

Stochastic Resonance Enhances the Electroreceptive Information Available to Paddlefish for Prey Capture

Priscilla E. Greenwood,¹ Lawrence M. Ward,² David F. Russell,³ Alexander Neiman,³ and Frank Moss³

¹Department of Mathematics, Peter Wall Institute for Advanced Studies, University of British Columbia, Vancouver, Canada V6T 1Z1

²Department of Psychology, Peter Wall Institute for Advanced Studies, University of British Columbia, Vancouver, Canada V6T 1Z1

³Center for Neurodynamics, University of Missouri at St. Louis, St. Louis, Missouri 63121

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Recent behavior experiments have demonstrated that paddlefish can make use of stochastic resonance while feeding on *Daphnia* plankton. Here we calculate the information content of the noisy *Daphnia* signal at the paddlefish rostrum using an exact statistical treatment of threshold stochastic resonance as a minimal neural model. These calculations compare well with experimentally obtained data on paddlefish strikes at *Daphnia* prey.

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Stochastic resonance (SR) has by now a well established history in a variety of fields [1] including sensory biology [2], human psychophysics [3], and medicine [4], as well as at the molecular level [5]. The mechanism of SR accounts for the presence of noise enhanced information about a weak signal input to systems with nonlinearities such as thresholds. However, in all experiments to date, with the sole exception of human psychophysics [3], SR has been demonstrated by computer analysis of data recorded from an afferent sensory neuron. This, of course, leaves open the question of whether or not the animal is aware of and can make use of the enhanced information available at the peripheral neurons. A recent behavioral experiment with the paddlefish *Polyodon spathula* has provided evidence in the affirmative [6]. This animal, as shown in Fig. 1, feeds on plankton which it locates and captures using exclusively its electroreceptive sense derived from an array of electroreceptor cells spread over a long rostrum [7]. *Daphnia*, a favorite prey of *P. spathula*, emit electrical signals a few tens of microvolts in amplitude (at 5 mm) with both dc and ac components. The *Daphnia* are only a millimeter or two in size, and their associated electric field is approximately dipolar. In this Letter, we consider them to be point dipole sources. Data on strikes at *Daphnia* presented to the fish in the space surrounding the rostrum with and without added electrical noise are given in [6]. Here we consider only the estimated strike probability, $P_s(d)$, in the vertical direction at distances d , above and below the rostrum. These estimates, which we call strike probability data, or simply strike data, are shown in Fig. 2 for strikes at prey above 2(a) and below 2(b) the rostrum. The open triangles and closed circles are the estimated strike probabilities without and with, respectively, optimal electrical noise added to the feeding environment. The optimal noise, approximately $0.5 \mu\text{V}/\text{cm}$, rms, was experimentally measured in Ref. [6]. It is that noise for which the strike probability at distant *Daphnia* is maximally enhanced. The curves are smoothed fits to the strike data for zero added noise (dashed) and optimal noise (solid) curve. The solid curves

are not symmetrical above and below the rostrum, possibly because of the asymmetry of the fish's anatomy. The two features upon which we focus here are shown by the crossing of the solid and dashed curves at small distances, and the enhanced strike probability at long distance, shown by the solid curves relative to the dashed curves.

Paddlefish locate, track, and capture *Daphnia* by means of complicated neural and brain functions that are largely unknown. Nevertheless, we show here that a simple statistical determination of the information available at the rostrum can reproduce the two aforementioned features of the strike data. This implies a close relationship between information in the model and strike probability in the data.

Our modeling approach is intended to be *minimal*, involving no neural encoding scheme and the use of only the threshold, or nondynamical, picture of stochastic resonance [8]. As a measure of detectability of the *Daphnia* we use the Fisher information [9], based on thresholded data, a natural measure since it was developed for analysis of behavioral experiments. Moreover, a clean knowledge of the input stimulus, obviously unavailable to the animal, is unnecessary for the present theory. In our study, the Fisher information is related to the variance of an optimal estimator of the signal level of the dipole electrical field generated by the *Daphnia*. We calculate the Fisher

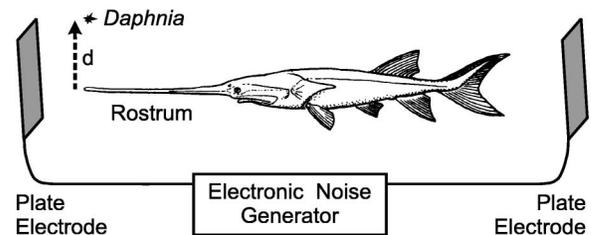


FIG. 1. The paddlefish, showing its rostrum, which supports an array of thousands of electroreceptor cells, and its prey, the plankton *Daphnia*, a distance d above the rostrum. The fish locates and captures its prey entirely by electroreception. For details see [6] and [7].

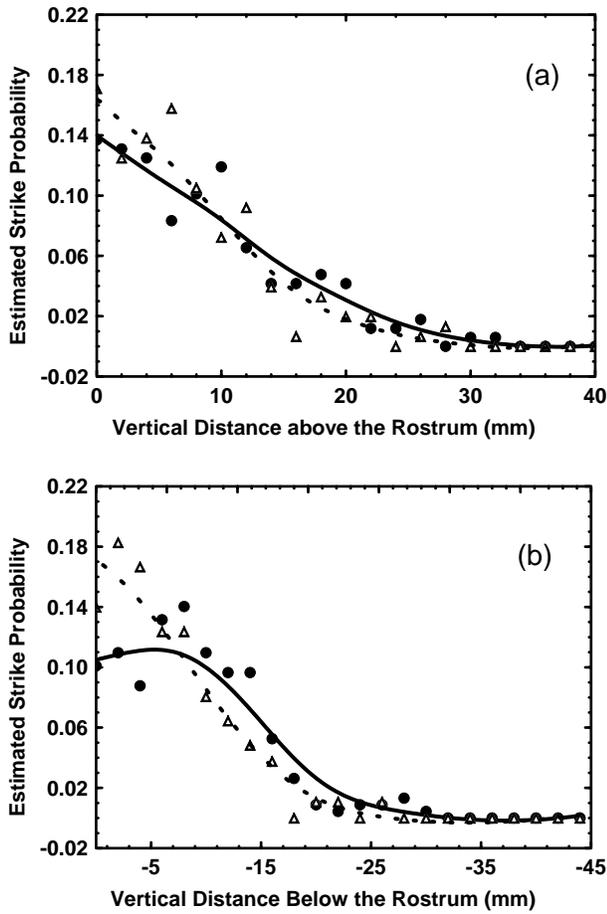


FIG. 2. The estimated strike probabilities from [6] for zero added noise (open triangles, dashed curve) and for the optimal level of noise, $0.5 \mu\text{V}/\text{cm}$, rms (solid circles, solid curve): (a) for strikes above the rostrum; (b) for strikes below the rostrum. The effects due to SR are small but statistically significant as demonstrated in Ref. [6]. The curves were obtained from a nonlinear, distance-weighted least squares fit.

information, I , from the noisy *Daphnia* signal level at the surface of the rostrum under the following assumptions: (1) The *Daphnia* are represented as point dipole sources whose amplitudes consequently decrease as $1/d^3$ with the vertical distance above and below the rostrum. (2) The noise is added to the *Daphnia* signal at the rostrum, as in the experiment [6], and hence is independent of d . Gaussian noise is added to the signal at a sequence of uniformly spaced times; the noise is independent and identically distributed for each time. We ask only whether the signal plus the noise exceeds a threshold a or not, at each noise sample time, as depicted in Fig. 3. We calculate the Fisher information contained in the temporal sequence of threshold exceedances (1's) and nonexceedances (0's). As in many psychophysics experiments [10], we assume that the probability of behavioral response, in this case $P_s(d)$, is mediated by the availability of information, in this case the Fisher information at the sensory periphery, $I(d)$, as defined below.

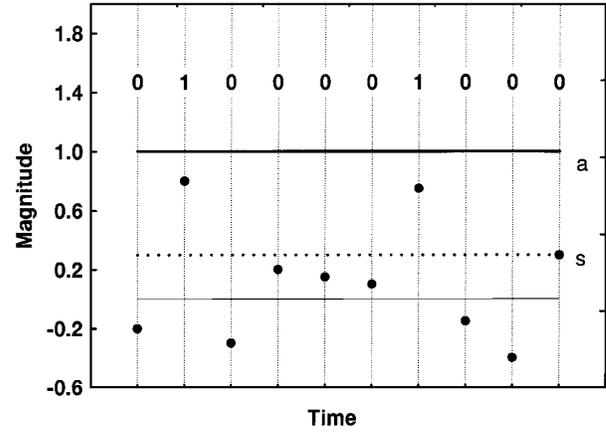


FIG. 3. Schematic representation of the signal level s (dashed horizontal line), threshold a (continuous horizontal line), and added Gaussian noise (mean zero, standard deviation σ , independent samples represented by uniformly spaced black dots of various magnitudes). The sequence of 1's and 0's displayed above the threshold line records the exceedances and non-exceedances of the threshold by s plus noise, respectively, at each sample time [e.g., for the first time point: $0.3 + (-0.2) = 0.1 < 1.0$ so a 0 is displayed].

A detailed statistical analysis of a general version of this process appears elsewhere for both single and multiple thresholds and for both constant [11] and periodic [12] signals. We summarize the theory here.

As noise we take n independent samples, $\varepsilon_1, \dots, \varepsilon_n$, with distribution function F , later chosen to be a Gaussian. We add these to the signal, s , and construct a time series of 0's and 1's that mark the threshold exceedances:

$$X_i^a = \begin{cases} 1, & \text{if } (s + \varepsilon_i) > a, \\ 0, & \text{otherwise,} \end{cases} \quad i = 1, \dots, n, \quad (1)$$

which are independent Bernoulli random variables with probabilities

$$p_s = P(X_i^a = 1) = P_s(a, \infty) = 1 - F(a - s). \quad (2)$$

The signal can be written as $s = a - F^{-1}(1 - p_s)$. An estimator for the probability, p_s , is $\hat{p} = (1/n) \sum_{i=1}^n X_i^a = \hat{n}/n$, where \hat{n} is the number of 1's in the sequence (1). The normalized error, $n^{1/2}(\hat{p} - p)$, is asymptotically normal with variance $p_s(1 - p_s)$. The corresponding estimator for the signal is $\hat{s} = a - F^{-1}(1 - \hat{p})$. The normalized error, $n^{1/2}(\hat{s} - s)$, is asymptotically normal with variance

$$v_s = \frac{p_s(1 - p_s)}{f[F^{-1}(1 - p_s)]^2} = \frac{F(a - s)[1 - F(a - s)]}{f(a - s)^2}, \quad (3)$$

the inverse of which is the Fisher information for estimation of s from the series of X_i^a . If the noise is Gaussian, $F = \Phi = \int_{-\infty}^x \phi dx$ with density $\phi = (1/\sqrt{2\pi}) \times \exp(-x^2/2)$, and the Fisher information is

$$I_{s\sigma}^a = \frac{[\phi(\frac{a-s}{\sigma})]^2}{\sigma^2 \Phi(\frac{a-s}{\sigma}) [1 - \Phi(\frac{a-s}{\sigma})]}, \quad (4)$$

where σ is the standard deviation of the noise distribution. This is an exact expression; that is, it extends to regimes beyond the linear response to the *Daphnia* signal. As a result, the optimal noise level that maximizes the Fisher information is a function of the signal s . We represent the *Daphnia* signal as $s = 1/(d + 1)^3$, which goes to zero as $d \rightarrow \infty$ and avoids becoming singular at $d = 0$. In Fig. 4(a) the Fisher information $I_{s\sigma}^a(d)$ from Eq. (4) is plotted as a function of σ and d with threshold $a = 1$. In Fig. 4(b) we show the Fisher information for two selected values of the noise intensity as a function of distance. Our results, drawn from a comparison of Figs. 2(a), 2(b), and 4(b) are qualitative and based on the following assumptions. In Fig. 4(b) the dashed curve is for noise $\sigma = 0.15$,

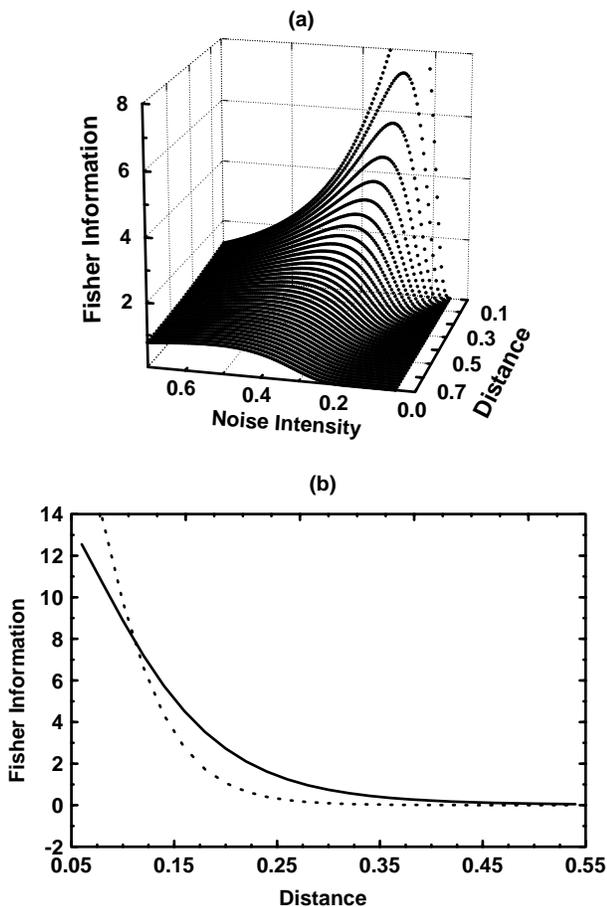


FIG. 4. (a) A three-dimensional plot of the Fisher information from Eq. (4) for the noise intensity, σ , and the vertical distance to a *Daphnia*, d . Note the shift of the information maximum towards smaller values of σ for smaller distances, d , which correspond to larger signal levels s . (b) The Fisher information at the surface of the rostrum as a function of d . The dashed curve is from Eq. (4) for $\sigma = 0.15$, simulating a low level of internal noise. The solid curve is from Eq. (4) with $\sigma = 0.2$, simulating an optimal level of externally applied noise. The distances are in arbitrary units. Note that this *minimal* theory does not capture the asymmetry observed in the experiment [6]; that is, it does not distinguish the strike probability above from that below the rostrum.

which we regard as a smaller noise that is internal to the paddlefish neural system and/or noise due to small erratic motions of the *Daphnia*. This is meant to model our results [6] for zero experimentally added noise. The internal noise avoids a sharp step function for the estimated strike probability at the detection threshold. The solid curve is for $\sigma = 0.2$ and is meant to model the detection process for experimentally added optimal noise. We note that the curves cross at small distance. This is the result of the shift of the maxima for smaller distances (larger signal amplitudes) towards lower noise intensity, together with the increase in the size of these maxima. Note also that the solid curve is slightly elevated at large distances. This represents the noise enhancement of the strike probability at large distances. These are the two features of the experimental data that our minimal model has captured qualitatively.

We assume that if σ were 0 there would be no strikes, i.e., that the *Daphnia* signal is below the threshold of a “comatose” paddlefish, and that the signal produced by a *Daphnia* very close to the rostrum is, in fact, near the threshold of this comatose paddlefish. This gives us a common location or initial point for the two figures. We have chosen the distance scale in Fig. 4(b) so that the size of the figure corresponds to Fig. 2. Hence no meaning can be attached to the similarity of scale in the two figures. The measure of detectability in Figs. 2(a) and 2(b) is the estimated strike probability, which corresponds to the Fisher information measure in Fig. 4(b) only in that each should be a monotonically increasing function of the other. Hence the conclusions we can draw from the similarities of these figures are strictly qualitative, and closer comparison must await further study.

The graphs of estimated strike probability versus distance presented in Fig. 2 resemble what is called in human psychophysics the “psychometric function” with the x axis plotted in reverse [10]. The psychometric function displays the probability of a signal being detected (or, the probability that signal plus noise exceeds a threshold) as a function of signal amplitude. It usually resembles the s -shaped graph of the normal distribution function. One interpretation of the sigmoid shape is that the function represents the interaction of an approximately normal distribution of signal plus noise with a fixed threshold (cf. [13]). In such a plot, the threshold is taken to be the signal amplitude at which the probability of detecting the signal is 0.5. Two psychometric functions that are shifted with respect to one another on the signal amplitude axis can be interpreted as exhibiting a difference in sensitivity, where the function with lower threshold, as just defined, represents the higher sensitivity. Such an interpretation can be made of the pairs of functions in Figs. 2(a), 2(b), and 4(b). Adding noise shifts the function to the right, which corresponds to weaker signals and indicates greater sensitivity at large distances. In each of Figs. 2(a), 2(b), and 4(b) an increase of noise also lowers the maximum value of the function so that the two curves cross. This is a feature

of the family of stochastic resonance curves exhibited in Fig. 4(a), which shows a decrease in the maximum information, as well as occurrence of this maximum at smaller distances, with increasing noise intensity. The repetition of this pattern in the strike probability data, Figs. 2(a) and 2(b), indicates that this aspect of the stochastic resonance phenomenon occurs in the responses of the paddlefish. Interestingly, such nonparallelism in psychometric functions is usually interpreted as a difference in the noise intensity between the two situations, with the “lower” function having the greater noise intensity, exactly as in Figs. 2 and 4. However, since the maximum of the function representing the higher noise intensity is not lowered in psychometric theory, that aspect of psychometric theory is not relevant in this context. Thus, the paddlefish strike probability data are compatible with our simple stochastic resonance model as well as with at least part of the psychophysical theory of psychometric functions.

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