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The optokinetic response in wild type and white zebra finches

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Abstract Optic flow is a main source of information about self movement and the three-dimensional composition of the environment during locomotion. It is processed by the accessory optic system in all vertebrates. The optokinetic response is elicited by rotational optic flow, e.g. in a rotating drum lined with vertical stripes. We investigated here the effect of rotational optic flow on the optokinetic response in wild type and white zebra finches. The highest stimulus velocity eliciting an optokinetic response (upper velocity threshold) was dependent on stimulus direction and illumination level, but was not different between the colour morphs. The upper velocity threshold was higher with temporal to nasal movements in monocularly exposed birds and symmetrical with binocular exposure. Its increase with illumination level followed Fechner's law and reached a plateau at about 560 Lux. In bright daylight, white birds did not show optokinetic responses. We conclude that the altered wiring of the visual system of white birds has no influence on accessory optic system function. The unwillingness of white birds to respond with optokinetic response in bright daylight may be due to a substantial lack of inhibition within the visual system as demonstrated earlier, which may enhance the sensibility to glare.

Keywords Albinism · Visual system · Birds · Optic flow · Accessory optic system

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Introduction

Moving around in an unpredictable environment appears to be an easy task, judged from the observation of animals walking or flying in their natural habitat. However, its complexity becomes obvious if one analyses the sensory and motor demands for perfect orientation and manoeuvring skills, which can be observed, for example, in birds. On the motor side, a lot of adaptations such as weight reduction, metabolism enhancement and the special construction of the wings are examples for the optimisation of the avian body for flight. On the sensory side, it is mainly the visual system that has to be optimized for fast processing of sensory information as it is necessary during flight.

This paper describes experiments aiming to investigate processing of optic flow by the visual system of birds. Self motion of the animal induces motion of the visual scene on the retina. This optic flow can be translational or rotational, depending on whether the motion is straight (forward, backward, up, down) or involves a rotation or turn of the head. Translational optic flow has been shown to be a major sensory cue, which the animal can use for navigation. It contains information about the three-dimensional composition of the environment, for example the distance between objects. Most support for this role of optic flow has been obtained with flying insects (rev. Lappe 2000; Kern et al. 2001), but there is also evidence that birds use it for manoeuvring (e.g. Davies and Green 1990, 1991; Lee et al. 1993). Rotational optic flow does not contain such information, and if occuring in combination with translational optic flow (simultaneous forward movement and turning), it makes the processing of translational flow information more difficult. Insects thus avoid contaminating translational optic flow by concentrating the necessary turns inducing rotational flow to short saccades (Kern et al. 2005).

A similar reaction to rotation, the optokinetic response (OKR), has been observed in all animals examined so far. When a subject is placed inside a rotating drum with vertical stripes, the eye (or head) responds to the optic stimulation by following the movement of the stripes. Traditionally, this has been interpreted as a mechanism that stabilizes an image on the retina for better object identification, but it may also play a role for stabilization of translational optic flow. Birds, like most other vertebrates, are following the rotation of a pattern with the head instead of just moving the eyes. It has been demonstrated that the head response in birds is coupled strongly with the eye response. Measurements of both the responses give almost identical results (Gioanni 1988).

The OKR has been examined to obtain information on the processing capacities of the visual system, for example to measure the upper velocity threshold, that is the maximal number of perceivable contrast changes, or the fastest speed detectable by the visual system (Bischof 1988). It has also been used as a diagnostic tool to detect deficits due to genetic or other disorders of the visual system (Mohn et al. 1986).

In all vertebrates examined so far, one of the three main visual pathways, the so called accessory optic system (AOS) is specialised for the processing of optic flow. Together with a closely connected pretectal nucleus (n. lentiformis mesencephali), it receives direct retinal input from the "displaced ganglion cells" of the contralateral retina (Brecha and Karten 1978; Fite et al. 1981), a subpopulation of retinal ganglion cells located outside the ganglion cell layer. Other afferents include projections from the visual wulst, and the telencephalic station of the thalamofugal visual pathway (Miceli et al. 1979; Rio et al. 1983). The information from these nuclei is then fed to optokinetic reaction control nuclei (oculomotor nuclear complex and vestibulocerebellum; Brauth and Karten 1977; Brecha and Karten 1978; Gioanni et al. 1983a, b). It also transfers information to brain areas calculating the time to collision of objects approaching on a collision course (e.g. N. rotundus, Wang and Frost 1992; Wylie et al. 1997; Diekamp et al. 2001) and controlling self motion (vestibulocerebellum, Brauth and Karten 1977; Wylie et al. 1997, 1998).

All information available for birds as yet stems from research on the pigeon. For the biggest avian group, the passerines, no information is available. We therefore decided to investigate the optokinetic response in the zebra finch, a small songbird from Australia, the visual system of which we have explored over the last 30 years.

Another reason to investigate the OKR was its suitability as a diagnostic tool for the function of the accessory optic system. The mammalian albino visual system differs from that of the normal animal by strongly reduced ipsilaterally projecting retinal ganglion cell fibres. This lack of binocular information may be responsible for the OKR deficit (Hoffmann et al. 2004).

A number of studies has demonstrated that in albino animals, the optokinetic reactions are reduced (albino rabbit, Collewijn et al. 1978) or absent (albino ferrets, Hoffmann et al. 2004). Collewijn et al. speculated that the reduction of the OKR might be due to normally nondecussating fibres from the temporal retina, which decussate in albino rabbits and cause an inversion of the OKR response in the anterior sector of the visual field. Hoffmann et al. were able to show that the deficit was due to changes within the NOT (nucleus of the optic tract), which is the mammalian homologue of the LM (n. lentiformis mesencephali) in birds, and not in motor areas. The mammalian albino visual system differs from that of the normal animal by strongly reduced ipsilaterally projecting retinal ganglion cell fibres. This lack of binocular information may be responsible for the OKR deficit (Hoffmann et al. 2004).

The white morph of the zebra finch is a partial albino. In contrast to full albinos, its eye is pigmented and normally structured. However, it develops strong deviations in the central visual system comparable to other albinotic animals (Bredenkötter et al. 1996). The optic nerve, which is totally crossing in birds, is unaffected, while recrossing fibres, conveying information of the eye from contralateral visual areas back to the ipsilateral hemisphere, are strongly enhanced. This is true for the projection from the tectum opticum to the contralateral n. rotundus and also includes a rotundo-rotundal crossing projection, which exists only in white and not in wild type animals (Leminski and Bischof 1996). Consequently, neuronal responses within the visual brain areas ipsilateral to the stimulated eye are enhanced, as has been shown for the entopallium by Engelage and Bischof (1988) and for the visual wulst by Bredenkötter et al. (1996). In addition, there is a general inhibition deficit in all visual areas examined so far in white zebra finches (optic tectum, n. rotundus, entopallium of the tectofugal visual system, visual wulst of the thalamofugal visual projection, Bredenkötter et al. (1996).

Given these strong anatomical and physiological changes, we proposed that behavioural reactions in white zebra finches may also be altered. The optokinetic nystagmus seemed to be a good first choice to investigate behaviour, because albinism has been shown to induce strong alterations in other albinotic animals (Collewijn et al. 1978; Hoffmann et al. 2004). Due to the wiring of the visual system of birds without direct visual input of the ipsilateral eye to the nuclei of the AOS, we expected asymmetries of the OKR for clockwise and counterclockwise rotation if only one eye could be used. Because the recrossing visual projections are stronger in white zebra finches, we speculated that this asymmetry could be smaller in white animals, based on the fact the AOS gets information from the visual

wulst (Miceli et al. 1979), which receives only minor ipsilateral input in wild type zebra finches, but has a quite strong ipsilateral component in white animals (Bredenkötter and Bischof 1990; Bredenkötter et al. 1996). The visual wulst of birds is homologue to the visual cortex in mammals (Shimizu and Karten 1993). In mammals, binocular backprojections from the cortex are the main source of binocularity the within AOS. The asymmetry of the OKR appears to depend on the degree of binocularity within the visual cortex (Hoffmann et al. 1996). Disturbance of the binocularity in frontally eyed animals leads to a stronger asymmetry of the OKR (Hoffmann et al. 1996). In analogy, one could speculate that an enhancement of the ipsilateral input to visual wulst (which should lead to a better balance of ipsi- and contralateral representation), could make the monocular OKR in white zebra finches more symmetric.

Materials and methods

Twelve white and 12 wild type zebra finches from the institute's stock were used for the experiments, testing the OKR with binocular and monocular viewing. Another six males of each morph were tested in the experiments under variable illumination conditions.

To cover an eye for monocular viewing conditions, we used eye caps made from soft plastic foil normally used as table cover. To manufacture these caps, the foil was firmly attached to one side of a plexiglass box that had numerous holes of 6 mm diameter on that side. The box was attached to a vacuum pump by high pressure tubing. By evacuating the box with the pump, the plastic foil was pressed onto the holes. The foil was then slightly warmed with a hot fan until it was soft enough to be sucked gently into the holes. With quite a lot of experience, hemispherical plastic caps could be produced, which were glued on the feathers around the eye with a silicone medical adhesive normally used for artificial stomata. The caps could be removed easily after the experiment.

The bird was wrapped into a poncho-like piece of cloth with its head free and then attached to a holder by a clamp. It was positioned in the middle of a rotating drum (59 cm inner diameter; 38.5 cm height) facing its walls, which were lined with vertical black and white stripes of equal width (3.24°). The drum was illuminated from above by a light bulb (200 W), which could be regulated at the power supply. The bird's head was monitored by a video camera from above to avoid distractions by direct observation.

The drum was rotated by a small electric motor. Velocities were adjusted by regulating the current supply and measured by a photo sensor monitoring the frequency of black–white transitions passing the point of measurement. A calibration curve was established to determine the velocity of the stripes as a function of the black and white transitions and, for an additional control, as a function of the applied voltage.

The illumination level was measured in lux [lx] by a handheld illumination metre positioned within the drum facing the same area of the drum's wall as the bird's head.

For determination of the effects of monocular and binocular viewing, the illumination was set to the highest level possible. The drum accelerated while the bird was watching. The angular velocity of the black and white stripes at the time the bird stopped its head movements (the upper velocity threshold), was recorded.

For experiments with variable light conditions, the lamp was first set to a certain illumination level and then turned off. In darkness, the rotation speed of the drum was set. Then the light was turned on again with the preset brightness. By this method, the resulting upper velocity threshold could not be contaminated by movements of the bird's head induced by lower speed of the drum before the threshold was reached. We measured in steps of 21°/s (0.5 V), starting with 93°/s (5 V). The frequency was registered at which the birds did not respond optokinetically when the light was turned on again.

To examine the upper velocity threshold under daylight, the method used in the previous experiment was not applicable. Therefore we accelerated the drum while the birds were able to see the moving stripes. We also measured a threshold curve under increasing light levels as we did in the experiment before, but with the difference that the birds were able to see the stripes when they were accelerated. Each frequency was measured once in each bird under the different experimental conditions.

Statistical comparison of the data was performed with one way ANOVA and subsequent post hoc tests (Newman–Keuls) using the "Statistica®" software.

Results

Monocular and binocular OKR

This experiment was run to examine the asymmetry of the OKR when only one eye was open. Because the symmetry of the optokinetic response may depend on the amount of ipsilateral input to the AOS, we presumed that the asymmetry would be smaller in white birds which have enhanced ipsilateral projections. The variable factor for this test was monocular (left or right) and binocular viewing. Twelve white and 12 wild type individuals were tested ten times during counterclockwise (ccw) and another ten times during clockwise (cw) rotation of the drum for each condition. The upper velocity threshold measured under the different conditions is given as mean ± standard error of the mean (SEM).

Wild type

For wild type animals, measurement of OKR with both eyes open revealed a mean upper velocity threshold of 363 ± 28°/s for clockwise and 370 ± 32°/s for counterclockwise rotations of the drum (Fig. 1). There was no significant difference between the two rotation directions (ANOVA; $F = 0.099$, $P = 0.755$). The mean of both the conditions was 366 ± 30.5°/s.

Monocular tests revealed a mean upper velocity threshold of 385 ± 41°/s for an open left eye, when the drum rotated clockwise. In counterclockwise condition, with the open left eye the mean upper velocity threshold was 192 ± 9.5°/s. When the right eye was open, we recorded mean velocity thresholds of 157 ± 24°/s for clockwise and 349 ± 32.5°/s for counterclockwise rotations. There was thus a strong asymmetry of the OKR in tests with monocular viewing (ANOVA, $F = 37.421$, $P < 0.001$).

Statistical analysis showed no significant difference between an open left eye paired with ccw stimulation and an open right eye paired with cw stimulation (post hoc Newman–Keuls: $P = 0{,}713$) and vice versa, but significant differences for all complementary pairings ($P < 0.003$). We therefore pooled the results to two classes: temporal to nasal (T–N; left eye open with cw rotation and right eye open with ccw rotation) stimulation and nasal to temporal (N–T; left eye open with ccw rotation and right eye open with cw rotation) stimulation. N–T stimulations resulted in significantly lower visual merging frequencies compared to T–N (Anova; $F = 50.38$, $P < 0.0001$).

Comparison of monocular and binocular conditions (Fig. 2) revealed differences (Anova; $F = 23.53$, $P < 0.001$).

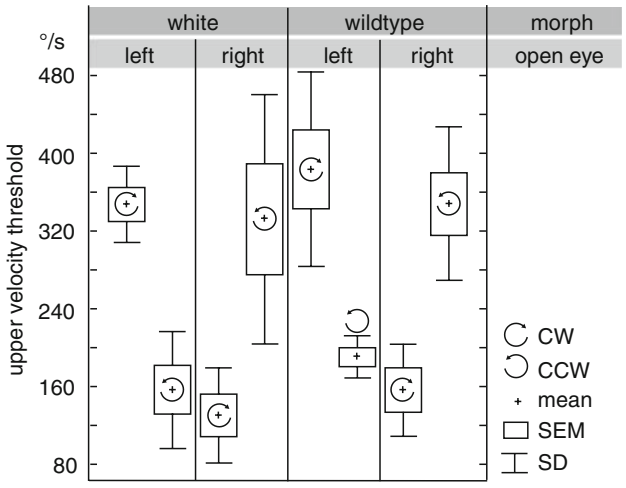

Fig. 1 Comparison of clockwise and counterclockwise stimulation. Mean for each morph (*wild type* and *white*) and each eye open (*left* and *right*), there is one mean value for clockwise (*CW*) and counterclockwise (*CCW*) stimulations as indicated by the *arrows*. *Boxes* indicate *SEM*, whiskers standard deviation (*SD*)

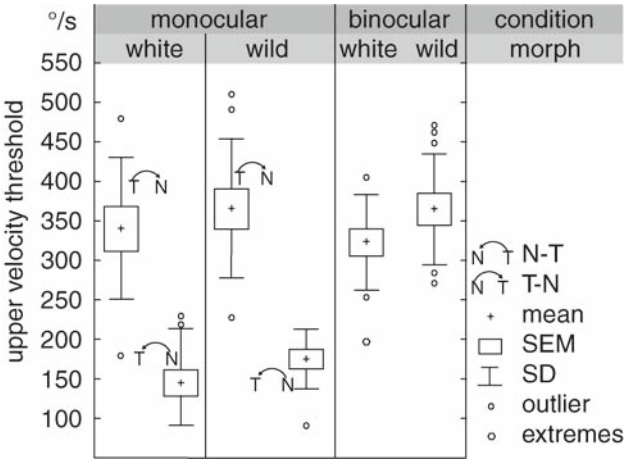

Fig. 2 Mean for *monocular* and *binocular* conditions. *Monocular* for each morph (*white* and *wild* type) there is the mean of the upper velocity threshold for *N–T* and that for *T–N* stimulation. *Binocular*: the mean of the upper velocity threshold for each morph. *Boxes* indicate *SEM*, and whiskers standard deviation

While T–N and binocular performances were not different (Newman–Keuls; $P = 0.975$), the OKR induced by N–T stimulation was lower than that of the binocularly induced ones ($P < 0.001$).

White morph

In contrast to our expectations, the results for white birds were very similar to those obtained in the wild type animals (Fig. 1). The upper velocity threshold for OKR with binocular viewing was 317 ± 19°/s for clockwise rotation of the drum and 332 ± 31°/s for counterclockwise rotation. The difference was not significant (Anova; $F = 3.234$, $P = 0.078$). The mean of both the conditions amounted to 324 ± 30.5°/s.

When the left eye was open, the mean upper velocity threshold was 157 ± 25°/s for counterclockwise rotation and 349 ± 17.5°/s for the clockwise condition. With the right eye open, we recorded the mean upper velocity thresholds of 131 ± 22°/s for clockwise and 334 ± 58°/s for counterclockwise stimulation.

There were significant differences between the different monocular conditions (Anova; $F = 11.87$, $P < 0.001$). Comparing the results of an open left eye paired with ccw stimulation and an open right eye paired with cw stimulation (Newman–Keuls; $P = 0.593$) and vice versa showed no significant difference ($P = 0.769$). Tests of the reverse conditions showed significant differences ($P < 0.003$). As in the wild type animals, this showed that there was a strong asymmetry in tests with monocular viewing, with higher merging frequencies for the temporal to nasal rotations compared to the nasal to temporal ones. Lumping together the two temporal to nasal and nasal to temporal conditions (Fig. 2), respec-

tively, revealed that this difference was significant (Anova, $F = 50.388$, $P < 0.0001$). Again, the binocular results were not different from the temporal to nasal condition ($P = 0.975$), but from the nasal to temporal one ($P < 0.001$).

Comparison of the morphs

The performances of both the morphs for binocularly induced OKR did not differ significantly (Newman–Keuls: $P = 0.36$). The same was found for T–N ($P = 0.672$) and N–T ($P = 0.310$) stimulations in the monocular condition (Figs. 1, 2).

Illumination level dependency of OKR

We tested each individual at 12 illumination levels from 1 to 200 lx once per stimulation direction. Figure 3 shows that upper velocity thresholds strongly correlated with illumination. There was no difference between white and wild type zebra finches (Anova; $F = 0.39$, $P = 0.5$). In agreement with the results of the experiments to test the influence of the eyes, we found no significant difference between stimulus directions (Anova; $F = 0.5$, $P = 0.89$).

Daylight

In daylight, all wild type, but only one white zebra finch showed optokinetic responses sufficient for data analysis. Each bird was tested three times for each stimulus; the corresponding illumination was measured directly thereafter.

As illumination undergoes fast changes during daylight, we were not able to achieve more than one measurement for a given illumination level. Therefore we calculated the mean of the illuminations and the corresponding upper velocity threshold to obtain one single value (Fig. 4). Mean daylight illumination was 8133.5 ± 2909 lx), and the corresponding merging frequency was 349 ± 67°/s.

Comparison of low illumination and daylight results

The daylight data points fit well to the calculated lines of best fit from the previously described results under low light (Fig. 3). But considering that the reaction to moving stripes should reach a plateau somewhere at higher illuminations, and because daylight should actually be at the saturation level, this result was not acceptable. So we conducted another experiment with other birds under low-light conditions. In contrast to the previous experiments, the light was not switched off before acceleration of the drum.

The results are shown in Fig. 4. This experimental variation lead to higher results for the upper velocity threshold, which got close to daylight results already at relatively low-illumination levels (between 240 and 290 lx). The standard

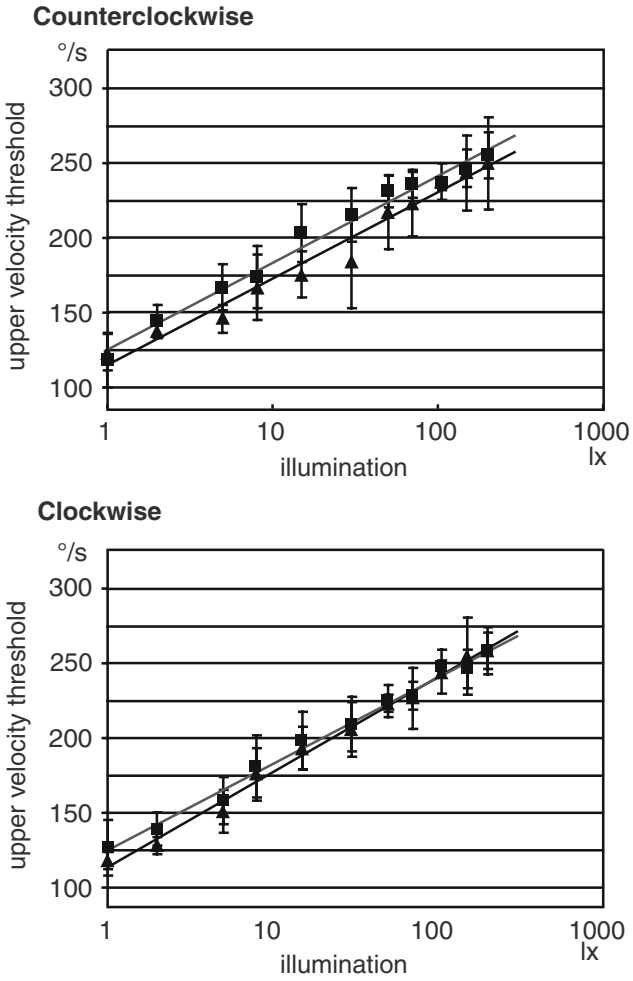

Fig. 3 Relation of the upper velocity threshold with illumination levels. Acceleration of the drum in the dark (see text). *CCW* Counter clockwise stimulation; *CW* clockwise stimulation; *grey squares* wild type zebra finches; *black triangles* white zebra finches; *grey line* line of best fit for wild type birds during low illumination [CCW: $R^2 = 0.9842$; $f(x) = 25.54 \ln(x) + 124.8$, CW: $R^2 = 0.991$; $f(x) = 25.28 \ln(x) + 126$]; *grey line* line of best fit for white birds during low illumination [CCW: $R^2 = 0.9724$; $f(x) = 25.29 \ln(x) + 114.24$, CW: $R^2 = 0.9931$; $f(x) = 27.66 \ln(x) + 115.14$]. *Bars* indicate SD

error of the mean became higher too (SEM between 18 and 26°/s when watching the acceleration and between ±2 and 13°/s when the light was turned off during acceleration).

The calculated line of best fit had a determination coefficient (R^2) of 0.95. According to its equation [$f(x) = 32.63 \ln(x) + 142.44$], we estimated the saturation point to be reached at about 530–590 lx, with a corresponding upper velocity threshold of about 348°/s.

Discussion

Our results concerning the optokinetic response in the zebra finch, a songbird, are comparable to findings in the pigeon

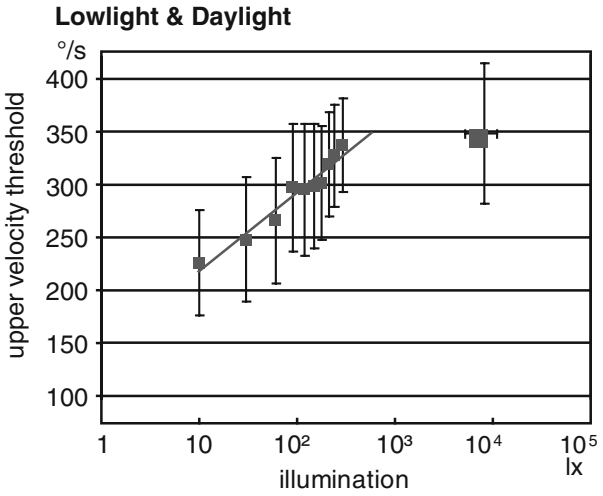

Fig. 4 Relation of the upper velocity threshold with illumination levels. Acceleration of the drum with light on (see text). *Small squares* mean upper velocity threshold for a given illumination; *big square* mean daylight data point; *line* line of best fit for low illumination [$R^2 = 0.9475$; $f(x) = 32.63 \ln(x) + 142.44$]. *Bars* indicate SD

(Gioanni 1988; Gioanni et al. 1981). Temporal to nasal (T–N) and nasal to temporal (N–T) movements of the stimulus exhibit different results if only one eye is open. A stimulus moving in T–N-direction leads to higher upper velocity threshold compared to stimulation in N–T direction. Performance during monocular T–N directed stimulation was equal to that achieved with both eyes open.

The information about the rotational optic flow is transferred from the retina to the pretectal nucleus LM (lentiformis mesencephali) and to nBOR (nucleus of the basal optic root) of the accessory optic system. LM receives additional input from the contralateral nBOR. Both nuclei project to the inferior olive where the input is combined and further transferred to the cerebellum. At least within the cerebellum, information from both the hemispheres is combined forming one output controlling the OKR. Neurons of the LM specifically represent the T–N direction of whole field movement with only a few units reacting to other stimulus directions (Winterson and Brauth 1985; Fu et al. 1998; Wylie and Crowder 2000), indicating that this nucleus is the main processing unit for the horizontal component of the OKR. nBOR exhibits responses for all other directions of environmental movements, with the exception of T–N directed ones. nBOR may thus probably modulate the OKR. (Burns and Wallman 1981; Wylie and Frost 1999). Fite et al. (1979) and Gioanni et al. (1983b) described contradictory results concerning such modulation. According to Fite, the nBOR has little to no effect on horizontal OKR, while Gioanni et al. described a complementary effect of nBOR to LM.

If there were an influence of nBOR on the OKR, there should be differences between monocular performance with T–N movement and binocular performance.

With both eyes open, the stimulus moves in T–N direction for one eye and in N–T direction for the other. Because there is a reciprocal connection between left and right nBOR and also between nBOR and LM, N–T coding cells in the nBOR might enhance the effect of T–N cells of the contralateral LM on OKR. With one eye covered, this activation of N–T neurons should not occur. If the contralateral nBOR enhances the ipsilateral LM performance, we would therefore expect the performance in monocular experiments with T–N stimulation to be weaker than that in binocular experiments. This is not the case, indicating that LM provides the dominant input for OKR control in zebra finches and is not additionally supported by contralateral nBOR input.

Dependency of OKR on illumination levels

Because we did not find significant differences between white and wild type zebra finches in the previous experiments, we also investigated whether there were differences concerning the dependency of the OKR on the illumination level. There were, however, again no significant differences between the colour morphs. When the light was turned off between the tests so that the birds were not able to see the drum accelerate, the results were very clear with small standard errors. When plotted on a logarithmic scale, the progression became linear indicating that the curves are following Fechner's law. The lines of best fit (least squares analysis) matched the data at the 97–99% level. The maximum upper velocity threshold reached in this experiment was about 260°/s at 210 lx illumination.

The experiment described above provided a very clear OKR-illumination relation with small standard deviations. It had, however, the disadvantage that the birds were adapted to the dark when they were asked to react to the moving stimulus. This may have effects on the upper velocity threshold that we measured. We therefore also investigated which velocity thresholds we achieved if the drums were accelerated with lights on. Indeed, they were between 50 and 80°/s higher in this case. If one considers that with this experiment, the frequencies measured might be slightly too high because of a "hysteresis" effect which may keep the birds moving their heads a bit longer than they perceived the moving stripes, the "real" upper velocity threshold may be between our two measurements.

The linearity of the curves in a logarithmic scale indicates that the illumination level, OKR curve is dependent on the function of the photoreceptors. In this case and also if the curve might be more determined by the motor response, a plateau should be reached where the velocity thresholds do not increase any longer. Because we did not reach this with the artificial light experiment, we transferred our experimental setup to daylight. According to these

daylight measurements, the limit of the upper velocity threshold measured under artificial illumination (~340°/s) was already close to the highest velocity that the birds are able to follow.

Comparison of white and wild type zebra finches

Although there were a couple of reasons to speculate about a difference between white and wild type zebra finches, we did find only one deviation in white birds, namely their unwillingness to perform OKR in bright daylight. Neither the performance under monocular conditions nor the dependency of the merging frequency on the illumination level was different. We can thus state that, in contrast to albino rabbits (Collewijn et al. 1978) and to albino ferrets (Hoffmann et al. 2004), the white zebra finches do not seem to have any defect of the OKR system. The reasons are as yet unclear. As stated above, the AOS receives binocular visual input from the visual wulst, and the ipsilateral component is enhanced in white birds. However, our results indicate that this higher ipsilateral input may not be sufficient to alter the OKR, or it does not reach the AOS. It might be that the accessory optic system, in contrast to the other visual projections, (Bredenkötter et al. 1996) is not affected by the albino mutation. It may also be that direct binocular interaction between AOS nuclei, (e.g. Wylie et al. 1997) is not as important in birds as to affect the OKR, because there were no differences between binocular performance and monocular performance with stimulation in the preferred direction. Such questions can only be solved by electrophysiological experiments.

The refusion of the white zebra finches to perform OKR under daylight conditions came not fully unexpected. Our initial reason to investigate the visual system of the white birds was the observation that they had big orientation difficulties at occasions where an animal caretaker entered the aviary. As yet, we presumed that it was the stressful situation causing the behavioural deficits. Our present results indicate that it could be the level of illumination (there is daylight in all our aviaries), which probably glares the birds and causes enhanced stress. The pupil reflexes, however, were normal in the white birds, and, as stated above, the retinal morphology is not altered in white birds. Possibly, the retinomotor system could be disturbed. This could be tested by dark adaptation of the birds before measuring the OKR, white zebra finches should have bigger problems with such a treatment compared to the wild type animals. The lack of inhibition, which we showed for the ipsilateral component of stimulus responses in all visual areas, could be also a phenomenon affecting other areas of the brain. This could probably lead to enhanced arousal of the birds, which may cause behaviour deficits if the arousal levels are yet too high. Probably this could be tested by the application of mild tranquilizers, or by adding arousing stimuli such as loud noise or air puffs to the experimental conditions.

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