

The Eye Movements of the Dark-reared Cat*

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Summary. Cats reared in total darkness to adulthood have abnormal eye movements. A spontaneous nystagmus is found in the dark before any visual experience. The eye movements evoked by vestibular or optokinetic stimulation are less effective at compensation than for a normal cat. The vestibulo-ocular reflex (VOR) has a low gain (around 0.3) and a frequency dependent phase relation. The efficiency of optokinetic nystagmus (OKN) is poorer than for a normal cat, except for downwards stimulus movement which is followed better than normal. OKN is poorest in response to a stimulus viewed monocularly moving in the nasal to temporal direction. Neither VOR nor OKN of a dark-reared cat recover in efficiency within 5 months of the animal being brought into the light. A normal cat put into the dark for 135 days shows none of these abnormalities except an occasional spontaneous nystagmus.

Key words: Eye movements – Dark-rearing – Cat – Vestibulo-ocular reflex – Optokinetic nystagmus

It is now well established that active visual experience is necessary for the normal development of the mammalian visual system. Depriving the organism of vision during early development results in profound visuomotor deficits (Riesen 1961; Wiesel and Hubel 1965a, b; Baxter 1966; van Hof-van Duin 1976). Prolonged visual deprivation also causes alterations in response characteristics of cells both in the

geniculostriate visual system (Wiesel and Hubel 1963, 1965a; Coleman and Riesen 1968; Buisseret and Imbert 1976; Cynader et al. 1976) and in the superior colliculus (Wickelgren and Sterling 1969; Cynader 1979). It is thus surprising that there have been no observations on the eye movements of cats reared in the dark to adulthood. The vestibulo-ocular reflex of kittens raised to the age of 4 months in the dark appears similar to that of normally reared kittens of the same age (Berthoz et al. 1975). The normal kitten at this age, however, does not yet have a fully developed oculomotor system, nor has the critical period for alteration of cortical connectivity yet ended in the animals (Olson and Freeman 1978; Cynader et al. 1980). Furthermore, the extent of recovery of visual function depends on the age at which the animal is first allowed visual experience (Timney et al. 1978). A 4 month old kitten reared in darkness from birth recovers considerably more visual acuity and cortical orientation selectivity over a few months than an older cat (Cynader et al. 1976; Timney et al. 1978; Cynader and Mitchell 1980).

We have therefore examined the eye movements of cats that were reared in darkness to adulthood. We have found substantial anomalies in the eye movements of such animals including those occurring spontaneously and those evoked by vestibular or visual stimulation.

Methods

Surgical Preparation of the Animals

Seven cats were used in this study. Four were normal and three were brought up in total darkness until the age of 11–15 months. All cats were implanted under Alfathesin anaesthetic with an eye coil for the measurement of eye position (Robinson 1963; Fuchs and Robinson 1966) and a pair of head-restraining tubes (Kopf) embedded in dental acrylic by means of which the head could be held firmly in the apparatus.

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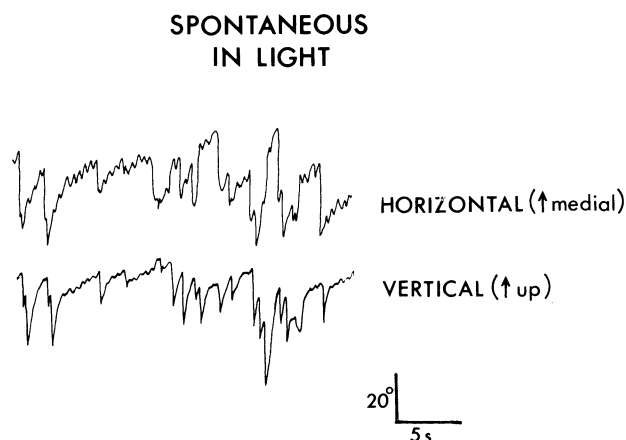


Fig. 2. The spontaneous horizontal and vertical eye movements of a dark-reared cat measured in the light. Typically both a horizontal and a vertical nystagmus were present. Note also the appearance of a low amplitude, high frequency pendular nystagmus not present in the dark

before the animal had any vision. The cat was mounted in the apparatus in dim light whilst wearing a light-proof bag over his head and the room lights were then extinguished.

The gain of the vestibulo-ocular response (defined as the ratio of the amplitude of slow phase response to the stimulus amplitude) to sinusoidal rotation is shown in Fig. 4. This figure compares the responses of dark-reared cats to those of normal cats. The gain is consistently low in the dark-reared cat while being very close to unity over this range in the normal adult cat. It is unlikely that this large gain difference could be due to a reduced state of arousal of the dark-reared cats. All animals were kept aroused by the experimenters frequently making a loud and varied series of noises.

The phase relation of the vestibulo-ocular response is also shown in Fig. 4. The phase of the VOR is defined with respect to a value of 0° corresponding to a perfect compensatory movement by the eyes (i.e., when the positions of the eye and table are 180° out of phase). A normal cat has a slight phase lead (eyes before head) throughout this frequency range (around 15° over this range of frequencies). The phase of the dark-reared cat's slow-phase response is dependent on the frequency of oscillation at this amplitude of sinusoidal rotation (10°). The dark-reared cat actually has a phase lead of 180° at a frequency of about 0.3 Hz (10° peak-to-peak; $9.4^\circ/\text{s}$ peak velocity). At this frequency the eye movement is actually in the *same* direction as the head and is therefore anti-compensatory.

The vestibulo-ocular reflex in response to sinusoidal oscillation was further investigated by varying the

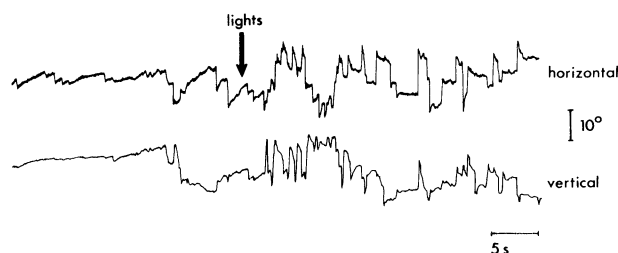


Fig. 3. The eye movements of a dark-reared cat upon the occasion of his first exposure to light. Note the great increase in frequency of both horizontal and vertical saccades. The lights remained on for the duration of the record right of the arrow

amplitude of oscillation. The effect of this on the phase of the response is shown in Fig. 5 in which the phase is plotted for three amplitudes of oscillation (10° , 30° , 60° peak-to-peak). Although the gain of the response was unaffected by the increase in amplitude (and thus of peak velocity), Fig. 5 shows that the phase is brought close to that of the normal cat (cf., Fig. 4). The points marked with asterisks on the three phase curves in Fig. 5 correspond to a constant peak velocity in each case. It is evident that different phase relationships of the VOR are associated with the same peak velocity in the dark-reared animals.

The efficiency of the vestibulo-ocular system was further measured by the ocular response to a step in angular velocity. Results are shown in Fig. 6 in which the response of a normal cat and a dark-reared cat are compared. The table was rotated at a constant angular velocity of $70^\circ/\text{s}$ for 2 min and then halted abruptly. The normal cat displayed a postrotatory nystagmus which persisted for some time after such a velocity step (Fig. 6, top two traces, corresponding to position and velocity) decaying with a time constant of 18.5 s. The response of the dark-reared cat to the same step is shown in the next two traces in Fig. 6. Two things are immediately apparent from a comparison of the normal and dark-reared traces. Firstly the peak "slow-phase" eye velocity of the dark-reared is much lower than that produced by the normal cat in response to an identical step. Secondly the response declines very much faster.

The decline of eye movement velocity of a normal cat after exposure to a step of velocity is only very roughly approximated by an exponential. This is particularly true as the eye velocity approaches zero (Fig. 6 top traces). Since the dark-reared cat's response to a velocity step reaches a maximum much closer to zero velocity, the lack of a truly exponential decline may contribute to the observed difference in the duration of post-rotatory nystagmus. The dark-reared cat was therefore subjected to a velocity step

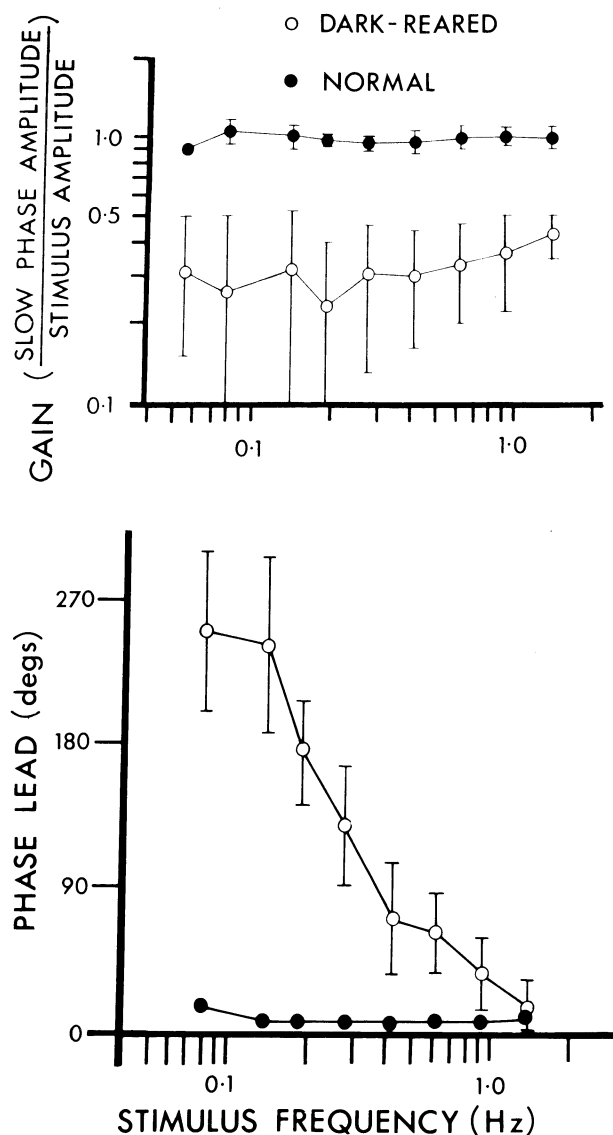


Fig. 4. The gain and phase of the vestibulo-ocular reflex of the dark-reared cat (open circles) compared to that of the normal cat (filled circles). The gain and phase were measured by hand. Each point is the average of five cycles for three cats on at least three occasions. The standard deviations are also plotted. Amplitude of rotation was held constant at 10° peak-to-peak

of three times that used for the normal cat (i.e., $210^\circ/\text{s}$). This resulted in a maximum slow-phase eye velocity very close to that of the normal cat's records shown in Fig. 6. The records thus obtained from the dark-reared cat are shown as the bottom two traces of Fig. 6. They demonstrate that the rate of decline is independent of the maximum velocity of the slow-phase response over this range of velocity steps. The time constant in this case was 6 s, a value very close to that achieved with the smaller step in velocity.

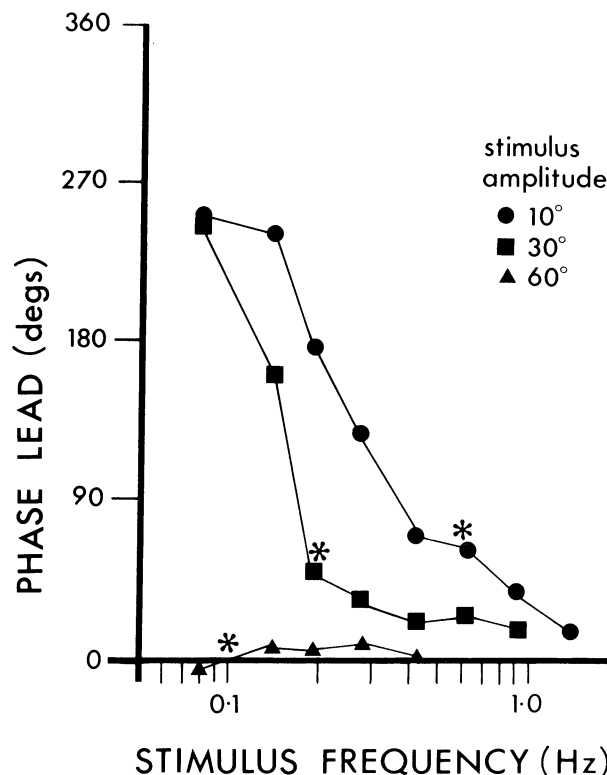


Fig. 5. As the amplitude of rotation was increased, the phase relation with frequency changed. The asterisks correspond to points on each graph that have the same peak velocity ($18.8^\circ/\text{s}$)

Optokinetic Nystagmus and Optokinetic After-nystagmus of the Dark-reared Cat. After the initial effects of the first visual exposure had subsided (Fig. 3) but before the dark-reared animals had been allowed to move freely in a normally lit environment, we measured the optokinetic response. The cats were held in the centre of an optokinetic drum which was rotated about a vertical axis. Figure 7A compares the response of a normal cat to that of a dark-reared animal. For normal cats the gain (defined as the ratio of eye velocity to the velocity of the drum) was close to unity indicating near perfect image stabilisation over the range of velocities used in these experiments. For the dark-reared cats the response was close to normal at low drum speeds but fell off rapidly at higher speeds. Above about $30^\circ/\text{s}$ the response was totally inadequate and reduced the image slip on the retina by less than 5%.

Figure 7B illustrates the optokinetic responses to monocular stimulation. Monocularly viewed stimuli moving medially are followed more efficiently than are laterally-directed stimuli even by the normal cat. This asymmetry is, however, much exaggerated in the dark-reared cat who shows virtually no response to a laterally-directed stimulus. The apparently *nega-*

Velocity Steps

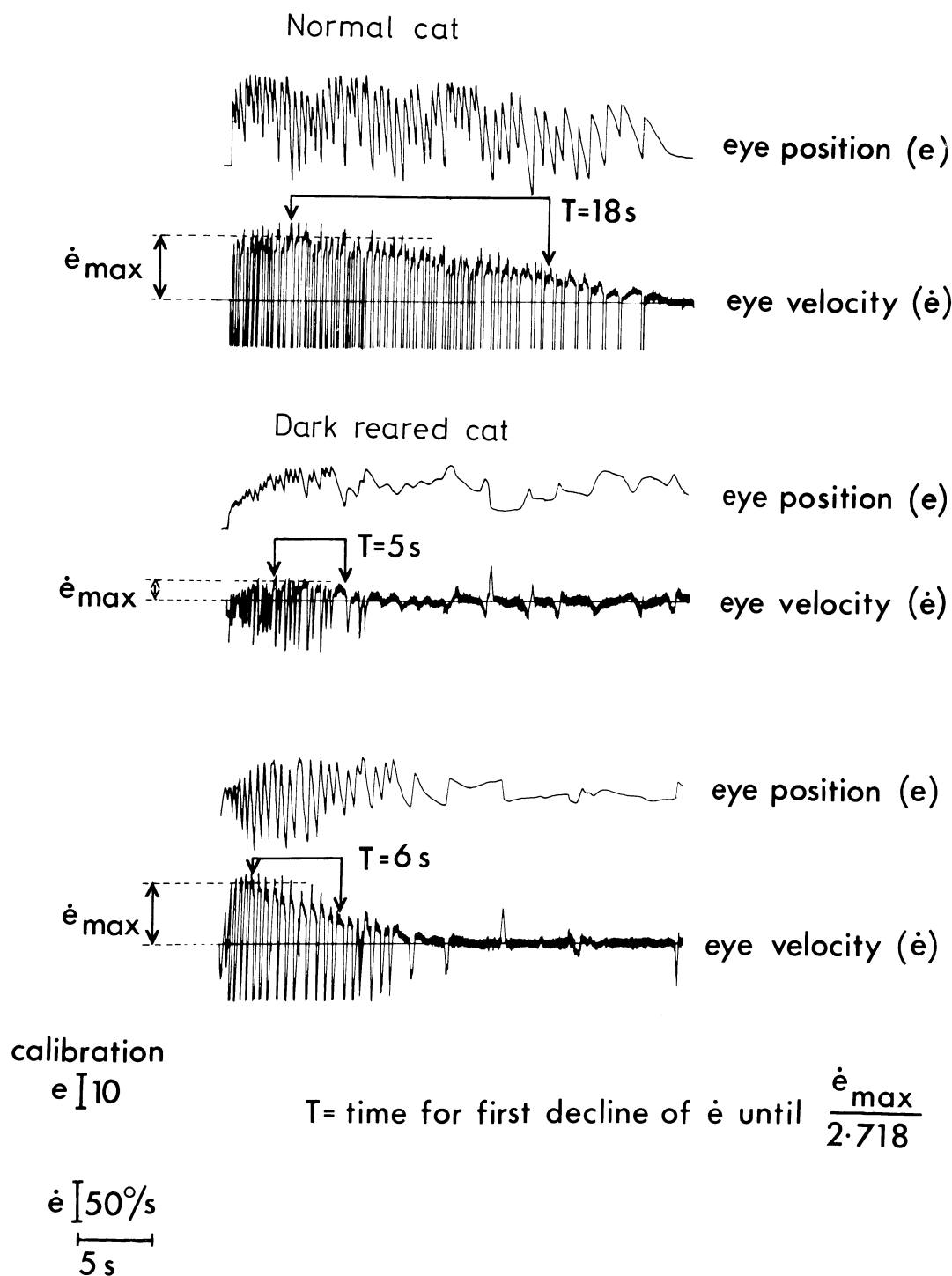


Fig. 6. The response of a normal cat (*top two traces*) and a dark-reared cat (*lower four traces*) to a step in velocity. The traces begin at the moment of the step. The responses to three steps are shown, each one giving rise to a pair of traces corresponding to eye position (*top trace of each pair*) and eye velocity (*lower trace of each pair*). The upper two steps were from $70^\circ/s$ to zero, and were applied to a normal cat (*top pair of traces*) and a dark-reared cat (*next pair of traces*). The results of a further step, of $210^\circ/s$ to zero, applied to the dark-reared cat is also shown (*lower two traces*)

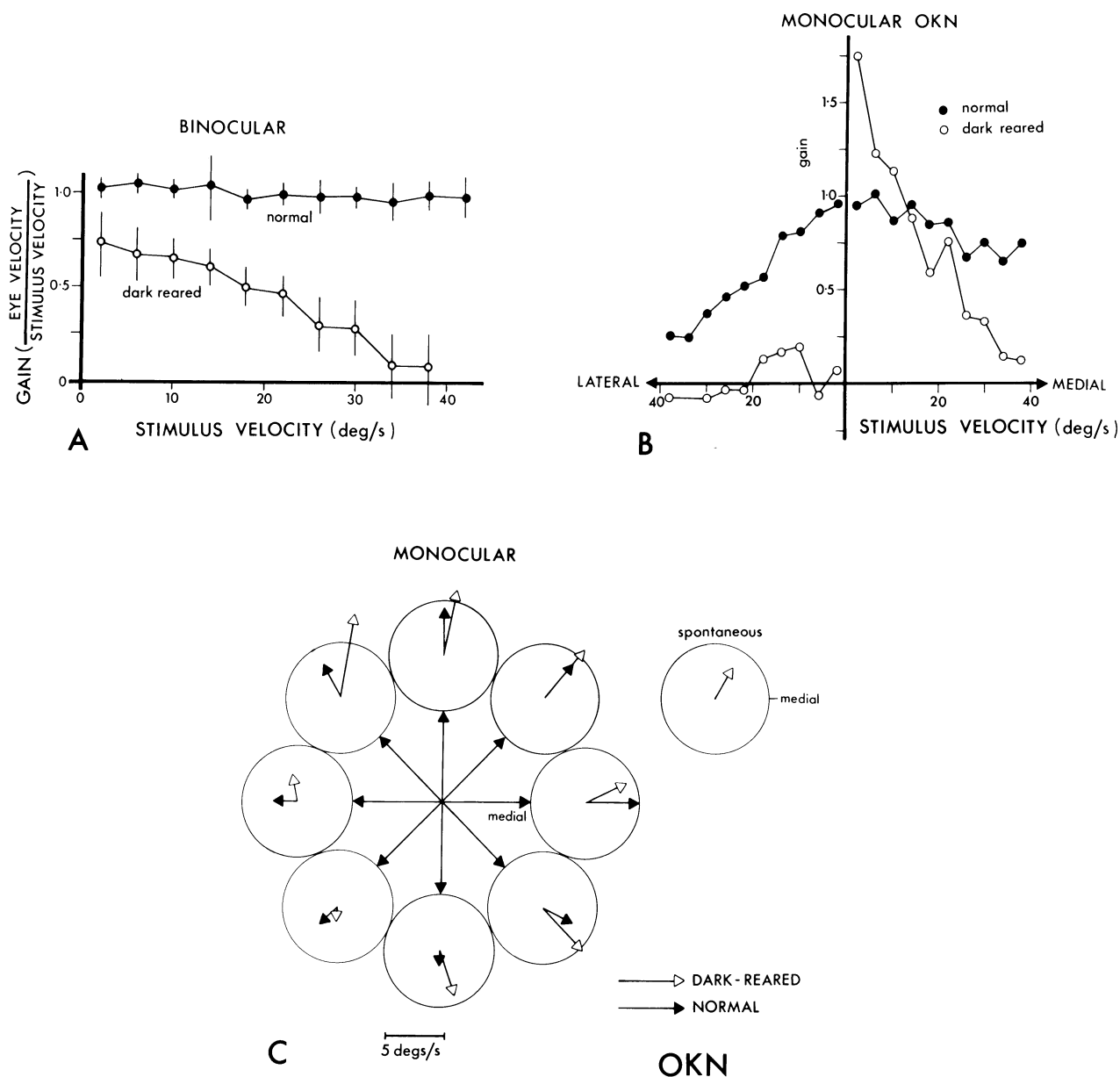


Fig. 7A-C. The gain of horizontal optokinetic nystagmus, measured with both eyes open **A** and monocularly **B**, as a function of drum speed for normal (filled circles) and dark-reared (open circles) cats. Gain is defined as eye velocity divided by stimulus velocity. The binocular data represent the means of at least two determinations of optokinetic slow phase gain in both horizontal directions of movement in each animal. The right hand part of **B** illustrates the responses of normal and dark-reared cats to monocularly viewed stimuli moving medially (towards the nose) while the left hand side shows responses to lateral movement. The drum consisted of a large cylinder (diameter 3 ft) on which high-contrast, vertical black and white stripes (period 20°) were painted. **C** shows the direction and velocity of the optokinetic response of normal (filled arrows) and dark-reared (open arrows) cats to a monocularly viewed grating drifting in various directions. The grating was back projected onto a tangent screen that was positioned 40 cm from the animal. The drift velocity was 10°/s at the centre but, of course, varied across the extent of the tangent screen. The direction of drift of the stimulus is shown by the position of the circle: the upper circle corresponds to upward drift etc. The velocity of the slow phase response is indicated by the length of the arrows; the direction of the arrow corresponds to the direction of the slow-phase. The circles have a diameter representing 5°/s

tive gain for laterally-directed stimuli and the apparent gain of greater than unity with low medial stimulus velocities can be accounted for in terms of the spontaneous eye movements described in Part 1.

Monocular stimuli were all viewed through the eye whose movements were being measured.

The monocular optokinetic reflex of the dark-reared and normal cats was also studied as a function

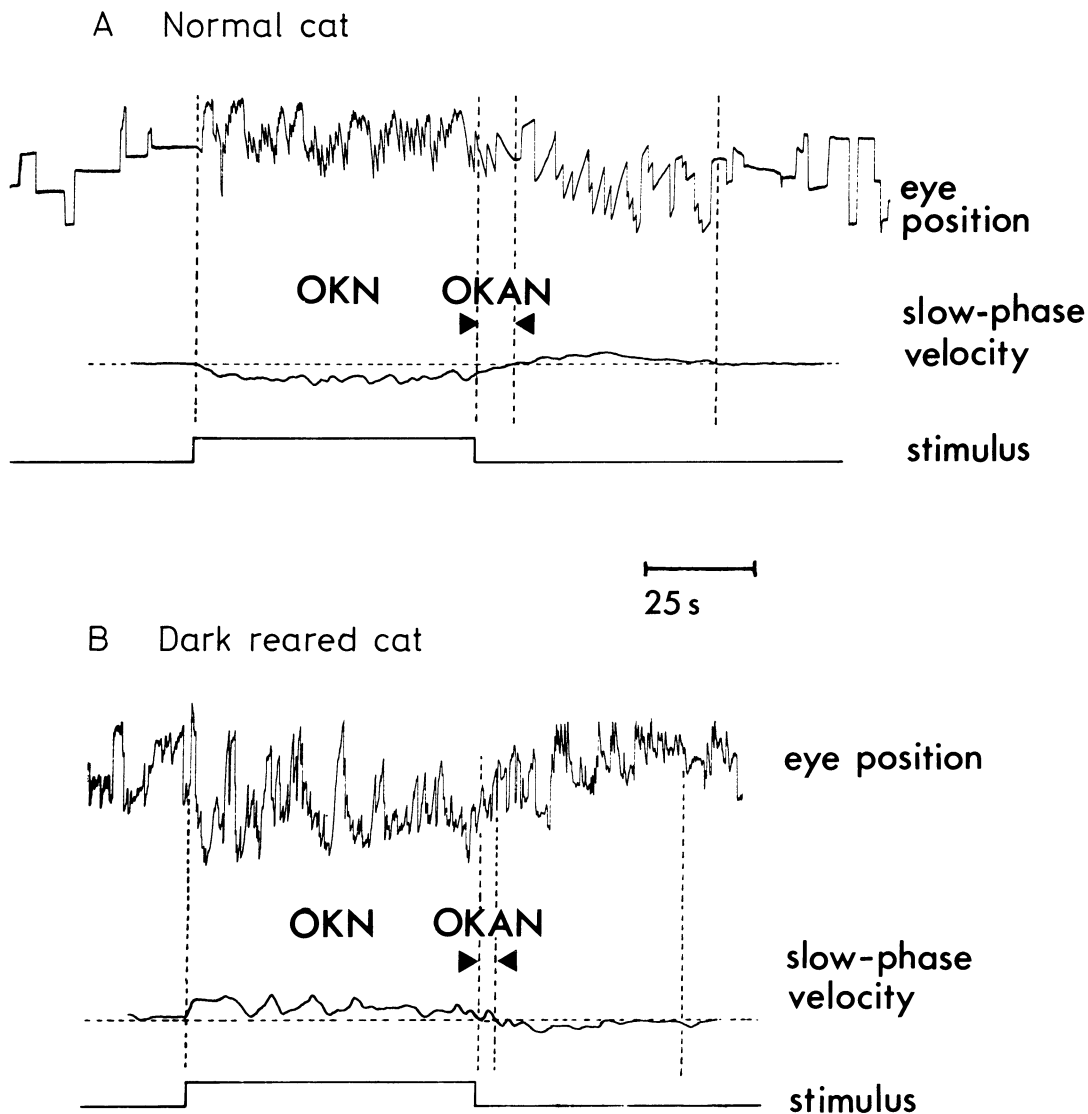


Fig. 8A, B. The characteristics of optokinetic following of **A** a normal and **B** a dark-reared cat. This figure illustrates typical eye movements recorded before during and after a short period of optokinetic stimulation (*lower trace in each set*). The upper trace represents eye position and the central trace is a fit by eye through the slow-phase component of the velocity trace

of direction of stimulus movement. Stimuli were back-projected onto a tangent screen (see Methods). The direction of drift of this stimulus was varied in 45° steps by tilting the projector. The velocity and direction of the slow-phase eye movement in response to each of the eight directions of movement are shown as arrows in Fig. 7C. The direction of the arrow indicates the direction of the slow-phase of the nystagmus. The length of the arrow represents the speed of the slow phase. The dark-reared cat shows a maximum response to a stimulus moving up and medial, but even for this stimulus responds only with

a gain of 0.6. Quantitative gain measures are, however, somewhat misleading in this situation for two reasons: first the tangent screen, unlike the optokinetic drum, did not entirely fill the visual field of the cat and second a grating projected onto a tangent screen cannot maintain a constant retinal velocity across the extent of the screen. At 45° eccentric (at the viewing distance used) the velocity of the grating was only 70% of the velocity at the centre.

Also shown on Fig. 7C are the data obtained from a normal cat under the same conditions. These normal data confirm the greater efficiency of follow-

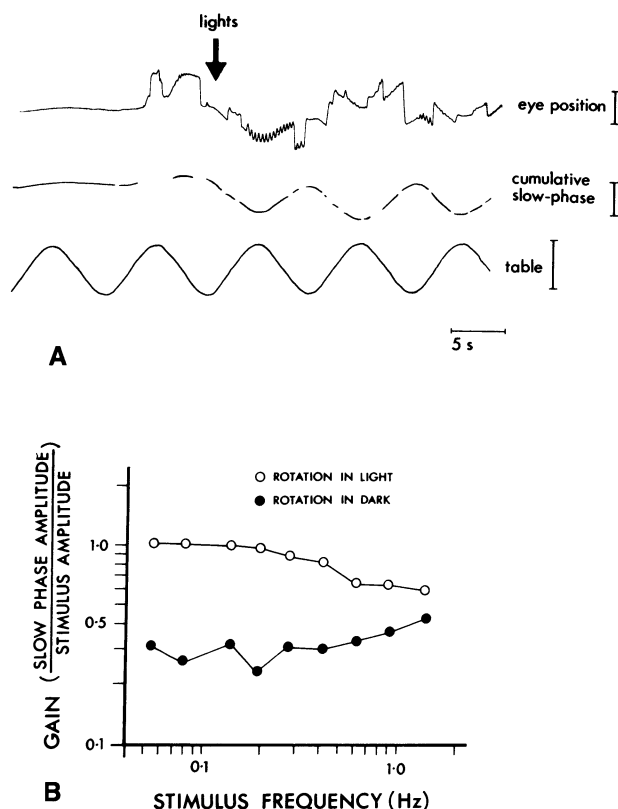


Fig. 9A, B. The effect of allowing vision to a dark-reared cat during sinusoidal oscillation. The records shown in A illustrate that when the lights are turned on (they remain on for the duration of the stretch of record to the right of the arrow) there is a dramatic improvement in compensatory eye movements as optokinetic cues are combined with vestibular information. The enormous phase lead is replaced by an almost negligible phase lag and gain becomes close to unity. Note also the sudden appearance of a pendular nystagmus. The calibration bars represent 10° . The efficiency of the combination of optokinetic and vestibular information is plotted against frequency in B. The gain of the VOR measured in the dark (closed circles) has been replotted from Fig. 4

ing medial vs lateral directed stimuli (cf. Fig. 7B) and also show a pronounced up/down asymmetry in the optokinetic response with movement downwards evoking only a weak response. The dark-reared cat is, however, apparently able to follow downward moving stimuli *better* than a normal cat. This is despite the presence of a slow-phase *upward* spontaneous nystagmus under these viewing conditions (see Fig. 2; Table 1 and right hand side of Fig. 7C).

The dark-reared cat displays further abnormalities in his optokinetic system. The normal animal's response when an optokinetic drum is moved from stationary to a constant velocity (velocity step) is shown in Fig. 8A. After a short delay the eyes rotate in the direction of the stimulus and the slow phase velocity builds up until the eyes are rotating

(interrupted by fast phases in the opposite direction) at the velocity of the stimulus (after about 5 s in the example shown). This velocity is then maintained for the duration of short periods of drum rotation. If the stimulus is removed, the velocity gradually declines to zero (optokinetic after-nystagmus; OKAN) and may even reverse direction (secondary optokinetic after-nystagmus). Three major differences can be observed in the responses of a dark-reared cat. These are illustrated in Fig. 8B. (1) The initial build up of the OKN in the dark-reared is much faster than for the normal cat, reaching the maximum velocity 1–2 s after the stimulus starts. (2) The eye velocity is not smoothly maintained during the presentation of the drum (note the increased variability evident in the velocity trace). (3) The eye velocity falls off extremely rapidly when the lights are extinguished (reaching zero after only 2–3 s in the example shown). The sharp fall off at the end of stimulus presentation in the dark indicates a deficiency in OKAN. This fall off is reminiscent of the unusually fast decline in eye velocity when vestibular stimulation ceases (post-rotatory nystagmus; Fig. 6).

Compensatory Eye Movements Evoked by Rotation in the Light:

Interaction Between Vestibularly and Visually Produced Eye Movements. The compensatory movements induced by either the vestibular or the visual system are, in general, inadequate in providing image stabilization in the dark-reared cat. Figure 9 shows the effect of allowing both systems to operate by turning on the lights while a dark-reared cat is being rotated sinusoidally. The records shown in Fig. 9A do not show the first exposure to light (cf. Fig. 3) but were obtained before the animal was allowed locomotor experience in the light. Several marked changes occur in the VOR when vision is permitted. In the dark, both the amplitude and phase of the vestibularly-induced compensatory eye movements are inadequate for an effective corrective movement (first half of Fig. 9A; also Fig. 4). As shown in Fig. 9 both of these anomalies are dramatically reduced by the addition of visual information. The phase lead is reduced from 180° at the beginning of the record to a phase lag of about 5° in the light. Simultaneously the amplitude of the corrective slow phase is increased to approximately the amplitude of the rotation (gain of one). Figure 9A also illustrates the striking pendular nystagmus which becomes manifest as the lights are turned on (see also Fig. 2 and Table 1).

Thus, although neither the optokinetic system nor the vestibular system works with normal efficiency in the dark-reared cat, the two systems are

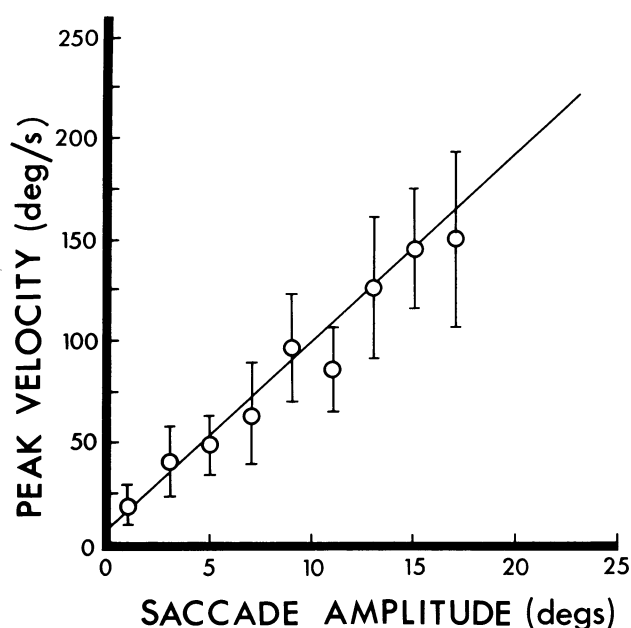


Fig. 10. The peak velocity of saccades is here plotted against saccadic amplitude for the dark-reared cat (open circles). The vertical bars represent standard deviations. The solid line through the data is a regression line fitted to the velocity/amplitude characteristics of a normal cat

able to combine to give a reasonable image stabilisation (better than 70%) up to a frequency of 0.9 Hz (at 10° peak-to-peak). This is shown in Fig. 9B in which gain of compensatory eye movements measured in the light (open circles) is compared to the gain in the dark (filled circles) when only vestibular information is available.

Part 3

The Saccades of the Dark-reared Cat. The saccades of the dark-reared cat resemble those of the normal cat in some ways but differ in others. The velocity-amplitude characteristics of saccades are similar in dark-reared and normal cats. This point is illustrated in Fig. 10 in which the peak velocities of saccades made by dark-reared cats in the dark are plotted as a function of amplitude. The solid line through these data is a regression line obtained from the velocity-amplitude characteristics of *normal* cats under a similar condition of alertness. Similar results are obtained with saccades made in the light. The saccades are, however, associated with a subsequent drift. Figure 11 shows some representative saccades of the dark-reared cat (further examples of which can be found in Figs. 1, 2, 3, 8, 9A) on an expanded time scale. A pronounced tendency to drift back towards the starting point after each saccade can be seen in

this figure. This tendency was very consistent and was seen in all cats for both horizontal and vertical saccades.

Part 4

The Eye Movements of a Normal Adult Cat Put into the Dark for 135 Days. In order to ascertain if the eye movement deficits described above were a consequence of prolonged deprivation or whether it was important that the deprivation occurred with no prior vision, an adult cat, whose eye movements had been measured and shown to be normal (see Figs. 4, 6–8) was put into the dark-room for 135 days. Her eye movements were then measured before she was allowed vision (measurements were taken, as with the dark-reared animal, in the dark with a light-proof hood over the animal's head). Spontaneous eye movements are indeed slightly affected by the experience in the dark. There is some post-saccadic drift reminiscent of that observed in the dark-reared cat. These slight post-saccadic drifts disappeared almost immediately the cat was exposed to light again and there was no greater medial/lateral asymmetry of monocular optokinetic responses than in a normal animal.

The vestibulo-ocular reflex as measured in response to sinusoidal oscillation was unaffected by the prolonged period of light deprivation. There was no change in the normal phase relation and no reduction (or increase) in the gain.

Part 5

The Effect of Allowing a Dark-reared Cat a Normal Visual Environment. The three dark-reared cats of this study were raised in the dark to the age of 11.5 months, 14 months and 15 months. Their oculomotor performance was then measured (spontaneous eye movements, vestibular and optokinetic evoked movements) over a period of 2 weeks during which time the animals were allowed vision only in the apparatus. Following this initial assessment the animals were released into a normally-illuminated cat colony³. The efficiency of the animals' oculomotor systems (VOR and OKN) was then measured at intervals over the next 5 months to trace any possible recovery.

Although the pattern of spontaneous eye movements did show clear changes over the course of a few weeks, the compensatory eye movements of the

³ One of the three cats went into convulsions for a brief period at this stage. This was the first time that he had been allowed to move around in a lit environment – all the OKN trials had taken place with the head immobilised

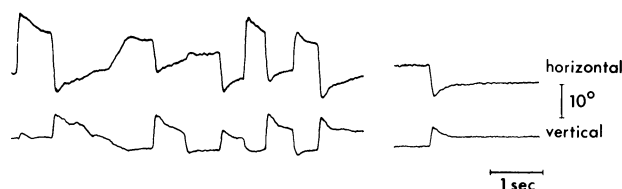


Fig. 11. Some examples of the saccades of a dark-reared cat. Note the tendency in both the horizontal and vertical components to drift back towards the starting position immediately after each saccade

dark-reared animals did not improve significantly over a 5-month recovery period. The improvement in the spontaneous eye movements are summarized in Table 2. After a few weeks of visual experience ocular deviations were held without return drift. In the dark, however, even after a 5-month recovery period, there were occasional post-saccadic drifts. The vertical spontaneous nystagmus was also still present, even in the light. However, there was a great improvement in the spontaneous horizontal nystagmus which was completely absent in the light for all cats after a few weeks, although it could occasionally be seen in records taken in complete darkness even after 5 months.

The compensatory eye movements, either of visual (OKN) or vestibular (VOR) origin hardly improved in efficiency at all over the 5-month "recovery" period. Figure 12A shows the efficiency of the optokinetic system (measured monocularly) over the recovery period in response to medially and laterally directed stimulus movement. There was very little improvement in either direction. What improvement there was was largely due to the correction of the spontaneous horizontal nystagmus, thus freeing the animal from a negative gain in response to the laterally moving stimulus. Only very low gain OKN responses were ever seen in response to even a very slow laterally directed stimulus. The vestibulo-ocular reflex also showed a surprising lack of recovery. This is shown in Fig. 12B for three frequencies of sinusoidal rotation. The gain remained very low and did not improve above about 0.5. The anomalous phase relation seen before any visual experience (Fig. 5) was still found after 5 months living in a normal cat colony.

Discussion

Our results demonstrate substantial deficits in virtually all types of eye movements examined in cats deprived of vision from birth to adulthood. Some of these deficits evidently require a considerable period

Table 2. The eye-movements of a dark-reared cat after 5 months of recovery in a normally lit environment. Directions as for Table 1

	Horizontal nystagmus	Vertical nystagmus	Pendular nystagmus	Deviations held
Dark	weak and occasional	clear	only present when very aroused	occasional return drifts
Light (Binoc)	rare	clear (especially during horiz. OKN)	present	normal
Light (Monoc)	rare	present	present	normal

of deprivation for their expression. Our results indicate considerably greater differences between the eye movements of normal and dark-reared cats than did the earlier studies of Berthoz et al. (1975) in which animals were deprived of vision only until the fourth postnatal month. Several studies (Cynader et al. 1976; Imbert and Buisseret 1975) suggest that prolonged visual deprivation results in progressive degradation of response properties among visual cortex neurones. It seems likely that similar processes at various levels of the nervous system may result in the substantial deficits observed here after prolonged deprivation.

Even in the dark, in the absence of stimulation, the eye movements of normal and dark-reared cats are readily distinguishable by the occurrence of the horizontal and vertical forms of nystagmus and by the presence of post-saccadic drift in the dark-reared animals. These stabilization deficits persist when the dark-reared cat is exposed to light and are in fact enhanced by a pendular nystagmus. They would in themselves be sufficient to prevent clear vision in these animals.

The Vestibulo-ocular Reflex of the Dark-reared Cat

A dark-reared cat exhibits eye movements in response to sinusoidal vestibular stimulation. These eye movements appear qualitatively normal and may be divided into slow compensatory movements interrupted by fast, saccadic movements in the opposite direction. Quantitative deficits in vestibular eye movements of the dark-reared cat were revealed however in the responses to both sinusoidal oscillation and steps in angular velocity. The rate of decline of post-rotatory nystagmus induced by a velocity step was much faster in dark-reared cats than in normal cats (Fig. 6). The time constant had a *maximum*

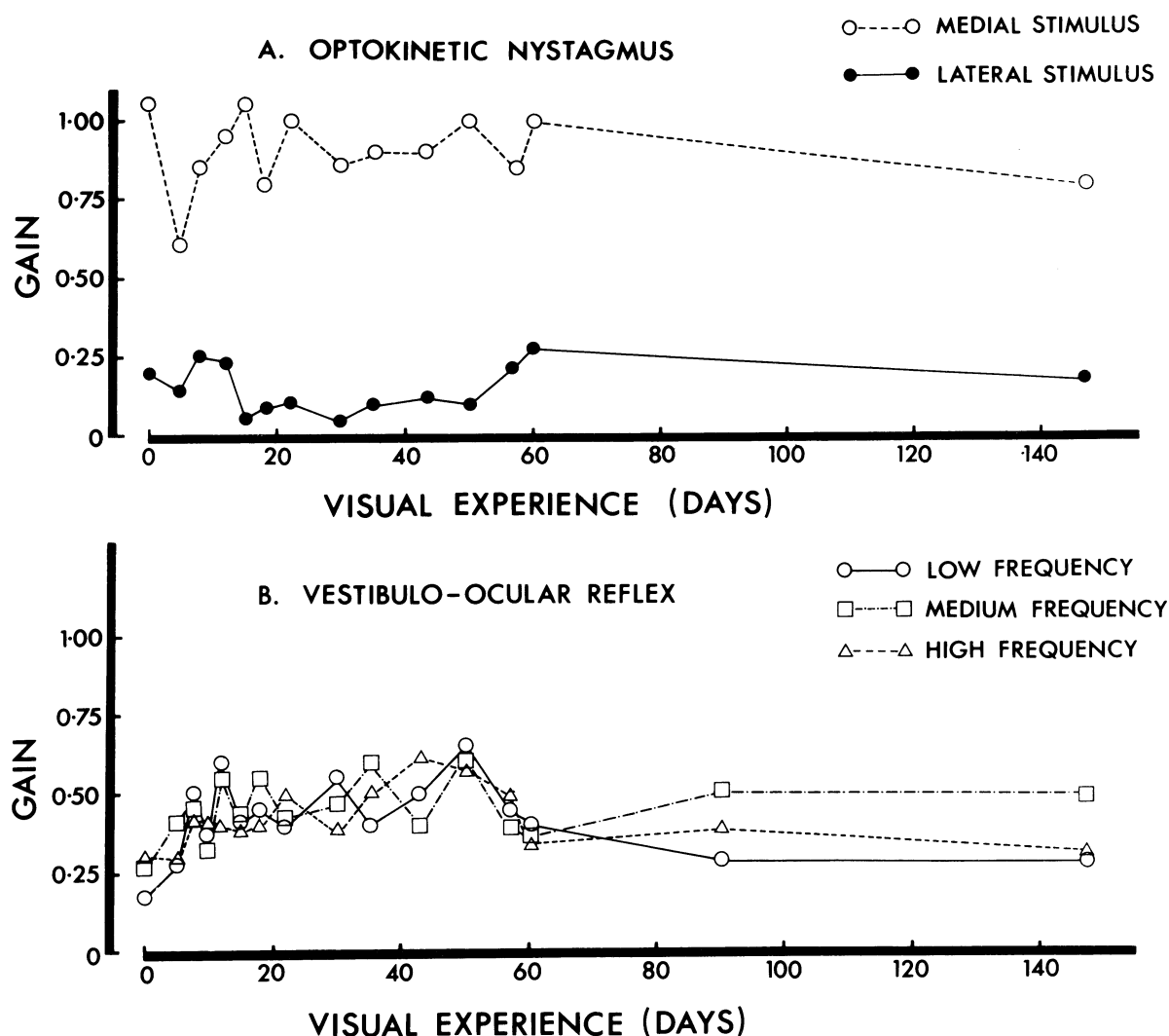


Fig. 12A, B. After more than a year of darkness the three dark-reared cats were released into a normally lit environment. Their optokinetic (**A**) and vestibular (**B**) performance was assessed regularly but there was no significant improvement in over 140 days. **A** shows the efficiency of the optokinetic response to a stimulus moving either medially (*open circles*) or laterally (*filled circles*) at 10°/s. **B** shows the gain of the VOR at low frequency (0.09 Hz; *open circles*), medium frequency (0.36 Hz; *open squares*) and high frequency (0.80 Hz; *open triangles*) of sinusoidal rotation. The amplitude was always 10° peak-to-peak

value of only 5–6 s in the dark-reared animals. This compares to 12–18 s for a normal cat (Fig. 6; see also Robinson 1976). The value of the time constant of the decline of post-rotatory nystagmus in the dark-reared cat is very close to the time constant of the cupula in the cat (about 4 s, Melvill Jones and Milsum 1971).

Sinusoidal oscillation revealed three further anomalies of the dark-reared cat's VOR: (1) the gain was approximately 1/3 of normal over the range 0.05–1.2 Hz, (2) the phase relationship between the movement of the eyes and that of the head varied with the frequency of oscillation, (3) the phase vs

frequency relationship was substantially altered by increases in the amplitude of sinusoidal stimulation. The anomalous phase relationship (Figs. 4 and 5) of the VOR would be sufficient, even without the reduced gain, to prevent the image stabilization by vestibular cues during head movement. In particular at 0.2 Hz (Fig. 4) the phase lead of 180° means that the VOR results in *anticompensatory* rather than compensatory movement. This anomalous phase relationship and its dependence on the amplitude of stimulation indicate substantial nonlinearities in the systems underlying VOR generation in the dark-reared cat.

A reduction in the gain of the vestibulo-ocular reflex has been observed in other studies of the effects of visual deprivation. The VOR of the dark-reared rabbit (Collewijn 1977) has a gain reduced, like that of the dark-reared cat, to about 1/3 of normal values. Furthermore, the dark-reared rabbit's VOR gain does not recover fully even after a 3-month period of visual experience. Berthoz et al. (1975) have also demonstrated deficits in the VOR of dark-reared kittens. Their use of the electro-oculogram does not allow firm quantitative conclusions, but their observations of a reduction of the number of fast phases also suggest a reduction of gain in agreement with the present findings. Older studies (e.g. Mowrer 1936 on dark-reared pigeons) indicate similar trends.

Vestibular responses are found in kittens between postnatal day 11 (Fish and Windle 1932) and day 30 (Flandrin et al. 1979) but, even by the fourth month (Berthoz et al. 1975 control group), have not fully reached the adult characteristics. Our results indicate that visual experience is necessary for this development and that deprivation of visual input for a prolonged period in early life has serious consequences for the developing vestibulo-ocular system. Our results further demonstrate that visual deprivation in adulthood has little or no effect on the VOR suggesting a critical period during early development for these alterations.

Optokinetic Responses

Optokinetic responses appear around postnatal day 15–25 in the normal kitten (Warkentin and Smith 1937; van Hof-van Duin 1976) and reach adult characteristics by day 50 (Flandrin et al. 1979). We have shown that OKN, while present (cf. Vital-Durand et al. 1974a, b; van Hof-van Duin 1976) is much reduced in gain by dark-rearing, especially at stimulus velocities above about 20°/s (Fig. 7). More detailed analysis, using monocular viewing, clarifies the nature of the deficit in the dark-reared animals (see also Harris and Cynader 1979a; Harris et al. 1980).

Monocularly viewed stimuli moving medially (from temporal to nasal, or rightward with the left eye viewing) are followed much better by the dark-reared cat than stimuli moving in the opposite direction. Analysis of the monocular data was hampered by the presence of a spontaneous nystagmus (Part 1) and the fact that even a normal cat has an asymmetry in OKN performance above a stimulus velocity of about 20°/s (Harris et al. 1980; Honrubia et al. 1967; but cf. Braun and Gault 1969). However,

it seems clear that the asymmetry in the dark-reared cat is considerably more pronounced than that of the normal cat. In this sense the dark-reared cat resembles rabbits, kittens and young children which also have a strong asymmetry in their monocular optokinetic response in favour of temporo-nasal stimuli (rabbit, Fukuda and Tokita 1957; Rademaker and ter Braak 1948; ter Braak 1936; Collewijn 1969; kittens, van Hof-van Duin 1978; children, Atkinson 1979). It has been suggested that symmetrical responses to stimulation in the two directions may require a fully developed fovea (Tauber and Atkin 1968) and, indeed, foveate human adults also show an asymmetry in OKN (Baloh et al. 1980). However, since adult cats show an asymmetry if dark-reared (Fig. 7) or strabismic (Cynader and Harris 1980) while the fovea remains unaffected (Wiesel and Hubel 1963; Chow and Stewart 1972) it is unlikely that the presence or absence of the fovea itself is the critical variable for the generation of symmetrical OKN. We believe rather that our results can be understood in the light of emerging studies on the neurophysiological basis of horizontal optokinetic nystagmus.

The nucleus of the optic tract (NOT) appears to be a centre of control for the horizontal optokinetic system. This role is assigned based on the appropriate visual response characteristics of NOT cells e.g., velocity and direction preference (Collewijn 1975a; Hoffmann and Schoppmann 1975), the abolition of OKN by lesions of the NOT (Collewijn 1975b), the production of nystagmus in response to microstimulation (Collewijn 1974, 1975b) and its appropriate anatomical connections (Berman 1977; Terasawa et al. 1979). Each NOT appears responsible for movement with the slow phase towards that side (Collewijn 1975b). There are two main inputs to each NOT: a direct retinal projection originates from the contralateral eye (Hoffmann and Schoppmann 1975) while the ipsilateral eye takes an indirect route through the visual cortex (Berman 1977). Removal of the cortex also abolishes OKN in response to a laterally moving stimulus (Braun and Gault 1969; Wood et al. 1973). Under these circumstances the left eye has no input to the left NOT. Dark-rearing in the cat also severely affects OKN to a laterally moving stimulus – producing the asymmetry of response in monocular viewing which is the norm in the rabbit (Collewijn 1969). Dark-rearing has severe effects on the response characteristics of neurones in the visual cortex (Wiesel and Hubel 1965a; Cynader et al. 1976) and consequently on the input pathways to the NOT (Hoffmann et al. 1977). It may be that dark-rearing produces a functional decortication with respect to the optokinetic system.

It is particularly surprising, in view of this horizontal asymmetry in OKN, that dark-rearing appears to abolish the normal up-down asymmetry of optokinetic nystagmus in the cat (Collins et al. 1970; Evinger and Fuchs 1978). Normally, stimuli moving up are better followed than stimuli moving down but this appears not to be the case in dark-reared cats who appear to be able to follow downward moving stimuli better than normal animals (Fig. 7). This *lack* of asymmetry in adult dark-reared's is also surprising in view of the Vital-Durand and Jeannerod (1974a) finding that OKN was particularly difficult to initiate in dark-reared kittens in response to downwards moving stimuli. They, however, had difficulty in initiating any OKN in control litters. The increase in efficiency of following downward movement is further surprising in view of the sustained spontaneous nystagmus (slow-phase up) which dominates the records of dark-reared cats eye movements. This could apparently be overcome by our stimulus although the stationary real world was inadequate. It is interesting here to note that bilateral labyrinthectomy in rabbits similarly abolishes an asymmetry in vertical OKN (Barmack et al. 1980).

Our results indicate that visual deprivation causes severe deficits in the "velocity storage mechanism" of OKN (Raphan et al. 1977; Robinson 1977). The dark-reared cat does not exhibit the slow rise in slow phase OKN velocity over the first 10 s of stimulation which characterises the normal cat (Fig. 8). In addition, the gain of the reflex during sustained drum rotation is more variable in the dark-reared cat than in the normal animal and the duration of OKAN is reduced (see also next paper: Harris and Cynader 1981). These are precisely the deficits which would be expected in a system in which the performance of the "velocity storage mechanism" was severely impaired (Raphan et al. 1977). Robinson's model (1977) further predicts that any condition which affects this mechanism and in particular shortens the duration of OKAN would also cause a reduction in the time constant of the post-rotatory *vestibular* nystagmus. This is in fact exactly what we observe in the dark-reared cat.

It might be argued that our measures of OKN are in fact not measures of the optokinetic system at all but rather measures of a pure smooth pursuit system of the dark-reared animals. It is difficult to separate these two systems in many cases. The lack of build-up of slow-phase velocity with drum movement, the weak after-effects of visual stimulation, and the limited maximum drum speed which could be followed, are all suggestive of the use of a smooth pursuit system rather than OKN by the dark-reared cat in this situation. It is important, however, to

remember the behavioural condition of the dark-reared animal at the time of testing. Our dark-reared animals tested outside the experimental apparatus displayed no evidence of vision and in particular were quite unable to pursue small moving objects with either their head or eyes (see also Timney et al. 1980). This inability to use the pursuit system under natural conditions suggests to us that our observations reflect the operation of a residual optokinetic system in the dark-reared animal rather than a smooth pursuit system.

The Saccades and Holding of Eye Deviation of the Dark-reared Cat

The saccades of the dark-reared cat appear normal in their velocity-amplitude characteristics (Fig. 10). However, a dark-reared cat is unable to maintain the eye deviation initially achieved by a saccade and there is a considerable amount of post-saccadic eye drift (as shown in the records of Fig. 11). Such eye drifts are occasionally seen after saccades in normal human subjects (Bahill and Stark 1979) but are more typically seen after cerebellar damage (Robinson 1974; Zee et al. 1976). Such an inability to hold eye deviation is indicative of a mismatch between the pulse and step inputs necessary for the generation of saccades (Robinson 1975). Robinson has discussed at length the need for an integrator in the mechanisms that underlie eye movement control (Robinson 1975). It appears from the effects of dark-rearing on both the time constant of the vestibulo-ocular system (Fig. 6) and on post-saccadic drift (Fig. 11) that dark-rearing, like cerebellectomy (Robinson 1974), affects the functioning of an integrator (Robinson 1975) that underlies both the vestibulo-ocular and saccadic systems.

The Lack of Recovery of Compensatory Eye Movements

Discussion on the extent of the development of visual ability after deprivation has been extensive since the seventeenth century (see Morgan 1977 for a philosophical review). We have shown that corrective eye movements demonstrate little recovery with light exposure but even the existing residual compensatory eye movements would provide a basis for the observed recovery of other aspects of visual function after deprivation (Cynader et al. 1976; Cynader and Mitchell 1980; Timney et al. 1980). Despite the inadequacies of both optokinetic and vestibulo-ocular reflexes, the two deficient systems can cooperate

to produce effective compensatory eye movements over quite a large range of head oscillation (Fig. 9). Retinal stability (apart from the frequent presence of vertical and pendular nystagmus) is therefore at least partially achieved.

Since the residual optokinetic system seems able to supplement the deficient vestibular system (Fig. 9B; see also Berthoz et al. 1975 Fig. 8) it is peculiar that the vestibulo-ocular reflex itself shows so little improvement over a 5-month period (Fig. 12). The gain of the vestibulo-ocular system of a normal adult cat is easily modified in response to vision (Robinson 1975; Melvill Jones and Davies 1976) like that of man (Gonshor and Melvill Jones 1976a, b). The situation in which the dark-reared cat finds himself when released into the light, with his vestibulo-ocular reflex being continuously corrected by the visual system during most head movements, is in fact the classic situation for VOR modification. Such modification, which would result in a normal VOR, however, does not occur and the vestibulo-ocular reflex remains virtually unchanged over a 5-month period. This lack of plasticity suggests that modifiability itself needs to be exercised before a certain point in development. This point is taken up in more detail in the following paper (Harris and Cynader 1981).

Comparison with the Eye Movements of Clinically Blind Patients

Blindness from birth (due to diseases affecting the anterior visual pathways) is associated with impaired vestibulo-ocular reflex in humans (Leigh and Zee 1980). Blind patients, like dark-reared cats, also show various forms of spontaneous nystagmus including pendular nystagmus (Ohm 1951). The vestibulo-ocular reflexes of blind people, like those of dark-reared cats, are weak (Forssman 1964) or may even be absent (Toglia 1967). The great similarity between the eye movement deficits of dark-reared cats and patients under comparable conditions suggests that the dark-reared cat may serve as an effective model for these clinical disorders.

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