SCOTOKINESIS IN THE BROWN BULLHEAD, *AMEIURUS NEBULOSUS* (LESUEUR, 1819)

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The last co-author started these experiments as a graduate internship at the Functional Neurobiology Group of Utrecht University in 1998; later the study was continued by the other co-authors intermittently.
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Abstract

Brown bullheads, *Ameiurus nebulosus* (Lesueur, 1819), seek shelter in daylight, and start exploration and swimming in the dark: the scotokinetic response. This behaviour can be induced under laboratory conditions by artificial manipulation of the light level. In order to investigate if the scotokinetic response occurs after a relative drop of illuminance or at a particular absolute low light level, we quantified locomotor activity of 5 individuals of *Ameiurus nebulosus* over periods of several weeks each, at illuminance levels between 0.05 lx and 5600 lx, and with photophase inter-trial intervals (ITI) of 15, 30, and 60 minutes. The scotokinetic response (SR) showed a threshold at reduction of the illuminance by 95%. Stronger reductions resulted in shorter reaction times. Weaker reductions had no effect within 10 minutes. The shortest response time was 3 seconds; the longest exceeded the 10 minutes observation window. The length of the inter-trial interval had a significant but weak effect on the scotokinetic response. An illuminance during the scotophase of 1400 lx reduced the locomotor activity to near zero. The illuminance during the scotophases had a major effect on the time to feed: the fish approached the food dispenser fastest at illuminance levels of 100 lx. Returning to a shaded shelter at the photophase occurred as a rule within 75 s. It is argued that the pineal organ rather than the visual system is involved in the control of the scotokinetic response.

Keywords

Catfish, brown bullhead, photokinesis, scotokinesis, locomotor behaviour, photophase, scotophase, non-habituating neural network, non-habituating response

Abbreviations

D Illuminance during the scotophase (lx)
DSS Dwelling in front of shaded shelter; interruption of IR-beam P2 (fig 1)
IR Infrared
ITI Intertrial interval; the photophase between two successive observation periods (trials)
L Illuminance during the photophase (lx)
R-F Return to shelter without having activated the food dispenser; the time between interruptions of IR-beam P2 and P1 (fig 1) after the transition of condition D to L
R+F Return to shelter after having received a food pellet; the time between interruptions of IR-beam P3 and P1 (fig 1) after the transition of condition D to L
SR Scotokinetic response time; the time between lowering the illuminance and the interruption of IR-beam P2 (fig 1)
TTF Time to feed; the time between interruptions of IR-beams P2 and P3 (fig 1)

Introduction

Light conditions play an important part in the locomotion and orientation behaviour of catfish, in particular the brown bullhead *Ameiurus nebulosus* (Lesueur, 1819). Brown bullheads are referred to as nocturnal or crepuscular in their activities. This is based on observations that adult brown bullheads prefer dark shelters near the bottom of ponds and predate at night, whereas the young ones are mostly active during twilight (Schiche, 1918, Breder, 1935, Darnell and Meierotto, 1965). The same type of locomotor activity is displayed by *Silurus asotus* (Linnaeus, 1758), another catfish (Tabata et al., 1989a, Tabata et al., 1989b). Under laboratory conditions brown bullheads behave similarly, although during high illuminance levels they can often be seen hiding in a dark place with their heads and barbels protruding in the light. In general they orient in the direction of the light source. In addition to orientation towards the light source they prefer a maximum of contact with objects in their surroundings. The latter is known as thigmotaxis. An extensive description of the thigmotactic and phototactic behaviour of *A. nebulosus* has been given by Schiche (1918).

During earlier laboratory experiments we noticed that locomotor activity of *A. nebulosus* can be induced almost instantaneously by lowering the light level. This locomotor response occurs without any form of training, and does not habituate. Over the past years we have been using lowering of the illuminance in all behavioural experiments with brown bullheads to signal the beginning of a trial, whereas a high illuminance level signified the end of a trial (Peters and Van Wijland, 1974, Peters et al., 1995, Peters and Baretta, 1998, Peters et al., 1999, Eeuwes et al., 2001, Eeuwes et al., 2004). Occasionally, low light levels were used in conditioning experiments as a reward, and high levels as a means for punishment. In the following we report quantification of some locomotor parameters in response to light changes in order to answer the question if the scotokinetic response depends on absolute levels of illuminance or on relative changes, and how this non-habituating response might be controlled by the nervous system. The locomotor

response of the brown bullheads to lowering of the light level will be called *scotokinesis*, meaning a dark-induced rise in locomotor activity (Edel, 1976, Van Ginniken et al., 2005) (see also the description of *photokinesis* in Fraenkel and Gunn, 1961).

Materials and Methods

The experiments were performed on the brown bullhead, *Ameiurus nebulosus* (Lesueur, 1819) (also *Ictalurus nebulosus.).* The responses to changes in illuminance were studied in two slightly different setups. Experiment 1 was intended as a pilot and range finding experiment. In experiment 2 care was taken to eliminate timing inaccuracies inherent of manually reducing the illuminance, and possible effects of spectral changes of the illuminance during the transition from light to dark and vice versa. In both experiments the illuminance was measured with a photometer Gossen Lunasix 3 with diffuser in the direction of the light source, just above the water surface. Hereafter the photophase is denoted as L, followed by the illuminance level in lx, for example L2800. The scotophase, intended to evoke the scotokinetic response, is denoted by D, followed by the illuminance level in lx, for example D100. The inter-trial time (ITI) is denoted by its duration in minutes. An experimental condition of 15-L2800/D100 for example means an inter-trial time (ITI) of 15 minutes and illuminance 2800 lx, followed by a scotophase with illuminance 100 lx.

*Experiment 1***.** One male individual of *A. nebulosus* of 240 mm total length was kept in an inflatable plastic basin with a diameter of 120 cm and a water height of 10 cm. The temperature was between 15 and 18 °C. The bottom of the basin was covered with sand, and the fish was daily fed *ad libitum* with pieces of fresh beef. The fish was kept on a basal light:dark regime of 10:14 hrs. It was provided with an artificial shelter, consisting of a lengthwise cut PVC tube with a diameter of 14 cm and a length of about 30 cm. A white, opaque PVC barrier was placed around the inside of the basin in order to keep the fish within the observational area, thus leaving the PVC tube as the only shelter possible. A 100 W light bulb was used with a variable transformer to vary the illuminance between 0.5 to 5600 lx. For the actual experiments, which were done during daytime, the room was made completely dark. The movements of the fish were followed with a Grundig electronic FA851 infrared sensitive video camera. Additional infrared background illumination was created with another 40 W light bulb and three gelatine filters (blue, red, and turquoise), which met the requirements.
A trial consisted of a photophase with the illuminance set at 1800 or 5600 lx for 30 minutes, after which the illuminance was lowered to the desired level by hand in 3 to 5 seconds. The scotokinetic response was quantified by measuring the response time upon switching from the photophase to the scotophase. The response time was defined as the time at which the illuminance was at the desired intensity until the moment at which the fish's tail was out of the shelter, head first. The reverse reaction, the shelter response, was also measured. In this case response time was defined as the time needed for the fish to completely disappear underneath the shelter. For the shelter response the illuminance of the scotophase was set at 0.5 lx and the illuminance of the photophase was varied per trial. In all cases the criterion for no response was 5 minutes, after which the trial was ended.

Experiment 2. One female and three male individuals of *A. nebulosus* with total lengths of 192 +/- 19 mm, were kept successively in a full glass container of 100 x 50 x 50 cm. The tank contained a dark shelter, an illuminated area and a food dispenser (fig. 1). The water height was 15 cm. The temperature followed the seasonal changes and varied during the experiment between 16 and 23 °C. The position of the fish was detected at three places by means of interruption of infrared (IR) beams Keyence PZ51 (fig 1: P1, P2, and P3). To make different illuminance levels with identical spectral compositions we used tube lights Sylvania luxlineplus 827 of 30 W and combinations of Lee neutral density filters 211 (0.9D) and 209 (0.3D). Activity was recorded at illuminance levels between 3600 and 0.17 lx, but

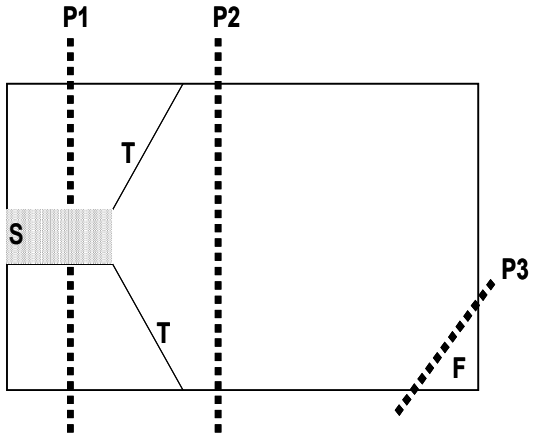

Fig. 1. Schematic drawing of the full glass observation tank used in experiment 2; top view. Shaded area S, dark shelter with opaque roof. Dotted lines P1, P2, and P3: IR-beams for the detection of the position of the fish. F: Place of the food dispenser. The food dispenser is placed above the tank and releases one food pellet if the IR-beam P3 is interrupted. T: Transparent plexiglass to keep the fish in the observation section.

mostly at of 2800, 1400, 175, 100, and 0.17 lx. The food dispenser was placed in a corner and provided one pellet of Trouvit when the IR-beam P3 near the dispenser was interrupted. The whole setup was housed in a dark container. The exposure to the light regime went on continuously**.** As a rule we collected between 25 and 65 responses per ITI and light condition. However, at a scotophase of 60-L2800/D1400 the fish did not respond at all, and only 8 and 15 responses were measured at conditions 15-L2800/D1400 and 30-L2800/D1400 respectively in the example treated under results.

At the start of a trial the fish had to be in the shelter and interrupt IR-beam P1. A trial consisted of lowering the illuminance instantaneously, and measuring the response time, i.e. the interval between lowering the illuminance and the interruption of IR-beam P2. We also measured how long the fish dwelled in front of its shelter (DSS), keeping IR-beam P2 interrupted. Then we measured how long it would take to return to its shelter without taking food (R-F), or how much time was needed to reach the IR-beam P3 at the feeding dispenser (TTF). Finally we measured the time between arrival at the feeding dispenser and returning to its shelter when the illuminance was raised after 10 minutes (R+F). After each trial a photophase inter-trial interval (ITI) was inserted of 15, 30 or 60 minutes. To understand unexpected response anomalies, we made occasional video recordings during the sessions. After delivery of a food pellet the fish was rewarded with 10 minutes feeding time, after which the light was switched on again. The time windows for SR, DSS, R-F, TTF and T+F were 10 minutes, after which the photophase followed. Each fish was monitored four to eight weeks.

We started the measurements with the photophase, immediately after introduction of the fish into the experimental tank.

Statistics

The statistical tests and graphs were made with the program Graphpad Prisma 4.03. In experiment 1 we tested the shift in response times (SR) with a non-linear regression method designed for sigmoidal dose-response curves, with as null hypothesis that both curves are equal. To test the effect of illuminance on the return-to-shelter times, we used a correlation paradigm. In experiment 2 we used unbalanced (unweighted means) two-way ANOVA with ITI and change of illuminance as factors, and post testing with Bonferroni (all columns) to analyze the behaviour of the selected fish.

Results

*Experiment 1.*Fig 2a shows the response times of 30 trials when the illuminance was lowered from L1800 lx to values above D0.7 lx. If the scotophase level was more than D95 lx the reaction time exceeded 5 min. Below the D95 lx level the reaction time decreased with decreasing illuminance. The transition from short reaction

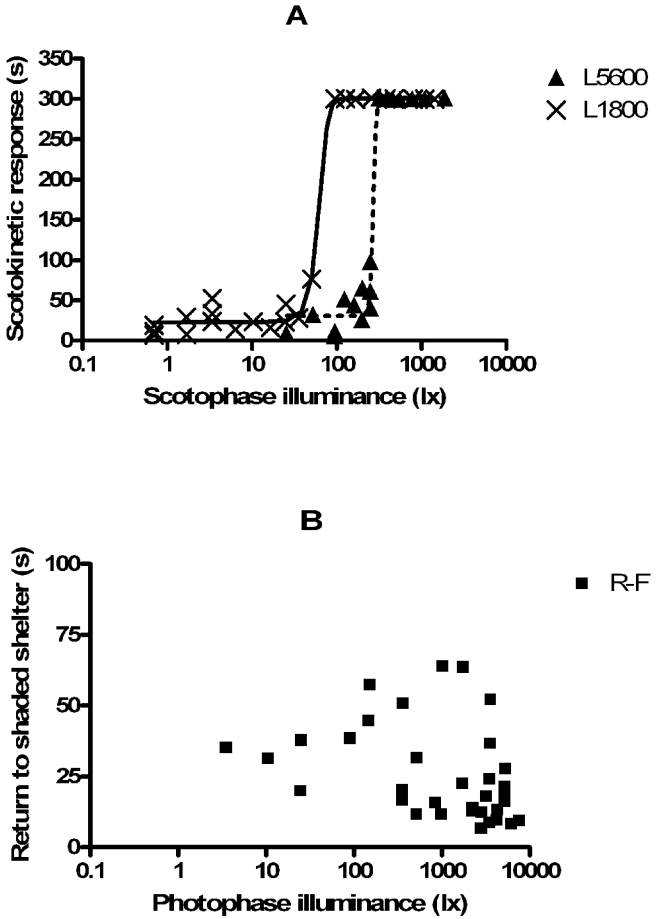

Fig. 2. Response times following the transition from the photophase to the scotophase and vice versa of experiment 1: ***A*** *Scotokinetic response time after lowering the light from 5600 (triangles) or 1800 (crosses) lx to different scotophase levels.* ***B****. Return times to the shaded shelter after raising the illuminance from 0.5 lx to different photophase levels.*

times to long reaction times was rather abrupt and seemed to indicate the presence of a threshold. Fig 2A shows also the reaction times of 22 trials when the illuminance was lowered from L5600 lx to D25 lx or higher. Above a scotophase level of D300 lx the reaction time exceeded the 5 minutes. The shift along the X-axis between the two curves was significant (spearman r = -0.43, p = 0.01).
Fig 2B shows 35 return-to-shelter times when the illuminance was increased from D0.05 lx to a value between L1 and L10,000 lx. The return times were always less than 70 s. The correlation between return times and illuminance levels was significant (p = 0.01).
If we take response times of 300 s as threshold criterion, it follows that a decrease in photophase illuminance with a factor 19 or more induces scotokinesis.

Experiment 2.

Analysis of the data of the four individuals of experiment 2 showed that the scotokinetic responses were dependent on the fish, illuminance and the ITIs. The scotokinetic response time of all four fish at ITI15, the experimental condition with the most consistent illuminance levels for all four fish, are given in fig 3A. Basically they support the findings of experiment 1. The other figures (Fig 3B ff.) represent the data of a single individual only, a male of 200 mm total length and a weight of about 100 g. The data of the other three fish are not presented, because of too strongly discordant experimental protocols.
During complete darkness the fish was lying in front of its shelter, thus continuously interrupting IR-beam P2 (fig 1). We observed this once, when the tube lights remained switched off unintentionally. If the photophase illuminance was L2800 lx, the fish was permanently hiding in its shaded shelter, interrupting IR-beam P1, to leave it only when the illuminance decreased. The scotokinetic response depended significantly on the illuminance during scotophases ($p<0.0001$), and almost significantly on the ITI ($P=0.06$). Further there was a significant interaction between illuminance during dark and ITI ($p=<0.0001$), meaning that light did not have exactly the same effect at all ITIs. Although the means and standard errors of the

scotokinetic response demonstrated nicely the effect of the scotophase on the response time (fig. 3B), the data were not normally distributed. If the scotokinetic response times were plotted as dot displays (fig. 3C), another feature emerged. Apparently the response times occurred in clusters. A frequency histogram (not presented here) of the response times at 15-L2800/D0.17 showed 2 clusters, one with a peak at 4 s, and another with a peak at 32 s. A similar plot at 30-L2800/D100 showed three clusters: a major one at 16 s, and two others at 4 s, and 512 s and higher. Once the fish had left its shelter it started exploring its tank and either returned in the dark without having taken food, or it swam towards the food dispenser. This could be concluded from the interruption time of IR-beam P2 (fig 1), which was always less than 1 s except in total darkness, and from experiment 60-L2800/D1400 when the fish was completely inactive. The effect of the scotophase on approaching the food dispenser (TTF) was extremely significant ($p<0.0001$); the effect of the ITI was very significant ($p=0.0077$). There was also a very significant interaction between the two factors (0.0032). In words: a scotophase of D100 lx resulted in the fastest approach of the food dispenser, that is within on average 80 s (fig. 3D). Under condition 60-L2800/D1400, there was no response at all. Further the different ITIs resulted in different clustering patterns (not shown here). The mean return-to-shelter times (R+F) at the photophase after feeding were less than 53 s in all sessions but those at the L2800/D1400 regime (fig. 3E), and thus also confirmed the results of experiment 1. In about 25 % of all trials the fish returned to its shelter without having interrupted IR-beam P3 of the food dispenser (fig. 3F). Figs 3E and 3F also show that if the scotophase was D1400 lx, the fish left its shelter after a long delay, or not at all, and returned in more than 50 % of the trials to its shelter without having approached the food dispenser.

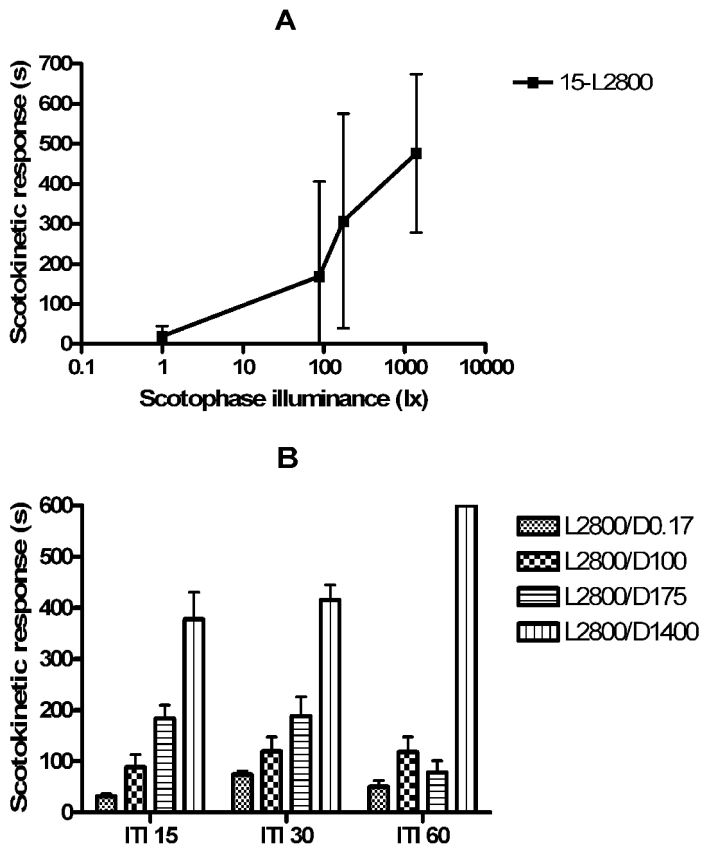

*Fig. 3. Experiment 2: **A** Mean scotokinetic response time of four fish with SD after lowering the light from 2800 lx to different scotophase levels of 1, 88, 175, and 1400 lx, with n = 91 (single fish), 185 (3 fish), 224 (four fish), and 143 (four fish) respectively. **B** Combined effects of ITI and illuminance change on the scotokinetic response time of a single fish. Bars are standard errors of the mean. At 60-L2800/D1400 the fish does not leave its shelter, which is interpreted as a response time exceeding the 600 s observation window.*

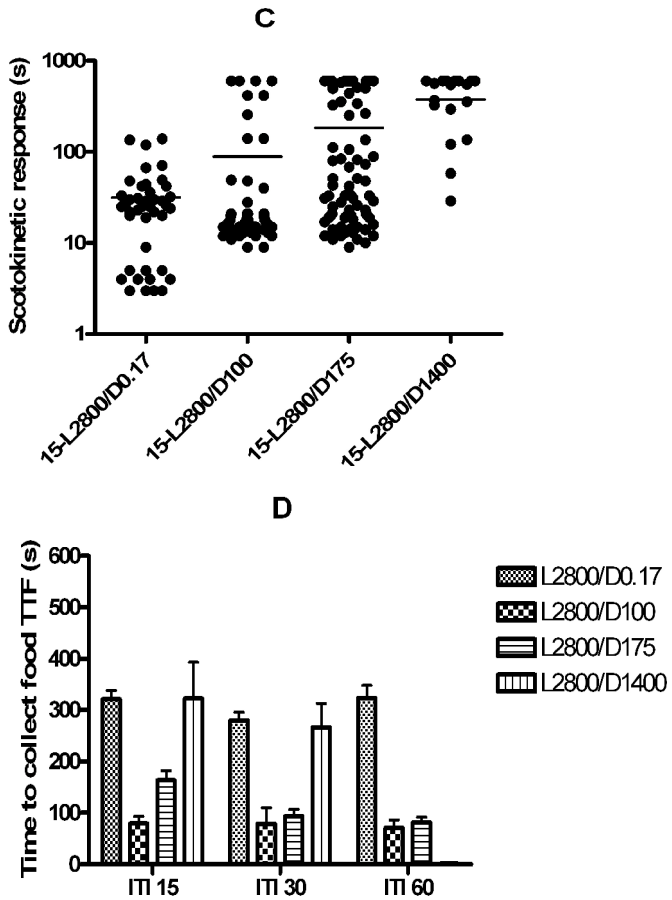

*Fig. 3. Experiment 2: **C** Scotokinetic response times at various illuminances and 15-ITI, plotted as dot display to show the clustering (non-gaussian distribution) of the data. **D** Time between interruption of IR-beam (P2) and arrival at the food dispenser (P3) during the scotophase (TTF). Note that at 100 lx this parameter is smallest at all ITIs.*

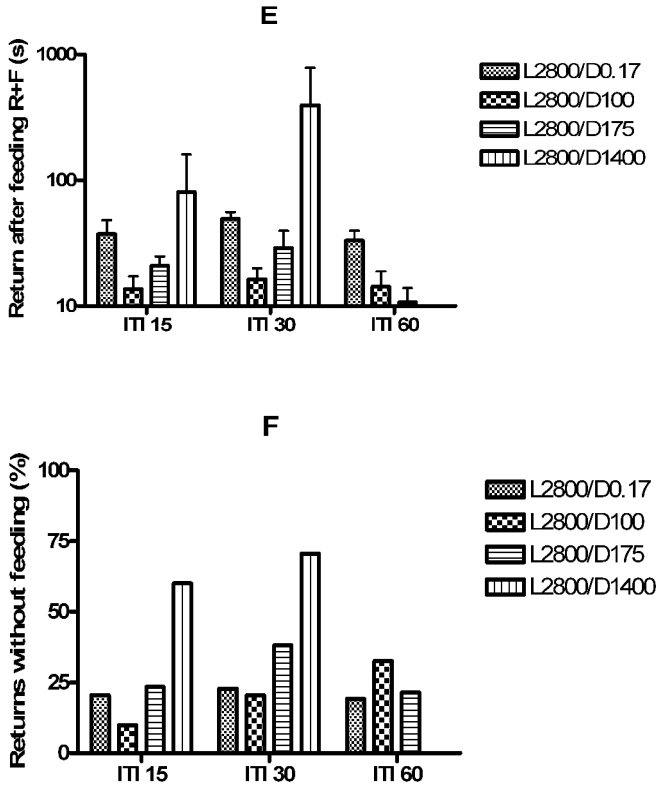

*Fig. 3. Experiment 2: **E** Return times to shaded shelter after having received food (R+F) after raising the illuminance to 2800 lx. The inverse of A. The number of returns per column varies from 17 to 34. At 60-L2800/D1400 the fish is inactive; at 15-L2800/D1400 and 30-L2800/D1400 only two returns were counted.*
***F** Percentage of returns to shaded shelter without having collected food (R-F) at different illuminances and ITIs. This percentage is high if the scotophase is 1400 lx. At 60-L2800/D1400 the fish does not leave its shelter.*

Discussion and conclusions

Both experimental approaches described above led to similar results and confirmed earlier observations: The brown bullhead seeks shelter under high illuminance levels, and leaves its shelter when the illuminance is reduced with about 95%. The scotokinetic response occurs after a relative drop in illuminance rather than at a particular absolute low light level.
If the illuminance is reduced with less than 95%, the scotokinetic response does not occur within the time window of the experiments: 5 minutes or 10 minutes for experiment 1 and 2 respectively. If the illuminance is reduced with more than 95%, the timing of the scotokinetic response is correlated with the change in illuminance level. The stronger the reduction of illuminance, the faster is the response. Once the fish has left its shelter it reaches the food dispenser fastest when the illuminance level is about 100 lx. Lower and higher levels lengthen the exploration time. In general, light suppresses exploratory locomotor activity.
The scotokinetic response does not habituate. Whenever the illuminance is lowered sufficiently, the fish is prepared to leave its shelter and explore its environment.
The response times shown in fig. 3C, appear clustered around 5 s, and at 600 s. The latter value is caused by the limit of the observation window. In between, response times are clustered around intermediate values – for instance 30 s – depending on the ITI and scotophase light levels of a particular session. We propose that these clusters may represent the alertness of the fish or its state of arousal that depend on the length of the ITI and on its position when the illuminance is decreased.

Since the scotokinetic response is a very typical response without habituation, one wonders by what neural mechanism or network it is controlled. The network must provide some kind of a threshold (cf. fig 2A, 3A), and generate a correlation between stimulus strength and response time. In neurophysiology, a short response time corresponds usually to a strong stimulus. In the present experiment the strong stimulus is represented by a reduction in illuminance with more than 95%. Three photoreceptor systems may be involved in the regulation of the scotokinetic response: the eye, the pineal organ, and the dermal photosensitivity. Let us first assume that the eyes are involved in locomotor regulation. Lowering the illuminance should then function as a releaser. When the illuminance is suddenly lowered, the eyes need some time to adapt to the lower illuminance. When the adaptation proceeds, the fish' sight improves. If the illuminance is lowered from 2800 lx to 1400 lx, adaptation would be completed sooner than when the illuminance would be lowered from 2800 lx to 1 lx. If 'being adapted' controls the response time, the fish would leave its shelter sooner at 1400 lx than at 1 lx. The opposite happens.
Another explanation could be that lowering the illuminance would deprive the fish temporarily from its visual input. Moving around could then provide additional sensory input via complementary sensory systems like the lateral line, chemical sense and electric sense. In this way, being not-adapted to the scotophase would induce locomotor activity. Though this explanation seems attractive, it somehow does not correspond with the time the fish takes to return to its shelter without having fed. Return without food (R-F) is on average slightly shorter at ITI-60 than at ITI-30 and ITI-15 (not shown). At ITI-60 it has been adapted to the photophase for 1 hour. In that case one would not expect a shorter time to adapt to the scotophase than at ITI-30 and ITI-15.

The pineal organ might be a better candidate for locomotor regulation. If the pineal is illuminated, firing of its afferent fibres is inhibited. Decrease of the illuminance results in an increase in firing rate of the pineal afferents. The greater the intensity drop, the higher the firing rate (Ekstrom and Meissl, 1997). Higher firing rates correspond well to shorter response times. Moreover, the pineal organ has been demonstrated to control the shadow response in an other aquatic vertebrate, *Xenopus laevis* (Jamieson and Roberts, 2000). There is, however, not much known of the neural wiring of the pineal and the locomotor system in fish. Connections between the pineal and limbic system have been demonstrated, but most studies deal with photoperiodism and the role of melatonin in diurnal activity. The

scotophase corresponds with a raised plasma level of melatonin, suppressing locomotor activity in the diurnal goldfish and without much effect on activity in nocturnal tench (Lopez-Olmeda et al., 2006a, Lopez-Olmeda et al., 2006b). Consequently it is unlikely that melatonin is the factor that controls the scotokinetic response. It is more likely that the pineal somehow controls the scotokinetic response via a direct neural pathway. The shortest response time in this experiment was 5 s. This corresponds well with the time constants of the achromatic ganglion cells of the pineal system in the rainbow trout (Tabata and Meissl, 1993) and illuminance levels between 660 and 0.6 lx.[1] The study of these authors shows full adaptation of the neural responses within 10 s at 15 and 20 °C.

The shelter seeking reaction in the photophase occurs usually within 70 s, irrespective of the magnitude of the intensity change. There is no reason why the pineal could not be involved in this reaction too. The response time of the pineal is short enough. On the other hand, returning to the dark shelter could also be under control of the visual system. Usually, more than one sensory system is involved in the control of behaviour. We may see evidence for dual photic control in the time needed to collect food after leaving the shelter (TTF) (fig. 3D). TTF is shortest, 70 s, at a scotophase of 100 lx. At lower and higher illuminances the TTF time increases. This seems to reveal two antagonistic neural systems. Another argument for the involvement of the visual system in dual control is that the fish retina seems to produce melatonin during photophases, whereas the pineal does so under scotophases (Vera et al., 2005, Besseau et al., 2006). Whereas the scotokinetic response time can be as short as 5 s, the R-T and R+T times are 70 s or longer. These relatively long times might betray hormonal control as would be the case if melatonin has a role.

A dermal photosensitivity as reported for some invertebrate and lower vertebrate species could also be involved in evoking the scotokinetic response (Ronan and Bodznick, 1991, Oshima, 2001). Evaluating the existing evidence, however, we favour a major role of the pineal organ.

Finally, one wonders if the scotokinetic response of *A. nebulosus* is somehow functional in finding food. Some invertebrate species show a response to lowering light levels opposite to the scotokinetic response in *Ameiurus* : the shadow reflex (Johnson and Forward, 2003, Samarova et al., 2005). It is thinkable that whereas *Ameiurus* starts to explore its surroundings upon darkening, its potential prey turns motionless upon under similar circumstances. The electric sense of *Ameiurus* would then faultlessly reveal the motionless prey when passing the electrical prey-field, and result in an easy catch.

Further, the scotokinetic response paradigm, seems a promising model for the neurological study of other non-habituating neural networks and behaviours .

1 *The illuminance values in lx were calculated from this reference by the following conversion: 1 lux = 4.5 * 10^{11} photons /cm^{-2}/s^{-1} from Foster, K. W. and Smyth, R. D., 1980. Light antennas in phototactic algae. Microbiol Rev. 44, 572-630.*

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