PERGAMON

Vision Research 43 (2003) 793–800

Vision Research

www.elsevier.com/locate/visres

Visual field defects in albino ferrets (*Mustela putorius furo*)

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Received 3 September 2002; received in revised form 9 January 2003

Abstract

The extent of the horizontal visual field was determined behaviourally in 4 pigmented and 5 albino ferrets (*Mustela putorius furo*, Carnivora, Mammalia) using perimetry. During binocular vision, all pigmented and three albino ferrets responded equally well to stimuli presented anywhere along the horizontal perimeter in the central 180° of the visual field. The remaining two albinos had a visual field defect in the right hemifield (>30° eccentricity). During monocular vision, a significant difference between the visual fields of pigmented and albino ferrets became apparent. In pigmented ferrets, the visual field of each eye included the ipsilateral (temporal) and a substantial portion of the contralateral (nasal) hemifield. In albinos, the visual field of each eye was limited to the ipsilateral hemifield and reactions to visual stimuli abruptly declined directly beyond the vertical meridian.

Keywords: Albinism; Perimetry; Visual orientation; Visual system; Mammals

1. Introduction

Albinism is a mostly hereditary condition affecting all animals. Its effects, however, have been studied most extensively in mammals. Its most obvious characteristic is a reduction or complete lack of pigment in the eye, the skin and the fur. This lack of melanin indicates a disruption in the tyrosine metabolism, specifically a faulty or lacking tyrosinase. The defects of the visual system in albinos have been investigated in detail in a number of mammals as different as mice, rats, rabbits, ferrets, cats, wallaby, monkey and man. A general finding is that the proportion of ipsilaterally projecting retinal ganglion cells is reduced. As a consequence the layering of the lateral geniculate nucleus (LGN) and the visual field representation in the LGN and the visual cortex are abnormal (e.g. mouse: Draeger & Olsen, 1980; rat: Lund, 1965; Creel & Giolli, 1976; ferret: Guillery, 1971; Huang & Guillery, 1985; Morgan, Henderson, & Thompson, 1987; Zhang & Hoffmann, 1993; siamese cat: Hubel & Wiesel, 1971; Shatz, 1977; cat: Creel, Hendrickson, & Leventhal, 1982; wallaby: Guillery, Jeffery, & Saunders, 1999; monkey: Guillery et al., 1984; man: Guillery, Okoro, & Witkop, 1975; Apkarian & Shallo-Hoffman, 1991; reviews: Creel, Summers, & King, 1990; Perez-Carpinell, Capilla, Illueca, & Morales, 1992; Jeffery, 1997). A more detailed investigation of the retina revealed that albinism mainly affects the central retina, i.e. visual streak, area centralis, and fovea, and that it specifically causes a significant reduction of rods. In addition, the nuclear layers in the central retina are thinner, and retinal maturation is delayed (for review see Jeffery, 1997). The severity of the defects in the central retina is not correlated with the degree of hypopigmentation (Donatien, Aigner, & Jeffery, 2002). Because the pathology of albinism is not always limited to the visual system but extends to the auditory system (Moore & Kowalchuk, 1988) it is suggested that the migration of neural crest cells is disturbed (for review see Lyle, Sangster, & Williams, 1997).

The ferret (*Mustela putorius furo*) is well suited for the study of albinism and its effects on the visual system. Albino strains are readily available, ferret retina is characterized by a visual streak in combination with an area centralis and, based on the position of the eyes in the head, the pigmented ferret possesses a considerable binocular overlap of the visual field and therefore a sizeable uncrossed projection of retinal axons, which is strongly decreased in albino ferrets (Guillery, 1971; Morgan et al., 1987; Zhang & Hoffmann, 1993).

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0042-6989/03/$ - see front matter © 2002 Elsevier Science Ltd. All rights reserved.
doi:10.1016/S0042-6989(03)00015-4

From a series of investigations characterizing the visual system of the ferret, we here report on behavioural studies using perimetry designed after Sherman (1973). Our question is whether the visual field of albino ferrets is normal or reduced as described by Elekessy, Campion, and Henry (1973). We therefore compared pigmented and albino ferrets for the extent of the binocular and monocular visual fields.

2. Methods

2.1. Subjects

The tests were performed in 4 male pigmented and 5 male albino ferrets ranging in age between 3 and 16 months. All but 2 animals that were purchased from Marshall Farms, North Rose NY, USA were bred and raised in the animal facility of the Department of General Zoology and Neurobiology, Ruhr-University Bochum. The animals were group-housed with access to an outdoor enclosure. Great care was taken to provide nesting material and hiding places as boxes and dark tubes so that the animals could avoid exposure to light at any time. All experiments were approved by the local ethics committee and were carried out in accordance with the European Communities Council Directive of 24 November 1986 (S6 609 EEC) and NIH guidelines for care and use of animals for experimental procedures.

2.2. Experimental setup and training procedures

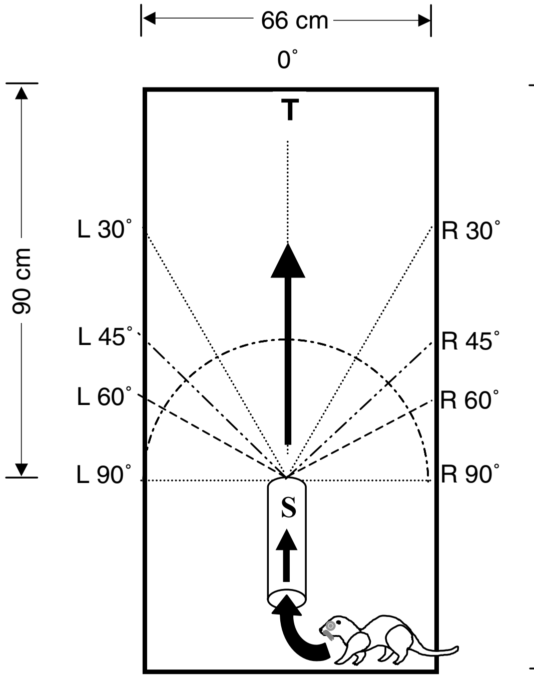

Fig. 1. Experimental setup. The animals were trained to run from the starting point (S) towards the target (T) or to a novel visual stimulus presented in either of the marked sectors of the left (L) or right (R) visual hemifield in order to receive a reward. For further explanations see text.

The experimental setup is demonstrated in Fig. 1. The tests were performed on a cloth-covered table (66 cm × 132 cm) on which the central 180° of the visual field were marked in 30°-sectors. For most monocular measurements the contralateral (nasal) sector between 30° and 60° was further divided in half to allow a more accurate assessment of the extent of the monocular visual field. Initially, the animals were trained to run to the target point straight ahead (thick arrow) when an acoustic or a visual stimulus was given at the target (T). If the animal ran straight without detour it received a food pellet from the assistant. During this training period, the experimentor held the animal's head at the starting point (S) until the stimulus appeared. The training sessions lasted for 30 min per day. After the animals had learned this task, a visual stimulus i.e. a black disc (diameter 3 cm) at the end of a transparent rod, was presented at other locations than the target point. If the animal ran to the novel stimulus it was rewarded by the assistant with a food pellet at the location where the stimulus had appeared. If it ignored the stimulus and ran straight to the target position it was only rewarded every third time. Care was taken not to touch the table with the stimulus as to avoid an additional acoustic cue for the animal. At intervals, no stimulus was presented. In these control trials the animal was supposed to run to the target position straight ahead to receive his reward. Within 2–9 days all animals had learned the tasks. During the training period a transparent tube was introduced to the setup through which the animal ran to the starting point (now the front opening of the tube) instead of having its head held by the experimentor. As soon as it emerged from the tube the visual stimulus was presented along a horizontal perimeter 33 cm in front of the starting point.

During the tests the same procedure was followed as during the training period. If the animal accurately ran to the stimulus this was taken as a positive trial, if it did not respond to the stimulus or made a detour this was judged as a negative trial. The judgement was performed independently by the experimentor and his assistant and compared after the test session.

Each animal was tested on average 7 times in the binocular viewing condition and on average 3 times in each monocular viewing condition comprising over all sessions on average 430 binocular trials and 354 monocular trials for the left and 322 for the right eye (see Table 1). For the monocular viewing one eye was completely covered with a black plastic lens.

During the training and testing periods the animals received their daily food rations exclusively in the experimental setup in order to encourage cooperation. The

Table 1
Training and testing scheme

Animal	Age (months)	Training sessions	Binocular trials (sessions)	Left eye trials (sessions)	Right eye trials (sessions)
P1	16	9	740 (12)	412 (4)	208 (2)
P2	16	5	581 (8)	431 (3)	583 (4)
P3	3	7	123 (2)	214 (3)	293 (3)
P4	3	2	551 (7)	416 (3)	314 (3)
A1	12	3	322 (8)	–	89 (2)
A2	12	2	396 (8)	–	242 (4)
A3	3	5	396 (4)	325 (3)	307 (3)
A4	15	4	416 (6)	224 (3)	386 (3)
A5	3	5	342 (5)	453 (3)	472 (3)
Average	–	–	430 (7)	354 (3)	322 (3)

P: pigmented ferrets, A: albino ferrets.

body weight was controlled daily to ensure that the animals did not loose more than 10–15% of their original weight. Water was offered between trials and ad libitum in the home range.

2.3. Data analysis

The sum of all runs in a given sector and the control runs (0°) in each session was set 100%, the number of correct trials was expressed as percent correct runs accordingly. Data were tested for statistical significance sector by sector using the rank sum test and the t-test. The data over all sessions for each ferret are presented on a half-circle perimeter representing the central 180° of the visual field.

3. Results

All animals learnt the task within 2–9 sessions. As indicated in Table 1, there is no indication that either genotype or age influenced the animals' learning ability in the task employed in the present study.

3.1. Binocular measurements

The primary aim of our study was to determine the extent of the monocular visual field of ferrets to uncover visual field defects in albinos. Thus, we restricted our tests to the central 180° (90° left–90° right) of the visual field both in the binocular and the monocular measurements. The binocular measurements served, first, to familiarize the animals with the task and, second, to determine if there was a general visual field deficit in any of the pigmented or albino ferrets.

The results of the binocular measurements in the best and worst performing pigmented ferrets are shown in Fig. 2A, D and in Table 2. All but one ferret reached more than 90% correct trials in all sectors of the visual field tested. Only ferret P3 showed a slight decrease in sector R 60°–90° (82%). During the control trials at 0° (no novel stimulus) no bias for spontaneous choices of any sector in the visual field was evident. In this condition animals ran most of the time straight ahead. There was no indication of any significant visual field defect in any of the pigmented animals.

In the albino ferrets, the results were more heterogenous (Table 3). Three of the animals (A1, A2, A3) reached more than 80% correct trials in all peripheral sectors (A3: Fig. 3A). By contrast, the remaining 2 albinos (A4, A5) showed a marked decrease in performance between 30° and 90° of the right hemifield indicating that these ferrets had a visual field defect (A4: Fig. 3D). Two albino ferrets (A1, A4) showed poorer performance in the control runs (0°, no stimulus). Because this was the case only in the binocular measurements it probably reflects poor motivation rather than a defect in the central visual field.

Statistical analysis shows that the performance in the binocular visual field of ferrets A1–A3 did not differ from those of wildtype ferrets whereas the performance of ferrets A4 and A5 was significantly lower than in pigmented ferrets in sector 30°–60° ($p = 0.001$) and sector 60°–90° ($p = 0.017$).

3.2. Monocular measurements

In 3 of the 4 pigmented animals the performance in the contralateral (nasal) 0°–30°-sector was still very high (78–89% correct trials) during monocular viewing (Fig. 2E and F). In the fourth (P1, Fig. 2B and C) only 44–49% correct runs could be recorded in this sector. A similar decline in performance was evident in the other pigmented ferrets only in the more peripheral sectors (30°–60°) (Table 2). Stimuli located in the far periphery of the contralateral field (>60°) only rarely elicited an orienting response (0–5% runs). Thus, in the normal pigmented ferret the monocular visual field includes at least 30°–45° of the contralateral hemifield. Beyond this point, recognition of stimuli declines rather rapidly and is virtually nil beyond 60°.

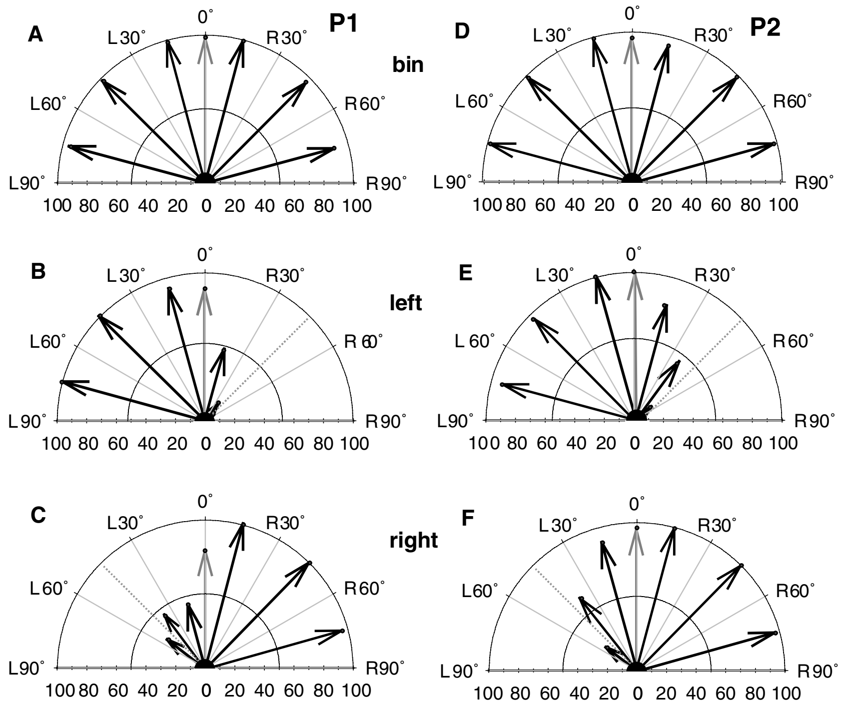

Fig. 2. Percentage of correct trials in pigmented ferrets P1 and P2 demonstrated in polar diagrams. The outer halfcircle represents 100%, the inner halfcircle 50% correct runs. The length of the arrows represents the percentage of correct runs, the direction of the arrows represents the sector in which the stimulus was presented. Control runs without novel stimulus are represented by grey arrows. The actual values are given in Table 2. L: left hemifield, R: right hemifield. A and D: binocular vision, B and E: monocular vision with the left eye, C and F: monocular vision with the right eye.

Table 2
Percentage of correct trials in the various sectors of the perimeter in pigmented ferrets (P1–P4) during binocular (Bin) and monocular left eye (L) and right eye (R) viewing

Sector	P1			P2			P3			P4		
	Bin	L	R	Bin	L	R	Bin	L	R	Bin	L	R
L 60°–90°	94	100	4	99	92	4	96	94	0	92	100	5
L 45°–60°			31			25			37			42
L 30°–60°	97	100		99	96		100	100		94	100	
L 30°–45°			44			61			75			78
L 0°–30°	98	92	44	100	100	89	100	100	86	99	100	100
Control	98	89	79	97	100	96	100	82	91	98	94	90
R 0°–30°	99	49	100	95	80	99	100	78	98	100	88	100
R 30°–45°	96	15	100	100	48	100	100	37	100	100	43	100
R 45°–60°		7			14			21			3	
R 60°–90°	90	0	96	99	5	97	82	0	95	100	4	85

In albino ferrets, the contralateral extent of the monocular visual field was dramatically reduced. Already in the 0°–30°-sector of the contralateral (nasal) hemifield performance was reduced to 0–18% correct runs and only in one of the animals tested could a response be elicited by stimuli located beyond the 30° mark. These results are demonstrated in Fig. 3B, D, E, F and Table 3.

This loss in the monocular visual field is further demonstrated by the medians of all monocular measurements given in Fig. 4. Whereas in pigmented ferrets monocular orientation to novel stimuli gradually declines beyond 30° in the hemifield contralateral to the seeing eye, performance in albino ferrets drops abruptly beyond the vertical meridian. This is particularly striking because in the sector 0°–30° ipsilateral to the seeing eye performance is as good as in pigmented animals. The difference to the performance of pigmented ferrets is statistically highly significant with significance levels increasing with increasing eccentricity (rank sum test; contralateral 0°–30° sector: $p = 0.043$, contralateral 30°–45° sector: $p = 0.016$, 45°–60° sector: $p = 0.001$).

Table 3
Percentage of correct trials in the various sectors of the perimeter in albino ferrets (A1–A5) during binocular (Bin) and monocular left (L) and right (R) eye viewing

Sector	A1			A2			A3			A4			A5		
	Bin	L	R	Bin	L	R	Bin	L	R	Bin	L	R	Bin	L	R
L 60°–90°	93	100		80	100		98	100	0	92	100	0	91	100	0
L 45°–60°							98	100	0	100	100	0	100	100	0
L 30°–60°	98	100		94	100										
L 30°–45°									12			0			0
L 0°–30°	100	86		96	100		100	100	13	98	97	6	98	100	18
Control	77	100		91	100		93	100	100	76	98	95	96	95	91
R 0°–30°	97	7		98	0		100	14	100	98	0	91	93	7	100
R 30°–45°							100	0	100	72	0	46	65	4	93
R 30°–60°	98	0		96	5										
R 45°–60°								0			0			0	
R 60°–90°	80	0		91	3		100	0	100	52	0	17	69	0	80

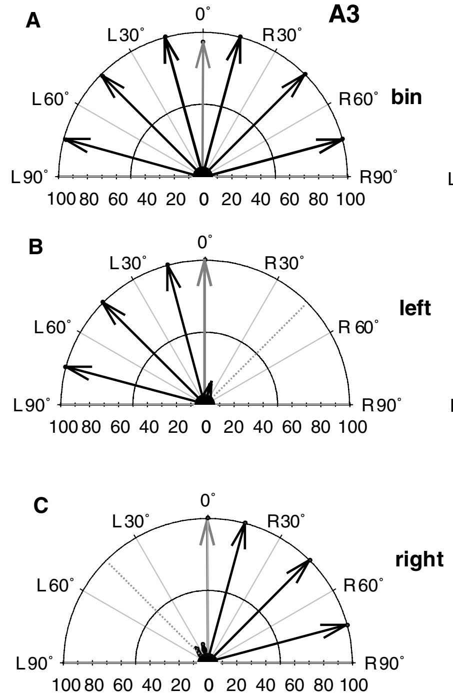

Fig. 3. Percentage of correct trials in albino ferrets A3 and A4. Values are given in Table 3. For further conventions see Fig. 2.

4. Discussion

In the present investigation we employed perimetry to determine the extent of the ferret's visual field with our main emphasis on the extent of the monocularly tested visual field. The animals had to learn to orient towards a frontal target and then turn towards a novel visual stimulus if presented anywhere along the horizontal meridian of a 180° perimeter. All animals learned the task regardless of their genotype (wildtype vs albino) or age (3 months old vs 16 months old) suggesting that the variability in the number of sessions needed to perform reliably was individual rather than group-related (Table 1).

We could demonstrate that the central visual field (90° left–90° right) as measured under binocular viewing conditions did not differ between pigmented and 3 of our albino ferrets. The remaining two albinos showed a restriction of the right peripheral visual field. This could be due to esotropia which went unnoticed despite careful inspection or due to specific defects of the nasal retina of the right eye, the left optic tract, lateral geniculate, colliculus superior or visual cortex, where this part of the visual field would be represented. Such a pathology is particularly probable for ferret A4 because in this animal the visual field defect was also seen during the monocular measurements of the right eye (Fig. 3F). Another possibility would be that due to an increased

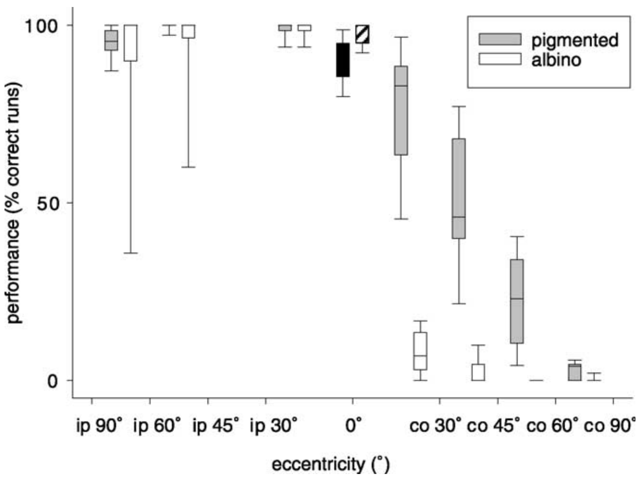

Fig. 4. Median of percentages of correct trials from all monocular measurements in pigmented (grey bars) and albino ferrets (open bars) over the various sectors of stimulus presentation in the ipsilateral (ip) and contralateral (co) hemifield. Values at 0° represent the scores for control runs (black: pigmented, striped: albino). Boxes represent the 25–75% range. Vertical bars indicate the 5–95% range. In pigmented animals the performance declines gradually in the contralateral hemifield and is below 40% in the contralateral 45°–60° sector. By contrast, performance in albino ferrets drops dramatically to almost zero directly beyond the vertical meridian.

photosensibility in A4 and A5 the illumination of the setup that came from above and slightly from the right affected ferrets A4 and A5 but not any of the other animals. We did not assess by physiological or anatomical means whether the albino ferrets were of the "Midwestern" or "Boston" type as described for Siamese cats by Shatz (1977) and for ferrets by Huang and Guillery (1985) and therefore cannot give a correlation between type and visual field deficit.

The main difference in the visual field between pigmented and albino ferrets revealed itself during monocular viewing. The monocular visual field in pigmented ferrets as assessed by our test reaches up to 45°–60° in the contralateral hemifield whereas in albino ferrets the ability to detect a stimulus in the contralateral hemifield abruptly declines directly beyond the vertical meridian so that already in the nasal 0°–30° sector performance is only between 0% and 18% correct runs. This finding correlates with anatomical findings that the ipsilateral retinal projection is severely reduced in albino ferrets (Guillery, 1971; Morgan et al., 1987; Zhang & Hoffmann, 1993). It also implies that the part of the visual field seen binocularly is significantly reduced from more than 90° in the pigmented to almost not existing in the albino ferret. Thus, the substrate for binocular mechanisms as for example depth perception is supposedly diminished or even missing in albino ferrets. Why do we see monocular orienting responses out to 60° into the the contralateral hemifield in pigmented ferrets although physiological evidence shows a visual field restricted to less than 40° contralateral to the seeing eye? It is extremely difficult to monitor the direction of gaze in these small and agile carnivores, especially because they tend to do small horizontal scanning translations of the head all the time. The gradual decrease of the detection rate with increasing contralateral eccentricity might also support the view that some of the detections beyond 40° were due to unnoticed gaze shifts. Thus, it is even more astonishing and significant that the albino animals had this complete neglect of stimuli presented in the contralateral hemifield of the seeing eye.

How do these findings relate to data from other species? Because albinism mainly affects the central and temporal retina and effects are much more pronounced in animals with retinal specializations as visual streak, area centralis or fovea as rabbit, cat and primate than in animals with homogenous ganglion cell distributions as rodents it is reasonable to compare the ferret with rabbit and cat. Rabbit is a typical lateral-eyed animal possessing a visual streak, cat is a typical frontal-eyed animal with a streak and a prominent area centralis. Both concerning the position of the eyes in the head and the retinal anatomy the ferret stands in between rabbit and cat. In rabbit, the overlap of the individual visual fields of the two eyes is maximally 30° (Hughes, 1972) and thus significantly smaller than in ferret. No data are available about the extent of the visual field in hypopigmented strains. By contrast, the extent of the visual field in normal cats closely corresponds to that of the ferret including 30°–60° contralateral and up to 90° ipsilateral to the tested eye (Elekessy et al., 1973; Sherman, 1973; Simoni & Sprague, 1976; Smith, Holdefer, & Reeves, 1982). There are no data available about albino cats. Siamese cats, however, also having a mutation at the albino locus have been studied in some detail. Comparison with data from the literature shows that our results about the monocular visual fields in albino ferrets very closely correspond to data reported by Elekessy et al. (1973) for the siamese cat where the visual field is limited to the ipsilateral hemifield during monocular viewing (but see also Simoni & Sprague, 1976). Comparison of our data with data from monocularly deprived cats shows that the albino visual field is more complete than that of the deprived eye that was reported to be limited to the monocular field (60°–90° ipsilateral) (Sherman, 1973; Sherman, 1974; Smith et al., 1982) or to include also parts of the binocular visual field (0°–90° ipsilateral) (Heitländer & Hoffmann, 1978; Hoffmann, Heitländer, Lippert, & Sireteanu, 1978; Van Hof-Van Duin, 1977). The performance in the central part of the ipsilateral hemifield was better in our albino ferrets (and the siamese cats of Elekessy et al., 1973) than in monocularly deprived cats. The monocular visual field of Siamese cats and albino ferrets resembles that of cats after binocular deprivation (Sherman, 1973) or with surgically induced strabismus (Sireteanu, 1991). Sherman hypothesizes that his animals use mainly their superior colliculus for orienting, Sireteanu (2000) suggests that the interocular suppression seen in amblyopic strabismic subjects might be a special form of physiological suppression, as revealed in binocular rivalry. In albino ferrets the collicular map contains a complete representation of the contralateral retina with almost no input from the ipsilateral temporal retina because the ganglion cell axons from the entire retina cross to a large extent at the chiasm (Quevedo, Hoffmann, Husemann, & Distler, 1996). Why do we nevertheless find that albinism causes a loss of orientation responses to stimuli in the contralateral (nasal) visual field of each eye at least in carnivores as closely related as cat and ferret? Does this imply that the abnormal representation of the nasal visual field in the contralateral visual brain (Hubel & Wiesel, 1971; Kaas & Guillery, 1973; Lomber & Payne, 2001; Quevedo et al., 1996) in albinos cannot be utilized for orienting towards novel stimuli due to interocular suppression as seen in strabismic amblyopes? (see also discussions of Elekessy et al., 1973 and Sireteanu, 2000). The mechanisms of such suppression of the activity from these parts of the visual map in the contralateral visual cortex and superior colliculus of albinos await further investigation. The initiation of this suppression may be due to the violation of a simple rule: the left visual brain is responsible for orienting towards stimuli in the right hemifield and vice versa. This is common sense for normal animals. Both eyes together with the partial decussation at the chiasm serve this purpose. However, in albino animals stimuli seen by the temporal retina are wrongly projected to the contralateral brain hemisphere, i.e. objects present in the right hemifield seen by the left eye are projected to the right half of the brain and would cause orienting responses to the left, which of course are never successful. Thus, they get eventually suppressed. This solves the problem of the same stimulus being represented in both hemispheres of the brain when both eyes are open in albinos or at noncorresponding locations in the same or across hemispheres in strabismic animals. The rule in such animals then could be: stimulus on the nasal retina of the right eye—orient to the left, stimulus on the nasal retina of the left eye—orient to the right. Stimuli on the temporal retinae—suppress.

Acknowledgements

We wish to thank M. Bronzel, M. Möllmann, and H. Pollmann for help during the experiments, D. Hupfeld and M. Klar for help with analysis, and C. Distler for her input to the study and for preparing the manuscript. The study was supported by DFG grant SFB 509 and a stipend from KOGNET to N. Garipis.

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