

Optokinetic Eye Movements in Albino Rabbits: Inversion in Anterior Visual Field

Abstract. When visual contrasts are restricted to the anterior sector (90° to 180°) of the albino rabbit's visual field, eye position is dramatically unstable, and when such contrasts are moved, horizontal optokinetic eye movements are inverted: the direction of pursuit is opposite to that of the stimulus. In the posterior visual field stability and optokinetic reactions are normal, as in all parts of the pigmented rabbit's visual field. This phenomenon may be one more of the complex of visual system defects linked to albinism.

Albinism, a genetic defect preventing normal synthesis of melanin, is accompanied by profound disturbances of visual function, such as low visual acuity, photophobia, strabismus, and nystagmus (1). This last phenomenon may be caused in part by the poor optical quality of an unpigmented eye but also by the systematic aberrant course of retinal fibers found in albinos. A large proportion of optic nerve fibers originating in the temporal retina, which normally do not decussate, are misrouted and terminate contralaterally. In the retino-geniculocortical pathway this anomaly has been documented in a variety of mammals (2). However, the projections to the pretectum and superior colliculus seem to be affected as well (3). We describe here for the first time, as far as we know, an oculomotor anomaly in albino rabbits which can be classified as a right-left inversion and which may be related to these subcortical aberrant projections.

Rotation of the visual surroundings around any animal elicits an optokinetic nystagmus consisting of a smooth pursuit movement which is occasionally interrupted by fast (saccadic) eye move-

ments that reset the eye to a more central position. In a stationary world, the slow component of this reflex contributes to the stability of the eye in space (4). In the Dutch pigmented rabbit, a nonfoveate mammal with a nearly full panoramic visual field (5), the optokinetic pursuit has been described as a negative feedback control system operating on retinal image movement as the input with an optimal function for low velocities of the visual surroundings (6).

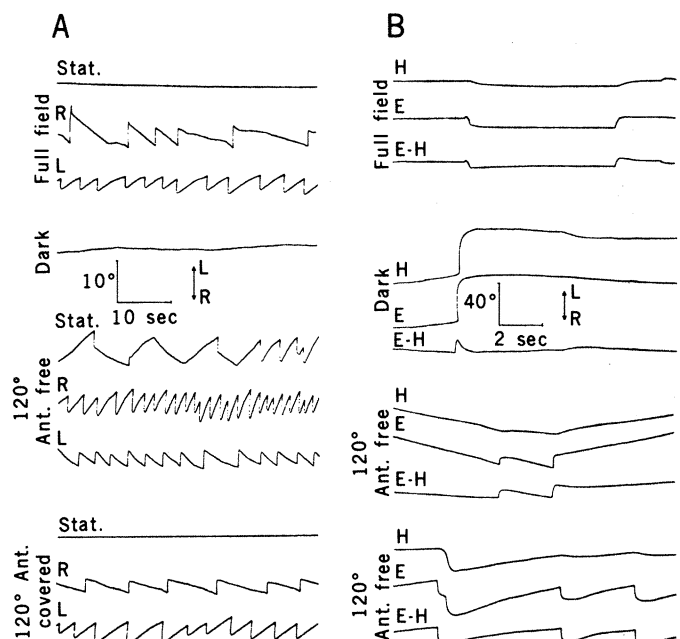
If anywhere in the system the sign of the signal were inverted so that a rightward motion of the world would cause a leftward pursuit, and vice versa, the system would become entirely unstable. This situation of positive feedback, never observed in normal animals, has been artificially created with a servo-controlled optokinetic drum in the rabbit (7) and in classical experiments in flies and fish, in which the eye was rotated 180° about its optical axis (8).

Serendipitously, we discovered a naturally occurring anomaly of this kind in the albino rabbit. A black screen covering the posterior visual field was placed around a New Zealand White rab-

bit. Immediately, a vigorous spontaneous horizontal nystagmus developed. It was abolished by darkness. This observation suggested a sign error in the optokinetic circuit related to the posterior part of the retina. We then systematically investigated optokinetic pursuit in five New Zealand White and four "Polish" albino rabbits, using pigmented Dutch rabbits as controls. Eye movements in alert animals were measured with permanently implanted scleral search coils (9).

Optokinetic reactions were elicited in a drum (diameter, 140 cm; height, 125 cm) centered around the head and lined with a random dot pattern with elements of 1° (10). Parts of the visual field could be screened by a black curtain. With a full visual field the reactions in albinos were relatively normal (Fig. 1A). The eye was stable in a stationary drum, and rotation induced a nystagmus in the normal direction. The pursuit was rather poor, particularly when rotation was in the posterior direction for the measured eye. In darkness some drift occurred, as is normal. Restriction of contrast to an anterior sector of 120° (60° on each side of the sagittal plane) resulted in permanent, severe instability. The spontaneous movements were smooth but frequently interrupted by saccades. Occasionally the smooth movement would change direction, often immediately after a saccade. This instability was always terminated by darkness. Illuminating a moving drum, visible only in the anterior sector, always induced a smooth movement in a direction opposite to the drum motion. The velocities of the spontane-

Fig. 1. Typical eye and head movements of Polish rabbits. (A) Angular eye position in optokinetic drum with full visual field (*Full field*), 120° anterior sector visible (120° Ant. free), and 120° anterior sector covered and posterior field visible (120° Ant. covered) to a stationary drum (*Stat.*), to rotation of the drum to the right (*R*) and left (*L*) at 1.2° per second, and in darkness (*Dark*). (B) Angular position of the head in space (*H*), eye in space (*E*), and eye in the head (*E-H*) in freely moving but quiet animals with full visual field (*Full field*), in darkness (*Dark*), and when 120° anterior sector was free (120° Ant. free). The rabbit's cubicle (80 by 80 cm) was draped with black and white gingham (elements, 1 cm).



ous smooth movements were typically about 3° per second, with peak velocities up to 18° per second. In darkness the same animals drifted only about 0.4° per second. The anterior visual field sector producing instability was about 120° in the Polish albinos but varied from 30° to 180° in the New Zealand White rabbits. No zone of the pigmented rabbit's visual field ever produced more instability than darkness.

The optokinetic pursuit of rotation of the entire visual field over a range of velocities was compared in albinos and pigmented rabbits. The effectiveness of the pursuit is expressed as gain = pursuit eye velocity/stimulus velocity (11). Pigmented (Dutch) rabbits show good pursuit (gain about 0.7) for stimulus velocities up to about 10° per second and fail progressively for higher velocities (Fig. 2A) (6). Performance was poorer in both strains of albinos, particularly in the Polish rabbits; gain was lower and decreased faster when the stimulus velocity was increased. Such poor pursuit could be due to the inverted reactions of the posterior retina; therefore, we

screened the anterior visual zone in both albinos and pigmented rabbits. We found an overall increase of gain in the albinos and a decrease in the pigmented rabbits. The performance of the two groups became comparable (Fig. 2B).

In the optokinetic drum, input-output relations of different parts of the retina were difficult to ascertain because retinal image position and velocity were influenced by the position and velocity of the eye. To circumvent this difficulty, an open-loop situation was created for the right eye. The left eye was covered. A small random pattern (20° horizontal by 40° vertical) was projected on a screen with two perpendicular servo-controlled mirrors (12). The stimulus position could be controlled by the eye position signal so that the stimulus border was stabilized on the retina; in this way stimulation could be restricted to a constant and known part of the retina. Within the stabilized border the pattern was moved at 1.2° per second in the four principal directions.

The results are summarized in Fig. 2C for the Polish albino rabbits, which

showed little individual variability. When the stimulus was positioned (13) in the posterior visual field or along the interocular axis, the eye was stable with a stationary pattern and slightly unstable when the pattern was locked to the retina (open-loop situation). Motion of the pattern caused eye movements in the same direction. Open-loop gain of these rabbits was comparable to that of pigmented rabbits. Anterior and posterior pursuit could be elicited but, as in normal rabbits, the response was much better to anterior motion. When the stimulus was positioned 30° or more anterior to the interocular axis, a stationary stimulus elicited horizontal instability similar to that seen in the drum with anterior vision only. Vertically the eye was stable. Horizontal drift velocities with a stable pattern, indicated in Fig. 2C, were maximal (3.5° per second) for a pattern 60° anterior to the interocular axis. This spontaneous drift was abolished not only by darkness but also by locking the stimulus to the retina. The instability is therefore due to the motion of the retinal image and not to the presence of the pattern as

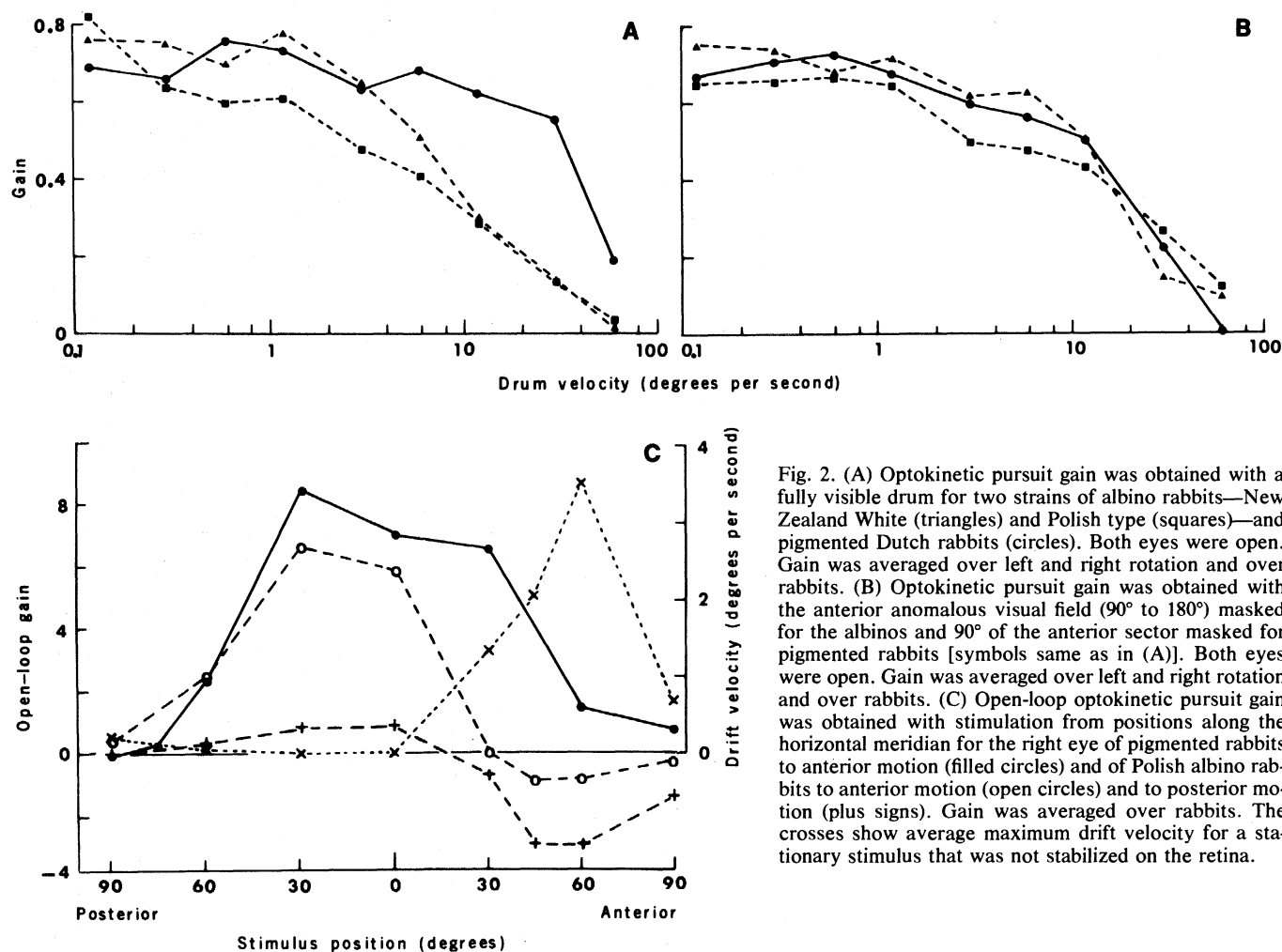


Fig. 2. (A) Optokinetic pursuit gain was obtained with a fully visible drum for two strains of albino rabbits—New Zealand White (triangles) and Polish type (squares)—and pigmented Dutch rabbits (circles). Both eyes were open. Gain was averaged over left and right rotation and over rabbits. (B) Optokinetic pursuit gain was obtained with the anterior anomalous visual field (90° to 180°) masked for the albinos and 90° of the anterior sector masked for pigmented rabbits [symbols same as in (A)]. Both eyes were open. Gain was averaged over left and right rotation and over rabbits. (C) Open-loop optokinetic pursuit gain was obtained with stimulation from positions along the horizontal meridian for the right eye of pigmented rabbits to anterior motion (filled circles) and of Polish albino rabbits to anterior motion (open circles) and to posterior motion (plus signs). Gain was averaged over rabbits. The crosses show average maximum drift velocity for a stationary stimulus that was not stabilized on the retina.

such. Horizontal motion of the pattern in this anterior zone again caused inverted pursuit and thus a negative open-loop gain. Posterior movement was more effective in this zone than anterior movement, which means that in general the eye had a preference to rotate in the anterior direction. Vertical motion of the pattern elicited pursuit in the correct direction, even in the anterior anomalous zone.

In the New Zealand White rabbits, the boundary of the anomalous zone was more variable than in the Polish albinos and was found 30° (two animals), 60° (two animals), and 75° (one animal) anterior to the interocular axis. For comparison, Fig. 2C also shows the result obtained in a similar series of experiments on pigmented Dutch rabbits; in these, gain was always positive. The magnitude depended upon retinal position. No stimulus position induced instability.

Finally, the spontaneous rotations of eye and head were measured in freely moving animals (14). The animals were provided with spectacles that masked different parts of the visual field.

In pigmented rabbits, the eye position in space was very stable between saccades, even for very long intersaccadic intervals.

Figure 1B illustrates typical findings for the albino rabbits. With an unrestricted visual field, the eyes were about as stable as in pigmented rabbits. Typical drift velocities were smaller than 0.2° per second. In darkness, drift velocities were higher and averaged about 0.7° per second; but, when vision was restricted to an anterior sector of 120°, stability was entirely lost. The eye and head usually drifted together, with typical average velocities of about 4° per second and 3° per second, respectively. Spontaneous reversals of direction occurred at irregular intervals, usually after a saccade. In pigmented rabbits, restriction of the visual field to the anterior sector did not noticeably affect stability.

The present experiments demonstrate that at least two strains of albino rabbits have inverted optokinetic reactions in the anterior parts of the visual field. Inverted optokinetic reactions in a few albinos were recently reported but because of its intermittent occurrence under those stimulus conditions it was merely mentioned, and its possible etiology was not discussed (15). Because much is known about the early neural stages, retinal and pretectal, controlling horizontal optokinetic pursuit movements, we believe a straightforward ex-

planation to this phenomenon can be given.

The direction-selective motion information necessary for optokinetic nystagmus is, at least in the rabbit, coded in the activity of a major class of retinal ganglion cells (16). This information converges on neurons in the nucleus of the optic tract in the pretectum, a nucleus related to the generation of horizontal nystagmus (17). A pretectal pathway for horizontal optokinetic reactions is therefore likely. According to Giolli and Guthrie (18), the nucleus of the optic tract in rabbits receives an ipsilateral projection. If this projection arises from temporal retina and terminates in the contralateral nucleus of the optic tract in albinos, the present findings could be explained.

These present findings also have implications for the plasticity of optokinetic reactions. The rabbits we used were fully adult, but apparently there was no correction or suppression of the incorrectly connected parts. However, the dominance of the larger correct input with full field vision might leave insufficient pressure for modification. It remains to be seen if some adaptation of optokinetic reflexes might occur in albino rabbits wearing spectacles that mask the posterior visual field for a long period. Another possibility is that the inversion in the processing of visual motion signals might induce a decrease or even inversion of vestibuloocular reflexes. Such an effect has been described in humans and cats in both of which vision was inverted by prisms for an extended time (19). Similar visual inversion experiments have been reported for the albino rabbit (20). The visual stimulus in the rabbit experiments consisted of a single vertical light slit, positioned laterally to the eye. The present findings indicate the perils of using albinos for such experiments. On the other hand our findings suggest plasticity experiments in which the naturally occurring anomaly is used.

If the optokinetic anomaly occurs generally in albinism, its effects on oculomotor control may be more profound in species that have a larger proportion of optic nerve fibers that remains ipsilateral, for example, in cat and man. Such optokinetic inversion could well be a cause of spontaneous nystagmus, which is often observed in albinos.

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11. Gain was determined once the nystagmus had increased to a steady state, which could take many seconds for the highest stimulus velocities (6). Drum rotation was always started in darkness, and the drum illumination was switched on when the drum had reached a constant velocity. Brightness of the white parts of the pattern was about 15 cd/m², of black parts about 1.5 cd/m².
12. General Scanning, Watertown, Mass.
13. Positioning was done with respect to the transverse axis through the center of both eyes (interocular axis). The stimuli were vertically centered on a horizontal plane through the axis. The visual streak is normally kept aligned with this plane, and the blind spot projects 10° anterior and 13° below the interocular axis (5). These relations were verified in our experiments by ophthalmoscopy to a precision of about ±10°.
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