

Near-infrared orientation of Mozambique tilapia *Oreochromis mossambicus*

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Abstract

Light plays a pivotal role in animal orientation. Aquatic animals face the problem that penetration of light in water is restricted through high attenuation which limits the use of visual cues. In pure water, blue and green light penetrates considerably deeper than red and infrared spectral components. Submicroscopic particles and coloured dissolved organic matter, however, may cause increased scattering and absorption of short-wave components of the solar spectrum, resulting in a relative increase of red and infrared illumination.

Here we investigated the potential of near-infrared (NIR) light as a cue for swimming orientation of the African cichlid fish (Cichlidae) *Oreochromis mossambicus*. A high-throughput semi-automated video tracking assay was used to analyse innate behavioural NIR-sensitivity. Fish revealed a strong preference to swim in the direction of NIR light of a spectral range of 850–950 nm at an irradiance similar to values typical of natural surface waters. Our study demonstrates the ability of teleost fish to sense NIR and use it for phototactic swimming orientation.

1. Introduction

Photoreception, the ability of organisms to sense the optical spectral range of electromagnetic radiation, plays a crucial role in the life cycle of most animal species including vertebrates (Cronin, 2008). Fish sense light by eyes and extraocular photoreceptors, including, for example, the pineal complex, deep brain and dermal photoreceptors (Blaxter, 1968; Yoshikawa and Oishi, 1998; Foster and Hankins, 2002). Visible light encompasses the small section of electromagnetic radiation covering wavelengths between 380 nm and 780 nm, determined by the spectral sensitivity of human photoreceptors for daylight vision. Many fish species are able to sense wavelengths invisible for humans. Ultraviolet (UV) sensitivity was shown both in freshwater (Bowmaker, 1995) and marine fish (McFarland and Loew, 1994; Siebeck et al., 2010) of different orders such as Cypriniformes (Schiemenz, 1924; Muntz and Northmore, 1970; Hawryshyn and Beauchamp, 1985; Hawryshyn and Harosi, 1991; Risner et al., 2006), Salmoniformes (Bowmaker and Kunz, 1987; Anderson et al., 2010) and Perciformes (Carleton et al., 2000; Hofmann et al., 2010). UV sensitivity may be important for foraging behaviour as an adaptation to planktivory (Bowmaker and Kunz, 1987; McFarland and Loew, 1994; Bowmaker and Loew, 2008; Cronin, 2008), as well as for species discrimination and communication (Partridge and Cuthill, 2010; Siebeck et al., 2010). Moreover, sensing UV radiation may be relevant for orientation and navigation (Hawryshyn and Beauchamp, 1985).

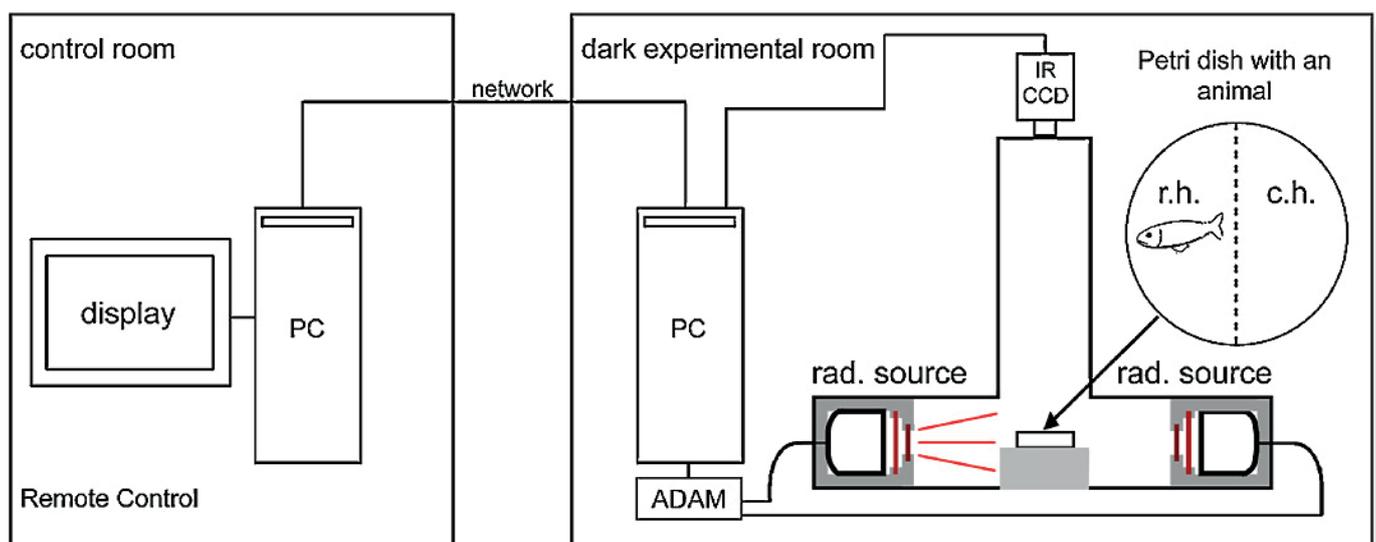


Fig. 1: Schematic diagram of the video tracking system for phototactic behavioural experiments. Abbreviations: rad. source = radiation source, r.h. = radiation source half, c.h. = control half, opposite to r.h.

Experimental evidence for near-infrared (NIR) sensitivity in some teleost species has been reported as well. Endo et al. (2002) and Takeuchi and Endo (2008) observed a dorsal light response in Nile tilapia (*Oreochromis niloticus*) under infrared illumination (750–1000 nm). Other studies showed an optomotor reaction to infrared light at 780–800 nm in the same species (Kobayashi et al., 2002). Cardiac conditioning elicited a response of carp and Nile tilapia to infrared LEDs of 865 ± 40 nm. A single carp showed a significant reaction to NIR light of 936 ± 45 nm (Matsumoto and Kawamura, 2005). These studies, despite their demonstration of NIR sensitivity in teleost fish, suffer from several shortcomings: (i) the applied spectral band width was wide, as no optical filters were used; (ii) only a low percentage of individuals showed a positive response to NIR light (Endo et al., 2002; Matsumoto and Kawamura, 2005; Takeuchi and Endo, 2008).

As the phototactic behavioural assay is an efficient method for investigating innate behavioural responses of fish to light (Blaxter, 1968), we developed a standardised high-throughput assay for Mozambique tilapia (*O. mossambicus*) to investigate NIR sensitivity and the ability of fish to use NIR for phototactic orientation. Specifically, the following hypotheses were tested: (1) *O. mossambicus* can sense NIR light of 850–950 nm; (2) fish are able to use NIR light as orientation cue, at least under laboratory conditions; (3) NIR-based orientation is native behaviour and does not require conditioning; (4) NIR sensation is phototaxis and not based on thermoreception.

2. Materials and methods

2.1. Animals

O. mossambicus (~4 months old), of unknown sex and a total body length of 2.0–2.5 cm, bred in the Institute of Zoology, University of Hohenheim, were kept in aquaria at 25 ± 1 °C and fed daily with TetraMin flakes (Tetra GmbH, Melle, Germany). White spectrum fluorescent lamps (Osram, Munich, Germany) with 90% emission between 400 and 750 nm produced a 12 h/12 h light/dark cycle with total irradiance at the water surface of $320 \mu\text{W}/\text{cm}^2$.

A non-invasive experimental procedure based on native untrained swimming behaviour of juvenile *O. mossambicus* was applied. The light intensities used were not higher than values observed under natural environmental conditions. The present study was carried out with the approval of the Animal Care Committee of the University of Hohenheim (permission number: S287/10 Zo).

2.2. Experimental equipment

Behavioural experiments were carried out in a dedicated bioassay device (Fig. 1) in a light-isolated dark room. The test area was shielded by black textile mate-

rial to eliminate potential residual light. The custom-built light-tight device of dark anodised aluminium had the shape of an inverted T (Fig. 1). Light sources were mounted in special housings and could be attached in opposite positions at the bottom of the T-shaped device. The housing consisted of a box of 10 mm thick light-tight PVC plates glued together, to which optical filters could be attached. Thus, different combinations of light sources and optical filters for emission of the experimental spectral range could be used.

A Petri dish at the central part of the T (diameter 35 mm) served as a swimming vessel. One fish was used per experiment. Preliminary experiments demonstrated that subadult *O. mossambicus* can perform different swimming movements in these vessels and reveal a clear orientation preference.

Light sources were placed in the T device at a distance of 10 cm from the dish. Fish behaviour was recorded using an infrared-sensitive camcorder (Sony DCR-HC23E; Sony Corp., Tokyo, Japan) with a disabled embedded NIR light source. The camcorder was mounted in a light-tight fashion on top of the T-device.

Videos were recorded using VirtualDub (available at <http://www.virtualdub.org>). The total number of tested individuals per experimental series was 30. Each set consisted of 15 specimens irradiated from the left or the right NIR source, respectively. Prior to the experiment each fish was kept in complete darkness for 1 min for behavioural adaptation, after which the selected right or left light sources were turned on for 5 min, computer-controlled from the control room next door. The temperature in the dark experimental room was maintained at 25 ± 1 °C. Videos were recorded at a frame rate of 25 fps.

2.3. Video tracking and data analysis

Video recordings were analysed using the custom-made software BioMotionTrack D.S. (Shcherbakov et al., 2010). For analysis, the frame rate of recorded videos was reduced to 2 fps. A semi-automatic mode was used for behavioural analysis: fish position was determined manually (by a mouse click between the eyes) followed by automatic behavioural analysis.

The following parameters of fish behaviour were analysed: (i) time spent in the left and right part of the vessel [s] to show light dependence of preference; (ii) covered distance [m] to determine the motivation level of fish for movement orientation behaviour. As fish tried to swim past the wall of the dish in the direction of light, revealing a wave-shaped swimming pattern with more oscillating movements at a lower speed and a higher turning rate, we included the following additional parameters: (iii) speed of motions [mm/s]; (iv) spatial rate of change of direction [°/mm] and (v) spatial rate of trajectory loops [loops/m].

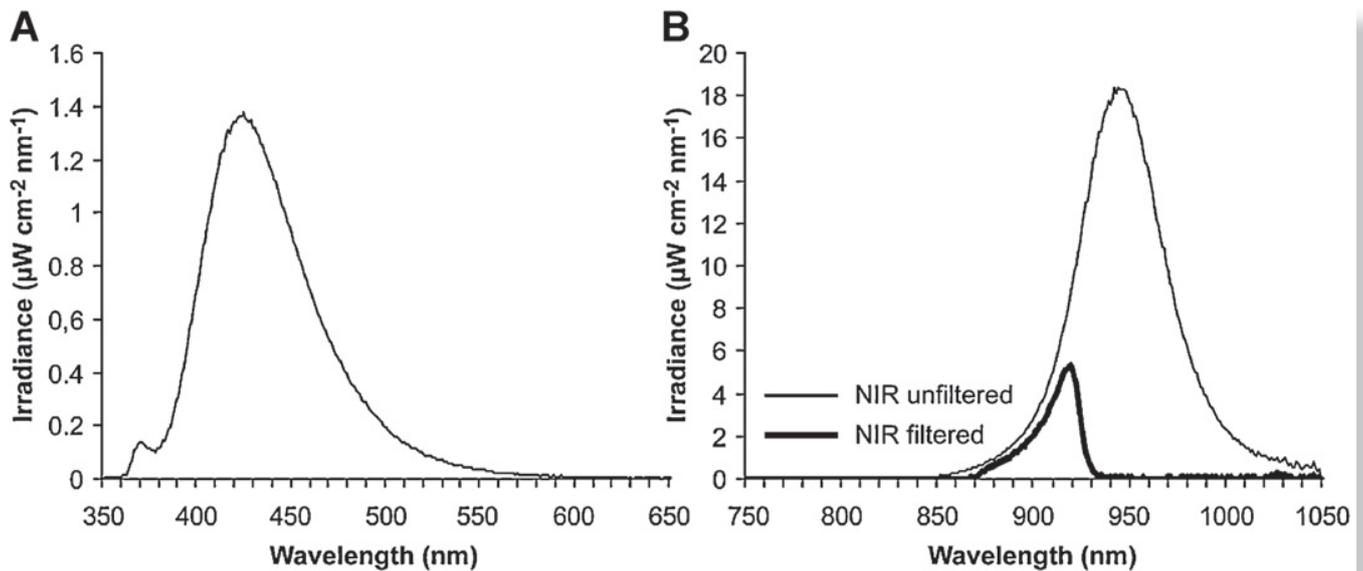


Fig. 2: Spectral characteristics of light sources used in the present study. (A) Blue light source without reduction of light intensity, with a peak wavelength at 430 nm and a spectral line half-width of 60 nm, as specified by the manufacturer. In the experiment the blue light intensity was reduced about 60-fold by using several layers of thin, semi-transparent synthetic foil. (B) Thin line = unfiltered infrared light emitted by an LED with an emission maximum at 940 nm and a spectral half-width of 50 nm, as specified by the manufacturer; thick line = filtered near-infrared light (as applied in the NIR experiments) emitted by the same LED (940 ± 50 nm) but modified by optical filters 850FG07-50 and D900/50X, thus covering a spectral range of 850–950 nm. For wavelengths above 950 nm only the noise in the detector was observed.

To determine the direction of mean vectors between the centre of the arena and the mean fish head positions, directional uniformity was calculated using a Rayleigh test (Gaile and Burt, 1980; Merkel, 1980). As a directional parameter, the length of the mean directional vector R was calculated, with $R = 0$ indicating uniform distribution in all directions and $R = 1$ representing vectors pointing in the same direction (e.g., in the direction of light).

The statistical significance of two-sided (light/control) results was calculated by the two-tailed Wilcoxon matched pairs test (Statistica 6.1; StatSoft, Inc., Tulsa, OK, USA). For calculation of the directional statistical significance, a Rayleigh test of uniformity was used (Gaile and Burt, 1980). Significance levels were $P \geq 0.05$ (not significant), $0.05 > P \geq 0.01$ (weakly significant *), $0.01 > P \geq 0.001$ (significant **), and $P < 0.001$ (highly significant ***).

2.4. Light sources and spectral measurements

The spectral intensity emitted by the light sources applied was measured by an **ILT 950 spectroradiometer** (International Light Technologies, Peabody, MA, USA). Spectral measurements were carried out at the position of the swimming vessel, 10 cm away from each light source. The surface temperatures of both radiation sources were measured by an infrared thermometer (VOLT-CRAFT IR-230; Conrad Electronic, Hirschau, Germany).

2.5. Behavioural experiments

The phototactic orientation behaviour of *O. mossambicus* was investigated in three experiments.

- (1) Behavioural patterns of *O. mossambicus* were tested with a blue light source (LED L-53MBC; Kingbright Elec. Co., Ltd., Taipei, Taiwan; $\lambda_{\text{max}} = 430$ nm; spectral line half width $\Delta\lambda_{1/2} = 60$ nm; Fig. 2A), as blue light is known to be visible to the closely related species Nile tilapia (*O. niloticus*; Bowmaker and Loew, 2008). Preliminary experiments revealed that light intensity was a crucial factor for behavioural patterns of fish. At moderate blue light intensity, *O. mossambicus* showed a strong positive phototactic behaviour with high reproducibility. No or negative phototaxis was observed when high blue light intensities corresponding to an irradiance peak of about $1.4 \mu\text{W}/\text{cm}^2 \text{nm}$ were applied. To reduce blue light intensity, several layers of thin synthetic foil, which were semi-transparent and reduced blue light intensity considerably, were installed between the light source and the vessel with the fish. In this setting, with the light intensity of the blue LEDs was reduced about 60-fold, *O. mossambicus* showed a strong positive phototactic reaction.

| Parameter | Blue light | P | Control | NIR (850–950 nm) | P | Control | P NIR (850–950 nm) | P | Thermal radiation |
|---|--------------|------|-------------|------------------|-----|-------------|--------------------|-----|-------------------|
| Mean allocation time [s] | 249.6 ± 69.9 | *** | 50.4 ± 69.9 | 218.8 ± 47.6 | *** | 81.2 ± 47.6 | 209.7 ± 48.2 | *** | 90.3 ± 48.2 |
| Mean covered distance [m] | 1.6 ± 0.8 | *** | 0.3 ± 0.4 | 2.9 ± 0.9 | *** | 1.2 ± 0.8 | 2.6 ± 1.0 | *** | 1.2 ± 0.7 |
| Mean speed of motions [mm/s] | 6.5 ± 2.5 | n.s. | 9.2 ± 7.7 | 13.5 ± 4.1 | * | 14.3 ± 4.8 | 12.4 ± 4.3 | ** | 14.2 ± 5.0 |
| Mean spatial rate of change of direction [°/mm] | 27.7 ± 7.2 | *** | 13.3 ± 9.6 | 14.8 ± 4.4 | *** | 11.2 ± 2.7 | 13.9 ± 4.0 | *** | 11.6 ± 3.3 |
| Mean spatial rate of trajectory loops [loops/m] | 57.8 ± 17.8 | *** | 21.5 ± 18.4 | 40.2 ± 8.9 | *** | 25.4 ± 8.5 | 36.5 ± 9.1 | *** | 27.9 ± 10.3 |
| Mean directional vector R | 0.77 *** | - | - | 0.85*** | - | - | 0.73 *** | - | - |
| Number of tested animals [N] | 30 | - | - | 30 | - | - | 30 | - | - |

n.s. $P \geq 0.05$ (not significant).
 * $0.05 > P \geq 0.01$ (weakly significant).
 ** $0.01 > P \geq 0.001$ (significant).
 *** $P < 0.001$ (highly significant).

Table 1: Movement behaviour of *O. mossambicus* under different illumination conditions (mean ± SD). Significance was calculated by a two-tailed Wilcoxon matched pairs test with the exception of the mean directional vector R, which was analysed by the Rayleigh test of uniformity (Gaile and Burt, 1980).

- Fish reactions to NIR were tested using an LED L-53F3C (King-bright Elec. Co., Ltd., Taipei, Taiwan) with an emission peak at 940 nm and a spectral line half width $\Delta\lambda_{1/2} = 50$ nm. The emitted spectrum of this LED was relatively broad (Fig. 2B, thin line). To exclude spectral components of visible light (e.g., dark red) and also to limit the spectral bandwidth of the incident NIR light, a combination of optical filters was used for the second and third experiments. A reduction to 850–950 nm was achieved by combining **a long-wave pass filter (850FG07-50; Quantum Design, Darmstadt, Germany) and a band pass filter (D900/50X; Chroma Technology Corp., Bellows Falls, VT, USA)** directly attached to the NIR light source housing (Fig. 2B, thick line).
- Control experiments were conducted to exclude thermal radiation, which was emitted by the NIR source as well, as a behavioural cue. As a thermal source we used the same type of NIR source equipped with an absorbing black filter which completely blocked NIR light without restricting thermal radiation. NIR light source and thermal radiation source were placed at opposite ends of the T-shaped device and were turned on simultaneously. The wavelengths of the radiation emitted by the thermal source were far above the sen-

sitivity range of the spectroradiometer as well as of the camcorder. The mean surface temperature of the NIR light source was 30.2 °C, and of the thermal source, 30.6 °C.

3. Results

3.1. Positive phototactic behaviour of fish towards blue light

The behavioural analysis showed that *O. mossambicus* spent 4.9 times more time in the half of the swimming vessel close to the blue light source compared to the distant half (Figs. 1 and 3A and Table 1; Wilcoxon matched pairs test: $T = 19$, $N = 30$, $P < 0.001$). The majority of tested individuals demonstrated an active swimming behaviour. Although no significant differences in the mean speed of motion were observed (Wilcoxon matched pairs test: $T = 155$, $N = 30$, $P = 0.11$), the mean covered distance in the blue light half was 5.3 times higher than that in the distant half (Wilcoxon matched pairs test: $T = 13$, $N = 30$, $P < 0.001$). Animals changed their movement direction more often in the half close to the light source as compared to the control side.

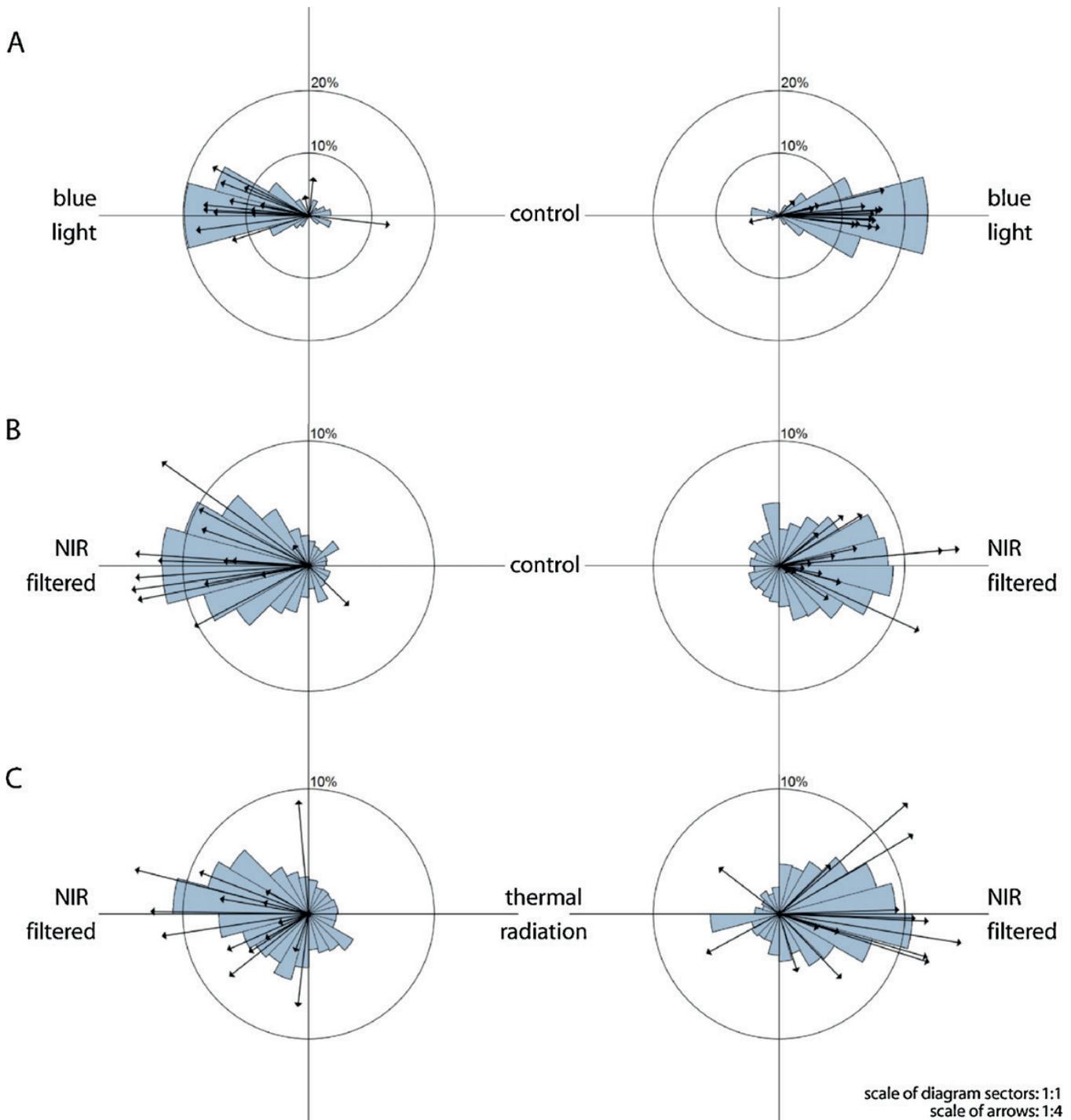


Fig. 3: Sector diagram of mean allocation time (in percent) with regard to mean head positions of fish in different sectors of the swimming vessel in experiments with different radiation stimuli: (A) blue light; (B) filtered NIR light (850–950 nm); (C) filtered NIR light (850–950 nm) vs. thermal source. Each sector represents 15°. Black arrows show the angle between the centre of the swimming vessel and the mean head positions for each fish. Arrow lengths were calculated in percent with regard to the distance between the vessel centre and the vessel border. The length of all vectors was reduced by a factor of 4.

The spatial rate of change of direction [$^{\circ}$ /mm] (Wilcoxon matched pairs test: $T = 34$, $N = 30$, $P < 0.001$) was higher than on the control side. In the blue light half, fish crossed their own trajectories more often, i.e. performed more trajectory loops [loops mm] (Wilcoxon matched pairs test: $T = 12$, $N = 30$, $P < 0.001$). The spatial preference of body orientation was such that the head was aligned to the blue light source (Fig. 3A). The length of the mean directional vector between the centre of the arena and the mean fish head positions was $R = 0.77$ ($P < 0.001$).

3.2. Positive phototactic behaviour of fish towards an NIR light source of 850–950 nm

Next, blue light was exchanged for an NIR light source. The fish, which demonstrated considerable swimming activity, spent 2.7 more time in the half of the swimming vessel next to the NIR source than in the control half (Figs. 1 and 3B and Table 1; Wilcoxon matched pairs test: $T = 8$, $N = 30$, $P < 0.001$). Although the mean speed of motion was slightly lower in the half of the dish close to the NIR source (Wilcoxon matched pairs test: $T = 124$, $N = 30$, $P < 0.05$), the mean covered distance was 2.4 times higher than that in the control half (Wilcoxon matched pairs test: $T = 8$, $N = 30$, $P < 0.001$). Animals also changed their movement direction more often in the NIR half. This was demonstrated by changes in the spatial rate of change of direction [$^{\circ}$ /mm] (Wilcoxon matched pairs test: $T = 15$, $N = 30$, $P < 0.001$). Furthermore, fish in the NIR half crossed their own trajectories more often, i.e. displayed more trajectory loops per mm of covered distance (Wilcoxon matched pairs test: $T = 12$, $N = 30$, $P < 0.001$). Again, the most frequent body orientation was such that the head was aligned to the NIR light (cf. supplementary video in Appendix A and Fig. 3B). The length of the mean directional vector between the centre of the arena and the mean fish head positions was $R = 0.85$ ($P < 0.001$).

3.3. No tactic behaviour of fish towards a thermal radiation source

The allocation time in the NIR half was 2.3 times higher than in the thermal half (Fig. 3C and Table 1; Wilcoxon matched pairs test: $T = 21$, $N = 30$, $P < 0.001$). The animals were slower on the side proximate to the NIR light source (Wilcoxon matched pairs test: $T = 101$, $N = 30$, $P < 0.01$), in accordance with the previous experiments without the thermal source. The mean covered distance in the NIR half was 2.2 times higher than that on the opposite side adjacent to the thermal source (Wilcoxon matched pairs test: $T = 24$, $N = 30$, $P < 0.001$). The tested individuals changed their movement direction more often in the NIR half. The spatial rate of change of direction [$^{\circ}$ /mm] (Wilcoxon matched

pairs test: $T = 26$, $N = 30$, $P < 0.001$) was higher than in the half of the swimming vessel adjacent to the thermal source. Tested fish crossed their own trajectories more often, i.e. displayed more trajectory loops per mm of covered distance (Wilcoxon matched pairs test: $T = 25.5$, $N = 30$, $P < 0.001$) in the half proximate to the NIR light source, and they preferred to align their heads in this direction (Fig. 3C). The length of the mean directional vector between the centre of the arena and the mean fish head positions was $R = 0.73$ ($P < 0.001$).

4. Discussion

This study provides strong and unambiguous evidence for an NIR sensitivity of *O. mossambicus*. Following the definition of phototaxis as the displacement of an organism towards or away from light, along a light gradient or its vector (Jekely, 2009), we demonstrated an innate untrained phototactic behaviour of fish to a limited spectrum of NIR light. Phototactic movement patterns of *O. mossambicus* were qualitatively and quantitatively similar, no matter whether NIR or blue light was applied. An influence of thermal radiation on the movement of fish could be excluded in experiments which simultaneously applied thermal and NIR sources. Our results thus demonstrate that *O. mossambicus* can sense NIR light of wavelengths ≥ 850 nm. Animals were able to use NIR light for phototactic orientation under experimental conditions without any conditioning, in line with our hypotheses 1–3. These were further supported by the preferred body alignment of *O. mossambicus* with the head pointing in the direction of the NIR light source. Moreover, the higher level of the mean spatial rate of change of direction [$^{\circ}$ /mm] on the NIR side of the swimming vessel is in good agreement with the preferred alignment of wave-shaped swimming motion in the direction of NIR radiation (cf. Table 1 and supplementary video in Appendix A). In addition, these results also support the fourth hypothesis, namely that NIR sensation in *O. mossambicus* is phototaxis and not based on thermo-reception. From studies in *O. niloticus* it is known that NIR light can be perceived by their eyes but not by the pineal organ (Matsumoto and Kawamura, 2005). This species is a close relative of *O. mossambicus* which prefers similar habitats. Evolutionary considerations thus argue for an eye-based NIR reception in *O. mossambicus* as well. In Nile tilapia, Kobayashi et al. (2002) reported a lack of optomotor reaction to infrared light at wavelengths above 800 nm. These conflicting results may be explained if *O. niloticus* were not able to see the moving drum stripes used in optomotor experiments. To prove that fish are able to detect objects by means of NIR-based visual cues, detailed behavioural experiments should be carried out under NIR conditions. Future experiments should discriminate

between phototactic light reaction and visual recognition of objects. NIR reception, like other forms of light sensation, could theoretically be relevant for foraging, avoiding predators and maybe also for intraspecific communication (Cerri, 1983; Bowmaker and Loew, 2008; Cronin, 2008; Michiels et al., 2008). Characteristics of photopigment spectral sensitivity in fish species depend on light conditions in their natural habitat (Lythgoe, 1984). *O. mossambicus* is an African cichlid which inhabits different water bodies such as rivers and lakes. It is euryhaline and can grow and reproduce in fresh, brackish and sea water (Bruton and Boltz, 1975; Chervinski, 1982; Philippart and Ruwet, 1982; Trewavas, 1982). Observations in a freshwater lake (Lake Sibaya, South Africa) with a maximal depth of 40 m indicated that *O. mossambicus* prefers depths of residence 0–12 m from the water surface (Bruton and Boltz, 1975). Due to a high tolerance to elevated water temperatures (Fiess et al., 2007; Ndong et al., 2007) and to extremely low oxygen concentrations (Wrigley et al., 1988), *O. mossambicus* can successfully survive in very shallow water and prefer waters with increased turbidity (Espinosa-Lemus et al., 2009). The electromagnetic radiation emitted by the sun covers a wide spectral range which is partially reflected, scattered and absorbed by constituent parts of the earth atmosphere. Therefore, the subaerial radiation of the sun and the light impinging the surface of the sea, lakes and rivers is modified with a characteristic spectral distribution of wavelengths above 300 nm to the long-wave infrared. Hence the light at water surfaces also contains near-infrared spectral components (Riordan, 1986; Bowmaker, 1995). Total irradiance by the NIR light source in our experiments was 13.3 W/m² m, and thus about 10–50 times lower than the natural solar irradiance values in the spectral range of 850–950 nm, measured at the earth's surface on the African continent (Adeyefa et al., 1995; Adeyefa and Holmgren, 1996). Usually only a negligible part of irradiance will be reflected from the water back to the atmosphere (Lavender et al., 2005; Doron et al., 2011). As the mean reflectance of light on the water surface usually reaches 6.5% (Wetzel, 1983), the NIR intensity applied in this study was similar to irradiance values which occur in nature, at least directly below the water surface. Due to the relatively high absorption coefficient of water for NIR radiation (approximately 103–105) compared to, e.g., blue light, the depth of penetration for near-infrared light is comparatively short. However, aquatic habitats of *O. mossambicus* often contain substantial amounts of suspended particles and dissolved coloured organic matter which may, for instance, cause increased scattering and absorption of short-wave components of the solar spectrum implying a relative increase of long-wave illumination (Seehausen et al., 2008), including red and infrared (Bowmaker, 1995; Borowiak, 2009).

The observed sensitivity shift to NIR light thus might improve the orientation of Mozambique tilapia in their natural habitat. Our study unequivocally demonstrated a strong influence of NIR light on the behaviour of Mozambique tilapia. Further studies of NIR sensitivity in different fish species are needed to determine the threshold of NIR reception, to unequivocally identify the sensing organ and to understand its mechanism and functional characteristics

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.zool.2012.01.005>.

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