Sensory coding in oscillatory electroreceptors of paddlefish

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Coherence and information theoretic analyses were applied to quantitate the response properties and the encoding of time-varying stimuli in paddlefish electroreceptors (ERs), studied *in vivo*. External electrical stimuli were Gaussian noise waveforms of varied frequency band and strength, including naturalistic waveforms derived from zooplankton prey. Our coherence analyses elucidated the role of internal oscillations and transduction processes in shaping the 0.5–20 Hz best frequency tuning of these electroreceptors, to match the electrical signals emitted by zooplankton prey. Stimulus-response coherence fell off above approximately 20 Hz, apparently due to intrinsic limits of transduction, but was detectable up to 40–50 Hz. Aligned with this upper fall off was a narrow band of intense internal noise at ~ 25 Hz, due to prominent membrane potential oscillations in cells of sensory epithelia, which caused a narrow deadband of external insensitivity. Using coherence analysis, we showed that more than 76% of naturalistic stimuli of weak strength, ~ 1 $\mu\text{V}/\text{cm}$, was linearly encoded into an afferent spike train, which transmitted information at a rate of ~ 30 bits/s. Stimulus transfer to afferent spike timing became essentially nonlinear as the stimulus strength was increased to induce bursting firing. Strong stimuli, as from nearby zooplankton prey, acted to synchronize the bursting responses of afferents, including across populations of electroreceptors, providing a plausible mechanism for reliable information transfer to higher-order neurons through noisy synapses. © 2011 American Institute of Physics. [doi:10.1063/1.3669494]

Rhythmical activity underlies various complex physiological processes in central nervous systems. Peripheral sensory receptors, on the other hand, are often considered as “passive” systems with relatively simple and linear dynamics. Nevertheless, self-sustained oscillations have been observed in several types of peripheral sensory receptors. This paper reports on stimulus encoding in electroreceptors (ERs) of paddlefish, which use passive electrosense to feed on zooplankton. A single peripheral electroreceptor in paddlefish is a complex system comprised of several thousands of sensory epithelial cells innervated by a few primary sensory neurons (afferents). It embeds distinct oscillators: one resides in a population of epithelial cells, synaptically coupled to another oscillator in afferent terminals. In contrast to auditory receptors, which resonate to sound waves of certain frequency, neither epithelial nor afferent rhythms of electroreceptors match the low-frequency bioelectric signals emitted by zooplankton prey. We applied Gaussian noise stimuli to study how oscillators embedded in paddlefish electroreceptors shape the linear and nonlinear responses of electroreceptors, and to characterize quantitatively how external stimuli, including bioelectrical signals from zooplankton prey, are encoded into the timing of afferent firing.

potential oscillations^{13,65} in auditory hair cells, regular firing of some vestibular afferents,³¹ epithelial oscillations in electroreceptors of marine rays,^{20,21,41} and periodic firing of electroreceptor afferents in catfish,^{7,67,71} rays⁷⁴ and sharks.⁸ These examples indicate that certain peripheral receptors are essentially non-linear systems whose dynamics are strongly governed by self-sustained (i.e., nonlinear) oscillators. Nevertheless, it is generally assumed that peripheral sensory receptors are linear encoders, at least for weak signals. This was verified in numerous experimental studies and is supported by linear response theory.³³ In particular, recent works have shown that the “phase response curve,” a metric of the dynamics of a neuronal oscillator perturbed by weak noise, is directly related to its linear transfer function,^{25,69} so that a direct link can be made between dynamics and information encoding into neuronal spike timing.⁶⁹ Physiological studies on several species have shown and discussed essential nonlinearities of sensory encoding in auditory,^{22,38} visual,^{40,56,59} vestibular,⁶⁶ mechanosensory,⁶¹ and electrosensory^{14,16} systems. In many cases, nonlinearities were associated with non-weak stimuli or with the existence of bursting patterns of neural firing.

In this paper, we study the response dynamics and sensory coding that take place in the peripheral ERs of paddlefish, *Polyodon spathula*. Among the several types of ERs in various species,^{10,12} those of paddlefish are of the most ancient ampullary “Lorenzian” type, like the famous ampullae of Lorenzini of marine sharks and ray fish. The name “ampullary” refers to the vase-like shape of an internal chamber. The unique feature of Lorenzian ERs is their

I. INTRODUCTION

Spontaneous oscillations have been observed in several types of peripheral sensory receptors. Examples include mechanical oscillations of hair bundles⁴⁴ and membrane

polarity of electrical sensitivity: afferents are excited to fire more frequently by weak ($\mu\text{V}/\text{cm}$) “cathodal” voltage gradients in the surrounding water, such that the skin pore of an ER becomes electrically negative relative to distant loci. Conversely, making the skin pore electrically positive (“anodal” stimulation) will slow down (inhibit) the spontaneous firing of an ER afferent. Certain other fish, e.g., catfish and weakly electric bony fish, have ERs with similar ampullary morphology but opposite polarity of sensitivity (excitation by anodal stimuli). Hence, the term “ampullary ER” is ambiguous in grouping at least two disparate types of ERs.⁵

Due to dense silt in the large North American rivers inhabited by paddlefish, vision is ineffective. Instead, paddlefish use passive electrosense as their primary 3-dimensional sensory modality, e.g., to locate zooplankton prey, as behavioral studies have shown.^{62,63,76,77} Thousands of peripheral electrosensors are located mainly on the elongated frontal appendage (rostrum), and also on the gill covers and head, and around the mouth. A single ER is a complex system composed of a cluster of 3–35 adjacent skin pores, each leading to a short canal ending in a sensory epithelium containing ~ 1000 sensory receptor cells. They synaptically excite the terminals of a few (3–5) primary afferents innervating the cluster of sensory epithelia, representing unidirectional coupling. Thus, paddlefish ERs have a two-stage feed-forward organization, similar to that of the hair cell—primary afferent sensory receptors for vertebrate hearing and balance.

Yakusheva and Moss mapped electrophysiologically the convergence of canals onto ER afferents, using microstimulation of one canal at a time by weak (~ 100 pA) sinusoidal currents from a glass micropipet inserted into a canal, driven by a constant-current generator circuit prototyped by Moss. A sensitive area of fish skin was photographed digitally through a microscope, and the canals tested were numbered on the photo during experiments. Out of many attempts, sometimes working all night, they succeeded in mapping the complete receptive field organization of 5 ER afferents. These high-resolution mapping data established that the receptive field of an ER afferent in paddlefish corresponds to a single cluster of canals.⁶⁴ Others have since extended these findings.¹⁸

Both major components of the ER system, i.e., receptor cells and afferents, demonstrate endogenous rhythms.⁴⁹ Populations of epithelial cells generate stochastic voltage oscillations across a sensory epithelium, which can be recorded extracellularly, at a fundamental frequency $f_e = 26 \pm 1.6$ Hz (at 22 °C). The many epithelial oscillators of all the canals in an afferent’s receptive field have similar frequencies (at a given temperature), and so can be collapsed together as a single noisy epithelial oscillator “EO.” These epithelial oscillations are coupled to another type of oscillator residing in each afferent’s terminal and driving neuronal spikes. The fundamental frequency of this afferent oscillator (AO), f_a , is distributed over a wide range of 30–70 Hz for different afferents, but has a stable value during spontaneous firing in any given afferent, which matches its mean firing rate. The 3–5 afferents from a given ER may have different f_a values. The unidirectional (that is, epithelial to afferent) synaptic

coupling of the two distinct types of oscillators results in quasiperiodic firing patterns of afferents.⁴⁹

Behavioral observations (by D.F.R.) suggest that paddlefish use their electrosensory system in two different ways: a far-field mode when the source is >5 cm distant from electroreceptors, as during initial detection of weak signals from approaching zooplankton prey, or a near-field mode when the source is in close proximity (<1 cm) to electroreceptors, as when a fish lines up to engulf prey into its mouth. Clearly, these two modes correspond to distinct regimes of stimulus intensity, weak, or strong respectively, relative to the lower limit of paddlefish electrosensory sensitivity at $0.5\text{--}1$ $\mu\text{V}/\text{cm}$ r.m.s., estimated behaviorally.^{62,63} In Ref. 51, we demonstrated and characterized two distinct classes of responses of single-unit afferents to time-varying noise stimuli. We showed that afferents undergo a transition from modulated tonic firing to parabolic burst discharges, as the standard deviation (SD) of a Gaussian noise stimulus (that matches the frequency band of ERs) is increased above approximately 2.5 $\mu\text{V}/\text{cm}$ r.m.s. Such non-weak stimuli may be of relevance for paddlefish tracking zooplankton prey at short distances, i.e., in the near-field mode.¹⁸ Bursting may signify to a fish that prey are nearby. Transition to bursting occurs for different types of noise stimuli, of varied frequency bands. Higher frequency stimuli, i.e., with frequency band significantly wider than that of ERs, required larger values of stimulus magnitude to induce bursting. This change from modulated tonic firing to bursting appears to be an example of a more general phenomenon, noise-induced transitions,³⁷ known to lead to new regimes in the operation of a system, in this case a bursting regime.

Initial studies of paddlefish ERs described responses to step and sinusoidal stimuli.^{34,76} Beyond that, stimulus encoding and information transfer in this class of sensory receptors, the Lorenzinian ampullary electroreceptors of freshwater *Acipenseriforme* fish (paddlefish and sturgeons), is an inviting topic. We have studied linear and nonlinear responses of the peripheral ERs of paddlefish to various types of Gaussian noise stimuli, ranging from band-limited white noise to low-frequency naturalistic stimuli derived from signals recorded from single zooplankton prey (*Daphnia*) or from swarms of large numbers of *Daphnia*. Coherence analysis and a stimulus reconstruction technique were used to estimate frequency tuning curves and the encoding of weak time-varying stimuli. Cross-bicoherence and synchronization metrics were used to assess nonlinear responses of ERs to stronger stimuli.

II. METHODS

A. Experimental

The data and results presented here were from 29 electroreceptor afferents of 19 paddlefish, from *in vivo* preparations <16 h old, and are representative of the qualitative features observed in all recordings. Experiments were conducted in the Center for Neurodynamics, University of Missouri St. Louis, under an IACUC-approved animal use protocol.

Experimental procedures and stimulation protocols were described in Refs. 49 and 51. Briefly, “uniform field”

stimulation was applied between two 6×15 cm Ag/AgCl plates, coated with agarose, which covered the ends of the elongated plastic experimental chamber, in front of a fish and behind it. The computer-generated noise stimulus waveforms had different frequency content:⁵¹ (1) Band-limited white noise stimuli with Gaussian-distributed amplitude had the SD (σ), and the power spectral density (PSD) $P_{ss}(f) = \sigma^2/(2f_c)$ within a low-pass frequency band limited at a cutoff frequency, f_c . Note that the stimulus SD was kept constant if the cutoff frequency was varied. (2) Exponentially correlated Ornstein-Uhlenbeck (OU) noise had the PSD $P_{ss}(f) = 2\tau_c\sigma^2/(4\pi^2f^2\tau_c^2 + 1)$, where the correlation time τ_c was set to 2 ms. (3) Recordings from an individual *Daphnia* zooplankton prey (Fig. 2(a)) that was glued to a post revealed its natural bioelectric signal (Fig. 2(b)) arising from muscle contractions to move appendages. This single-*Daphnia* signal was not Gaussian, but a Gaussian “naturalistic” surrogate was constructed by matching the power spectrum of Gaussian noise to the power spectrum of the original *Daphnia* signal, as in Ref. 60. (4) Natural electrical noise (Fig. 2(c)) recorded from a swarm of *Daphnia* zooplankton prey was Gaussian.²⁶ Two types of noise presentations were used: (a) as sequences of 180 s segments of different randomly chosen noise variances, or cutoff frequencies, separated by 10 s of no stimulus; or (b) as repeated identical 13.2 s segments of a noise realization, i.e., “frozen noise,” separated by 5 s of no stimulus, to study cross-trial variability of afferent responses.

B. Data analyses

Data analyses were performed offline using custom software programmed in MATLAB. A sequence of N spike times t_n , $n = 1 \dots N$, was resampled together with the stimulus, $s(t)$, at 2 kHz. A spike train was represented as a sequence of delta functions centered at the spike times: $x(t) = \sum_{n=1}^N \delta(t - t_n)$. The mean firing rate $\bar{r}$ was subtracted from $x(t)$ for further analyses. In the following, the subscript “S” refers to a stimulus waveform, “X” refers to an observed afferent spike train during the stimulus, “R” refers to the averaged response, lower case refers to instances, and upper case refers to averaged global estimates.

Tuning properties of afferents were characterized by standard methods using two metrics: gain and coherence. The system transfer function or *gain* was calculated⁴ as the ratio

$$G(f) = \frac{|P_{sx}(f)|}{P_{ss}(f)}, \quad (1)$$

where $P_{sx}(f)$ is the cross spectral density of a stimulus $s(t)$ and the coincident afferent spike train $x(t)$, while $P_{ss}(f)$ is the PSD of the stimulus. The coherence function⁴ between a stimulus and afferent firing (stimulus—response “SR coherence”) is defined as

$$C_{SR}(f) = \frac{|P_{sx}(f)|^2}{P_{xx}(f)P_{ss}(f)}, \quad (2)$$

where $P_{xx}(f)$ is the PSD of the coincident afferent spike train. It was calculated using procedure *mccoher* of

MATLAB’s signal processing toolbox. SR coherence is a measure of linear relations between a stimulus and a spike train (response). Unlike the gain, which in our case had units of (spikes/s)/(μ V/cm), the coherence is a dimensionless normalized function of frequency and changes in the range $0 \leq C_{SR}(f) \leq 1$. For a linear system which has no internal or measurement noise, the coherence between input and output is always 1. Otherwise, coherence can be less than 1 due to noise, or to nonlinearity in stimulus transduction, or both. To exclude spurious baseline values for coherence, 10 *shuffled surrogates* of a spike train were generated by random reordering of the interspike intervals (ISIs), to destroy cross-correlations between a spike train and the noise stimulus. For each surrogate spike train, its maximum value of SR coherence over the whole frequency range was determined. The maximum value averaged over the ensemble of surrogates, $\bar{C}$, was compared to the coherence of the original spike train, $C(f)$, whose value was then set to 0 for frequencies at which $C(f) \leq \bar{C}$.

Calculation of the coherence from a long recording of a stimulus and a simultaneous afferent spike train was used to estimate information metrics. Encoding of a noise stimulus was analyzed using the linear stimulus reconstruction technique explained in Refs. 6, 29, 30, and 75. Briefly, an estimate of the stimulus, $s_{est}(f)$, can be obtained by convolving the afferent spike train with an optimal Wiener-Kolmogorov filter, $h(t)$: $s_{est}(t) = (h * x)(t)$. The filter is given (in the frequency domain) by its transfer function $H(f) = [P_{sx}(-f)]/[P_{xx}(f)]$. The effective noise contaminating the reconstruction, $n(t) = s(t) - s_{est}(t)$, has the power spectral density $P_{nn}(f) = P_{ss}(f) [1 - C_{SR}(f)]$. A normalized measure of the quality of reconstruction is the *coding fraction* γ , defined as

$$\gamma = 1 - [\text{var}(n)/\text{var}(s)]^{1/2}. \quad (3)$$

It gives the fraction of a stimulus that can be correctly estimated from a spike train, ranging from 0 (no encoding) to 1 (complete encoding). An estimate of the information transmitted by an afferent was obtained in terms of the lower bound of the mutual information rate, calculated as

$$I_{LB} = - \int_0^{f_c} \log_2[1 - C_{SR}(f)] df, \quad (4)$$

in units of bits/s.

To reveal nonlinearities in stimulus transduction by paddlefish ERs, higher-order spectral densities that quantify the degree of nonlinear coupling of Fourier harmonics were calculated, including the *cross bicoherence*, $B(f_1, f_2)$, a normalized measure that quantifies the extent of quadratic nonlinear coupling as a function of two frequencies that can be varied independently. It is defined in the frequency domain^{54,72} as

$$B(f_1, f_2) = \frac{|P_{ssx}(f_1, f_2)|}{[P_{ss}(f_1 + f_2)P_{ss}(f_1)P_{ss}(f_2)]^{1/2}}, \quad (5)$$

where $P_{ssx}(f_1, f_2)$ is the cross bispectrum.⁵⁴ It was calculated using the higher order spectral analysis toolbox (HOSA) of

FIG. 1. Raw spontaneous firing (a) of a paddlefish electroreceptor (ER) afferent, and its responses (b)–(d) to uniform-field stimulation between large plate electrodes with Gaussian white noise, band-limited to frequencies below 200 Hz, for 3 different r.m.s. amplitudes (*bottom traces* in (b)–(d), scaled identically; the noise SDs are labeled). Uppermost traces show instantaneous firing rate, per calibration in (c); note the parabolic trajectory of the firing rate during bursts in (d).

MATLAB (Ref. 72). Whereas the stimulus—response coherence (Eq. 2) is built upon first-order correlations and thus is a measure of linear relations between various frequency components of a stimulus and response, in contrast, the cross bicoherence involves the cross bispectrum, a two-dimensional Fourier transform of second-order cross-correlations,⁵⁴ which thus characterize non-linear relations of components at triplets of frequencies, f_1 , f_2 , and $f_1 + f_2$. Bicoherence and higher order spectra have been utilized successfully to reveal quadratic coupling of phases at various frequency bands in electroencephalographic data^{2,11,39} and in multiple micro-electrode recordings from visual cortex of cats and monkeys.⁶⁸

In certain cases, nonlinearities still allow for optimal linear encoding.⁴⁶ To check whether a linear encoding scenario was adequate to describe (inherently nonlinear) bursting regimes, we used an approach proposed by Roddey *et al.* in Ref. 61, namely stimulation with repeated sequences of identical noise segments, 13.2 s long, also known as “frozen noise,” followed by comparison of the *response—response* (RR) coherence, $C_{RR}(f)$, to the usual (linear) SR coherence,

$C_{SR}(f)$. To explain, suppose that an afferent is stimulated by a sequence of K identical segments of noise, $s(t)$, resulting in K response spike trains, $x_k(t)$, with $k = 1, 2, \dots, K$. The stimulus—response coherence is calculated according to Eq. (2) with $P_{sx}(f) = \frac{1}{K} \sum_{k=1}^K P_{sk}(f)$ and $P_{xx}(f) = \frac{1}{K} \sum_{k=1}^K P_{kk}(f)$, where $P_{sk}(f)$ is the cross spectrum between the stimulus and the k th trial response, while $P_{kk}(f)$ is the power spectrum of the k th trial spike train. The response—response coherence is then¹⁴

$$C_{RR}(f) = \frac{\left| \frac{2}{(K-1)K} \sum_{k=1}^K \sum_{j < k} P_{kj}(f) \right|^2}{\left[\frac{1}{K} \sum_{k=1}^K P_{kk}(f) \right]^2}, \quad (6)$$

where $P_{kj}(f)$ is the cross spectrum between k th and j th responses. The stimulus does not enter into Eq. (6) since RR coherence quantifies variability of responses that cannot be accounted for by the stimulus. The RR coherence changes from 0 to 1 and satisfies an inequality, $C_{SR}(f) \leq \sqrt{C_{RR}(f)}$. While the SR coherence characterizes an optimal linear encoding model, the RR coherence sets an upper bound for the performance of the optimal nonlinear model, as shown in Ref. 61. Therefore, RR coherence is used to estimate an upper bound of mutual information rate.^{24,45} Closeness of the SR coherence to the square root of the RR coherence indicates that a linear encoding scenario is optimal, whereas large departures indicate that a linear encoding model is not appropriate.

III. RESULTS

Our aim was to estimate separately the linear and non-linear encoding properties of afferents from ampullary ERs of paddlefish. Experimental variables were the source, frequency band, and SD of several types of noise stimulus waveforms, all Gaussian and zero-mean. Our theme is introduced in Fig. 1, showing raw recordings of an afferent's spike trains. All afferents studied fired spontaneously at a near-stationary frequency in the 30–70 Hz range (Fig. 1(a)). This continuous tonic firing was quasiperiodic.⁴⁹ Weak broad-band Gaussian noise stimuli, from ~ 0.5 up to $2\text{--}7 \mu\text{V/cm}$ in

FIG. 2. Bioelectric signals recorded from *Daphnia* zooplankton, a prey of paddlefish. Similar data were reported previously, e.g., Ref. 26. (a) Body length: a few mm. (b) Electrical signals recorded from an individual *Daphnia* glued to a post in water, arising from contracting muscles, corresponded to beating motions of feeding legs at 5–7 Hz, plus intermittent swimming motions of antennae. Voltage differences in the water were detected by a 1 mm Ag/AgCl ball electrode near the *Daphnia*, relative to a large distant Ag/AgCl plate electrode, connected to a high impedance differential voltage preamplifier. The water was also grounded. (c) A similar electrode setup was used to record noise-like signals from a swarm of *Daphnia* in a large aquarium. The Ag/AgCl ball electrode amongst the swarm was encased in agarose to prevent *Daphnia* from colliding with it. (d) A large DC potential difference between head and tail was revealed by rotating a vertical post that a *Daphnia* was glued to, for 3.5 turns, so that the head and tail passed alternately near a stationary Ag/AgCl ball recording electrode. Small ripples: feeding leg beating.

FIG. 3. Frequency tuning. ((a), grey line) PSD of spontaneous ER afferent firing. ((a), black line) The ER was stimulated by 180 s long epochs of white noise band-limited to below 200 Hz, and $SD = 5.9 \mu V/cm$. For the same afferent, gain (b) and SR coherence (c) were calculated, as functions of frequency. (d) Comparison of SR coherence (5 superimposed black lines, left vertical scale) and gain (5 superimposed grey lines, right vertical scale) for a sample of 5 different ERs stimulated by identical noise stimuli as in (a)–(c).

r.m.s. amplitude, modulated the tonic firing (Fig. 1(b)). However, less-weak stimuli induced a qualitative change to a parabolic bursting mode of afferent firing (Figs. 1(c) and 1(d)).⁵¹ Our focus in this article was to characterize the sensory performance of ERs during these disparate tonic and bursting modes of afferent firing.

A. Gain and coherence tuning curves

Previous studies of frequency tuning in paddlefish ER afferents used sinusoidal stimulation, and an index of firing rate modulation, or a synchronization index, to reveal that the frequency response of ERs is limited to a 0.1–30 Hz range,^{34,57,76,78} like other Lorenzian ERs. Instead, we used broad-band noise stimuli, which have the advantage of testing responsiveness at all frequencies within the stimulus pass band. As metrics of frequency tuning, we calculated the gain according to Eq. (1) or alternately the SR coherence (Eq. (2); Methods). The latter is a normalized *linear* cross-correlation measure in the frequency domain. Thus, if an afferent's firing responds well to a stimulus waveform, there will be high coherence between them at certain frequencies. We compared the gain and coherence tuning curves for a noise stimulus that was weak (i.e., did not produce afferent bursts) and had uniform power (i.e., “white” noise) at all frequencies below its cutoff frequency at $f_c = 200$ Hz (i.e., higher frequencies were not relevant).

Fig. 3(a) shows the PSD of spontaneous and noise-stimulated spike trains for a representative afferent. Biphasic spontaneous firing of the afferent is reflected in its PSD (grey line) containing a characteristic series of peaks,⁴⁹ including a peak at the fundamental frequency of the AO, $f_a = 57$ Hz, and at its second harmonic, $2f_a$, along with a peak at the fundamental frequency of the EO, $f_e = 24$ Hz, and also sideband peaks at combination frequencies, $f_a \pm f_e$. The PSD of stimulated firing (Fig. 3(a), black line) shows that noise acted to increase the power in the low-frequency

(<20 Hz) part of the spectrum, and to widen and suppress significantly the main peak associated with the AO, and to obscure the sideband peaks. However, the position, maximum value, and width of the EO peak did not change. Both the gain (Figs. 3(b) and 3(d)) and SR coherence (Figs. 3(c) and 3(d)) grew with the frequency up to a few Hz, reached a broad peak at 2–20 Hz, and fell off steeply at higher frequencies. However, frequency tuning estimated from SR coherence covered significantly wider band, with high coherence values extending towards lower frequencies, compared to tuning estimated from the gain.

The coherence of broadband noise stimuli to afferent firing always showed a “notch” at 23–27 Hz (at 22 °C), corresponding to the fundamental frequency of the EO, f_e . Coherence values fell abruptly in this notch, and could reach zero (Figs. 3(c), 3(d), and 6(a) arrow). Reduced coherence is a characteristic effect of strong noise. Thus, the reduced coherence in a narrow band around f_e is consistent with epithelial oscillations acting as a strong source of additional narrow-band noise, “internal” to an electroreceptor system,⁴⁹ which makes ER afferents unresponsive to external stimuli at frequencies near f_e . The frequency value of f_e is known to not be affected by external non-strong electrical stimuli,^{21,41,49} as already noted for Fig. 3(a), and neither was the notch band. The notch at f_e was not detected in earlier reports using discrete sinusoidal stimuli.

At higher frequencies, the coherence rose again just above f_e , but never to values greater than 0.5. Coherence then fell progressively, to nil at 40–50 Hz and higher (Figs. 3 and 6(a)). This falloff of coherence at higher frequencies, well above the EO frequency band, cannot be attributed to the narrow-band EO noise. Therefore, the responsiveness of paddlefish ERs presumably would decline over a similar upper boundary of stimulus frequencies even if epithelial oscillations were absent. Hence, the narrow band of EO noise appears to be *aligned* with an intrinsic upper frequency limit of electrosensory transduction. They act in concert to

FIG. 4. Linear stimulus reconstruction technique applied to an ER afferent stimulated by Gaussian noises with PSDs matched to the PSDs of original signals recorded from a swarm of *Daphnia* zooplankton prey or from a single *Daphnia*. (a) PSDs of Gaussian stimuli. Grey line: *Daphnia* swarm-like stimulus with $\text{SD} = 1.4 \mu\text{V/cm}$. Black line: Single *Daphnia*-like stimulus with $\text{SD} = 1.3 \mu\text{V/cm}$. (b) Coherence between Gaussian *Daphnia*-like stimuli and the resulting afferent spike trains. (c), (d) Segments of *Daphnia*-like stimuli to the ER (dotted lines) are compared to reconstructed stimuli (solid lines), derived from afferent spike trains (lower traces). Calibration bars apply to the stimulus waveforms in both (c) and (d).

achieve a relatively steep roll-off, ~ 13 dB/octave in the example of Fig. 3(c), about twice the falloff slope expected for a resistor-capacitor network.

B. Linear encoding and information rates

Information metrics, including the coding fraction and the mutual information, that quantify the linear encoding properties of electroreceptor afferents, were estimated from SR coherence and by linear reconstruction of a stimulus from the resulting afferent spike train to obtain an estimate of distortion, the mean square error between a stimulus reconstruction and the original. The coding fraction (Eq. (3)) gives the fraction of a stimulus waveform represented in a spike train and changes from 0 (no encoding) to 1 (100% representation of a stimulus in its reconstruction from a spike train or zero effective noise). The mutual information is a measure of how much information can be obtained about one random variable by observing another. Using the linear reconstruction method, we assessed the rate at which the reconstruction transmits information about Gaussian stimuli, which yields a lower bound of the mutual information rate.²⁸

The method is illustrated in Fig. 4 for an afferent stimulated by 180 s segments of Gaussian signals derived from

previously recorded bioelectric signals from individual *Daphnia* or from a swarm of many *Daphnia* (Methods, Fig. 2). For both types, most of the stimulus power was at low frequencies < 10 Hz, as shown by PSDs of the stimuli (Fig. 4(a)), and was within the frequency response band of ERs (Fig. 3(d)). While the signal from a *Daphnia* swarm could be represented as exponentially correlated noise,²⁶ the signal from a single *Daphnia* possessed essential periodicities due to 7 Hz beating of feeding legs, interrupted by large pulses due to antennal motions for swimming (Fig. 2(b)).²⁶ These naturalistic stimuli were faithfully encoded into afferent spike trains, as indicated by high values of SR coherence for both types of stimuli (Fig. 4(b)). The high fidelity of encoding is also seen in Figs. 4(c) and 4(d), comparing original stimulus waveforms (dotted lines) to their reconstructions from afferent spike trains by the optimal linear filter (solid lines). Both types of *Daphnia*-like stimuli gave high values of coding fraction (labels).

The dependence of the coding fraction or the lower bound of information rate on noise intensity (SD) was non-monotonic for all types of noise used, including naturalistic stimuli or band-limited Gaussian noise with 20 Hz cutoff frequency (Figs. 5(a) and 5(b)). Both measures increased with low SD values, but then saturated or passed through

FIG. 5. Coding fraction (a) and (b) the lower bound of mutual information rate, I_{LB} , versus noise SD, for 3 different ER afferents (different symbols), stimulated by the *Daphnia* swarm-like stimulus (triangles), or by the single *Daphnia*-like stimulus (squares), or by band-limited white noise with 20 Hz cutoff. All 3 stimulus waveforms had comparable power in the frequency response band of ERs.

TABLE I. Maximum values of the coding fraction, and the lower bound of the mutual information rate, for 13 paddlefish ER afferents; 3 were tested with both classes of stimuli. Naturalistic stimuli included swarm or single *Daphnia*-like waveforms with Gaussian amplitude distributions.

Type of stimulus	# ERs, n	CV	Coding fraction	Lower bound of mutual information rate (bits/s)
Naturalistic prey signals	7	0.19 ± 0.05 Range 0.13–0.27	0.76 ± 0.05 Range 0.70–0.83	30.2 ± 6.0 Range 25.0–37.6
White noise, 20 Hz cutoff	9	0.17 ± 0.04 Range 0.13–0.22	0.65 ± 0.04 Range 0.59–0.72	61.5 ± 7.2 Range 51.1–73.8

maximum values at SDs of $1\text{--}2\ \mu\text{V}/\text{cm}$, for these and other stimuli matching the frequency band of ERs.

Table I summarizes results for the maximal values of the coding fraction and the information rate obtained for ER afferents from 3 paddlefish stimulated by Gaussian naturalistic stimuli or by Gaussian white noise band-limited to 20 Hz. The table lists the sample size, n , for each type of stimulus used, the coefficient of variation (CV) of spontaneous sequences of interspike intervals, the coding fraction, and the lower bound estimate of the mutual information rate, I_{LB} . The fraction of a stimulus that was linearly encoded into afferent spike trains was significantly larger for naturalistic stimuli than for the band-limited noise (t-test, $P = 0.0003$), indicating that ER afferents are better suited for encoding signals from zooplankton prey. I_{LB} was larger for band-limited noise, because such a stimulus was less autocorrelated than naturalistic stimuli, and thus contained more information. On average, paddlefish ER afferents encoded 76% of weak naturalistic stimuli and transmitted their information at the rate of 30 bits/s.

C. Nonlinear responses

Indications of nonlinearities in the responses of paddlefish ERs to noise stimuli can be seen already in Fig. 5 from

the peaked dependence of the coding fraction and the lower bound of mutual information rate on the SD noise stimuli. These information metrics increased, but then saturated and decreased for strong stimuli. Linear response theory predicts, however, a monotonic increase of the coherence with higher stimulus intensity,⁵² and thus an increased coding fraction or information rate. The observed non-monotonic behavior of the mutual information rate can, therefore, be attributed to nonlinear effects^{56,61} acting to decrease SR coherence. We used two distinct approaches to assess nonlinearities in signal encoding.

The cross bicoherence is a normalized measure that ranges from 0 to 1 (Eq. (5)) and quantifies the extent of quadratic coupling as a function of two frequencies that can be varied independently (Methods). Since our stimulus waveforms were continuous and Gaussian, the cross bicoherence should be nil for a linearly coupled stimulus and response.⁵⁴ Frequency-dependent non-zero values of the cross bicoherence would instead indicate nonlinear coupling of the two frequency sources. Fig. 6 compares linear and nonlinear responses of an afferent stimulated by broad-band (up to 200 Hz) noise, at 3 intensities ranging from small to large SD, which, respectively, elicited none, moderate, or pronounced bursting. As a linear metric, the coherence curves shown in

FIG. 6. (Color online) Nonlinearities of afferent bursting responses measured with cross bicoherence. (a) and (b) Comparison of linear to nonlinear metrics for the same ER stimulated with broadband white noise (200 Hz cutoff) of 3 different SDs, as labeled. (a) [Linear] SR coherence between noise stimuli and simultaneous afferent spike train. (b) Contour lines of [nonlinear] cross bicoherence showing significant nonlinearities (i.e., non-zero, frequency-dependent values) for moderate and large noise. (c) Maximal value of [nonlinear] cross bicoherence, of spiking of two different afferents, to white noise stimulus with 20 Hz (triangles) or 200 Hz (circles) cutoff, over a wide range of SDs. Arrows: Threshold values of bursting determined from Arrhenius plots, i.e., plots of mean interburst interval vs. noise SD (not shown). (d) Maximal value of [linear] SR coherence, calculated from same data as (c).

Fig. 6(a) had similar shapes for all 3 stimulus SD's, reflecting afferent frequency tuning properties already described above, including a zero-coherence notch at the frequency of epithelial oscillations (f_e), and regrowth of coherence in the f_e to 50 Hz band (*asterisk*), especially at higher stimulus intensity.

The cross bicoherence yields 3D graphs, as in Fig. 6(b), shown using contour lines. As a metric of nonlinearity, the cross bicoherence was nil for weak noise, when the afferent was in tonic firing mode, indicating linear response (not shown). For larger noise (25 $\mu\text{V}/\text{cm}$), the cross bicoherence grew significantly, reaching 0.04 in the frequency band of best afferent tuning at 10–20 Hz (Fig. 6(b), left panel). For strong noise (Fig. 6(b), right panel), the cross bicoherence reached maximal value of ~ 0.22 in the frequency band 10–20 Hz, but also displayed significant values around 30 Hz, where the second band of SR coherence was observed for broadband stimuli (Fig. 6(a), *asterisk*). This indicated essentially nonlinear coupling of Fourier harmonics of the broadband Gaussian stimulus to the spike train response, which was strongly in the bursting mode.

The maximal value of the cross bicoherence across all frequencies served as another metric of nonlinearity. Its threshold-like behavior established a causal link between nonlinearity and bursting. As the intensity of a noise stimulus was increased, the maximum value of the cross bicoherence was negligible up to a certain level of stimulus intensity, as expected for a linear stimulus—response relation, but grew abruptly at higher stimulus intensity, demonstrating sharp threshold behavior (Fig. 6(c)). We observed this for both band-matched noise (*triangles*, 20 Hz cutoff) and broadband noise (*circles*, 200 Hz cutoff). We note again that since total power was held fixed for stimuli of different bandwidths (Methods), broadband stimuli had less power in the response

band of electroreceptors, so the apparent threshold for bursting was higher.⁵¹ These threshold values, at which the cross bicoherence grew abruptly, corresponded well to the threshold values to elicit bursting, estimated from Arrhenius plots as in Ref. 51, shown by arrows in Fig. 6(c). For comparison, the maximal value of SR coherence, used as a metric of linear responsiveness, grew with stimulus intensity until saturating (Fig. 6(d)), resembling the behavior of the coding fraction and the lower bound of the mutual information rate (Fig. 5), also metrics of linear responsiveness.

Our second approach to assessing nonlinearities in signal encoding was to compare the performance of the best linear encoding model, quantified by the SR coherence, to a theoretical upper limit of encoding set by the RR coherence.^{14,61} The square root of RR coherence (Eq. (6)) is always greater than or equal to the SR coherence at a given frequency. The RR coherence is calculated between response trials, does not consider the stimulus, and quantifies the reliability of repeated responses that cannot be accounted for by the stimulus. If encoding is linear, the SR and the square root of RR coherences are close. Significant elevation of the square root of RR coherence above the SR coherence indicates nonlinear stimulus—response relations. A “frozen noise” procedure was used: for $n=6$ afferents in 3 paddlefish, we stimulated ERs with 30–100 identical trials of broadband noise, each 13.2 s long, with 5 s of no stimulus between trials. A qualitative impression of the reliability of spike timing was obtained from raster plots of afferent spike times, relative to the noise stimulus segment, which showed emergence of bursts as the stimulus SD was augmented (Fig. 7(a)). At intermediate stimulus SDs, e.g., 10 $\mu\text{V}/\text{cm}$, bursting started to appear, but spikes inside bursts were aligned poorly and thus responses were not “reliable” at short time scales (high frequencies). Reliability increased

FIG. 7. Reliability of responses of an electroreceptor afferent to “frozen noise” stimulation. One trial was a 13.2 s long segment of Gaussian white noise, 200 Hz cutoff frequency. This was repeated 100 times for each indicated value of stimulus SD. (a) Raster plots of afferent spikes (*dots*) in relation to the stimulus noise segment (*bottom*), for 4 stimulus intensities ranging from weak to strong. (b) Comparison of stimulus—response coherence (SR coh, *black line*) and the square root of response—response coherence (RR coh, *grey line*), for labeled values of noise SD.

dramatically at larger noise SDs, until at $97 \mu\text{V}/\text{cm}$, not only the burst onsets but also the spikes inside bursts were almost perfectly aligned.^{9,32,42,55}

This extra reliability of spike timing during bursts was quantified by comparing the RR and SR coherences (Fig. 7(b)). For weak and intermediate stimuli ($\text{SD}=3$ or $10 \mu\text{V}/\text{cm}$), when the afferent was in the tonic firing mode, the SR and RR coherences coincided, indicating that a model assuming linear encoding was appropriate. However, for the well-developed bursting during larger noise ($\text{SD}=30$ or $97 \mu\text{V}/\text{cm}$), dramatic departures of the RR and SR coherences were observed. The RR coherence exhibited large values at high frequencies extending well beyond the linear frequency response band of ERs, due to the high degree of reliability of afferent spike timing inside bursts. In the important low-frequency domain ($0.4\text{--}20 \text{ Hz}$), the RR coherence was high and flat, indicating amplification of encoding of low-frequency components of the stimulus by bursts. This elevation of RR coherence manifested at frequencies $<1 \text{ Hz}$ even for weak stimulus intensities (Fig. 7(b); 3 or $10 \mu\text{V}/\text{cm}$), attesting to the tendency of ER afferents to fire in bursts. In contrast, even for strong stimuli, the SR coherence still showed frequency tuning typical for ERs, with lower coherence values at low frequencies ($\leq 1 \text{ Hz}$). We conclude that the best linear encoding model was not optimal for strong stimuli and that the bursting regime represents highly nonlinear responses of ER afferents.

D. Synchronization of burst events

We showed previously⁴⁹ that the spontaneous dynamics (afferent spike timing and epithelial oscillations) of different ERs located on the paddlefish rostrum are statistically independent. Thus, the rostrum ERs form parallel arrays of independent sensors. Moreover, the spontaneous firing rates of ER afferents are heterogeneous, distributed over a wide $30\text{--}70 \text{ spikes/s}$ range. Despite this heterogeneity and lack of coupling, noise stimuli can act to synchronize the activity of different afferents, on the slow timescale of bursts.⁴⁸ That is, burst events elicited in pairs of ERs by shared adequate-strength stimuli were tightly time-locked. This was true despite recording from ER pairs having receptive fields on opposite sides of the rostrum, and up to $10\text{--}15 \text{ cm}$ apart, to ensure that there was no coupling between them.

We tested the effectiveness of several types of noise waveforms for eliciting such stimulus-mediated coupling of bursts in $n=9$ pairs of afferents. Gaussian-matched naturalistic noise of an individual *Daphnia* zooplankton prey (Fig. 8(a1)), as well as other types of low-frequency noise matching the best tuning of paddlefish ERs were more effective for inducing synchrony of ER afferent pairs, being operative at lower stimulus intensity than was required for broadband OU noise (Fig. 8(a2)), on account of band matching.

Cross-correlograms (Figs. 8(b1) and 8(b2)) allowed quantitation of how tightly the burst or spike events were

FIG. 8. Synchronization of burst events in pairs of electroreceptor afferents of different ERs, stimulated and recorded simultaneously. (a) Segments of raw recordings. Burst onsets are marked by short vertical lines. Bottom traces show the simultaneous stimulus waveforms, either (a1) Gaussian-matched naturalistic signal of a single *Daphnia*, $\text{SD}=12 \mu\text{V}/\text{cm}$, or (a2) broadband OU noise, $\text{SD}=55 \mu\text{V}/\text{cm}$. ((b1) and (b2)) Cross-correlograms between a pair of afferents during noise co-stimulation, of spikes (black line) or burst onsets (grey line), from the same respective recordings as (a1) and (a2). Horizontal dashed line: Control cross-correlogram of spontaneous spiking activity. (c) Dependence on stimulus intensity of the width of cross-correlogram peak for spikes (black) or bursts (grey), for the pair of afferents stimulated with OU noise (in (a2) and (b2)).

coordinated between two afferents, recorded simultaneously and co-stimulated with noise. The *width* of a peak in a cross-correlogram is a measure of how tightly the events in two channels are linked; for perfectly synchronized events, the width would be zero (a delta function). The widths of cross-correlogram peaks from the *burst onsets* in a data segment were always several-fold narrower than from all the individual *spikes*, for either type of stimulus, of a given strength (Figs. 8(b1) and 8(b2)). As the stimulus SD was raised (Fig. 8(c)), cross-correlogram peaks became narrower, until reaching saturating minimum width values, estimated at the half-maximum of peaks as 6 ± 2 ms for the burst onsets only, compared to 26 ± 15 ms for complete spike trains, for $n = 9$ pairs of ERs. Saturation was reached at lower stimulus strength for burst onsets than for spikes (Fig. 8(c)). Thus, stimulus-driven *bursts* were well-synchronized across different afferents, for moderate and higher stimulus intensities. This marked propensity to synchronization suggests homogeneity in the bursting dynamics of different ER afferents.

Although the existence of a peak shows that individual *spikes* in a pair of afferents (from different ERs) were correlated during co-stimulation, they were not tightly synchronized, because the positions and numbers of spikes inside bursts differed for different afferents, and fluctuated from burst to burst, resulting in a wide cross-correlogram peak. Even though a given afferent's spikes became reliably locked to a stimulus waveform at high strength (Fig. 7(a)), the positions and numbers of spikes inside bursts could still differ for different afferents. As a control, cross-correlograms between the spontaneous tonic firing of afferent pairs yielded uniform distributions (flat dashed lines in Figs. 8(b1) and 8(b2)), indicating independence, as expected.

Further insights into the functional roles of nonlinear responses, and their relation to synchronization, were obtained by stimulating pairs of afferents, recorded simultaneously from different ERs, with raw signals emitted by individual *Daphnia* (Fig. 2(b)), presented as “uniform field” stimulation between plate electrodes (Methods) at moderate strength ($SD = 10.5 \mu\text{V/cm}$). This real prey signal was non-Gaussian and contained an almost periodic 5–7 Hz component resembling a sine wave (Fig. 9(a), bottom trace), due to beating motions of feeding legs, along with intermittent large-amplitude short pulses (*arrows*) during antennal motions, which boosted the signal's power at lower frequencies. ERs responded to both the sine wave and the pulse components. The periodic (feeding legs) component of the *Daphnia* signal modulated the tonic firing of afferents, like responses to moderate sine wave stimuli. By contrast, each large antennal pulse, of positive (anodal) polarity in this example, led to a period of silence in both afferents, followed by a burst of tightly spaced spikes that occurred simultaneously and stereotypically in both afferents.

To quantitate the latter behavior, we used an index developed for analysis of transient synchronization⁷³ to compare the spike times of two afferents (recorded simultaneously, from different ERs) in relation to antennal pulse stimuli. Such analysis required that each afferent's spike train, a point process, be converted to phase, a continuous function of time, by defining the spike train phase as increas-

FIG. 9. Transient synchronization of individual spikes in two afferents by shared abrupt input. (a) Simultaneous firing of a pair of afferents (two upper traces) from different ERs, co-stimulated by a raw original signal recorded from a single tethered *Daphnia* (bottom trace) with $SD = 10.5 \mu\text{V/cm}$. Small stimulus oscillations correspond to the motions of feeding legs, while large pulse-like excursions correspond to antennal motions. Dashed horizontal line: Baseline. Arrows: Peaks of antennal pulses were used as *trigger points* for averaging of the *Daphnia* stimulus waveform (panel b), using a 1 s sliding window centered at trigger points (dashed vertical line at time = zero), and for calculation of synchronization index between the pair of afferent spike trains (panel c). (c, black line) Synchronization index versus time relative to stimulus trigger points. (c, grey shading) Synchronization index for surrogate spike trains obtained by random shuffling (resequencing) of interspike intervals for both afferents, as a “computational control.”

ing by 2π at every spike time, and by interpolating the phase linearly between consecutive spikes. This treatment implicitly viewed the afferent firing as a cyclical process, with each ISI corresponding to a cycle, of variable duration. *Daphnia* antennal pulses which were separated from others by at least 1 s were treated as uncorrelated “stimulus trials”; trigger points were set at their peak values (*arrows*, Fig. 9(a)), and a 1 s time window was attached to each chosen pulse, centered at the trigger point, such that time t in each window ran from -0.5 to $+0.5$ s. An ensemble of trial responses was created by aligning the windows. The degree of stimulus-locked synchronization between two different afferents was assessed using a time-dependent synchronization index, $\sigma^2(t) = \langle \cos \psi(t) \rangle^2 + \langle \sin \psi(t) \rangle^2$, where $\psi(t) = \varphi_1(t) - \varphi_2(t)$ was the instantaneous phase difference of the two afferents within a trial window, and averaging $\langle \rangle$ was performed across the ensemble of trials. This index ranges from 0 to 1. A maximum value of $\sigma(t) = 1$ would indicate that at time t relative to stimulus trigger points, the phase differences were the same for all trials, so that the two afferents were perfectly

synchronized at that time. A minimum value of 0 would mean that the phase differences were distributed uniformly across trials, i.e., that synchronization was completely absent at that time. As shown in Fig. 9(c), spikes in an afferent pair were tightly but transiently synchronized by antennal pulses, as evidenced by the time-dependent synchronization index reaching high values of ~ 0.98 near trigger points. Index values were small before and after antennal pulses because they occurred more-or-less randomly in time. As a simple statistical “control,” the interspike intervals within trial windows were randomly shuffled. The synchronization index calculated for these surrogate data (shown by grey shading in Fig. 9(c)) fluctuated near zero, without systematic variation at different time offsets from trigger points, as expected for abolition of time dependencies. In sum, large natural stimulus excursions acted to reset the phases of afferent neurons, evoking transient synchronization of individual spikes in different afferents.

IV. CONCLUSION AND DISCUSSION

We have characterized the linear and nonlinear response properties of Lorenzinian ampullary ERs of paddlefish, and their encoding of various kinds of time-varying stimuli, ranging from artificial broad-band Gaussian noise to natural waveforms recorded from zooplankton prey. Our main results are: (1) Measurements of the linear frequency tuning properties of ER afferents, using coherence and gain metrics, in response to white Gaussian noise stimuli, confirmed that ERs are tuned to a “best” frequency band of 0.5–20 Hz, matching the frequency band of naturalistic electrical stimuli emitted by zooplankton prey. (2) Coherence analysis revealed the role of epithelial oscillations as a source of narrow-band noise at ~ 24 –30 Hz. This band is aligned with the upper margin of ER frequency responsiveness and contributes to its roll-off. (3) On average, 76% of naturalistic stimuli of weak strength, $\sim 1 \mu\text{V}/\text{cm}$, was linearly encoded into afferent spike trains, which transmitted information at a rate of 30 bits/s. Coding efficiency was highest for naturalistic stimuli (see Table I), indicating that ERs are tuned to encode signals from zooplankton prey. (4) Stimulus transfer to afferent spike timing became essentially nonlinear as the stimulus strength was increased to induce bursting. Nonlinearity was manifested as growth of cross bicoherence between stimulus and afferent spikes, and as reliable spike timing in response to “frozen noise” trials, quantified using response-response coherence. (5) Stimulus-induced bursts were synchronized across populations of ERs. (6) Large pulse-like stimuli acted to synchronize the individual spikes in pairs of afferents, as shown using a synchronization index. Both types (5 and 6) of stimulus-mediated fictive coupling between electroreceptors provide a plausible mechanism for redundant and hence reliable information transfer to higher-order neurons through (presumably) noisy synapses.

A. Functional roles of oscillations in electroreception

We have documented several types of oscillatory activity in paddlefish electroreceptors, including: (1) a dominant oscillator in the peripheral terminal of each afferent, whose fre-

quency corresponds to its mean firing rate, in the range of 30–70 Hz; (2) prominent ongoing epithelial oscillations at ~ 26 Hz; (3) a parabolic bursting mode of afferent spiking in response to stimuli of moderate or higher intensity; and (4) correlations of sequential ISI durations that alternate in sign, and decay over several tens of ISIs after a given afferent spike.^{1,47,50} That the oscillatory activities in paddlefish electroreceptors have functional significance, and represent optimizations governed by Darwinian selection, is our working hypothesis.

As in other “lateralis” sensory receptors of vertebrate animals, e.g., for hearing and balance, the afferent axons from paddlefish ERs fire action potentials continuously, without external stimulation, in what is termed “spontaneous” or background firing. This ongoing “tonic” discharge allows sensory receptors to respond to both excitatory and inhibitory external stimuli. That is, the afferent firing rate speeds up or slows down, depending on stimulus polarity. Several mechanisms for background firing have been documented: (1) Synaptic mechanisms drive the background firing of vestibular and auditory afferents, whereby vesicles of excitatory glutamate-like neurotransmitter are released continuously at the ribbon synapses found in (presynaptic) hair/receptor cells, and this stochastic “quantal release” evokes spikes in (postsynaptic) afferents in a nearly one vesicle—one spike manner, such that the background firing of afferents follows (random) Poisson statistics, like the quantal transmitter release. Supplemental excitation of certain afferent terminals comes from accumulation of potassium ions around stimulated hair cells. (2) “Pacemaker” mechanisms can be likened to integrate-fire-reset models having an internal bias such that they cross threshold and fire again after a delay. This describes how the rhythm and rate of the heartbeat arise in cardiac cells of the sinoatrial node, due to time-dependent decay of a “pacemaker” membrane current through certain ion channels. Pacemaker mechanisms depend on spike generation for resetting. (3) In contrast, certain well-documented “endogenous burster” neurons possess a distinct mechanism for producing slow oscillations of membrane potential, which then drive fast repetitive firing of axon spikes. The slow oscillator may remain intact and active even if spikes are abolished pharmacologically. In certain sensory receptors, a similar mechanism has been proposed to account for “skipping” and “preferred intervals” in the firing statistics of afferents.^{43,67}

While the background firing of paddlefish ER afferents appears tonic and random, our statistical analyses have revealed that it is actually quasiperiodic. Evidence for an afferent oscillator includes the high-power peak in power spectra of afferent spike trains coincident with the mean firing rate, along with synchronization and serial ISI phenomena which imply the existence of an oscillator in each afferent’s peripheral terminal. These lines of evidence point to a functional role of the afferent oscillator as a major driver of background periodic firing. However, it cannot be the sole driver of background firing, because it cannot explain that ER firing slows in response to inhibitory stimuli. Hence, another drive component for the background firing must come from continuous synaptic excitation by the receptor cells, consistent with their known possession of ribbon-type synapses.

B. Epithelial oscillations

Epithelial oscillations were well-documented in the Lorenzinian ERs of other fish^{20,21,41} before our results on paddlefish ERs. The primary functional role of these prominent oscillation is unproven, but a plausible working hypothesis is that the primary functional role of epithelial oscillations may be to drive secretion of the proteinaceous gel that fills the ampulla and canal of Lorenzinian ERs. There are many examples of secretory cells being auto-active. Besides conducting electrical signals, the gel is likely to be involved in defending the canal interior and the sensory epithelium against invasion by microbes and parasites.

Nonetheless, three functional consequences of epithelial oscillations, for electroreception, that we have identified, appear to be more than merely coincidental. First, the narrow-band large noise of the EO acts as a tuning mechanism, contributing to the steep upper roll-off of ER frequency response (Results, part A). This large drop in detection of external stimuli occurs because the EO injects large noise, presumably at the stage of synaptic transmission from receptor cells to afferents. This noise-masking of stimulus input is akin to the phenomenon of “sound masking” in hearing. However, as already explained, electrosensory transduction probably declines intrinsically over a similar upper boundary, to which the narrow-band ER noise is *aligned*, resulting in steeper roll-off. The behavioral significance, if any, of this steeper roll-off is unknown. Perhaps, this arrangement simply serves to put the EO noise, an unavoidable side effect of gel secretion, outside of the best frequency band for electrosense to avoid interference. On the other hand, the EO frequency should not be any higher, to avoid synchronization interactions with the afferent oscillator that would occur if their frequencies were close. In sum, paddlefish electroreceptors provide an example of a plausible general mechanism for sharply limiting the frequency band of a neural transmission channel, based on frequency-specific masking by narrow-band noise from stochastic oscillators.

A second functional effect of the EO, on electroreception, is suppression of low-frequency noise, by inducing ISI correlations in conjunction with the afferent oscillator. The high-pass filtering property of ERs, at ~ 0.1 Hz, is presumably due to slow adaptation processes which tend to filter out slow variations in stimulus amplitude, as in certain ERs of weakly electric fish.³ Despite such adaptation, the coherence tuning curves that we measured retained high values at lower frequencies, owing to a specific correlation structure of the afferent spike train. We have shown previously that the spontaneous spike timing of ER afferents in paddlefish is non-renewal, instead showing prominent extended serial correlations for tens of ISIs.^{1,47,49,50} These correlations suppress spiking variability on time scales longer than the mean interspike interval, resulting in decreased power of internal noise at low frequencies in the power spectrum.^{23,27,50} This boosts the signal-to-noise ratio at low frequencies, and consequently the SR coherence, and enhances the coding efficiency of a neuron. We note that the low frequency band of 0.5–2 Hz is indeed represented in the PSDs of naturalistic stimuli from

zooplankton²⁶ and of moving DC electrical sources in water.³⁶ Although the gain of paddlefish ER afferents was low in this 0.5–2 Hz frequency range, the SR coherence showed high values, indicating effective stimulus encoding, and demonstrating the advantages of SR coherence for measuring frequency tuning.¹⁷ Similar results were reported for “P-unit” afferents from tuberous ERs of weakly electric fish,^{15,58} in which negative serial correlations over just a few afferent ISIs shape the power spectrum by lowering internal noise power at low frequencies, dubbed “noise shaping,” thus enhancing SR coherence. However, the mechanism of generating serial correlations in paddlefish ampullary Lorenzinian ERs is very different. Periodic forcing of the afferent oscillator by the epithelial oscillations is the main source of long-lasting serial ISI correlations.⁵⁰ Modeling studies have shown that this novel mechanism depends strongly on the frequency ratio of the epithelial and afferent oscillators, with the longest series of ISI correlations occurring at epithelial/afferent frequency ratios near 0.5. It seems like more than coincidence that real ERs tend to show just this frequency ratio.⁴⁹

Third, recent modeling studies have shown that self-coherent epithelial oscillations enhance significantly both the coding of sensory information^{27,53} and the discrimination capacity of electroreceptors.²³ Other functional roles of epithelial oscillations are possible. In sum, it appears that natural selection has turned a liability, the noisy electrical activity of sensory epithelia (for gel secretion?), into assets for electroreception.

C. Linear and non-linear responses and coding

For weak and moderate stimuli, when afferents responded in the “tonic” mode, the SR and RR coherences were close, indicating that a linear encoding model was adequate. The coding fraction was in the range of 59–83% for stimuli with frequency content matching the ER response properties and was maximal for stimuli derived from natural zooplankton signals. We conclude that the ampullary electroreceptors of paddlefish are perfectly suited to linearly encode weak low-frequency stimuli. As Fig. 5 shows, linear information metrics for naturalistic stimuli started to rise below $0.1 \mu\text{V}/\text{cm}$ r.m.s amplitude, peaked at $1\text{--}2 \mu\text{V}/\text{cm}$, and declined at stronger values (as bursting appeared). This is surprising, since a stimulus strength of $1 \mu\text{V}/\text{cm}$ has long been cited as near “threshold” for electrosensitivity in fresh water fish.¹⁰ In fact, linear metrics are nearly saturated at $1 \mu\text{V}/\text{cm}$. Of course, information metrics involve averaging.

Afferents transitioned to the bursting mode at increased stimulus strength.⁵¹ We have shown that noise-induced bursting is an essentially nonlinear process, using two distinct approaches to assess nonlinearities (Results, part C). In the bursting regime, the lower bound metric may severely underestimate the true mutual information rate, which should instead be estimated directly.⁷⁰

Interestingly, a wide uniform frequency response was reported for higher-level electrosensory neurons in the paddlefish brain.^{19,35} They, unlike primary afferents characteristically show low background firing rates and thus may work

as rectifiers, which are a canonical example of a nonlinear decoder.

Another type of nonlinear encoding is stimulus-evoked synchronization of different afferents. We distinguished between co-stimulation effects on bursts vs. individual spikes. Burst events can be synchronized across pairs of different afferents receiving identical stimulation,^{48,51} with a precision of a few milliseconds (Fig. 8(a)). We used a synchronization index to show that large pulse-like bioelectrical signals from zooplankton prey could evoke transient synchronization of firing in different afferents, at the level of individual spikes (Fig. 9(c)). This could provide yet another mechanism of signal detection. Synchronization of several afferents from the *same* receptive field, due to external stimuli, is an attractive scenario for reliable stimulus detection in higher-level electrosensory processing in the brain. On the other hand, lag synchronization of afferents from *different* receptive fields may be useful for spatial localization of a stimulus.

D. Notes on methods

For all the types of noise stimuli that we utilized, the SR coherence to afferent firing had a broad peak, tailed off at lower frequencies (to ~ 0.1 Hz), and fell precipitously at frequencies above 26–30 Hz (Figs. 3(c), 3(d), and 6(a)). Therefore, band-limited white noise with 200 Hz cutoff frequency was effectively broadband or “white” for these low-frequency ERs of paddlefish.

Despite being repeatedly confirmed,^{20,21,41,67} epithelial oscillations and other oscillatory phenomena exhibited by electroreceptors continue to be dismissed by some authors as epiphenomena or artifacts. This prejudice originates in part from inappropriate past procedures of recording from ERs while they were in air or oil, such that normal electrical loading due to connection of canals to surrounding water was absent, which tended to induce instability. Mindful of this, all of our results have come from fully immersed ERs. Another concern is that the physiological status of an *in vivo* fish preparation should be monitored quantitatively during an experiment, to have criteria for distinguishing “neurodynamics” from “necrodynamics.” To this end, we report only data from healthy fish and “fresh” *in vivo* preparations less than 16 h old.

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¹Bahar, S., Kantelhardt, J. W., Neiman, A., Rego, A., H. H., Russell, D. F., Wilkens, L., Bunde, A., and Moss, F., “Long-range temporal anti-correlations in paddlefish electroreceptors,” *Europhys. Lett.* **56**(3), 454–460 (2001).

²Barnett, T. P., Johnson, L. C., Naitoh, P., Hicks, N., and Nute, C., “Bispectrum analysis of electroencephalogram signals during waking and sleeping,” *Science* **172**, 401–402 (1971).

- ³Benda, J., Longtin, A., and Maler, L., “Spike-frequency adaptation separates transient communication signals from background oscillations,” *J. Neurosci.* **25**(9), 2312–2321 (2005).
- ⁴Bendat, J. S. and Piersol, A. G., *Random Data Analysis and Measurement Procedures* (Wiley, New York, 2000).
- ⁵Bennett, M. V. and Obara, S., “Ionic mechanisms and pharmacology of electroreception,” in *Electroreception*, edited by T. H. Bullock and W. Heiligenberg (Wiley, New York, 1986), pp. 157–181.
- ⁶Bialek, W., Rieke, F., de Ruyter van Steveninck, R. R., and Warland, D., “Reading a neural code,” *Science* **252**(5014), 1854–1857 (1991).
- ⁷Braun, H. A., Schafer, K., Voigt, K., Peters, R., Bretschneider, F., Pei, X., Wilkens, L., and Moss, F., “Low-dimensional dynamics in sensory biology. 1: Thermally sensitive electroreceptors of the catfish,” *J. Comput. Neurosci.* **4**(4), 335–347 (1997).
- ⁸Braun, H. A., Wissing, H., Schafer, K., and Hirsch, M. C., “Oscillation and noise determine signal transduction in shark multimodal sensory cells,” *Nature* **367**(6460), 270–273 (1994).
- ⁹Bryant, H. L. and Segundo, J. P., “Spike initiation by transmembrane current: A white-noise analysis,” *J. Physiol.* **260**(2), 279–314 (1976).
- ¹⁰Bullock, T. H., “Electroreception,” *Ann. Rev. Neurosci.* **5**, 121–170 (1982).
- ¹¹Bullock, T. H., Achimowicz, J. Z., Duckrow, R. B., Spencer, S. S., and Iragui-Madoz, V. J., “Bicoherence of intracranial EEG in sleep, wakefulness and seizures,” *Electroencephalogr. Clin. Neurophysiol.* **103**(6), 661–678 (1997).
- ¹²Bullock, T. H., Bodznick, D. A., and Northcutt, R. G., “The phylogenetic distribution of electroreception: evidence for convergent evolution of a primitive vertebrate sense modality,” *Brain Res.* **287**, 25–46 (1983).
- ¹³Catacuzzeno, L., Fioretti, B., Perin, P., and Franciolini, F., “Spontaneous low-frequency voltage oscillations in frog saccular hair cells,” *J. Physiol.* **561**, 685–701 (2004).
- ¹⁴Chacron, M. J., “Nonlinear information processing in a model sensory system,” *J. Neurophysiol.* **95**(5), 2933–2946 (2006).
- ¹⁵Chacron, M. J., Longtin, A., and Maler, L., “Negative interspike interval correlations increase the neuronal capacity for encoding time-dependent stimuli,” *J. Neurosci.* **21**(14), 5328–5343 (2001).
- ¹⁶Chacron, M. J., Longtin, A., and Maler, L., “To burst or not to burst?,” *J. Comput. Neurosci.* **17**(2), 127–136 (2004).
- ¹⁷Chacron, M. J., Maler, L., and Bastian, J., “Electroreceptor neuron dynamics shape information transmission,” *Nature Neurosci.* **8**(5), 673–678 (2005).
- ¹⁸Chagnaud, B. P., Wilkens, L. A., and Hofmann, M. H., “Receptive field organization of electrosensory neurons in the paddlefish (*Polyodon spathula*),” *J. Physiol. Paris* **102**(4–6), 246–255 (2008).
- ¹⁹Chagnaud, B. P., Wilkens, L. A., and Hofmann, M. H., “Response properties of electrosensory neurons in the lateral mesencephalic nucleus of the paddlefish,” *J. Comput. Physiol. A* **194**(3), 209–220 (2008).
- ²⁰Clusin, W. T. and Bennett, M. V. L., “The ionic basis of oscillatory responses of skate electroreceptors,” *J. Gen. Physiol.* **73**(6), 703–723 (1979).
- ²¹Clusin, W. T. and Bennett, M. V. L., “The oscillatory responses of skate electroreceptors to small voltage stimuli,” *J. Gen. Physiol.* **73**, 685–702 (1979).
- ²²Eguiluz, V. M., Ospeck, M., Choe, Y., Hudspeth, A. J., and Magnasco, M. O., “Essential nonlinearities in hearing,” *Phys. Rev. Lett.* **84**(22), 5232–5235 (2000).
- ²³Engel, T. A., Helbig, B., Russell, D. F., Schimansky-Geier, L., and Neiman, A. B., “Coherent stochastic oscillations enhance signal detection in spiking neurons,” *Phys. Rev. E* **80**, 021919 (2009).
- ²⁴Engelmann, J., Gertz, S., Goulet, J., Schuh, A., and von der Emde, G., “Coding of stimuli by ampullary afferents in *Gnathonemus petersii*,” *J. Neurophysiol.* **104**(4), 1955–1968 (2010).
- ²⁵Ermentrout, G. B., Galan, R. F., and Urban, N. N., “Relating neural dynamics to neural coding,” *Phys. Rev. Lett.* **99**(24), 248103 (2007).
- ²⁶Freund, J. A., Schimansky-Geier, L., Beisner, B., Neiman, A., and Russell, D. F., Yakusheva, T., and Moss, F., “Behavioral stochastic resonance: how the noise from a *Daphnia* swarm enhances individual prey capture by juvenile paddlefish,” *J. Theor. Biol.* **214**(1), 71–83 (2002).
- ²⁷Fuwape, I. and Neiman, A. B., “Spontaneous firing statistics and information transfer in electroreceptors of paddlefish,” *Phys. Rev. E* **78**, 051922 (2008).
- ²⁸Gabbiani, F., “Coding of time-varying signals in spike trains of linear and half-wave rectifying neurons,” *Network Comput. Neural Syst.* **7**(1), 61–85 (1996).

- ²⁹Gabbiani, F. and Koch, C., "Principles of spike train analysis," in *Methods in Neuronal Modeling. From Ions to Networks*, edited by C. Koch, and I. Segev (MIT Press, Cambridge, Mass, 1998), pp. 313–360.
- ³⁰Gabbiani, F. and Metzner, W., "Encoding and processing of sensory information in neuronal spike trains," *J. Exp. Biol.* **202**, 1267–1279 (1999).
- ³¹Goldberg, J. M., "Afferent diversity and the organization of central vestibular pathways," *Exp. Brain Res.* **130**(3), 277–297 (2000).
- ³²Goldobin, D. S. and Pikovsky, A., "Synchronization and desynchronization of self-sustained oscillators by common noise," *Phys. Rev. E* **71**, 045201 (2005).
- ³³Hanggi, P. and Thomas, H., "Stochastic-Processes - Time Evolution, Symmetries and Linear Response," *Phys. Rep.-Rev. Sec. Phys. Lett.* **88**(4), 207–319 (1982).
- ³⁴Hofmann, M. H., Chagnaud, B., and Wilkens, L. A., "Response properties of electrosensory afferent fibers and secondary brain stem neurons in the paddlefish," *J. Exp. Biol.* **208**, 4213–4222 (2005).
- ³⁵Hofmann, M. H., Jung, S. N., Siebenaller, U., Preissner, M., Chagnaud, B. P., and Wilkens, L. A., "Response properties of electrosensory units in the midbrain tectum of the paddlefish (*Polyodon spathula* Walbaum)," *J. Exp. Biol.* **211**, 773–779 (2008).
- ³⁶Hofmann, M. H. and Wilkens, L. A., "Temporal analysis of moving DC electric fields in aquatic media," *Phys. Biol.* **2**(1–2), 23–28 (2005).
- ³⁷Horsthemke, W. and Lefever, R., *Noise-Induced Transitions. Theory and Applications in Physics, Chemistry, and Biology* (Springer, Berlin, 1984).
- ³⁸Hudspeth, A. J., Julicher, F., and Martin, P., "A critique of the critical cochlea: Hopf-a bifurcation-is better than none," *J. Neurophysiol.* **104**(3), 1219–1229 (2010).
- ³⁹Johnson, L. C., Nute, C., Austin, M. T., and Lubin, A., "Spectral analysis of the EEG during waking and sleeping," *Electroencephalogr. Clin. Neurophysiol.* **23**(1), 80 (1967).
- ⁴⁰Lesica, N. A. and Stanley, G. B., "Encoding of natural scene movies by tonic and burst spikes in the lateral geniculate nucleus," *J. Neurosci.* **24**(47), 10731–10740 (2004).
- ⁴¹Lu, J. and Fishman, H. M., "Localization and function of the electrical oscillation in electrosensory ampullary epithelium from skates," *Biophys. J.* **69**(6), 2458–2466 (1995).
- ⁴²Mainen, Z. F. and Sejnowski, T. J., "Reliability of spike timing in neocortical neurons," *Science* **268**(5216), 1503–1506 (1995).
- ⁴³Manley, G. A., "Preferred intervals in the spontaneous activity of primary auditory neurons," *Naturwiss.* **66**(11), 582–584 (1979).
- ⁴⁴Martin, P., Bozovic, D., Choe, Y., and Hudspeth, A. J., "Spontaneous oscillation by hair bundles of the bullfrog's sacculus," *J. Neurosci.* **23**(11), 4533–4548 (2003).
- ⁴⁵Massot, C., Chacron, M. J., and Cullen, K. E., "Information transmission and detection thresholds in the vestibular nuclei: single neurons vs. population encoding," *J. Neurophysiol.* **105**(4), 1798–1814 (2011).
- ⁴⁶Metzner, W., Koch, C., Wessel, R., and Gabbiani, F., "Feature extraction by burst-like spike patterns in multiple sensory maps," *J. Neurosci.* **18**(6), 2283–2300 (1998).
- ⁴⁷Neiman, A. and Russell, D. F., "Stochastic biperiodic oscillations in the electroreceptors of paddlefish," *Phys. Rev. Lett.* **86**(15), 3443–3446 (2001).
- ⁴⁸Neiman, A. B. and Russell, D. F., "Synchronization of noise-induced bursts in noncoupled sensory neurons," *Phys. Rev. Lett.* **88**(13), 138103 (2002).
- ⁴⁹Neiman, A. B. and Russell, D. F., "Two distinct types of noisy oscillators in electroreceptors of paddlefish," *J. Neurophysiol.* **92**(1), 492–509 (2004).
- ⁵⁰Neiman, A. B. and Russell, D. F., "Models of stochastic biperiodic oscillations and extended serial correlations in electroreceptors of paddlefish," *Phys. Rev. E* **71**, 061915 (2005).
- ⁵¹Neiman, A. B., Yakusheva, T. A., and Russell, D. F., "Noise-induced transition to bursting in responses of paddlefish electroreceptor afferents," *J. Neurophysiol.* **98**(5), 2795–2806 (2007).
- ⁵²Neiman, A., Schimansky-Geier, L., and Moss, F., "Linear response theory applied to stochastic resonance in models of ensembles of oscillators," *Phys. Rev. E* **56**(1), R9 (1997).
- ⁵³Nguyen, H. and Neiman, A. B., "Spontaneous dynamics and response properties of a Hodgkin-Huxley-type neuron model driven by harmonic synaptic noise," *Eur. Phys. J. Spec. Top.* **187**(1), 179–187 (2010).
- ⁵⁴Nikias, C. L. and Petropulu, A. P., *Higher-Order Spectral Analysis. A Nonlinear Signal Processing Framework* (Prentice Hall, Englewood Cliffs, NJ, 1993).
- ⁵⁵Pakdamian, K. and Mestivier, D., "External noise synchronizes forced oscillators," *Phys. Rev. E* **64**, 030901 (2001).
- ⁵⁶Passaglia, C. L. and Troy, J. B., "Information transmission rates of cat retinal ganglion cells," *J. Neurophysiol.* **91**(3), 1217–1229 (2004).
- ⁵⁷Pei, X., Russell, D. F., Wilkens, L. A., and Moss, F., "Dynamics of the electroreceptors in the paddlefish, *Polyodon spathula*," in *Computational Neuroscience: Trends in Research 1998*, edited by J. Bower (Plenum, New York, 1998), pp. 245–249.
- ⁵⁸Ratnam, R. and Nelson, M. E., "Nonrenewal statistics of electrosensory afferent spike trains: implications for the detection of weak sensory signals," *J. Neurosci.* **20**(17), 6672–6683 (2000).
- ⁵⁹Reinagel, P., Godwin, D., Sherman, S. M., and Koch, C., "Encoding of visual information by LGN bursts," *J. Neurophysiol.* **81**(5), 2558–2569 (1999).
- ⁶⁰Rieke, F., Bodnar, D. A., and Bialek, W., "Naturalistic stimuli increase the rate and efficiency of information transmission by primary auditory afferents," *Proc. Biol. Sci.* **262**(1365), 259–265 (1995).
- ⁶¹Roddey, J. C., Girish, B., and Miller, J. P., "Assessing the performance of neural encoding models in the presence of noise," *J. Comput. Neurosci.* **8**(2), 95–112 (2000).
- ⁶²Russell, D. F., Tucker, A., Wettering, B. A., Neiman, A. B., Wilkens, L. A., and Moss, F., "Noise effects on the electrosense-mediated feeding behavior of small paddlefish," *Fluctuation Noise Lett.* **1**, L71–L86 (2001).
- ⁶³Russell, D. F., Wilkens, L. A., and Moss, F., "Use of behavioural stochastic resonance by paddle fish for feeding," *Nature* **402**(6759), 291–294 (1999).
- ⁶⁴Russell, D. F., Yakusheva, T., Neiman, A. B., and Moss, F., "The receptive field of an electroreceptor afferent in paddlefish corresponds to a single cluster of canals," (unpublished).
- ⁶⁵Rutherford, M. A. and Roberts, W. M., "Spikes and membrane potential oscillations in hair cells generate periodic afferent activity in the frog sacculus," *J. Neurosci.* **29**(32), 10025–10037 (2009).
- ⁶⁶Sadeghi, S. G., Chacron, M. J., Taylor, M. C., and Cullen, K. E., "Neural variability, detection thresholds, and information transmission in the vestibular system," *J. Neurosci.* **27**(4), 771–781 (2007).
- ⁶⁷Schafer, K., Braun, H. A., Peters, R. C., and Bretschneider F., "Periodic firing pattern in afferent discharges from electroreceptor organs of catfish," *Pflügers Arch.* **429**(3), 378–385 (1995).
- ⁶⁸Schance, T. and Eckhorn, R., "Phase correlation among rhythms present at different frequencies: spectral methods, application to microelectrode recordings from visual cortex and functional implications," *Int. J. Psychophysiol.* **26**(1–3), 171–189 (1997).
- ⁶⁹Schleimer, J. H. and Stemmler, M., "Coding of information in limit cycle oscillators," *Phys. Rev. Lett.* **103**(24), 248105 (2009).
- ⁷⁰Strong, S. P., Koberle, R., de Ruyter van Steveninck, R., and Bialek, W., "Entropy and information in neural spike trains," *Phys. Rev. Lett.* **80**(1), 197 (1998).
- ⁷¹Struik, M., Bretschneider, F., and Peters, R., "Spontaneous nerve activity and sensitivity in catfish ampullary electroreceptor organs after tetanus toxin application," *Pflügers Arch.* **443**(5–6), 903–907 (2006).
- ⁷²Swami, A., Mendel, J. M., and Nikias, C. L., HOSAHigher Order Spectral Analysis Toolbox, <http://www.mathworks.com/matlabcentral/fileexchange/loadFile.do?objectId=3013&objectType=FILE> (2003).
- ⁷³Tass, P., "Stimulus-locked transient phase dynamics, synchronization and desynchronization of two oscillators," *Europhys. Lett.* **59**(2), 199–205 (2002).
- ⁷⁴Tricas, T. C. and New, J. G., "Sensitivity and response dynamics of elasmobranch electrosensory primary afferent neurons to near threshold fields," *J. Comput. Physiol. A* **182**(1), 89 (1998).
- ⁷⁵Wessel, R., Koch, C., and Gabbiani, F., "Coding of time-varying electric field amplitude modulations in a wave-type electric fish," *J. Neurophysiol.* **75**(6), 2280–2293 (1996).
- ⁷⁶Wilkens, L. A., Russell, D. F., Pei, X., and Gurgens, C., "The paddlefish rostrum functions as an electrosensory antenna in plankton feeding," *Proc. R. Soc., London, Ser B* **264**(1389), 1723–1729 (1997).
- ⁷⁷Wilkens, L. A., Wettering, B. A., Wagner, E., Wojtenek, W., and Russell, D. F., "Prey detection in selective plankton feeding by the paddlefish: is the electric sense sufficient?," *J. Exp. Biol.* **204**, 1381–1389 (2001).
- ⁷⁸Wojtenek, W., Pei, X., and Wilkens, L. A., "Paddlefish strike at artificial dipoles simulating the weak electric fields of planktonic prey," *J. Exp. Biol.* **204**, 1391–1399 (2001).