



Changes in signalling during agonistic interactions between male weakly electric knifefish, *Apteronotus leptorhynchus*

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Signals emitted preceding and during combat can aid in sequential assessment of opponent quality and motivation. Signal reliability can be maintained by physical constraints, by costs of production or receiver retaliation, or can be cost-free, when contestants have a common interest. In staged dyadic contests over a shelter, male brown ghost knifefish, *Apteronotus leptorhynchus*, modulate the frequency of their electric organ discharge (EODF) and perform increasingly costly behaviours as fights escalate. Relative body length was the best predictor of fight duration and victory, and although there were initially no differences in electrical signalling rates between contestants, through the course of the interaction ultimate winners made increasingly more abrupt EODF increases ('chirps') and fewer gradual frequency rises ('GFRs') than losers. This is consistent with previous hypotheses that chirps signal aggression and dominance, whereas GFRs indicate submission. However, fine temporal analysis revealed that both signal types are good predictors of impending attack: paradoxically, just prior to bouts of combat, combat initiators gradually increase EODF significantly more than receivers and continue to do so throughout the bout. We discuss the putative functions of these signals.

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Agonistic encounters often involve threat displays that presumably help contestants gauge each other's relative resource-holding potential (RHP: fighting ability and/or motivation) without having to incur the potentially lethal costs of combat (Huntingford & Turner 1987; Bradbury & Vehrencamp 1998). Fights do escalate when assessment becomes more difficult however: the sequential assessment model (Enquist & Leimar 1983; Enquist et al. 1990) predicts longer and more costly fights between individuals that are more closely matched in RHP than those with obvious differences in quality. Despite many models generated to explain variation in signal structure and function, much remains unresolved about what information is contained in agonistic signals and under what conditions they serve in escalating or resolving conflicts

(Maynard Smith & Harper 1988; Vehrencamp 2000; Hurd 2001).

An ongoing issue in animal communication theory is understanding how signal reliability is maintained when a conflict of interest between two individuals provides an incentive to cheat by exaggerating or lying about one's quality (e.g. Johnstone 1995). As a result, recent signal classification schemes have focused on examining the nature of costs imposed on the sender, whether in the form of a physiological constraint, a production expense or a risk of retaliation from the receiver (Vehrencamp 2000; Maynard Smith & Harper 2004; Hurd & Enquist 2005). Performance signals (Hurd & Enquist 2005) are those that are directly constrained by an individual's RHP and are thus unbluffable. For example, the lowest frequencies in frog calls are achievable only by larger males, as only larger males have the capacity to harbour the larger vocal cords necessary to create vibrations of sufficiently long wavelengths (Gerhardt 1994). Unlike performance signals, strategic signals are those that all signallers can make, but whose reliability can be maintained by costs of production

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(handicap signals; e.g. Zahavi & Zahavi 1997) or receiver retaliation (conventional signals; e.g. Guilford & Dawkins 1995; Vehrencamp 2001). Strategic signals may also be cost-free if sender and receiver have a common interest in avoiding conflict (Vehrencamp 2000; Hurd & Enquist 2005). These signals may indicate not only aspects of a sender's fighting ability such as body size and stamina, they may also contain information about motivation to attack (Zahavi & Zahavi 1997), which varies temporally and is expected to take the form of a graded behavioural signal (Vehrencamp 2000). Darwin (1899) was the first to note that signals conveying opposite states, such as aggression and submission, often occupy opposite extremes of some variable in signal space, presumably reducing receiver error (Morton 1977; Hurd et al. 1995).

The weakly electric brown ghost knifefish, *Apteronotus leptorhynchus*, provides an intriguing system to study changes in signalling during agonistic encounters. During dyadic interactions and when played back conspecific electric organ discharge frequency (EODF) mimics, all brown ghosts produce modulations of categorically distinct frequency excursion, duration and onset slope. Signals with relatively rapid onset and offset (and variable frequency excursion and duration) are termed 'chirps'. Playback stimuli of similar frequency to an individual's EODF elicit bursts of ~ 15 ms, ~ 60 Hz chirps that are hypothesized to function in intrasexual aggressive communication (type II chirps; e.g. Engler et al. 2000; Engler & Zupanc 2001; Triefenbach & Zakon 2003). More gradual frequency rises (GFRs) of much lower-frequency excursion but often longer duration have been presumed to function in signalling submission (Hopkins 1974; Serrano-Fernandez 2003; Triefenbach & Zakon 2003). However, recent evidence suggests that GFRs are proactively emitted in aggressive contexts (Tallarovic & Zakon 2005), conflicting with their proposed role in submissive signalling.

While previous studies on weakly electric fish have examined agonistic behaviours in other species (Black-Cleworth 1970; Bell et al. 1974; Westby 1974, 1975; Crockett 1986; Hagedorn & Zelick 1989; Moller 1995; Franchina et al. 2001; Terleph 2004), in this paper we provide a more detailed analysis, correlating EOD frequency modulations with overt behaviour and recording when each signal type is used and by whom, thus allowing speculations on signal function. Despite numerous studies, such information usually is sparse. We describe putative performance and strategic signals and examine how two contesting males change their use of these signals over the course of bouts of escalated assessment. We tested whether (1) contest duration, physical escalation and (2) electrical signalling rate are related to status asymmetry between opponents. We looked for general correlations between signalling rates and relative status over the course of an entire trial, but also asked whether electrical displays signal impending attack by comparing display rates before, during and after individual bouts of aggressive physical contact on a narrower temporal scale (within several seconds preceding and following escalated combat bouts). We predicted (1) contest duration and the degree of escalation to correlate inversely with opponent size asymmetry and (2) signal types to correlate with the

variations in number of attacks of each combatant at each stage. Thus, as opponents increasingly clarify their relative status, the signals they emit should reflect this loss in ambiguity.

METHODS

Animals

Fish were purchased from a commercial vendor (Segrest Farms, Gibsonton, FL, U.S.A.) and isolated in their home tanks (dimensions: $W \times H \times L$: $23 \times 20.5 \times 49$ cm; temperature: $26 \pm 2^\circ\text{C}$; conductivity ~ 400 mS/cm) for several months. We selected males ($N = 14$) initially based on their morphology (Hagedorn 1986). We then measured their body lengths (20.9 ± 0.4 cm, range 17.6–23.0 cm) and weights (22.8 ± 0.8 g, range 19.7–28.6 g) and confirmed sex by recording their EODFs (852 ± 11 Hz, range 802–943 Hz); adult males typically discharge at frequencies greater than 800 Hz. We randomly grouped 14 males into seven pairs, recording their body lengths.

Behavioural Arena and Recording Procedures

Dyads were tested in a neutral arena that was a rectangular 70-litre aquarium ($W \times H \times L$: $30 \times 20 \times 60$ cm) containing water from their home tank system. Five of these seven dyadic interactions were filmed in incandescent light with a hand-held Sony PC-9 Mini-DV camera, and electrical activity was recorded at a sampling rate of 22 050 Hz (16-bit) with a PC (Cool Edit, Syntrillium, Phoenix, AZ, U.S.A.) through a pair of Ag electrodes attached to the short sides of the tank with suction cups. To later synchronize the video and audio tracks, we filmed the monitor screen showing the Cool Edit audio timeline (in bins of 33 ms/frame) at the beginning and end of a continuously filmed trial and imported video and audio into Vegas Video (Sonic Foundry, Madison, WI, U.S.A.). Here we matched the times displayed on the filmed computer screen with the time of the computer-recorded audio track.

Procedure for Staged Interactions

Each dyad was simultaneously transferred to the neutral arena. Individuals were allowed nontactile interactions across a plastic mesh barrier dividing the arena into two halves (Tallarovic & Zakon 2005) for 5–10 min before the barrier was removed and replaced by an opaque plastic tube, a preferred shelter (Dunlap & Oliveri 2002) over which fish will fight. We then recorded their behaviour and electrical signals until a winner was determined. We defined the winner as the individual who spent at least 10 s and 10 times more time than the other fish in and/or within 10 cm of the tube, without being approached.

To facilitate analysis and because different periods of time elapsed until determination of the winner, we quantified behaviour during four periods of this interaction (shown in Fig. 1). The first was the 'barrier' phase,

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