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Independent and conjugate eye movements during optokinesis in teleost fish

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Summary

In response to movements involving a large part of the visual field, the eyes of vertebrates typically show an optokinetic nystagmus, a response in which both eyes are tightly yoked. Using a comparative approach, this study sets out to establish whether fish with independent spontaneous eye movements show independent optokinetic nystagmus in each eye. Two fish with independent spontaneous eye movements, the pipefish *Corythoichthyes intestinalis* and the sandlance *Limnichthyes fasciatus* were compared with the butterflyfish *Chaetodon rainfordi*, which exhibits tightly yoked eye movements. In the butterflyfish a single whole-field stimulus elicits conjugate optokinesis, whereas the sandlance and pipefish show asynchronous optokinetic movements. In a split drum experiment, when both eyes were stimulated in opposite directions with different speeds, both the sandlance and the pipefish compensated independently with each eye. The optokinetic response in the butterflyfish showed some disconjugacy but was generally confused. When one eye was occluded, the seeing eye was capable of driving the occluded eye in both the butterflyfish and the pipefish but not in the sandlance. Monocular occlusion therefore unmasks a link between the two eyes in the pipefish, which is overridden when both eyes receive visual input. The sandlance never showed any correlation between the eyes during optokinesis in all stimulus conditions. This suggests that there are different levels of linkage between the two eyes in the oculomotor system of teleosts, depending on the visual input.

Key words: eye movement, fish, optokinesis, conjugate eye movements, independent eye movement, teleost fish, *Corythoichthyes intestinalis*, *Limnichthyes fasciatus*, *Chaetodon rainfordi*.

Introduction

The optokinetic response is one of the most fundamental oculomotor reactions (McCrea et al., 1986; Carpenter, 1988), because it stabilises the gaze during head rotation. Stabilisation is achieved by matching eye rotation to the rotation of the visual surround. The nystagmus shown to a global movement of a whole-field stimulus consists of a smooth phase following the stimulus direction (slow phase) and a saccade-like resetting movement in the opposite direction (fast phase). Both phases tend to be linked between eyes in most animals studied so far (i.e. Easter et al., 1974; Maioli and Precht, 1984; Collewijn, 1991); however, most animals studied such as goldfish, rabbits or primates show coupling of both eyes' movements during most oculomotor behaviours.

Among teleost fishes, spontaneous eye movements range from yoked movements of the very laterally placed eyes of goldfish (Easter, 1971), to the chameleon-like independent eye movements seen in the sandlance (Pettigrew et al., 1999; Fritsches and Marshall, 1999). The present study uses this variability of oculomotor strategies in teleosts to investigate the extent to which the eyes are coupled or uncoupled during optokinesis. We recorded the animal's eye movement behaviour while each eye was presented with separate optokinetic stimuli moving in different directions and at different speeds. Furthermore, we used monocular stimulation with or without visual feedback to the contralateral eye.

We also tested for variations in the strength of the optokinetic response with respect to stimulus direction. For instance, the chameleon is one of the very few animals for which an uncoupled optokinetic nystagmus has been reported (Tauber and Atkin, 1967; Kirmse, 1988; Gioanni et al., 1993). The animal is well known for its ability also to show highly independent spontaneous eye movements, and it possesses a specialised area of best vision, a fovea (Müller, 1862). During optokinesis, the chameleon responds equally well to stimulation in either direction, back-to-front (tempo-nasally) or front-to-back (naso-temporally) (Tauber and Atkin, 1967). On the other hand, most afoveate, lateral-eyed animals with coupled eye movements, such as the goldfish (Easter, 1972), many lizards (Tauber and Atkin, 1968), birds (Tauber and Atkin, 1968; Wallman and Letelier, 1993) and mammals such as rabbits or guinea pigs (Ter Braak, 1936; Tauber and Atkin, 1968), show a reduced or abolished response to movement from front-to-back. This adaptation in lateral-eyed animals is thought to prevent optokinetic stimulation by translational

movements during forward locomotion while preserving sensitivity to rotational movements of the head and body (Collewijn, 1991; Wallman and Letelier, 1993). The lack of image stabilisation and the resulting retinal slip during locomotion are crucial to produce optic flow, which is an important cue for determining self-motion in relation to the environment (Nakayama, 1985; Koenderink, 1986).

The chameleon shows equally strong responses in either stimulus direction, which suggests that these animals dissociate locomotion and rotation in a different way. This led us to test if the fishes studied also show equal optokinesis in both directions, especially those with independent, chameleon-like eye movements such as the sandlance (Pettigrew et al., 1999). Our comparative approach allowed us to look for explanations by differences in lifestyle and hence different requirements for the oculomotor system.

We studied a lateral-eyed fish with goldfish-like yoked eye movements, the butterflyfish *Chaetodon rainfordi*, and two fish with independent spontaneous eye movements, the pipefish *Corythoichthyes intestinalis* and the sandlance *Limnichthyes fasciatus*. All three species are members of the Perciformes, Teleostei, and inhabit the coral reef, but their locomotion and feeding behaviours are quite different, as are their general lifestyles.

Butterflyfish are predominantly algal grazers and coralivores (Allen et al., 1998) and move quickly over quite large areas of the coral reef. Restrained fish exhibit strongly yoked eye movements (K. A. Fritsches and N. J. Marshall, unpublished observations), similar to those of the goldfish (Easter, 1971). The animals do not show fixational saccades or other signs of more highly developed oculomotor behaviour, which strongly suggests the absence of a fovea (Walls, 1962).

The eye movements of the pipefish, on the other hand, are strikingly independent between eyes when the animal moves slowly among coral rubble in search of small benthic invertebrates (Myers, 1991). The independent eye movements of pipefish and seahorses (Syngnathidae) were recognised by many early workers (Kahmann, 1934; Walls, 1942), who correlated this behaviour with the presence of a fovea (Krause, 1886; Kahmann, 1934, 1936; Collin and Collin, 1999).

Sandlances maintain a motionless posture while buried in the sand, with only their prominent eyes showing. Extensive eye movements, covering a range of 160 ° longitude and 90 ° latitude, allow the animal to observe its environment without moving head or body (Fritsches, 1999; Pettigrew et al., 2000), and both eyes move independently from each other. These small fish (2–3 cm in length) catch planktonic prey by darting out of the sand and back again, a movement usually completed within 100 ms (Pettigrew et al., 2000) and therefore amounting to a ballistic strike. This lifestyle has led to a highly developed visual system, including a fovea, and eye movement strategies with many unusual features (Collin and Collin, 1988; Pettigrew et al., 1999; Fritsches and Marshall, 1999).

The choice of animals was influenced by existing knowledge about their visual systems and behaviours (Collin and Collin, 1988, 1999; Pettigrew and Collin, 1995; Pettigrew et al., 2000), and also by their behaviour in captivity under physical constraint. For instance, members of the wrasse family (Labridae) or triggerfish (Balistidae) show a high degree of independence between the two eyes when observed in the wild. Under constraint, however, these animals freeze and are generally unhappy, precluding observation under experimental conditions (K. A. Fritsches and N. J. Marshall, unpublished observation).

In specimens of all three chosen species, the optokinetic response was initially investigated by stimulation with one whole-field stimulus, in order to characterise the response under normal experimental conditions. Further experiments introduced stimulation with a split-field stimulus, challenging each eye with a stimulus direction and speed different from the stimulus seen by the contralateral eye. We also tested the response to monocular stimulation while the contralateral eye received stationary input or was occluded.

Materials and methods

Recordings

For the experiments, eight specimens of each of the species *Lymnichthyes fasciatus* Waite (sandlance), *Corythoichthyes intestinalis* Ramsay (pipefish) and *Chaetodon rainfordi* McCulloch (Rainfords butterflyfish) were used. The animals were collected on the Great Barrier Reef off Heron Island Research Station and maintained in aerated saltwater tanks. The butterflyfish and the pipefish were restrained during the recording. Light anaesthesia was induced using clove oil (0.2 mol l^{-1}, stock 85–95 % clove oil, Sigma; see Munday and Wilson, 1997), and the animal was wrapped in tissue paper and restrained in a purpose-built holder. The sandlance did not require restraint due to its naturally motionless pose.

All videos were recorded from a dorsal viewpoint, with the camera positioned above the animal to record both eyes at a similar angle (Fig. 1A). To achieve sufficient magnification the camcorder (Sony CCD-TR1E) was positioned to record through the eyepiece of a stereoscope (Wild Heerburg photomacroscope M400). An alternative arrangement included a CCD video camera (Sony DXC 151P) with an extension tube (Navitar, 1×), zoom lens (Navitar) and magnifying lens (×0.75). In both setups, the resulting image was displayed on a screen (Sony RGB monitor).

Optokinetic stimulation

Whole-field rotation

A cylinder with vertical black and white grating (spatial frequency 0.05 cycles/°) was rotated horizontally around the holding aquarium, covering 360 ° of the horizontal visual field and 55 ° of the vertical field. We were able to vary the speed of the drum by using a modified kymograph. The animal's response to both clockwise and counter-clockwise rotation was recorded at different drum speeds.

Split half-field rotation

To stimulate each eye separately, two half-field optokinetic drums were used. We constructed two semicircular devices,

each moving a grating around one half of the holding aquarium (Fig. 1). Each device consisted of a wooden frame, shaped in a semicircle and matched in height and width to cover almost 180° of the circular observation tank. The top part of the structure had cogs attached, driving a toothed belt, which was maintained in a semicircular shape using small runners. A cloth with a grating printed on it (spatial frequency 0.06 cycles/°) was attached to the toothed belt, providing a semicircular curtain of vertical stripes (Fig. 1B). Each of the semicircles was driven by an independent power supply. This allowed the two half-field optokinetic stimuli to be moved in opposite directions and at different speeds independently of each other.

The advantage of this novel design was twofold. Firstly, it was possible to elicit continuous movement in one direction in each half-field, which allowed investigation of the slow and fast phases of the nystagmus. Secondly, the drum design used here provides a rotational stimulus for each eye separately. Rotation of a large field stimulus provides equal stimulation at constant speeds to the entire retina, which is the best stimulus for optokinesis. Tangent screens that have been used in other studies (Easter, 1972; Collewijn and Noorduin, 1972b) provide mainly translational movement, with components such as different slip speeds added in different parts of the retina. Since we wanted to test the optokinetic response in isolation, the new circular half-field design used was ideal.

The optokinetic response to naso-temporal and temporo-nasal stimulation was recorded with the drums operating at equal or different speeds. The fish was placed facing the touching point of the two semicircles, which ensured that each eye was maximally stimulated by the grating in its respective hemi-field (Fig. 1C).

Monocular stimulation with visual feedback to the contralateral eye

In order to record the optokinetic response to unilateral stimulation, the split half-field set-up was used, except that one half of the drum was kept stationary while the other drum was moved either temporo-nasally or naso-temporally. Care was taken to cover the area of binocular overlap, estimated at 45° in front of the animal. This stimulus paradigm was intended to record unilateral optokinesis while the other eye was visually stabilised.

Monocular stimulation with occlusion of the contralateral eye

This stimulus condition elicited the optokinetic response in one eye while the other eye was deprived of visual input. To occlude one eye the animals were lightly anaesthetised with clove oil (0.2 mol l^{-1}, stock 85–95% clove oil; Sigma). A small disk of non-transparent black plastic was attached to one eye of the fish using superglue. For the sandlance, which has small protruding eyes, a conically shaped occluder was formed from aluminium foil and attached to the eye. The animal was then stimulated with a single whole-field grating as used for whole-field rotation. Great care was taken to ensure that the occluder covered all of the pupil and did not leave any residual vision. This was checked by observing whether the animal responded to a small moving object in the visual field of the blinded eye. Additionally, the visual surrounding of the occluded eye was shielded off to avoid possible visual stimulation.

Analysis

Tracing

The video recordings of eye movements were hand-digitised by overlaying the video image with the computer screen using a half-silvered mirror. The movements of each eye were then traced using 'Object Image' (program by N. Vischer). Only horizontal eye movements were considered and traced as angular displacements of the pupil from the centre of rotation (Fig. 2A).

The tracing of the movement was slightly different in the different species of fish. In the sandlance, which has more

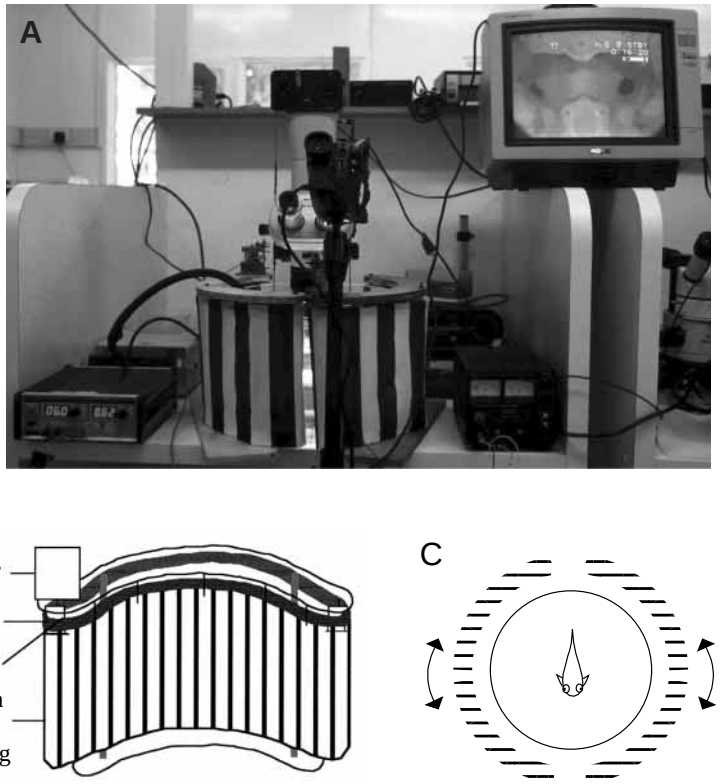

Fig. 1. (A) Photograph of the experimental set-up using the half-field stimulus drum. Two of these semicircular constructions are placed around a circular observation tank, covering 360° of the animal's horizontal and 55° of its vertical visual fields. The video monitor displays a field of view of 3 mm and in the photograph shows the eyes and head of a sandlance. (B) Illustration of one semicircular construction. (C) Diagram to illustrate the position of the fish relative to the two semicircular parts of the drum. Each half-circle is powered by a separate power supply, allowing independent variations in stimulus speed and direction.

dorsally placed eyes than the other fish (Fig. 2B), the centre of rotation was defined when the sandlance looked directly up. On the screen, a circle was drawn around the outline of the eye using the cursor, and the centre of this circle was defined as the centre of rotation of the eye (Fig. 2A). The horizontal angular displacement of the pupil in subsequent movements was recorded in two steps. A circular or oval object was drawn around the outline of the large black pupil for the software to calculate the centre of the pupil. Then the program drew a line from the centre of rotation to the centre of the pupil and recorded the angle of horizontal movement in relation to the anterior–posterior axis (Fig. 2A). For the movement traces shown in Figs 3, 4, 6–8, the position of the pupil was recorded in 100 ms intervals.

In both the pipefish and the butterflyfish the eyes were more laterally placed (Fig. 2C,D), hence the shape of the pupil was mostly invisible. Instead, landmarks on the eye near the pupil or the apex of the circular lens were used for tracing the movement, and the centre of rotation was defined when the eye pointed exactly lateral, at a 90° angle from the anterior–posterior axis of the body.

Measurement of the eye speed in the split drum arrangement

In order to test if the sandlance and the pipefish followed different stimulus speeds accurately with each eye in the split-drum arrangement, we measured the eye speed quantitatively. In three specimens of the pipefish and the sandlance the response to tempo-nasal stimulation was recorded while one eye was viewing a stimulus speed of $5\,^\circ s^{-1}$ and the other eye viewed the stimulus moving at $15\,^\circ s^{-1}$. For comparison we also recorded the eye movements elicited by a whole-field optokinetic stimulus (see above) at stimulus speeds of 5 and $15\,^\circ s^{-1}$. Suitable 20 s long sections were traced from the recordings for each specimen and for each stimulus condition at 200 ms sampling intervals. The criterion for following the optokinetic stimulus in a slow phase was a smooth movement with a minimum duration of 1 s. The slope of the slow phase was determined by a linear regression through the data points from start to termination of each slow phase. This procedure reduced noise introduced by inaccuracies during tracing.

Results

To provide an overview, the results of all three species for each stimulus condition are summarised in Table 1.

The normal optokinetic response

All three species show consistent optokinetic nystagmus to a moving grating (Fig. 3). The nystagmus is executed with a slow tracking movement in the direction of the stimulus movement (slow phase) and a fast resetting movement in the opposite direction (fast phase).

Butterflyfish

Both slow and fast phases are executed simultaneously in both eyes, and the position, amplitude and timing of the optokinetic response in each eye are tightly yoked in this fish (Fig. 3A). Without optokinetic stimulation, butterflyfish show a regular spontaneous shift of gaze, moving both eyes conjugately. Slow optokinetic stimulation of 0.5 and $1\,^\circ s^{-1}$ did not have an obvious effect on this stereotypical behaviour. However, the tracing technique was not sufficiently accurate to detect possible pursuit movements between saccades at these slow stimulus speeds.

Drum speeds of $5–30\,^\circ s^{-1}$ elicited eye movements in the drum direction and resetting fast-phase movements, although some saccades in the stimulus direction were observed. At stimulus speeds above $30\,^\circ s^{-1}$ and faster, the animal showed a clear unidirectional nystagmus even at the highest testing speed of $120\,^\circ s^{-1}$. This maximum speed was followed easily without signs of breakdown of the response. At no time did the optokinetic nystagmus in these animals show any disconjugacy between the two eyes. The fast phase was always synchronous between eyes.

Table 1. *Correlation of the two eyes during optokinesis under different stimulus conditions*

	Butterflyfish	Pipefish	Sandlance
Normal optokinesis	**Yoked** fast phase	Mainly **independent** fast phase	**Independent** fast phase
Split drum stimulation	**Disjunctive** fast and slow phase, slow phase gain linked, convergence to temporo-nasal stimulation	**Independent** fast and slow phase, independent slow phase gain	**Independent** fast and slow phase, independent slow phase gain
Monocular stimulation with visual feedback to contralateral eye	**Yoked** optokinesis, seeing eye drives eye that views stationary grating	**Independent** slow phase, fast eye movement sometimes linked, but no optokinesis in contralateral eye	**Independent** slow and fast phase, no optokinesis in contralateral eye
Monocular stimulation, contralateral eye occluded	**Yoked** optokinesis, seeing eye drives occluded eye	**Yoked** slow phase, fast phase largely independent	**Independent** slow and fast phase, no optokinesis in contralateral eye

The results clearly show differences in the degree of correlation between the two eyes in the species studied. The emerging picture is that of a sliding scale of conjugacy, revealing different linkage strengths between the eyes of the different species.

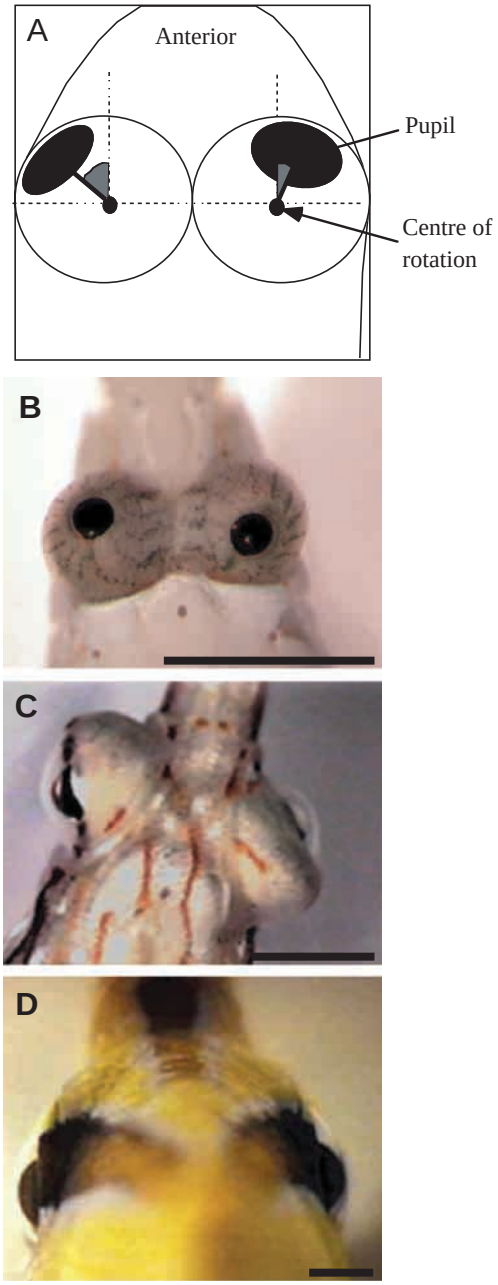

Fig. 2. (A) Tracing of eye movements using 'Object Image'. The horizontal eye position was measured as an angle from the centre of the pupil to the anterior–posterior axis. (B–D) Dorsal viewing angle of the three species of fish used in this study: the sandlance (B), the pipefish (C) and the butterflyfish (D). In all images the animals' nose points towards the top of the photograph. Scale bars, 2.5 mm.

Pipefish and sandlance

Both the pipefish (Fig. 3B) and the sandlance (Fig. 3C) show nystagmus following the stimulus direction, although the response of both is less regular than in the butterflyfish. The fast phase in the sandlance was very rarely elicited simultaneously in both eyes while the pipefish showed more incidences of simultaneous fast phases in both eyes.

In sandlance and pipefish, no optokinetic eye movements could be elicited at slow stimulus speeds of 0.5 or 1 °s^{-1}, similar to the situation in the butterflyfish. Higher speeds of 5–30 °s^{-1} resulted in a good optokinetic response, although many saccades were also elicited in the stimulus direction. The number of these saccades declined with increasing drum speed, and in the pipefish no eye movements other then those belonging to the nystagmus were shown if the drum speed exceeded 30 °s^{-1}. In the sandlance, some saccades in the stimulus direction were seen even at the highest stimulus speeds.

Fast drum speeds of 60 °s^{-1} and 120 °s^{-1} elicited optokinetic nystagmus in both species of fish; however, in many specimens the response ceased periodically during the stimulation. There was a strong individual variability between specimens of both species, with two out of the four pipefish tested showing a nystagmus without interruption, while the other two pipefish showed periodical break-downs of the response at the highest stimulus speed. In all four sandlances the response usually ceased for a short interval when the eye was at the edge of its oculomotor range, either in a rostral or a caudal position.

Split optokinesis

The fish were stimulated with two independently moving gratings to test if the optokinetic response could be dissociated between the eyes. The half-fields of the split drum were operated in opposite directions, both moving either naso-temporally with respect to the animal or in a temporo-nasal direction.

Temporo-nasal stimulation

Butterflyfish. In response to the split half-field stimulus moving from back-to-front for both eyes, the butterflyfish showed a variety of responses. Many animals showed stereotypic spontaneous saccades for most of the time with no hint of a nystagmus in response to the stimulation. However, as shown in Fig. 4A (left, 1–3 s; right, 3–4 s), some animals responded with binocular, convergent following movements to temporo-nasal stimulation, interrupted by unidirectional saccades in both eyes. Occasionally the butterflyfish showed another strategy in trying to follow the two half-field stimuli. While one eye followed the drum direction in a smooth pursuit, the other eye moved in the same direction showing step-like smaller saccades against the stimulus direction it was seeing (Fig. 4A, right). Hence the animals showed spontaneous gaze shifts with both eyes moving in the same rotational direction (i.e. either left or right), similar to what is seen during unstimulated viewing. At the same time, however, the gaze shift was overlayed by dissociated fast -and slow-phase movements in response to the split optokinetic stimulation. It was not possible to see or trace clearly whether the smooth phase in this animal was in fact smooth or the result of many small, step-like saccades.

Sandlance and pipefish. Unlike the butterflyfish, the sandlance and the pipefish show a clearly independent optokinetic response for each eye (Fig. 4B,C). Each slow phase

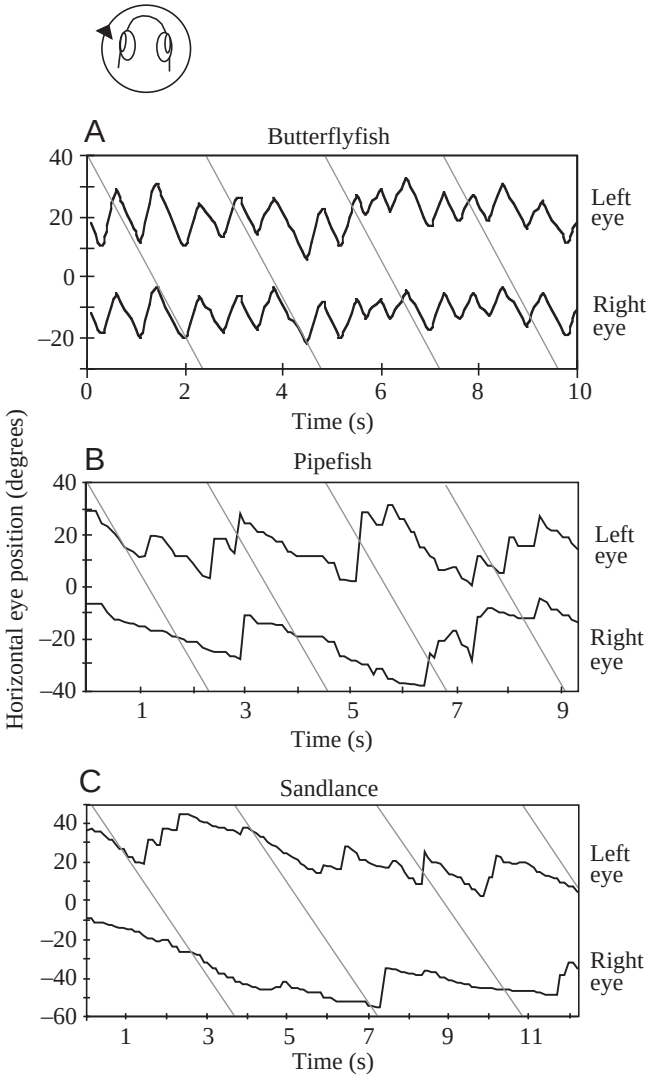

Fig. 3. Normal optokinetic response to a whole-field stimulus, displayed as horizontal eye position (degrees) over time (s). (A) Butterflyfish, (B) pipefish, (C) sandlance. The stimulus speed varied from 25 to 35 °s^{-1} between animals and the speed and direction of the stimulus are indicated by the grey lines. Note the regular and conjugate response in the butterflyfish while the sandlance shows asynchronous fast phases. In the pipefish, some linked fast phases can be seen, although the amplitude of the movement in each eye is mostly different.

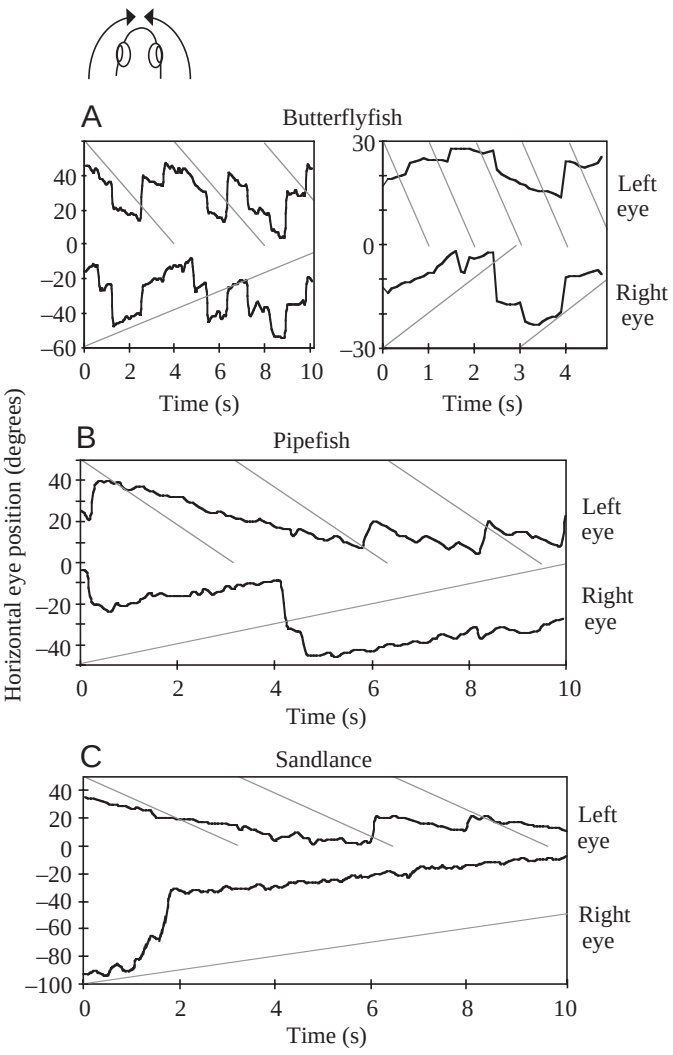

Fig. 4. Optokinetic response to split optokinesis in the temporo-nasal direction for both eyes with a stimulus speed of 15 °s^{-1} for the left eye and 5 °s^{-1} for the right eye. Otherwise the conventions are the same as in Fig. 3. The butterflyfish (A) does not show a fully developed optokinetic nystagmus in both eyes; however, some compensatory strategies can be observed. Left: converging eye movements following the respective stimulus can be observed in both eyes and independent saccades are shown (example at 5 s). Right: both eyes move in the same rotational direction (i.e. to the left or the right of the fish), however, while one eye shows a smooth slow phase in the stimulus direction, the other eye makes several fast phase movements (1–1.5 s; 2.5–4 s), dissociating slow and fast phases between the two eyes. Pipefish (B) and sandlances (C) both respond independently to the different stimuli to each eye.

follows the direction of the stimulus it was seeing, and the fast phase resets mostly independently against the movement of the drum.

When the speed of the two drums differed, the eye speed of the slow phase of each eye was matched to the respective stimulus speed it was seeing (Fig. 5). For instance, in response to temporo-nasal stimulation with speeds of 15 °s^{-1} and 5 °s^{-1}, all specimens of the pipefish (N=3) responded with an eye speed of 9.4±1.1 °s^{-1} (mean ± S.E.M.) in one eye and 3.5±0.2 °s^{-1} (mean ± S.E.M.) in the other eye. In similar stimulus conditions the sandlance specimens (N=3) showed an eye speed of 5.6±0.4 °s^{-1} (mean ± S.E.M.) and 3.2±0.3 °s^{-1} (mean ± S.E.M.). To test how well eye speed matches stimulus speed in general in these species, we compared the above results with the measurements gained from recordings of eye speeds in both eyes using a whole-field (rather than split) stimulus moving at 15 °s^{-1} and 5 °s^{-1}. A similar difference of eye speeds following the respective stimulus speed became apparent; for pipefish (N=3): 9.0±1.1 °s^{-1} and 3.9±0.4 °s^{-1}; for sandlance (N=3): 6.9±1.3 °s^{-1} and 2.6±0.2 °s^{-1}; see Fig. 5.

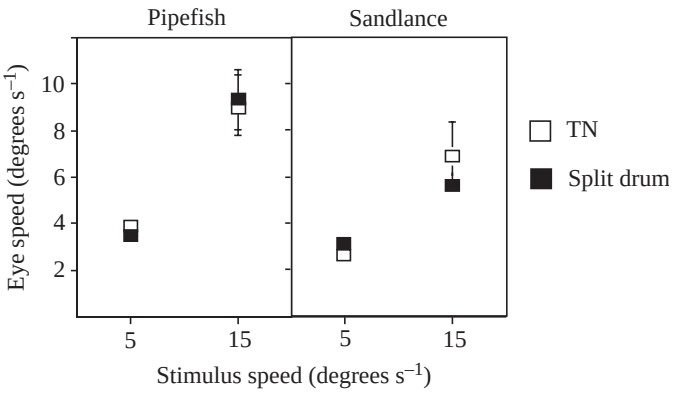

Fig. 5. Comparison of eye speeds at stimulus speeds of 5 °s^{-1} and 15 °s^{-1} during normal optokinesis (white square; temporo-nasal, TN, direction) and split optokinesis, during which each eye responds to a different stimulus speed (black square; both eyes are stimulated in TN direction). Pipefish (left) and sandlances (right) show the appropriate eye speed to the respective stimulus speeds, suggesting that the slow-phase response in each eye is independent of that of the other eye.

Naso-temporal stimulation

During front-to-back stimulation the butterflyfish showed very little sign of following the optokinetic stimulus (Fig. 6A). In some instances weak smooth eye movements in stimulus direction might have been present (Fig. 6A; left eye, 1–3 s); however, the response was considerably weaker than during temporo-nasal stimulation. Particularly when stimulated in the naso-temporal direction, the animal appeared to ignore the stimulation and showed normal spontaneous eye movements.

In both pipefish and sandlance, an independent optokinetic response was shown to naso-temporal stimulation (Fig. 6B,C). Individual variability was noticeable, as in some animals, the naso-temporal stimulus appeared to be less effective in eliciting optokinesis than in other specimens. However, in these two species, front-to-back stimulation clearly resulted in optokinetic compensatory movements.

Monocular stimulation

To test for evidence of a linkage between the two eyes when only one eye is stimulated, two sets of experiments were conducted. In the first experiment, one eye was stimulated, while the other eye viewed a stationary grating. In the second experiment, one eye was exposed to optokinetic stimulation, while the other was occluded to deprive it of visual input, removing possible mechanisms of visually stabilising this eye.

Monocular stimulation with visual feedback to the other eye

Butterflyfish. The butterflyfish showed a strong link between the two eyes: the optokinetically stimulated eye drove the non-stimulated eye also to perform an optokinetic nystagmus (Fig. 7A).

Sandlance and pipefish. In contrast, in both the pipefish and the sandlance the stimulated eye showed an optokinetic response

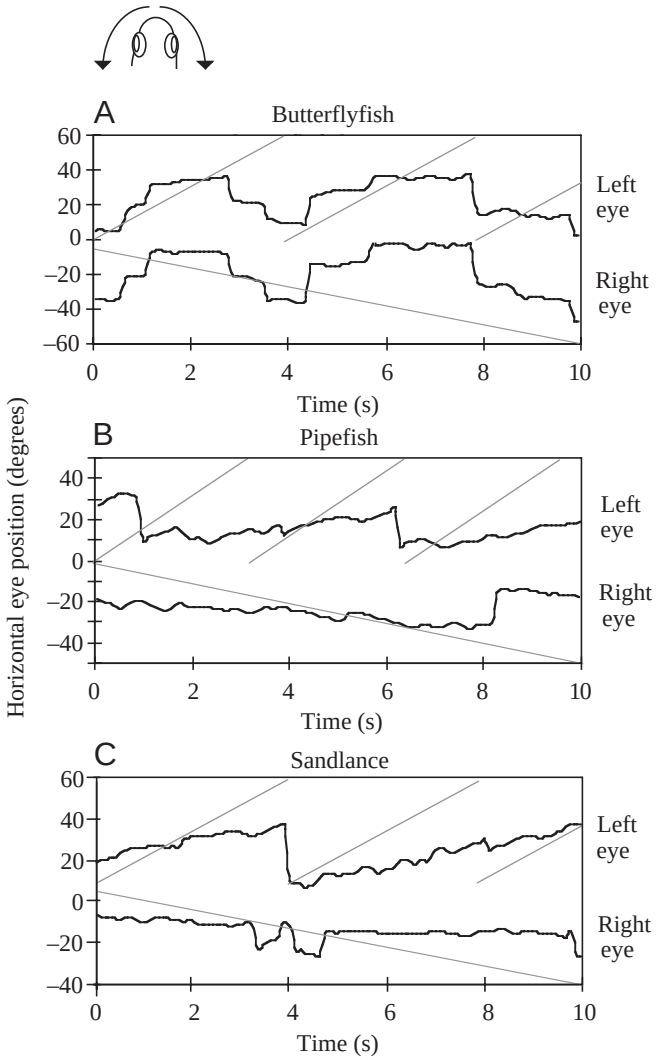

Fig. 6. Optokinetic response to split optokinesis in the naso-temporal direction for both eyes, stimulus speed 15 °s^{-1} for the left eye and 5 °s^{-1} for the right eye. (A) The butterflyfish shows no response to the stimulus, apart from a potential small following movement in the left eye (1–3 s). Instead, the eye movements are normal spontaneous ones. (B,C) Both pipefish and sandlances show independent slow and fast phase movements to naso-temporal stimulation. In these animals the response to the slower drum speed (right eye) was not as strong as during temporo-nasal stimulation.

while the eye that viewed the stationary grating did not show a nystagmus (Fig. 7B,C). In the pipefish, a correlation in gaze direction similar to that described during spontaneous saccades could be seen between the two eyes (Fritsches, 1999). The eyes tend to keep their visual axes parallel, so that the direction of saccades in the eye that views the stationary grating appears to be coupled with the fast phases in the eye stimulated optokinetically. The eye viewing the stationary grating, however, showed no slow phase; hence, by definition, no nystagmus was observed in that eye.

In summary, the butterflyfish shows linked optokinesis during monocular stimulation, whereas the optokinetic

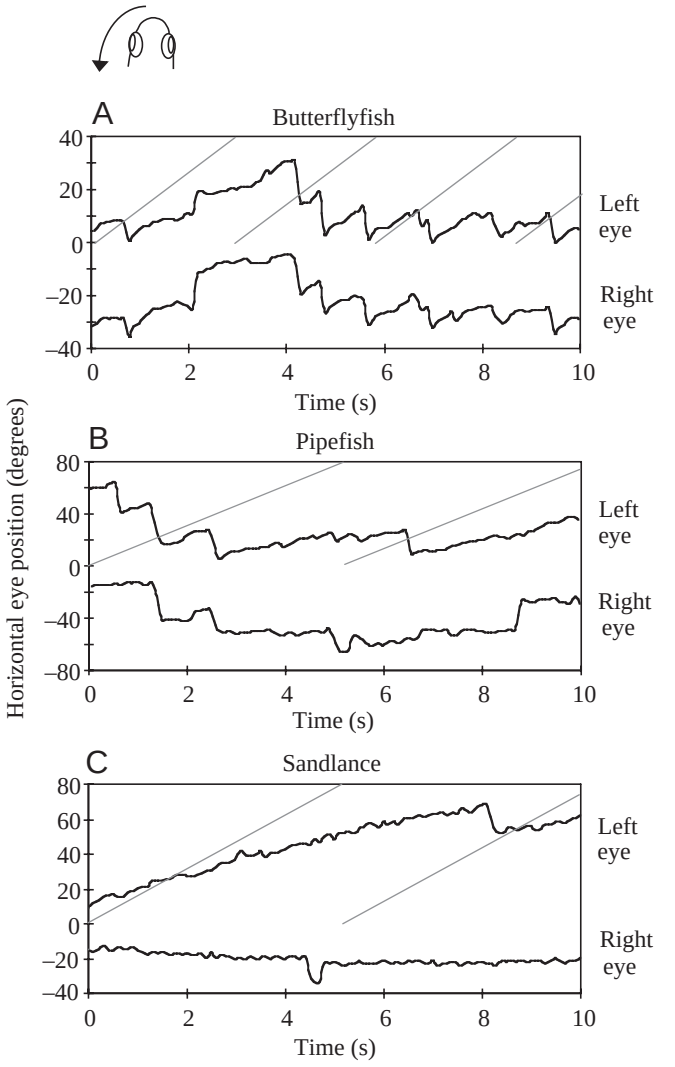

Fig. 7. Monocular optokinetic stimulation to the left eye (at 15 ° s^{-1}) while the right eye receives visual input in the form of a stationary grating. The butterflyfish (A) shows conjugent optokinesis in both eyes, whereas in both the pipefish (B) and the sandlance (C) the eyes are unlinked and only the stimulated eye shows a slow phase in the stimulus direction. However in the pipefish, the eyes are approximately correlated in the direction in which they are moving, as seen during spontaneous eye movements.

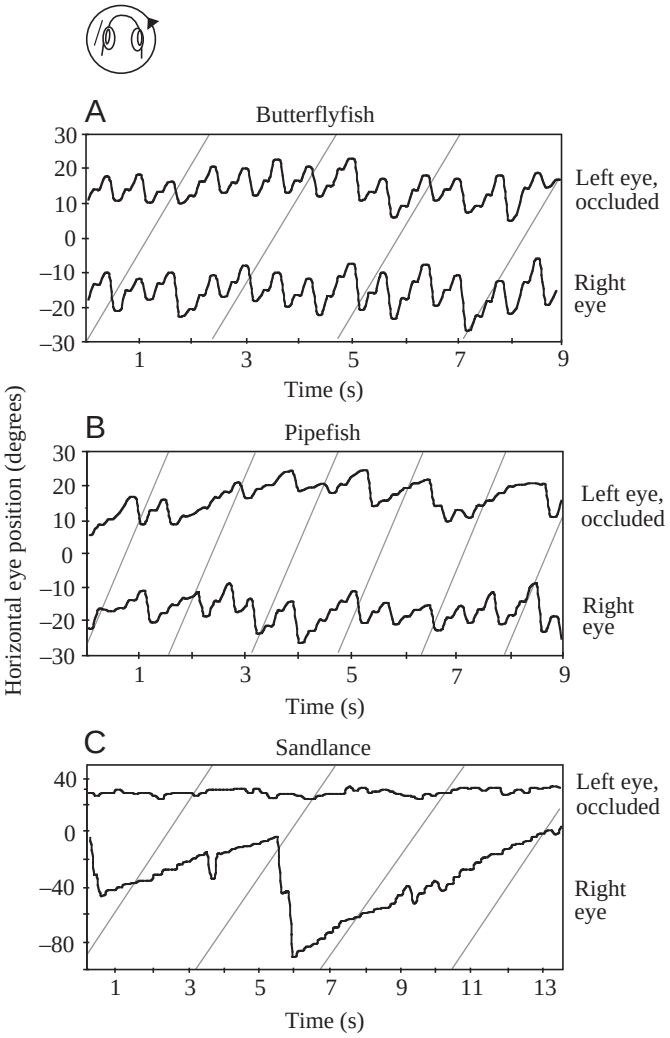

Fig. 8. Monocular stimulation to the right eye while the left eye is occluded. The response in both the butterflyfish (A) and the pipefish (B) is linked, whereas in the sandlance (C) only the stimulated eye shows optokinesis. Note that in the pipefish only the slow phase is clearly linked while the fast phase is frequently asynchronous between eyes.

response between the two eyes in both the pipefish and the sandlance appears to have no link (Table 1).

Occlusion experiments

The animals were stimulated by an optokinetic stimulus to one eye, while the contralateral eye was occluded. Great care was taken to occlude the entire eye and it is very unlikely that any of the animals perceived the whole-field stimulus, even at the far periphery. Any possible residual stimulation would furthermore have been too small to elicit optokinetic nystagmus (Easter, 1972). The movement described above was also unlikely to be a smooth pursuit response to a small area visible to the occluded eye. Repeated attempts were made to elicit smooth pursuit eye movements in the fish species studied, but none of them showed smooth pursuit at any time.

Butterflyfish. Again the butterflyfish showed strong linkage between the eyes; the seeing eye was driving the occluded eye. There was no apparent difference between the responses of the two eyes, apart from a slightly larger amplitude of the fast phase in the seeing eye (Fig. 8A). However, this could have been a residual effect of the physical presence of the occluder.

Sandlance. No influence of the seeing eye on the occluded eye was detected in the sandlance (Fig. 8C). While the right eye clearly showed an optokinetic nystagmus, the occluded left eye did not show any optokinetic response. At times the occluded eye made spontaneous saccades of large amplitude, followed by a drifting movement back to the primary position. This was a very stereotypic response, and the directions of the saccade and the drift did not coincide with the direction of the

stimulus. These spontaneous saccades in the occluded eye showed clearly that the occluder did not obstruct the eye. Occlusion was successful in four animals, and none of these showed any nystagmus in the occluded eye. However, the frequency of these spontaneous saccades in the blinded eye depended on stimulation of the seeing eye. In a stimulus-deprived environment, saccade frequency decreased for both eyes, probably linked with a decrease in general alertness.

Pipefish. Interestingly, the pipefish revealed a link between the two eyes when one eye was deprived of visual input. The occluded eye showed an optokinetic response in conjunction with the seeing eye (Fig. 8B). The fast phase, however, was executed less frequently in the occluded eye, and there was no strong link in fast-phase onset or amplitude between the eyes. This result indicates that the deprivation of visual input unmasks a link between the two eyes, which is not seen when the eye receives visual feedback.

In both the sandlance and the pipefish, no detectable bias between naso-temporal and temporo-nasal stimulation was noticed when one eye was occluded. Surprisingly, the butterflyfish also showed optokinetic nystagmus in the seeing eye to movement in both directions. However, the response to naso-temporal stimulation was weaker and more irregular than to temporo-nasal stimulation.

Discussion

Optokinetic response in animals with independent eye movements

The optokinetic response to a single whole-field stimulus in both the sandlance and the pipefish shows a large extent of independence between the two eyes. Slow and most fast phases of the response are executed without obvious correlation between the two eyes. The sandlance is even able to point one of its eyes upwards to fixate a stationary object above it while the other eye proceeds to follow the optokinetic stimulus (K. A. Fritsches and N. J. Marshall, unpublished observations). Among vertebrates, similar observations have only been made in the chameleon *Chamelio* sp., which can follow optokinetic stimulation independently with each eye (Tauber and Atkin, 1967; Kirmse, 1988; Gioanni et al., 1993). Among invertebrates, the mantis shrimp *Odontodactylus scyllarus* shows the most remarkable independent optokinetic response, quite similar to that shown by the fish in this study (Cronin et al., 1991). This ambush predator has very specialised foveate eyes and complicated spontaneous eye movements, including scans, which occur independently in the two eyes (Land et al., 1990; Marshall et al., 1991; Cronin et al., 1992). An intermediate degree of uncoupling of the eyes during optokinesis is seen in the turtle *Pseudemys scripta* (Ariel, 1990). In these animals the fast phase is tightly conjugate, whereas the slow phase shows very different gains, depending on stimulus direction.

By using two independent half-field stimuli in this study, the true independence of optokinetic compensation in each eye could be observed. The sandlance, the pipefish (this study) and the chameleon (Kirmse, 1988) show compensatory responses in each eye separately. This strongly suggests that each eye processes the visual input independently. In this study, it was also shown that when presented with different stimulus speeds to each eye, both the sandlance and the pipefish respond with different eye speeds in each eye, well matched to the stimulus speed perceived. These findings can only be explained by assuming an independent feedback loop for each eye without modulation of the response by visual input to the contralateral eye (Dell'Osso, 1994).

Disjunctive optokinetic movements in animals with yoked eye movements

Vertebrates with laterally placed eyes and yoked eye movements such as the goldfish *Carassius auratus* (Easter, 1972) and the rabbit *Oryctolagus cuniculus* (Collewjin and Noorduin, 1972a) were tested using translational image motion shown on a tangent screen. As with butterflyfish, stimulus motion that imitated forward motion (naso-temporal stimulation to both eyes) did not elicit stabilisation of the eyes; the animals appeared to be insensitive to this stimulation. Confronted with a pattern moving in the temporo-nasal direction for both eyes, the goldfish (Easter, 1972) showed convergence of the two eyes, similar to the butterflyfish (this study). The vergence movements appeared to be more regular and frequent in the goldfish than in the butterflyfish; however, in both species no clear nystagmus was shown because saccades were elicited both in the direction of the stimulus and against it.

In the rabbit (Collewijn and Noorduin, 1972a) and possibly the goldfish (Easter, 1972) the vergence movements show the same gain, suggesting a link of slow-phase speed in the two eyes, even though the slow-phase direction is not linked. Convergence movements in the butterflyfish were not sufficiently frequent for quantitative gain analysis; however, from visual inspection of Fig. 4A, for instance, it appears that the gain is similar in both eyes. In the rabbit, the speed of vergence movements in both eyes is constant regardless of the speed of the tangent screen (Collewijn and Noorduin, 1972a). This might indicate that these vergence movements are controlled by a different mechanism from the slow-phase movements, but more experiments are needed to investigate this point.

The butterflyfish shows a second strategy to compensate for binocular image motion in the temporo-nasal direction, which is also seen in the turtle *P. scripta* (Ariel, 1990). Both eyes shift in the same rotational direction (i.e. either left or right), but slow and fast phases alternate between the two eyes (Ariel, 1990). It therefore appears that, regardless of the visual stimulus, maintaining both eyes 'back to back' by moving them in the same direction (i.e. both left or both right) is the strongest link between the eyes in these two lateral-eyed animals. In order to achieve this in a stimulus situation in which both eyes see a pattern that moves in the opposite direction, these animals are able to elicit disjunctive fast and slow phases which, under normal circumstances, are always

yoked between the eyes. Hence several lateral-eyed animals with a yoked optokinetic response can show a degree of dissociation of the two eyes, a decoupling of the eyes, if this is required in response to a certain stimulus.

Different levels of linking the eyes

In the sandlance, both the slow and fast phases of the optokinetic nystagmus appear to be executed entirely independently in each eye. Monocular stimulation does not elicit any optokinetic response in the contralateral eye, whether it is visually stabilised by a stationary grating or deprived of visual feedback with an occluder. Similar results have been obtained in the chameleon (Gioanni et al., 1993). The seeing eye cannot drive the occluded eye, unlike in most other vertebrates (Carpenter, 1988).

Interestingly, when deprived of visual input to one eye, the pipefish displays optokinetic nystagmus in the occluded eye, obviously driven by the seeing eye. However, when one eye views a stationary scene, the visual input it receives seems strong enough to decouple the eyes. This strongly suggests a link between the two eyes that is overridden during normal viewing conditions. Since there is no obvious advantage of a linked optokinetic response in a blinded eye, it appears as if this link represents a residual condition that is usually subordinate to independent control of the two eyes. On the other hand, the butterflyfish, which shows strongly conjugate eye movements, is capable of partially decoupling its eye movements when confronted with half-field stimuli that require disjunctive compensatory movements.

Coupling and decoupling of the eyes during optokinetic nystagmus in these fish is therefore to some extent an active process rather than a hard-wired oculomotor condition. This contradicts Hering's law of equal innervation (Hering, 1868), assuming a single system to control the movement of both eyes in animals with yoked eye movements. Supported by several neuroanatomical (McCrea et al., 1986; Moschovakis et al., 1990) and neurophysiological (Mays, 1984; Judge and Cumming, 1986; Zhang et al., 1991) studies, Hering's law was considered a most fundamental dogma of the oculomotor system (Westheimer, 1989). Recently, however, support for the idea of binocular coupling as an active process rather than a hard-wired condition in vertebrates has increased, to describe oculomotor behaviour in mammals which cannot be explained by a single control system for both eyes (Enright, 1984; Williams and Dell'Osso, 1993; Dell'Osso and Williams, 1995; King and Zhou, 1995; Enright, 1996; Zhou and King, 1996, 1997, 1998).

Zhou and King (1998) obtained evidence to support their suggestion that the monocular organisation of the oculomotor system in primates is an evolutionary inheritance of lateral eyes that move independently. The underlying linkage of the eyes in the pipefish indicates, however, that the facultative decoupling of the two eyes may be achieved as a secondary requirement for the appropriate use of the fovea in a lateral-eyed animal. Dubois and Collewijn (1979) suggested that the assumed monocular control in the usually binocularly yoked rabbit allows independent small corrections of drifts or inaccuracy in one eye, without influencing the other eye too much. An even more basic evolutionary rationale to account for monocular control of usually yoked eye movements can be found in fish. Easter et al. (1974) showed that compensatory saccades and slow phases in the goldfish are not equal in each eye during swimming, which allows the animal to compensate for head rotation during swimming while stabilising a part of its visual field short of infinity. This might have been the primary reason for a monocular basic plan of the oculomotor system. The strongly yoked binocular situation in primates or the entirely independent eye movements of the sandlance are more likely to be secondary deviations from that basic plan.

Optokinesis during locomotion

The compensatory role of optokinesis for head turns is universally found in animals that can move their eyes (Carpenter, 1988), but the role of optokinesis for locomotion is not obvious. In fact, optokinetic gaze stabilisation during locomotion or visual tracking will 'clamp' the eye to the visual surround, making gaze shifts impossible (Carpenter, 1988; Land, 1992). The nystagmus shown to an optokinetic stimulus is a very strong response that cannot be easily suppressed (Carpenter, 1988) unless the animal freezes all movement when frightened (Collewijn, 1981). It appears that animals with different oculomotor strategies have found various ways to override optokinetic gaze stabilisation.

Afoveate animals with yoked eye movements

In many lateral-eyed vertebrates only the temporo-nasal direction is a stimulus for optokinetic nystagmus, so locomotion that moves the world naso-temporally for both eyes does not elicit a nystagmus (Tauber and Atkin, 1968; Easter, 1972; Carpenter, 1988; Collewijn, 1991; Wallman and Letelier, 1993). This could also be seen in the butterflyfish, which did not show optokinetic compensation when the eyes were stimulated in the naso-temporal direction. The strong preference for nasal movements will make the optokinetic response insensitive to locomotion, while sensitivity to rotation, and therefore image stabilisation during head turns, remains maximal (Collewijn, 1991). The undulating swimming motion of most fish means that the eyes show a nystagmus to compensate for rotational head movements. Compensatory eye movements are unequal and change with every turn to stabilise a different part of the visual field (Harris, 1965; Easter et al., 1974; Fernald, 1985). Since the image is only stabilised on parts of the retina during translation, optic flow is experienced, which is a very rich source of cues to relative location and self-motion relative to the environment (Nakayama, 1985; Koenderink, 1986).

Foveate animals with independent eye movements

Both the sandlance and pipefish show a fully developed optokinetic response to stimuli in the naso-temporal direction, and when shown a stimulus moving naso-temporally for both

eyes (which imitates forward locomotion), these fish, like the chameleon (Kirmse, 1988), show independent optokinesis in the two eyes. Forward locomotion in the sandlance, the pipefish or the chameleon should therefore result in stabilisation of the moving background, which in other lateral-eyed animals is strongly inhibited.

Sandlances can deactivate their optokinetic response, as reported in this study. Despite a whole-field stimulus, these fish show phases of stationary eye position and even drifts against the stimulus direction (Fritsches and Marshall, 1999; this study). The frequent spontaneous saccades during locomotion in pipefish and seahorses also suggest that optokinetic stabilisation during forward motion is suppressed.

Very little work has been done on foveate animals without binocular vision, hence little is known about how these animals deactivate their optokinetic response in order to maintain foveal fixation on a target during locomotion; but studies in other animals suggest possible mechanisms. Even in afoveate animals such as the goldfish or the rabbit, the optokinetic response depends on both the size of the stimulus and on its position on the retina; i.e. the more eccentric the stimulus, the less strongly it elicits an optokinetic response (Easter, 1972; Dubois and Collewijn, 1979). Hence, if a foveate animal fixates on a stationary target, a whole-field stimulus to the periphery might not be effective in eliciting optokinesis (Howard and Ohmi, 1984). Locket (1992) pointed out that if an animal with a deep fovea such as a sandlance or a pipefish fixates on an object and accommodates, the foveal image is magnified and sharply focussed against a slightly blurred background. The human optokinetic response is greatly reduced or even abolished when, within a whole-field stimulus, the central part perceived by the fovea is occluded and the edges blurred (Howard and Ohmi, 1984).

The combination of fixating an object and a blurred peripheral retinal image might therefore be sufficient to abolish the optokinetic response in foveate animals. If the animal then accommodates so that the periphery is in focus and the foveal image appears blurred (Locket, 1992), the optokinetic stimulus might regain its efficacy. With these mechanisms at a retinal level, based on accommodation, fish such as the sandlance or the pipefish might be able to activate fixation and pursuit or optokinetic stabilisation selectively, depending on the behavioural context.

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