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Research report

Motion perception in rats (*Rattus norvegicus* sp.): Deficits in albino Wistar rats compared to pigmented Long-Evans rats

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Abstract

Motion perception was tested in pigmented Long-Evans and albino Wistar rats (*Rattus norvegicus* sp.) using moving random dot patterns. Pigmented as well as albino rats could distinguish a fully coherently moving pattern from dynamic noise. However, motion coherence thresholds were significantly lower in pigmented compared to albino rats (12% and 30% coherence, respectively). These results indicate that pigmented rats have well developed motion coherence perception, whereas albino rats are severely impaired but not motion blind.

Keywords: Albinism; Visual; Motion detection; Motion coherence; Rodents

Albino mammals are an important model for studying the development, function and pathology of the visual system [18]. The albino phenotype is characterized by reduced pigmentation of the skin, iris and retinal pigment epithelium. The reduced action of the enzyme tyrosinase leads to a lack of L-DOPA (L-3,4-dihydroxyphenylalanine) which in turn causes a cascade of spatiotemporal perturbations during retinal development [18]. These maturational alterations lead, e.g. to a reduced number and a reduced peak density of rods, a reduced ipsilateral projection of ganglion cell axons, as well as physiological deficits in cortical visual centres [3,8,17]. These anatomical changes result in various visual perception deficits [1,4,10,11].

Albino mammals have reduced visual acuity, depth perception and a limited monocular visual field. They also show various impairements in their optokinetic reaction, i.e. their ability to stabilize the image of the environment on the retina [7,14]. In albino Wistar rats, the optokinetic reaction is strongly reduced or absent [27,31]. The rat, together with the mouse, is an important laboratory animal serving for many pathological studies. Various strains including models for degenerative deficits of the visual system are available. As the visual system of this species is being studied more thoroughly, the animals' visual capacities have to be analysed in detail also on the behavioural level. We therefore investigated whether albino rats have a deficit in visual motion perception which could explain their optokinetic deficit, thus whether albino rats are motion blind.

1. Animals

The investigation of motion perception in albinos was started with eight experienced Wistar rats (ALB$_e$: four males and four females). They had previous experience with the setup and the training stimuli and were 12-months old at the beginning of the experiments. Then two other age matched groups of naive Wistar (ALB$_n$: two males and two females) and black-hooded Long-Evans rats (PIGM$_n$: four males and four females), 12–20 weeks old at the beginning of the training, were tested for their motion coherence threshold. Five Long-Evans rats were bred and raised at the animal facility of our institute, three female Long-Evans rats were bought from a commercial breeder (Harlan UK, strain Hsd:Blu). Wistar rats were bred and raised in the departmental animal facility, and were offspring of parents derived from Harlan Winkelmann, Hannover (strain: Wistar Unilever Hsd-Cpb). All rats were grouphoused in environmentally enriched (60 cm × 50 cm × 50 cm) cages under natural daylight. The rats could avoid exposure to light by hiding in wooden huts, which were placed beneath opaque shelves covering about a third of the floor area, to provide maximal protection from light. Light intensities inside the cages were below 50 cd/m^2 at ground level and below 20 cd/m^2 in front of their huts. These light intensities are significantly lower than under conventional housing

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conditions with artificial light (100–200 cd/m^2). Rats were food-deprived and kept at a minimum of 85% of their free feeding body weight. Water was available ad libidum in the homecages. All experiments were conducted in accordance with the European Communities Council Directive of 24 November 1986 (S6 609 EEC) and the National Institutes of Health guidelines for the care and use of animals for experimental procedures. The experiments were approved by the local ethics committee.

2. Setup and procedure

A two alternative forced choice paradigm was used in a modified Lashley jumping stand (Fig. 1). The setup consisted of a wooden box with a small central platform, high above the ground in the centre of the box, and two choice platforms in front of a monitor. Stimuli were presented side by side on the monitor, creating a left–right choice situation. Operant behaviour of the rat consisted of crossing the gap by stepping over to one of the choice platforms. In case of a correct choice, the rat was rewarded by single sunflower seeds, a false choice resulted in no food reward. Rats were handled for 2 weeks and habituated to the setup and the sunflower seeds used as reward. The experiments began with a handshaping to the desired operant behaviour after which the first visual discrimination stimulus was introduced. Usually 30–40 trials per session were performed by trained rats, after each session rats received additional food in a separate cage.

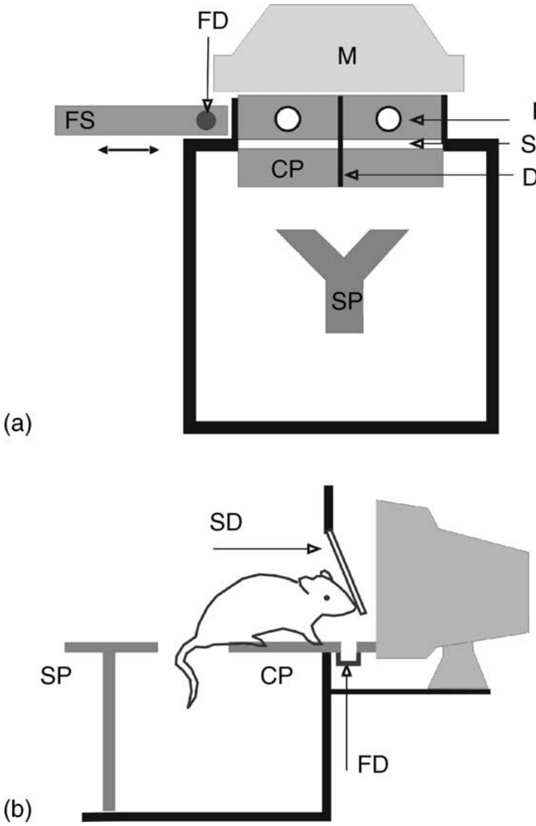

Fig. 1. Illustration of visual discrimination setup: (a) setup illustrated as seen from above and (b) illustration of the setup as seen from the right. Elements: CP, choice platforms (left, right); D, divider; FD, food dish; FH, food hole; FS, food slide; M, monitor; SD, swinging door; SP, start platform. A horizontal start platform (SP) is adjusted in half height inside a wooden box. The monitor (M) outside the box can be watched by the rat through a rectangular opening. The left and right choice platforms (CP), adjusted at the same height as the central platform, are separated from each other by an opaque vertical divider (D). The swinging door (SD) can be pushed towards the monitor (see (b)), allowing access to the food holes (FH). The food slide (FS) can be moved so that the food dish (FD), containing a single sunflower seed, is placed below the corresponding food hole (FH).

3. Stimuli

Limited lifetime moving random dot patterns were created and presented by the software “randomdots”, developed by B. Krekelberg. Dots were white squares, $2^\circ \times 2^\circ$ in size, mean dot density was 0.1 dots/deg^2 and the visible area of the stimulus was $35^\circ \times 35^\circ$ for each side. Dot speed was kept at $10^\circ\ \mathrm{s}^{-1}$, lifetime of each dot was limited to 1 s, after which the dot vanished and was replaced at a new random position. A coherent movement was created by a proportion of dots moving to the right. Equal proportions of dots moving in different directions created an incoherently moving dynamic noise pattern. The proportion of coherently moving dots among dynamic noise is referred to as percentage of coherence. A strong avoidance reaction of the rats to the coherent stimulus was observed, the dynamic noise pattern was chosen as the rewarded stimulus (S+). Rats were initially trained to discriminate a dynamic noise pattern (0% coherence) from a black (B) screen. This first training level is referred to as 0|B, indicating the type of S+ and S− (S+|S−), and was followed by several training levels during which dot density of S− was increased from 0 to the final dot density. Once criterion performance was reached, which was set to 80% correct choices over two sessions of at least 20 trials each, the next training level began. Motion coherence detection ability was finally investigated with a stimulus of 0% versus 100% coherence.

For the second experiment, the method of constant stimuli was used to obtain motion coherence thresholds from Wistar and Long-Evans rats. Stimulus intensity (i.e. percentage of coherence) of S− was varied, 11 levels (5% and values between 10% and 100% coherence in steps of 10%), were presented versus 0% coherence as reference stimulus. Sets of four coherence values were presented in randomised order within one session, sets were changed between sessions.

4. Analysis

Target and choice positions for each trial were protocolled by hand. The outcome of a training session was given as percentage of correct choices over all trials. The mean percentage of correct choices was calculated over at least 100 trials for level 0|B and 0|100 and for about 60 trials per level for motion coherence threshold assessment. The threshold was determined as the percentage of coherence at criterion performance, which was calculated individually as the mean between lapse rate (best performance) and guess rate (50% correct choices), resulting in about 70% correct choices. Statistical analysis consisted of comparing performance of albino and pigmented rats using the

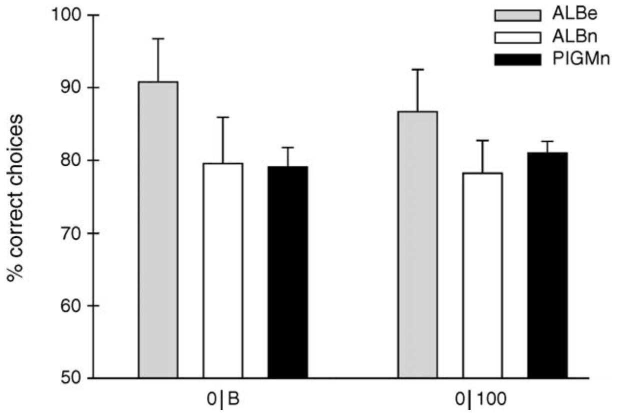

Fig. 2. Motion coherence detection in albino rats. The ordinate shows the mean (±S.D.) percentage of correct choices on level 0|B (0% coherence vs. a black screen) and 0|100 (0% vs. 100% coherence) for the experienced albino Wistar rats (ALB_e: $n = 8$) and for the age matched naïve Wistar and Long-Evans rats (ALB_n: $n = 4$, $PIGM_n$: $n = 8$).

Wilcoxon rank-sum test, for error probabilities of and below 5% the difference between the groups was regarded as significant ($p \leq 0.05$). There was no difference between male and female rats, thus data were pooled to obtain group values.

5. Visual discrimination and motion coherence detection in albino rats

The Wistar rats investigated in the first experiment (ALB_e) as well as the albino rats used in the second experiment (ALB_n) had a high performance on level 0|B (Fig. 2). Performance for the discrimination of dynamic noise (0% coherence) from a completely coherent (100% coherence) pattern exceeded criterion performance for each Wistar rat, thus a visual discrimination based on motion coherence was achieved by these albinos.

6. Motion coherence thresholds of albino and pigmented rats

The performance of the first group of Wistar rats (ALB_e) was higher for both levels (0|B, 0|100) compared to the albino as well as pigmented rats tested in the second half of the experiment. This can be caused by the additional training that the experienced rats (ALB_e) received throughout previous visual discrimination experiments. Discrimination performance of the two matched groups of Wistar and Long-Evans rats was above criterion and not significantly different for level 0|B and level 0|100, the highest stimulus intensity used within the scope of coherence threshold assessment (Fig. 2). In albino and pigmented rats, discrimination performance decreased with decreasing stimulus coherence of S− (Fig. 3a). Mean performance of pigmented rats was always higher than of albino rats, however, the difference in performance at each single coherence level of and above 30% was not significant. By contrast, for 20% coherence the performance was significantly higher ($p < 0.01$, rank-sum test) in pigmented rats, which kept a significantly above chance discrimination performance up to 10% coherence, for lower stimulus intensity performance did no longer exceed chance level. Motion coherence thresholds (Fig. 3b) were significantly lower in pigmented Long-Evans rats than albino rats ($p < 0.01$, rank-sum test). Pigmented rats could on an average discriminate a pattern of about 12% coherence from dynamic noise, albino rats needed about 30% coherence for this discrimination.

7. Motion perception in optokinetically blind albino rats

All Wistar rats were able to discriminate coherent from incoherent visual motion. This for the first time shows that the well documented optokinetic deficit shown with 100% coherently moving dots or stripes in Wistar rats cannot be caused by a lack

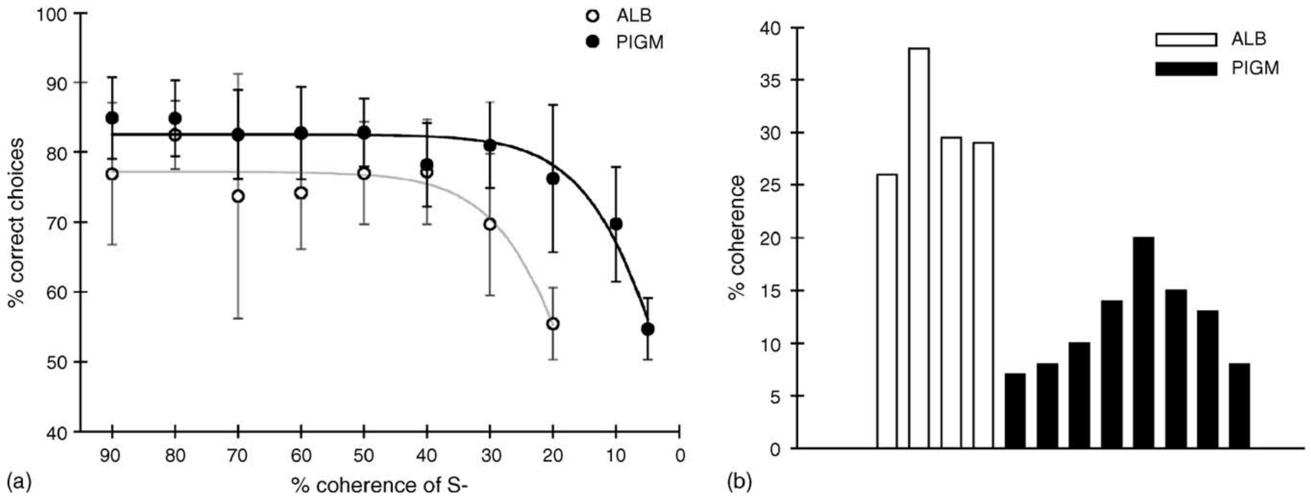

Fig. 3. Motion coherence threshold assessment in albino and pigmented rats. (a) The ordinate shows the mean (± S.D.) percentage of correct choices, different coherence levels for S− are shown on the abscissa (S+: dynamic noise). Performance of albino rats (ALB_n; $n = 4$) shown as open circles, pigmented rat data ($PIGM_n$; $n = 8$) as filled circles. The difference between albino and pigmented rats is significant at 20% coherence (0|20). ALB, albino; PIGM, pigmented. (b) Motion coherence thresholds, expressed as percentage of coherence, are shown on the ordinate. The difference between rats of both phenotypes is significant ($p < 0.01$, rank-sum test). ALB, albino; PIGM, pigmented.

of perception of such stimuli, because as shown in this study, albino rats are not motion blind.

8. Differences between phenotypes

To compare albino and pigmented animals, two different strains were used. The Long-Evans strain was chosen as pigmented reference model based on the common origin of this and the Wistar strain [22]. We suggest the differences in motion perception to be mainly based on the pigmentation phenotype, thus being an effect of albinism. There are known behavioural differences between albino and pigmented rat strains [2,30,32]. However, the differences between Long-Evans and Wistar rats in exploration and anxiety can be reduced by prolonged habituation and training (own observations). As the experiments lasted several months, these strain related behavioural differences were presumably reduced in our study.

9. Impaired motion coherence perception in albinos

Visual acuity and spatial contrast sensitivity differ between albino and pigmented rats [4,28]. Therefore, stimulus parameters were chosen so that dot size and separation of the random dot patterns were well above resolution limits for both albino and pigmented rats. Thus, a reduced visibility of the stimulus pattern could not explain the higher coherence threshold in the albino rat. To prevent light damage of the albino rat retina animals were housed under natural daylight in enriched cages providing significantly lower light intensities than conventional housing conditions. There was no difference in performance for the training stimuli, or in the discrimination of completely coherent stimuli from dynamic noise. Even though no histological data are available on the retinae, these results indicate that the animals were neither generally visually impaired nor were they motion blind. However, Wistar rats had significantly higher motion coherence thresholds. Compared to pigmented rats albinos required about twice to three-fold the coherence level to discriminate coherent motion patterns from dynamic noise. Wistar rats in our studies never showed eye or head movements comparable to a regular horizontal nystagmus as seen in pigmented animals. The lack of an optokinetic response can, however, not be explained with impaired coherence thresholds. Optokinetic stimulation consists of patterns which move coherently in one direction. The results of the present study therefore cannot explain why the Wistar rat seems optokinetically blind. We can, however, exclude a general lack of motion perception as a possible cause.

10. Comparison with other species

There is only one other report of motion coherence thresholds for Long-Evans rats, the authors used different experimental conditions and obtained higher thresholds (25%) compared to our study (12%) [20]. Motion coherence thresholds of cats are reported to be higher, about 25% coherence, than those obtained for rats in this study [16]. A study in pigeons revealed thresholds of 22–60% coherence [5]. Motion coherence thresholds of primates are generally lower, values differ between studies but thresholds down to 5% coherence have been obtained [21]. Ferrets were investigated in parallel to this study, revealing motion coherence thresholds of 20% for wildtype and 42% for albino ferrets [15]. No further comparison of motion coherence thresholds between albino and pigmented conspecifics is available in the literature. Thus, it is difficult to ascertain whether the deficit in motion perception observed in our study reflects an albino characteristic or specific features of the visual systems of these strains. Further studies are necessary to extrapolate this conclusion to humans.

11. Neuronal substrate for motion perception

For global motion processing, the extrastriate cortical areas of the dorsal pathway are crucial in carnivores and primates. The posteromedial lateral suprasylvian area (PMLS) of the cat, the posterior suprasylvian area (PSS) of the ferret, the medial temporal and medial superior temporal area (MT, MST) of monkeys, and the homologue visual area in humans, visual area V5, are characterised by a high proportion of direction selective neurons [19,21,26,34]. Lesions in these areas affect both visual motion perception and optokinetic performance [9,21,23,29,34]. A recent study comparing albino and pigmented ferrets revealed a significantly lower proportion of direction specific neurons of area PSS and an impaired direction selectivity of these neurons in albino compared to pigmented ferrets [26]. As in other species, direction specific neurons are present in primary and secondary visual cortical areas of the rat [12]. However, cortical lesions have nearly no impact on optokinetic performance in the pigmented Long-Evans rat [13]. A specialized motion sensitive area comparable to MT/MST, PMLS or PSS has yet to be identified in the rat. If such an area exists, we would expect differences between albino and pigmented rats comparable to those found in ferrets.

Alternatively, the discrimination defects could be based on retinal deficits which in turn could impair cortical mechanisms of motion processing in areas 17 and 18. With the exception of the reduced ganglion cell density in albino rats, no anatomical differences were found regarding horizontal cells, amacrine cells and ganglion cells between albino and pigmented rats [17,24,25,33]. However, the number of GABA-rich ON-starburst amacrine cells is slightly reduced in albino Wistar compared to pigmented Long-Evans rats [6] indicating that on the physiological level the retinal wiring may be altered in albinos. ON-amacrine cells are involved in generating direction selectivity in retinal ganglion cells which innervate, e.g. the optokinetic system. This retinal defect, probably together with physiological alterations in the accessory optic system, may be responsible for the deficits in the optokinetic reflex. The visual motion discrimination ability described in the present study certainly relies on other, i.e. the geniculo-cortical and the colliculo-thalamo-cortical pathways.

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