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RESEARCH ARTICLE

Disembodying the invisible: electrocommunication and social interactions by passive reception of a moving playback signal

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ABSTRACT

Mormyrid weakly electric fish have a special electrosensory modality that allows them to actively sense their environment and to communicate with conspecifics by emitting sequences of electric signals. Electroreception is mediated by different types of dermal electroreceptor organs for active electrolocation and electrocommunication, respectively. During electrocommunication, mormyrids exhibit stereotyped discharge sequences and locomotor patterns, which can be induced by playback of electric signals. This raises the question: what sensory information is required to initiate and sustain social interactions, and which electrosensory pathway mediates such interactions? By experimentally excluding stimuli from vision and the lateral line system, we show that *Mormyrus rume proboscirostris* can rely exclusively on its electrosensory system to track a mobile source of electric communication signals. Detection of electric playback signals induced discharge cessations, followed by double-pulse patterns. The animals tried to interact with the moving signal source and synchronized their discharge activity to the playback. These behaviors were absent in control trials without playback. Silencing the electric organ in some fish did not impair their ability to track the signal source. Silenced fish followed on trajectories similar to those obtained from intact animals, indicating that active electrolocation is no precondition for close-range interactions based on electrocommunication. However, some silenced animals changed their strategy when searching for the stationary playback source, which indicates passive sensing. Social interactions among mormyrids can therefore be induced and mediated by passive reception of electric communication signals without the need for perception of the location of the signal source through other senses.

KEY WORDS: Weakly electric fish, Mormyridae, Passive electroreception, Electrical playback, Sensory systems

INTRODUCTION

Mormyrid weakly electric fish have a multitude of sensory systems at their disposal, which they use to navigate their environment, detect predators and food, and mediate social interactions between individuals. Mormyrids share the ability to passively detect low-frequency electric signals via ampullary receptor organs with a variety of electroreceptive fishes (Kalmijn, 1974; Engelmann et al., 2010). More prominent is their capability to probe their immediate environment by means of self-generated electric organ discharges (EOD) during active electrolocation (von der Emde, 1999). These signals are produced by an electric organ located within the caudal peduncle and generate an instant, three-dimensional dipole field around the fish (Bennett, 1971a). Animals detect their own discharges by means of mormyromast electroreceptor organs (Bell et al., 1989), which are distributed over large areas of the body surface (Harder, 1968; Hollmann et al., 2008). Object-induced local modulations of EOD amplitude and waveform, which are registered by mormyromasts, constitute an electric image that allows the fish to detect and differentiate objects based on their size and shape (von der Emde et al., 2010), as well as material composition (von der Emde, 2006). Active electrolocation is thus used for finding food (von der Emde, 1994; von der Emde and Bleckmann, 1998; Arnegard and Carlson, 2005) and for orientation and navigation in the environment (Cain et al., 1994; Cain and Malwal, 2002; Walton and Moller, 2010; Schumacher et al., 2017b).

Electrocommunication relies on a third electrosensory system with its own electroreceptor organs and brain pathway. Like mormyromasts, knollenorgans are electroreceptors that respond to the high frequencies contained in an EOD, but their input to the central nervous system is inhibited by a centrally evoked corollary discharge each time an animal discharges its own electric organ (Bell and Grant, 1989). Instead, the knollenorgans relay information about the timing of EODs emitted by other electric fish to the brain. Through their knollenorgan pathway, fish can thus detect variations in waveform and inter-discharge interval (IDI) of the signals of nearby conspecifics (Baker et al., 2013). While the EOD waveform mainly conveys information about the identity and status of the sender (Hopkins, 1980; Bass and Hopkins, 1983; Graff and Kramer, 1992; Carlson et al., 2000; Terleph and Moller, 2003; Hanika and Kramer, 2005), immediate changes in IDI distribution enable mormyrids to communicate behavioral states and motivations. Instantaneous discharge frequencies are also linked to the current needs of active electrolocation in a given behavioral context, such as resting, swimming or foraging (Bauer, 1974; Gebhardt et al., 2012a) or the detection and analysis of novel stimuli in the environment (Toerring and Moller, 1984; von der Emde, 1992; Post and von der Emde, 1999). Systematic variations in IDI duration additionally result in specific temporal signal patterns that can encode intentional information (Kramer, 1976; Bratton and Kramer, 1989; Carlson and Hopkins, 2004; Baier and Kramer, 2007), and interactive signaling can lead to synchronization of discharge activity between individuals, which is also likely to play a role during communication (Arnegard and Carlson, 2005; Gebhardt et al., 2012a,b).

Social communication consists not only of detection and decoding of the sender's signal and its content by the receiver, but often aims at initiating physical interactions, which requires the receiver to also determine its spatial relationship to the signal source. Social behaviors in mormyrids are quite versatile and include overt aggression and territorial behavior as well as social

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interactions and shoaling depending on both context and species (Moller, 1976; Gebhardt et al., 2012b; Carlson, 2016). A multitude of context-depending motor patterns and behavioral sequences during social encounters have been described, many of which could be associated with stereotypical displays of electric discharge activity (Bell et al., 1974; Kramer and Bauer, 1976; Wong and Hopkins, 2007), or were shown to depend on the capability to produce EODs (Moller, 1976; Crockett, 1986).

Many fishes are highly vision-dominated animals, as apparent from the innumerable amount of visual displays of postures, markings and coloration during agonistic encounters, mate choice or group integration (Simpson, 1968; Bakker and Milinski, 1993; Denton and Rowe, 1998). Due to their nocturnal lifestyle (Moller et al., 1979), social interactions among mormyrids cannot often rely on their visual system, which is adapted to dim light and turbid water conditions (Landsberger et al., 2008; Kreysing et al., 2012). Although the pulse-type electric signals emitted by mormyrids are well suited to encode information into temporal sequences, they do not provide directional information about the shortest distance towards the position of the signal source, because they exist as electrostatic dipole fields (Hopkins, 2005). Weakly electric fish therefore approach an electric dipole source describing a curvilinear trajectory along the electric field lines of the emitted signal (Schluger and Hopkins, 1987). However, these experiments involved the detection of stationary signal sources and little is known about the relative roles of active and passive electrolocation during close-range encounters between mormyrids when both sender and receiver are in motion. Can social interactions among weakly electric fish in these cases still be mediated by passive reception of electric communication signals alone? Or do mormyrids require input from other sensory modalities as well, to sustain close range interactions between individuals during electrocommunication? These questions can only be addressed by restricting the source of the signal to its 'disembodied' electric signaling properties from the perspective of an electric fish.

Weakly electric *Mormyrus rume* have been shown to follow a mobile dummy fish emitting electrical playback of natural IDI sequences from a shelter into an open area, apparently without relying on visual or motility cues (Donati et al., 2016). Under non-visual conditions, the spatial relationship between the moving dummy and the following fish was affected by the presence of electric playback signals (Worm et al., 2017), raising the question of what sensory systems are actually involved when following another individual. In that study, we hypothesized that mormyrids can rely on the spatial information contained in the electrostatic dipole fields generated by the EODs of a conspecific, and thus are capable of spatially interacting with a moving signal source based on information processed via the knollenorgan pathway during electrocommunication. In the current study, we used a similar design as in Worm et al. (2017) to confront single individuals of *M. rume* with a mobile dummy electrode emitting EOD to entice them out of a shelter and into a testing area. We experimentally excluded all sensory cues from the signal source such as vision, the lateral line system, and eventually also active electrolocation. This approach should render the physical properties of the signal source undetectable for *M. rume* and allowed us to conclude on the significance of passive electroreception via the knollenorgan pathway during interactive social behaviors. We thus disembodied the invisible signal source and tested whether this sufficed to induce normal social following behavior. Our results show that presentation of electric playback signals reliably attracted the tested fish and triggered the emission of stereotypical signaling sequences, which can usually be observed during electrocommunication. Even animals that were deprived of their capability to generate EODs were still able to locate the moving signal source, track its movement throughout the testing area and orient themselves relative to its position during spatial interactions. Thus, passive perception of electrocommunication signals was sufficient to initiate following behavior in *M. rume* and sustained interactions with an otherwise imperceptible signal source.

MATERIALS AND METHODS
Experimental animals
A total of 27 *Mormyrus rume proboscirostris* Boulenger 1898 (abbreviated to *M. rume* throughout the paper) were used during the experiments, all of which were bred in captivity by imitation of rainy season conditions following the method described by Schugardt and Kirschbaum (2004). Animals were kept under tropical conditions and a 12 h:12 h light:dark cycle, with water temperatures around 26°C. Food was provided at least five times a week in the form of defrosted chironomid larvae. All experiments were carried out in accordance with the guidelines of German law and with the animal welfare regulations of the University of Bonn. All procedures and methods were approved by the LANUV NRW (Landesamt für Natur, Umwelt und Verbraucherschutz Nordrhein-Westfalen, reference number: 84-02.04.2015.A444).

In a first set of experiments, 24 *M. rume* with standard lengths between 6.4 and 11.4 cm were used to test the reaction of intact fish to a mobile dummy dipole that was basically reduced to the emitted playback signal (see below). These animals were approximately two years of age at the time of experimentation and of undetermined sex. They were kept as a group in a communal tank, from where they were individually transferred to the experimental tank at least one day prior to testing.

Experimental set-up
The experimental tank had a base area of 200×50 cm and was subdivided into three compartments (Fig. 1): the first compartment (closed area) measured approximately 60 cm in length. It was made inaccessible to the tested fish using a fly screen and contained the inlet and outlet of the water filter, a heater and an aeration device, all of which were switched off during the experiments. The second compartment measured around 50 cm in length and served as a hiding area, which was connected via a 10 cm wide gate to the testing area, which had a length of 90 cm. The floor of both the hiding and testing areas was covered with gravel. Water level was
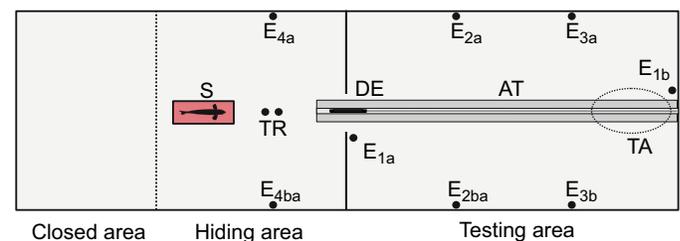

Fig. 1. Experimental set-up. Top view of the experimental set-up (base area: 200×50 cm). Upon registration of electric activity by a pair of trigger electrodes (TR), the mobile dummy electrode (DE) crossed the testing area through an electrically transparent agarose tube (AT) while emitting playback of a natural IDI pattern. Fish that left the shelter (S) and reached the target area (TA) within 15 s of onset of the experiment were defined as following the dummy electrode. Experiments were videotaped by an infrared-sensitive camera and electric activity was recorded by a multielectrode array (E) for further analysis.

maintained at approximately 20 cm. In the testing area, an electrically transparent agarose tube was embedded in the ground, which served as the track for the moving electric dipole source. During all experiments, water temperature and conductivity were kept at 26.0±1°C and 100±5 µS cm^{-1}, respectively.

The agarose tube had a length of 1000 mm and defined the trajectory of the mobile playback electrode inside the third compartment, the testing area. It had a cubic outer cross-section of 55×50 mm and an inner diameter of 15 mm and was made using 20 g l^{-1} Universal Agarose (Seakem LE, Axon Labortechnick, Kaiserslautern, Germany). Water with a conductivity of 100 µS cm^{-1} was used to manufacture the tunnel to ensure electric transparency during the experiments (Heiligenberg, 1973). The tunnel was embedded in the gravel, running in parallel to the longitudinal axis of the tank, through the gate and centrally through the testing area. The upper surface of the tunnel was planar with a final layer of fine white sand (Sansibar Snow; JBL, Neuhofen, Germany) which provided good contrast for subsequent video tracking, but did not cover the surface of the tunnel.

The hiding area was provided with a single shelter made from a 20×5 cm red transparent plastic tube (Bioscape, Castrop-Rauxel, Germany), with the opening directed towards the gate at a distance of 30 cm. The front end of the shelter was endowed with a pair of trigger electrodes. Electric activity of the test fish was amplified differentially (Brownlee Precision model 440, Palo Alto, CA, USA) between these electrodes and was used to generate a transistor–transistor logic (TTL) pulse via a digital oscilloscope (Yokogawa DL1620, Tokyo, Japan) once a certain threshold was passed. This threshold was determined for each fish prior to an experimental session. Its sensitivity was set to trigger the onset of an experiment once the test fish stuck its snout out of the front end of the shelter.

Electrical playback and EOD recordings

A playback dipole was made from a 9 cm plastic rod with a diameter of 8 mm, which was fitted with a pair of carbon electrodes situated at the front and rear ends of the rod. This dummy electrode was placed inside the agarose tunnel and could be dragged at a speed of 0.11 m s^{-1} by a wire through the tunnel using a small DC motor (Modelcraft RB350050-2273R, 12 V/50:1) to which it was connected via a cable linkage and a set of pulleys. The wire also connected the dummy electrode to a stimulus isolator (model 2200, A-M Systems, Carlsborg, WA, USA) that also served as a power source for electrical playback generation.

An electrical playback sequence was generated in MATLAB (version R2013b, The MathWorks Inc., Natick, MA, USA) using a custom-written script to concatenate single EODs to a highly regular, but natural pulse sequence with an average IDI duration of 59±9 ms (mean±s.d.) and a total duration of 14 s. This sequence had previously been recorded during a similar experiment. Template EODs were recorded head-to-tail (Brownlee Precision model 440, high-pass: 1 Hz) from a *M. rume*, digitized at a sampling rate of 50 kHz (CED Power 1401, Cambridge Electronic Design, Cambridge, UK) and averaged from 50 signals using Spike2 (version 5.21, Cambridge Electronic Design). The second positive phase of the EOD (Kramer, 2013) was omitted from the playback signal because it declines 'asymptotically' and arguably contains low-frequency signal components. The output of the assembled playback sequence occurred at 50 kHz via the Spike2 sequencer, a D/A converter (CED Power 1401), a dB attenuator (University of Regensburg, Germany) and the stimulus isolator to the playback electrode inside the agarose tube. The stimulus isolator was also turned on during trials without electrical playback to control for

effects of any low-frequency offsets it may have caused. Signal strength was adjusted to match the EOD amplitude of a living fish of similar size, resulting in maximum signal strength of 118 mV cm^{-1} measured outside the agarose tube.

The EODs of the fish and the dipole were recorded differentially (Brownlee Precision model 440) via a five-channel multi-electrode array (Fig. 1), which included the trigger electrodes in order to account for all signals irrespective of the test fish's position in the tank. Recording electrodes, which consisted of single wires funnelled through 5 mm plastic tubes with a short silver wire (AG-8W, Science Products, Hofheim, Germany) soldered to the tip, were placed closely above the gravel. Waveform data were digitized (CED Power 1401) and recorded to disk using Spike2 software. All experiments were performed under infrared illumination only (850 nm, IR Illuminator model SA1-60-C-IR, Itakka, Wattens, Austria). They were recorded using a Spike2 video recorder and monitored remotely via a pair of infrared-sensitive cameras (DBK 21AF04 FireWire Camera with varifocal T4Z2813CS-IR CCTV lens, The Imaging Source, Bremen, Germany) mounted above the hiding compartment and the testing area to avoid the possibility of visible light influencing the behavior of the tested fish.

Experimental protocol

Single animals were taken from the communal tank and adapted to the experimental tank overnight. To establish basic parameters for random swimming, electric communication patterns and communication distances, trials with the moving electrode were preceded by a set of baseline experiments, during which the playback electrode was placed stationary at the farthest position within the testing area. During these baseline experiments, movement patterns and electric activity of each fish were recorded 10 times with and without playback presentation for 15 s after activation of the trigger by the test fish. The presentation order was pseudo-randomized, allowing no more than three consecutive repetitions of the same condition. For each trial it was noted whether the fish entered the testing area, and whether it subsequently reached the stationary dummy dipole, which was defined by a perimeter criterion (see below).

Following the baseline experiments after a short break, each fish was presented three times with the moving dummy electrode emitting the electric playback sequence and three times with the silent control condition without playback. The dummy dipole arrived at the target positions after 7 s and remained there motionless while continuing to emit electrical playback for another 7 s. Again, the presentation order was pseudo-randomized, allowing no more than two consecutive repetitions of the same condition. Half of the animals were confronted first with the control, and the other half with the playback sequence. Inter-trial intervals of at least 5 min were maintained in between experimental trials. Again, all movement patterns and electrical activity were recorded to disk for 15 s after the fish had activated the trigger.

To investigate a possible influence of active electrolocation for detecting the moving playback electrode, three additional fish (standard length: 10.9–12.9 cm) were subjected to the same experimental protocol with the only difference that the number of trials with the moving electrode was increased to 10 repetitions per condition. After this initial experimental session, these animals were electrically silenced and then tested again 6–8 days later. As after silencing the animals were no longer capable of producing EODs, the start of each experimental trial had to be initiated manually by the experimenter once the test fish stuck its snout out of the front end of the shelter.

Electric silencing was achieved by sectioning the spinal cord directly in front of the electric organ with a needle. Animals were anesthetized with 150 mg l^{-1} MS 222 (Acros Organics, Geel, Belgium) before the procedure. The success of the intervention was verified by an audio monitor (RadioShack mini amplifier-speaker, Tandy, Fort Worth, TX, USA) after the operation, as well as directly before re-testing these animals in the behavioral experiments.

Data analysis

Two criteria were defined to quantify the effectiveness of moving and stationary playback presentations on following behavior, and to distinguish the effect of these treatments from random swimming. For each condition, the proportion of trials, in which the test fish entered the testing area completely within 15 s of onset of the experiment, was determined. For the second criterion, fish had to cross an elliptic perimeter around the dummy dipole at its final position (Fig. 1) with any part of their body. Ellipses were drawn in ImageJ (version 1.46r, National Institutes of Health, USA) with a major axis of 190 mm and a minor axis of 110 mm, defining an area extending about 50 mm around the dipole. All videos were evaluated manually. The relative proportion of trials in which each fish fulfilled this perimeter criterion during all experimental conditions was determined 7 and 15 s after onset of the experiment. Additionally, for both the experimental sessions with the stationary and the moving dummy electrode, fish that had fulfilled the perimeter criterion within 14 s of onset of the experiment at least once during playback presentation and the control condition were selected for further analysis. Of the 24 *M. rume* that were used in these experiments, this was the case in 15 animals for the stationary and 13 animals for the moving condition. For these animals, those trials in which they reached the criterion for the first time were used for more detailed analysis of electric signaling and swimming trajectories.

Spike 2 waveform data from these experiments were converted into time series by marking the occurrence of each EOD in time. Signal sequences of playback and test fish were then separated into individual time series from which IDIs were subsequently calculated. Histograms of the relative occurrence of IDI distributions were calculated for each experimental condition by pooling IDIs into bins of 2 ms duration. IDI sequences were then analysed for communicative signaling patterns, in particular double-pulses and long cessations, as well as discharge synchronizations with the playback sequence.

Double-pulses are signaling sequences involving alternations of long and short IDIs. The minimal requirement for a double-pulse sequence was defined by setting a lower and an upper threshold at 50 and 60 ms, respectively. A double-pulse sequence had to consist of at least five pulses, where IDI1, IDI3 and IDI5 had durations of ≥60 ms, and IDI2 and IDI4 had durations of ≤50 ms. All signals in that sequence were then treated as double-pulses. This analysis was performed automatically using a custom-written MATLAB script.

Long cessations were characterized by the absence of electric signals and were defined as periods of at least 1000 ms without an EOD by the tested fish. Using ImageJ, the distance between the test fish and the dummy electrode was determined within that video frame which was recorded simultaneously with the last EOD before a cessation for each trial involving the stationary playback condition.

Discharge synchronizations were quantified by calculating adaptive cross-correlations between the IDI sequences of the fish and the electrical playback according to the procedure described in Gebhardt et al. (2012b). Maximum correlation values occurring within a 100 ms response time between EODs of the playback sequence and the fish were averaged over the time course of an experimental trial for the moving playback condition (N=24) and the stationary playback condition (N=13). As a control, randomly occurring correlations between the playback and IDI sequences of *M. rume* recorded independently during the moving control condition (N=23) were also calculated.

Detailed swimming trajectories of the fish were obtained by video tracking using Ctrax (Branson et al., 2009) for all trials involving the moving dummy electrode. Video tracking was also performed for the three fish before and after silencing of their electric organs in the trials involving the moving dummy electrode and electrical playback.

All statistical tests were performed in SPSS (version 22.0, IBM, Armonk, NY, USA). Normality of data was assessed by a Shapiro–Wilk test, and parametric or non-parametric tests were used accordingly. Statistical significance was accepted at the α=0.05 level.

Data availability

Recorded data and custom MATLAB routines used for evaluation are stored on the server of the Zoological Institute/Department of Neuroethology and can be provided upon request by the corresponding author.

RESULTS

Attraction of the dummy

Once they detected the electric playback signals, all 24 animals were highly attracted to the dummy dipole and responded with communicative signaling patterns and physical interactions. In a first set of trials featuring the stationary playback electrode, the active space for electrocommunication was determined, and a basic value for explorative behavior into the testing area, as well as for the detection of the dummy dipole based on a perimeter criterion, was established. For the experiments with the stationary dummy dipole, the average ratio of animals entering the testing area was 0.47±0.03 (mean±s.e.m.) during the silent controls compared with 0.50±0.03 during electric playback presentations from the target area. This indicates that the intensity of the playback from the end position of the dipole was not sufficient to recruit animals from the hiding area into the testing area at a rate higher than what would be expected due to normal exploring behavior (paired samples *t*-test, t_{23}=−0.88, P=0.39; Fig. 2A).

Similarly, the fish were not attracted by the moving dummy dipole alone when it did not emit electric playback signals. Median values for the relative number of trials in which animals entered the testing area were 0.50 for the silent stationary and 0.33 for the silent moving control, respectively, and did not differ significantly from each other based on a paired-samples Wilcoxon signed rank test (z=−0.80, P=0.42; Fig. 2B).

Of the 24 *M. rume* participating in these trials, a total of 15 animals reached the perimeter criterion at least once during both the stationary playback experiments and the stationary silent control tests. The latency for reaching the criterion did not differ significantly between the control condition (9.64±0.84 s; mean± s.e.m.) and electrical playback presentation (8.96±1.00 s; paired samples *t*-test, t_{14}=0.47, P=0.64), indicating that the playback signal at the end position was not strong enough to recruit animals reliably from the hiding area to reach the perimeter criterion (Fig. 2C).

This was not the case for the moving conditions, during which 13 animals reached the perimeter criterion at least once during both playback presentation and the silent control condition. Here, the latency for reaching the criterion was significantly longer for the silent controls (8.58±0.78 s) compared with when electrical
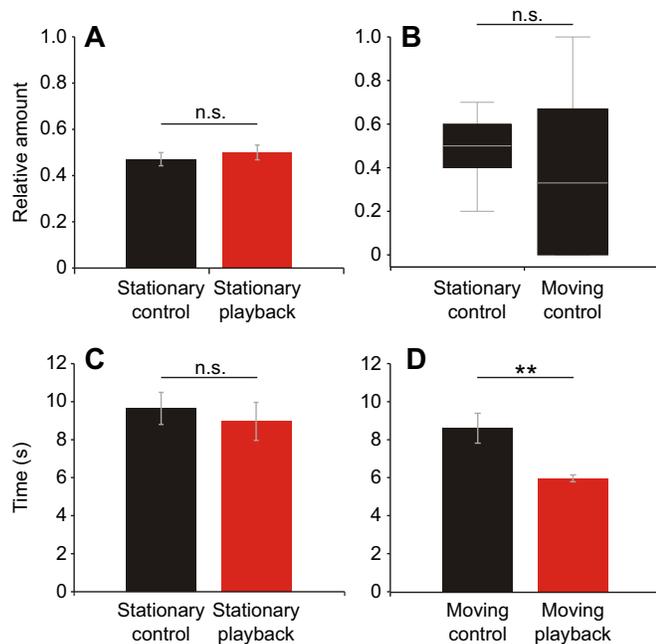
Fig. 2. Influence of experimental condition on attraction. (A) Relative number (mean±s.e.m.) of trials for 24 *Mormyrus rume proboscirostris* where animals entered the testing area during presentation of stationary playback and stationary silent control. (B) Relative proportion of trials where 24 fish entered the testing area during stationary and moving silent controls. Box plots depict medians and quartiles, with whiskers extending to minimum and maximum values. (C) Average time (mean±s.e.m.) when 15 *M. rume* reached the perimeter criterion for the first time during stationary playback presentation and stationary silent control. (D) Average time when 13 *M. rume* reached the perimeter criterion for the first time during moving playback presentation and moving silent control. **P≤0.01; n.s., not significant.

playback was emitted (5.96±0.18 s; paired samples *t*-test, t_{12}=3.73, *P*=0.003). In this case, the fish reliably reached the criterion as soon as the dummy electrode stopped at its target position, indicated by the smaller error bars compared with the control (Fig. 2D).

To determine the recruitment efficiency of the mobile dummy dipole, the relative number of trials where 24 *M. rume* had reached the perimeter criterion was determined 7 and 15 s after onset of an experimental trial for all experimental conditions (Fig. 3). Most individuals had already fulfilled the criterion after 7 s in response to the moving playback condition (median=1), whereas very few

animals reached the criterion at that time during all other conditions (median values: 0.0–0.1; Friedman test for repeated measures, χ^2_3=56.79, *P*<0.001; *post hoc* tests, *P*<0.001 for all comparisons with the moving playback condition; Fig. 3A). After 15 s, *M. rume* had followed the mobile dipole almost without exception when it emitted electrical playback (median=1), still differing significantly from all other conditions (Friedman test for repeated measures χ^2_3=52.49, *P*<0.001; *post hoc* tests, *P*≤0.001 for all comparisons with the moving playback condition; Fig. 3B). By that time, the stationary playback condition (median=0.35) had, however, also attracted test fish at a significantly higher rate than the stationary control (median=0.1; *post hoc* comparison, *P*=0.04). The playback dipole was therefore within the active space of the sheltered fish when placed at the starting position, but at the target position was only detected if animals were already swimming in the testing area.

Electric signaling and locomotor behavior
Signaling sequences by *M. rume* in response to electrical playback were highly stereotypical. IDI distributions during the silent control conditions were irregular, with a high variability resulting in wide distributions and modes at relatively long IDIs between 71 ms (moving control) and 55 ms (stationary control; see upper panels of Fig. 4A,B). In contrast, signaling sequences emitted in response to electrical playback were characterized by long cessations, double-pulse patterns and regularizations at higher frequencies (see lower panels of Fig. 4A,B). Typical IDI sequence of *M. rume* in response to the moving playback dipole (Fig. 4A, lower panel) started with a cessation upon detection of the electric playback signals, continued with a short sequence of double-pulses and ended with a regularized discharge sequence, synchronized at approximately the same frequency as the playback sequence. This pattern is reflected in the overall histogram on the right-hand side of the lower panel of Fig. 4A, with a narrower IDI distribution around the mode at 59 ms, and additional modes at 71 and 27 ms, representing the alternation of long and short intervals during double-pulse sequences, compared with the histogram of the moving control condition in the panel above.

Fundamentally different reactions based on whether the moving dummy dipole emitted electrical playback were also observed in the swimming trajectories of *M. rume* (Fig. 4C). During the electric silent control condition (upper panel), swimming trajectories dispersed throughout the testing area with a tendency of the fish to swim along the walls of the tank, but without obvious relation to the trajectory of the moving dummy dipole. In contrast, fish stuck
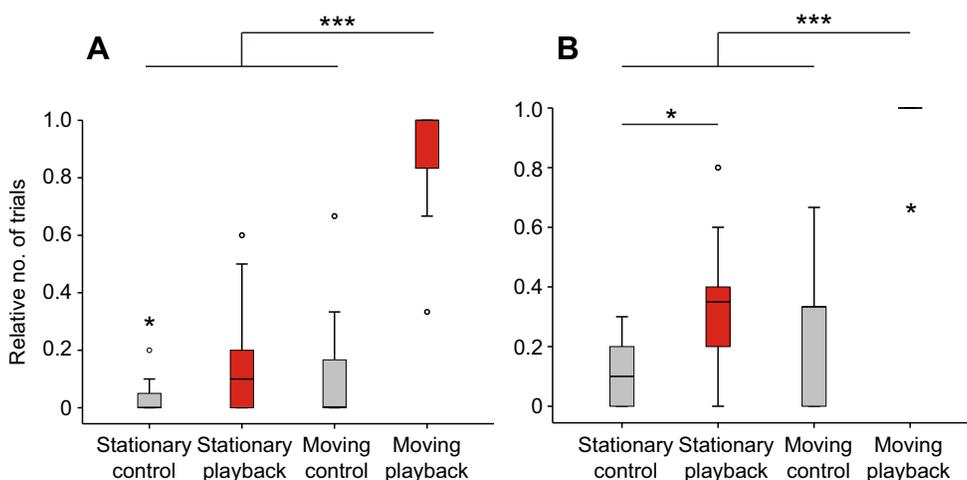

Fig. 3. Recruitment efficiency. Relative number of trials for 24 *M. rume* where animals reached the perimeter criterion within 7 s (A) and 15 s (B) of onset of the experiment during the presentation of stationary and moving playbacks and controls. *P≤0.05, ***P≤0.001.
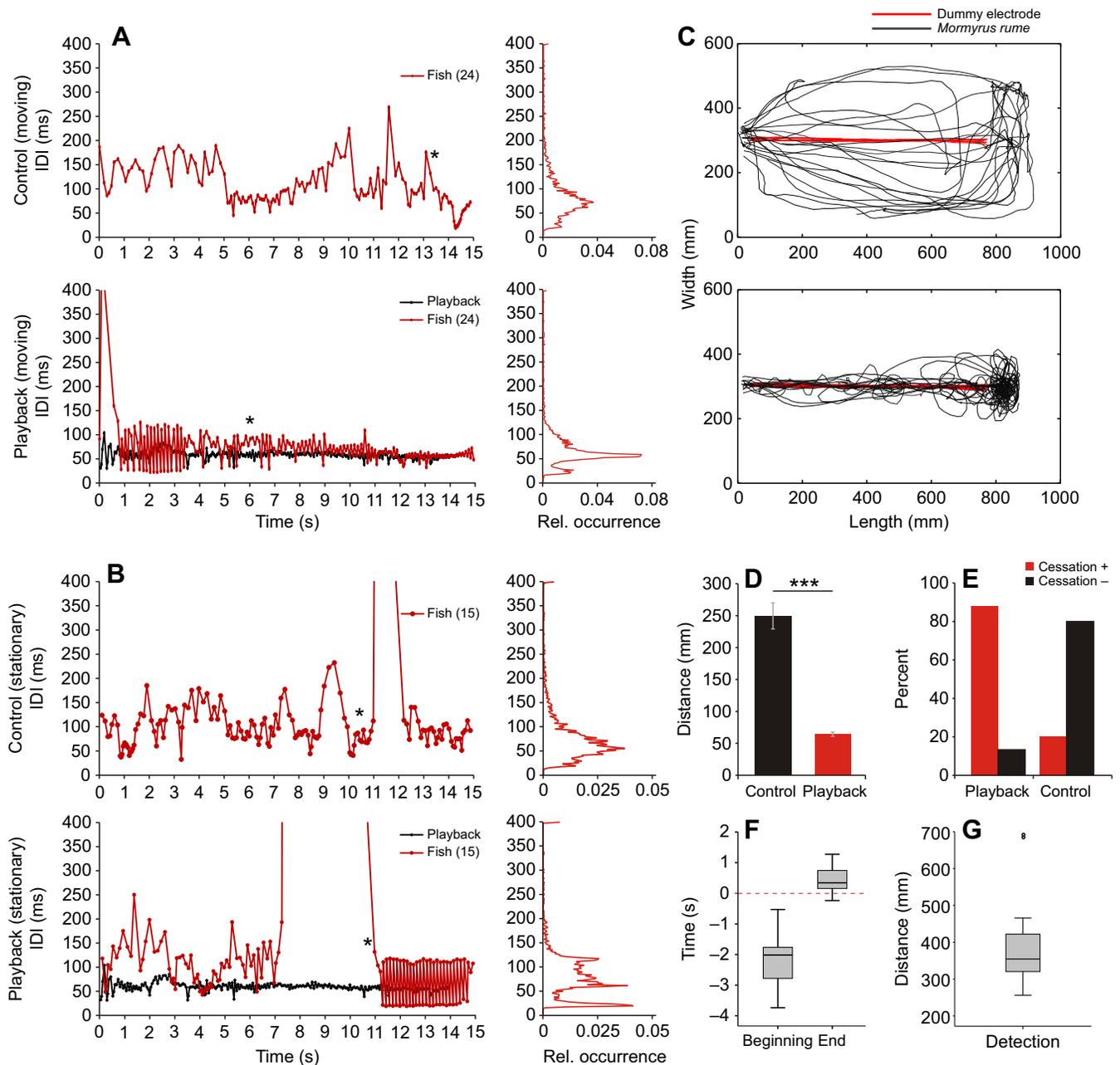
Fig. 4. Electric signaling and motor behavior patterns. Exemplary IDI sequences of individual *M. rume* reaching the target area within 15 s of onset of the experiment during presentation of electrical playback (lower panel) and the silent control (upper panel) for the moving (A) and the stationary (B) dummy electrode. Asterisks mark the points in time when the perimeter criterion was met. Histograms to the right represent pooled IDIs of $N=13$ (A) and $N=15$ (B) fish that reached the perimeter criterion during the four experimental conditions. (C) Swimming trajectories of $N=13$ fish (black) that followed the mobile dummy electrode (red) emitting electrical playback (lower panel) and during silent controls (upper panel). (D) Average (mean±s.e.m.) of the mean distance between test fish and dummy electrode for the trajectories depicted in C. ***$P \leq 0.001$. (E) Relative number of IDI sequences featuring at least one discharge cessation ≥ 1000 ms during experiments with the stationary dummy electrode; pairwise comparisons for 15 individuals that had reached the perimeter criterion during playback presentation and the control condition. (F) Time differences for beginning and end of discharge cessations ≥ 1000 ms in relation to the point in time where the perimeter criterion was met (dotted red line) shown by 20 individuals in response to stationary playback presentation. (G) Distance between test fish and dummy electrode at the time of the last EOD before the discharge cessations shown in F.

close to the dummy trajectory in case of electric playback presentation (lower panel), showed multiple instances of circling and trajectory cut-off, and did not leave the dummy electrode after it reached its target destination, as they would do during the silent control condition. Instead, animals kept searching the surface of the agarose tube at the front end of the dummy electrode until the

playback stopped. This difference in following behavior is reflected in a highly significant difference in average distances between *M. rume* and the dummy dipole during the two conditions (paired samples *t*-test, $t_{12}=8.49$, $P<0.001$; Fig. 4D). With an average distance of 250±20 mm (mean±s.e.m.), *M. rume* spent most of the time out of reach for active electrolocation during silent controls,
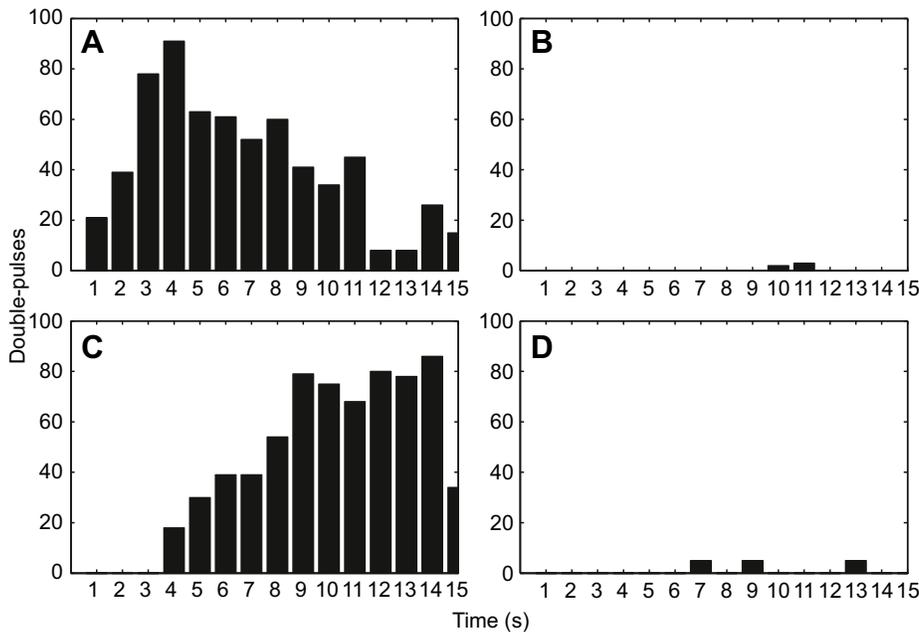
Fig. 5. Double-pulse patterns. Total number of double-pulses displayed over the time course of the experiments by 13 individuals in response to the moving dummy electrode emitting electrical playback (A) and during silent controls (B), and for 15 individuals that reached the perimeter criterion during the experiments with the stationary dummy electrode in response to electrical playback (C) and control (D).

whereas the average distance of 64±3 mm during electric playback presentation was well within the range of active electrolocation (von der Emde, 1999).

Typical IDI sequences in response to the stationary playback condition (Fig. 4B, lower panel) started with the same irregular discharge pattern as observed during the silent control condition (upper panel). Upon detection of the electric playback stimulus, *M. rume* usually responded with a long cessation of up to several seconds, directly followed by a highly regular double-pulse pattern, which is reflected by additional modes at 19 and 117 ms in the overall IDI histogram. The onset of the double-pulse pattern usually occurred directly after the test fish had crossed the perimeter criterion (asterisk in the lower panel of Fig. 4B). Long cessations occurred with 87.7% significantly more often during the playback trials compared with the control trials with only 20% (exact McNemar's test *P*=0.002; Fig. 4E). An evaluation of onset and offset times of long cessations during playback trials (Fig. 4F) demonstrated that long cessations always occurred before the fish crossed the perimeter criterion (median=−2.02 s) and usually stopped shortly thereafter (median=0.34 s). The median distance between *M. rume* and the dummy dipole where 20 animals first responded to the detection of the playback signal with a long cessation, was 355 mm (Fig. 4G). *Mormyrus rume proboscirostris* thus marked the outer limit of the playback's active space with the onset of a long cessation. It then approached the signal source silently and started to discharge double-pulse patterns when it was near it. Double-pulses were only produced in response to electrical playback (Fig. 5A,C). They were virtually absent during the control conditions (Fig. 5B,D) and were not displayed prior to long cessations during stationary playback presentation (Fig. 5C), suggesting that *M. rume* attempted to interact socially with the discharging dummy dipole.

Discharge synchronizations of *M. rume* to the electric playback sequence were frequently observed in response to the moving playback condition (Fig. 6). In contrast, during the stationary playback condition, correlations did not exceed those calculated for an independently recorded IDI sequence, suggesting that detection and initial approach of a stationary conspecific are not associated with interactive signaling in *M. rume*.

Silenced fish

To determine the importance of active electrolocation during social interactions, three additional animals were tested before and after silencing of their electric organs. When the moving dummy electrode produced electrical playback, all animals reached the perimeter criterion in 10 out of 10 trials both before and after surgery. This was in all cases significantly more often than during the silent control condition (Fisher's exact test, α=0.05; Fig. 7). Animals did not seem to behave differently during the post-surgery trials and were similarly active as before the intervention. While following, silenced *M. rume* remained close to the moving dummy electrode and displayed the same type of circling behavior previously observed in intact fish, even though they could not use their active electrolocation system. Exemplary
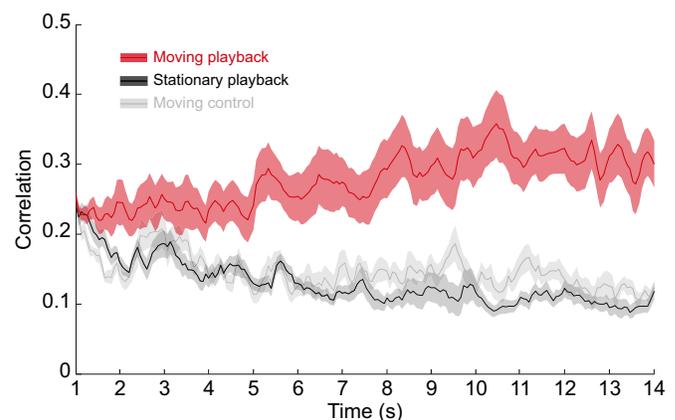

Fig. 6. Signaling interactions of *M. rume* with the playback sequence. Averaged maximum cross-correlation coefficients for a 100 ms response time window over the time course of an experimental trial. Correlations represent synchronization of the test fish's signaling sequence to the electrical playback during the experiments with the moving playback (red), the stationary playback (black) and an independently recorded control using the signals emitted by the fish during the moving control condition (gray). Shaded areas represent the standard error of the mean.
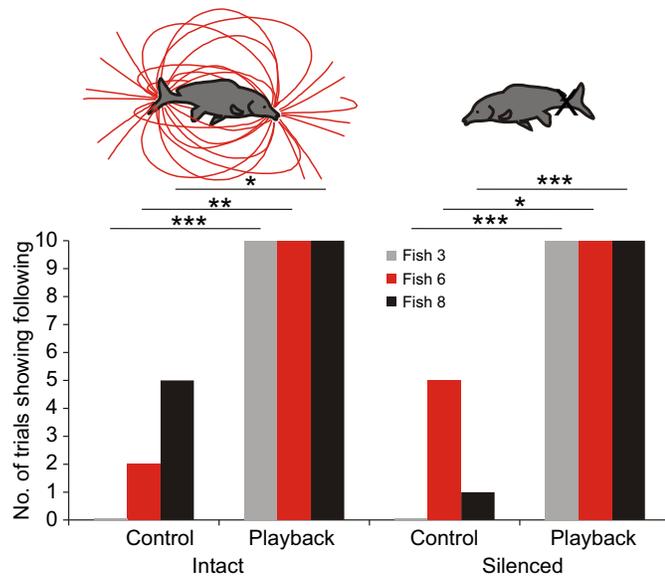
Fig. 7. Comparison of following behavior between intact and electric silenced fish. Number of trials out of 10 for three fish reaching the target area during playback presentation and controls both before and after silencing of their electric organs. Fish follow significantly more often during playback presentation, independent of the functionality of their active electrolocation system. Scores differ significantly based on Fisher's exact test (α=0.05). *$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$.

swimming trajectories of fish number 6 are shown on the left-hand side of Fig. 8. This demonstrates that the fish do not require active electrolocation in order to locate the physical source of a communication signal and to determine their position relative to the signaler. However, once the playback electrode stopped moving but continued emitting electrical playback, intact fish vigorously tried to reach the positive electrode of the dummy dipole (Fig. 8, upper right panel), whereas swimming trajectories after silencing of the electric organ described a symmetrical, curvilinear path (Fig. 8, lower right panel), which would be expected if fish followed the field lines along the dipole source. This distinction in searching strategies was observed in fish numbers 3 and 6, whereas fish number 8 employed the latter strategy both before and after surgery
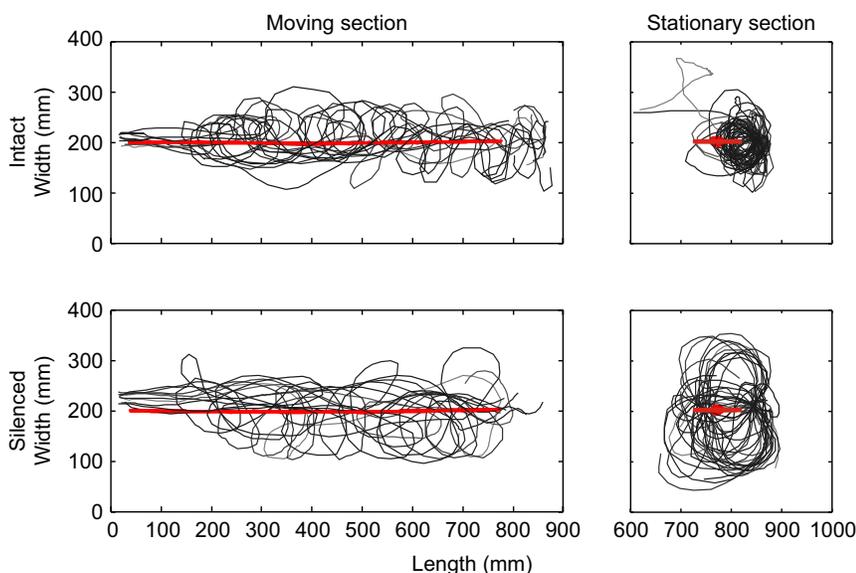
(data not shown), suggesting that knollenorgans play the major role in spatial inter-relations between socially interacting mormyrids.

DISCUSSION

Like most animals, mormyrids use multiple sensory systems synergistically to perceive their environment, and the loss of a particular modality may be compensated for by a different sense to accomplish a specific goal (von der Emde and Bleckmann, 1998; Rojas and Moller, 2002; Schumacher et al., 2016, 2017a). In our experiments, the behavior of *M. rume* when following the disembodied dummy electrode moving along the ground closely resembled the behavior of single *M. rume* following an EOD-emitting fish replica moving through the water (Worm et al., 2017). In both cases the following fish moved at comparable distances from the dummy (Fig. 4) and communicated with it electrically by producing double-pulses (Fig. 5) and synchronizing their EODs to the electrical playback sequence (Fig. 6). By experimentally excluding all sensory cues mediated through vision, the lateral line system and active electrolocation, we demonstrated that only passive electroreception of EODs, probably mediated through the knollenorgan pathway, is sufficient to initiate and perpetuate following behavior and evoke electric signaling typical for electrocommunication in *M. rume*.

Based on electrical playback of natural EOD sequences, the fish in our experiments followed a mobile dummy dipole from a shelter into an open area and to a final position, which was outside the communication distance from that shelter under non-visual conditions. The active space of the playback signal was pre-determined in control trials with a stationary playback source, using the onset of long discharge cessations as a means to define the outer limit where fish reacted to the signal. Animals then silently approached the dummy electrode and subsequently resumed discharge activity by displaying a double-pulse pattern that was only observed in response to electrical playback. These behavioral sequences were very similar to those observed by Moller et al. (1989) in *Brienomyrus niger*, another pulse-type weakly electric mormyrid. Taken together, the combination of discharge cessations and double-pulse patterns clearly demonstrates that live fish attempted to interact socially with the electrically active dummy dipole and engaged in electrocommunication.

Visual guidance during following behavior was excluded by performing all experiments under infrared illumination only, which

Fig. 8. Swimming trajectories before and after electric silencing. Exemplary depiction of 10 swimming trajectories (black) in response to the moving dummy electrode emitting electric playback. Tests were performed before (upper panel) and after (lower panel) silencing the electric organ of fish number 6. Trajectories are split between the first half of the trial, where the dummy electrode was moving, and the second half, where it remained motionless in the target area. Dummy trajectories are shown in red. On the right-hand side, the size of the dummy electrode is indicated by a red bar.

is invisible to the fish (Ciali et al., 1997). Under these non-visual conditions, the fish could, in principle, use either active electrolocation or the mechanosensory lateral line system (Walton and Moller, 2010) to follow a moving object. In the present study, lateral line stimuli were ruled out by moving the playback dipole inside an electrically transparent agarose tube. Active electrolocation is a close-range sensory system that allows weakly electric fish to detect objects up to a distance of approximately one body length, but discrimination performance rapidly drops at distances greater than 4 cm in *Gnathonemus petersii* (von der Emde et al., 2010; Fechler and von der Emde, 2013) and probably at similar distances in *M. rume*. Given the distance of 30 cm between the shelter and the gate, it is unlikely that *M. rume* detected the moving electrode by active electrolocation from within the shelter. The following distance under the electric playback condition was, however, well within that detection range. Active electrolocation could therefore have been employed during close-range interactions in all experiments with intact fish. The significance of active electrolocation for interactive behaviors in *M. rume* was controlled for by comparing three animals before and after surgically silencing their electric organs, making it impossible for them to use active electrolocation. The silenced animals showed the same tendency to follow the mobile dipole as before the intervention. They also showed the same motivation to interact with the moving dummy by circling around it, a behavior never observed in response to the silent controls. Although active electrolocation might in principle be used synergistically with passive electric sensing during close-range encounters between weakly electric fishes, our results demonstrate that active electrolocation is not required to track and interact with a moving signal source mimicking a swimming conspecific. Hence fish only require the information contained in the electric fields generated by a conspecific's EODs to position themselves with respect to the signaler during close-range interactions.

A functional electric organ was also no precondition for the searching behavior that the fish displayed once the moving electrode had come to a stop but continued producing electrical playback. However, two out of three animals changed their searching strategy after silencing (the third animal had used this strategy already before silencing). Instead of probing for the positive pole of the dipole, which represents the rostral part of a *M. rume* producing an EOD, they circled the dummy dipole along curvilinear trajectories. These would be expected if animals orient themselves along the current lines of the electric dipole field established during EOD emission. The application of such a strategy for approaching a signaling conspecific from outside the range of active electrolocation was demonstrated by Schluger and Hopkins (1987) for the mormyrid *Brienomyrus brachyistius*. This behavioral response was proposed to be mediated through the directional sensitivity of knollenorgan electroreceptors by analogy to similar behaviors of the gymnotiform weakly electric fish *Hypopomus*, which possesses functionally similar time coding tuberous electroreceptor organs with directional sensitivity characteristics (Yager and Hopkins, 1993).

As other senses could not have mediated recruitment from the shelter and active electrolocation was apparently not essential for following the moving dipole, we propose that it was passive electroreception of the electric signals of the dummy dipole, essentially mediated through the knollenorgan system, which effectuated these behaviors. However, ampullary receptor organs can also be used for passive electroreception in weakly electric fish (Engelmann et al., 2010). Due to the experimental design, a significant contribution of the low-frequency ampullary receptor system to the recruitment of the fish from the hiding area is not very

likely, because animals did not follow in the absence of high-frequency EOD signals. However, during following behavior, a combined use of ampullary receptor organs and knollenorgans cannot be completely ruled out. It is, however, not very likely, as ampullary receptors are tuned to low frequencies of <10 Hz (Engelmann et al., 2010), whereas knollenorgans are broadly tuned to the higher frequencies contained in the species-specific EODs (Hopkins, 1981) that were used for playback in this study. It was shown by Bell and Russell (1978) that in *G. petersii* ampullary receptor organs do not respond to EOD-like biphasic positive–negative signals with phases of equal amplitudes. Thus if ampullary receptors are involved, they would have to respond to the low-frequency component of the playback EODs used in our experiments, which had, however, a significantly lower amplitude than the high-frequency components. An involvement of mormyromast electroreceptor organs in mediating the observed behavior cannot be ruled out completely, but is also rather unlikely. The sensory threshold of mormyromasts is approximately one order of magnitude higher compared with that of the knollenorgans (Bennett, 1971b). This probably makes the mormyromasts not sensitive enough for the perception of the dummy's playback EODs. Afferent electrosensory input from mormyromasts is enhanced by a corollary discharge at the level of the electrosensory lateral line lobe in the hindbrain, which makes the system most sensitive only when the fish produce their own EODs during active electrolocation (Bell and Maler, 2005).

The conditions presented in this experiment were highly artificial and may have resulted in mismatched sensory information that would not normally be encountered in a natural situation. Although vision has traditionally been considered to be of minor importance due to their nocturnal lifestyle and reduced neuronal correlates in the visual system (Lázár et al., 1984), mormyrids are in principle capable of performing visual tasks (Schuster and Amtsfeld, 2002; Schumacher et al., 2016, 2017a). A loss of vision under dim-light conditions reduced group cohesion in *G. petersii* (Moller et al., 1982), indicating a contribution of vision to social behaviors. However, imitation of visual appearance and motility patterns by a mobile fish dummy had no noteworthy effect recruiting individual *M. rume* from a sheltered area, when compared with playback of electric signaling sequences (Donati et al., 2016), supporting the notion that electroreception is the dominant modality when it comes to social interactions. In a previous study (Worm et al., 2017), *M. rume* also followed a mobile dummy fish, which did not emit any electrical playback, even in complete darkness. Swimming trajectories obtained from these experiments suggested an involvement of the lateral line in following behavior, as they closely reproduced the swimming path of the mobile dummy fish. Path-following behavior based on lateral line information has previously been described in piscivorous catfish tracking their prey (Pohlmann et al., 2001). In *M. rume*, however, such path-following behavior was mainly observed in the absence of electric playback signals, whereas following behavior in response to electrical playback caused a shift of swimming trajectories to a more lateral position in relation to the dummy (Worm et al., 2017). This supports our hypothesis that passive electroreception by knollenorgans constitutes a major determinant of spacing during social interactions in *M. rume*.

The importance of active electrolocation for detection and characterization of animate and inanimate objects is well established. Whether mormyrids make use of active electrolocation during intraspecific interactions has rarely been addressed. Evidence that mormyrids might be capable of recognizing conspecifics by

active electrolocation comes from the observations by Moller et al. (1982), who found blind *G. petersii* to be still attracted by electrically silent conspecifics. Terleph (2004) suggested that regularized discharge patterns during parallel line-ups could have been ritualized into a communication signal from mutual size estimation during sequential assessment between opponents (Enquist and Leimar, 1983). Insights from modeling active and passive electric images in the gymnotid *Gymnotus omarorum* suggest that both active and passive electroreception could be used during assessment of an opponent, but passive information is more likely to trigger aggressive interactions (Pedraja et al., 2016). The notion that information from passive electroreception serves in triggering following behavior and social interactions in mormyrids is also supported by the experiments with *M. rume* presented in this paper.

In conclusion, it is suggested that passive location via the knollenorgan pathway serves in mediating communication with respect to detecting EOD waveform differences and variations in IDI sequences. The evidence presented in this study supports the hypothesis that this sensory pathway is also used to mediate spatial interactions between individuals, where it is sufficient, although not necessarily exclusively employed, during close-range encounters between mormyrid weakly electric fish.

Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: M.W., G.v.d.E.; Methodology: M.W., G.v.d.E.; Software: M.W.; Validation: M.W., G.v.d.E.; Formal analysis: M.W.; Investigation: M.W.; Resources: F.K., G.v.d.E.; Writing - original draft: M.W.; Writing - review & editing: F.K., G.v.d.E.; Visualization: M.W.; Supervision: G.v.d.E.; Project administration: M.W., G.v.d.E.; Funding acquisition: G.v.d.E.

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