Report

Current Biology

Electric-Color Sensing in Weakly Electric Fish Suggests Color Perception as a Sensory Concept beyond Vision

Highlights

- The weakly electric fish *G. petersii* perceives electric colors for prey recognition
- Animals, plants, or prey provide specific electric colors during electrolocation
- Electric color shares perceptual traits with visual color
- Electric-color sensing in electric fish implies color perception beyond vision

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In Brief

Using stimulus recordings and behavioral experiments, Gottwald et al. show that nocturnal, weakly electric fish utilize a color-like electrical cue for fast and reliable prey recognition. Electric-color sensing during active electrolocation suggests the perception of "colors" as a sensory concept beyond vision and passive sensing.

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Electric-Color Sensing in Weakly Electric Fish Suggests Color Perception as a Sensory Concept beyond Vision

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SUMMARY

Many sighted animals use color as a salient and reliable cue [1] to identify conspecifics [2–4], predators, or food [5–7]. Similarly, nocturnal, weakly electric fish *Gnathonemus petersii* might rely on "electric colors" [8] for unambiguous, critical object recognitions. These fish identify nearby targets by emitting electric signals and by sensing the object-evoked signal modulations in amplitude and waveform with two types of epidermal electroreceptors (active electrolocation) [9–12]. Electrical capacitive objects (animals, plants) modulate both parameters; resistive targets (e.g., rocks) modulate only the signal's amplitude [11, 12]. Ambiguities of electrosensory inputs arise when object size, distance, or position vary. While previous reports suggest electrosensory disambiguations when both modulations are combined as electric colors [8, 13, 14], this concept has never been demonstrated in a natural, behaviorally relevant context. Here, we assessed electric-color perception (1) by recording object-evoked signal modulations and (2) by testing the fishes' behavioral responses to these objects during foraging. We found that modulations caused by aquatic animals or plants provided electric colors when combined as a ratio. Individual electric colors designated crucial targets (electric fish, prey insect larvae, or others) irrespective of their size, distance, or position. In behavioral tests, electrolocating fish reliably identified prey insect larvae of varying sizes from different distances and did not differentiate between artificial prey items generating similar electric colors. Our results indicate a color-like perceptual cue during active electrolocation, the computation [15], reliability, and use of which resemble those of color in vision. This suggests "color" perception as a sensory concept beyond vision and passive sensing.

RESULTS

Electric Colors Reliably Designate Relevant Environmental Targets

Several targets (fish, electric fish, different types of insect larvae, and plants) were used to test for electric colors of natural, capacitive objects during active electrolocation. In addition, artificial stimulus objects were recorded to select items, which did or did not electrically resemble the natural electrolocation targets (small capacitive or resistive items). The object-evoked amplitude and waveform modulations of the fish's signals (examples shown in Figure 1) were recorded close to the skin of a *G. petersii* at a fixed position (STAR Methods; Figures S1A and S1B). Measurements were mainly conducted at the fish's "electroreceptive fovea" [12, 16], a movable chin appendix, which is used for object inspection and prey recognition [9]. The second object and recording position was at the side of the fish's head (STAR Methods; Figure S1A). Electric colors were calculated as waveform-to-amplitude modulation ratios. They were evaluated for different object sizes, different object distances, and the two recording positions (Figures 2A–2C).

For each stimulus object, the waveform modulation was plotted versus the amplitude modulation in a two-dimensional space [8, 11–14] (Figures 2A and 2B). In these graphs, amplitude and waveform modulations recorded at the fovea, e.g., for differently sized animals, and plants could be aligned with five linear functions (Figure 2A, colored lines). Each line was obtained only for objects with a similar waveform-to-amplitude modulation ratio (electric color). Different color lines therefore represented individual electric colors. As indicated by the line labels, electric colors corresponded to basic categories of natural objects (fish, electric fish, water plants, insect larvae). Interestingly, insect larvae generated two very distinct electric-color lines: one for chironomids (mosquito larvae) and one for all other insect larvae tested. Chironomids are the main food item of *G. petersii* [17], and due to their specific electric color, they clearly stand out among larval prey insects.

Because modulation ratios caused by all stimulus objects showed close alignments to their specific color lines irrespective of object size, electric color was size invariant (Figure 2A). When recorded for different object distances from the fovea (Figure 2B), amplitude and waveform modulations of stimulus objects fitted

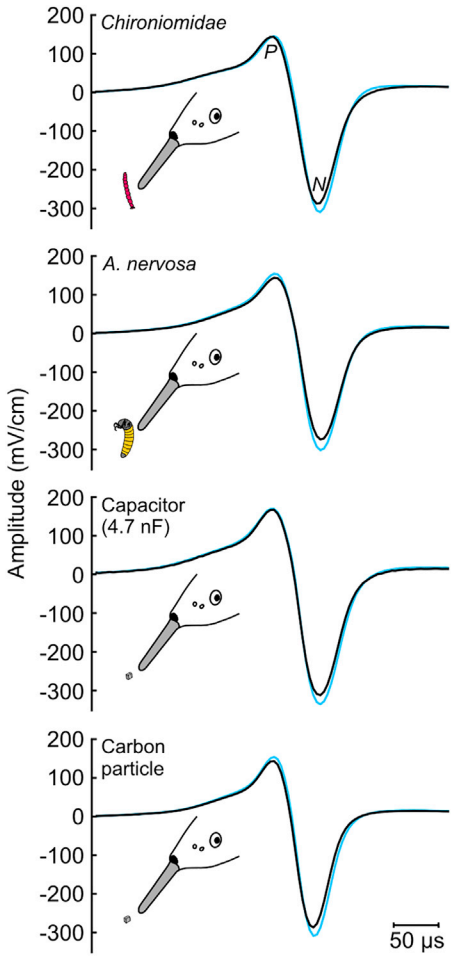

Figure 1. Object-Evoked Amplitude and Waveform Modulations of *G. petersii*'s Electric Signal

Biphasic signals recorded at the tip of fish's electric fovea (gray) with stimulus objects (see insets) present (blue signals) and absent (black signals). Electrical capacitive targets (e.g., insect larvae and capacitor) slightly modulate the signal (peak-to-peak) amplitude and waveform (ratio of the peak amplitude of the positive [P] and negative [N] phase) by scaling N considerably stronger than P. Purely resistive stimulus objects (e.g., a carbon particle) only cause an amplitude modulation, scaling N relative to P to a much lower extent.

the same color lines, which were obtained before for stimulus objects of different types and sizes. This suggests that electric color is also distance invariant.

Electric colors of stimulus objects, which were recorded successively at the fovea (Figure 2A) and at the side of the fish's head, showed no significant differences when statistically compared (Figure 2C). Thus, electric colors were stable for different "electric viewing" positions (i.e., when an object is inspected with the fovea or the head). Our measurements also showed that amplitude or waveform modulations alone varied non-systematically for different stimulus objects, distances, and sizes (Figures 2A and 2B). Hence, only electric color, i.e., the ratio of waveform-to-amplitude modulations, provided an unambiguous active electrolocation cue for identifying relevant environmental objects, especially larval prey insects.

Electrolocating Fish Use Electric Color to Reliably Identify Prey

In behavioral experiments, we tested whether fish might rely on electric-color cues for prey recognition. If so, they should be able to spontaneously identify chironomid larvae and to reject non-prey items, irrespective of their size or distance (i.e., the burial depth within the soil). However, as natural objects might also provide additional cues, e.g., odors for their identification, we also used artificial objects, which possess solely electrical properties (Figures 1 and 2D) during the tests (STAR Methods). Based on recordings close to the fovea (Figure 2D), we selected small resistors and capacitors, which caused different amplitude and waveform modulations but provided stable electric colors of either a chironomid larva (capacitors) or of the other larval prey insects (resistors). Note that, with their metal and plastic enclosure exposed to the fish's electric emissions, resistors had additional weak capacitive properties and thus evoked weak waveform modulations. Pure electrical resistors usually do not change the waveform of the fish's electric signal. We additionally used small carbon or plastic particles, which generated only amplitude modulations (Figure 1) and thus did not provide electric colors (Figure 2D).

In the first series of behavioral experiments, three *G. petersii* (fish 1–3) were trained to feed from a sandbox (STAR Methods; Figure S1C) containing a single buried chironomid larva or a non-prey item (plant stem or a metal rod). Like the carbon particle (Figures 1 and 2D), a metal rod is an electrical conductor (i.e., purely resistive) and causes only amplitude modulations and thus does not generate an electric color. Stimulus items were either large (~15 mm) or small (~8–10 mm) and were presented at a depth of 1 or 5 mm (Figure 3). During trials, fish electrically scanned the sandbox for food with their chin appendix. Items identified as prey were then sucked into the mouth (intake).

In all three fish, intakes of chironomids reached 100% (Figure 3), irrespective of sizes or burial depths. Non-prey items evoked, if at all, only minor intake rates, which were statistically inseparable (Figure 3). Some plant stems were erroneously judged as chironomid prey only when they were large and deeply buried (5 mm) or when they were small and buried at shallow depth (1 mm). Our recordings revealed that in these perceptual situations, modulations evoked by plant stems tended to scatter near the chironomid color line (see *Hydrocotyle vulgaris* with 10 mm length, Figure 2A, or at 5 mm distance, Figure 2B). The rare choices of plant stems might have therefore been driven by this minor electric-color bias.

The constant choice behavior for chironomid larvae suggests the use of electric color for prey identification in *G. petersii*. We are aware of no other active electrolocation cue, which could have guided prey choice as performed by the fish. While foraging relies mainly on the active electric sense, it probably was assisted by the perception of odor cues and/or passive electrolocation cues (i.e., low-frequency electric stimuli) [18–20]. However, such additional cues are far less important, especially for triggering prey choice (i.e., intake) [19], and can be considered to be attenuated for our buried stimulus items.

In a second series of behavioral experiments, five *G. petersii* (fish 2–6) were offered chironomids or artificial prey or non-prey items (STAR Methods; Figure S1D). The artificial items do not generate low-frequency stimuli or chemical cues and thus

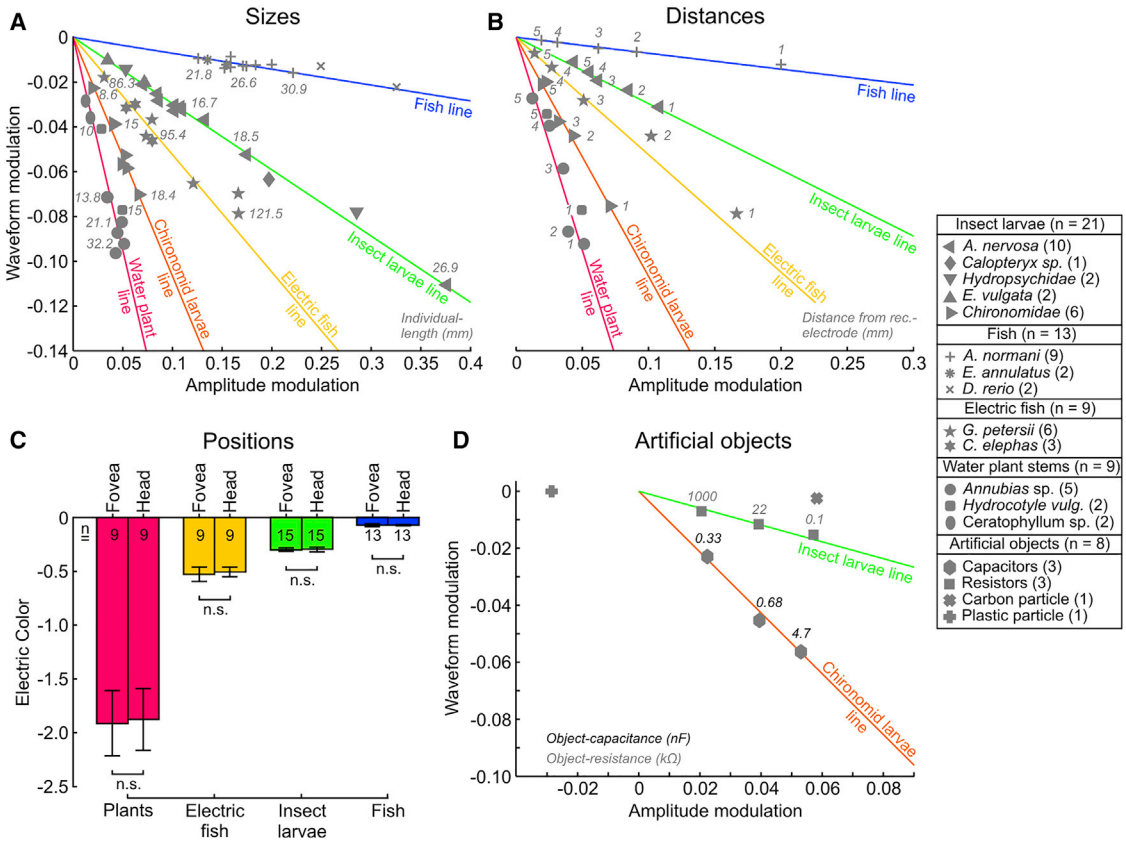

Figure 2. Object-Evoked Electric Colors

(A) Recordings of animals and plants of various sizes (lengths) at the electric fovea (1 mm distance from the recording electrode). Individuals with a similar waveform-to-amplitude modulation ratio (electric color) fall onto a linear function (color line). Indicated by the lines labels, electric color defines categories of stimulus objects, irrespective of their sizes.

(B) Single-target items recorded at different distances to the electric fovea fall onto their respective color lines obtained from the data in (A).

(C) Statistical comparison (paired two-tailed t test) of electric colors recorded from the same target items at the fovea (data in [A]) and at the side of the head (shown as means ± SD). Data had passed Shapiro-Wilk normality test in advance ($p > 0.05$ for all groups).

(D) Artificial objects recorded at the electric fovea (0.5 mm distance to the recording electrode). Certain capacitors and resistors (values written next to the symbols) generate electric colors of natural prey and fit the color lines, obtained from the data in (A). The resistors provided electric colors as a result of a weak additional capacitance evoking amplitude and waveform modulations (refer to main text for details). Carbon and plastic particles, as purely resistive objects, only caused amplitude modulations and thus no electric colors.

provided only active electrolocation cues for their identification (STAR Methods). Therefore, artificial prey could only be identified reliably by means of electric color. In all five fish, intake rates of artificial objects having the same electric color did not differ statistically (Figure 4). In addition, objects that did not generate electric colors (plastic and carbon particles) were completely rejected by the fish (Figure 4). Intake rates for capacitors (60%–75%) with the electric color of chironomids or resistors (25%–38%) with the electric color of the insect larvae line (Figure 2) statistically differed from one another and from intake rates of real chironomid larvae (93%–100%) (Figure 4).

The intake rates of artificial items show that fish rely on electric color to reliably identify prey by means of active electrolocation. Even though different intake rates for chironomids and capacitors suggest a use of additional parameters, e.g., odors or passive electric stimuli [19], the high intake rates for capacitors reveal electric color as the dominant cue for prey identification. The lower intake rates of resistors indicate that the fish recognized them as their "secondary" insect prey, which is preferred less compared to chironomid larvae [17]. Electrical differentiation of primary from secondary prey larvae might be an easy task for *G. petersii* due to the clear difference in their electric color revealed by our recordings (Figure 2).

DISCUSSION

Our results show that the weakly electric fish *G. petersii* uses a color-like perceptual cue to identify crucial environmental objects such as prey. Although vision and the active electric sense rely on different physical stimuli, color perception in the two modalities results from similar aspects of color formation. Electric colors can be represented as distinct lines (color lines) in a two-dimensional space with amplitude and waveform modulation at its axis (Figure 2) [8, 13, 14]. This bears close resemblance to the representation of visual color hues, e.g., in the human visual system, which form distinct color lines within their

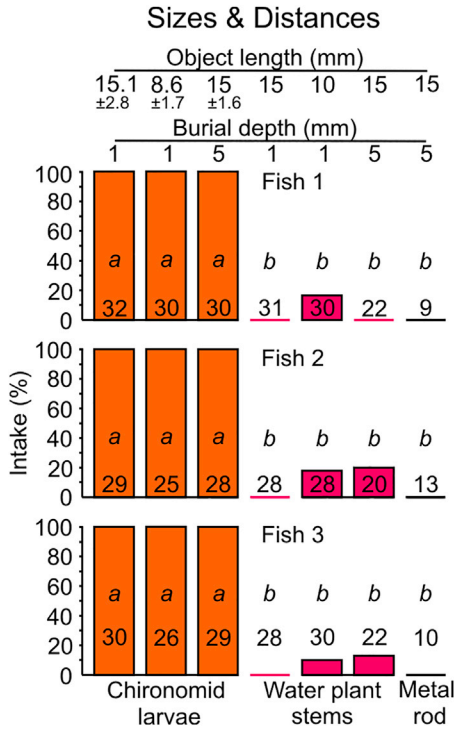

Figure 3. Prey Recognition for Differently Sized and Positioned Stimulus Objects

Relative intake of small and large prey and non-prey items, buried at two different depths ("distances") in the sandbox. Three fish were tested. Plant stems belonged to species *Hydrocotyle vulgaris*. For each condition, 32 trials were conducted. The number of detected items is given within or above the bars. A Fisher's exact test (two-tailed) was used to compare the relative object intake under the different conditions for each fish. Bars, which do not differ significantly ($p > 0.05$) or show constant values, are indicated by the same italic letter. Bar colors indicate the electric colors of the objects (see Figure 2).

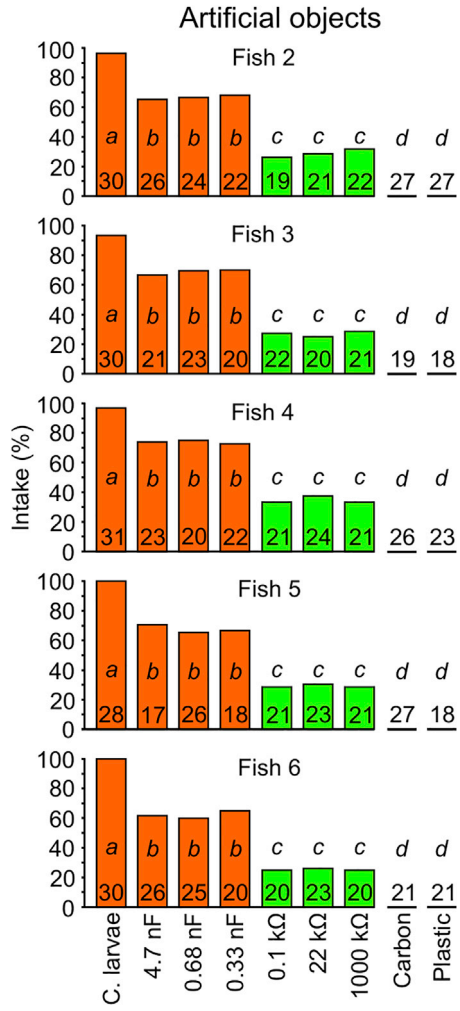

Figure 4. Prey Recognition for Artificial Stimulus Objects

Relative intake of artificial objects and chironomid larvae for five fish. For each condition, 32 trails were conducted. The number of objects found is given within or above the bars. Fisher's exact tests (two-tailed) were used to compare the relative object intake under the different conditions for each fish. Bars, which do not differ significantly ($p > 0.05$) or show constant values, are indicated by the same italic letter. Different italic letters indicate significant differences ($p \leq 0.05$) in intakes. Bar colors indicate the electric colors of the objects (see Figure 2).

respective color space (isoluminant plane only). Here, both axes are opponent color channels [e.g., in 21], which recombine the information from different types of cones [22] via subtraction. Also in *G. petersii*, central subtraction of its two electroreceptor channels is required to extract waveform modulations as counterpart to amplitude modulations. Sensory processing at the receptor level only provides amplitude or amplitude-and-waveform information combined, each of which is transduced by one of the two electroreceptor types of the fish's epidermal sense organs [10, 23, 24]. While both sensory streams project to separate zones in first order central regions, waveform extraction is suggested to take place at a higher brain level [24, 25].

Visual and electric colors are advantageous for object detection in a similar way. Compared to pure intensity contrasts, which can be very ambiguous when lightness changes, color enhances the contrast of relevant objects (e.g., fruits, flowers, etc.) against their backgrounds more reliably and clearly [1, 26]. During active electrolocation, the voltage of the fish's electric emissions varies around the animal [27] and thereby the "electric illumination" of nearby targets. Object-evoked amplitude modulations and contrasts change accordingly [27]. In turn, the electric color of capacitive objects makes, e.g., prey items stick out more robustly and distinctively from resistive backgrounds (soil, sand, stones), which only cause amplitude modulations [9].

Electric colors also render the fish's active electric sense reliable for the identification of relevant objects (prey, other animals, plants). Our recordings revealed that electric colors were remarkably stable, irrespective of an object's size, distance, or position (Figures 2A–2C). We thereby verify and extend on previous simulation [8, 13] and recording [14] results obtained with artificial objects, which suggested electric color as a distance-invariant cue. Without being combined, amplitude or waveform modulations do not provide these qualities mentioned above (Figures 2A and 2B).

Interestingly, horseshoe bats apply a partly reminiscent strategy for identifying prey insects irrespective of position during active

echolocation [28]. To do so, the prey-evoked amplitude and frequency modulations of their acoustic signals are combined. Unlike *G. petersii*, passive electroreceptive animals such as sharks, rays, or platypus [29, 30] rely on only a single electric cue during foraging that can be varied (i.e., attenuated) when prey freezes, slows breathing, or covers its body openings [e.g., 31]. Our behavioral tests (Figures 3 and 4) suggest that *G. petersii* only minimally uses such passive electric information but mainly benefits from the stability of electric color (i.e., color constancy) during prey identification through active electrolocation.

Also in the visual sense, color constancy is a basic requirement for the functionality of color vision in many animals (e.g., bees, fish, monkeys) and in humans [32]. Here, it provides a stable color sensation for different distances (in non-aquatic environments) or positions of an object [33, 34]. To achieve visual color constancy, the brain has to tackle spectral variations caused by changes of the illuminant (e.g., at day or dusk) or by interactions of light and atmospheric particles (e.g., over a larger distance) [33, 34]. Additional compensation is required for variations caused by changes in background reflectance (e.g., when an object is seen against different backgrounds [35]). During active electrolocation, object-to-background interferences also occur [36]. Foraging of actively electrolocating *G. petersii*, however, is only minimally affected by varying backgrounds (i.e., substrates) [18].

The dominant role of active electrolocation during object and especially prey identification might be further explained by another trait of electric color. The electrical properties, which generate the electric colors of natural capacitive objects, depend on their integral cellular and acellular structures [37]. We assume that these, and thus also electric color, cannot be changed easily, e.g., by prey items. In contrast, changes of visual coloration "only" require the manipulation of pigments and thus can serve for adaptive concealment against predators [38]. As mentioned above, also passive electric cues can be masked by prey animals providing bioelectric crypsis [e.g., 31] against passively electrolocating predators (e.g., sharks). Electric color, during active electrolocation, bypasses usual anti-predator behavior of chironomid larvae [e.g., 39] and does not easily allow prey (and other animals) to camouflage their identity or to blend into the background.

Our recording experiments demonstrate that electric colors indicate categories of environmental capacitive objects to *G. petersii*. This is in line with an earlier suggestion [8] that fish might be able to determine and discriminate "families" of capacitive objects by recognizing their individual electric colors. Here, we show that two different electric colors divide insect larvae into primary (chironomids) [17] and secondary prey items (other insect larvae). Accordingly, fish did prefer capacitors with the electric color of chironomids over resistors, which have the electric color of secondary prey (Figure 4).

Because our fish were caught in the wild, we do not know whether these electric-color preferences are innate or were initially learned through sensory experience. However, the fish's quick and almost reflex-like foraging responses to artificial prey items, which also did not change (adapt) throughout the course of the experiments, may suggest an inborn and "hardwired" choice behavior. Without the need of elaborate processing in the brain, the strategy of electric-color perception might be suited best to capture small and inconspicuous insect prey. Similarly in color vision, innate color preferences enable an effective response to relevant food sources, e.g., in various insects, in spiders, or in fish [1, 5–7].

In conclusion, we found that weakly electric fish *G. petersii* employ a color-like cue to identify relevant items such as prey. As steady markers, electric colors designate those targets selectively and reliably. This makes electric-color sensing a critical adaption of the active electric sense to its specific environment and renders it more robust than (passive) electric sensing in other animals (sharks, platypus, etc.). Despite the different physical inputs and neuronal machineries used in vision and active electrolocation, color turns out in both senses as the appropriate percept for enabling crucial, selective, and reliable object recognitions (e.g., during foraging). On a broader scope, the similar computational "goals and strategies" [15] underlying both types of color sensing and resembling aspects of color traits suggest color perception as a sensory concept beyond vision and passive sensing. Beyond biology, our findings might help improve recent biomimetic applications (i.e., technical versions of the active electric sense) used, e.g., for analysis of atherosclerotic plaques in blood vessels [40] or underwater object inspections [e.g., 41].

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- CONTACT FOR REAGENT AND RESOURCE SHARING
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
  - Experimental Animals
- METHOD DETAILS
  - Recordings
  - Behavioral experiments
- QUANTIFICATION AND STATISTICAL ANALYSIS
- DATA AND SOFTWARE AVAILABILITY

SUPPLEMENTAL INFORMATION

Supplemental Information includes one figure and can be found with this article online at https://doi.org/10.1016/j.cub.2018.09.036.

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AUTHOR CONTRIBIUTIONS

Conceptualization, M.G. and G.v.d.E.; Methodology, M.G. and G.v.d.E.; Software, M.G.; Formal Analysis, M.G.; Investigation, M.G., N.S., A.N.H., and S.R.; Resources, G.v.d.E.; Writing – Original Draft, M.G.; Writing – Review & Editing, M.G., G.v.d.E., N.S., A.N.H., and S.R.; Visualization, M.G.; Supervision, M.G. and G.v.d.E.; Project Administration, M.G. and G.v.d.E.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological Samples		
Weakly electric fish	Aquarium Glaser GmbH	https://www.aquariumglaser.de
Other fish	Fressnapf	https://www.fressnapf.de
Chironomid larvae	Fressnapf	https://www.fressnapf.de
Other insect larvae	Local creek (Nette)	N/A
Water plants	Fressnapf	https://www.fressnapf.de
Chemicals, Peptides, and Recombinant Proteins		
Hypnomidat (Etomidat)	JANSSEN	Local pharmacy
Tricoine methansulfonate MS 222	Sigma-Aldrich	https://www.sigmaaldrich.com
Experimental Models: Organisms/Strains		
Gnathonemus petersii	Aquarium Glaser GmbH	https://www.aquariumglaser.de
Software and Algorithms		
SPSS Statistics 24	IBM	https://www.ibm.com/analytics/us/en/technology/spss
LabVIEW 8.2 or higher	National Instruments	http://www.ni.com
Other		
SMD Capacitors/Resistors G0805	YAGEO	https://www.reichelt.com

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Martin Gottwald (martingottwald@uni-bonn.de).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Experimental Animals

Seven wild-caught *Gnathonemus petersii* of unspecified sex and age were used and obtained from a commercial fish dealer. Fish were housed in separate tanks (23 cm × 40 cm × 40 cm) with a 12 h:12 h light:dark cycle. Water conductivity (~100 μS cm^{-1}) and temperature (~27°C) were kept constant. One fish was used for recording experiments. The other six fish attended behavioral experiments. All procedures and methods performed in the recording experiments were approved by the authorities of the State of North Rhine-Westphalia (Landesamt für Natur, Umwelt und Verbraucherschutz Nordrhein-Westfalen, LANUV-NRW), reference number: 84- 02.04.2015.A444. All behavioral experiments were carried out in accordance with the guidelines of German law and with the animal welfare regulations of the University of Bonn.

METHOD DETAILS

Recordings

Amplitude and waveform modulations of insect larvae (prey), fish, electric fish and water plants (see Figure 2 for details) were measured close to the chin appendix of a *G. petersii* (Figure S1A). The chin appendix is considered to be an electroreceptive fovea and is used for object and prey recognition [9]. Prior to recordings, stimulus animals were killed in an Etomidat (2 mg ml^{-1}, Janssen-Cilag) solution (insect larvae) or in an MS 222 (2 g l^{-1}, Acros Organics) solution (fish, electric fish).

The *G. petersii* was narcotized in an Etomidat solution (0.6 mL Etomidat in 1 l of water). It was then fixed onto a plastic holder (9 cm × 1.5 cm × 6 cm) in the center of the experimental tank (28.7 cm × 38.5 cm × 18.8 cm) with cloth strings and wooden sticks (Figure S1A). The tank water (11 l, 99.3 ± 2.6 μS cm^{-1}, 25.6 ± 0.4°C) was mixed with 3.3 ml Ethomidat to maintain anesthesia. Under sedation, the animal discharges its electric organ in the tail at a slow and regular rate. 15 electric signals (so-called 'local electric organ discharges', lEODs) were recorded, 1 mm away from the fish's skin, with a carbon dipole electrode (pole-length: 2 mm, inter-pole-distance: 1 mm) in the presence and the absence of a stimulus object. In doing so, the electrode was placed between the object and the fish skin with its two poles orientated perpendicular to the skin surface (Figure S1A).

The biphasic waveforms of the lEODs (Figures 1 and S1B) were amplified (× 100, custom-built differential amplifier), filtered (band-pass: 1 Hz to 100 kHz) and digitized (sampling rate: 250 kHz, A/D converter PCIe 6341, National Instruments). lEOD amplitude was

defined as peak–to–peak amplitude (PP) of the signal's positive (P) and negative (N) phase and the IEOD waveform was determined by the peak amplitude ratio of the two signal phases (P/N) (Figure S1B). The IEOD amplitude and waveform parameters obtained with and without a stimulus object were each calculated and averaged with a self-designed LabVIEW (Version 8.2, National Instruments) program. The modulation of the IEOD amplitude or waveform was defined as the ratio between the changes produced by the stimulus object and the amplitude or waveform in its absence and then subtracted by one. Amplitude and waveform modulations of animals and plants were recorded for several conditions (different object sizes or distances to the recording electrode).

The modulations of some individuals were also measured close to the side of the head of the *G. petersii*. Here, the electrode was positioned between the eye and the gill opening (Figure S1A).

Small resistors or capacitors (YAGEO Corp.) and self-made carbon or plastic particles (all of equal size: 2 mm × 1.25 mm × 1.25 mm) were recorded close to the fish's fovea. Doing so, we selected artificial stimulus objects that did or did not generate modulations similar to larval prey insects.

Behavioral experiments

Prey identification by *G. petersii* was tested under different foraging conditions. The tanks (23 cm × 40 cm × 40 cm) in which the six fish were housed contained an experimental arena (23 cm × 10 cm). Water conductivity (103 ± 4.7 μS cm^{-1}) and temperature (27.2 ± 1.1°C) were kept constant during experiments.

Different sizes/distances of prey/non-prey items

The experimental arena consisted of a sandbox (20 cm × 10 cm × 3 cm), which was divided into eight feeding areas (2 × 4, with each area sized 5 cm × 5 cm × 3 cm) (Figure S1C). Three *G. petersii* (fish 1-3), which were trained to feed from the sandbox, were tested. Before trials, an opaque plastic divider blocked the access to the sandbox, while a prey- (dead chironomid larva) or non-prey item (plant stem *Hydrocotyle vulgaris,* or metal rod) was buried in one of the areas. Presentation of stimulus objects and selection of feeding areas was pseudorandomized during trials. Burial depth was either 1 or 5 mm. Object size (length) was either large (~15 mm) or small (~8-10 mm). Buried objects did not provide visual cues for their identification. Burying also attenuated possible odors or passive electrolocation cues. A fish had 30 s per trial to search the sandbox for prey. In doing so, fish scanned the sand with their chin appendix (electroreceptive fovea). After detection, fish dug for the object and when also judged as prey, sucked it into the mouth (intake). Digging was therefore chosen as the criterion that fish had found the object and object intake as the criterion that fish had identified the object as prey item. After every second trial, an interim-trial was conducted with a chironomid larva to keep fish motivated.

Artificial objects

Five *G. petersii* (fish 2-6) were tested. Fish were trained to feed from a plastic table (20 cm × 10 cm × 3 cm, Figure S1D). Capacitors and resistors, which evoked similar electric colors as prey (chironomid or other insect larvae) or plastic and carbon particles (non-prey items) were presented (see recordings section). Small, dead chironomid larvae (8.6 ± 1.7 mm length) were used as a control for natural prey. During object placement, the plastic divider restricted access to the feeding table. A stimulus object was placed pseudo-randomly on the table in one of eight position markers (Figure S1D). Stimulus objects were presented in a pseudorandomized order. In each trial, fish had 30 s to electrically probe an object and to suck it in. Trials were conducted at an ambient light level of 113 ± 5.5 lx at which visual object discrimination is no more reliable in *G. petersii* [42]. Stimulus objects were also too small to be visually recognized due to the poor spatial resolution of the fish's grouped retina [9]. Identification of artificial objects was therefore restricted to active electrolocation cues. An object was considered found when a fish had approached it very closely (~1 mm) with its chin appendix or had touched it. Object intake was chosen as the criterion that the fish had identified an artificial object as a prey item. After every third trial, an interim-trial was conducted with a real chironomid larva to maintain motivation of the fish.

QUANTIFICATION AND STATISTICAL ANALYSIS

Statistical analyses of the recording and behavioral data were performed using SPSS (Version 24, IBM Corp.). Statistical significance of differences ($p \leq 0.05$) between electric colors, recorded successively at the fovea and the side of the fish's head, was determined by paired t test (2-tailed) (see Figure 2 for details). All data was normally distributed (Shapiro-Wilk normality test, $p > 0.05$ for all groups). Statistical significance of difference ($p \leq 0.05$) between relative intakes of different stimulus objects by a fish was determined by Exact Fischer test (2-tailed) (see Figures 3 and 4 for details).

DATA AND SOFTWARE AVAILABILITY

Recording and behavioral data are stored on the server of the Zoological Institute/ Department of Neuroethology and can be provided upon request by contracting the Lead Contact, Martin Gottwald (martingottwald@uni-bonn.de).