Eye movements of laterally eyed birds are not independent

Joe Voss* and Hans-Joachim Bischof

Lehrstuhl Verhaltensforschung, Universität Bielefeld, Postfach 100131, D-33501 Bielefeld, Germany

*Author for correspondence (e-mail: joe.voss@uni-bielefeld.de)

SUMMARY

Most birds have laterally placed eyes with two largely separated visual fields. According to studies in pigeons laterally eyed birds move their eyes independently in most situations, eye coordination just occurred during converging saccades towards frontal stimuli. Here we demonstrate for the first time that laterally eyed zebra finches show coordinated eye movements, regarding direction and amplitude. Spontaneous and visually elicited movements of the two eyes were recorded simultaneously, using a newly developed eye tracking system. We found that, if one eye moves in a certain direction, the other eye simultaneously performs a counter-movement in the opposite direction. Based on these data we developed a hypothesis of how laterally eyed birds cope with the situation in which the left and right eye simultaneously obtain images with different content. We suggest that the counter-movements maintain the spatial relationship of the two visual fields. 'Oculospatial constancy', as we call it, facilitates the combination of the left and right visual percept on the level of peripheral or unattended viewing, and the localization of appearing stimuli within the whole visual field. As soon as two visual stimuli simultaneously appear in the left and right visual field, the birds decide on one stimulus and direct the fovea of the appropriate eye towards it for high resolution analysis, the other eye simultaneously performing a counter-saccade. This leads to the assumption that, in contrast to simultaneous peripheral perception with two eyes, the processing of foveal information is possible only for one eye at one time.

Key words: birds, vision, eye tracking, eye coordination, oculospatial constancy.

INTRODUCTION

Animals with frontally placed eyes have 'binocular vision', and they combine two almost identical images from the two eyes to one single percept. The foveal axes of the two eyes are directed on the same site, analysing the attended object with high resolution. The visual periphery is, however, also perceived by the visual system on a different, maybe lower level of processing. Such 'unattended vision' is well adapted to detect some novel, mostly moving objects appearing in visual space.

A lateral position of the eyes, typical for the majority of birds (Mayer, 1988), results in two visual fields which are largely separated, with a small overlapping zone in the frontal part of the birds (Bischof, 1988; Schmidt and Bischof, 2001). The question arises of how the two images from the eyes are processed perceptually. At the very least the foveal processing of the attended part of the visual scene may be a problem, because the foveal axes of the two eyes cannot be directed to the same site in laterally eyed animals. At least theoretically, these animals could process two different stimuli at the same time, one with the left, the other with the right fovea. However, there is as yet no example of such 'split attention', not even in animals like chameleons and certain fish species that move their eyes with considerable independence (Ott, 2001; Pettigrew et al., 1999). Instead of splitting their visual attention, the birds may focus it on the left or the right visual field alternately. Kirmse (Kirmse, 1990) suggests a mechanism called 'selective internal attention' that uses visual information obtained from unattended vision to select the most conspicuous object within the entire visual field (including the fields of both eyes) and define it as the target for an eye movement which brings the object into one of the foveal foci. According to this idea, only one object within the visual space is attended at any time, and the foveal channel of the other eye is blocked.

Inhibition mechanisms for blocking or at least suppressing information from the unattended fovea have been demonstrated within the tectofugal visual system (Engelage and Bischof, 1988; Voss and Bischof, 2003), which is the main visual pathway in laterally eyed birds (Hellmann and Güntürkün, 2001) and can be seen as homologue of the extrageniculocortical pathway in mammals (Shimizu and Karten, 1990). In all birds, information from the eye is conveyed by the optic nerve to the contralateral hemisphere, at first glance suggesting that the eye information is completely processed there (Cowan et al., 1961). However, each brain hemisphere also receives information from the ipsilateral eye, recrossing from the optic tectum of the contralateral side to the nucleus rotundus of the ipsilateral hemisphere (Benowitz and Karten, 1976; Bischof and Niemann, 1990). Comparable to interocular inhibitory effects in cats (Sengpiel et al., 1995), in birds this recrossing visual information can be suppressed by activity of the contralateral eye (Engelage and Bischof, 1988). The suppression is controlled by pretectal nuclei mediating information from the tectum to n. rotundus (Voss and Bischof, 2003; Theis et al., 2003) and might also be affected by top down processes coming from the visual wulst (Folta et al., 2004).

The existence of such a suppression mechanism supports the view of Kirmse (Kirmse, 1990) that in attended vision only one of the foveal channels may be selected. It does not, however, solve the question of how one foveal channel is selected, whether this selection works on both attended and unattended vision, and how the necessary eye movements are coordinated between the eyes.

Eye movements have been studied in different avian species. Investigation of saccadic eye movements of chickens indicated that they are synchronized with head-bobbing movements to optimize visual sensing during walking (Pratt, 1982). The characteristics of spontaneous saccades in pigeons (Lemeignan et al., 1992) and in

predatory birds (Wallman and Pettigrew, 1985) have also been investigated; the studies showed that in most cases the left and right eye moved simultaneously. In pigeons the observed saccades were parallel with the beak axis in the frontal and parallel with the horizon in the caudal part of the visual field (Lemeignan et al., 1992). Stimulus related eye movements have also been investigated in pigeons. During food pecking, the birds move head and eyes in a coordinated manner, both eyes performing convergent saccades towards the food grain (Martinoya et al., 1984). Based on observations of eye movements, Bloch and colleagues (Bloch et al., 1984; Bloch et al., 1986) concluded that pigeons possess two different modes of viewing: a frontally presented stimulus might be processed binocularly after targeting with coordinated converging saccades, a stimulus presented on one lateral visual field is attended with the appropriate eye without any coordination of the other one.

The hypothesis of such bimodal (frontal and lateral) viewing is supported by anatomical and functional specializations of the pigeon retina. In contrast to human eyes with one fovea, pigeons and other avian species possess two areas with high cell density and high visual resolution: the fovea centralis, pointing to the lateral visual field, and the area dorsalis which is directed to the frontal part where the hemifields of the two eyes overlap (Galifred, 1968). Our anatomical investigations of the retina of zebra finches showed similar results. These birds have the typical fovea centralis pointing to the lateral visual field and a second area of high retinal ganglion cell density in the caudal retina, directed to the frontal field. The two sites are connected by a band of higher cell density (Voss, 2005).

In this study we investigated the characteristics of spontaneous and stimulus elicited eye movements in zebra finches, with an emphasis on the coordination of the two eyes. With a newly developed eye tracking system for laterally eyed birds we recorded eye movements of both eyes and evaluated corresponding movement directions and amplitudes concentrating on two questions. First, does the way eye movements are performed provide information on how laterally eyed birds process the two visual images from the left and right visual field? And second, how far can the oculomotor mechanisms of laterally eyed birds and those of animals with frontally directed eyes be compared?

MATERIALS AND METHODS

The experiments were performed on five adult wild-type zebra finches (*Taeniopygia guttata*, Vieillot 1817; three male, two female) from the institute's breeding colony. To isolate the birds from external visual stimulation during the experiment, they were tested in a cylindrical arena of white plastic with a diameter and a height of 60 cm (Fig. 1). In the wall of the arena three windows for TFT screens were located: one in the frontal part where the birds' left and right visual fields overlap and one each at the left and right side, to stimulate the lateral visual fields.

The setup allowed visual stimulation from +30 deg. to –30 deg. azimuth for the frontal field and from 50 deg. to 120 deg. azimuth for each lateral field (0 deg.=beak axis). The vertical extension of all three TFT screens ranged from –20 deg. to +40 deg. elevation, based on the horizontal plane of the birds' eyes.

The birds were wrapped in cotton cloth to prevent them from moving and placed in a mounting device in the centre of the arena. The head was fixed with an inclination of 21 deg., which is the natural head posture during flight (H.-J.B., unpublished observation).

For head fixation a small Teflon pin was cemented on the scull of each bird. First, the birds were anaesthetized with Equithesin $(0.03\,ml\,10\,g^{-1})$ and mounted on a head holder for small birds (Bischof, 1981). Feathers on the head were removed and the skin
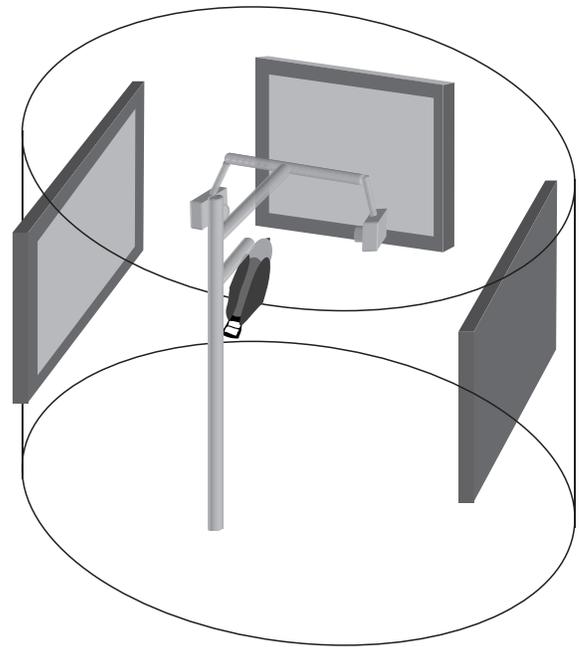

Fig. 1. Schematic drawing of the experimental setup. TFT screens for presenting frontal or bilateral stimuli are inserted in the wall of the arena. CCD cameras record the movements of both eyes. A third camera (not shown in the drawing) records the stimuli from above.

opened to access the skull. The outer bone layer was removed to provide access for the Teflon pin; the inner bone layer was left intact. The resulting cavity was filled with dental cement (Richter and Hoffmann, Harvard, Berlin, Germany), and the pin was embedded. After curing, the skin was replaced over the pin base and fixed with tissue adhesive (Histoacryl®, Aesculap/Braun, Tuttlingen, Germany). The eye track experiments began 2 weeks after surgery.

Eye movements were recorded with two small CCD cameras, positioned at a fixed distance of 4.5 cm in front of each eye. A third camera above the arena monitored the whole scene including the stimuli. The three video signals were merged on a split screen monitor to obtain a video sequence with time correlated information on both eye movements and the stimulus presentation. The video was digitized to DIV format, then sequences starting 0.4 s before and ending 1.6 s after the appearance of a stimulus were selected and cut out using the video editing software Premiere® (Adobe Systems Software, Dublin, Ireland). To obtain controls with spontaneous eye movements without stimulation, sequences with a length of 2 s were selected randomly from the video material. All video sequences were deinterlaced. With the resulting frame rate of 50 frames s^{-1} the eye positions could be determined every 20 ms. The *x*- and *y*-coordinates of the centre of each eye pupil were recorded frame by frame. The coordinate data were then converted by custom made Java® software (Kai Essig, Bielefeld University), drawing the eye movement trajectories and calculating the time marker for the left and the right eye. The resulting trajectories served as a basis for the final evaluation of the eye movements.

The birds were tested under three conditions. (a) Spontaneous movements of both eyes: no conspicuous stimulus was presented, the windows for the TFT screens were covered with white plastic. (b) Bilateral stimulation: both eyes were stimulated by the appearance of stationary objects (black and red circles and crosses)

of 4 deg. diameter which were presented simultaneously for 2 s on the TFT screens in the left and right lateral visual field. The inter-stimulus time varied from 4 to 10 s. The stimuli appeared at random positions on the TFT screens, but were always symmetrical on the two screens. (c) Frontal stimulation: one stationary stimulus appeared for 2 s at 0 deg. (beak axis), where the visual fields of the left and right eye overlap.

Each bird was tested twice a day and for no longer than 6 min per trial. During one test trial the two stimulation conditions were presented in pseudo-random order. Spontaneous eye movements in the 'no stimulus' condition were tested in separate trials.

The x/y-coordinates of the start and end point of the eye movements on the video had to be transformed into angular and amplitude data within an eye related coordinate system. The eye track system was therefore calibrated using an eyeball model with the same dimensions as a natural eye. It was positioned in front of the cameras at the same distance as that of the birds' eye during the experiment. The surface of the artificial eye was covered with a grid of parallels and meridians; the distance between these lines was equal to 10 deg. visual angle. The image of the grid on the video picture was then used to calibrate the whole eye tracking system.

An eye movement was defined as stimulus related if it occurred no later than 1 s after stimulus onset and if its deviation was no more than ±15 deg. from the stimulus direction.

The latency, direction and amplitude of the eye movements of both eyes were evaluated. Due to the calibration procedure the resulting trajectories of the left and right eye arose from the same coordinate system and could be compared directly.

Movement directions of the eyes were analysed from the perspective of the screens/cameras and expressed as angles in a circular coordinate system. To illustrate the directions of spontaneous eye movements, the absolute directional data of all birds were sorted in 20 deg. wedges and depicted in a circular diagram, where movements towards the beak were defined as 0 deg.; correspondingly, movements to the caudal visual field were defined as 180 deg., and dorsal and ventral movements as 90 deg. and 270 deg., respectively (Fig. 2A).

For simultaneously performed saccades by the two eyes, the relationship of the movement directions was evaluated by calculating the difference between the angles of the left and right eye directions. To sum up the data and find prospective regularities, the measured angle of the direction of one eye (in the case of stimulation of the targeting eye) was then set to 0 deg. The direction of the other eye was depicted in the graphs as the corresponding angle. For example, if the targeting eye moved upwards to a dorsally presented stimulus, and the other eye simultaneously performed a saccade downwards to the ventral visual field, the direction of the attending eye was set to 0 deg., and the corresponding angle of the other eye was 180 deg. and pointed to the opposite direction.

The relationship of the movement amplitudes of the left and right eye were calculated as a ratio using the formula:

$$\text{Ratio}_{l/r} = \left(\frac{\text{amplitude}_l}{\text{amplitude}_r} \right)^{\Sigma\,(\text{amplitude}_r - \text{amplitude}_l)} . \quad (1)$$

This ratio can vary between zero and one, and is independent of the absolute distances of the eye movements. The more it approximates one the more the two amplitudes are of equal length. The resulting amplitude ratios were sorted into 0.25 classes and the frequency of values in each class was counted for every single bird. On the basis of these data mean scores for each class were calculated, representing the frequency of different amplitude ratios.

To evaluate whether, in a situation where stimuli appeared simultaneously on the two lateral sides, the birds prefer one of the two eyes for targeting, a preference score was determined. The targeting movements of the left and the right eye were counted for each bird and the score was calculated using the formula:

$$\text{Preference score} = \frac{\text{left eye counts}}{\text{left eye counts} + \text{right eye counts}} . \quad (2)$$

A score higher than 0.7 was defined as a preference for the left eye and a score lower than 0.3 as a preference for the right eye. Statistical calculations are based on means obtained for every experimental bird.

All circular data, e.g. direction of eye movements and the correlation angle between simultaneous movements of the left and right eye, were analysed using software for circular statistics (Oriana, version 2.02a; Kovach Computing Services, Pentraeth, Isle of Anglesey, Wales, UK). Bimodal directional distribution was calculated using axial values. Axial data consist of an undirected line; either end of the line could be taken as the direction. Unimodal directions were evaluated using classical circular statistics. The resulting mean vector in all circular statistics has two properties; its direction (the mean angle, μ) and its length (r-value). The r-value ranges from 0 to 1; a larger value indicates that the data are clustered more closely around the mean (Mardia and Jupp, 2000). For linear statistical analysis, Prism4 (Graphpad Software, Inc., La Jolla, CA, USA) and Statistica (StatSoft, Inc., Tulsa, OK, USA) was used.

The original research reported here was performed under guidelines established by the German Welfare Law.

RESULTS
Spontaneous eye movements

Five birds were tested in an environment without any suspicious visual cue. Sixty-three video sequences of 2 s length, comprising 405 eye movements of both eyes, were analysed. Spontaneous movements occurred approximately two times per second; the mean of the interval between two eye movements was 519±98 ms.

The birds performed eye movements with amplitudes up to 21 deg. (visual angle) and with a movement velocity up to 250 deg. s^{-1}, which is comparable to the velocity of human saccades (Smeets and Hooge, 2003). Based on this result the observed eye movements of zebra finches can be characterized as saccades.

The direction of spontaneously performed saccades was evaluated by calculating the angle of each direction: 0 deg.–180 deg. describes an anterior–posterior saccade (beak axis), 90 deg.–270 deg. a dorsally–ventrally directed one. Fig. 2A shows the frequency of movement directions in 20 deg. wedges; the data of each single bird are depicted in a different colour.

The data show that eye movements in this situation have a distinct bimodal distribution. The mean axial direction (blue arrow) was calculated from the means of the directions measured for each bird (arrowheads), resulting in an angle of 16.5 deg. related to the beak axis. As the head was held with a beak inclination of 21 deg., the mean eye movement direction is with –4.5 deg. almost aligned with the 0 deg.–180 deg. axis. Spontaneous saccades are thus not randomly distributed, but have a preferred direction roughly along the horizontal plane.

In 95% of all cases, eye movements were accompanied by a simultaneous movement of the other eye. Evaluation of the
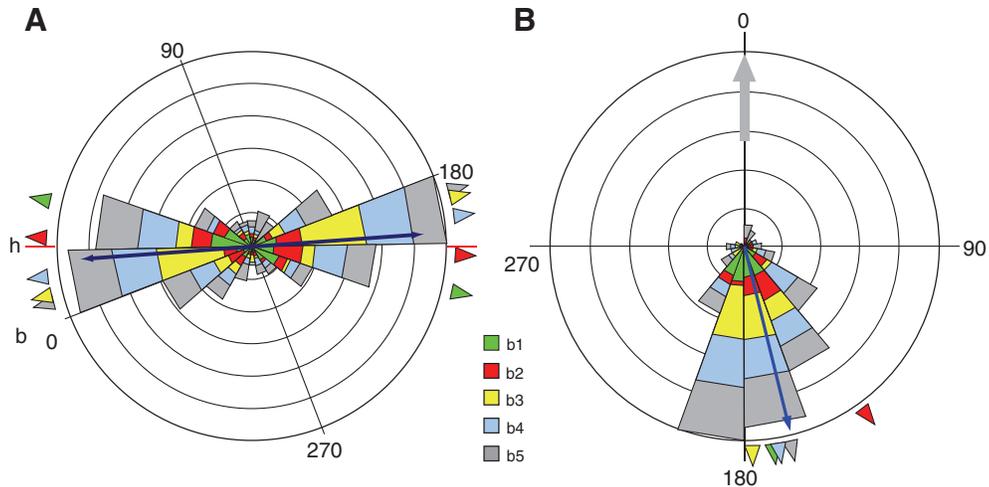
Fig. 2. (A) Circular diagram showing the frequency of spontaneous eye movement directions of both eyes without a conspicuous stimulus in 20 deg. wedges (the colours code for different birds, b). The mean axial direction (blue arrow) is based on the mean axial direction of each bird (coloured arrowheads) and shows that the birds move their eyes close to the axis of the visual horizon. 0 deg.–180 deg.=beak axis, 90 deg.–270 deg.=upward–downward directions, h=horizontal plane. (B) Circular diagram showing the directional relationship of simultaneously performed spontaneous eye movements. 0 defines the movement direction of one arbitrary eye (grey arrow), the frequency of directions of the other eyes' corresponding movement is depicted in 20 deg. wedges. The mean corresponding direction 166.3 deg., r-value=0.98 (blue arrow) is based on the mean directions of each bird (coloured arrowheads). If one eye moves in one direction, the other eye performs a saccade in the opposite direction.

relationship of movement directions of the left and right eye shows that if the two eyes move simultaneously, the movements are not performed independently but have a high degree of coordination in that the eyes move in opposite directions (Fig. 2B). The mean corresponding direction (the direction of the second eye in relation to that of the first eye), based on the mean of the directions measured for each bird, is 166.3 deg. (variance, r=0.98). If one eye moves towards the frontal part of the visual field, the other eye simultaneously performs a saccade into the caudal field, and *vice versa*.
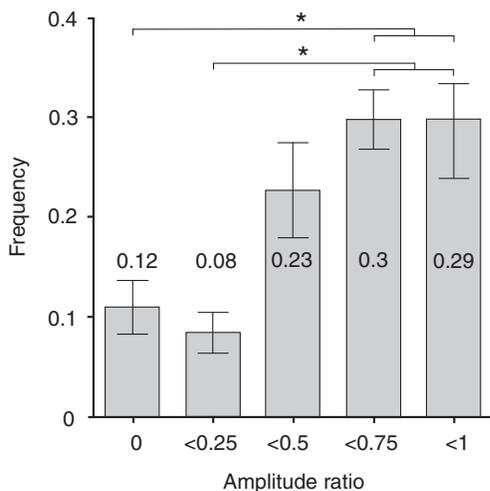

Fig. 3. Relationship of movement amplitudes of the left and right eye when they are moved spontaneously, sorted into classes. 0, only one eye moves; 1, the two amplitudes are of the same length. Simultaneously performed movements of the two eyes tend to have amplitudes of similar or same length (ANOVA: F=6.057, P=0.0036, N=5; Tukey's multiple comparison test: *P<0.001). Data are means ± s.e.m.

To evaluate the relationship of the amplitudes of simultaneous saccades, the ratio of the left and right amplitude was calculated and sorted into classes, representing the average frequency of amplitude ratios (Fig. 3).

The classes for similar (0.5–0.75) and almost equal amplitudes (0.75–1) included more than half of all cases. In contrast, single eye movements (0) and saccades with explicitly different amplitudes (<0.25) were quite rare (scores 0.1 and 0.08). The significance of the frequency differences was evaluated using an ANOVA for repeated measurements (N=5, P=0.0036, F=6.057). A *post hoc* test revealed that the differences between the classes 0.5–0.75/0.75–1 and 0/<0.25 were significant (Tukey's multiple comparison test, P<0.05).

The results show that spontaneous saccades were not performed independently, but were coordinated in most cases. If one eye was moving, the other eye moved in the opposite direction with an amplitude of similar or the same length.

Eye movements evoked by visual stimuli
Bilateral stimulation

The coordination of the left and right eye as a reaction to visual stimuli was investigated by recording their movements during stimulation of both eyes. Sixty-six stimulus targeting eye movements were evaluated in cases where two objects were presented simultaneously at symmetrical positions in the two lateral fields. From these saccades 60 (90.9%) were accompanied by movement of the other eye. We examined first whether the birds used one eye to target one of the stimuli or whether they used two eyes simultaneously. Analysis of simultaneous eye movements showed that in almost all cases (95%) the birds targeted either the left or the right stimulus by moving the appropriate eye towards it. To examine the reaction of the other, not attending eye, the directional relationship between the two eyes was analysed by calculating the angle between saccades of the targeting and the simultaneously moved non-targeting eye. Fig. 4A shows movement directions of the non-targeting eye for all birds (20 deg. wedges) in relation to the targeting one (0 deg.).
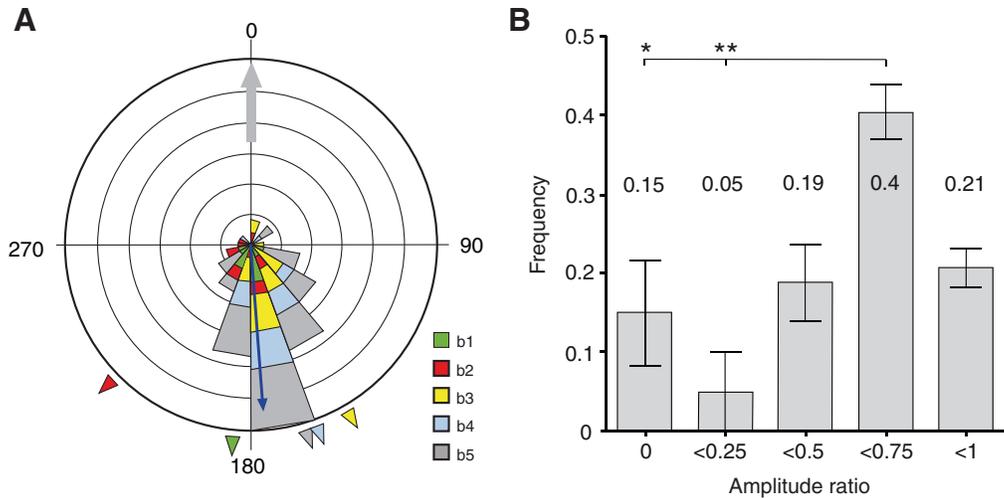
A

B

Fig. 4. (A) Circular diagram showing the relationship of the movement directions of the targeting eye and of the corresponding eye after simultaneous stimulation in the two lateral fields. 0 defines the movement direction of the targeting eye (grey arrow); the frequency of directions of the other eyes' corresponding movements is depicted in 20 deg. wedges (the colours code for different birds). The outer arrowheads show the mean corresponding direction for each bird. The birds decide on one eye and target the stimulus on its side; the contralateral eye simultaneously moves in the opposite direction (mean corresponding direction=176 deg., r=0.89). (B) Relationship of the saccade amplitudes of the left and right eye, sorted into classes. If one eye is used to target the stimulus, the other eye moves with similar amplitude (ANOVA: F=6.01, P=0.0038, N=5; Tukey's multiple comparison test: *P<0.05, **P<0.01).

The mean correspondence angle (blue arrow) of the non-targeting eye was 176 deg. (r=0.89).

Our results show that in the case of two stimuli of the same shape and dimension appearing simultaneously in the left and right visual field, one of the two stimuli is selected and the appropriate eye is directed towards it. The other eye ignores the stimulus that is simultaneously appearing in its visual field and moves in the opposite direction.

Fig. 4B depicts the distribution of amplitude ratios of simultaneous eye movements following bilateral stimulation. There were

significant differences between classes (ANOVA, F=6.01, P=0.0038, N=5). In most cases the amplitudes of the non-targeting eye were between 50 and 100% of that of the targeting eye. If the two eyes were stimulated simultaneously not only did they move in opposite directions but also the amplitudes of the two eye movements were similar.

Frontal stimulation

Eye movements elicited by stimulation of the frontal visual field with a single stimulus were characterized using 104 eye movements.
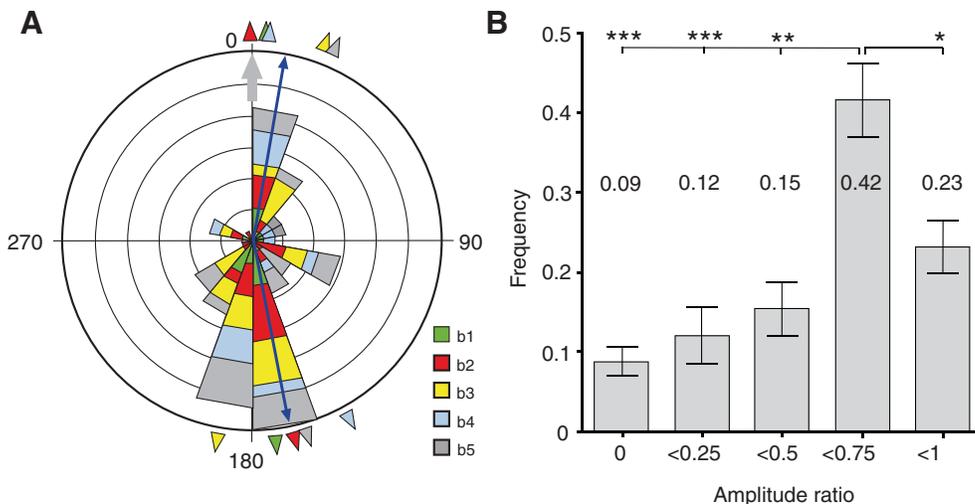
A

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Fig. 5. (A) Circular diagram showing the directional relationship of simultaneously performed eye movements after stimulation in the frontal visual field. If a stimulus appears frontally, the birds react in two different modes. Either they decide on one of the eyes to target the stimulus, and the other eye simultaneously moves in the opposite direction (wedges around 180 deg.), or in 22% of the cases the two eyes simultaneously perform converging saccades towards the stimulus (wedges around 0 deg.). The outer arrowheads depict the mean direction for each bird for converging movements (around 0 deg.) and for counter-movements (around 180 deg.). The blue arrows show the mean corresponding directions in the two modes (mean corresponding direction of one eye targeting: 168.8 deg. (r=0.98), mean corresponding direction of convergent targeting: 10.0 deg. (r=0.99). (B) Relationship of the saccade amplitudes of the left and the right eye (including both modes) after frontal stimulation, sorted into classes. The two eyes move with equal amplitudes (ANOVA: F=11.6, P=0.0001, N=5; Tukey's multiple comparison test: *P<0.05, **P<0.01, ***P<0.001).
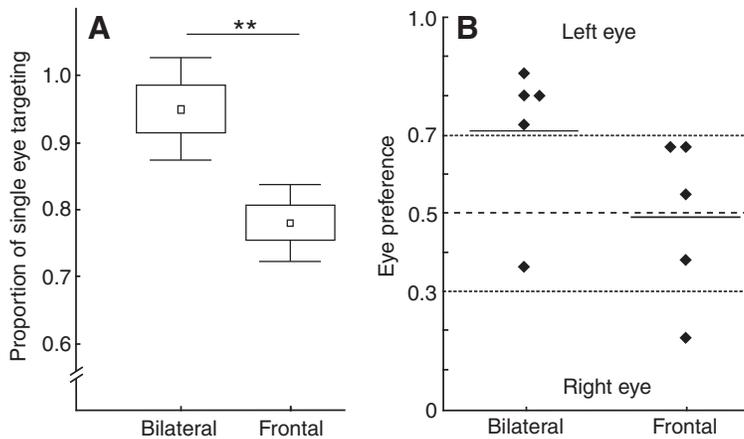
Fig. 6. (A) Frequency of single eye targeting after bilateral and frontal visual stimulation. After bilateral stimulation in almost all cases the birds decide on one eye to target one of the two stimuli; in contrast after frontal stimulation only 78% of the targeting saccades are performed with one single eye, and 22% are converging saccades (unpaired *t*-test: *t*=4.04, **P=0.0037, N=5). (B) Eye preference scores of each bird (diamonds) in bilateral and frontal stimulus situation (means are given by solid horizontal lines). After bilateral stimulation four out of five birds decide on the left eye to target the left stimulus. After frontal stimulation (single eye targeting mode) only one bird has a preference for the right eye; mean values show no eye preference.

From these 104 reactions, 96 (92.3%) were performed with the two eyes simultaneously. The relationship between the movement directions of the two eyes was calculated as described in the experiment above and expressed as corresponding angles (Fig. 5A). In contrast to bilateral stimulation, the relationship between movement directions showed a distinct bimodal distribution: 78% of all stimulus targeting saccades were performed with one single eye, while at the same time the other eye moved in the opposite direction (Fig. 5B), as already found in the experiments with lateral targeting.

In 22% of the cases, however, the frontally appearing object was targeted with the two eyes simultaneously, the eyes converging towards the direction of the stimulus. The mean corresponding angle for single eye targeting movements was 169 deg. (r=0.98), indicating a movement in the opposite direction. For convergent saccades the mean corresponding angle amounted to 10 deg. (r=0.99).

The amplitude relationship of left and right eye movements was similar to that obtained with lateral stimulation. Again, most relationships were within the 0.5–0.75 class (mean=4.2±0.1; ANOVA: P=0.0001, F=11.6; R^2=0.7436; Fig. 5B).

For targeting saccades after bilateral stimulation and for frontally elicited saccades with a single eye, we evaluated whether the birds showed a preference for the left or the right eye. Fig. 6B shows the preference scores for each bird (diamonds) and the resulting mean scores (solid horizontal lines) in both situations. With bilateral stimulation (lateral targeting), four out of five birds showed a preference for the left eye (mean 0.71±0.12), while there was no preference in the frontal stimulation group (mean 0.49±0.12)

DISCUSSION

Our study shows not only that the eyes of zebra finches are moved simultaneously, as has already been shown for pigeons (Lemeignan et al., 1992) and predatory birds (Wallman and Pettigrew, 1985), but also that there is a high degree of coordination between the left and right eye concerning movement direction and amplitude. We can show that if one eye moves in a certain direction, the other eye performs a counter-movement, a saccade of comparable amplitude in the opposite direction.

Such coordination can already be found in a situation without any conspicuous visual stimulation. Zebra finches move their eyes spontaneously approximately two times per second along the horizontal plane in both directions. If one eye moves frontally, at the same time the other eye moves caudally, and *vice versa*. This is in contrast to pigeons, which perform frontally directed saccades towards the beak axis and caudally directed saccades along the horizon (Lemeignan et al., 1992).

Eye coordination has also been found in eye movements of visually stimulated zebra finches. If stimuli are presented frontally, the birds react in two different ways: in most cases one eye moves frontally to attend the stimulus; the other, as described before, performs a counter-movement in the opposite (caudal) direction. In 22% of the reactions to frontal stimulation, however, the two eyes were used simultaneously to target the frontal object with converging saccades. In accordance with our results, Bloch and colleagues describe converging binocular saccades towards frontally presented stimuli in pigeons, but in contrast to our results in zebra finches, the pigeons reacted to lateral stimulation with only one attending eye, the other eye showing no coordinated movements (Bloch et al., 1986). The pigeon results are in accordance with observations in chameleons where left and right eyes are synchronized during prey tracking (Ott, 2001), and spontaneous eye movements can be independent in direction and amplitude (Gioanni et al., 1993). In contrast, zebra finches only use one eye to move towards a target after stimulation in both lateral visual fields. The other eye, obviously not attending the target on this side, simultaneously performs a counter-saccade in the opposite direction, away from the stimulus. Whether this is a species difference or is due to differences in the experimental procedure has to be examined in further experiments.

Concerning the question of how laterally eyed birds cope with two foveal images, that is, whether they are able to split attention in order to process the two foveal images simultaneously or whether they alternate attention between the right and the left image, our experiment provides a clear answer. With simultaneous stimulation of the two lateral fields the birds directed only one eye towards the target, and the other eye performed a counter-movement in the opposite direction, away from the stimulus. Simultaneous processing of the two foveal images is therefore unlikely. In contrast, our results indicate that the birds shift their attention selectively to the left or right foveal field, if laterally placed objects are attended.

In our experiments with simultaneous stimulation of the two lateral fields four of five zebra finches preferentially attended the stimulus in the left lateral field; only one bird showed a tendency to use the right eye/right stimulus. This is consistent with earlier behavioural findings in chicks, which prefer the left eye/right hemisphere to react to novel objects in visual space (Rogers, 2000). Whether this finding in zebra finches is due to lateralization of visual

processing (Rogers et al., 2004) has to be examined with bigger sample sizes and more complex stimuli.

The converging movements after frontal stimulation are reminiscent of converging saccades of the eyes in frontally eyed animals. For frontally eyed birds like owls and diurnal raptors it has been shown that information from the two eyes converges on binocular neurons within the visual wulst (Bravo and Pettigrew, 1981), the avian homologue of the visual cortex of mammals (Shimizu and Karten, 1990). Stereopsis is, however, possible if the overlapping images of the two eyes are of sufficient resolution. Accordingly, the above mentioned bird species have a second fovea within each eye looking into the frontal visual field (Inzunza et al., 1991).

It is doubtful whether the area of enhanced ganglion cell density, which is named the 'red area' in the pigeon (Nalbach et al., 1990), and has also been found in the zebra finch retina (Voss, 2005), has enough resolution to serve for stereopsis. Accordingly, zebra finches do not use frontal vision for location of food. Instead, they fixate a grain with one of the lateral foveae and then grasp it with a mostly ballistic head movement (Bischof, 1988).

However, the present experiment demonstrates the existence of converging eye movements in the zebra finch, reminiscent of the converging saccades seen in frontally eyed animals. It may well be that we have as yet underestimated the importance of convergent eye movements in laterally eyed birds for tasks like distance estimation during flight and landing or for enhancing the contrast between frontal objects and the background (Nieder, 2003).

Convergent movements of the two eyes are, however, an exception. In the majority of all stimulus related reactions, the eyes are moved in opposite directions, and only one fovea targets the stimulus. We have already explained this by the idea that only one stimulus can be attended at a time. The question remains, however, of why the other eye is moved in the opposite direction in almost every case, away from the stimulus. It would have been more plausible if the eye not attending to the stimulus would not perform any coordinated movement.

To explain this we come back to the issue raised in the Introduction. Attended, foveal vision is not the only mode of processing in the visual system. It is also important, besides focusing on a sharp foveal image, that an animal keeps track of what is happening in the entire visual field. We have pointed out that this is performed by 'unattended vision', a process of the visual periphery which locates new conspicuous objects within the environment. We propose here that the counter-movement of the non-attending eye may facilitate this location process, in that it helps to maintain the spatial relationship between the left and right visual hemifield, a phenomenon we shall hereafter call oculospatial constancy.

Oculospatial constancy

The advantage of a mechanism that maintains the spatial relationship between the left and right hemifield could be a simplification of visual processing in laterally eyed birds. Even if the birds focus attention to the fovea of one eye, the periphery of the same eye and the visual field of the other eye cannot be left totally unattended, because the detection of suddenly appearing objects within the whole visual surrounding has to remain possible.

We suggest that such unattended or indirect vision from both eyes is processed simultaneously at any time. At the level of unattended vision, the images coming from the peripheral parts of the left and right eye may be fused to one percept, resulting in panoramic vision. The combination of the panoramic view of the two eyes to one percept would be highly difficult if the spatial relationship of both images changes permanently, because at any time the spatial position of the left and right eye image within the whole scenery has to be recalculated before a fusion to one percept is possible. In contrast, oculospatial constancy, resulting from the counter-movement of the eyes, keeps the spatial relationship of both visual fields quite unchanged, and in this situation a fusion process may be comparably simple.

As our experiments were performed on birds with restrained heads, the question arises of whether the eye movements we have measured do also occur in freely moving animals because, according to earlier claims, birds are moving their head instead of their eyes. Gioanni (Gioanni, 1988), however, has shown in a study of the optokinetic response in the pigeon that the head movements account only for 80–90% of the overall gaze shift; 10–20% are thus due to eye movements. This indicates that birds like other animals are adjusting the gross direction of view with the head or the whole body, and that the fine tuning is done with eye movements. Because head movements affect the two eyes simultaneously, they do not change the relationship of the two visual fields. Birds with restrained heads may extend the saccade amplitudes to compensate for the lack of head movements and the extensive movements clearly reveal the oculospatial constancy mechanism. However, the mechanism that maintains the spatial relationship of both visual fields should work identically under unrestrained conditions when the saccades are used for fine tuning processes.

Species that move their eyes largely independent of each other, e.g. chameleons, might have advanced the strategy of shifting their visual attention to either the left or the right visual field. The inhibition of visual information coming from the unattended eye might also affect indirect peripheral viewing, resulting in a much stronger or general suppression. In that case maintenance of the spatial relationship of the left and right visual field, like we suggest for oculospatial constancy in laterally eyed birds, would not make sense in these animals.

The method of visual processing we describe here might be very useful for birds with laterally placed eyes. Due to oculospatial constancy, the two visual fields are represented with equal processing power at the level of unattended vision and the resulting panoramic vision provides the advantage of observing the whole visual field without disregarding one side. As soon as an object within the scenery is of special interest, it is targeted by the fovea of the appropriate eye. At that moment, information from the fovea of the contralateral eye may be suppressed, but information from the periphery is still processed. However, the described oculomotor strategy may also be an advantage in predatory birds, which are themselves preyed upon by other animals. Accordingly, simultaneous counter-movements of the eyes have also been found in the frogmouth (*Podargus strigoides*), a nocturnal predator with frontally directed eyes, which is taken itself as prey by hawks and owls (Wallman and Pettigrew, 1985).

The oculomotor mechanism of oculospatial constancy in laterally eyed birds is the same as that used by frontally viewing animals to simultaneously direct the two eyes towards a new target. For example, if a stimulus appears in the right half of the binocular field of frontally eyed animals, the right eye has to perform a nasal to temporal movement, the left eye a temporal to nasal one. These are exactly the oculomotor properties we observed in the laterally eyed birds during counter-movements, maintaining oculospatial constancy.

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