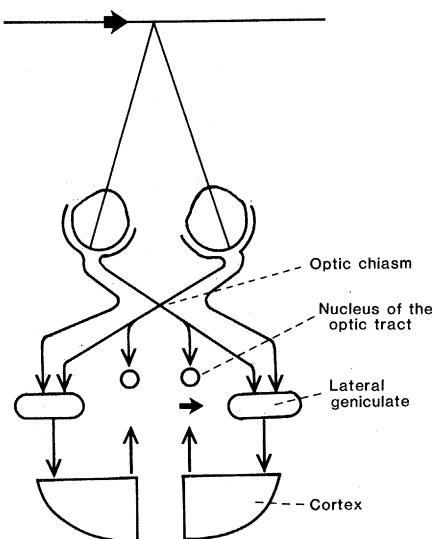
References and Notes

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5. At least two cats were subjects in each condition. The dark-reared cats were raised from before the time of natural eye opening at 1 week of age until 11 to 14 months in total darkness. Thereafter the coil and restraining tubes were implanted and the cats were allowed at least 2 weeks to recover before recording began. The dark-reared cats in which the optic chiasm was sectioned underwent the operation at about 8 months of age and then recovered for at least 1 month in the dark. Vision was minimized during surgery by the use of opaque scleral occluders and by an opaque black hood placed over the animal's head. The optic chiasm was sectioned under askeptic conditions through a ventral (transbuccal) approach.
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8. We monitored the movements of only one eye of each cat. This means that, although the spontaneous nystagmus of the monitored eye of the dark-reared cats was medial, we cannot be certain of the direction of movement of the other eye and thus of whether the movements were conjugate or disconjugate. The direction of the dark-reared cats' spontaneous nystagmus did not change depending on which eye was open. The dark-reared cat results (Fig. 2) were all obtained by stimulation of the monitored eye.
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