BLIND MEXICAN CAVE FISH (ASTYANAX HUBBSI) RESPOND TO MOVING VISUAL STIMULI

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Summary

In apparatus for measuring optomotor behaviour, blind Mexican cave fish, Astyanax hubbsi, increase their swimming velocity upon rotation of a striped cylinder, i.e. in response to a solely visual stimulus. The fish follow the movements of the stripes at (i) rotation velocities between 60 degrees s\(^{-1}\) and 80 degrees s\(^{-1}\), (ii) light intensities of less than 20 lx and, (iii) stimulus widths subtending an angle of less than 1°.

Extrapolation of the vestigial eye structures does not affect the response to the moving visual stimulus, which indicates that the response is mediated by extra-ocular photoreceptors.

An optomotor response can be reliably evoked in a round test aquarium. Fish do not respond when the test aquarium contains environmental cues, such as bars on the wall or when a section of the round aquarium is divided off. This indicates that the fish obtain information about their environment from different sensory sources and that the visual stimulus is effective only when no other means of orientation are available. We suggest a modified theory of the optomotor response, which emphasizes the crucial role of the environment in eliciting the response and which permits behaviours more complex than just following the stimulus.

Introduction

There is mounting evidence that in various animals extra-ocular photoreceptors (EOPs) play an important role in eliciting different behaviours (for reviews, see Underwood and Groos, 1982; Oliver and Bayle, 1982). It was shown that experimentally blinded (and pinealectomized) fishes respond to light (Scharer, 1928; de la Motte, 1964) and utilize this capacity in a behaviourally relevant manner, such as changing their skin colour (Frisch, 1911) or controlling motor activity (van Veen et al. 1976). A few studies have employed blind Mexican cave fish (Astyanax hubbsi), which have no superficially discernible eye structures and thus seem to be an advantageous model for comparing the functional role of EOPs with that of lateral eyes in fish. The remnants of the eyes, called optic cysts, are highly atrophic and are buried deep within the tissue in the orbital region (Gresser and Breder, 1940; Kähling, 1961; Wilkens, 1988). Blind cave fish were found to be unresponsive to direct stimulation with points of light (Voneida and Fish, 1984), but

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could distinguish minute differences in ambient lightness (Breder and Gresser, 1941a; Kuhn and Kähling, 1954; Lüling, 1954; Kähling, 1961). It was suggested that this sensory capability is dependent upon the remnants of the eyes (Breder and Gresser, 1941b).

However, evidence that extra-ocular photoreceptors, not the eyes, are responsible for the perception of light appears to be equally convincing (Kuhn and Kähling, 1954; Kähling, 1961). In blind cave fish, as in other fish, extra-ocular photoreceptors have been located in the pineal organ (Herwig, 1976). Extra-pineal photoreceptors have not been identified in blind cave fish yet, but their presence and location can be inferred from studies in other fish (see, for example, Hartwig and Oksche, 1982; Dodt and Meissl, 1982).

It is important to keep in mind that the results of different studies on the visual capabilities of the blind cave fish Astyanax are not immediately comparable since different populations of cave fish, found in different pools within the cave, differ considerably in the degree of reduction of their eyes and disorganization of the retinal structures and, correlated to that, in their visual potential (Breder and Gresser, 1941a). Therefore, it is imperative to determine the visual abilities of our experimental fish by comparing their behaviour with that reported for the different populations of blind cave fish.

*Blind cave fish are blind fish*

Our observations indicated that our experimental fish behave in a manner typical of fully blind fish believed to be incapable of forming a retinal image and thus having no visual capacity (see Breder and Gresser, 1941a). (1) They swim continuously through the aquarium; (2) they do not respond to visual stimuli, such as points of light directed at them or shadows from above; (3) they do not school; (4) they perform a typical searching behaviour on the bottom of the tank when food is tossed into the aquarium and (5) they occasionally collide with objects in unfamiliar environments.

Preliminary morphological studies have revealed that the eyes of our experimental fish are reduced to a considerable extent. A residual ‘optical cyst’ is located under layers of fatty tissue deep within the orbital region. The eye is small (about 1 mm in diameter) and highly atrophic: (1) the front is coated with a dark, reflective pigment; (2) there is no lens and (3) the retina shows hardly any stratification. Serial sections indicated that several retinal cell types are present, but photoreceptors could not be identified.

These findings indicate that our breeding stock of blind Mexican cave fish, Astyanax, is characterized by the highest degree of optical reduction observed in blind cave fish (see also Wilkens, 1988) and suggest that they are not able to obtain visual information by means of their eyes.

We now report that fully ‘blind’ cave fish show a reliable behavioural response to white vertical stripes that are rotating around an aquarium in apparatus used for testing optokinetic behaviour. Our observations indicate that this behaviour is independent of the eyes, suggesting that extra-retinal photoreceptors are responsible for detecting the visual stimulus provided by the rotating bars.

**Materials and methods**

*Behavioural testing*

Adult blind cave fish of body lengths between 4 and 6 cm were kept in separate holding
Individual fish were placed in a circular test aquarium (12 cm diameter) suspended in the centre of a vertically striped cylinder (20 cm in diameter). The cylinder consisted of white stripes (2 cm wide, unless otherwise noted) arranged in a regularly alternating pattern and driven by an electric motor. A black velvet curtain provided a uniform background and shielded the apparatus from outside light. Illumination was provided from above, and the fish were monitored with a video camera from below.

After placing a fish in the test aquarium, it was permitted to explore and become accustomed to the environment for 2 h. Control experiments indicated that an exploration period of 2 h was sufficient for blind cave fish to become familiarized with their environment, as indicated, for example, by the reduction of their swimming velocities to low-level cruising speeds (see Teyke, 1989). After the exploration period, the spontaneous swimming behaviour of the fish was video taped for 2 min, followed by a recording of the same duration during rotation of the striped cylinder. Frame-by-frame analyses of the video recordings were carried out to determine the angular position of the fish in circular coordinates. The projection of the tip of the head (perpendicular to the body axis of the fish) to the perimeter of the aquarium was utilized to determine the angular position of the fish. By doing this, straight swimming and translational turning movements of the fish were converted into a circular movement which could be measured in degrees. These data were then used to calculate the velocity of the fish (given in degrees s\(^{-1}\)). Based on this we computed (1) the average velocity of the fish (irrespective of the swimming direction – with or against the turning direction of the cylinder); (2) the average absolute velocity (which took the turning direction into account); and (3) the error (the angle between the position of the fish and the stripe closest to it). As shown below, the average velocity of the fish (regardless of the direction of swimming) was found to be an appropriate measure of the fish’s behaviour. For each experiment, the fish’s spontaneous velocity before testing was compared with that during rotation of the cylinder. For statistical analysis of the data of individual experiments, \(t\)-tests were employed. ANOVA was utilized for assessment of overall effects.

Animal preparation

For surgical extirpation of the eyes, the fish were anaesthetised with MS 222 (Sandoz). A small incision was made in the skin overlying the orbital region and the optic cyst was removed after transection of the optic nerve and connecting tissue. The fish recovered quickly and without discernible complications from this procedure and were tested 14 days and again 8 weeks after surgery.

Results

Blind cave fish increase their velocity upon rotation of white stripes

In the experiments described below the fish were selected randomly and different experiments were performed in a random sequence to avoid conditioning, habituation and other unrelated effects. Experiments in which a fish swam spontaneously at velocities at, or above, 60 degrees s\(^{-1}\) were discontinued. Of the six experimental fish tested, one fish
was dismissed from the group after the experiments had been completed, because it increased its velocity during two control recordings.

A good example of the change in the behaviour of a blind cave fish to a moving visual stimulus is shown in Fig. 1. In Fig. 1A the typical swimming behaviour of a fish 2 h after release in the test aquarium is illustrated by plotting the angular position of the fish over time. The spontaneous swimming behaviour of the fish is contrasted to its behaviour during rotation of the striped cylinder (Fig. 1B). Spontaneously, the fish swam slowly, at an average velocity of 36.7 degrees s$^{-1}$, during the 1 min period shown in the figure. During rotation of the cylinder at 80 degrees s$^{-1}$ (Fig. 1B), the fish noticeably increased its velocity. The fish seemed to follow the movement of a stripe by swimming at a velocity similar to the rotation velocity of the cylinder. From time to time, when the fish fell behind one stripe, it continued swimming close to the next one. The average velocity of the fish (during the 1 min recording period shown in the figure) was 69.7 degrees s$^{-1}$, which is an increase of about 90% compared to spontaneous swimming.

Fig. 2A illustrates the results of a series of experiments in which the striped cylinder was rotated at different speeds. The spontaneous ‘cruising’ velocity of the fish in these experiments was between 40 and 50 degrees s$^{-1}$ (open symbols; means of five animals ± S.E.M.). If the bar cylinder was rotated at velocities of 20 or 40 degrees s$^{-1}$, which are lower or similar to the cruising speed of the fish, there was no change in the fish’s swimming behaviour. The average velocity of the fish during rotation in both cases was increased only by about 3 degrees s$^{-1}$ compared with spontaneous swimming, and this is
not a significant increase (20 degrees s\(^{-1}\) rotation velocity: \(P=0.5\); 40 degrees s\(^{-1}\): \(P=0.45\)).

Rotation of the cylinder at velocities exceeding the cruising speed of the fishes prompted them to increase their swimming velocities. As shown in Fig. 2A, at drum velocities of 60 and 80 degrees s\(^{-1}\), the velocities of the fish increased from the spontaneous level to levels that were considerably higher than the cruising speeds (asterisks indicate statistically significant differences). During rotation at 60 degrees s\(^{-1}\), the fish significantly increased their velocities from a mean cruising speed of 44.4 degrees s\(^{-1}\) to a mean velocity of 59.4 degrees s\(^{-1}\) (\(P<0.01\)), which is very similar to the rotation velocity of the cylinder. At 80 degrees s\(^{-1}\), the mean velocity of the fish was 72.2 degrees s\(^{-1}\), a significant increase from cruising speed (\(P<0.05\)); (one fish swam at 79 degrees s\(^{-1}\), three swam at 70 degrees s\(^{-1}\), and one swam at 65 degrees s\(^{-1}\)). At 100 degrees s\(^{-1}\) the mean velocity of the fish was 50.6 degrees s\(^{-1}\), which is not significantly different from that during spontaneous swimming (\(P=0.3\)). Inspections of the video recordings, however, indicated that even at 100 degrees s\(^{-1}\), the fish
occasionally tried to follow the stripes, but managed to do so only for a short period and then continued swimming at low speeds.

In the majority of cases, the fish followed the movement of the stripes, i.e. they swam in the turning direction of the cylinder. At the onset of the movement, the likelihood of fish swimming in the turning direction was about the same as swimming against it (turning direction: 46% with \textit{versus} 54% against). Thus, we hypothesized that a considerable number of fish should change their direction in order to follow the movement of the cylinder. In our combined experiments, 65% of the fish that were swimming against the turning direction reversed their swimming direction within the first 15s of cylinder movement. In contrast, fish that were swimming in the turning direction continued in 80% of the cases. In general, we observed an increased propensity of the fish to turn during rotation of the cylinder. Within the initial 15s of cylinder rotation, 55% of the fish executed a turn, as opposed to only 16% during control recordings. A recurring observation was that fish, even though they were swimming in the turning direction of the cylinder, reversed their swimming direction and swam – for a short period – against the turning direction of the cylinder. Episodes of swimming in the turning direction alternated with those of swimming against the turning direction. In a few experiments (7/180), the fish swam against the turning direction for the entire recording period. Contrary to our expectations (considering the relative movement of fish and cylinder), the fish appeared to swim at similar velocities in both directions. One should expect that swimming against the turning direction should lead to lower velocities, as the fish attempt to counteract the increase in the rate of the stimulus. We examined this observation more closely by calculating the velocities separately for the two swimming directions. We found that the velocities of the fish during rotation of the bars was increased, for both directions, from that during spontaneous swimming. In one experiment in which a fish swam exclusively in the counter direction, it also increased its velocity to 60.3 degrees s\(^{-1}\), which was very close to the 60° turning velocity of the cylinder.

\textit{Removal of optic cysts does not affect the response}

The functional role of the eyes in blind cave fish is controversial, and it is conceivable that the eyes may be responsible for (or at least contribute to) the detection of the visual stimulus. To test this possibility, we surgically removed the optic cysts in three fish. Observations of the lesioned fish revealed that they behave in a way indistinguishable from intact fish (see also Kähling, 1961). Moreover, when tested according to the standard protocol (Fig. 2B), the ‘eyeless’ fish increased their velocity from their spontaneous cruising speed of 40 degrees s\(^{-1}\) to above 60 degrees s\(^{-1}\) during rotation of the cylinder ($P<0.05$). During both spontaneous swimming and rotation of the cylinder, the ‘eyeless’ fish swam at velocities comparable to those of normal fish recorded under standard conditions ($P=0.7$; standard: 60 degrees s\(^{-1}\) rotation velocity; 3000lx illumination; 2 cm wide stripes; data taken from Fig. 2A). This indicates that photoreceptors, other than those located in the eyes, may be responsible for eliciting the optomotor response. Furthermore, preliminary experiments in which the cylinder was illuminated with either blue or red light indicated that fish are considerably more sensitive to red illumination. This supports a role for EOPs in eliciting the response, since it has
been shown that red light penetrates deeper into the tissue than blue light (see Hartwig and van Veen, 1979) and thus red light more efficiently stimulates photoreceptors embedded deep in the tissue. We have obtained two independent lines of evidence which indicate that extra-ocular photoreceptors and not the eyes are responsible for mediating the optomotor response in blind cave fish: (1) the unchanged response of the fish after extirpation of the eyes; and (2) the higher sensitivity of fish to red light than to blue light.

**Limiting stimulus conditions of optomotor response**

The following experiments address the effectiveness and the limiting conditions of the visual stimulus in eliciting an optomotor response.

**Control experiments**

To test for unspecific effects, such as the sound stimulus from the motor during rotation of the cylinder, we performed two series of control recordings, interspersed among the regular set of experiments. In control recordings in which the cylinder did not turn (the electric motor was turned on but the cylinder was not connected to the axle), the fish did not increase their velocity. As shown in Fig. 2B, in the control experiments (Cont), the velocity of the fish was found to be very similar to that during spontaneous swimming \( (P=0.3) \), which contrasts with the behaviour recorded under standard conditions (Stand: the cylinder was rotating; data taken from Fig. 2A).

**Random light stimulus**

To examine further whether the response of the fish is caused by the movement of the stripes, as opposed to an unspecific response to stimulation with light, we challenged the fish with a random pattern of flashing lights. Fifteen lights flashed (approximately 1 s on/off cycle) independently behind a diffusor to generate a stimulus situation with spatial characteristics similar to those of the striped cylinder (at an increased contrast). Stimulating the fish with random light flashes (Fig. 2B, Rand) did not promote a change in swimming behaviour and the average swimming velocity was very similar to that during spontaneous swimming \( (38.1 \text{ degrees s}^{-1} \text{ versus } 39.4 \text{ degrees s}^{-1}; P=0.66) \).

Based upon the two experiments outlined above, we conclude that the increase in velocity of the fish is a response specifically evoked by the movement of the visual stimulus.

**Intensity of illumination**

To evaluate the sensitivity of the sensory system responsible for the detection of the visual stimulus, we reduced the intensity of the light that illuminated the striped cylinder by using neutral grey filters. Bar width was 2 cm and the turning velocity of the cylinder was 60 degrees s\(^{-1}\). As shown in Fig. 3A, under high-intensity illumination of 3000, 1000 and 125 lx, the fish significantly increased their velocities above the spontaneous swimming velocity and closely matched the turning velocity of the cylinder (asterisks indicate statistically significant differences). At intensities of 20 lx, the fish still responded to the rotating bars with a slight increase in their velocity, and the increase from the spontaneous level was significant at the 90% level. At intensities below 2 lx,
rotation of the bars did not lead to a significant increase in the velocity of the fish (2 lx, 
P > 0.25; 0.3 lx, 
P > 0.1). Statistical analysis indicated a significant overall effect of the intensity of the illumination on the velocity of the fish during rotation of the drum (ANOVA; 
P < 0.03). The spontaneous velocities did not differ between the experimental groups (ANOVA; 
P = 0.89).

Spatial resolution

To determine the acuity of the sensory system, we kept the number of stripes the same (15) and reduced the width of the stimulus (i.e. we decreased the duty cycle by shortening the white period and increasing the dark period). Fig. 3B shows that the fish responded reliably when the stimulus width was reduced to 10 %, 5 % and 2 % of the total cycle, which correspond to subtended visual angles of 4 \degree, 2.2 \degree and 1.2 \degree, respectively. Reducing the width of the stimulus to 1 % of the cycle (0.5 \degree subtended angle) caused a slight, but insignificant, increase in the fish’s velocity (P > 0.1), indicating that the threshold of the resolution of the sensory system is at stimulus widths subtending an angle of about 1 \degree.

Blind cave fish perform the optomotor response only in certain environments

The blind cave fish responded readily to the moving visual stimulus in the circular aquarium. Since a previous report has emphasized the importance of spatial features of
the environment as determinants of the behaviour of blind cave fish (Teyke, 1989), we used aquaria of different shapes and tested the response. As shown in Fig. 4, provision of the round aquarium with three 1 cm bars glued to the side wall of the aquarium (see schematic drawing in Fig. 4) almost completely eliminated the responses of the fish to the visual stimulus. Upon rotation of the cylinder, the fish increased their velocities only by 5 degrees s\(^{-1}\) above the spontaneous level, which is not a significant increase (\(P=0.3\)). When the circular aquarium was equipped with a small cylinder placed in the centre (see schematic drawings in Fig. 4), the mean velocity of the fish during spontaneous swimming was 40 degrees s\(^{-1}\) compared with 48 degrees s\(^{-1}\) during rotation of the cylinder. This increase – even though significant at the 90 % level (\(P<0.1\)) – is far from the 60 degrees s\(^{-1}\) swimming velocity of the fish usually observed in the round aquarium during rotation of the cylinder. Experiments in which the shape of the aquarium was further modified led to more striking results. In an aquarium in which a portion of the ground area was sectioned off (see schematic illustration of the shape of the aquarium in the right column in Fig. 4), the mean velocity of the fish during rotation of the cylinder was 39.6 degrees s\(^{-1}\), which is very similar to the 37.4 degrees s\(^{-1}\) measured during spontaneous swimming (\(P=0.67\)).

The finding that the shape of the aquarium determines whether the optomotor response
occurs indicates that spatial features of the environment can override the visually evoked behaviour in blind cave fish.

Discussion

We have shown that blind cave fish, which supposedly have very limited or no visual potential, reliably increase their velocity in response to rotation of a striped cylinder, i.e. they perform an optomotor response. There are several constraints that determine whether the response can be observed, which might explain why it has been overlooked (e.g. Voneida and Sligar, 1976). First, if a fish is tested during its initial exploration phase in a novel environment, the response is more difficult to observe, since the fish’s high velocity during exploratory swimming does not differ much from that during rotation of the cylinder. Furthermore, the stimulus velocity (rotation velocity of the striped cylinder) has to be within a certain window – it must exceed the spontaneous swimming velocity of the fish (about 40 degrees s$^{-1}$) and be below a maximum velocity of 100 degrees s$^{-1}$. As further expected, the intensity of the illumination and the size of the stimulus have to be above certain threshold values to initiate the response. In addition, we have found that for the response to occur the experimental aquarium has to be without spatial bearings for the fish.

Strong evidence leads us to believe that the increase in velocity of blind cave fish is an optomotor response, specifically elicited by the moving visual stimulus, even though we cannot fully exclude the possibility that it is a visually induced exploration phase. Our evidence is as follows. First and most importantly, even during exploration, when the fish swim at increased velocities, the rotating visual stimulus promotes a further increase in velocity (data not shown). Second, the fish reduce their velocity to the spontaneous level within the first minute after the cylinder stops turning. On the basis of previous experiments (Teyke, 1989), one would expect an exploration phase to last considerably longer. Third, we have found that slow turning velocities of the cylinder, as well as stimulation with random light flashes, do not initiate the response. Since any change of the environment leads to renewed exploration, slow stimulus velocities and random lights should both evoke exploration and thus cause an increase in the fish’s swimming velocity.

As we have shown, the remnants of the eyes are not necessary for the detection of the visual stimulus. After extirpation of the optic cyst, the responses of the fish to the moving visual stimulus were indistinguishable from those of control animals. This is in accordance with previous findings (Käihling, 1961; Voneida and Fish, 1984), which indicated that the eyes of blind cave fish do not contribute to visually evoked behaviour and thus appear to be nonfunctional. In various other animals it has been shown that, after removal of the eyes, visual stimuli remained effective in eliciting certain behaviours. In fish (van Veen et al., 1976; Ronan and Bodznick, 1991; Morita et al., 1992), molluscs (Andresen and Brown, 1982; Nishi and Gotow, 1992), reptiles (Underwood, 1973) and birds (Menaker and Keatts, 1968; Menaker et al., 1970; Oliver and Bayle, 1982), extra-ocular photoreceptors located within the brain were found to be responsible for eliciting behaviours as diverse as changing the colour of the skin to controlling circadian activity. By extending previous studies, we have now shown for blind Mexican cave fish that extra-ocular photoreceptors – in the pineal organ or yet unidentified extra-pineal photoreceptors – enable the fish to
detect a moving visual stimulus. This capability can be achieved by the receptors in two
ways. The receptors could detect the moving white and dark stripes as a sequence of light
and dark events, prompting the fish to alter its behaviour. Alternatively, some kind of
elementary motion detector could be employed within the receptor system. On the basis of
the results of our current experiments, we cannot distinguish between the two alternatives.
morphological and additional behavioural studies are scheduled to address this issue.
Regardless of how the fish accomplish the detection of the moving stimulus, to our
knowledge this is the first demonstration of motion detection with a visual system other
than the eyes, thus adding another topic to the variety of behaviours elicited by EOPs.

Another key finding of this paper is that blind cave fish respond to moving visual
stimuli only in certain environments. This complements previous findings that the
structure of the environment influences the exploratory behaviour of the fish (Teyke,
1989) and supports the role of the environment as a crucial determinant of behaviour. The
results of our current experiments can be explained by postulating that visual stimuli are
of minor relevance for orientation when other kinds of information about the environment
– such as input from the lateral line system, for example – are available. When a point of
reference in the environment provides spatial cues for orientation (such as the three bars
or the sectioned off aquarium; see schematic drawing of the shapes of the aquaria used in
Fig. 4), the fish do not respond to the visual stimulus. One can speculate that the position
of the objects provides the fish with unequivocal information that the environment has not
changed and, therefore, they do not respond to the visual stimulus. In contrast, the round
aquarium, and to a lesser degree the round aquarium with a cylinder in the centre,
provides no point of reference for the fish’s orientation. Under these circumstances, the
moving visual stimulus might indicate that the environment is changing and prompt the
fish to respond accordingly. In other words, when the fish have access to spatial bearings
within the aquarium from other sensory systems, the moving visual stimulus does not
cause an optomotor response. If, however, the fish are deprived of other environmental
cues for orientation, they do respond to the moving visual stimulus. These findings
indicate that the response of blind cave fish to moving visual stimuli is directly associated
with knowledge of the stability of the environment.

The optomotor response has mostly been employed to study motion detection in
animals, and a variety of characteristics of the response and the underlying movement
detectors have been worked out (see, for example, Borst and Egelhaaf, 1989). In our
study, we have employed a typical optomotor response stimulus paradigm but our
experiments connote a functionally different response. This difference became apparent
in the experiments in which different environments were employed and concerns the
behavioural relevance of the response. We have therefore deliberately abstained from
analyzing our data according to the established premises. Our results suggest that the
behaviour elicited by the moving stimulus is specifically adapted to cope with changes in
the environment, which fish might experience when drifting in currents, for example. A
mechanism to counteract these environmental changes can encompass a group of
different behaviours, and it is not imperative that these behaviours be coupled to the
moving stimulus (i.e. these behaviours do not necessarily have to comply with previous
findings regarding the optomotor response, such as a close coupling between the pattern
movements and the evoked movements of the animals). We hypothesize that a fish can engage in several different behaviours to counteract changes in its environment brought about by a moving stimulus. One of these behaviours might be to swim at a velocity which corresponds to that of the stimulus. It is also conceivable that, in some cases, the fish might continue to swim against the turning direction.

We would like to extend our conclusion to other fish by suggesting that at least some of the responses observed and described under the umbrella of optomotor responses conform more closely to the category of behaviour that we have described. It has been reported that frogs and newts stopped responding to the moving visual stimulus as soon as they were able to establish tactile contact with the walls of the tank (Birukow, 1950). In addition, comparative studies on fish showed that bottom-dwelling fish do not perform optomotor behaviour (Harden Jones, 1963; see also Arnold, 1974). These findings can be explained by our hypothesis: bottom-dwelling fish maintain contact with the substratum and thus have access to tactile cues which can be used as tell-tale signs that the environment has not changed. Similarly, frogs and newts perform optokinetic behaviour when they are swimming freely in a tank, but as soon as they establish tactile contact with the walls (i.e. they have acquired a point of reference in their environment), they cease to respond.

This notion is further supported by our recent studies on goldfish in which two competing stimuli were delivered, one in the nearfield and one ‘environmental’ stimulus at a distance (Teyke and Schaerer, 1993). We found that stimuli moving at a distance override stationary proximate stimuli and effectively initiate an optomotor response. And, vice versa, stationary stimuli at a greater distance reduce or abolish the response to moving stimuli close to the fish. These findings support the hypothesis that the environment per se is the critical determinant for the response to occur.

Our notion suggests that information about the environment, which can be acquired via different interacting sensory systems and can be differentially weighted, determines whether the fish respond to a moving stimulus. We further propose that the optomotor response consists of various behavioural strategies developed by the animals to offset the changes in their environment.

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References


