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Gradual frequency rises in interacting black ghost knifefish, *Apteronotus albifrons*

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Abstract The present paper highlights the relationship between social status and production of gradual frequency rises in interacting *Apteronotus albifrons*. The gradual frequency rise production was mathematically inferred and a discrete classification deliberately avoided. The results showed little gradual frequency rise production before the hierarchy settlement. Afterwards, only the dominant fish kept this gradual frequency rise production at low levels, while the subdominant fish drastically increased it in all following interaction contexts. The hypothesis of gradual frequency rises being involved in communication as submissive signals was thus strengthened.

Keywords *Apteronotus* · Electric fish · Electrocommunication · EOD · GFR

Abbreviations EOD electric organ discharge FM frequency modulation GFR gradual frequency rise IQR interquartile range JAR jamming avoidance response

Introduction

According to their kind of electric organ discharge (EOD) we distinguish between weakly electric fish of the pulse type and the wave type. The former generate short EODs (from approximately 100 μ s up to many milliseconds) separated by longer, highly variable intervals,

while the latter discharge continuously at a stable frequency (ca. 15–1800 Hz), for instance the apteronotids (Gymnotiformes), which were the subject of this study.

Some wave fishes make use of EOD interruptions to encode messages relevant for social interaction (Hopkins 1974b; Hagedorn and Heiligenberg 1985), but the most common social signals among them are frequency modulations (FMs). The baseline frequency range is characteristic, although not exclusive, for each species and may also depend on the sex and age of each individual, as demonstrated for *Sternopygus macrurus* (Hopkins 1974a). This baseline frequency is kept almost constant (Bullock 1970; Moortgat et al. 1998) under stable temperature conditions, but is often modulated in the presence of conspecifics. FMs can take various forms, for example to avoid frequency-overlapping (reviewed in Heiligenberg 1986), a behaviour known as jamming avoidance response (JAR). JAR has been demonstrated in the genera *Eigenmannia* and *Apteronotus*, and implies mainly a frequency shift (other FMs can also be evoked under experimental jamming).

Other FMs involved in communication are more complex (Larimer and MacDonald 1968; Bullock 1969; Hopkins 1974a, 1974b; Hagedorn and Heiligenberg 1985), but they have been sometimes reduced to two main types, namely chirps and gradual frequency rises (GFRs). Chirps are very brief (between 10 and a few hundred milliseconds), conspicuous frequency rises, while GFRs involve smoother rises and a slow return to the baseline frequency, with a total duration ranging from ca. 100 ms up to several minutes. Both have been described in *Apteronotus leptorhynchus* (Engler et al. 2000), but although the chirps could be clearly separated in classes, a systematic classification of the GFRs failed due to their vast diversity in shape and duration. Other recent studies followed that example and focused on chirping behaviour (Engler and Zupanc 2001; Dunlap et al. 2002; Dunlap 2002), while GFRs remained out of the research foreground.

GFRs in *A. leptorhynchus* were analysed by Zupanc et al. (2001), who pointed out a variation in the

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frequency of GFR production, depending on the light-dark cycle, but not coupled to an internal circadian rhythm. They were generated more often during the light phase than during the dark phase, as opposite to other gymnotiforms (Schwassmann 1971). *Apteronotus* are nocturnal fish, so this finding raises the question whether or not the GFRs are voluntarily controlled signals relevant for electrocommunication.

Hagedorn and Heiligenberg (1985) pointed out the possible involvement of GFRs ("long rises" and "short rises" in their paper) in the courtship of the sternopygid *E. virescens* and of *A. leptorhynchus*. But in spite of the recent technical advances in computer-based data acquisition and analysis, the reference point is still the comprehensive study by Hopkins (1974b) on *E. virescens* in agonistic contexts. He found out that GFRs ("long rises" in his paper) were produced more often by subordinate fish and were significantly associated with the motor behaviour "retreat". The recent study of Tallarovic and Zakon (2002) on *A. leptorhynchus* females has been the only additional systematic attempt to unravel the social implications of GFR production in interacting apteronotids since then. They proposed a GFR classification on the basis of both their physical characteristics and their possible communicative function.

In contrast to chirps, GFRs are extremely variable in time-course and often may not terminate with a return to the baseline frequency. In addition, there is no established minimum frequency shift to consider a FM as a GFR. In spite of these delimitation problems, previous studies chose the number of recorded GFRs as a dependent variable (Hopkins 1974b; Zupanc et al. 2001). Therefore the results were strongly influenced by the observer's operative definition of GFR. Other methods like cluster analysis, as used by Engler et al. (2000) or Tallarovic and Zakon (2002), also imply a previous manual identification of the signals and a reduction of the quantitative information. These information losses may mask underlying relationships.

The present paper tries to elucidate the possible social relevance of GFRs in interacting *A. albifrons*, exploring Hopkins' (1972) hypothesis of GFRs being a submissive signal.

Materials and methods

Animals

The research was based upon observations on 12 individuals of *A. albifrons*, purchased from a tropical fish importer. They could be individually identified by idiosyncratic pigmentation patterns and morphological characteristics. The fish were not sorted in any way and thus the expected sex ratio is, a priori, 1:1.

Experimental design

The experimental tank was a 512-l rectangular aquarium, in which temperature was kept between 26.1 and 26.7 °C and water conductivity between 150 and 170 $\mu\text{S cm}^{-1}$. The light-dark cycle was

12:12 h. The tank had only one hiding place on each side, so that motor behaviour could be thoroughly followed. Fish were fed daily with frozen *Chironomus* larvae, always 30 min before the beginning of the night phase. Observations were based on a continuous event recording model under two different conditions; observations within each phase had no time gap (Bakeman and Gottman 1997).

The first phase of each series of experiments was for control. A pair of fish that had no previous contact with each other were put each into one half of the experimental tank that was symmetrically divided by a plastic wall. Their motor and electric behaviours were monitored during the 1st hour after onset of the dark phase. This phase allowed the fish to acclimatise to the new aquarium and the data recorded during this stage were taken as a reference for comparison with the next phase. In the second phase (experimental phase), the plastic wall was removed before recording and the fish were able to interact directly. Observations were made over the 1st hour after dawn.

Data acquisition and analysis

The tank was illuminated with infrared lamps and activity recorded with an infrared camera (Pieper FK 6990-IQ) connected to a hi-fi S-VHS video recorder (Panasonic Video Cassette Recorder AG-7330).

The EODs were detected with two vertically positioned carbon electrode pairs forming two horizontal dipoles, one at each side. The dipole axes formed an almost right angle so that the EOD signal was detectable independently of the position of the fish. A ground electrode was placed at a corner of the tank. Water filtering was air driven and heaters were disconnected during measurements to minimise electrical noise.

The signal was amplified using an adjustable dual-channel differential amplifier (GVJ, Electronics Workshop of the University Regensburg, gain 1–1000 \times , bandwidth 1 Hz–10 kHz), one channel for each electrode pair. One output channel was connected to the audio-input of the video recorder, while the other output channel was added to the output of an external signal generator (Hewlett Packard Function Generator 3314A) before reaching the audio-input of the video recorder. Every 10 s the signal generator produced a synchronisation signal consisting of a short sinusoidal burst that was set manually at about 200 Hz below the lowest baseline frequency of the interacting fish to avoid overlapping.

The signal generator was simultaneously connected to a pulse-marker (Electronics Workshop, University of Regensburg), where every incoming burst triggered a video marker that was directly added to the corresponding image at the video-input of the video recorder. After each recording session, the audio track was digitised using the sound card of a computer (Pentium III, 800 MHz) at a rate of 44.1 kHz and 16-bit resolution. Data were analysed with self-programmed software for MatLab (Version 5.1, The MathWorks). The program yielded the time-course of the EOD frequencies in which the FMs could be clearly detected (± 0.3 Hz) and localised in time (± 25 ms) separately for each fish. Independently, the motor behaviour was monitored thanks to the video images and assigned to a certain time with a maximum accuracy of ± 20 ms.

GFRs and motor behaviour were put together for statistical analysis only post hoc so that a possible observer bias (the assumption of GFRs as a kind of submissive signal) could be ruled out. The synchronisation of both data pools was very reliable thanks to the simultaneous audio and video markers, with a maximum error of ± 25 ms.

Motor behaviour

Interactive behaviour was broadly defined as every behaviour occurring when the observed fish was within less than two times its own total length to the other fish. Non-interactive behaviour comprised the rest.

Signal behaviour

Two complementary variables were taken as measurement for the GFRs similar to those used by Engler et al. (2000) to classify chirps in *A. leptorhynchus*. The first dependent variable, the “duration”, was the time a fish spent modulating its EOD frequency. All measurement points deviating at least 0.5 Hz from the previous one were added and divided by the total number of measurement points in that interval.

The second dependent variable was the “amount of the EOD frequency shift”, comparable to the “relative frequency deviation” used by Engler et al. (2000), but the deviation measured here did not have a fixed reference level or baseline frequency. Instead, I took the absolute value of the difference between the EOD frequency measured at each point and the mean within the given time interval divided by the total number of measurement points in that interval.

For longer intervals a subdivision was necessary because of the irregularity of the EOD frequency in interactive contexts. In contrast to the great frequency stability known for wave-type weakly electric fish (Fig. 1A), it is almost impossible to find a stable baseline frequency when the fish is interacting with another conspecific (Fig. 1B). By subdividing longer sequences in 5-s segments the variability of the EOD frequency was minimised so that the mean was a reasonable reference point for the calculation of the amount of the EOD frequency shift within the segment. Steep FMs lasting less than 200 ms were filtered out to exclude chirps from the data set.

To summarise, one could say that GFRs, as interpreted here, were not a qualitatively delimited FM, but rather quantitatively inferred from both dependent variables, the FM duration and the amount of the EOD frequency shift.

Two additional variables were also used, namely the inter-quartile range (IQR) and the kurtosis of the distribution curve of the EOD frequency. They are easily understandable, but they are unfortunately not very sensitive to small variations at the tails of the distribution curve. They were therefore only used to obtain an overview of the EOD frequency changes over long time sequences. The kurtosis values were previously standardised to a range of 70 Hz centred at the value of the mean EOD frequency of the given interval to allow meaningful comparisons.

IQR and kurtosis provide us with complementary information about the frequency distribution histogram of the EOD frequency. The former can be described as an indicator of the sparseness of the data at the tails of the distribution histogram and the latter as an indicator of the convexity degree of the same histogram. The higher the kurtosis value and the lower the IQR value, the shorter the tails of the distribution histogram and the steeper the distribution around the median, in other words, a limited variability of the data.

Results

Fish hierarchy

Fish hierarchy was assessed on account of two different variables: the number of butts received and directed to the other fish, and the approach-retreat ratio. This ratio represents the total time spent swimming towards the opponent divided by the total time spent swimming away from the opponent. It was assumed that a dominant fish would butt the other more often and spend more time approaching the neighbour than swimming away from it. The result was a list of hierarchical relationships without contradictory values in both variables, and mostly coherent with the fish size measured as body length (see Table 1). The only exceptions were fish 5 and 6, where the smallest individual turned out to be dominant.

GFRs in social contexts

The following question was the first to be addressed: does *A. albifrons* modulate the frequency of its EOD to a greater extent during the experimental than during the

Fig. 1 Complete time-course of the electric organ discharge (EOD) frequency of fish 1 (dominant, grey line below) and fish 2 (subdominant, black line above), during the control phase (A) and the experimental phase (B). An increase in the EOD frequency variability is most obvious in the subdominant fish

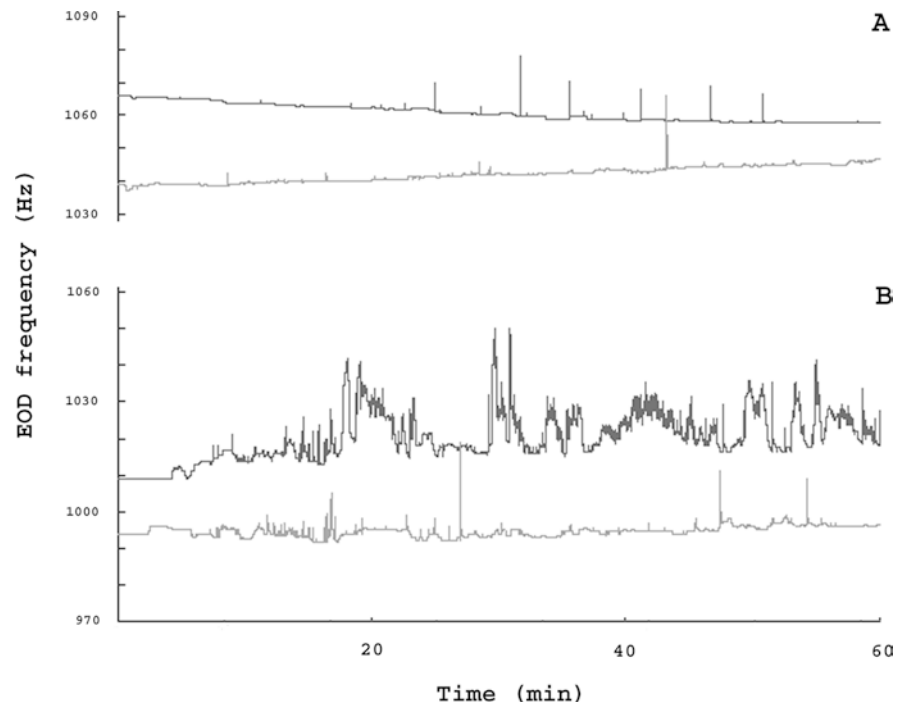
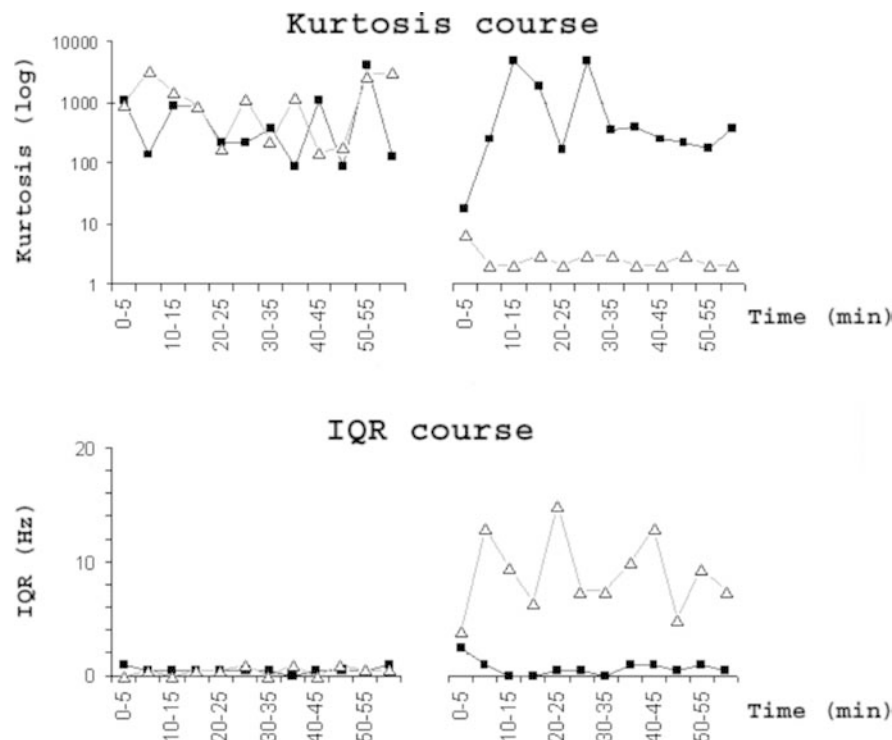


Table 1 The fish hierarchy (fourth column) is assessed considering the number of butts received, the proportion of time spent swimming to and swimming away from the opponent, and body length. The average electric organ discharge (EOD) frequency measured for each individual is attached in the fifth column

	Received butts	Approach-retreat ratio	Body length (cm)	Hierarchy	Average EOD frequency (Hz)
Fish 1 vs. 2	19 vs. 37	6.1 vs. 0.2	25.2 vs. 21	Fish 1 > 2	1019 vs. 1040
Fish 3 vs. 4	1 vs. 100	2.2 vs. 0.7	23.5 vs. 19.3	Fish 3 > 4	1033 vs. 1206
Fish 5 vs. 6	143 vs. 165	5.7 vs. 0.5	28.9 vs. 32.8	Fish 5 > 6	938 vs. 852
Fish 7 vs. 8	107 vs. 114	3.7 vs. 3.0	28.3 vs. 27.4	Fish 7 > 8	1028 vs. 1156
Fish 9 vs. 10	0 vs. 49	29.5 vs. 0.1	27.5 vs. 22.5	Fish 9 > 10	1195 vs. 987
Fish 11 vs. 12	0 vs. 18	4.8 vs. 0.2	30.0 vs. 10.1	Fish 11 > 12	1196 vs. 1167

Fig. 2 Kurtosis and interquartile range (IQR) time-course for fish 7 (black squares) and fish 8 (open triangles). The first interval series (left side) show the values during the control phase and the second series (right side) show the values during the experimental phase. Kurtosis values are standardised to a range of 70 Hz centred at the value of the mean frequency of each interval



control phase? The time-course of the EOD frequencies was first analysed for possible trends to test whether time subdivisions for the calculation of the amount of frequency shift were meaningful or unnecessary (see Materials and methods). A clear positive or negative trend was always found in the time sequence for every fish both in the control and in the experimental phase (Cox-Stuart trend test, $P < 0.01$, $n = 12$), so subdivisions proved to be necessary. The sign of the trend was not always consistent within fish pairs and neither within the same individual in the different phases.

The Wilcoxon matched-pairs signed-ranks test was chosen to test the question whether the fish modulate more in duration and amount of the EOD frequency shift during the experimental phase than during the control phase. Dominant and submissive fish were examined separately and the null hypothesis could be rejected in both cases. In the case of the submissive fish it could be demonstrated an increase both in duration and amount of the EOD frequency shift during the experimental phase ($P < 0.05$, $n = 6$), but in the case of the

dominant fish only an increase in duration was detected ($P < 0.05$, $n = 6$).

There was no detectable difference between both groups of dominant and submissive fish during the control phase (Mann-Whitney U -test, $n = 12$), but in the experimental phase submissive fish modulated their EOD frequency more than the dominant ones both in duration and amount of the EOD frequency shift (Mann-Whitney U -test, $P < 0.025$, $n = 12$).

Although the fish were not separated during the experimental phase, they did not interact constantly. The next step was to determine if *A. albifrons* modulates its EOD frequency to a greater extent when it really interacts with other conspecifics than when it does not.

In the case of the dominant fish no significant difference between the interactive and the non-interactive sequences of the experimental phase was found, neither in duration nor in amount of the EOD frequency shift (Wilcoxon matched-pairs signed-ranks test, $n = 6$). In contrast, an increased EOD frequency shift during the interactive situations in the group of submissive fish was

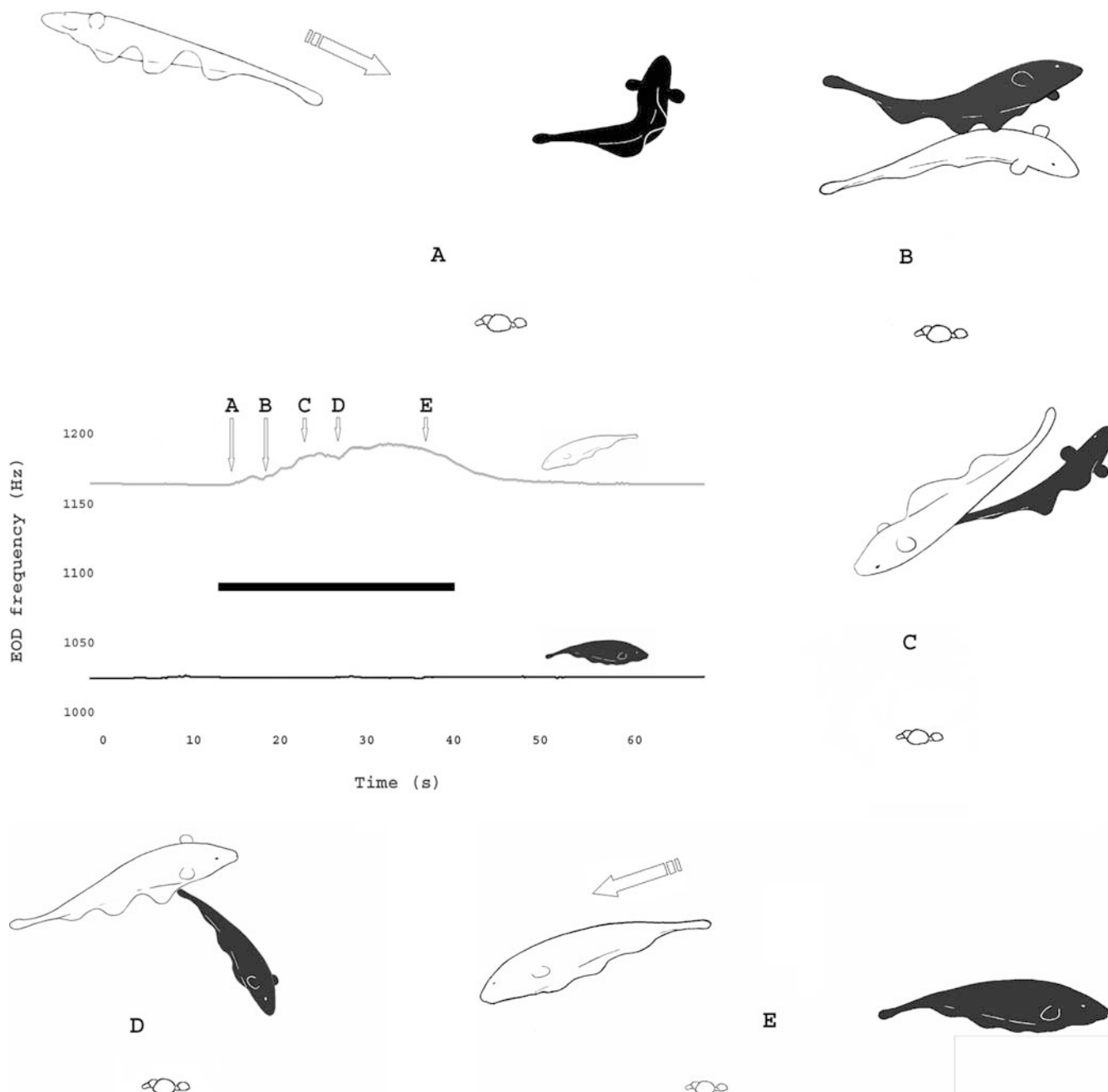


Fig. 3A–E Gradual frequency rise (GFR) during interaction after hierarchy settlement between fish 9 (dominant, *black silhouette*) and fish 10 (subdominant, *white silhouette*). **A** Fish 10 approaches fish 9 backwards and increases its EOD frequency. **B, C** Parallel and antiparallel displays. **D, E** Longer intense interaction. **E** Fish 10 swims away from fish 9 and slowly lowers its EOD frequency back to the start level. The signal behaviour of both fish during this sequence is shown in the *middle* of the figure (EOD frequency of fish 10 *above*, of fish 9 *below*). The *black bar* symbolises the interval matching the behaviour category “interaction”)

very noticeable (Wilcoxon matched-pairs signed-ranks test, $P < 0.05$, $n = 6$).

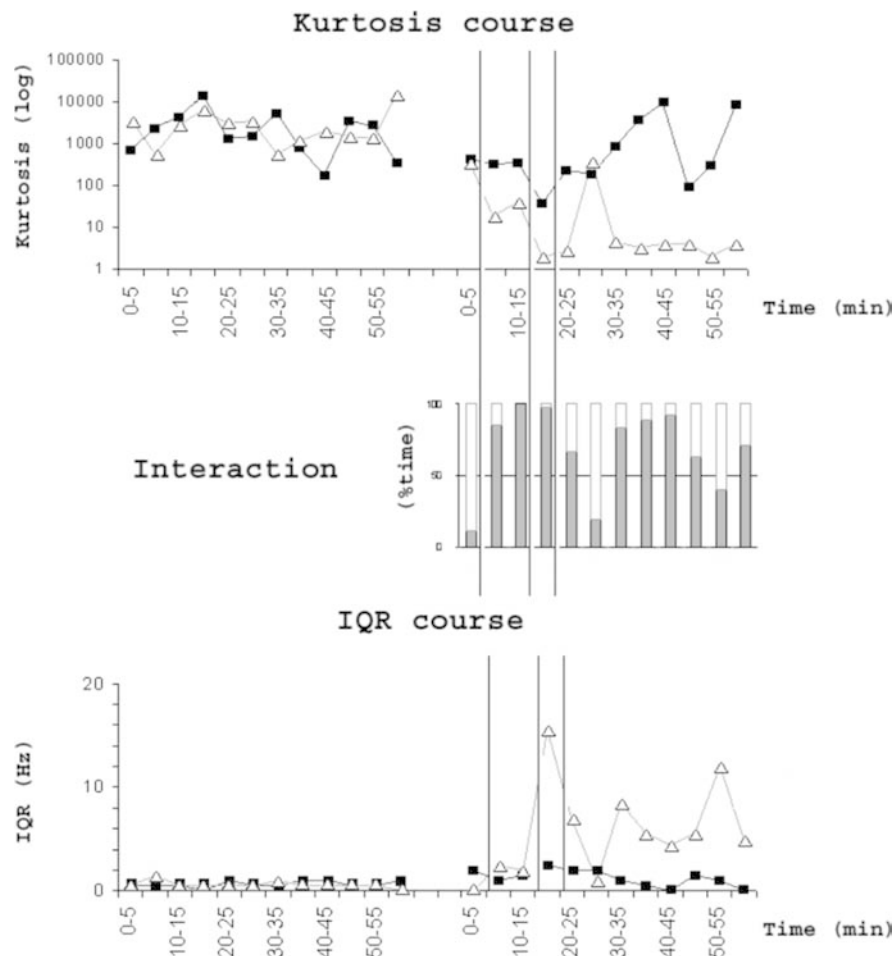
Comparing both fish groups during the non-interactive sequences, it was found that submissive fish had greater amount of EOD frequency shift (Mann-Whitney

U -test, $P < 0.005$, $n = 12$), but not a greater duration. The differences were more obvious during the interactive sequences where submissive fish modulated more than the dominant ones both in duration (Mann-Whitney U -test, $P < 0.025$, $n = 12$) and in amount of EOD frequency shift ($P < 0.005$).

Time-course of the GFRs

In the time-course analysis the results consistently showed a very low variability (high kurtosis and low IQR values) in all distribution histograms of the EOD frequency during the control phase, as anticipated by the

Fig. 4. Kurtosis, interaction and IQR time-course for fish 1 (black squares) and fish 2 (open triangles). The first interval series (left side) shows the values during the control phase and the second series shows the values during the experimental phase (right side). Kurtosis values are standardised to a range of 70 Hz centred at the value of the mean frequency of each interval. Hierarchy was assessed during minutes 5–15 of the experimental phase (vertical lines), afterwards the subdominant fish (fish 2) strongly increases its EOD frequency variability



foregoing results. During the experimental phase dominant fish kept their EOD frequency variability also at low values, while submissive fishes quickly began to increase it (low kurtosis and high IQR values). An example can be seen in Fig. 2, which shows the IQR and kurtosis values of fish 7 and 8 during control and experimental phases.

A detailed example of a typical interaction sequence after hierarchy settlement is shown in Fig. 3. The submissive fish generates a stable EOD frequency until it approaches the dominant one. During the interaction the submissive fish strongly modulates its EOD frequency and only returns to the initial level when the interaction comes to an end. In contrast, the dominant fish hardly changes its EOD frequency during the whole sequence.

Figure 4 represents the more complex case of the first fish pair (cf. Fig. 1). The histogram with the relative amount of time spent interacting during each time segment is attached as a control. A stable and low EOD frequency variability was recorded for this first fish pair during the control phase that contrasted with the higher values during the experimental phase. This was most remarkable in the case of the submissive fish, which strongly increased its EOD frequency variability. At the

beginning of the experimental phase, between 5 and 15 min, a lower variability for both fish coupled with high interaction levels is apparent. The greatest variability was met by the submissive fish 2 between 15 and 20 min coinciding with the second highest interaction level. That change in the signal behaviour of the submissive fish occurred coupled with intense aggressions. At this time fish 1 directed 39% of its “butts” towards the opponent, which answered with 37% of its own “butts”. After that interval fish 2 never attacked its opponent again. The dominant fish maintained its EOD frequency variability at a low level during the whole encounter. Low interaction levels such as observed in the first and sixth intervals were coupled with low EOD frequency variability levels in both fish.

Discussion

The positive result of the trend test for every EOD frequency time-course in every phase gave support to the decision to subdivide longer sequences into shorter segments of 5 s, in which the effect of the global trend of the curve was not so relevant for calculation of the EOD frequency shift. The underlying cause for these trends is

unclear. Active phase coupling (Langner and Scheich 1978) or JAR could be explaining that global frequency shifts (reviewed in Kramer 1990).

The first investigation addressed the question of whether the fish would modulate their EOD frequency to a greater extent during the experimental phase than during the control phase. The results demonstrated this to be only partially true. The modulation, measured as duration, was significantly higher in the experimental phase than in the control phase for both groups of dominant and submissive fish. The modulation, measured as amount of EOD frequency shift, was significantly higher in the experimental phase than in the control phase only for the submissive fish.

This result does not prove a communicative function of GFRs, but the other alternatives—a failure to reject the null hypothesis in both groups or an even greater modulation level in the control phase—would have seriously damaged the credibility of the communicative function, and this was not the case.

The second investigation dealt with the modulation of the EOD frequency during non-interactive sequences of the experimental phase in comparison with the intervals when the fish interacted directly. Once again the results supported the hypothesis of the communicative function of GFRs. Submissive fish significantly increased the amount of their EOD frequency shift during direct interactions as opposed to the dominant ones, which showed no change.

The results for the duration of the EOD frequency modulation were not so clear-cut, since there was no significant difference between interactive and non-interactive sequences either among the dominant or among the submissive fish. This result may reflect the small sample size, but it is very probable that the duration does not play such an important role as the amount of the EOD frequency shift: on the one hand, the variable “duration” is composed to a great extent of small EOD FMs of about 0.5 Hz that may be irrelevant for the fish, and on the other hand, we know these fish to be very sensitive to extremely brief but abrupt EOD frequency rises, namely the chirps. Therefore, it seems likely that the amount of EOD frequency shift in GFRs may play an essential role for communication purposes.

The time-course of the variability of the EOD frequency provided additional information. At the beginning of the experimental phase the EOD frequency variability of both dominant and subdominant fish was not very high, although it coincided with high motor interaction levels. Only after a certain time did the subdominant fish start to modulate to a very high level in comparison with the dominant fish, coupled with high interaction and aggression levels. From that moment on, the difference between dominant and subdominant fish was most obvious. The submissive fish reduced its EOD frequency variability only during the sequences when they interacted least.

A possible interpretation is that the hierarchy is not yet assessed at the beginning of the interaction. There-

fore, both fish groups would interact most, but show little differences in their EOD frequency variability. Once the hierarchy is established, the subdominant fish modulate their EOD frequency to a much higher degree, while the dominant keep their EOD frequency much more stable. This is also consistent, on a smaller time scale, with the signal behaviour in a typical interaction after hierarchy assessment as described in Fig. 3. Therefore, all results lead to the same conclusion: GFRs are mostly produced by subdominant fish and mostly during interactions. The hypothesis of the GFRs being signals involved in communication and probably indicating submission is clearly supported by these results.

Finally, I want to point out the possible relationship between the general activity level of the fish and the variability in modulation of its EOD frequency. The increased variability of the signal could be simply explained as a consequence of its increased motor activity, a more parsimonious hypothesis than that implying an active communicative function. This alternative hypothesis is severely discredited by the previous work of Zupanc et al. (2001) and two of the results described here. During interactive sequences submissive fish modulated their EOD frequency to a greater extent than the dominant fish. In contrast, during these interactive sequences the general motor activity was similar for both fish groups (see Fig. 3). Additionally, the increase in the EOD frequency variability was only obvious after the hierarchy was settled (Fig. 4, fourth time interval); before, both fish were interacting at high levels of motor activity and none of them showed an increased EOD frequency variability (Fig. 4, second and third time intervals). Definitive proof of the communicative function of the GFRs requires playback experiments to assess the effect of GFRs on the receiver fish. Further research in this direction promises to be fruitful since evidence supporting that hypothesis has now doubtless increased.

The quantitative approach of analysing GFR proved to be a successful alternative to former methodologies. The loss of quantitative information inherent to any clustering is prevented and changes in the EOD frequency variability are prominent even if they do not correspond to any concrete class structure.

An analysis of this type may be particularly rewarding early on in investigations of signal behaviour, to detect underlying relationships between motor behaviour and signal characteristics that might be masked by following subdivisions. A next step might be to try to classify the signals using cluster analysis or self-organising maps.

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