Electric pulse characteristics can enable species recognition in African weakly electric fish species

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Communication is key to a wide variety of animal behaviours and multiple modalities are often involved in this exchange of information from sender to receiver. The communication of African weakly electric fish, however, is thought to be predominantly unimodal and is mediated by their electric sense, in which species-specific electric organ discharges (EODs) are generated in a context-dependent and thus variable sequence of pulse intervals (SPI). While the primary function of the electric sense is considered to be electrolocation, both of its components likely carry information regarding identity of the sender. However, a clear understanding of their contribution to species recognition is incomplete. We therefore analysed these two electrocommunication components (EOD waveform and SPI statistics) in two sympatric mormyrid Campylomormyrus species. In a set of five playback conditions, we further investigated which components may drive interspecific recognition and discrimination. While we found that both electrocommunication components are species-specific, the cues necessary for species recognition differ between the two species studied. While the EOD waveform and SPI were both necessary and sufficient for species recognition in C. compressirostris males, C. tamandua males apparently utilize other, non-electric modalities. Mapped onto a recent phylogeny, our results suggest that discrimination by electric cues alone may be an apomorphic trait evolved during a recent radiation in this taxon.

Communication signals that convey sex and species identity from a sender to a receiver are vital to intra- and interspecific recognition and discrimination, often driving reproductive and behavioural isolation.1–3. Understanding the communication mechanisms responsible for species recognition is therefore of importance for our understanding of both speciation and hybridization events.4

African weakly electric fish communicate by means of a pulse-like electric organ discharge (EOD) generated by a specialized electric organ situated in the caudal peduncle of adult fish. This form of communication, termed electrocommunication, is of particular interest for communication studies because these electric signals can be reliably recorded under natural conditions, as well as be reproduced and manipulated in experimental settings.

Two major components of mormyrid electrocommunication are thought to carry information – the EOD and the temporal pattern in which EODs are emitted, i.e. the sequence of inter-pulse-intervals (sequence pulse interval, SPI). The EOD waveform is species-specific, and the duration, number, and polarity of phases in the discharge are determined by the genetic (e.g., expression pattern of ion channels) and morphological (e.g., histology of electrocytes) structure of the electric organ. Electrolocation is generally considered the primary function of the electric discharges. Given the intraspecies stability but notable interspecies variation in the EOD waveform, numerous studies have suggested its additional importance in mate selection and species recognition. In contrast, the SPI is a volitional component and varies within an individual depending on behavioural context (reviewed in ref.14,15). Changes in the SPI in mormyrid fish have been correlated with, for

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example, different swimming patterns and feeding behaviours16–18, in response to external electrical stimulation19, aggressive and agonistic interactions20–22, courtship displays23,24, and solving sensory tasks25–28. A wide range of SPI patterns observed at short timescales (e.g., bursts, cessations, and/or regularizations of approximately 20 inter-pulse-intervals) have also been defined and linked to specific behavioural contexts14,22.

Notwithstanding this large body of research addressing numerous aspects of mormyrid electrocommunication, a clear understanding of the contribution of the two major electrocommunication components (EOD waveform and SPI) for species recognition has not yet been achieved (but see ref.23 for experiments with the sound producing mormyrid Pollimyrus isidori). In this study, we therefore investigate the contributions of these components in two African weakly electric fish species, Campylomormyrus compressirostris and Campylomormyrus tamandua.

Campylomormyrus species are endemic to the river systems of the Congo, Niger, Chad, Shari, Zaïre, and Volta, and both C. compressirostris and C. tamandua occur in sympathy in the Congo Basin26,29. While most morphological divergence between these two species is confined to the snout, the EOD waveforms differ significantly26,30. The biphasic C. compressirostris EOD waveform is characterized by a short, head-positive peak followed by a second head–negative phase with an average duration of 164 μs. The EOD waveform of C. tamandua, in contrast, is triphasic with an initial head–negative pre-phase of low amplitude followed by a head-positive phase and a final head-negative phase. The EOD has an average total duration of 316 μs (Fig. 1a). Neither species displays a sexually dimorphic EOD waveform3.

Previous research on C. compressirostris and C. tamandua suggests that males may mediate species recognition and pre-zygotic reproductive isolation11. It is, however, as of yet unknown which components of the electrocommunication signal are necessary for discrimination or how the EOD and SPI components interact for successful species recognition. In the current study, we therefore investigated SPIs of C. compressirostris and C. tamandua individuals. In contrast to the stereotypic SPI patterns that have been successfully defined at short timescales14,27, our aim was to investigate SPI statistics at longer timescales and determine if (1) these statistics differ between species and if so, (2) if species can recognize and distinguish between these differences. In playback experiments, we further tested the behavioural relevance and contribution of each of the electrocommunication components (EOD waveform vs SPI) for species recognition. Our findings establish that not only the EOD waveform but also the SPI statistics differ significantly between these two species, but that those components responsible for species recognition and discrimination vary depending on species.

Results

SPI statistics. To establish possible species and sex differences in SPI statistics during electrocommunication, 29 SPI trains were recorded from unrestrained, isolated C. compressirostris (male n = 13, female n = 4) and C. tamandua (male n = 10, female = 2) individuals during the resting phase, i.e. during the day. Six additional SPI trains were recorded from unrestrained, isolated female C. compressirostris (n = 4) and female C. tamandua (n = 2) during the active phase, i.e. at night. A segment (time span: 1 second) of a resting phase SPI for each species and sex, where each vertical line represents a generated EOD, is shown in Fig. 1a. From two individuals, three 30-minute SPI trains were recorded on separate dates to show individual variation in SPI statistics; a summary of these results is provided in the Supplementary Information Table S1.

A visual analysis of the SPI patterns from C. compressirostris individuals suggests that during the resting phase, inter-pulse-intervals follow trends, such as cycles of bursts or periods of highly variable inter-pulse-intervals (IPIs; cf. formula 1 in methods). In C. compressirostris individuals, bursts were often followed by short periods of regularized IPI sequences. C. tamandua individuals recorded during the resting phase displayed a broad range of intervals and produced notably fewer bursts than C. compressirostris. For the SPI trains recorded during the active phase, less variation in the IPI was observed in both species (Supplementary Information Fig. S1).

From the resting phase SPI recordings, EOD interval histograms were produced for each species and sex to visualize absolute changes in SPI distributions. For both male and female C. compressirostris individuals, the histograms were bimodal with prominent peaks at 14 and 23 milliseconds, respectively (Fig. 1b,c). In contrast, the resting phase SPIs of C. tamandua individuals were broadband, with intervals occurring at a relatively similar probability between 25 and 150 milliseconds. Clear predominant modes like those seen in C. compressirostris were not consistently apparent across C. tamandua individuals, but the comparison of individual histograms suggests that an alternating activity pattern with transitions between long and short intervals might occur (Fig. 1d,e; for details see Supplementary Information Fig. S2).

Given potential species-specific differences in the IPIs, the 29 resting phase SPIs were further analysed using a principle component analysis (PCA). Five variables were extracted from each individual SPI train: (1) the total number of EODs produced in the 120-second sequence, (2) the mode inter-pulse-interval (i.e. the most frequent EOD interval), (3 & 4) the range (i.e. longest and shortest interval between two adjacent EODs), and (5) the number of runs, as derived from the runs test (please see Table 1 and the Methods for more detailed information). First, to identify those variables that may explain variability between the two species’ SPIs, sex was ignored and the C. compressirostris and C. tamandua species were compared. The two species form distinct clusters and are divided primarily along PC1 (Fig. 2a). Accounting for 71.7% of variance between species, PC1 is loaded mainly with the total number of EODs (loading: −0.517) and the predominant inter-pulse-interval (loading: 0.492). Downstream analysis shows that C. tamandua individuals did produce significantly fewer EODs in the 120-second recording period than C. compressirostris (two sample t-test; p < 0.001). Second, to identify any sex differences in the SPIs, we performed a subsequent, within-species PCA. The male and female C. compressirostris SPIs show a weak but insignificant division along PC2, loaded almost exclusively with the recorded range (i.e. the largest inter-pulse-interval for a given individual) (loading: 0.992) (Fig. 2b). Given that only two SPIs could be recorded from C. tamandua females, a statistical comparison across sex was not possible within this species.
A Pearson correlation matrix and probability values for each pair of variables is provided in the Supplementary Information Table S2.

Under the assumption that the SPI component of the electric activity contains information for a receiver, we calculated serial correlations (SC) of the SPI trains to test if the sequential order of emitted EODs is influenced by memory effects (i.e. a dependency of a given EOD interval and its past) or if EOD emission is a renewal process (i.e. EOD intervals occur randomly). For all natural (recorded and unaltered) SPIs, we found serial correlations that exceeded chance level (at a type I error rate of $p = 0.01$) and could extend up to approximately 100 inter-pulse-intervals (IPIs; Fig. 3a–d). In contrast, the artificial (scrambled) SPIs are a renewal process, with the serial correlation never increasing above or decreasing below chance level (at a type I error rate of $p = 0.01$; Fig. 3e). We also used the median IPI to calculate the duration of SC for each individual. These differed between species and were significantly smaller for *C. compressirostris* than for *C. tamandua* in resting phase SPIs (Fig. 3f; Kruskal-Wallis test; $p = 0.008$). The same trend was evident for SPIs recorded from active fish, but the difference was not statistically significant (Fig. 3f; Kruskal-Wallis test; $p = 0.064$). We suspect the limited volume of data available for active fish ($n = 6$) prevents a clearer distinction. The serial correlation durations within a species did not significantly differ depending on activity phase (Kruskal-Wallis test; $p = 0.361$ (*C. tamandua*) and $p = 0.474$ (*C. compressirostris*)).

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**Figure 1.** Inter-pulse-interval (IPI) histograms from resting phase SPIs show species-specific differences. Panels show relative histograms (bin width 2 milliseconds) of the IPI for a given species and sex. (a) A 1 second excerpt of a recorded SPI from each species and sex, where each vertical bar represents an emitted EOD. The EOD waveform visualized represents the characteristic waveform of each species. Note the initial head-negative pre-phase of low amplitude in the *C. tamandua* EOD waveform. (b–e) The IPI histograms from resting phase SPIs. Each coloured line represents a single individual. Plot insets show the population averages (with SEM: dark grey; STD: light grey). (b) *C. compressirostris* males ($n = 13$) (c) *C. compressirostris* female ($n = 4$) (d) *C. tamandua* male ($n = 10$) and (e) *C. tamandua* female ($n = 2$; population averages not shown because of small sample size). F = female; M = male.
Mormyrids have a unique electric organ discharge (EOD) system, which is used for communication, electrolocation, and navigation. The species-specific differences in the electric organ discharges (EODs) and sequence pulse intervals (SPIs) can provide information about sex, age, and dominance status. The SPIs are context-dependent and have been linked to courtship and spawning behaviors.

### Table 1. Definitions of the five variables examined for the principle component analyses of resting phase SPIs and their group mean ± SE.

| Description of term | Total Nr. EODS | Nr. Runs | SPI | Range (high) | Range (low) |
|---------------------|---------------|---------|-----|-------------|------------|
| C. compressirostris M; n = 13 | 3157 ± 116 | 1836 ± 72 | 23 ± 4 ms | 394 ± 101 ms | 10 ± 0.190 ms |
| C. compressirostris F; n = 4 | 3131 ± 434 | 1987 ± 296 | 14 ± 1 ms | 1062 ± 271 ms | 10 ± 0.005 ms |
| C. tamandua M; n = 10 | 1303 ± 96 | 855 ± 71 | 104 ± 10 ms | 790 ± 281 ms | 17 ± 0.949 ms |
| C. tamandua F; n = 2 | 1238 ± 717 | 1300 ± 370 | 48 ± 25 ms | 194 ± 38 ms | 14 ± 0.119 ms |

### Discussion

Over three decades ago, Hopkins and Bass (ref.19) established that species recognition can be mediated by the electric organ discharge (EOD) and sequence pulse interval (SPI), the two major components of electrocommunication in mormyrid fish. Here, we present further evidence that both of these electrocommunication components exhibit species-specific features. We also suggest that while they may be relevant for species recognition and discrimination, the cues mediating recognition may vary depending on species.

While the adult EOD waveform clearly differs between species, differences in the SPI are not as easily quantifiable. SPIs are volitional and context dependent, related to the dual function of discharges in electrocommunication and electrolocation. Nonetheless, a wide range of stereotypic SPI patterns have been categorized in mormyrid species, including bursts (brief accelerations, smooth accelerations, rasps, etc.), cessations, and regularized intervals of EODs (see, e.g., Table 2 in ref.22). Here, we could also identify similar patterns qualitatively. Most notable was the tendency of resting C. compressirostris to produce bursts, while resting C. tamandua displayed a more heterogeneous discharge pattern. Additional analyses of the SPI across a longer timescale also suggest that certain aspects of the resting phase SPI are species-specific, such as the average EOD frequency. We were also able to quantify a species-specific difference in the average duration of SPI serial correlations in the two investigated species, which are shorter in C. compressirostris than C. tamandua. This coincides with a significantly lower number of total discharges in the 120-second C. tamandua recordings compared to C. compressirostris. This species specificity suggests that the SPI may transmit relevant information to the receiver, possibly regarding species identity. Previous studies on a wide range of mormyrid species have already suggested that the sequential manner of impulse discharges can carry information, with alternative EOD interval patterns hypothesized to correlate with sex, age, and/or dominance status. Specific SPI patterns have also been linked to courtship and spawning behaviour (Pollimyrus22,24,25 and Marcusenius26) and various other social interactions (Brienomyrus27, Gnaithonomus28, Marcusenius26).

### Behaviour Choice Experiments

To investigate the contribution of both electrocommunication components (EOD waveform and SPI) towards species recognition in C. compressirostris and C. tamandua, we presented sexually mature male individuals with different communication stimuli consisting of combinations of an EOD waveform (con- or heterospecific) and SPI (conspecific, heterospecific, or artificially scrambled). The two differing communication stimuli were presented simultaneously through spatially separated playback electrodes. Based on video recordings under IR illumination, the responsiveness of male fish (i.e. association time near each playback electrode) was evaluated post-hoc using strength of preference (SOP) values. Each individual was tested in five different conditions (Fig. 4).

During playback conditions, C. compressirostris males spent significantly more time associating with the conspecific EOD waveform, regardless if the playback was combined with a con- or heterospecific SPI (Fig. 5a; one-sample t-test against a random distribution of SOP = 0; p < 0.001 in conditions I and II; p = 0.031 in condition III). However, if the SPI was artificial (scrambled), no significant preference between the two playback electrodes was detected (Fig. 5a; p = 0.159 in condition IV). The playback of heterospecific EOD waveforms combined with a conspecific SPI or a heterospecific C. tamandua SPI also elicited no significant association preference (Fig. 5a; p = 0.672 in condition V). Pairwise comparisons of the SOP values across conditions identified a significantly different response between condition I (natural conditions) and V (SPI discrimination), and condition II (EOD waveform discrimination 1) and V (SPI discrimination) (Fig. 5a; Tukey HSD: p = 0.009 and 0.003, respectively). In summary, C. compressirostris males spent significantly more time near the conspecific signal only if the EOD waveform was paired with a natural (recorded and unaltered) SPI.

During playback recordings with C. tamandua (n = 10), male individuals displayed no significant association preference during the first four experimental playback conditions (Fig. 5b; one-sample t-test against a random distribution of SOP = 0; p = 0.130 in condition I; p = 0.305 in condition II; p = 0.145 in condition IV). In condition V for SPI discrimination, C. tamandua individuals showed a significant association preference for the heterospecific C. compressirostris EOD waveform and SPI (Fig. 5b; one-sample t-test against a random distribution of SOP = 0; p = 0.049). No significant differences in SOP values across conditions was identified (ANOVA on arcsine transformed SOP values; all p-values > 0.100). In summary, C. tamandua males did not show a significant association preference for the conspecific EOD waveform or SPI.

During playback conditions, the responsiveness of C. compressirostris and C. tamandua males to the playback signals, calculated as the total respective time spent outside of the neutral zone, did not significantly differ across the five conditions (ANOVA on square transformed time data; p = 0.968 and 0.645, respectively).
Given the possibility that both the EOD and SPI components of electrocommunication may be relevant for species recognition and discrimination, we conducted a series of playback experiments where con- and hetero-specific EOD waveforms and SPIs were artificially combined. Our results from these five conditions suggest that for *C. compressirostris* males, the EOD waveform may be the predominant cue used for species recognition (conditions I–III). Interestingly, a previous playback study found that female *C. compressirostris* do not discriminate between conspecific EOD waveforms and that of *C. tamandua*12. This sex-based asymmetric response to playback cues has been observed in other mormyrid studies as well. In the genus *Brienomyrus*, for example, preferential association with the conspecific EOD waveform was observed for male *B. brachyistius triphasic* and Gabon’s *Brienomyrus* species flock40,41 (now revised to the genus *Paramormyrops*)41. In contrast, females were relatively unresponsive to electrical playback signals40. This suggests that in both *C. compressirostris* and possibly other mormyrid species, males may mediate species recognition and discrimination.

**Figure 2.** Principle components of SPIs differ between species and sex. Five variables (see Table 1) were examined across the 29 resting phase SPIs recorded from *C. compressirostris* and *C. tamandua* individuals. (a) A comparison between the two species: *C. compressirostris* (n = 17; red) and *C. tamandua* (n = 12; blue). (b) A comparison between the two species, including sex as a group variable, with *C. compressirostris* females (n = 4; red), *C. compressirostris* males (n = 13; green), *C. tamandua* females (n = 2; blue) and *C. tamandua* males (n = 10; purple). PC = principle component; F = female; M = male.
While *C. compressirostris* males associated significantly more with the conspecific EOD waveform, their preference was not absolute. Such a pattern is commonly seen in preference tests (not only in mormyrids 11, but also, e.g., in mollies 42,43 and swordtails44), and may be a result of varying and overlaying motivations, e.g., mate search and exploratory behavior ('selective responsiveness')11. It further suggests that the fish were not avoiding proximity to heterospecific signals.

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Figure 3. SPI serial correlation durations differ between species. (a–d) Average serial correlations for 120-second recordings of the discharge behaviour of *C. compressirostris* (a: resting, n = 17; c: active, n = 4) and *C. tamandua* (b: resting, n = 12; d: active, n = 2). Population averages are shown with SEM (dark grey) and STD (light grey). The red line depicts the chance level (at a type I error rate of *p* = 0.01) at which serial correlations could be found in the respective datasets. (e) Same as (a–d), but for the artificial (scrambled) SPIs (n = 6). (f) Distribution of average serial correlation durations. Stars (*) represent significance. comp = *C. compressirostris*; tam = *C. tamandua*.

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Figure 4. Experimental playback setup. The aquarium used for playback experiments was divided into five sections (marked A–E). The playback electrodes were located behind gridded partitions in sections A and E, with the positive pole facing the centre of the aquarium. The focal fish was positioned in the centre, which was divided in space into three equal sections (marked B–D). Sections B and D represent the respective preference zones for A and E; section C was considered a neutral zone. The five (I–V) playback conditions conducted are listed in the table, along with the EOD waveform and SPI combinations. During playback experiments, the actual physical location (section A vs. E) of the synthesized playback combinations was randomly interchanged to control for side-bias. EOD = electric organ discharge; SPI = sequence pulse interval.
While male *C. compressirostris* showed a clear association preference for the conspecific EOD waveform when it was paired with a natural (recorded and unaltered) SPI, the conspecific EOD playback did not elicit a preference response in all conditions. When the conspecific EOD waveform was combined with an artificial (scrambled) SPI (condition IV), no association preference was evident. While a lack of response is not in and of itself evidence for a lack of perceptual discrimination, our SPI statistics confirm (as shown previously in, e.g.\(^ {23,27,33,34,36,37} \)) that the temporal pattern of EOD intervals is not random under natural conditions and contains species-specific features in the species and contexts studied here. The lack of response to the scrambled SPI may therefore suggest that natural SPIs carry valuable information, which is lacking when the SPI has a randomized temporal structure. Both the SPI and EOD waveform may therefore be relevant, necessary, and sufficient for species recognition and discrimination by *C. compressirostris* males.

In contrast to *C. compressirostris* males, *C. tamandua* males did not show an association preference for conspecific electric signals. Only in condition V, where the heterospecific EOD waveform was combined with a conspecific or heterospecific SPI, did males show a greater strength of preference for the heterospecific *C. compressirostris* SPI. A type-I error could possibly explain this unexpected and marginally significant result (\(p = 0.049\)), or these observations may – at first glance – suggest that *C. tamandua* males are willing to undermine reproductive isolation. Sympatric species often display asymmetric sexual isolation behaviours, with one species discriminating more strongly than vice versa\(^ {45,46} \). However, an effort to obtain natural hybrids in breeding groups between female *C. compressirostris* and male *C. tamandua* led to several spawning events, but never fertilization\(^ {47} \). This corresponds with previous research showing that *C. tamandua* males do preferentially associate with female conspecifics (over female *C. compressirostris*) when live fish are used as stimuli\(^ {31} \). A recent genetic analysis also shows no evidence of gene flow between the two species, although incipient speciation is apparent\(^ {30} \). Artificial reproduction between *C. compressirostris* and *C. tamandua* individuals produces fertile offspring and F1-hybrids produce viable fish\(^ {47} \).
The apparent absence of a behavioural preference by *C. tamandua* males is not *per se* evidence that the species cannot discriminate between conspecific and heterospecific signals, but the playback results may suggest that the cues used for species recognition differ among mormyrid species. While the EOD waveform and SPI are both relevant for species recognition and discrimination in *Campylomormyrus compressirostris*, electric cues alone may not be sufficient for discrimination in *C. tamandua*. Molecular phylogenies of the *Campylomormyrus* genus show *C. tamandua* as the sister species of all other *Campylomormyrus* representatives and morphological investigations into the electric organ suggest that the rostral position of the stalk found in *C. tamandua* is the ancestral state. Discrimination by electric cues alone may, therefore, be an apomorphic trait evolved during a more recent radiation (i.e., after separation from *C. tamandua*), while electric cues alone may not be sufficient for species recognition and discrimination in *C. tamandua*.

In addition to electrocommunication, various modalities may act either synergistically with the electrosensory system or as a ‘back-up’ signal. The lack of discrimination among *C. tamandua* males during our behavioural experiments could, therefore, be due to the absence of suitable cues of other modalities. Overt behavioural interactions, such as the distinct swimming patterns observed during courtship and spawning in the mormyrid *P. isidori* and the anti-parallel displays of dominance and aggression observed in *G. petersii* (i.e., the interaction between the electric and mechanosensory sense) may have been a key factor missing during our playback setup.

In addition to the wide scope of studies addressing electrocommunication in mormyrid weakly electric fish, the electric gymnotiform of South America have also been extensively studied. Although these two electric fish lineages arose independently from non-electrogenic teleost ancestors after the separation of South America and Africa, both groups show striking convergence in electric organ development, reproductive behaviour and ecology. While the majority of gymnotiforms have developed quasi-sinusoidal EOD waveforms, a number of species have developed pulse-like EODs similar to that in mormyrids. In those species, both components of the electrocommunication signal (EOD waveform and frequency) have been shown to play a role in species and sex recognition.

The complexity and variation of the comparatively simple electrocommunication used by weakly electric fish for species recognition emphasizes that our understanding of inter- and intraspecies communication is still largely incomplete. Weakly electric fish are therefore a particularly interesting model for communication studies because many species occur in sympathy, where effective communication is vital for species recognition and discrimination. In our study, we have been able to unravel species-specific characteristics of the SPI and present further evidence for the contributions of the EOD waveform and SPI for *Campylomormyrus* species recognition and discrimination. Future investigations are needed to elaborate upon the various other communication modalities acting synergistically to electrocommunication in African weakly electric fish.

**Methods**

**Study species.** Two mormyrid weakly electric fish species were investigated in this study - *Campylomormyrus compressirostris* and *C. tamandua*. All specimens were imported from Kinshasa (Democratic Republic of the Congo), where they occur in sympathy. Individuals were held in the laboratory at the University of Potsdam, Germany under a 12/12 hour dark/light cycle and fed daily with Chironomidae and Chaoborus larvae.

**Recordings of discharge behaviour.** The inter-pulse-interval (IPI) is under volitional control and consequently varies depending on behavioural context. We therefore standardized the time and conditions for recording SPIs (tank: L 32 × W 50 × H 50 cm; conductivity: 700 ± 20 μS/cm; temperature: 25 ± 1 °C). During SPI recordings, a plastic tube was placed in the tank for shelter and movement was not restricted in any way. From 17 recordings, a plastic tube was placed in the tank for shelter and movement was not restricted in any way. From 17 *C. compressirostris* (n = 13 males; n = 4 females) and 12 *C. tamandua* (n = 10 males; n = 2 females), we recorded SPIs over a period of 30 minutes, four hours after light onset (i.e., within the resting phase of the day-cycle) after separation from *C. tamandua*), while electric cues alone may not be sufficient for species recognition and discrimination in *C. tamandua*.

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To explore which electrocommunication component (s) (EOD waveform and SPI) mediate species recognition, we artificially combined conspecific and heterospecific SPIs and EOD waveforms from *C. compressirostris* and *C. tamandua* in five experimental playback conditions. For the purpose of this experiment, the heterospecific signal (EOD waveform or SPI) presented to *C. compressirostris* was that of a *C. tamandua* individual, and vice versa. The artificial (scrambled) SPI presented was from conspecifics. All focal fish were males with a kink in their anal fin base indicating sexual maturity.

Our initial playback (condition I) was a “natural” playback, combining the conspecific EOD waveform and conspecific SPI presented against a heterospecific EOD waveform and SPI. To then test if the EOD waveform...
alone is sufficient for species recognition, we tested focal fish in three different conditions (II–IV). In condition II, a conspecific EOD waveform and SPI was presented against a heterospecific EOD combined with a conspecific SPI. Condition III combined the conspecific EOD waveform with a heterospecific SPI presented against a heterospecific EOD waveform and heterospecific SPI. In condition IV, a conspecific and heterospecific EOD waveform were respectively combined with an artificial (scrambled) SPI to test if the EOD is both necessary and sufficient for species recognition. Finally, in condition V the heterospecific EOD was paired with a conspecific and heterospecific SPI to test if the SPI is both necessary and sufficient for species recognition (Fig. 4).

Behavioural experiments were conducted in an observation aquarium (L 160 × H 50 × W 50 cm; conductivity: 690 ± 20 μS/cm; temperature: 26 ± 1 °C) divided by plastic, grid partitions into three sections (Fig. 4; tank sections A, B–D, E). The playback electrodes were placed in the far right and left partitions (Fig. 4; tank sections A, E). The centre section (Fig. 4; tank sections B–D) was not physically divided, but ‘preference zones’ of 32 cm each were marked on the exterior of the tank. The focal fish was transferred to the tank 3.5 hours before each experiment began for acclimation. There was a clear plastic tube for shelter centred equidistant to the two playback electrodes.

For playback, we used a randomly selected pre-recorded active phase SPI (Spike2 and MICRO 1401) to trigger the outputs of a waveform generator (DG1032Z, Rigol Technologies, Beijing, China). The EOD waveforms were pre-recorded, averaged waveforms (across approximately 400 EODs) and could be triggered on two separate channels simultaneously. The signals were isolated from ground (2200 Analog Stimulus Isolator, A–M Systems, Carlsborg, WA, USA) and played into the water through dipole carbon electrodes spaced 104 cm apart, meaning the two electrodes were each 52 cm from the centre of the tank (Fig. 4; tank sections A, E). Each electrode was oriented with positive and negative poles (3.5 cm apart) parallel to the long axis of the aquarium. The output amplitude of each channel was adjusted to be level and match that of a live fish at equal distance (52 cm).

Data analysis — Recordings of discharge behaviour. For each of the 29 resting phase SPIs, we used the time stamp occurrence of each EOD in a given sequence to calculate the inter-pulse-interval of the EODs (IPI) as:

\[ IPI_t = t_i - t_{i-1} \]  

where \( t \) is the time at which an EOD occurred and \( i \) is the index of the given EOD. Sequences of IPIs were then plotted as a function of time and visually scanned for SPI patterns that have been linked to specific behavioural contexts in previous research. These included bursts (brief accelerations, scallops, rasps, etc.), cessations, pulse pairs, regularizations, and random SPI patterns. IPI histograms (bin width 2 milliseconds) were also plotted, separately for species as well as sex. Population averages (arithmetic mean) and errors (standard error of the mean, SEM; standard deviation, STD) were calculated at a resolution of 2 milliseconds.

Principle Component Analyses (PCAs) are often used to identify communication signal differences between individuals and species, including in fish, bird, and insect species. We therefore investigated possible species and sex variation in the resting phase SPIs of our weakly electric fish using a PCA. Five variables were incorporated: (1) the total number of EODs produced in the 120-second sequence, (2) the mode inter-pulse-interval (i.e. the most frequent EOD interval), (3 & 4) the range (i.e. longest and shortest interval between two adjacent EODs), and (5) the number of runs (Table 1). For the runs analysis, IPIs were compared in sequential pairs; if the second interval in a pair was larger, smaller, or equal in duration to the first interval, it was assigned as positive, negative, or equal, respectively. A run was then defined as a series of increasing, decreasing, or constant IPIs. This definition of a run is derived from the runs test, an established statistical test to determine if two or more nominal events occur in random sequence or if the probability of a given event is a function of the outcome of a previous event. Similar methods have been used previously to investigate the temporal organization of successive SPIs. Two PCAs were conducted with these five variables clustered by species (n = 17 C. compressirostris; n = 12 C. tamandua) or by sex and species (n = 13 C. compressirostris males; n = 4 C. compressirostris females; n = 10 C. tamandua males; n = 2 C. tamandua females). Both PCAs were calculated using the prcomp function in R (singular value decomposition). All five SPI characteristic were log transformed to centre and scale variables. We calculated the Pearson correlation coefficient for each pair of variables using the R add-on package psych. To visualize the data, we used the R add-on package ggbiplot. A normal contour line with an ellipse probability of 68% for each defined group is visualized.
where $k$ is the index of a given interval and (...) means the average over all $k$. Species-specific population averages for active and resting phase recordings were obtained as a function of lag $i$. To test whether the results differed significantly from chance level, we recalculated serial correlations according to the above formula, while randomly permuting the IPI sequences 250 times. From this, chance level was defined as the 99% confidence interval above the mean, averaged over all possible intervals (red lines in Fig. 3a–e).

We calculated the average duration of the SC for each recording by multiplying the interval number at which serial correlations first decreased under chance level with the median IPI interval duration in that specific recording. The distributions of SC durations for active and resting phase SPIs were compared between species with an individual non-parametric test (Kruskal-Wallis).

**Data analysis – Behaviour choice experiments.** Across all five experimental playback conditions, the behaviour of the male focal fish was evaluated offline based on video recordings. We scored responses as total time spent within each pre-defined preference zone. Data was analysed according to Plath et al.\(^\text{a}\) using strength of preference (SOP) as a measure of association preference. SOP was calculated as:

$$SOP = \frac{t_B - t_D}{t_B + t_D}$$

(3)

where $t_B$ is the time the focal fish spent in preference zone $B$ and $t_D$ is the time the focal fish spent in preference zone $D$. SOP values can range from $-1$ (complete avoidance of preference zone $B$) to $1$ (complete preference of preference zone $B$). A one-sample $t$-test was used to compare SOP values to a random distribution of SOP $= 0$. Significant differences in the SOP values between conditions were tested with a repeated measures ANOVA, with individual male and SPI identifiers as random variables. If significant differences were identified, the post-hoc Tukey’s HSD pairwise comparison test was performed with a confidence interval of 95% using the R add-on package multcomp\(^7\). Data was tested for normality using the Shapiro-Wilk normality test and visualized with the qqnorm and hist functions in R\(^2\).

**Ethics statement.** All experiments were approved by the Deputy for Animal Welfare of the University of Potsdam and are in accordance with the national legal requirements.

**References**

1. Braune, P., Schmidt, S. & Zimmerman, E. Acoustic divergence in the communication of cryptic species of nocturnal primates (Microcebus spp.). BMC Biol. 6, 19 (2008).
2. Wilkins, M. R., Seddon, N. & Safran, R. J. Evolutionary divergence in acoustic signals causes and consequences. Trends Ecol. Evol. 28, 156–166 (2013).
3. Honda-Sumi, E. Difference in calling song of three field crickets of the genus Teleogryllus: the role in premating isolation. Anim. Behav. 69, 881–889 (2005).
4. Jones, G. Acoustic signals and speciation: the roles of natural and sexual selection in the evolution of cryptic species. Adv. Study Behav. 26, 317–354 (1997).
5. Bennett, M. V. L. Electric Organs in Fish Physiology (eds Hoar, W. S. & Randall, D. J.) 347–491 (Academic Press, 1971).
6. Lissmann, H. W. & Machin, K. E. The mechanism of object location in Gymnarchus niloticus and similar fish. J. Exp. Biol. 35, 451–486 (1958).
7. Nagel, R., Kirschbaum, F. & Tiedemann, R. Electric organ discharge diversification in mormyrid weakly electric fish is associated with differential expression of voltage-gated ion channel genes. J. Comp. Physiol. A 203, 183–193 (2017).
8. Paul, C. et al. Comparative histology of the adult electric organ among four species of the genus Campylomormyrus (Teleostei: Mormyridae). J. Comp. Physiol. A 201, 357–374 (2015).
9. Bass, A. H. Species differences in electric organs of mormyrids: substrates for species-typical electric organ discharge waveforms. J. Comp. Neurol. 244, 313–330 (1986).
10. Hopkins, C. D. & Bass, A. H. Temporal coding of species recognition signals in an electric fish. Science 212, 85–87 (1981).
11. Moller, P. & Serrier, J. Species recognition in mormyrid weakly electric fish. Anim. Behav. 34, 333–339 (1986).
12. Feulner, P. G. D., Plath, M., Engelmann, J., Kirschbaum, F. & Tiedemann, R. Electrifying love: electric fish use species-specific discharge for mate recognition. Biol. Lett. 5, 225–228 (2009).
13. Schmid, D. & Kramer, L. B. Sexual selection by female choice prevents speciation reversal in a hybridizing trio of mormyrid fish in southern Africa: evidence from playback experiments of electric organ discharges. Behaviour 151, 1703–1734 (2014).
14. Carlson, B. A. Electric signaling behavior and the mechanisms of electric organ discharge production in mormyrid fish. J. Physiol. Paris 96, 405–419 (2002).
15. von der Emde, G. Active electrolocation of objects in weakly electric fish. J. Exp. Biol. 202, 1205–1215 (1999).
16. Teysedre, C. & Serrier, J. Temporal spacing of signals in communication, studied in weakly-electric mormyrid fish (Teleostei, Pisces). Behav. Processes 12, 77–98 (1986).
17. Gehhardt, K., Böhme, M. & von der Emde, G. Electrocommunication behaviour during social interactions in two species of pulse-type weakly electric fishes (Mormyridae). J. Fish Biol. 81, 2235–2254 (2012).
18. Arnegard, M. E. & Carlson, B. A. Electric organ discharge patterns during group hunting by a mormyrid fish. Proc. R. Soc. B 272, 1305–1314 (2005).
19. Forlim, C. G., Pinto, R. D., Varona, P. & Rodríguez, F. Delay-dependent response in weakly electric fish under closed-loop pulse stimulation. PLoS One 10, e0141007, https://doi.org/10.1371/journal.pone.0141007 (2015).
20. Kramer, B. & Bauer, R. Agonistic behaviour and electric signalling in a mormyrid fish. Gnathonemus petersii. Behav. Ecol. Sociobiol. 1, 45–61 (1976).
21. Wernery, M. & Kramer, B. Intraspecific agonistic interactions in freely swimming mormyrid fish, Marcusenius macrolepidotus (South African form). J. Ethol. 20, 107–121 (2002).
22. Moller, P., Serrier, J. & Bowling, D. Electric organ discharge displays during social encounter in the weakly electric fish Brienomyrus niger L. (Mormyridae). Ethology 82, 177–191 (1989).
23. Crawfield, J. D. Sex recognition by electric cues in a sound-producing mormyrid fish. Pollimyrus isidori. Brain. Behav. Evol. 38, 20–28 (1991).
24. Bratton, B. O. & Kramer, B. Patterns of the electric organ discharge during courtship and spawning in the mormyrid fish, Pollimyrus isidori. Behav. Ecol. Sociobiol. 24, 349–368 (1989).
25. Hofmann, V., Sanguinetti-Scheck, J. I., Gómez-Sena, L. & Engelmann, J. Sensory flow as a basis for a novel distance cue in freely behaving electric fish. J. Neurosci. 37, 302–312 (2017).

26. Schwarz, S. & von der Emde, G. Distance discrimination during active electrolocation in the weakly electric fish Gnathonemus petersii. J. Comp. Physiol. A 186, 1185–1197 (2001).

27. Hopkins, C. D. Behavior in Mormyridae in Electroreception (eds Bullock, T. H. & Heiligenberg, W.) Ch. 8, 527–576 (John Wiley & Sons, 1986).

28. Feulner, P. G. D., Kirschbaum, F., Mamonekena, V., Ketaiwa, V. & Tiedemann, R. Adaptive radiation in African weakly electric fish (Teleostei: Mormyridae: Campylomormyridae): a combined molecular and morphological approach. J. Evol. Biol. 20, 403–414 (2007).

29. Gosse, J.-P. Mormyridae in Check-list of the Freshwater Fishes of Africa (eds Daget, J., J.-P. G. & Thys van den Audenaerde, D. F. E.) Ch. 16, 63–122 (Office de la Recherche Scientifique et Technique Outre-Mer, 1984).

30. Lamanna, F. et al. Species delineation and phylogenetic relationships in a genus of African weakly-electric fishes (Osteoglossiformes, Mormyridae). Mol. Phylogen. Evol. 101, 8–18 (2016).

31. Nagel, R. et al. Male-mediated species recognition among African weakly electric fishes. R. Soc. Open Sci. 5, 170443, https://doi.org/10.1098/rsos.170443 (2018).

32. Plath, M. et al. Complementary effect of natural and sexual selection against immigrants maintains differentiation between locally adapted fish. Naturwissenschaften 97, 769–74 (2010).

33. Kramer, B. Spontaneous discharge rhythms and social signalling in the weakly electric fish Polliamyrus isidori (Cuvier et Valenciennes) (Mormyridae, Teleostei). Behav. Ecol. Sociobiol. 4, 61–74 (1977).

34. Moller, P. “Communication” in weakly electric fish, Gnathonemus niger (Mormyridae) I. Variation of electric organ discharge (EOD) frequency elicited by controlled electric stimuli. Anim. Behav. 18, 768–786 (1970).

35. Lareo, A., Forlorn, C. G., Pinto, R. D., Varona, P. & Rodriguez, F. de B. Temporal code-driven stimulation: definition and application to electric fish signalling. Front. Neuroinform. 10, 41, https://doi.org/10.3389/fninf.2016.00041 (2016).

36. Graff, C. Firing activity of the weakly electric fish Marcusenius macrolepidotus (Mormyridae, Teleostei): logarithmic repartition of inter-pulse intervals, and sequential inequality testing. Behaviour 109, 258–284 (1989).

37. Kramer, B. & Kühn, B. Species recognition by the sequence of discharge intervals in weakly electric fishes of the genus Gymnotus (Mormyridae, Teleostei). Anim. Behav. 48, 435–445 (1994).

38. Baier, B. & Kramer, B. Electric communication during courtship and spawning in two sibling species of dwarf stonebasher from southern Africa, Polliamyrus castelnauæ and P. marianne (Mormyridae, Teleostei): evidence for a non species-specific communication code? Behaviour 144, 115–142 (2007).

39. Hanika, S. & Kramer, B. Intra-male variability of its communication signal in the weakly electric fish, Marcusenius macrolepidotus (South African form), and possible functions. Behaviour 142, 145–166 (2005).

40. Arnegard, M. E., Jackson, B. S. & Hopkins, C. D. Time-domain signal divergence and discrimination without receptor modification in sympatric morphs of electric fishes. J. Exp. Biol. 209, 2182–2198 (2006).

41. Gallant, J. R., Arnegard, M. E., Sullivan, J. P., Carlson, B. A. & Hopkins, C. D. Signal variation and its morphological correlates in Paramormyrus kingsleyae: data revealed that evolution of electric organ discharge in mormyrid electric fish. J. Comp. Physiol. A 197, 799–817 (2011).

42. Riesch, R., Schlupp, I., Töbler, M. & Plath, M. Reduction of the association preference for conspecifics in cave-dwelling Atlantic mollys, Poecilia mexicana. Behav. Ecol. Sociobiol. 60, 794–802 (2006).

43. Plath, M., Seggel, U., Burmeister, H., Heubel, K. U. & Schlupp, I. Choozy males from the underground: male mating preferences in surface- and cave-dwelling Atlantic mollys (Poecilia mexicana). Naturwissenschaften 93, 103–109 (2006).

44. Wong, B. B. M., Fisher, H. S. & Rosenthal, G. G. Species recognition by male swordtails via chemical cues. Behav. Ecol. 16, 818–822 (2005).

45. Svennson, E. L., Karlsson, K., Friberg, M. & Eroukhmanoff, F. Gender differences in species recognition and the evolution of asymmetric sexual isolation. Curr. Biol. 17, 1943–1947 (2007).

46. Kaneshiro, K. Y. Sexual isolation, speciation and the direction of evolution. Evolution 34, 437–444 (1980).

47. Kirschbaum, F. et al. Intraspecific variation in Campylomormyridae and intergeneric hybrids in mormyrid fish: physiological and histological investigations of the electric organ ontogeny, J. Physiol. Paris 110, 281–301 (2016).

48. Sullivan, J. P., Lavoûé, S. & Hopkins, C. D. Molecular systematics of the African electric fishes (Mormyroidea: Teleostei) and a model for the evolution of their electric organs. J. Exp. Biol. 203, 665–680 (2003).

49. Moller, P. Multimodal sensory integration in weakly electric fish: a behavioral account. J. Physiol. Paris 96, 547–556 (2002).

50. Schumacher, S., Burt de Perera, T., Thenert, J. & von der Emde, G. Cross-modal object recognition and dynamic weighting of sensory inputs in a fish. Proc. Natl. Acad. Sci. 113, 7638–7645 (2016).

51. Bell, C. S., Myers, J. P. & Russell, C. J. Electric organ discharge patterns during dominance related behavioral displays in Gnathonemus petersii (Mormyridae). J. Comp. Physiol. A 92, 201–228 (1974).

52. Alves-Gomes, J. Systematic biology of gymniform and mormyriform electric fishes: phylogenetic relationships, molecular clocks and rates of evolution in the mitochondrial rRNA genes. J. Exp. Biol. 202, 1167–1183 (1999).

53. Lavoûé, S. et al. Comparative ages for the independent origins of electrogenesis in African and South American weakly electric fishes. PLoS One 7, e36287, https://doi.org/10.1371/journal.pone.0036287 (2012).

54. Bass, A. H. Electric organs revisited: evolution of a vertebrate communication and orientation organ in Electroreception (eds Bullock, T. H. & Heiligenberg, W.) Ch. 2, 13–70 (Wiley, 1986).

55. Denizot, J.-P., Kirschbaum, F., Westby, G. W. M. & Tsuji, S. On the development of the adult electric organ in the mormyrid fish Polliamyrus isidori (with special focus on the innervation). J. Neurocytol. 10, 547–556 (1982).

56. Kirschbaum, F. Myogenic electric organ precedes the neurogenic organ in aperotomid fish. Naturwissenschaften 70, 205–207 (1983).

57. Szabo, T. Development of the electric organ of Mormyridae. Nature 188, 760–762 (1960).

58. Kirschbaum, F. Reproduction and development in mormyriform and gymniform fishes: convergence of a specialized foraging mode in Mormyridae. Environ. Biol. Fishes 94, 175–186 (2001).

59. Marrero, C. & Winemiller, K. O. Tube-snouted gymniform and mormyriform fishes: convergence of a specialized foraging mode in Mormyridae. Environ. Biol. Fishes 38, 299–309 (1993).

60. Hopkins, C. D. & Westby, G. W. M. Time domain processing of electric organ discharge waveforms by pulse-type electric fish. Brain. Behav. Evol. 29, 77–104 (1986).

61. Hagedorn, M. Ecology and behavior of a pulse-type electric fish, Hypopomus occidentalis (Gymnotiformes, Hypopomidae), in a fresh-water stream in Panama. Copeia 1988, 324–335 (1988).

62. Shumway, C. A. & Zelack, R. D. Sex recognition and neuronal coding of electric organ discharge waveform in the pulse-type weakly electric fish, Hypopomus occidentalis. J. Comp. Physiol. A 160, 465–478 (1988).

63. Malavasi, S., Collatuzzo, S. & Torricelli, P. Interspecific variation of acoustic signals in Mediterranean gobies (Percoidei, Gobiidae): comparative analysis and evolutionary outlook, Biol. J. Linn. Soc. 93, 763–778 (2008).
66. Boyle, K. S., Colleye, O. & Parmentier, E. Sound production to electric discharge: sonic muscle evolution in progress in *Synodontis* spp. catfishes (Mochokidae). *Proc. R. Soc. B* **281**, 20141197. https://doi.org/10.1098/rspb.2014.1197 (2014).

67. Aubin, T., Mathévenon, N., Da Silva, M. L., Vielliard, J. M. E. & Sebe, F. How a simple and stereotyped acoustic signal transmits individual information: the song of the White-browed Warbler *Basileuterus leucoblepharus*. *An. Acad. Bras. Cienc.* **76**, 335–344 (2004).

68. Henry, C. S., Wells, M. L. M. & Simon, C. M. Convergent evolution of courtship songs among cryptic species of the Carnea group of green lacewings (Neuroptera: Chrysopidae: Chrysoperla). *Evolution* **53**, 1165–1179 (1999).

69. Sokal, R. R. & Rohlf, F. J. Test for randomness of nominal data: runs test in *Biometry*. 3rd Edition. Ch. 18.2, 797–803 (W.H. Freeman, 1995).

70. Zar, J. H. Serial randomness of nominal scale categories in *Biostatistical Analysis*, 2nd Edition. Ch. 23.6, 416–417 (Prentice-Hall, 1984).

71. Brudno, S. & Marczynski, T. J. Temporal patterns, their distribution and redundancy in trains of spontaneous neuronal spike intervals of the feline Hippocampus studies with a non-parametric technique. *Brain Res.* **125**, 65–89 (1977).

72. R Core Team R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org (2014).

73. Revelle, W. psych: Procedures for Psychological, Psychometric, and Personality Research. Northwestern University, Evanston, Illinois, USA, https://CRAN.R-project.org/package=psych (2018).

74. Vu, V. Q. ggbiplot: A ggplot2 based biplot. R package, version 0.55. https://github.com/vqv/ggbiplot (2011).

75. Hothorn, T., Bretz, F. & Westfall, P. Simultaneous inference in general parametric models. *Biometrical J.* **50**, 346–363 (2008).

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Author Contributions

F.K. and R.T. supervised the study. R.N., F.K. and R.T. designed the experiments. R.N. performed the experiments, analysed the data, and wrote the draft manuscript text. J.E. and V.H. implemented the computer code used for data collection and helped in conceptualization of the experiment. V.H. assisted further with data analysis. All authors reviewed and approved the manuscript.

Additional Information

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