

The electric fish *Brachyhypopomus pinnicaudatus* produces jamming avoidance responses to signals that are harmonically related to its own discharges

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Summary

Jamming avoidance responses (JARs) are exhibited by pairs of pulse type electric fish that discharge with similar frequencies whenever their individual pulses are about to coincide: responses consist of the transient shortenings in inter-discharge intervals in the fish with the higher frequency. This study describes and models novel forms of JARs observed in sexually mature male or female *Brachyhypopomus pinnicaudatus*.

One novel JAR was observed in male–female pairs in their natural habitat. It happened when the baseline frequencies were not similar but, rather, when one was almost twice that of the other; moreover, the transient interval shortenings occurred not in the fish with the higher frequency but in the slower one.

Transient interval shortenings similar to those in all natural JARs were observed in individual fish in tanks and submitted to periodic electrical pulse trains. They happened not only when pulse frequencies were slightly

lower than the unperturbed frequency emitted by the fish but also when slightly lower than the frequency's sub- or higher harmonics (e.g. one half or twice).

The proposed model satisfactorily reproduces all experimental observations. In it, forthcoming inter-pulse intervals reflect the differences between the cophasings of pulses that arrive within the 'sensitive windows' belonging to either consecutive (i.e. one and the next) or alternating (e.g. every other, every three) intervals.

Paired pulse fish embody interacting oscillators, and, in particular, JARs embody either quasiperiodic phase walk-throughs and intermittencies or periodic and locked forms. Hence, their study would profit by the powerful theories and approaches advanced by nonlinear dynamics.

Key words: electric organ discharge, jamming avoidance response, electric fish, inter-pulse interval, transient interval shortening.

Introduction

South and central American electric fish use a specialized electric organ in their tail to generate an electric organ discharge (EOD). The EOD generates in the surrounding water a field detected by electroreceptors in the skin of the fish. Primary afferent fibers transmit this information to the electric lobe and other sensory nuclei, in turn connected to pre-pacemaker centers that provide direct synaptic input to the medullary pacemaker centers controlling the electromotoneurons: thus, a closed loop is involved (for comprehensive reviews, see Carr and Maler, 1986; Bastian, 1986). This active electrosensory system has the main function of electrolocation in the watery environment, recognizing distortions of the EOD waveform by surrounding objects, as well as that of social electrocommunication using EOD rate modulations.

Electric fish species have been classified according to their EOD. In wave-type species, the duration of the individual

discharges are of the same order as the intervals between them and the EODs are quasi-sinusoidal. In pulse-type species, the individual discharge is very brief in comparison with the intervals.

When several fish are close to one another, the discharges of one fish may perturb and jam the electrolocating abilities of others, regardless of whether socially interacting or not. Such interferences are minimized by changes in their EOD called jamming avoidance responses (JARs; Heiligenberg, 1977, 1986, 1991). JAR strategies differ with species type and, in some cases, between species of the same type (Heiligenberg, 1986). The best-understood strategy is that of the wave-type electric fish *Eigenmannia* and *Apteronotus leptorhynchus* (Watanabe and Takeda, 1963; Bullock et al., 1972; Heiligenberg, 1986; Kaunzinger and Kramer, 1995; Metzner, 1999). To avoid interference between the respective waves, the fish with the higher EOD frequency slightly increases its

frequency, while the fish with the lower frequency may slightly decrease it. This increases the frequency difference, prevents jamming and protects electrolocation. This type of JAR is also observed using an artificial jamming sinusoidal stimuli whose frequency is close to higher harmonics of the fish frequency but not to their subharmonics (e.g. Kaunzinger and Kramer, 1995). Other reports also indicate that wave-type fish can synchronize their EOD to sinusoidal stimuli during episodes where the EOD–stimulus phase relations remain constant (Gottschalk and Scheich, 1979).

In pulse-type species, EODs consist of short pulses separated by comparatively long intervals, and jamming occurs when two fish discharge simultaneously. Typical JARs arise when temporal coincidences are imminent and the fish whose EOD has the higher rate briefly shortens its EOD intervals, thus reducing the probability of jamming (Heiligenberg, 1974, 1976, 1986; Scheich et al., 1977; Heiligenberg et al., 1978; Capurro et al., 1998, 1999; Capurro and Malta, 2004). In some species, these transient interval shortenings in the faster fish may associate with simultaneous lengthenings in the fish with the lower rate (Heiligenberg, 1986; Perrone, 2003).

Studies of electromotor responses under jamming with artificial pulse trains have shown that the pulse-type fish is particularly sensitive to pulses that coincide with the EOD or occur just prior to it (e.g. 1 ms). These pulses distort the perceived map of the environment and perturb the electromotor response. The electrolocation performance tolerates well a single pulse–EOD coincidence and deteriorates only after multiple coincidences have involved successive EODs (e.g. 3–6 EODs; Heiligenberg, 1974, 1976, 1986; Heiligenberg et al., 1978).

Studies of the response to artificial pulses in pulse-type South American species have shown that the necessary condition for a single pulse to have an effect on the fish EOD is that it arrives within the late portion, referred to as the ‘sensitive window’, of the EOD period; thus, at least a minimum time after the preceding EOD referred to as ‘phase’ or ‘delay’ or, equivalently, at most a maximum time (5–15 ms) before the following EOD referred to as ‘cophase’ (Capurro et al., 1998). When this happens, the pulse induces a shortening of several successive EOD intervals, starting in the interval that follows the one containing the pulse. The maximum shortening is usually reached one or two intervals after the beginning of the response and from this point the intervals return exponentially to their value before the perturbation (Capurro et al., 1998). When two or more pulses arrive in sensitive windows, veritable JARs that involve 4–10 shortened intervals are observed. The JAR happen only when the successive phases of the pulses relative to the EOD slowly increase: there is, therefore, a sensitivity to the direction of the phase and cophase shifts (Heiligenberg, 1974; Baker, 1980, 1981; Capurro et al., 1999).

Some South American pulse-type species, in addition to the JARs with transient EOD interval changes described above, also perform JARs involving sustained EOD frequency shifts and synchronization bouts during which phases remain almost constant (Heiligenberg, 1974; Westby, 1979, 1981; Capurro et al., 1999; Perrone, 2003).

The present paper has two related purposes. The strictly biological purpose is to describe JARs not yet reported as far as we know: they arise in pairs of pulse-type fish in their natural habitat and are evoked by signals harmonically related to the EOD. The formal purpose is to describe a mathematical model that reproduces the transient interval shortenings evoked in an isolated fish by pulse trains at harmonic and subharmonic frequencies with respect to the EOD.

Materials and methods

Recording of interactions in the natural environment and the laboratory

The field recording that motivated the present study was performed immediately after sunset (the active moment in the circadian cycle of the fish) during the breeding season at the natural habitat (Laguna del Tigre, Departamento de Treinta y Tres, Uruguay) (Capurro, 1999; Silva, 2002; Perrone, 2003). A pair, one male and one female, of sexually mature 10–15 cm-long *Brachyhyppopomus pinnicaudatus* (Hopkins) (Hopkins et al., 1990) was captured and allowed to move freely in a fenestrated plastic tank (50 cm×50 cm×20 cm height) with circulating lake water (conductivity 300 μ S, temperature 20–25°C). Two pairs of electrodes, consisting of 45 cm-long wires along the four bottom edges of the tank, detected the EOD voltages. Voltage differences were measured between each pair of parallel wires, thus the paired electrodes were oriented orthogonally. Voltages were amplified and displayed on an oscilloscope and stored on a stereo audio tape.

Other recordings were obtained in the laboratory after sunset from other sexually mature fish pairs in a tank filled with water from the lake and using the same recording and display setups. Storage was on stereo video tapes.

The voltage records were digitized at 5–20 kHz. A peak detection algorithm recognized the peak of the EOD’s head positive wave. Although the recorded voltages depend on the position of the animals relative to the electrodes, generally the male has higher voltages. As two orthogonal electrode pairs were used, amplitude differences in at least one of the pairs could often be found. Hence, the discharges of the male and the female were discriminated by amplitude, within data segments where the voltage reached by the two EOD peaks was clearly different to the naked eye. Lists, one for the male and another for the female, of the instants when each EOD pulse occurred were obtained and used to construct the interval and delay plots and to detect and count the number of simultaneous discharges.

When the two EODs coincided in time it was possible to miss one of them because the two peaks may appear as only one in the digitized file. However, when comparing the digitized and analog records it was clear that the sampling rate was sufficiently high to avoid most of these errors. In the few cases where coincidences were not distinguished in the digitized files, the same time was adjudicated to both signals. In certain cases, the position of the animals made detection of the positive EOD peak of one fish impossible. As, in some of

these cases, the negative peak of the fish could be easily detected, the time between the positive and the negative EOD peaks was subtracted from the list of discharging times of the fish, so as to consider always the peaks of the positive wave.

Mature animals during the breeding season exhibit sexually dimorphic EOD waveforms (Hopkins et al., 1990; Silva, 2002). The head negative wave lasts longer and has larger amplitude in the male, providing a reliable criterion for separation in voltage recordings. Using this criterion, we checked whether all individual discharges had been detected and assigned correctly to the male or the female. Errors apparent to the naked eye were corrected by typing into the ASCII files of the EOD times.

Stimulation with artificial pulses

Electric pulses, evoking in discharging fish responses similar to those observed in natural interactions, are used widely to study pulse-type fish (e.g. Heiligenberg, 1974; Westby, 1975; Heiligenberg et al., 1978; Baker, 1980, 1981). Stimuli were tested in sexually mature isolated fish (10–12 cm length) at day time (room temperature 15–20°C). Individual fish (male or female) were placed in a tank (50 cm×25 cm×25 cm height). They spontaneously entered a plastic tube, open at both ends, and did not change their position during the recordings. The recording electrodes were a pair, one close to the head and the other to the tail, and the recorded signal was amplified and displayed on an oscilloscope. The stimulating pair was one positive 4 cm lateral from the tail and one negative 4 cm lateral from the head. A stimulator delivered square, 2 ms-duration pulses such that the head electrode was negative with respect to the first wave of the fish EOD and arising at equal intervals with different frequencies. Pulse voltage was set to about half that of the EOD head negative wave. This arrangement emulates the EOD of a second fish placed at a short distance from the first.

As the oscilloscope was triggered with the EOD, the relative position of the pulses on the screen served to adjust their generation to the beating frequency. Using this guide, the stimulus frequency was set with a hand-wheel to exhibit ratios of 1:1, 2:1, 3:1 and 1:2 relative to the EOD (corresponding to different harmonics and to the first sub-harmonic). Observations lasted 1–5 min. As explained above, records were obtained and digitized, events (EODs, pulses) were identified, and lists with the respective times of occurrence were obtained. These lists served to construct the joint ‘interval and delay’ plots whose abscissa is ongoing time. Each point in the graph of intervals corresponds to a single EOD, the abscissa corresponds to the instant when that EOD occurred and the ordinate corresponds to the interval between it and the preceding EOD. Each point in the graph of delays corresponds to a single pulse, the abscissa corresponds to the instant when that pulse occurred and the ordinate corresponds to the interval between it and the preceding EOD (delay or phase).

Mathematical model

A model referred to here as X and published previously first

used autoregressive (AR) procedures to reproduce the resting EOD (see Unperturbed inter-discharge intervals; Capurro et al., 1998, 1999, 2001). In addition, it realistically postulated that only single pulses in a sensitive window far from the last EOD event and close to the anticipated next one would shorten the next intervals (see Response to single pulse). It also postulated that JARs would be triggered only if consecutive pulses swept consecutive sensitive windows from left to right (see Response to pulse trains); this meant that intervals separating each pulse from the preceding EOD (phases or delays) slowly increased from one to the next; i.e. intervals to the forthcoming EOD (cophases or co-delays) slowly decreased. Model X accounts for the transient interval shortenings observed in a *Gymnotus carapo* after a single pulse arrives within the sensitive window, as well as for the response to trains of pulses at frequencies close to that of the EOD.

In *Brachyhypopomus pinnicaudatus*, model X reproduced the interaction in which the two fish discharged at close rates. However, it did not reproduce findings when the frequency of the second fish EOD or of the pulse trains was twice as fast or twice as slow. So as to accommodate these failures, a new model, referred to as Z+, will be proposed. Model Z+, as with model X, used AR procedures to reproduce the resting EOD and postulated that only pulses arriving in a sensitive window would shorten the intervals. Two other rules were incorporated. One rule allowed the perturbing events (EODs, pulses) in consecutive sensitive windows to not be consecutive, so that other perturbing events arrive between two consecutive sensitive windows. This means that perturbations can exhibit higher frequencies than the EOD, including those slightly lower than two or more times that of the fish. It means also that the sweeping velocity, i.e. the changes in phases and cophases, is evaluated for pulses within successive, not necessarily consecutive, sensitive windows. It is as if the fish, when deciding whether to generate a JAR, concentrates on the pulses within sensitive windows and ignores those outside of it. The model with this first addition is referred to as Z. The final rule that completed Z+ was that JARs would be triggered when pulses swept from left to right (increasing delays or phases, decreasing cophases) successive sensitive windows that did not have to be consecutive. This means that perturbations can exhibit lower frequencies than the EOD, including those slightly lower than half that of the fish. In the following, the mathematical formulation of models X, Z and Z+ is presented together with the parameter set used in the simulations.

Unperturbed inter-discharge intervals

In both models (X and Z+), each inter-pulse interval of the spontaneous EOD is assigned according to the following equations:

$$I_{n+1} = M_{n+1} + N_{n+1}, \quad (1)$$

$$N_{n+1} = \rho_1 \times N_n + \rho_2 \times N_{n-1} + \rho_3 \times N_{n-2} + \rho_4 \times N_{n-3} + \sigma \times W_{n+1}, \quad (2)$$

where I_{n+1} is the (n+1)th interval, and M_{n+1} is the mean of all preceding intervals. N_{n+1} , representing the variability of the

spontaneous discharge, is computed with the AR scheme of equation 2, where the W_i are independent identically distributed truncated centered Gaussian random variables, σ controls the noise amplitude and the coefficients ρ_i control the level of autocorrection (Capurro et al., 2001).

Response to single pulse

The ‘cophase $C(t)$ ’ (or co-delay) of a perturbing pulse is the interval from it to the next EOD. The ‘phase’ or ‘delay’ of the pulse is the interval from it to the previous EOD and will be used in the interval and delay plots. The interval containing the pulse equals the sum of the delay or phase plus the cophase. In both models, the response of the system to a pulse arriving at time t_0 between the n (th) and $(n+1)$ th discharges depends on its location within the interval between these discharges, thus on its delay and cophase $C(t_0)$; this model uses the cophase but could be enunciated equivalently in terms of the delay.

So as to be effective and shorten the following intervals, pulses must arrive within the sensitive window: this is represented by the condition that the cophase must be smaller than a value C_H called ‘maximal cophase’. When $C(t_0) < C_H$, the means of the following inter-discharge intervals are shortened according to:

$$M_n^+ = M_n^- - G_1[C(t_0)], \quad (3)$$

$$M_{n+1}^+ = M_{n+1}^- - G_2[C(t_0)], \quad (4)$$

where M_n^+ and M_{n+1}^+ represent the new values of the mean intervals after the perturbation, while M_n^- and M_{n+1}^- are those before the perturbation. G_1 and G_2 are piece-wise linear functions given by:

$$G_i(X) = 0, \text{ if } X > C_H, \quad (5)$$

$$G_i(X) = \lambda_i [(C_H - X)/C_H], \text{ if } B < X < C_H, \quad (6)$$

$$G_i(X) = \lambda_i X [(C_H - B)/(BC_H)], \text{ if } 0 < X < B, \quad (7)$$

where λ_1 , λ_2 and B ($< C_H$) are positive constants that depend on the strength of the stimulation. After an interval shortening, if no further perturbation occurs during the sensitive window, the following mean intervals are computed according to:

$$M_{n+1} = (1 - \alpha) \times M_n + (\alpha \times M^*), \quad (8)$$

where α is the recovery factor, and M^* is the natural interval. Hence, following interval shortenings due to the perturbation, their means, M_n , return monotonically to M^* .

Response to pulse trains

Other conditions must be complied with for pulse trains (i.e. two or more pulses) to evoke the interval shortenings; these conditions differed in models X and Z. In model X (Capurro et al., 1998), the condition reads:

$$0 < C(i) - C(i+1) < K, \quad (9)$$

where $C(i)$ and $C(i+1)$ are the cophases of the i th and $(i+1)$ th pulses, falling in the sensitive windows of two consecutive EOD intervals; no other pulses arrive between the i th and

$(i+1)$ th pulses, which, therefore, are consecutive [in the particular cases where the $(i+1)$ th pulse falls in the sensitive window but the n th does not, the response also occurs]. This condition requires that, for EOD interval shortenings to occur, consecutive pulses must sweep consecutive EOD cycles from left to right advancing by less than K . Parameter K prevents responses to fast left to right sweeps and to right to left sweeps at the moments when the cophase jumps from a large value (just under that of the interval) to a small value close to 0. At this moment, $0 < C(i) - C(i+1)$ is met (i.e. the cophases are decreasing) but not $C(i) - C(i+1) < K$.

In model Z, the condition to evoke interval shortenings reads:

$$0 < C(i) - C(i+j) < K, \quad (10)$$

where $C(i)$ and $C(i+j)$ are the cophases of the i th and $(i+j)$ th pulses falling in the sensitive windows of two consecutive EOD intervals; $j-1$ pulses arrive between the i th and $(i+j)$ th pulses, which, therefore, are not necessarily consecutive. Hence, for the JAR at close EOD periods $j=1$ (Fig. 2), and for the JAR in which the EOD period of the slower fish is close to twice the period of the faster fish (Fig. 2B) $j=2$ [in the particular cases where the $(i+1)$ th pulse falls in the sensitive window but the n th does not, the response also occurs].

For low-frequency stimulation, not all sensitive windows receive pulses. For this reason, the condition for interval shortenings was further modified, giving rise to the model Z+. The pulses i th and $(i+j)$ th need not arrive in consecutive sensitive windows; i.e. between the two pulses there may be one (or more) EOD cycles that did not receive a pulse. In other words, the condition that the pulses must arrive in consecutive sensitive windows to evoke a response was relaxed. The impact of this last property of model Z+ is that it allows reproduction of the response to pulse trains at sub-harmonic frequencies with respect to the EOD.

Selection of parameter values

Parameter values were maintained invariant in each simulation with the exception of M^* values, which changed from one to another. The AR coefficients, ρ_i , were estimated from the EOD intervals of an isolated fish using methods in Capurro et al. (2001). The parameters that control the magnitude of the interval shortenings, λ_i , as well as those that control the amplitude of the background variability (σ) and the recovery of the intervals after an interval shortening (α) were set to reproduce the record in Fig. 2B. C_H and B , which affect the sensitive window as judged by the interval shortening vs cophase curve, allowed phase-cophase plots similar to those of a fish stimulated with low-frequency (0.2 Hz) artificial pulses (e.g. Capurro et al., 1999); they reproduced adequately interval and delay plots such as that in Fig. 2B. The commonly used parameter set was the following: $\lambda_1=2.9$ ms; $\lambda_2=3.0$ ms; $C_H=6.0$ ms; $B=0.2$ ms; $K=5.0$ ms; $\alpha=0.4$; σ of the slow train=0.3; σ of the fast train=0.0025; AR coefficients of both trains, $\rho_1=0.6662$, $\rho_2=0.2108$, $\rho_3=0.0685$, $\rho_4=0.0052$.

The critical interval and frequency ratios are those of the

EODs when not perturbed by pulses. M^* , the mean interval without perturbations, varied in each numerical simulation. The values used for each fish are provided in the figure captions. As such values were not available in the field, they were estimated from the interacting fish record using the low-variability EOD period of one fish and the portions without shortened intervals between JARs in the other.

Coincidences

As suggested by behavioral work, we call ‘coincidence’ the presence of a perturbing event within 1 ms back and/or forward from a reference EOD event. ‘Successive coincidences’ are those that involve several consecutive EODs; they are ‘double’, ‘triple’, etc. when happening in two, three, etc. consecutive EODs. Coincidences were counted with a program based on a cumulative algorithm that scanned the series of discharging times from fish or numerical simulations. Every time a single coincidence was repeated in the next EOD cycle, the algorithm added a double coincidence to the list (plus a second single one); if the coincidence repeated again in the following cycle, a triple coincidence was counted together with a second double coincidence and a third single one, and so forth. The slower fish EOD was used as the reference event. When both fish exhibit almost the same instantaneous frequency, the number of coincidences is the same using the fast or the slow fish as reference, but this does not hold in cases when the fast fish discharges at higher harmonics of the slow fish frequency because the faster fish can fire more than once between coincidences. We focused upon multiple coincidences that are physiologically more significant than single ones (see Introduction) and, in particular, on double ones because the coincidences of higher order (i.e. those repeated in three or more successive EOD cycles) can occur only if a double coincidence has already taken place.

Results

This section describes JARs observed in freely behaving fish and in response to artificial stimuli, together with possible models for both situations.

JARs in freely behaving fish pairs

Fig. 1, with the inter-EOD intervals of the female (red) and the male (blue) plotted against time, shows the electromotor interactions of freely swimming sexually mature fish. Records in Fig. 1A were obtained in a tank in the laboratory: the female:male mean interval ratio was just under 1:1, with the female’s intervals shorter (i.e. instantaneous rates higher) than the male’s. During the interaction, the male’s intervals (blue trace) are practically invariant. The female’s intervals (red trace), on the other hand, fluctuate. Fluctuations include first brief epochs where intervals are longest, having almost the same duration as those of male’s; these longer intervals are close to those of the female’s EOD when unperturbed. Interspersed between these epochs are irregularly recurring transient interval shortenings (instantaneous rate increases),

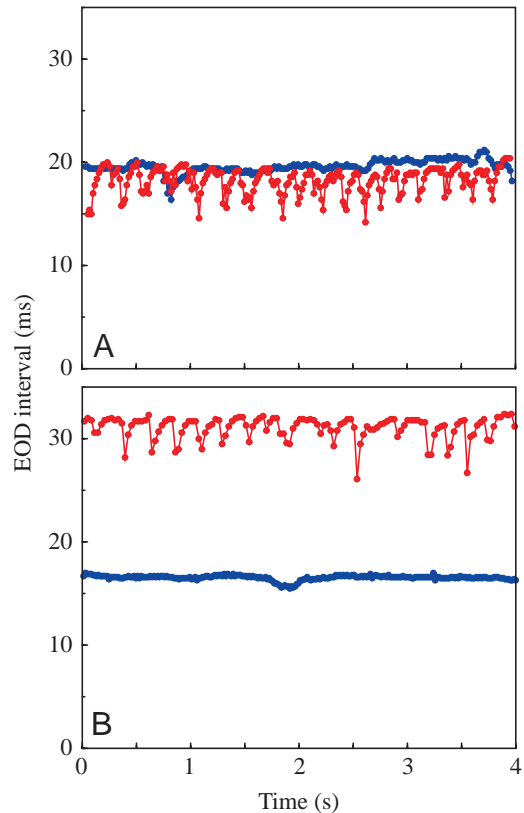


Fig. 1. Jamming avoidance responses (JARs) in interacting pairs of *Brachyhypopomus pinnicaudatus*. Different pairs in A and B. Inter-EOD event intervals (ms) as a function of ongoing time (s). Female, red trace; male, blue trace. Mean intervals estimated from portions without transient interval shortenings. (A) Interval ratio of female to male close to 1:1 (in the laboratory). Mean intervals during the interaction: female, 19.5 ms; male, 20 ms. (B) Interval ratio of female to male close to 2:1 (natural environment). Mean intervals during the interaction: female, 36.0 ms; male, 18.0 ms.

which are installed rapidly, reaching local interval minima over a few steps, and then return gradually to the longer values. These transient shortenings by the female prevented EOD coincidences and, therefore, constitute veritable JARs; there were no double coincidences in the record.

Records in Fig. 1B were obtained from a fish pair studied in their natural environment (Laguna Tigre). The female:male mean interval ratio was just under 2:1, with the female’s intervals longer (i.e. instantaneous rates lower) than the male’s. As in Fig. 1A, the male’s intervals (blue) are invariant but the female’s (red) fluctuate between alternating epochs with relatively stationary longer intervals at about twice those of the male and rapidly installed, slowly recovering transient shortenings. Also these transient shortenings prevented EOD coincidences and thus also constitute veritable JARs; there was only one double coincidence in the record. This, as far as we know, is the first report in pulse fish of JARs where the slower fish shorten their EOD intervals and the male discharges just under the first harmonic of the female’s EOD.

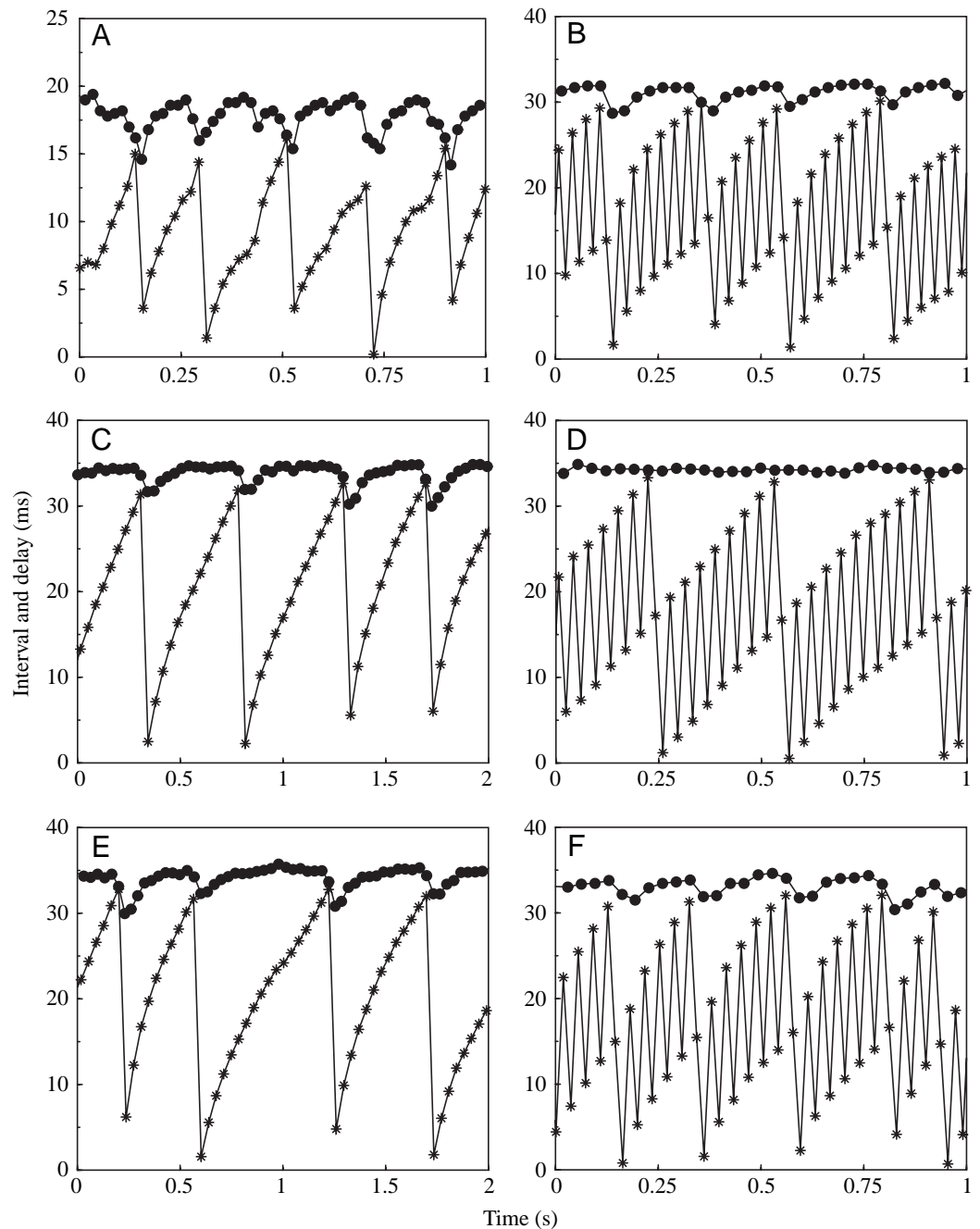
Fig. 2A,B shows interval and delay plots, with the EOD

intervals (circles) of one fish and the delays (asterisks) with respect to the first fish of the EOD pulses from the second. These data are selected segments from the records shown in Fig. 1. In Fig. 2A, the female:male mean interval ratio is about 1:1 (mean rates about the same). Delays increase monotonically, sweeping, sliding or walking across the interval of the first fish; when reaching a maximum value just under that interval, they jump to a small value close to 0 and grow along steps that individually are similar to (although not identical) and are in about the same number as those of the previous sweep. A coincidence exists when delays are practically equal to the interval and plots superimpose or, as at 0.75 s, delays are equal to zero. When the monotonically increasing delays approach the interval's value, the paired

EODs drift towards a coincidence, and, when sufficiently close, interval shortenings (Fig. 2A) occur rapidly over a few EODs: shortenings avoid coincidences and thus constitute JARs.

In Fig. 2B, the female:male mean interval ratio is about 2:1 (mean rate ratio about 1:2). Delays increase along a zigzag path, with alternating larger and smaller values; considered separately, the larger and smaller values have the same slopes, similar to those in Fig. 2A. The faster fish fires twice within each interval of the slower EOD: the first time is with a shorter delay and prior to the sensitive window; the second, with a longer delay, is within the sensitive window and shortens the extant interval. This finding provides the key for model Z to reproduce this novel behavior (see Response to pulse trains).

Fig. 2. Jamming avoidance responses (JARs) in different settings or simulated. Interval and delay plots. (A,B) Female electric organ discharge (EOD) intervals are represented by circles; male EOD delay with respect to the female EOD are represented by asterisks plus lines. (A) Fish pair in laboratory settings (depicted in Fig. 1A). (B) Fish pair in natural environment (depicted in Fig. 1B). (C–F) Data generated numerically. Female train shown as interval vs time (circles); male train shown as delay vs time (asterisks plus lines). M^* , mean interval in the absence of perturbations. (C) Data generated with model X attempting to mimic the situation in A; female faster train ($M^*=36.0$ ms); male slower train ($M^*=36.5$ ms). (D) Data generated with model Z attempting to mimic the situation in B. Female slower train ($M^*=36.0$ ms); male faster train ($M^*=18.0$ ms). (E) Data generated with model Z attempting to mimic the situation in A. Female faster train ($M^*=36.0$ ms); male slower train ($M^*=36.5$ ms). (F) Data generated with model Z attempting to mimic the situation in B. Female slower train ($M^*=36.0$ ms); male faster train ($M^*=18.0$ ms).



While model X reproduces results in Fig. 2A well, with the two fish discharging at close EOD frequencies (Fig. 2C), it fails to reproduce the case where one fish fires close to twice as fast as the other (Fig. 2D). Using model Z, both cases could be reproduced (Fig. 2E,F).

Fig. 3A shows the same data set as Fig. 2B but, in this case, represents the male's faster EOD as interval *vs* time and the female's EOD as delay *vs* time. Note the absence of transient interval shortenings in the male's EOD. Fig. 3B shows the same data set as Fig. 2F but, in this case, represents the male's faster EOD as interval *vs* time and the female's EOD as delay *vs* time. These data were generated numerically with model Z attempting to reproduce the situation shown in Fig. 3A. Note that the train representing the male does not produce transient interval shortenings.

The number of coincidences found in the fish interactions depicted in Fig. 1 is within the confidence intervals of the distribution produced by 20 realizations of model Z having the same duration as the recordings; simulation segments are in Fig. 2E,F. The very low number of coincidences (i.e. 0 for Fig. 1A and 1 for Fig. 1B) is indicative of the high efficiency

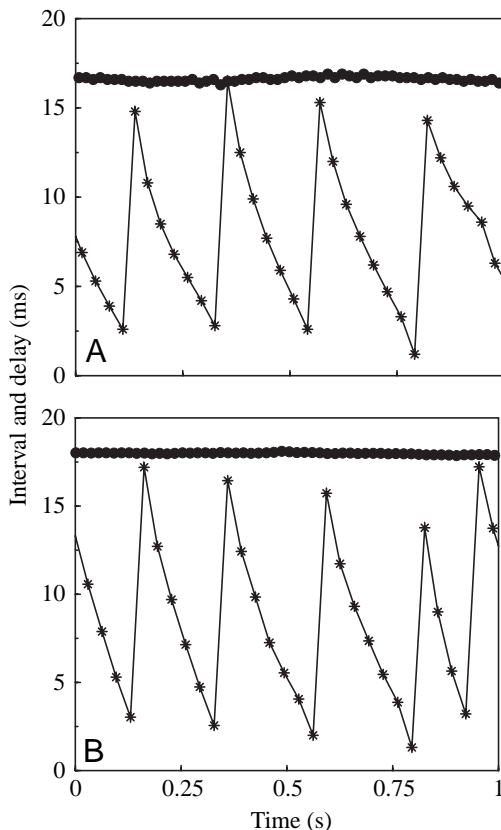


Fig. 3. Jamming avoidance responses (JARs) with 2:1 female:male period ratios: natural and simulated. Interval and delay plots. Fast male electric organ discharge (EOD) represented by intervals (circles); slow female EOD represented by its delay with respect to the male EOD (asterisks plus lines). (A) Fish pair in natural environment (same as in Fig. 2B). (B) Simulation using the incomplete version of model Z (same as in Fig. 2F). Male fast train ($M^*=18.0$ ms); female slow train ($M^*=36.0$ ms).

of the JAR. Control simulations of the same duration and relation of periods but without transient interval shortenings ($\lambda_i=0$) included more than 10 successive coincident discharges. When $\lambda_i=0$, successive coincidences occur only when one simulated train fires close to integer multiples of the discharging rate of the other. If transient interval shortenings are allowed in the simulations, model X removes only coincidences when EOD period ratios are close to 1:1. Model Z also removes most of the coincidences that occur when periods are at integral multiples.

JARs to artificial pulses

The same reactions observed during the behavioral interactions (Fig. 1A,B) could be evoked in isolated specimens of both sexes stimulated with artificial pulse trains. The responses were the same, even though, because fish were studied during the inactive period of the circadian cycle, the EOD intervals were larger than those depicted in Figs 1B, 2B.

Fig. 4 displays interval and delay plots, with fish EODs represented by intervals (black circles) and pulse trains represented by delays (asterisks); the pulse train is also represented by intervals (thick gray line). Responses in Fig. 4A,B are very similar to those in Fig. 2A,B, respectively, and can be described in the same manner.

Fig. 4C includes separate EOD portions, both stationary but each at different interval values; the pulse train is the same throughout. The first half, where the longest intervals were practically equal to twice the interpulse interval (rates about one half), shows obvious JARs. The second half, where visibly the EOD intervals were shorter and the alternating delay slopes greater than in the first, had no JARs. Fig. 4B and C (first part) illustrate JAR's in, respectively, male and female specimens: therefore, JARs depend on mechanisms and computations shared by both sexes. In Fig. 4D, the period of the stimulus train (thick gray line) was varied: JARs were present in the first 3 s, where the longest EOD intervals were practically equal to twice the pulse intervals (rates about one half), but disappeared when pulse intervals were lengthened. Thus, Fig. 4C,D shows that JARs vanish whenever the regime departs, because either EODs or pulses changed, from the 2:1 ratio.

JARs also occurred when the mean EOD to pulse interval ratio was about 3:1, as in Fig. 4E, and 4:1 (not shown). These situations have not been observed in naturally behaving fish pairs but should be looked for: conceivably, they are hard to encounter because, as the higher order lockings between interacting pacemakers, their domains may be small and susceptible to the inevitable noise. As in Fig. 4B–D, delays increase along zigzags with successively larger, intermediate and smaller values that, taken separately, have similar slopes.

Fig. 5A illustrates JARs arising when a first spike train (generated with the same parameter set used for the slower train of Fig. 2D,F) and a slower second train, whose frequency was almost half that of the first, are present. Model Z+ reproduces this situation (Fig. 5C), but model Z does not (Fig. 5B). Model Z+ also shows JARs at 1:1, 2:1 and 3:1 relation of periods (not shown).

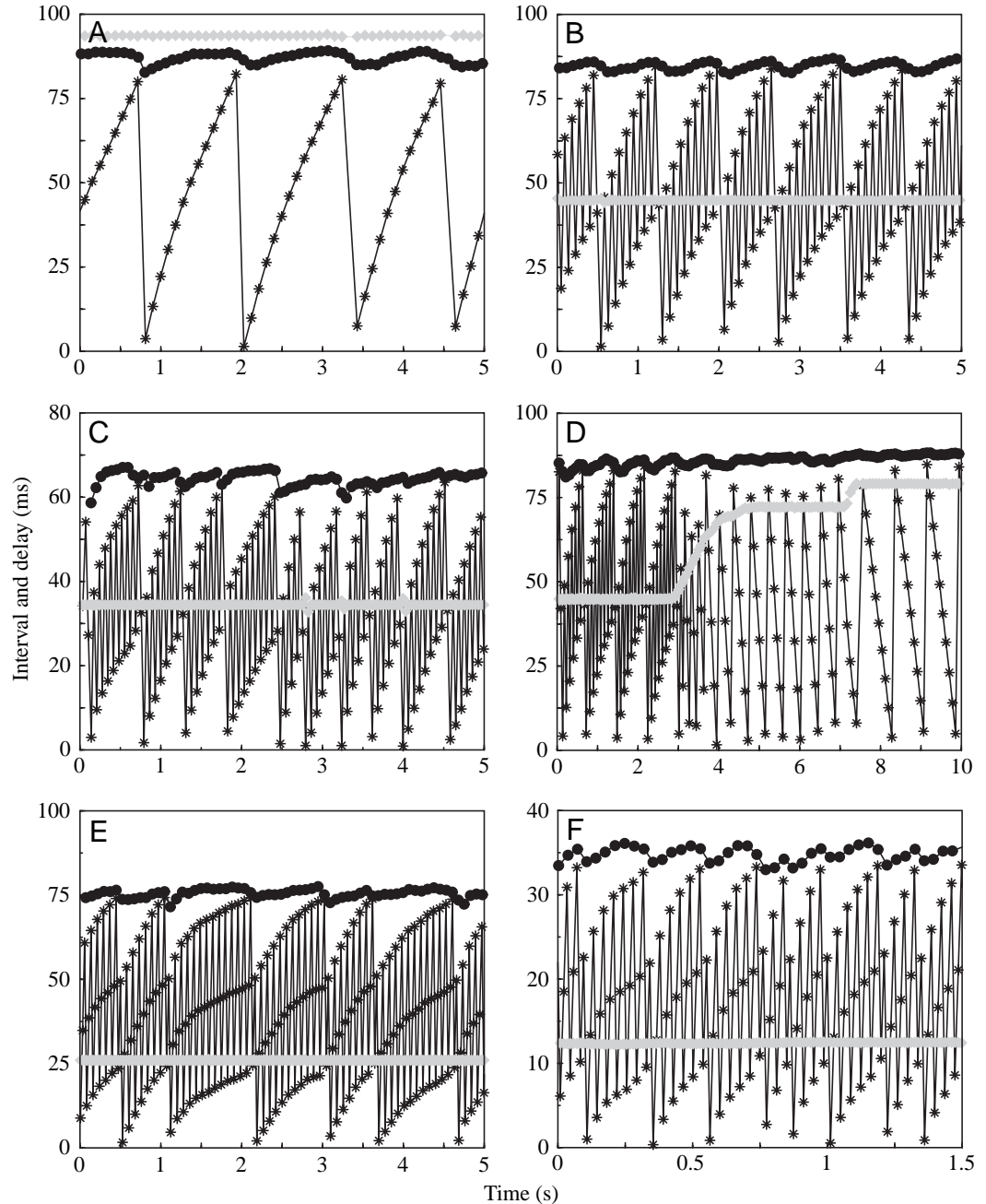


Fig. 4. Jamming avoidance responses (JARs) and artificial pulses. Interval and delay plots. Isolated fish electric organ discharge (EOD) represented by intervals (circles); artificial pulses represented by delays relative to the EOD (asterisks with lines) and intervals (thick gray line). (A) 1:1 period ratio (male EOD). (B) 2:1 period ratio (male EOD). (C) JARs (female EOD) arise with 2:1 period ratios but not when those ratios vary because EOD intervals change. (D) JARs (male EOD) with 2:1 period ratios but not when those ratios vary because pulse intervals change. (E) 3:1 period ratio (female EOD). (F) Numerically generated data referring to the situation depicted in E. The slow train is plotted as interval vs time with black circles and represents the fish. The fast train represents the artificial pulses and is plotted both as delay vs time (asterisks plus lines) and as interval vs time (thick gray line). M^* of the fast train=12.0 ms; M^* of the slow train=36 ms.

Discussion

This study adds novel features to the catalog of JARs performed by pulse-type electric fish. The main finding is that the fish is able to respond by JARs to pulse trains delivered not only at frequencies close to its EOD but also at frequencies close to its higher harmonics and sub-harmonics. This responsiveness is broader than that of the wave-type fish that, while responding to frequencies close to the EOD and its higher harmonics, does not respond to its sub-harmonics (Kaunzinger and Kramer, 1995). The second contribution of the paper is to develop a mathematical model able to reproduce the reported behaviors. The ethological relevance of the JAR at 2:1 relation of periods, the models and the conjectures about the dynamical behaviors involved are discussed below.

Ethological significance of the JAR at 2:1 relation of periods

From an ethological point of view, the more relevant finding reported here was the JAR triggered in one fish by another's EOD whose period was close to half its own and thus whose frequency was close to its first harmonic. This JAR was witnessed in fish behaving freely in their natural habitat and, therefore, can safely be assigned a genuine ethological significance. The situation in which the period of one fish reaches near twice the period of the other fish can occur often during the breeding season. In the first hours of the night, when the animals have their active period, the male increases its frequency and maintains it with low variability in a high value. This sustained frequency increase is correlated with the locomotor display and electrocommunicatory signals of

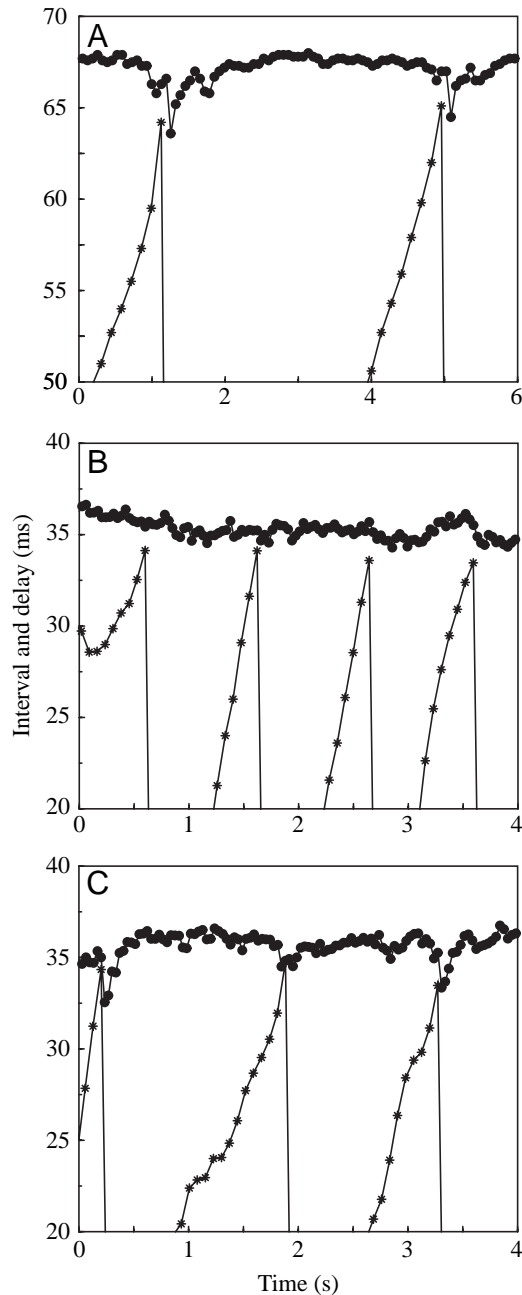


Fig. 5. Jamming avoidance responses (JARs) with 1:2 'electric organ discharge (EOD) to pulse' period ratios: natural and simulated. Interval and delay plots. EODs represented by intervals (black circles); artificial pulses represented by delays relative to the EOD (asterisks with lines). (A) Live fish: mean interval=68.0 ms; pulse interval=141.3 ms. (B) Failure of incomplete model Z, which responds only if pulses occur at consecutive sensitive windows. For B and C, fast train $M^*=36.0$ ms; slow train $M^*=73.0$ ms. (C) Success of complete model Z+, which responds to pulses arriving either at consecutive or every other sensitive window.

courtship and exceeds those during the active period in sexually immature specimens (Macadar et al., 2001; Quintana et al., 2002; Silva, 2002; Perrone, 2003). It may lead to a 2:1 relation of periods (e.g. Fig. 1B). When, as can happen, the

female also increases her mean frequency, interactions may be without transient interval shortenings (if the frequencies are far from harmonical relations) or an interaction with transients may be produced by the faster fish (if both frequencies are close to one another; e.g. Fig. 1A).

Observations in the laboratory using artificial pulses showed that JARs were identical in both sexes, suggesting that, in spite of different EOD wave-shapes and external phenotypes (Hopkins et al., 1990; Silva, 2002), both sexes use the same computations. Moreover, the same kind of JARs triggered by harmonically related pulse trains were found in immature specimens with minor sexual dimorphism in their external phenotypes; hence, contrary to the general behavioral aspects of courting, the JAR does not depend on full maturity. Longer observations of natural interactions are needed, however, to evaluate a possible sexual influence in the behavioral determination of the M^* values.

Models for JARs

This study improves on an earlier model (X), proposing models Z and Z+. In all three models, the fish performing the JAR responds only to pulses within a sensitive window that starts at a characteristic instant preceding the forthcoming EOD (C_H). Also, in all models, successive effective pulses have to scan the EOD's sensitive windows slowly and from left to right, i.e. with increasing delays and decreasing cophases. This requires a mechanism that stores the position in the cycle of each perturbation and compares it with that of later ones. However, models differ in the identities of the arriving pulses involved in the influential scans.

In model X, proposed previously (Capurro et al., 1998, 1999), the response occurs only if windows in consecutive EOD cycles are scanned by successive pulses that are also consecutive. This model reproduces only situations in which the frequencies and periods of the two EODs are close. With this model, coincidences are avoided through brief interval shortenings in the discharge of the fish having the higher rate (shorter period) of the pair. In model Z, the response occurs if windows in consecutive EOD cycles are scanned by successive pulses that need not necessarily be consecutive. This model also reproduces situations in which the frequency of one EOD is close to two or three times that of the first. Coincidences are avoided through brief interval shortenings in the discharge of the fish having the slower rate (larger period) of the pair.

In model Z+, the response occurs if windows in either consecutive EOD cycles or windows belonging in every other EOD cycle are scanned; perturbations need not be consecutive pulses. Sensitivity to perturbations in every other window requires storage across EOD cycles without arrivals, one at least. Model Z+, reproducing satisfactorily all outcomes encountered in natural habitats and using artificial pulse trains, accounts well for fish behavior. These experiments showed that JARs arise also when EOD to pulse interval ratios are 1:2, involving one interposed cycle without perturbation; further work in progress is examining their maximum number and thus the duration of this memory. Also in progress are experiments

using pulse trains with interval ratios such as 2:3 and 3:2, as well as pulses with different amplitudes.

JARs as dynamical behaviors

Below, we attempt to justify briefly the potential usefulness for studying electric fish interactions of formal approaches inspired by nonlinear dynamics, a powerful theory with widespread practical applications. EODs are periodic so their behaviors, JARs included, embody oscillator interactions. The theory indicates that these, depending on the driver period (relative to the unperturbed driven one) and the coupling strength, can be periodic, quasiperiodic or aperiodic (chaotic). Periodic behaviors, where intervals are invariant and phases locked, have been reported in interacting electric fish (Gottschalk and Scheich, 1979; Westby, 1979; Capurro et al., 1999; Perrone, 2003). We contend that, when performing JARs, fish also embody the quasiperiodic behaviors called 'phase walk-throughs'. Indeed, JARs exhibit the essential characteristics of walk-throughs: namely, the phases (delays) of the driven oscillator move monotonically – walk, sweep, slide – across the driver period, reach a large value, jump to a small value and start the next walk, which, though similar, is not identical to the previous one. Simultaneously, the driven oscillator, mostly periodic, unpredictably destabilizes briefly. Moreover, both walk-throughs and JARs arise when driver period ratios are close to 1:1, 2:1, etc. Walk-throughs, modeled by Ermentraut and Rinzel (1984), appear in interacting fireflies and pacemaker neurons (Segundo, 2003). It is also suggestive that the EODs intervals illustrate a special kind of intermittency. 'Intermittency' is a qualitative concept describing behaviors, most of the time almost periodic, that unexpectedly irregularize briefly in unpredictable ways (Bergé and Dubois, 1988); it has been applied profitably to numerous practical situations. Clearly, the individual EODs with transient interval shortenings behave intermittently (Fig. 1A,B red and others). Further discussion is postponed for a separate publication (A.C. and K.P., manuscript in preparation).

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