

Vestibulo-ocular Reflex and Optokinetic Nystagmus in Adult Cats Reared in Stroboscopic Illumination

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Summary. Cats reared in stroboscopic illumination (strobe reared cats) have been found to have abnormal eye movements. Visual and vestibular evoked compensatory eye movements were inefficient. Vestibulo-ocular reflex in the dark had a maximum gain of 0.6 (1.0 in normal animals). Optokinetic nystagmus had a mean gain which approached unity only at stimulus velocities around 7°/s (up to 30°/s in normal animals). The asymmetry of the optokinetic nystagmus resulting from monocular stimulation was more pronounced in strobe reared cat than in normal animals. Interaction between vestibulo-ocular reflex and optokinetic nystagmus to give adequate compensatory eye movements was absent in strobe reared cats: visual suppression of vestibulo-ocular reflex was absent when the animal was rotated in an illuminated environment which remained stationary with respect to the head. Optokinetic nystagmus failed to improve the gain of the vestibulo-ocular reflex when the animal was rotated in a normally lit environment. The deprived animals showed no signs of recovery after 5 months exposure to normal lighting.

Key words: Eye movements – Strobe reared cat – Vestibulo-ocular reflex – Optokinetic nystagmus

Introduction

There is considerable experimental evidence to suggest that the functioning of the adult visual system is dependent on experience during development. Rearing animals at low frequencies of stroboscopic illumination deprives them of visual motion signals, resulting either from movement in the outside world or from movement of the retina, whilst allowing them

normal stationary visual input. Deprivation of visual motion during development gives rise to marked deficits in neuron response both at the level of the superior colliculus (Flandrin et al. 1976; Kennedy et al. 1980) and the visual cortex (Cynader et al. 1973; Olson and Pettigrew 1974; Cynader and Chernenko 1976; Orban et al. 1978; Pasternak et al. 1981; H. Kennedy and G.A. Orban, submitted for publication).

Animals reared in total darkness show an impaired visuomotor activity (Riesen 1961; Vital-Durand et al. 1974; Berthoz et al. 1975; Van Hof-Van Duin 1976; Flandrin and Jeannerod 1977; Harris and Cynader 1981). Strobe rearing could also be expected to have a detrimental influence on the development of the oculomotor system. As stroboscopic illumination eliminates retinal slip, strobe reared cats will not have experienced the necessity to perform compensatory eye movements in order to stabilize the retinal image during eye and/or head movements.

In order to investigate the effects of rearing in the absence of visual movement we have investigated vestibulo-ocular reflex (VOR) and optokinetic nystagmus (OKN) in adult strobe reared and normal cats. The capacity of strobe reared cats to visually explore a normally illuminated environment was evaluated by examining VOR and OKN interaction.

A preliminary report of the results obtained has appeared elsewhere (Amblard et al. 1981).

Methods

Rearing Procedure and Surgical Preparation

Five adult cats were used in this study (three normal and two strobe reared). The deprived cats were reared from birth for 14 months in light tight cages illuminated stroboscopically. Movement of the retinal image was abolished by using a flash duration

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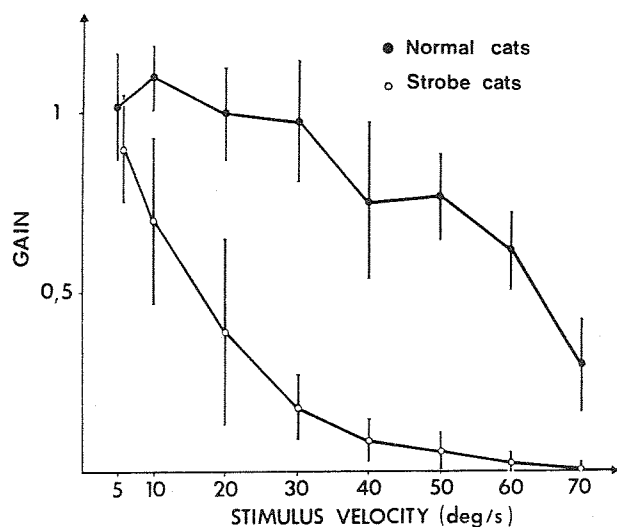


Fig. 1. The gain of the horizontal optokinetic nystagmus as a function of stimulus velocity. Mean values and S.D. shown for two determinations made on the strobe (open circles) and the normal cats (closed circles)

of 0.2 ms and a frequency of 2/s. Animals were implanted under nembutal anaesthesia (35 mg/kg i.p.) with silver-silver chloride electrodes for recording eye-movements in the horizontal plane. A head-fixation device was cemented to the skull (Magnin and Jeannerod 1973). The animals were allowed at least 1 week to recover from anaesthesia before commencing recording sessions. During this time the deprived animals were returned to a stroboscopic illuminated environment.

Calibration of Eye Movements

Horizontal eye movements were displayed on a paper chart and stored on FM tape. Eye movements were calibrated by comparing simultaneous TV recordings of eye movements in the light adapted animals and the accompanying oculogram (Stryker and Blakemore 1972). Calibration was carried out at the end of the recording sessions. The accuracy of this method of calibration depends on the reliability of data concerning the dimensions of the cat's eye (Vakkur and Bishop 1963) and the magnification of the cat's eye obtained with the TV camera. The results obtained with this method of calibration agreed to within at least 15% with that assuming a gain of unity when the normal animal is rotated sinusoidally at a frequency of 0.25 Hz with an amplitude of $\pm 20^\circ$ in an abnormally illuminated environment (Keller and Precht 1979). The degree of imprecision of this method of calibration is reflected by the maximum gain values of 1.14 at low velocities in response to optokinetic stimulation (Fig. 1).

Experimental Procedure

During experimental sessions the cat was secured in a hammock and placed with the head centered on a servo-controlled turntable which could be rotated sinusoidally or at constant velocity. A drum (1 M dia) could be placed over the turntable and either rotated independently at constant velocity or coupled mechanically to the turntable. The light tight cylinder could be illuminated from within

(background luminance 0.9 Cd/m^2) and had vertical black and white stripes which subtended a visual angle of 10° . The cylinder itself subtended a vertical visual angle of 70° .

VOR was tested in the dark. Different velocity profiles were applied to the turntable: velocity steps of $160^\circ/\text{s}$, from $80^\circ/\text{s}$ in one direction to $80^\circ/\text{s}$ in the other. Sinusoidal stimulation was made at constant peak velocities of $70^\circ/\text{s}$ and at frequencies of 0.01, 0.03, 0.05, 0.07, 1 Hz.

In both the deprived and normal animals care was taken to make sure that animals were fully aroused during recording sessions of VOR. Auditory stimulation helped to maintain the animals vigilance. The animal's level of arousal is reflected in the characteristics of the nystagmus (Flandrin et al. 1979), and as soon as the cat showed signs of drowsiness the recording session was suspended.

Visual suppression of VOR was tested by illuminating the drum and coupling it mechanically to the turntable. During rotation of the table and drum the visual surround was therefore stationary with respect to the head of the cat. Sinusoidal oscillations as above were applied to the turntable and drum.

In order to investigate the capacity of OKN to improve the performance of VOR, the animals were rotated sinusoidally in the illuminated stationary cylinder. The same frequencies of rotation were used as for testing VOR in the dark.

OKN was tested by rotating the illuminated cylinder around the stationary cat. The cylinder was rotated in both directions at velocities ranging from 7 to $70^\circ/\text{s}$. OKN was tested in two conditions: with both eyes open (binocular OKN) and with one eye occluded (monocular OKN).

Recording sessions were carried out over a period of 5 months. During this period the deprived animals were placed in a normally illuminated environment.

Data Processing

Vestibular nystagmus was analyzed by constructing manually the slow cumulative eye position (SCEP) (Meiry 1965). In the case of step responses, the parameters C_m (peak value of SCEP), and t_o (time to SCEP peak), were computed (see Jeannerod et al. 1976, for a more detailed definition of these parameters). In the case of responses to sinusoidal oscillations, the average peak to peak values of SCEP over several cycles of clockwise and anticlockwise rotations were computed. The phase shift between the inversion of the slow compensatory eye movement and the corresponding inversion of the head position during responses to sinusoidal oscillations were measured and averaged.

The efficiency of compensatory eye-movements was expressed as the gain which is the relationship of the movement of the eye to that of the stimulus. The C_m divided by the amplitude of rotation of the table defines the gain of VOR. A gain of unity corresponds to an equal amplitude of displacement of eye and head. In OKN the slope of SCEP gives the velocity of eye movement which when divided by the velocity of the visual stimulus gives the gain of the nystagmus. At a gain of one, therefore, eye velocity equals stimulus velocity.

Binocular OKN had a gain which did not depend on direction of stimulus and the results for rotation in either direction were pooled. Monocular OKN in the normal cat is asymmetrical (Braun and Gault 1969), stimuli moving in the temporal-nasal direction (stimuli moving from left to right viewed by the left eye and right to left moving stimuli viewed by the right eye) elicits a stronger OKN than nasal-temporal moving stimuli. Therefore, the gains of OKN resulting from nasal-temporal and temporal-nasal motion were computed separately.

Results

During the first trials it was noticed that both strobe cats showed a deviation of eye position when placed in the dark. The ability to maintain a fixed gaze in the dark was found to improve after exposure of a few days to normal lighting. This deficit, which has also been found in dark reared cats (unpubl. observ.), was not quantified and will not be described further.

Optokinetic Nystagmus

Binocular OKN. Under our conditions of stimulation the normal cat maintained a gain of unity for OKN up to stimulus velocities of around 30°/s (Fig. 1). At velocities in excess of 30°/s there was a progressive decrease in gain to 0.6 at 60°/s. In the strobe reared cats the response approached normal values only at the very slowest velocities (Fig. 1). At 10°/s, the mean gain was 0.7 and with increasing stimulus velocities fell to progressively lower values. At 30°/s the slow phase velocity of OKN was considerably below that of stimulus velocity and the mean gain was less than 0.2. The variability of the response was greater in the strobe reared animals than in the normal. This is reflected by the large standard deviation values in Fig. 1.

Monocular OKN. Stimulating only one eye in the normal animal gives a response which up to 30°/s is as strong as the binocularly viewed OKN (Fig. 2). At velocities in excess of 30°/s the gain of monocular OKN drops faster than does the response to binocular stimulation and at 60°/s the monocular OKN had a gain not higher than 0.31 whereas at the same velocity the mean gain of the binocular response was 0.64. Not only was the gain lower at high stimulus velocities but there appeared a consistent asymmetry according to the direction of stimulation. As expected, stimulus moving in the temporal-nasal direction elicited a more vigorous response than did a stimulus moving in the nasal-temporal direction. In the normal animal the mean difference in gain between the two directions is around 25%. In the strobe reared animal this asymmetry was much more pronounced (Fig. 2). Stimuli moving in a temporal-nasal direction at 7°/s elicited a nystagmus with a mean gain (0.8) only slightly less than that resulting from binocular stimulation (0.9). Stimuli moving in a nasal-temporal direction at the same velocity gave a considerably weaker nystagmus which did not exceed a gain of 0.2 and disappeared at velocities over 30°/s. The monocular optokinetic response in the preferred direction fell off much quicker than that following

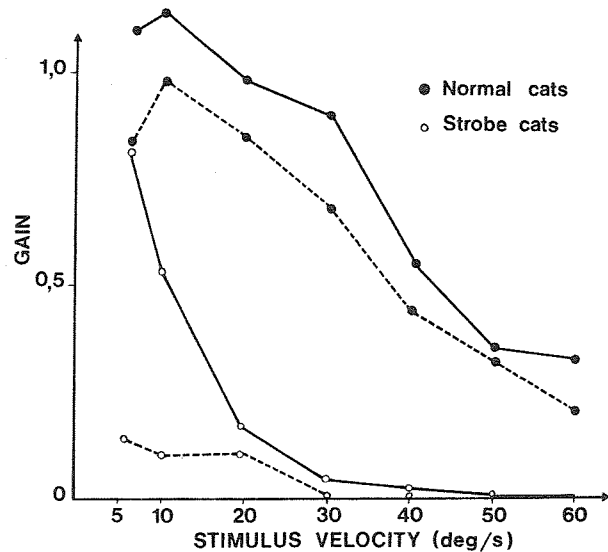


Fig. 2. The gain of the horizontal optokinetic nystagmus following monocular stimulation as a function of stimulus velocity. Mean values are shown for two measurements made for the normal (filled circles) and strobe reared animals (open circles). In both sets of animals the mean gain values for temporal-nasal directed stimuli are shown by a continuous line and for nasal-temporal directed stimuli by a discontinuous line

binocular stimulation. At 30°/s monocular stimulation in the temporal-nasal direction gives rise to a gain of 0.05 compared to a gain of 0.18 during binocular stimulation at the same velocity. It should be mentioned that at the gain values of OKN approaching zero in strobe reared cats the few eye movements which did occur were always found to be in the correct direction i.e., the slow phase of the eye movement was in the direction of stimulus movement.

Vestibulo-ocular Reflex

Normal animals did not show a significant variation in mean VOR gain with the frequencies used, confirming the results of Robinson (1976). Strobe reared cats showed a reduction in mean gain values of 45–47% at the lower frequencies and of 38% at 0.1 Hz. The differences in gain and the variability of response for the two sets of animals are shown in Fig. 3. Despite a large degree of variability in the responses, there was no overlap in the gain values obtained from normal and strobe reared animals.

Although the gain of VOR was lower in the strobe reared animal than in the normal, other aspects of VOR appeared quite normal (see trace 2 in Figs. 5 and 7). In the normal animal deceleration at

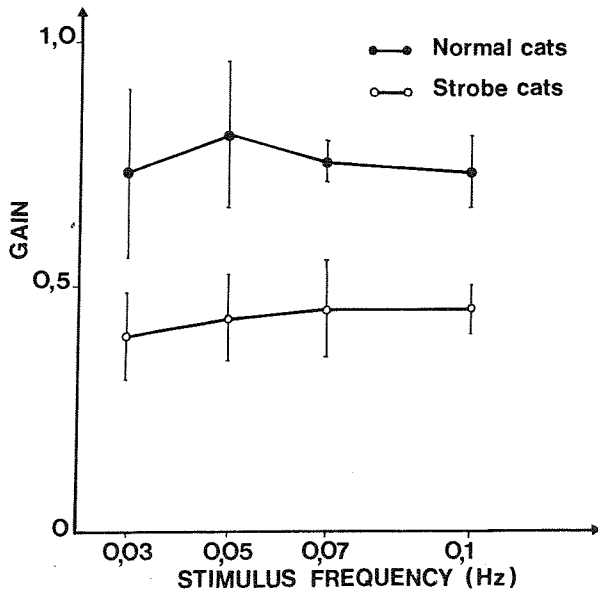


Fig. 3. The gain of the vestibular ocular reflex in the horizontal plane as a function of frequency of sinusoidal rotation at constant maximum velocity. The gain is defined as the ratio of amplitude of slow cumulative eye position to the amplitude of head movement. Mean values and S.D. from two determinations for normal (filled circles) and strobe reared cats (open circles)

low frequencies of sinusoidal rotation in the dark causes the eye-movements to change direction before reversal of head rotation. The time interval between inversion of the slow phase of the eye movement and the zero velocity of the head defines the phase lead. This phase lead reflects the dynamics of the vestibular system and was found to be similar in normal and strobe reared animals (Fig. 4).

The parameter t_0 of VOR was estimated from the response to steps in angular velocity ($160^\circ/s$). The time interval measured was between the initiation of the step and the inversion of the slow phase of the nystagmus. The value of t_0 was found to be between 22 and 28 s in both the deprived and normal animals.

Visuo-vestibular Interactions

Visual Suppression of VOR. Sinusoidal rotation in a lighted environment stationary with respect to the cat's head changes VOR gain. Although rotating the normal cat in the dark for instance at a frequency of 0.03 produces a VOR with a gain of 0.7 (Fig. 3), illumination of the cylinder during rotation results in a decrease in the velocity of the slow phase of the nystagmus as well as in the number of beats (Fig. 5, trace 3). Comparison of the SCEP obtained in the two conditions shows that the gain during rotation in

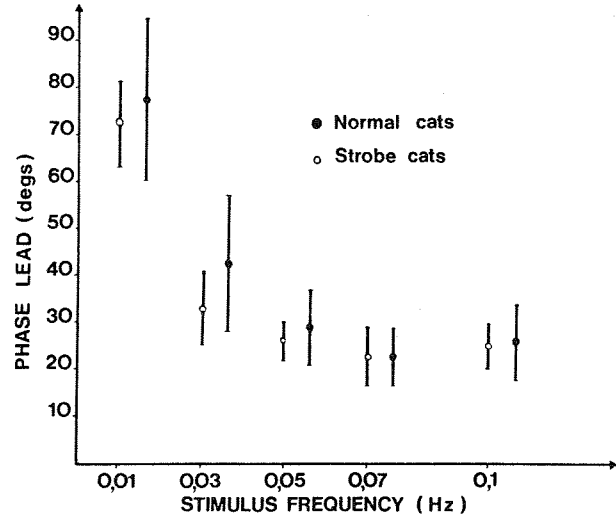


Fig. 4. The phase relation of the vestibulo-ocular response as a function of stimulus frequency. Mean values and S.D. are shown for two determinations in the strobe reared cats (open circles) and for normal cats (filled circles)

the light is reduced more than twofold. The slope of the SCEP during rotation in the light not only is less steep than that obtained in the dark, reflecting a lower slow phase velocity but also shows a plateau instead of an inversion of the slow phase of the eye (Fig. 5, trace 4). Rotation at higher frequencies produces larger accelerations and visual suppression of VOR is decreased. This is shown in Fig. 6 where the percentage of visual suppression $\frac{(C_{md}-C_{ml})}{C_{md}} \times 100$ where the suffix l and d refer to rotation in the light and in the dark is expressed as a function of frequency of sinusoidal rotation. At increasing acceleration values the percentage of visual VOR suppression dropped off from nearly 100% at 0.01 Hz to 15% at 0.1 Hz. In contrast strobe reared cats showed a considerably reduced capacity to suppress their VOR. At 0.03 Hz the SCEP in the dark and in the light was quite similar (Fig. 5, trace 4). At the lowest frequency tested (0.01 Hz) they showed a suppression of only about 20% which dropped to 10% at higher frequencies. In one test the frequency of the beats was slightly higher during rotation in the light.

Improvement of VOR During Sinusoidal Rotation in the Light. Sinusoidal rotation in a lighted environment has been shown in the normal animal to improve the gain to approximately unity (Keller and Precht 1979). We tested the effect of the interaction between vestibular and visually provoked eye-movements by sinusoidally rotating the cats whilst the cylinder was illuminated and kept stationary with respect to the laboratory. The mean percentage of

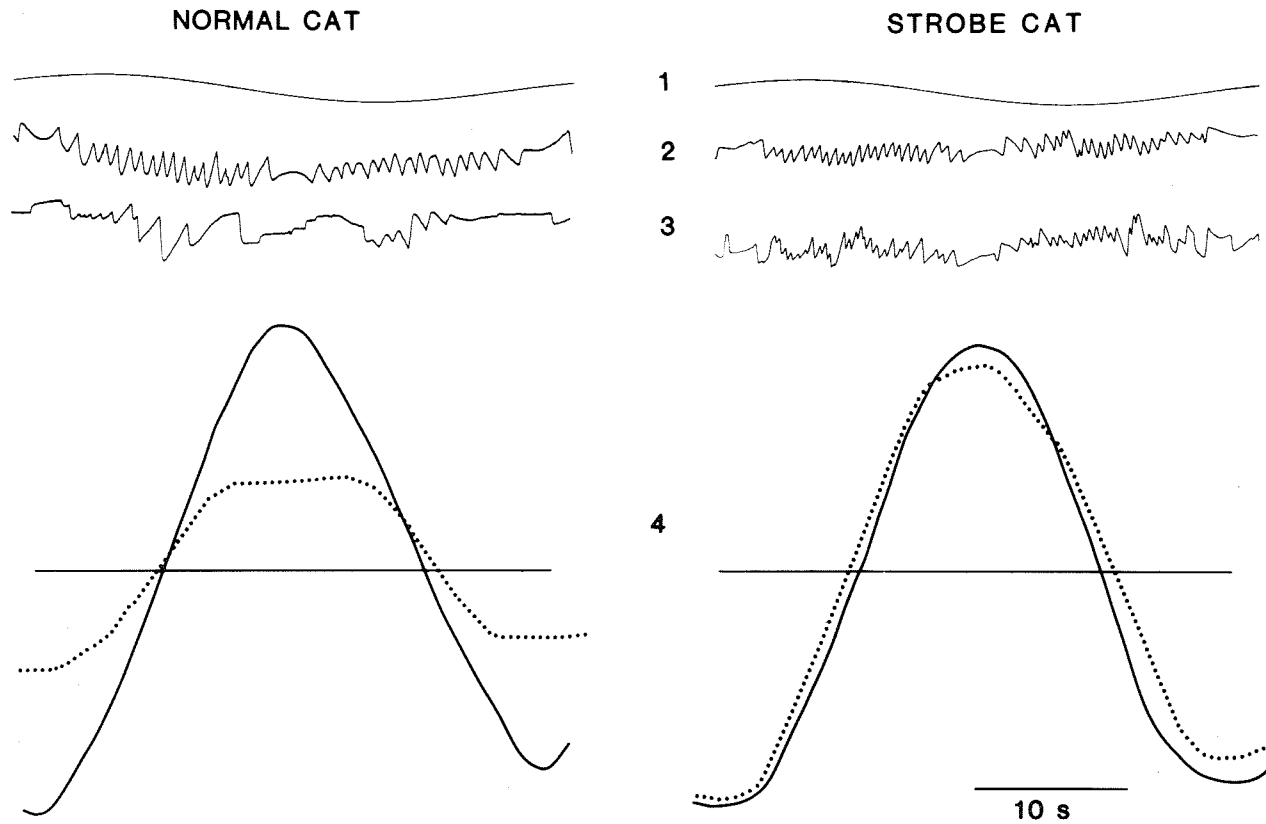


Fig. 5. Visual suppression of the vestibulo-ocular reflex evoked by sinusoidal rotation (frequency 0.03 Hz, maximum velocity 80°/s) for a normal and a strobe reared cat. (1) Head position, upward deflection clockwise rotation, (2) Electro-oculogram in the dark, (3) Electro-oculogram with a visual environment stationary with respect to the head, (4) Slow cumulative eye position corresponding to the records displayed in 2 (continuous line-vestibulo-ocular reflex in the dark) and 3 (discontinuous line-vestibulo-ocular reflex in the light)

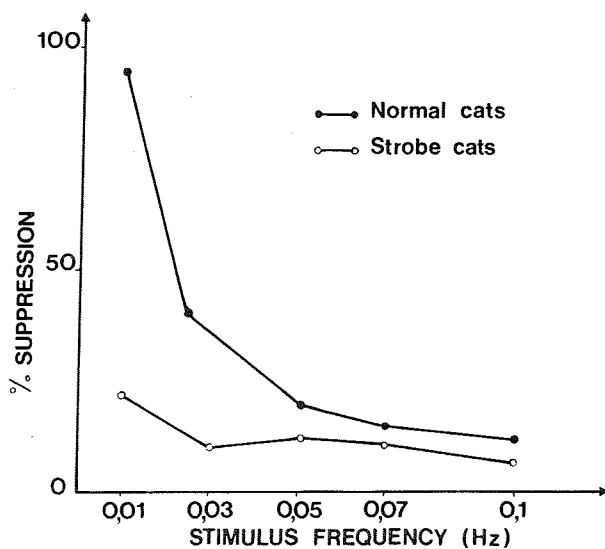


Fig. 6. Percentage of visual suppression of the vestibulo-ocular reflex as a function of the frequency of sinusoidal rotation. The percentage of visual suppression of the VOR obtained was calculated for each frequency and the mean value obtained from two determinations in normal (filled circles) and strobe reared (open circles) cats

increase of the response from the two strobe reared and the three normal animals are shown in Table 1. It can be seen that the normal animals were able to improve the strength of their nystagmus, the degree of improvement being greater at lower frequencies. The maximum extent of improvement was in the order of 30%. Although the gain of VOR of strobe reared cats was very low in the dark (see Fig. 3), they were unable to increase the strength of their nystagmus when rotated in the light. Rotation in the light gave little or no difference in the gain and therefore SD of the multiplication factor was very small.

During sinusoidal rotation in the dark the nystagmus inversion leads the inversion of the head position (e.g., Fig. 7, trace 2). The magnitude of this phase lead is dependent on the frequency of stimulation (lower curves in Fig. 6). The normal animal, when rotated in the light shows a considerable reduction in phase lead to near zero values and, therefore, vestibular stimulation in the light produces fully compensatory eye movements (Fig. 7, trace 3). Strobe reared cats showed a similar phase lead during sinusoidal rotation in the dark. However, they could

Table 1. Enhancement of the VOR in the light

| | Stimulus frequency | Multiplication factor ¹ |
|--------------------|--------------------|------------------------------------|
| Normal cats | 0.03 Hz | 1.15 ± 0.18 |
| | 0.05 Hz | 1.15 ± 0.16 |
| | 0.07 Hz | 1.13 ± 0.11 |
| | 0.1 Hz | 1.08 ± 0.06 |
| Strobe reared cats | 0.03 Hz | 0.93 ± 0.03 |
| | 0.05 Hz | 1.01 ± 0.05 |
| | 0.07 Hz | 0.96 ± 0.04 |
| | 0.1 Hz | 0.97 ± 0.06 |

¹ $\frac{\text{VOR in the dark}}{\text{VOR in the light}}$

Mean increase of VOR in the light expressed as a multiplication factor of VOR in the dark in two trials in normal and strobe reared cats.

not reduce their phase lead when rotated in an illuminated environment. Eye inversion still preceded head inversion during rotation in the light by similar values as those found during rotation in the dark. Therefore, vestibular stimulation in an illuminated environment in the strobe reared animals gave

rise during part of the cycle to anticompany eye movements.

Discussion

There is evidence for two pathways mediating OKN, (1) a largely crossed subcortical pathway in which temporal-nasal directed stimulation predominates in eliciting a nystagmus and, (2) a cortical pathway which is responsible for a symmetrical oculomotor response (Fukuda 1959; Braun and Gault 1969; Wood et al. 1973; Hoffmann and Schopmann 1975; Montarolo et al. 1981). The visual cortex has been shown to increase the gain of OKN particularly at higher velocities resulting from both directions of horizontal stimulation, although more so for uncrossed fibers and for the nasal-temporal direction (Montarolo et al. 1981). The absence of a temporal directed monocular OKN in the strobe cat and the drop off in gain at high velocities of the binocular OKN indicate, therefore, a failure of the cortex to contribute to visually elicited reflex eye-movements.

The absence of cortical participation in OKN in strobe reared cats could be the result of a disruption

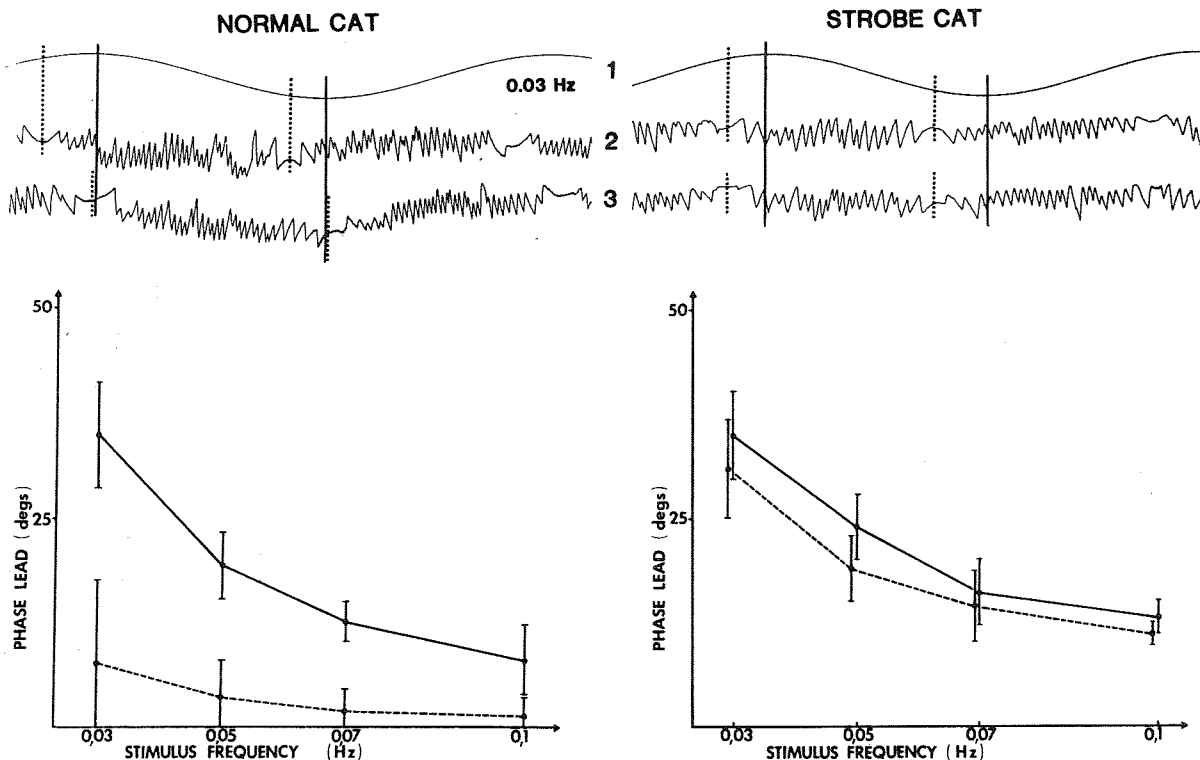


Fig. 7. Phase lead of inversion of the slow phase of the VOR and the effect of sinusoidal rotation in the light. *Upper part of figure:* oculograms obtained at 0.03 Hz. (1) head position, (2) VOR in the dark, (3) VOR in the light. Continuous line indicates inversion of rotation of the head and dotted line the inversion of the slow phase of the nystagmus. *Lower part of figure:* phase lead of the inversion of the slow phase of the nystagmus in the dark (continuous line) and in the light (dotted line) as a function of the frequency of sinusoidal rotation. Values and S.D. from two determinations in the normal and strobe reared cats

of cortical influences on midbrain structures. Strobe rearing has been shown to lead to deficits in neuron response in the superior colliculus which can be best explained by a disruption of the descending corticotectal pathway (Flandrin et al. 1976; Kennedy et al. 1980). There is evidence that the cortical projections to the nucleus of the optic tract (NOT) arise from collaterals of cortico-tectal cells (Schopmann 1981). The NOT has been suggested as playing a privileged role in controlling the slow phase of OKN (Collewyn 1975a, b; Hoffmann and Schopmann 1975) and developmental manipulation and decortication gives rise to neuron deficits in the NOT which can be interpreted as a functional disconnection of the ipsilateral input to this pretectal nucleus via the visual cortex (Hoffmann 1979, 1982).

VOR gain in strobe reared cats was very much reduced, although it appeared quite normal in other respects. Velocity steps of $160^\circ/\text{s}$ in the dark produced a post rotatory nystagmus with a first component which lasted for about 25 s. This is similar to the value obtained for normal animals. The phase relationship between the movement of the eyes and the head decreased with increasing oscillation frequency in a similar way as in the normal cat. The normal time constant of the post-rotatory nystagmus and the phase lead of eye position during sinusoidal rotation in the dark would suggest that the dynamics of the vestibular control of eye movements have remained essentially similar to those in the normal animals (Robinson 1977). The reduced gain of VOR however indicates that the efficiency of the vestibular input has decreased and shows that experience of visual movement during development is necessary for its proper maturation.

In the normal adult perfect stabilization of the retinal image is achieved by a cooperation between vestibular and optokinetic compensatory eye movements. Movement of the head evokes compensatory eye movements in the opposite direction and movement of the visual world in the same direction as the visual stimuli. Accordingly rotation of the animal in an illuminated, earth fixed environment gives an improved nystagmus efficiency with respect to that obtained from purely vestibular stimulation and the gain reaches unity (Keller and Precht 1979; Montarolo et al. 1981). This is not the case in strobe reared cats where rotation in the light failed to give an improvement in gain, thus indicating an impossibility in additive interaction between VOR and OKN. Rotation of animals with a visual environment which is stationary with respect to the head gives rise to a displacement of the retinal image resulting from the slow phase eye-movement of the VOR. In the normal animal this displacement of the retinal image

gives an OKN of opposite sign to that of rotation. At low frequencies of sinusoidal rotation the two types of nystagmus cancel each other out and the cat can maintain a fixed retinal image. At higher frequencies visual suppression breaks down at maximum velocities. In the strobe reared animal NOK is very low except at very slow stimulus velocities and is not sufficient to suppress VOR.

In many ways deprivation of visual movement during development gives rise to similar deficits of the oculomotor system as does rearing animals in total darkness (Vital-Durand et al. 1974; Berthoz et al. 1975; Collewyn 1977; Harris and Cynader 1981). Both types of developmental manipulation give rise to a reduced gain of VOR and OKN and can be interpreted as a perturbation of the influence of the visual cortex on these two types of nystagmus. Adult strobe reared cats failed to develop normal VOR and OKN after 5 months of exposure to normal light. A similar lack of recuperation was also found in adult dark reared cats (Harris and Cynader 1981). Adult strobe reared cats differed from dark reared cats in that simultaneous activation of both the OKN and the VOR did not lead to effective compensatory eye movements. In their study Harris and Cynader (1981) found that dark reared cats rotated in the light had a gain of unity. Therefore, the dark reared cat is able to achieve stabilization of the retinal image. In this respect strobe reared cats appeared to be more incapacitated than dark reared cats as sinusoidal rotation in an illuminated environment did not give an improvement in gain. This failure of the strobe reared cat to supplement VOR with OKN is coherent with its incapacity to use visual input to suppress its VOR and also the failure of the visual system to adjust VOR during the 5 months period after the animal had been brought into the light. OKN and VOR deficits found after strobe and dark rearing suggest that normal development of the oculomotor system is not dependent on visual input per se but on movement of the retinal image, resulting either from saccadic eye-movements or from movement of visual stimuli.

The oculomotor deficits in strobe reared cats revealed in this study could indicate a failure of the visual cortex to participate in compensatory eye movements. A clue to understanding the perturbation of the behavior of strobe reared cats may, therefore, reside in a consideration of the deficits at the cortical level. Single unit recording in the primary visual cortices of adult strobe reared cats reared in an identical fashion to those used in this study have shown that nearly every aspect of neuron response is perturbed in these animals. The neuron deficits encountered in areas 17 and 18 included a modifica-

tion of the spatial characteristics of the receptive fields, a decrease in the number of neurons receiving an input from both eyes, a disappearance of cells selective to the direction of movement of a visual stimulus and a modification of velocity sensitivity including a loss of neurons responding to high velocities (Orban et al. 1978; Kennedy et al. 1981). In normal animals, neurons in area 18 subserving the central visual field show a greater degree of direction selectivity, sharper velocity tuning and respond to lower velocities than do neurons in cortex subserving the peripheral visual field (Orban et al. 1981a, b). In strobe reared cats this specialization of the cortex subserving the central visual field is lost and there is a flat distribution of neuron properties across the cortex.

The asymmetrical response of the monocular OKN is the outstanding deficit of the strobe reared cat. The asymmetrical response probably originates from a cortical deficit and could be linked to the lack of direction selective neurons at this level. The absence of neurons in the visual cortices of these animals responding to fast velocities might be responsible for the incapacity of the cortex to maintain OKN gain at high stimulus velocities. However, it has been suggested by Tauber and Atkin (1968) that optokinetic symmetry has developed in relation to foveal organization. A symmetrical response would provide better conjugate performance of the two eyes and result in improved binocular vision. It may be therefore that in strobe reared cats, where there is no specialization of cortex subserving the area centralis and where there is an absence of binocular interaction, that the need or the capacity to elaborate a symmetrical monocular OKN is comprised.

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References

- Amblard B, Courjon JH, Cremieux J, Flandrin JM, Kennedy H (1981) The influence of stroboscopic rearing on the optokinetic nystagmus in the cat. *J Physiol (Lond)* 317: 74–75 P
- Berthoz A, Jeannerod M, Vital-Durand F, Oliveras JL (1975) Development of vestibulo-ocular responses in visually deprived kittens. *Exp Brain Res* 23: 425–442
- Braun JJ, Gault FP (1969) Monocular and binocular control of horizontal optokinetic nystagmus in cats and rabbits. *J Comp Physiol Psychol* 1: 12–16
- Collewijn H (1975a) Direction-selective units in the rabbit's nucleus of the optic tract. *Brain Res* 100: 489–508
- Collewijn H (1975b) Oculomotor areas in the rabbit's midbrain and pretectum. *J Neurobiol* 6: 3–22
- Collewijn H (1977) Optokinetic and vestibulo-ocular reflexes in dark reared rabbits. *Exp Brain Res* 27: 287–300
- Cynader M, Berman N, Hein A (1973) Cats reared in stroboscopic illumination: Effects on receptive fields in visual cortex. *Proc Natl Acad Sci USA* 70: 1353–1354
- Cynader M, Chernenko G (1976) Abolition of direction selectivity in the visual cortex of the cat. *Science* 193: 504–505
- Flandrin JM, Jeannerod M (1977) Developmental constraints of motion detection mechanisms in the kitten. *Perception* 6: 513–527
- Flandrin JM, Kennedy H, Amblard B (1976) Effects of stroboscopic rearing on the binocularity and directionality of cat superior colliculus. *Brain Res* 101: 576–581
- Flandrin JM, Courjon JH, Jeannerod M, Schmid R (1979) Vestibulo-ocular responses during the states of sleep in the cat. *Electroencephalogr Clin Neurophysiol* 46: 521–530
- Fukuda T (1959) The unidirectionality of the labyrinthine reflex in relation to the unidirectionality of the optokinetic reflex. *Acta Otolaryngol (Stockh)* 50: 507–516
- Harris LR, Cynader M (1981) The eye movements of the dark-reared cats. *Exp Brain Res* 44: 41–56
- Hoffmann KP (1982) The control of the optokinetic reflex by the nucleus of the optic tract in the cat. In: Hein A, Jeannerod M (eds) *Spatially oriented behavior*. Springer, Berlin Heidelberg New York (in press)
- Hoffmann KP (1979) Optokinetic nystagmus and single cell responses in the nucleus tractus opticus after early monocular deprivation in the cat. In: Freeman RD (ed) *Developmental neurobiology of vision*. Plenum, New York, pp 63–72
- Hoffmann KP, Shoppmann A (1975) Retinal input to direction selective cells in the nucleus tractus opticus of the cat. *Brain Res* 99: 359–366
- Jeannerod M, Magnin M, Schmid R, Stefanelli M (1976) Vestibular habituation to angular velocity step in the cat: A new description. *Biol Cybern* 22: 39–48
- Keller EL, Precht W (1979) Visual-vestibular responses in vestibular nuclear neurons in the intact and cerebellectomized alert cat. *Neuroscience* 4: 1599–1613
- Kennedy H, Flandrin JM, Amblard B (1980) Afferent visual pathways and receptive field properties of superior colliculus neurons in stroboscopically reared cats. *Neurosci Lett* 19: 283–288
- Kennedy H, Orban GA, Maes H (1981) The effects of stroboscopic rearing on cat visual cortex. *Neurosci Lett [Suppl]* 7: 202
- Magnin M, Jeannerod M (1973) Fixation non traumatique de la tête chez le chat éveillé. *C R Séances Soc Biol Paris* 167: 996–998
- Meiry JL (1965) The vestibular system and human dynamic space orientation. Sc D. Thesis M.I.T.
- Montarolo PG, Precht W, Strata P (1981) Functional organization of the mechanisms subserving the optokinetic nystagmus in the cat. *Neuroscience* 6: 231–246
- Olson CR, Pettigrew JD (1974) Single units in visual cortex of kittens reared in stroboscopic illumination. *Brain Res* 70: 189–204
- Orban GA, Kennedy H, Maes H (1981a) Response to movement of neurons in areas 17 and 18 of the cat: Velocity selectivity. *J Neurophysiol* 45: 1043–1058
- Orban GA, Kennedy H, Maes H (1981b) Response to movement of neurons in areas 17 and 18 of the cat: Direction selectivity. *J Neurophysiol* 45: 1059–1073
- Orban GA, Kennedy H, Maes H, Amblard B (1978) Cats reared in stroboscopic illumination: Velocity characteristics of area 18 neurons. *Arch Ital Biol* 116: 413–419
- Pasternak T, Movshon JA, Merigan WH (1981) Creation of direction selectivity in adult strobe-reared cats. *Nature* 292: 834–837
- Riesen AH (1961) Studying perceptual development using the technique of sensory deprivation. *J Nerv Ment Dis* 132: 21–25

- Robinson DA (1976) Adaptive gain control of vestibulo-ocular reflex by the cerebellum. *J Neurophysiol* 39: 954-969
- Robinson DA (1977) Vestibular and optokinetic symbiosis. An example of explaining by modelling. In: Baker R, Berthoz A (eds) *Control of gaze by brain stem neurons*. Elsevier, Amsterdam, pp 49-58
- Schopmann A (1981) Projections from areas 17 and 18 of the visual cortex to the nucleus of the optic tract. *Brain Res* 223: 1-17
- Stryker M, Blakemore C (1972) Saccadic and disjunctive eye movements in cats. *Vision Res* 12: 2005-2013
- Tauber ES, Atkin A (1968) Optomotor responses to monocular stimulation. Relation to visual system organization. *Science* 160: 1365-1367
- Vakkur GS, Bishop PO (1963) The schematic eye in the cat. *Vision Res* 3: 357-381
- Van Hof-Van Duin J (1976) Development of visuomotor behavior in normal and dark-reared cats. *Brain Res* 104: 233-241
- Vital-Durand F, Putkonen PTS, Jeannerod M (1974) Motion detection and optokinetic response in dark-reared kittens. *Vision Res* 14: 141-142
- Wood CC, Spear PD, Braun JJ (1973) Direction-specific deficits in horizontal optokinetic nystagmus following removal of the visual cortex. *Brain Res* 60: 231-237

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