



Behavioral Stochastic Resonance: How the Noise from a *Daphnia* Swarm Enhances Individual Prey Capture by Juvenile Paddlefish*

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Zooplankton emit weak electric fields into the surrounding water that originate from their own muscular activities associated with swimming and feeding. Juvenile paddlefish prey upon single zooplankton by detecting and tracking these weak electric signatures. The passive electric sense in this fish is provided by an elaborate array of electroreceptors, Ampullae of Lorenzini, spread over the surface of an elongated rostrum. We have previously shown that the fish use stochastic resonance to enhance prey capture near the detection threshold of their sensory system. However, stochastic resonance requires an external source of electrical noise in order to function. A swarm of plankton, for example *Daphnia*, can provide the required noise. We hypothesize that juvenile paddlefish can detect and attack single *Daphnia* as outliers in the vicinity of the swarm by using noise from the swarm itself. From the power spectral density of the noise plus the weak signal from a single *Daphnia*, we calculate the signal-to-noise ratio, Fisher information and discriminability at the surface of the paddlefish's rostrum. The results predict a specific attack pattern for the paddlefish that appears to be experimentally testable.

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Introduction

Paddlefish, *Polyodon spathula*, are among the largest freshwater fish found in the river basins of North America, yet they feed exclusively on planktonic prey. They are found most often near the bottoms of rivers and lakes where turbulence

and muddy water obscure normal vision but where plankton are plentiful. In order to adapt to this environment, paddlefish, primitive creatures whose fossil record extends into the Cretaceous (65 million years ago) (Grande & Bemis, 1991), have evolved an elaborate array of electroreceptor organs spread over an elongated rostrum anterior to the mouth and head, see Fig. 1(a). The organs consist of clusters of Ampullae of Lorenzini which communicate with the water through short (0.1 mm) canals that terminate in pores on the skin surface, as shown in Fig. 1(b). Prey, for example *Daphnia*, are detected and tracked exclusively by means of an entirely passive electric sense provided by the rostral array (Wilkens *et al.*, 1997; Neiman *et al.*, 2000;

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FIG. 1. (a) A juvenile paddlefish. (b) Close-up view of clusters of electroreceptor pores on the rostrum.

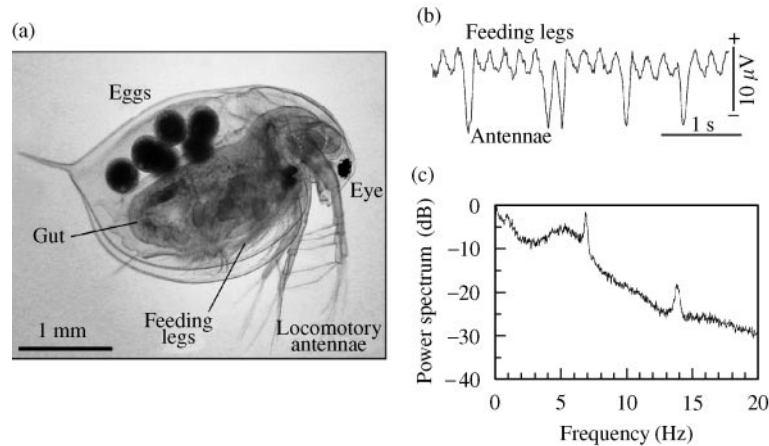


FIG. 2. (a) A single *Daphnia*. (b) Electric potential from a tethered *Daphnia* measured at a distance of 0.5 cm. The oscillations result from higher frequency feeding motions of the legs and lower frequency swimming motions of the antennae. (c) Power spectrum of the signal from a single, tethered *Daphnia* showing the approximately 7 Hz feeding frequency as the sharper peak and the broader 5–6 Hz swimming frequency.

Neiman & Russell, 2001). This sensory system has evolved to detect the weak electric fields emitted into the surrounding water by the *Daphnia*'s muscular activity associated with its swimming and feeding motions. The electric fields from the *Daphnia* are approximately periodic in time and dipolar in spatial shape (Neiman *et al.*, 2000).

We have recently shown that juvenile paddlefish make use of stochastic resonance (SR) in the detection and capture of *Daphnia* at the threshold of their perception (Russell *et al.*, 1999, 2001). This, together with the 65 million year evolutionary history and some recent physiological evidence (Jaramillo & Wiesenfeld, 1998), suggests that SR is an evolved survival strategy. Juvenile paddlefish (of less than 1 year old) locate, track and feed on single plankton (Wilkins *et al.*, 1997; Neiman *et al.*, 2000), whereas older fish, after having developed gill rakers, filter feed on swarms. A favorite food of the paddlefish is the

Daphnia, a plankton of 1–2 mm length commonly found in North American fresh water, see Fig. 2(a). *Daphnia* emit weak dipole-shaped electric fields with both DC and oscillatory (4–15 Hz) components [see Fig. 2(b) and (c)]. In this paper, we assume the individual *Daphnia* to be the source of a single-frequency sinusoidal “signal” [the approximately 5 Hz feeding frequency as shown by the power spectrum in Fig. 2 (c)]. The intensity of the signal on the surface of the fish's rostrum decreases approximately as the inverse cube of the distance to the *Daphnia* because of the dipole-like shape of the field. Indeed, it has recently been shown, using the $1/r^3$ drop-off characteristic of the dipole field, that the Fisher information at the rostrum from a single *Daphnia* follows the prey capture probability exhibited by the fish (Greenwood *et al.*, 2000). *Daphnia* that appear at larger distances from the fish are less likely to be detected and/or captured, because their signals on the rostrum are weaker owing to

the $1/r^3$ law. However, external or environmental noise can enhance the detectability of subthreshold signals at the edge of the animal's perception. Consequently, the probability that distant *Daphnia* are captured can be enhanced by the noise in a process called *behavioral SR* (Russell *et al.*, 1999).

But where should paddlefish in the wild expect to encounter sources of environmental electrical noise? Our hypothesis is that the noise originates from the *Daphnia* themselves. *Daphnia* tend to form *swarms*, or large concentrations of individuals clustered in rather well-defined regions in space. Oscillatory signals from the individuals in such swarms are expected to be incoherent with one another. Moreover, their dipole vectors are expected to point in all possible directions and to be uncorrelated with one another. Thus, the sum of signals at a single point in space from a large number of *Daphnia* is expected to look like Gaussian noise as a result of the Central Limit Theorem (see, for example, Reichl, 1980).

Indeed, a swarm does produce noise. Figure 3(a) shows a swarm of *Daphnia* in an aquarium together with measuring and reference electrodes, and (b) shows an example time course measured near the swarm. Figures 3(c) and (d) show examples of the probability density and power spectrum, respectively. Below, we show that the power is well represented by the Ornstein–Uhlenbeck (or band-limited) noise spectrum (Uhlenbeck & Ornstein, 1930) shown by the smooth solid curve in Fig. 3(d). Moreover, the density is well approximated by a Gaussian function indicated by the smooth solid curve in Fig. 3(c). We can conclude that a swarm of *Daphnia* therefore is a source of band-limited, Gaussian, electrical noise in the water.

A single *Daphnia* swimming as an outlier near a swarm therefore provides to the paddlefish all the necessary ingredients for SR: a subthreshold signal, a threshold (characteristic of its electro-sensory and perceptive systems) and noise (from the swarm). In this paper, we use the threshold

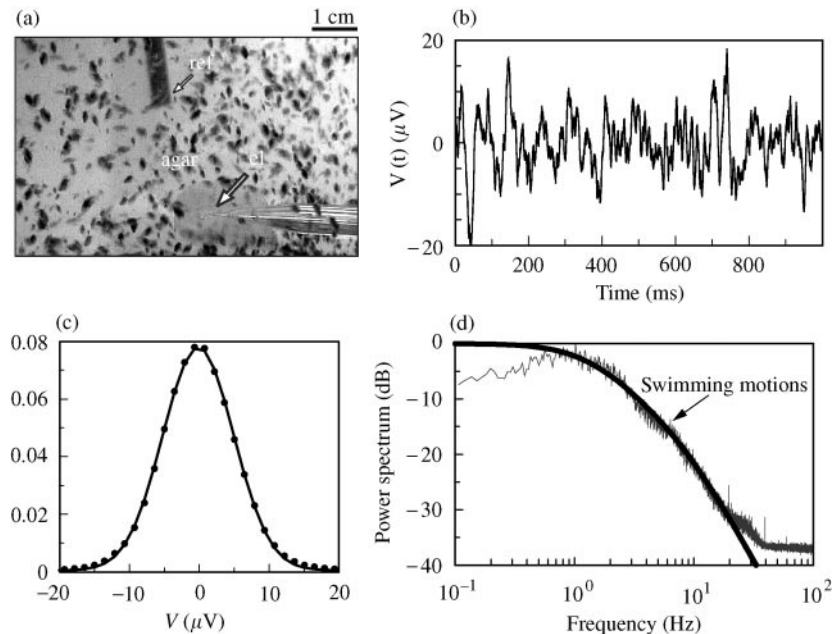


FIG. 3. (a) A *Daphnia* swarm shown in an aquarium together with measuring and reference electrodes. The measuring electrode is coated with a bead of agar, an electrically conducting substance. This is to minimize the effects from individual *Daphnia* colliding with the electrode tip and to thus more accurately measure the collective potential from the swarm. (b) Electrical noise from the swarm, a time course of the potential measured at the electrode shown in (a). (c) The probability density of the time course of the potential. The solid curve is a Gaussian fit with $A = 0.078$ and $\sigma = 5.09$. (d) The power spectrum of the potential. The small bump at around 7 Hz is from the antennae swimming motions. (—) curve denotes theoretical band-limited noise from eqn (4) with $\tau_1 = 0.13$ s and $\tau_2 = 0.017$ s.

theory of SR (Gingl *et al.*, 1995) to calculate the signal-to-noise ratio (SNR), the Fisher information (Fisher, 1949), and the discriminability (Stemmler, 1996) at the rostral surface of a fish due to an individual *Daphnia* swimming in the vicinity of the swarm. This approach has the great advantage that it is not dependent on any specific neural encoding scheme. We consider only the time course of simple crossings of the fish's perceptive threshold by the external signal and noise. It has been shown that the essential features of the experimentally determined prey strike probability are captured by this simple scheme (Greenwood *et al.*, 2000). We have previously considered a variant of this problem wherein the synchronization of electroreceptor activity with the *Daphnia* signal was calculated using the dynamical SR theory together with a bistable potential (Freund *et al.*, 2001).

SR is a phenomenon occurring in stochastic nonlinear systems whereby the addition of random forcing, or noise, to a weak information-carrying signal can enhance its detectability and/or the information transmitted through the system. SR theory originated in efforts to understand the periodicities in the recurrences of the Earth's Ice Ages (Benzi *et al.*, 1981; Nicolis, 1993). The introduction of SR into experimental sensory biology (Douglass *et al.*, 1993; Levin & Miller, 1996) and its observation in membrane ion channels (Petracchi *et al.*, 1994; Bezrukov & Vodyanoy, 1995, 1997) stimulated wide interest. A report (Wiesenfeld & Moss, 1995) plus several reviews (Moss, 1994; Moss *et al.*, 1994; Gammaitoni *et al.*, 1998; Anishchenko *et al.*, 1999; Moss, 2000) provide further information. SR was for many years thought to occur only in dynamical systems with double- or multi-well potentials. Indeed, in the original biological application of SR, the information contained in the barrier crossings of the state point in a weakly, periodically modulated bistable potential provided the first quantitative explanation of the famous "phase locking" phenomenon widely observed in sensory biology. Example data from the auditory nerve fibers of the squirrel monkey and from the visual cortex of a cat were presented in support of that explanation (Longtin *et al.*, 1991). More recently, however, a much simpler realization of SR was discovered in non-dynamical

systems that include a threshold, a subthreshold signal and noise (Gingl *et al.*, 1995; Moss *et al.*, 1994). Called "threshold SR", this view also provides the simplest description of excitable systems, such as single sensory neurons (Wiesenfeld *et al.*, 1994), or arrays of receptors, as in the paddlefish rostrum, which together represent a sensory threshold of perception for the animal. SR has also been experimentally observed in human neurophysiological (Chiou-Tan *et al.*, 1996; Cordo *et al.*, 1996) and perceptual (Collins *et al.*, 1996, 1997; Richardson *et al.*, 2001) experiments as well as in psychophysics (Simonotto *et al.*, 1997; Ward, 1999; Ward *et al.*, 2001; Usher & Feingold, 2000). We adopt this view here, and outline the theory of threshold, or non-dynamical, SR below.

We consider an outlier *Daphnia* in the vicinity of the swarm as the source of a weak periodic signal. The oscillatory dipole-shaped signal from this single *Daphnia*, described by the vector \mathbf{p}_d , is detected at the rostrum of a paddlefish. The swarm is assumed to be spherical with diameter A . In the reference frames of the single *Daphnia* and the center of the swarm, the two vectors \mathbf{r} and \mathbf{R} represent the distances to the paddlefish rostrum, respectively. A schematic diagram of this geometry is shown in Fig. 5. At the rostrum, noise from the swarm is added to the weak signal from the single *Daphnia*. The noise-enhanced SNR , the Fisher information and discriminability are calculated from the time series of threshold crossings using the non-dynamical, threshold SR theory outlined below. We suppose that the temporal sequence of threshold crossings carries all the necessary information regarding the location and velocity of the *Daphnia* in order that the paddlefish can capture it.

In the following section, we briefly describe the swarming behavior of *Daphnia* populations and outline some ideas regarding their interactions with one another. We also summarize what is known about the feeding behavior of juvenile paddlefish in the vicinity of swarms. We describe the nature of the signal from an individual and the noise from the swarm and show that band-limited theoretical noise fits the measured power spectrum very well. We then outline the threshold theory of SR and show how SNR and the related Fisher information and discriminability are obtained from the theory.

Eventually, we calculate the noise and signal intensities on the rostrum and apply these calculations to the detection problem faced by a juvenile paddlefish seeking to capture a single *Daphnia*. Contours of constant SNR and discriminability in the neighborhood of the swarm delineate optimal tracking and capture strategies for juvenile feeding. Our predictions appear to be experimentally testable.

Daphnia Swarms

Daphnia inhabit the pelagic (open-water) zones of lakes and slow-moving rivers and are an important prey for planktivorous fish. They swim with a hopping motion induced by a powerful downbeat of the modified second antennae, that is followed by a brief period of sinking. *Daphnia* and other zooplankton species are known to form swarms consisting of very high-density aggregations (1000–9000 individuals per liter) (Colebrook, 1960; Brandl & Fernando, 1971; Davies, 1985; Kvam & Kleiven, 1995). These swarms may be formed by physical processes in the water column, for example Langmuir circulations, but there are also several key biological drivers. The main biological drivers are avoidance of predators (including diel vertical migration), location of food patches, and location of mates (reviewed in Folt & Burns, 1999). Swarms are formed when many individuals modify their swimming patterns (turning frequency) and speed in response to predator detection (Jensen *et al.*, 1998), food density (Young & Getty, 1987; Cuddington & McCauley, 1994), and light intensity (Ringelberg, 1987). Individuals may use photons emitted by other individuals to recognize each other and determine inter-neighbor distances within a swarm (Galle *et al.*, 1991).

A major hypothesis is that swarms in *Daphnia* are formed for predator avoidance. Swarming more often occurs during daylight hours than at night (Jakobsen & Johnsen, 1988; Kvam & Kleiven, 1995) when visual predators like planktivorous fish and invertebrates would be most threatening. The strongest evidence for swarms induced by predation is from predator kairomone studies (Pijanowska & Kowalczewski, 1997; Jensen *et al.*, 1998). Kairomones are chemical compounds that act as cues for the prey and

are released by fish, invertebrate predators or even crushed bodies of *Daphnia*. When such kairomones are experimentally introduced into the water of *Daphnia* cultures, swarming behavior is induced (Pijanowska & Kowalczewski, 1997). When predators are present, formation of a group benefits the individual, because many identical prey individuals in random motion (noise) can distract or confuse predators and decrease their attack rates (Milinski, 1986). Thus, the dilution effect affords a degree of safety to an individual within a group. The probability of an individual being attacked within a group is lower than for a solitary individual (Bertram, 1978). Thus, swarming in *Daphnia* is likely a permanent behavioral strategy in systems where predators are abundant (Jensen *et al.*, 1998).

The feeding mode of paddlefish on *Daphnia* depends on the size (related to age) of the individual fish. Adult paddlefish (age greater than approximately 1 year) feed as if they were giant plankton nets. Mouth open, they cruise through the swarms of zooplankton, filtering the water as it passes over their gill-rakers. In juvenile paddlefish (typically < 1 year of age and 120 mm in length), the gill rakers are as yet undeveloped, and consequently this form of filter feeding is not available to them (Michaletz *et al.*, 1982). They must rely on selecting individual *Daphnia* from the water column (Rosen & Hales, 1981).

We have observed that juvenile paddlefish in the lab only select individual *Daphnia* as prey. Others have also observed that young paddlefish tend to swim right through swarms of *Daphnia* without feeding unless an individual passes very close to the rostrum (Michaletz *et al.*, 1982). Juvenile paddlefish appear to actively seek and consume individual prey, especially of the genus *Daphnia* (Rosen & Hales, 1981; Michaletz *et al.*, 1982). Other planktivorous fish are also known to avoid feeding in dense patches of swimming prey, probably because of the confusion effect (see, for example, Milinski, 1986). An alternative explanation of why juveniles tend to avoid feeding within swarms may be that the benefit of potentially high feeding rates is outweighed by the cost of possible attacks by predators in the form of adults attracted by the swarm (Milinski, 1986). Gill rakers begin development in paddlefish when individuals reach a length of 70 mm,

and a full shift to the adult filter-feeding mode occurs around 120 mm (Michaletz *et al.*, 1982) at approximately 1 year of age.

Since juvenile paddlefish prey on individual plankton that are not located within a swarm, it is possible that they can use the swarm noise together with the SR process to enhance their capture success.

Characteristics of the Noise and the Signal

The signatures of the electric fields from single *Daphnia* and from the swarm can be measured. In Fig. 3(a), we show a photograph of a swarm in an aquarium. Figure 3(b) shows the time course of the noise potential obtained at the location of the measuring electrode shown in (a). The probability density of the amplitude of the potential is shown in (c), and we note that it is well described by a Gaussian function as shown by the solid curve. Figure 3(d) shows the measured power spectrum of the *Daphnia* swarm. The power spectrum is clearly representative of band-limited noise. Consequently, we shall approximate the noise from the swarm as Ornstein-Uhlenbeck (OU) “doubly filtered” noise (Uhlenbeck & Ornstein, 1930; see also Jung, 1994; Dolan *et al.*, 1999). This noise, $\xi(t)$, is generated by a double-pole linear filter of white noise according to

$$\frac{d^2\xi}{dt^2} + \left(\frac{1}{\tau_1} + \frac{1}{\tau_2}\right) \frac{d\xi}{dt} + \frac{1}{\tau_1\tau_2} \xi = \frac{\sqrt{D}}{\tau_1\tau_2} \Gamma(t), \quad (1)$$

where D is the noise intensity, and $\Gamma(t)$ is white noise with zero mean and a delta autocorrelation function:

$$\langle \Gamma(t) \rangle = 0 \quad \text{and} \quad \langle \Gamma(t)\Gamma(t') \rangle = 2\delta(t - t'). \quad (2)$$

The filtered noise, $\xi(t)$, has two correlation times, τ_1 and τ_2 , resulting in the stationary autocorrelation function (for $\tau_1 > \tau_2$),

$$C(\tau) = \frac{D}{\tau_1^2 - \tau_2^2} \left[\tau_1 \exp\left(-\frac{|\tau|}{\tau_1}\right) - \tau_2 \exp\left(-\frac{|\tau|}{\tau_2}\right) \right] \quad (3)$$

and the (one-sided) power spectrum is given by

$$S_{\xi\xi}(f) = \frac{4D}{[1 - \tau_1\tau_2(2\pi f)^2]^2 + [\tau_1 + \tau_2]^2(2\pi f)^2}, \quad (4)$$

where f is the frequency. The two time constants are characteristic of the dynamics of a system that would reproduce the swarm noise. The case $\tau_2 \ll \tau_1$ corresponds to the overdamped limit of the OU process, and the correlation function reduces to a simple single exponential and the power spectrum reduces to a Lorentzian. However, in the following, we shall need to calculate the mean threshold crossing rate of this noise, and this quantity must be finite. In the strict overdamped limit it is not, so we must retain both correlation times (Stratonovich, 1964; Jung, 1994). We note that the experimental power spectrum of the swarm, shown by the dots in Fig. 3(d), is very well described by this doubly filtered OU noise [eqn (4) with $\tau_1 = 0.13$ s and $\tau_2 = 0.017$ s] as shown by the solid curve.

Moreover, in this work we assume that the signal to be detected originates from a single *Daphnia* as shown in Fig. 2(a). Figure 2(b) shows the time course of the potential measured at a distance of about 0.5 cm. The shape of the potential at distances of 1 cm or more is approximately a dipole, and in this work we shall assume it to be a dipole. The power spectrum of the experimental *Daphnia* signal is shown in Fig. 2(c). There are two main frequency components, a broader one around 5 Hz, which results from swimming motions of the appendages, and a narrower one at about 7 Hz resulting from feeding motions. Note that both these oscillatory components are superimposed on a broad noise background. For the sake of simplicity we shall concentrate on the 5 Hz feeding frequency f_0 and neglect the broadband background entirely. Thus, we take the temporal part of the *Daphnia* signal $\mathbf{A}(\mathbf{r}, t)$ to be a single-frequency sinusoid:

$$\mathbf{A}(\mathbf{r}, t) = \mathbf{A}(\mathbf{r}) \sin(2\pi f_0 t). \quad (5)$$

Later, we will show that the spatial dependence of the magnitude of the signal, i.e. $\max |\mathbf{A}(\mathbf{r})| \sim 1/r^3$, as expected for a dipole, and use this in order to

calculate the sum of the noise plus the signal at the rostrum.

Threshold Theory of Stochastic Resonance

In this work, we make use of the *non-dynamical*, or *threshold*, theory of SR which has been detailed in prior publications (Gingl *et al.*, 1995; Moss *et al.*, 1994). Thus, only an outline is necessary here. For the occurrence of non-dynamical SR, only three ingredients are essential: a threshold, a subthreshold signal and noise. Since these three quantities are ubiquitous in the real world, we expect that SR will appear in a wide variety of natural phenomena, and indeed it has been widely observed (see for example, Anishchenko *et al.*, 1999; Moss, 2000).

The system paradigm is that it cannot respond to any stimulus unless its threshold is crossed, whereupon it responds with a stereotypical signal: a rectangular pulse of amplitude Q and width δt . The subthreshold signal alone cannot

stimulate a response. But the signal plus the noise, assumed to be Gaussian, produces a sequence of stereotypical pulses that mark the times of the positive-going threshold crossings, see Fig. 4(a). The noise serves as a random sampling function for the signal, and thus its upper cutoff frequency, $f_n \cong (1/\tau_1)$ must be equal to or larger than the Nyquist frequency of the signal, $2f_0$ (see for example, Stremler, 1990).

Two major approximations are adopted: (1) the adiabatic approximation, $f_0 \ll \langle v \rangle$ and f_n , where $\langle v \rangle$ is the mean threshold crossing rate (due largely to the noise); and (2) the threshold crossing times are uncorrelated, that is, they are described by a renewal process. The mean threshold crossing rate (Rice, 1954), scaled for Gaussian noise with standard deviation σ and a mean distance Δ below the threshold, is

$$\langle v \rangle = \exp\left(-\frac{\Delta^2}{2\sigma^2}\right) \left[\frac{\int_0^\infty f^2 S(f) df}{\int_0^\infty S(f) df}\right]^{1/2}, \quad (6)$$

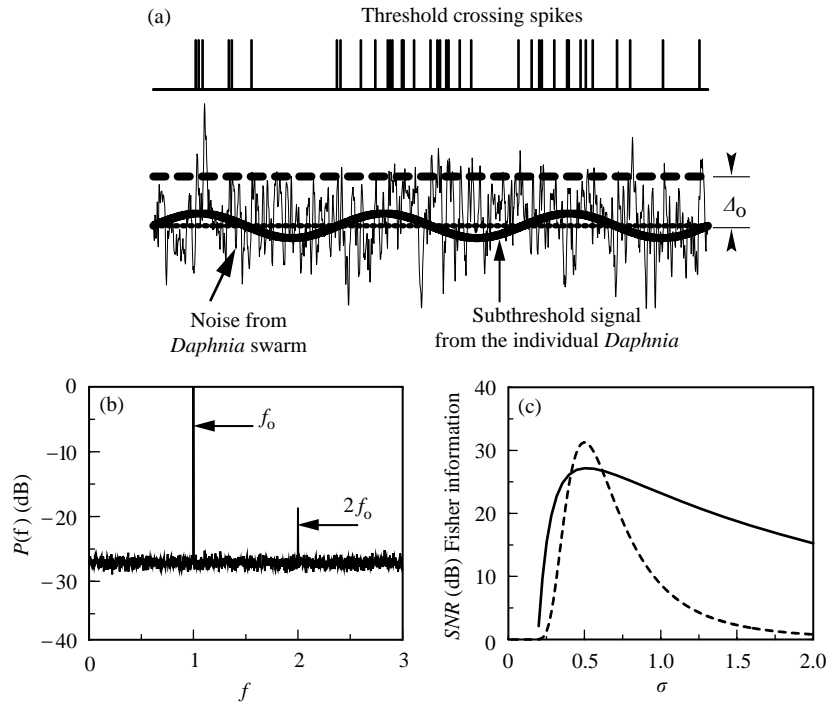


FIG. 4. Threshold stochastic resonance. (a) The threshold (----), subthreshold signal (—) plus noise (—). Mean of the signal is shown by the (—) line lying Δ_0 below the threshold. Stereotypical pulses that mark the threshold crossing events are shown above. The horizontal axis is time. The parameters are, for the signal, $f_0 = 1.0$, $A = 0.25$; and for the Gaussian noise, $\sigma = 0.6$, $\Delta_0 = 1$, and $f_n = 500$. (b) Power spectrum of the pulse train of threshold crossings showing the signal feature f_0 , and its second harmonic. The SNR is the ratio of the power in the signal feature to the noise power in a unit bandwidth centered on the signal frequency f_0 . The noise power is shown by the horizontal trace at -27.5 dB. (c) Stochastic resonance shown by a local maximum of both the SNR (—), eqn (12), and the Fisher information (FI) (----), eqn (18). The time window for the FI measure is $T = 0.05$.

where $S(f)$ is the (one-sided) power spectrum of the noise which, here, is assumed to be a rectangular function of height D and width f_n . Thus, the mean threshold crossing rate is

$$\langle v \rangle = \frac{f_n}{\sqrt{3}} \exp\left(-\frac{\Delta^2}{2\sigma^2}\right). \quad (7)$$

A stereotypical pulse marks each threshold crossing. If the threshold crossings are not correlated, Campbell's Theorem gives the power spectrum of the pulse train (Stremler, 1990) due to noise alone,

$$P_n(f) \approx \frac{1}{2} \langle v \rangle Q^2 \delta t^2 = \frac{Q^2 \delta t^2 f_n}{2\sqrt{3}} \exp\left(-\frac{\Delta^2}{2\sigma^2}\right). \quad (8)$$

Actually, for a single pulse $P_{pulse} = Q^2 \delta t^2 \text{sinc}(\pi f \delta t)$ but we are only interested in the low-frequency amplitude of this function, as given by eqn (8), since $\delta t \ll 1/\langle v \rangle$. The mean amplitude of the pulse train due to the noise alone is

$$\langle V \rangle_n = Q \delta t \langle v \rangle = Q \delta t \left(\frac{f_n}{\sqrt{3}}\right) \exp\left(-\frac{\Delta^2}{2\sigma^2}\right). \quad (9)$$

Since $f_0 \ll \langle v \rangle$, both $\langle v \rangle(t)$ and $\langle V \rangle(t)$ become slow functions of time. Adding the signal and the mean threshold, $\Delta(t) = \Delta_0 + A \sin(2\pi f_0 t)$, where $A \ll \Delta_0$. The mean amplitude of the pulse train is

$$\begin{aligned} \langle V \rangle(t) &= \left(\frac{Q \delta t f_n}{\sqrt{3}}\right) \\ &\times \exp\left[-\frac{\Delta_0^2 + 2\Delta_0 A \sin(2\pi f_0 t) + A^2 \sin^2(2\pi f_0 t)}{2\sigma^2}\right] \\ &\approx \left(\frac{Q \delta t f_n}{\sqrt{3}}\right) \left[1 - \frac{\Delta_0 A}{\sigma^2} \sin(2\pi f_0 t) \right. \\ &\quad \left. + \frac{A^2}{4\sigma^2} \cos(4\pi f_0 t) - \frac{A^2}{4\sigma^2}\right] \exp\left(-\frac{\Delta_0^2}{2\sigma^2}\right), \quad (10) \end{aligned}$$

where the approximation arises from $\exp[-\Delta^2(t)] \cong [1 - \Delta^2(t)]$ and $A \ll \Delta_0$ plus a trigonometric identity for $\sin^2(2\pi f_0 t)$. Neglecting the constant terms and dropping the second harmonic,

the power spectrum of eqn (10) is

$$P_s(f) = \left(\frac{Q^2 \delta t^2 f_n^2}{3}\right) \times \left[\left(\frac{\Delta_0 A}{\sigma^2}\right)^2 \delta(f - f_0)\right] \exp\left(-\frac{\Delta_0^2}{\sigma^2}\right). \quad (11)$$

A numerical simulation of the threshold crossing process has been implemented. The power spectrum from the simulation is shown in Fig. 4(b). Note that the threshold-crossing rate is maximized at the maxima of the subthreshold signal. Thus, only positive crests of the signal are enhanced by the crossings. This constitutes an effective rectification process leading to the strong second harmonic as shown in Fig. 4(b). However, here we are concerned only with the SNR derived from the fundamental frequency f_0 . The SNR is the ratio of the coefficient of the delta function in eqn (11) to that in eqn (8).

$$SNR = \left[\frac{2f_n \Delta_0^2 A^2}{\sigma^4 \sqrt{3}}\right] \exp\left(-\frac{\Delta_0^2}{2\sigma^2}\right). \quad (12)$$

The SNR computed from this formula is shown in Fig. 4(c) as a function of noise intensity σ . The maximum value of the SNR at an optimal noise intensity is the signature of SR.

The SNR, Fisher Information and Discriminability

In the previous section SR was described in terms of the SNR. As shown, this approach requires calculation of the power spectrum by a long time average, which in turn requires advance knowledge of the noise-free, or clean, signal, $A(t) = A \sin(2\pi f_0 t)$. These requirements are rather inappropriate for sensory systems of biological objects. In fact, the paddlefish must make a decision about the existence of a prey in much < 1 s, and typically the decision is made within 125–200 ms (based on observations of behavioral cues, see Russell *et al.*, 2001). Moreover, it is difficult to imagine that it has a clean copy of a *Daphnia* signal, as implied by eqn (5). That is why we discuss here a different measure of SR, which does not require advance knowledge of

a signal. Such a measure can be constructed from a sequence of threshold crossings, for example the crossings of neural action potentials, or spikes. The threshold crossing probability distribution can be obtained either from behavioral experiments, where threshold crossings are associated with certain reactions of the animal to the presentation of stimuli, or from the train of spikes generated by a sensory neuron.

Let us denote a stimulus as Δ_0 and its estimate from a spike train as $\tilde{\Delta}_0$. In the section above, Δ_0 is the threshold below which lies the mean of a distribution. Here, we shall be concerned with the ability to discriminate between the spike count distributions due to Δ_0 alone and that of $\Delta_0 + A$, where $A \ll \Delta_0$ as in eqn (10) above, i.e. we shall consider A a small signal that the animal must detect. We also suppose that the stimulus is constant. The theoretical limit of how accurate this estimation can be is given by the following formula:

$$\text{Var}(\Delta_0 - \tilde{\Delta}_0) \geq \frac{1}{J(\Delta_0)}, \quad (13)$$

where Var stands for the standard error of stimulus estimation, and $J(\Delta_0)$ is the Fisher information (Fisher, 1949). The Fisher information can be calculated based on the spike count probability distribution $P(N, \Delta_0)$, the probability to observe N spikes within an observation time $T \ll f_0^{-1}$ for a given stimulus Δ_0 (Cover & Thomas, 1991):

$$J(\Delta_0) = \int \frac{1}{P(N, \Delta_0)} \left[\frac{\partial}{\partial \Delta_0} P(N, \Delta_0) \right]^2 dN. \quad (14)$$

A lower bound of the Fisher information can be written as (Stemmler, 1996)

$$J_{LB}(\Delta_0) = \frac{1}{\sigma_N^2(\Delta_0)} \left(\frac{\partial \mu_N}{\partial \Delta_0} \right)^2, \quad (15)$$

where μ_N and σ_N are the mean and standard deviation of the spike count probability distribution, respectively. The greater the Fisher information, the more accurate the estimate of the stimulus *from the spike train alone*.

Another way to characterize the encoding efficiency of a sensory neural system is to measure

directly how far apart are two spike count distributions for two different stimuli Δ_0 and $\Delta_0 + A$. The discriminability, d' is a normalized measure of this distance:

$$d' = 2 \frac{|\mu_N(\Delta_0 + A) - \mu_N(\Delta_0)|}{\sigma_N(\Delta_0 + A) + \sigma_N(\Delta_0)}. \quad (16)$$

For small signal amplitude A , such that the difference between the mean values of two spike count distributions is also small, the discriminability and the lower bound of the Fisher information are connected by a simple relation, $d' \approx A \sqrt{J_{LB}}$ (Stemmler, 1996).

Stemmler (1996) has calculated the Fisher information for several neuron models and proved the existence of SR as manifested in the maximum of the Fisher information vs. noise intensity. He also showed that for a simple threshold model of a neuron (McCulloch & Pitts, 1943), similar to our threshold theory for SR outlined above, the lower bound of the Fisher information follows the same dependence on the noise variance as the SNR. Spike generation in our threshold model of SR is a renewal process. Thus, in the asymptotic limit the mean and the variance of the spike count distribution in a window T can be related to the mean μ_T and variance σ_T^2 of the interspike time intervals (Cox, 1962), whence $\mu_N = T/\mu_T$ and $\sigma_N^2 = T\sigma_T^2/\mu_T^3$. Further, we assume that the point process generated by threshold crossings is Poissonian, so that $\sigma_T = \mu_T$. Then, taking into account that $\mu_T = 1/\langle v \rangle$, the estimation for the lower bound of the Fisher information reads (Stemmler, 1996) as

$$J_{LB}^{Pois}(\Delta_0) = T \left[2 \frac{\partial \sqrt{\langle v \rangle}}{\partial \Delta_0} \right]^2. \quad (17)$$

Substituting the mean crossing rate, $\langle v \rangle = (f_n/\sqrt{3}) \exp(-\Delta_0^2/2\sigma^2)$, into the last expression we obtain

$$J_{LB}^{Pois}(\Delta_0) = \frac{T f_n \Delta_0^2}{\sqrt{3} \sigma^4} \exp\left(-\frac{\Delta_0^2}{2\sigma^2}\right), \quad (18)$$

which possesses the same dependence on noise variance σ as the SNR. The Fisher information

obtained from this formula is shown also in Fig. 4(c) where it can be compared to the *SNR*.

But our fish must discriminate the spike train due to $\Delta_0 + A$ from that due to Δ_0 alone. Substituting $\mu_N = \sigma_N^2 = T\langle v \rangle$ into eqn (16) and squaring we obtain the square discriminability,

$$d'^2 = \frac{4Tf_n}{\sqrt{3}} \left[\exp\left(\frac{A(2\Delta_0 + A)}{4\sigma^2}\right) - 1 \right]^2 \times \exp\left(-\frac{(\Delta_0 + A)^2}{2\sigma^2}\right), \quad (19)$$

which in the limit of small signal amplitude A reduces to

$$d'^2 \approx \frac{Tf_n A_0^2 A^2}{\sqrt{3}\sigma^4} \exp\left(-\frac{\Delta_0^2}{2\sigma^2}\right) = A^2 J_{LB}^{Pois}(A, \Delta_0) = \frac{T}{2} SNR. \quad (20)$$

This expression connects the discriminability with the Fisher information and the *SNR* as obtained from threshold theory, eqn (12).

The Noise and Signal Intensities at the Rostrum

It is now necessary to find the amplitudes of the signal and noise at the rostrum as functions of the distance of the fish from the single *Daphnia* and the swarm. We assume that the electric field of the single *Daphnia* is a near-field dipole. This field is defined by

$$\mathbf{E}(\mathbf{r}) \sim \frac{3\mathbf{n}(\mathbf{n} \cdot \mathbf{p}_d) - \mathbf{p}_d}{r^3}, \quad (21)$$

where r is the vector distance from the single *Daphnia* to the rostrum, \mathbf{n} is a unit vector in the direction of \mathbf{r} , and \mathbf{p}_d is the dipole moment, as shown in Fig. 5. The maximum value of the field component of \mathbf{E} directed along \mathbf{n} at the rostral surface is (Freund *et al.*, 2001)

$$A = \frac{C_1}{r^3}, \quad (22)$$

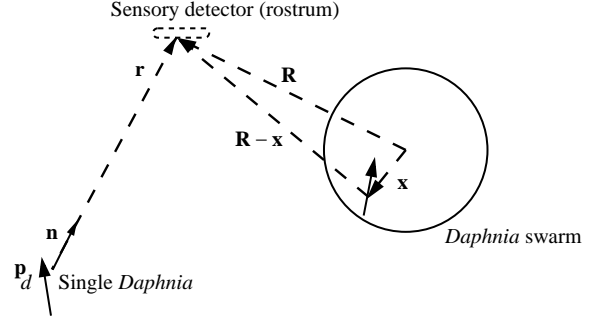


FIG. 5. Schematic diagram of the spatial locations of the single *Daphnia*, the swarm, assumed to be spherical, and the “sensory detector”, that is the paddlefish rostrum. Noise from the swarm combines with the periodic signal from the individual *Daphnia* at the rostrum of the paddlefish where the theory of threshold stochastic resonance is applied.

where the magnitude of the first proportionality constant C_1 is determined from measurements on a single tethered *Daphnia*: $C_1 = 125/8 \mu\text{V cm}^3$.

Next, we need to determine how the noise intensity D depends on the distance R from the center of the swarm to the rostrum. We assume a density of *Daphnia* $\rho(x)$ which is described by a spherically symmetric distribution as shown in Fig. 5. The field of each single *Daphnia* is given by the near-field dipole formula, but all dipole moment directions are random. Moreover, the frequencies and phases of the AC components of the individual *Daphnia* fields are randomized. Averaging over frequency, phase and dipole direction results in the following simple integral:

$$D \sim p_d^2 \int \frac{\rho(x)}{|\mathbf{R} - \mathbf{x}|^6} d^3x, \quad (23)$$

which for a constant density within the swarm, $\rho(x) = N/(4/3)\pi(A/2)^3$, yields

$$D = C_2 \frac{N}{R^6} \left(1 - \frac{A/2}{R}\right)^{-3} \left(1 + \frac{A/2}{R}\right)^{-3} \approx C_2 \frac{N}{R^6} \quad \text{for } R \gg A, \quad (24)$$

where N is the total number of *Daphnia* in the swarm and A is the swarm diameter (cf. Fig. 5).

The second proportionality constant C_2 has been experimentally determined (Russell *et al.*,

1999; Freund *et al.*, 2001). For $D = 1 (\mu\text{V})^2 \text{Hz}^{-1}$, $A/2 = 2 \text{ cm}$, $R = 3 \text{ cm}$, and $N = 200$, we obtain $C_2 = 5/8 (\mu\text{V})^2 \text{cm}^6 \text{Hz}^{-1}$. The standard deviation of the noise at the rostrum is $\sigma^2 = D/(\tau_1 + \tau_2)$ with $\tau_1 + \tau_2 = 0.147 \text{ s}$ (see Fig. 3 caption).

We can fix the threshold by choosing $A/\Delta_0 = 1$ when the distance to the *Daphnia* is 1 cm. These assumptions then yield the threshold value, $\Delta_0 = 125/8 \mu\text{V}$. Thus, we now have all numbers in hand to calculate the *SNR* and/or the discriminability using Eqns (12), (19) or (20).

Detection Contours

We can visualize these results in the following way. We place the single *Daphnia* at the origin of a coordinate system and the center of the *Daphnia* swarm is placed along the x -axis at $(L, 0, 0)$. Then, at each point on the sphere $r = \sqrt{x^2 + y^2 + z^2}$, where the rostrum of a paddlefish is located at a distance $R = \sqrt{(x - L)^2 + y^2 + z^2}$ from the center of the swarm (see Fig. 5), we can determine the *SNR* and d'^2 . Assuming the swarm diameter to be $A = 100 \text{ cm}$ together with reported swarm densities in the range $1000\text{--}9000 \text{ l}^{-1}$, we estimate a maximum number for the total *Daphnia* population of $N = 5 \text{ million}$. With these numbers we can finally compute the *SNR* and d'^2 .

We choose to plot both the *SNR* from eqn (12) and the square discriminability from eqn (19) as contours of constant value in the neighborhood of the swarm and single *Daphnia*. The contours are plotted in the X - Y plane containing the single *Daphnia* and the center of the swarm. Though the forms of the two formulae are similar (they are essentially identical in the limit of small A), we plot them both to show how, for example, the $\text{SNR} = 1$ contour relates to the discriminability for the same parameters. Figure 6 shows the contours of constant *SNR* ranging from 0.01 to 10.0. The dashed circle surrounding the individual *Daphnia* indicates the region where the threshold theory does not apply, since in this region the signal is greater than the threshold. Figure 7 shows similar results for the square discriminability, d'^2 . The contours $\text{SNR} = 1$ and $d'^2 = 1$ can be compared as indicators of standard signal detectability. Both plots show that

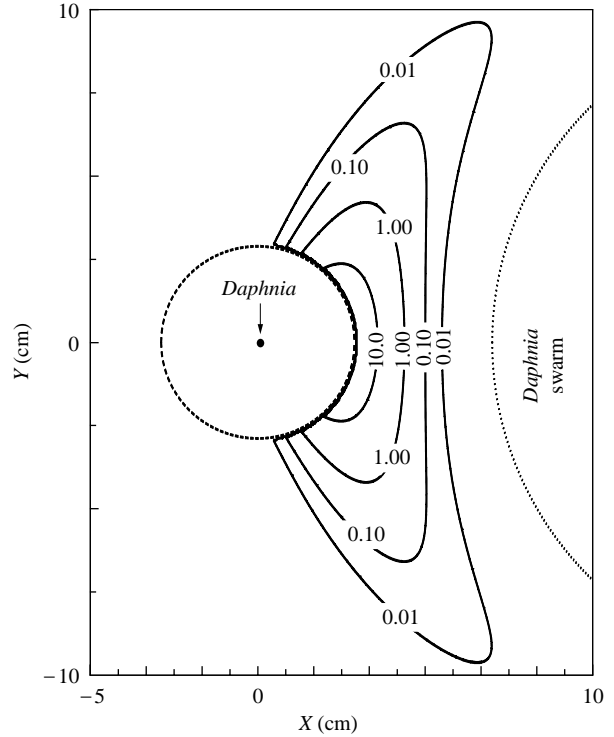


FIG. 6. Contours of constant *SNR* from eqn (12). The theory does not apply within the dashed circle.

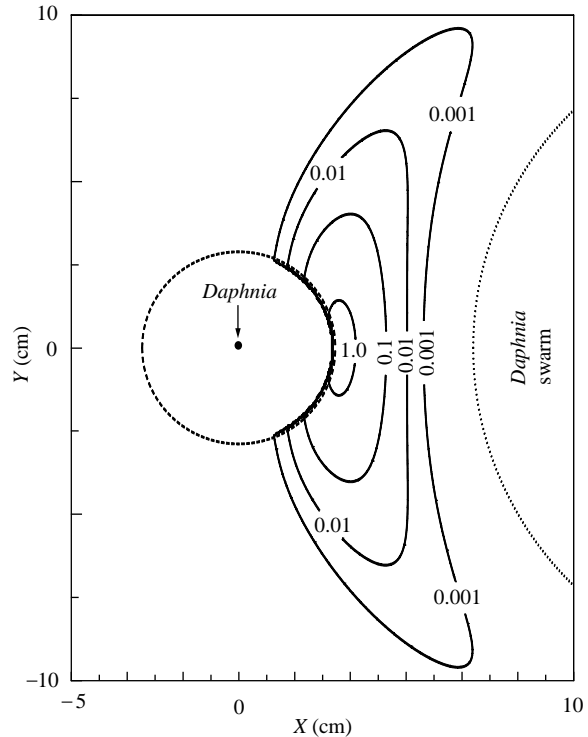


FIG. 7. Contours of constant square discriminability, d'^2 , from eqn (19). The theory does not apply within the dashed circle.

steep gradients exist in the vicinity of the single *Daphnia*. While the steepest gradient is realized by a “head-on” approach from the direction of the center of the swarm, this approach may not be optimal for a juvenile that is uncomfortable swimming within the swarm. Moreover, the gentler gradients that encircle the swarm on the outside offer substantial detectability at a longer distance. These gradients form a curved path toward the single *Daphnia* which may indicate an optimal approach trajectory for a juvenile paddlefish.

Summary and Conclusions

In this paper, we have examined the idea, first proposed in Russell *et al.* (1999), that juvenile paddlefish may make use of the electrical noise from a swarm of *Daphnia* in order to enhance their ability to detect and presumably to capture individuals in the vicinity of the swarm. Guided by experimental measurements we modeled the swarm noise, generated by incoherent *Daphnia* activity, as Ornstein–Uhlenbeck noise. We outlined how threshold stochastic resonance can be used to calculate the SNR and its relation to the Fisher information and the discriminability at the rostrum of a juvenile paddlefish cruising in the vicinity of a swarm. We obtained contours of constant SNR and d'^2 around the single *Daphnia* and the swarm. The rapid decrease in noise intensity from the swarm ($\sim 1/R^6$) and in signal intensity from the single *Daphnia* ($\sim 1/r^3$) result in steep gradients in the SNR and d'^2 . These in turn indicate an optimal path of approach to the single *Daphnia* for the cruising paddlefish, a result that appears to be experimentally testable.

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