

Visual prey detection by near-infrared cues in a fish

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Abstract Many animal species are able to perceive light wavelengths beyond those visible to humans. While numerous species are additionally sensitive to short wavelengths (UV), long wavelengths such as the near-infrared spectrum (NIR) are supposed to be unsuitable for visual perception. Here, we experimentally show that under exclusive NIR illumination, the cichlid fish *Pelvicachromis taeniatus* displays a clear foraging response towards NIR reflecting prey. Additional control experiments without prey indicate that the observed behavior is not a mere response to the NIR environment. These results give first evidence for NIR visual sensitivity in a functional context and thus challenge the current view about NIR perception.

Keywords *Pelvicachromis taeniatus* · Visual perception · Foraging behavior · Near-infrared sensitivity

Abbreviations

UV Ultraviolet
NIR Near-infrared

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Introduction

The solar radiation that reaches the earth's surface consists of wavelengths between 290 nm in the ultraviolet (UV) and 2,000 nm in the far infrared (Knowles and Dartnall 1977). The human visual system is able to perceive wavelengths between 400 and 780 nm. Many animal species are able to perceive light that is invisible to humans (Jacobs 1981) such as short UV-A (Tovée 1995) (315–400 nm) or UV-B (Li et al. 2008) wavelengths (280–315 nm) and use these wavelengths in visual communication (Rick and Bakker 2008). In contrast to short wavelengths, infrared light is supposed to be unsuitable for visual perception due to the noise produced in visual pigments by thermal energy (Luo et al. 2011). Far-infrared wavelengths (3×10^3 – 1×10^6 nm) can be perceived by highly sensitive thermoreceptors as radiant heat, for instance by fire beetles and some snake species (Evans 1964; Newman and Hartline 1982). However, theoretical models suggest that photoreceptor spectral sensitivities might extend into the NIR range (780–1,000 nm) (Lythgoe and Partridge 1989; Pelli and Chamberlain 1989; Lamb 1995). NIR radiation is present in different habitats (Knowles and Dartnall 1977), and several animal species display NIR-reflecting patterns (Schwalm et al. 1977) or NIR bioluminescence (Widder et al. 1984). Furthermore, visual pigments in some deep-sea fish are sensitive to wavelengths in the far-red spectral region (Douglas et al. 1998), but little is known about the sensitivity to even longer wavelengths such as the NIR. In aquatic habitats, especially the scattering of the seston and dissolved humic substances facilitate natural NIR availability in shallow, nutrient-rich, stained, and turbid waters (Rijkeboer et al. 1998; Ranåker et al. 2012).

Here, we examined whether the fish *Pelvicachromis taeniatus*, a cichlid species inhabiting shallow streams in Western Africa, is capable of using visual NIR cues in a functional

context. Visual cues play an important role in the communication in cichlids in general (Maan et al. 2006) and in *P. taeniatus* in particular (Baldauf et al. 2011). We tested the response of *P. taeniatus* towards a NIR reflecting prey stimulus (*Gammarus pulex*) under exclusive NIR illumination (780–920 nm) in an experimental setup which excludes other prey detection cues. To control for potential NIR habitat preferences, we re-tested the fish in the same setup in the absence of prey stimuli.

Materials and methods

Five adult males and females of *P. taeniatus* (F2 lab-raised) were housed individually in 20×30×20 cm (L×W×H) tanks and were fed with live *G. pulex* 2 days prior to experiments. For the experiments, fish were introduced to the experimental setup (Fig. 1a) under full-spectrum illumination, acclimatized overnight during darkness, and were kept under NIR illumination for 1 h prior to trials. During trials, individual fish was given the choice between *G. pulex* presented behind a NIR+ (Schott RG780, transmittance 780–920 nm, see Fig. 2a) or NIR– filter (Schott KG5, transmittance 300–780 nm, see Fig. 2a), respectively, under exclusive near-infrared illumination (Conrad IR-lamp, see Fig. 2b). *G. pulex* reflect in the near-infrared (see Fig. 2c for the reflectance spectrum). We used NIR filters in order to control for possible perception of non-infrared-based visual signals such as bioluminescence emission. *G. pulex* presented behind the NIR+ and NIR– filter did not significantly differ in size (two-tailed paired *t* test, $t=-1.464$, $df=9$, $p=0.177$). Trials were recorded with a NIR-sensitive camera (EQ 150, EverFocus, Taipei, Taiwan) for 10 min after the fish had entered both association zones and subsequently re-entered one zone (at least 1-s duration of stay per zone). Between trials, prey was replaced and filter positions alternated; each fish was re-tested in the same setup without prey after an intermission period of 12 days. Videos were analyzed using an animal tracking software (Biobserve Viewer²) to measure the time fish spent in each association zone. Furthermore, a naïve observer quantified the number of bites directed towards each prey chamber. Association times and bites were converted to relative data. Relative data as well as absolute association times did not significantly differ from normality according to Shapiro–Wilk tests. To examine the effect of the filters (NIR+ and NIR–) on the association time and the proportion of attacks, we applied linear-mixed-effect models (LME, R library “nlme”). To compare the absolute association times before the respective filters of the main experiment with prey with those of the control experiment without prey, we conducted a LME with association time as dependent variable and prey presence (yes/no) as explanatory variable. In all models, fish identity was entered

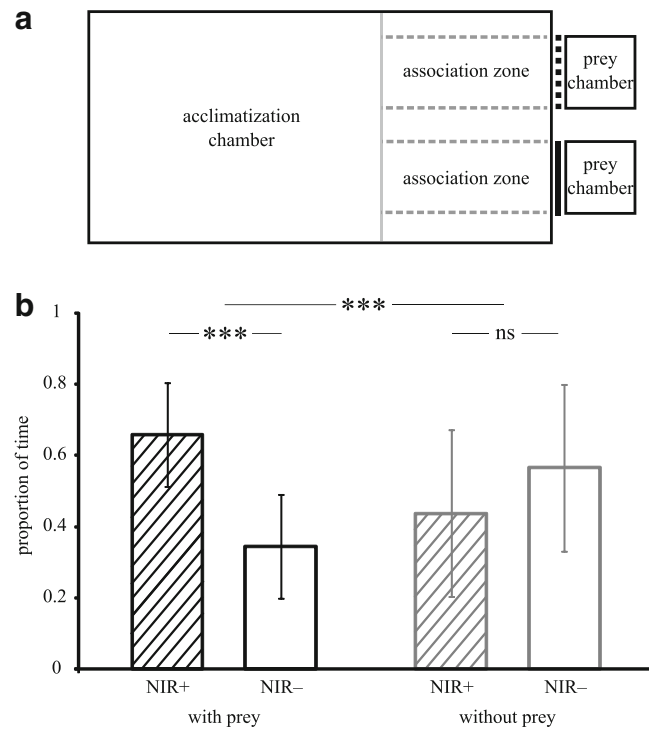


Fig. 1 **a** Top view of the experimental apparatus. The test fish was individually placed into the acclimatization chamber (20×20×20 cm) of the glass test tank (20×30×20 cm, water level 10 cm) for habituation. Prey stimuli (three *G. pulex*) were presented in two chambers (each 5×5×5 cm) behind vertically placed optical filters, either transmitting (NIR+, dotted line) or blocking NIR wavelengths (NIR–, solid line). Because the experiment was conducted under exclusive near-infrared illumination and *G. pulex* reflects in the NIR, fish could perceive the prey only through the NIR+ filter, but not through the NIR– filter if sensitive to NIR light. The distance between prey chambers was 3.5 cm. The side of the prey chamber facing the test tank was made of glass, whereas the three other walls consisted of opaque gray plastic partitions which do not reflect in the NIR range (DM, personal observation). With the start of the trial, fish were allowed to visit the association zones (each 10×5 cm) by raising an opaque barrier. **b** Mean proportion of time ± SD fish spent in the association zones in front of prey presented behind NIR+ (hatched bars) or NIR– (open bars) filters. The two left bars represent the results of the main experiment with prey (black contour lines, $n=10$), whereas the two right bars represent the results of the control experiment (controlling for potential habitat preferences) without prey (right bars, gray contour lines, $n=9$). Triple asterisk above the bars indicate $p<0.001$, ns denotes $p>0.05$

as random factor to account for repeated use of the same fish. All tests of statistical significance were based on likelihood ratio tests; hence, degrees of freedom always differ by 1.

Results

Test fish spent significantly more time next to prey located behind the NIR+ filter than next to prey located behind the NIR– filter (LME, $\chi^2=16.644$, $p<0.001$, Fig. 1b). In addition, test fish bit more often towards prey presented behind

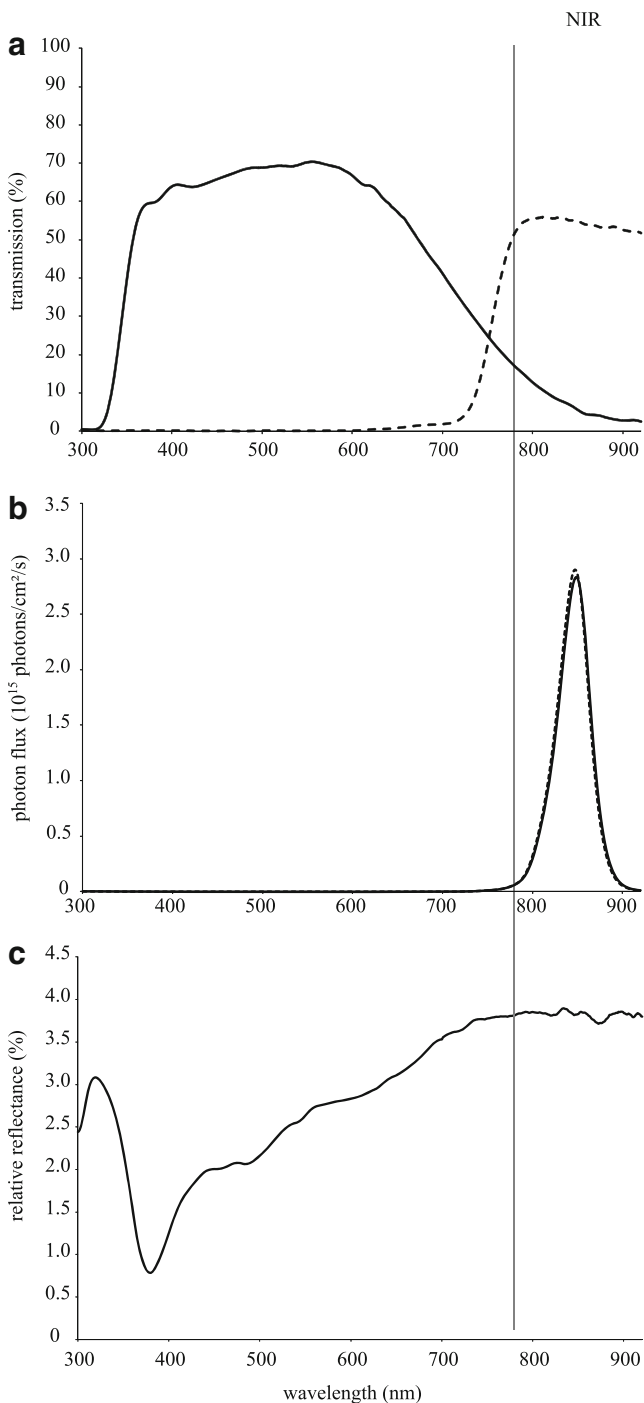


Fig. 2 **a** Transmittance spectra of NIR+ (dashed line) and NIR- (solid line) filters, positioned between two layers of tank glass (thickness 4 mm each) to simulate the experimental conditions. Given is the mean transmission curve of five measurements performed with an Avantes Avaspec 2048 spectrophotometer connected to an Avantes DHs deuterium-halogen light source for wavelengths between 300 and 920 nm. **b** Spectra of downwelling irradiance measured under experimental lighting conditions within the NIR+ (dashed line) and NIR- (solid line) prey chambers at 5 cm below water level. Spectra display a combination of unfiltered light from above and filtered light collected through the front side of each chamber. Measurements were obtained with an Avantes CCUV/VIS cosine corrector; irradiance calibration was performed versus an Avantes NIST traceable irradiance application standard. **c** Mean reflectance spectrum of the *G. pulex* carapace ($n=3$) involving the fourth and fifth thoracal segments. Reflectance was measured relative to a 98 % Spectralon white standard with a bifurcated 200- μm small tip fiber-optic that was held at a 90° angle to the body surface connected to the same apparatus used during transmittance measurements. A mat black fabric background prevented light transmission and scattering caused by translucent body parts

filter independent of prey presence (prey present: mean $81.78 \pm \text{SD } 62.48$ s, prey absent: mean $61.36 \pm \text{SD } 36.38$ s, LME, $\chi^2=2.591$, $p=0.108$).

Discussion

In our experiment, *P. taeniatus* displayed a clear foraging response towards prey under exclusive NIR illumination when all other signaling pathways were excluded. Because of the additional use of NIR filters, we furthermore controlled for other visual cues than NIR, such as bioluminescence emission. As fish did not differentiate between NIR+ or NIR- habitats without prey in the control experiment, our study provides first evidence for the use of NIR wavelengths in a functional context in an animal species.

The underlying mechanism of NIR visual perception, however, requires further research addressing not only retinal but also the poorly understood extraretinal photoreceptors whose photopigments can differ considerably from retinal receptors (Foster and Hankins 2002). The existence of visual pigments with absorption maxima capable of absorbing NIR wavelengths was questioned because NIR quanta display low energy levels; therefore, visual pigment isomerization usually cannot be achieved using this energy alone (Lythgoe 1984). Even if thermal energy contributes the required additional energy, the expected noise levels due to spontaneous isomerizations are hypothesized to grow too large for visual perception (Luo et al. 2011). Nevertheless, either a boosted absolute photon capture of the rods or an extended cone pigment spectral sensitivity beyond 780 nm could make NIR perception possible (Lamb 1995). Accordingly, visual cone pigments such as reported in the deep-sea dragon fish (*Malacosteus niger*) with an absorption maximum of 666.8 nm (Douglas et al. 1998) might very well be capable of NIR absorption (Lythgoe and Partridge 1989).

the NIR+ filter compared to prey behind the NIR- filter (mean $87.77 \pm \text{SD } 17.29$ % of all bites, LME, $\chi^2=29.763$, $p<0.001$). In the control experiment without prey, fish neither bit in the direction of either prey chamber nor spent a different amount of time between filters (LME, $\chi^2=1.449$, $p=0.229$, Fig. 1b). In the presence of prey, fish spent on average three times more time in the NIR+ filter association zone (mean $149.11 \pm \text{SD } 75.21$ s) compared to prey absence (mean $44.41 \pm \text{SD } 34.25$ s, LME, $\chi^2=13.362$, $p<0.001$). In contrast, fish spent similar amounts of time near the NIR-

Generally, the spectral composition of natural aquatic habitats is spatially and temporally highly heterogeneous (Lythgoe 1972). This is also true for NIR wavelengths, whose availability in aquatic habitats depends on both abiotic and biotic factors. Clear water attenuates NIR with increasing depth, whereas phytoplankton, non-living suspended matter, and dissolved humic substances scatter NIR light, facilitating NIR transmission in nutrient-rich, stained, and turbid aquatic habitats (Rijkeboer et al. 1998; Ranåker et al. 2012). Furthermore, absorption is temperature-dependent, leading to increased NIR transmission at approximately 800 nm with increasing temperature (Langford et al. 2001). Moreover, during certain times of the day, the proportion of NIR is increased, e.g., during twilight (Munz and McFarland 1975). Our study species *P. taeniatus* inhabits small tropical streams and prefers shallow littoral regions (Lamboj 2004). In such habitats, the NIR amount of surface waters in the spectral range between 780 and 855 nm is comparable to the lighting conditions used in our experiment (unpublished data). Consequently, NIR wavelengths have the potential to play a role in the visual ecology of *P. taeniatus* under natural conditions.

A future challenge will be to examine whether the effects of artificially manipulated light conditions can also be applied to predator–prey interactions under a range of natural light environments. Furthermore, as some fish are capable of producing NIR signals (Widder et al. 1984) and *P. taeniatus* shows sex-specific reflectance of NIR (DM, personal observation), the potential involvement of NIR in intraspecific communication, especially in sexual selection and the interplay with other ornamental traits present in our model system (Baldauf et al. 2010, 2011), should be investigated.

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical standards All experiments comply with the current laws of Germany.

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