

Coding accuracy is not fully determined by the neuronal model

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It is automatically assumed that the accuracy, with which the stimulus can be decoded, is entirely determined by the properties of the neuronal system. We challenge this perspective by showing that the identification of pure tone intensities in an auditory nerve fiber depends both on the stochastic response model and on the arbitrarily chosen stimulus units. We expose an apparently paradoxical situation in which it is impossible to decide whether loud or quiet tones are encoded more precisely. Our conclusion reaches beyond the topic of auditory neuroscience, however, as we show that the choice of stimulus scale is an integral part of the neural coding problem and not just a matter of convenience.

Keywords: Fisher information, Neuronal coding, Coding precision

INTRODUCTION

One of the primary goals of neuroscience is to understand how neurons encode and process information about their environment. The problem is often approached by examining the degree to which the neuronal response reflects the stimulus feature. The coding accuracy, with which the stimulus can be ultimately decoded from the observed responses, is of particular interest. Comparing this precision for different types of responses (e.g., counts of action potentials or intervals in between them) then yields an important evidence about the principles of neural coding. The evaluation of the best decoding precision can be quite involved mathematically [1], instead it is often more practical to employ the Cramér-Rao bound on the mean square error (MSE) [2–10].

In this paper we show how the deduced coding precision changes under one-to-one stimulus re-parameterizations where, intuitively, no information loss or gain is expected. Such behavior differs from the properties of the Shannon and Kullback information measures [11]. From this perspective, the choice of stimulus units *is not* a matter of convenience, a fact whose consequences seem to have been overlooked in the neuroscience literature so far.

METHODOLOGY

The observed neuronal response varies randomly across trials [12–14]. The stimulus-response relationship is therefore defined probabilistically, in terms of the distribution function $R \sim f(r; \theta)$, where θ is the stimulus value and R is the random variable describing the response [13, 15]. It is known from statistics that any unbiased decoding procedure based on the elicited response cannot identify the true stimulus with MSE smaller than the the Cramér-Rao bound [16],

$$\text{MSE}(\theta) \geq \frac{1}{J(\theta)}, \quad (1)$$

where $J(\theta)$ is the Fisher information,

$$J(\theta) = \text{E} \left[\frac{\partial \log f(R; \theta)}{\partial \theta} \right]^2. \quad (2)$$

The Cramér-Rao bound is usually tight for the maximum-likelihood decoder, as the response variability decreases or the size of neuronal population increases [13].

The stimulus value θ can be *equivalently* expressed in different physical units as $\lambda = \varphi(\theta)$, where the function φ is one-to-one. The models $f(r; \theta)$ and $f(r; \lambda)$ describe *the same* neuronal system equally well and the bound on the decoding precision of λ becomes [16, p. 115],

$$\text{MSE}(\lambda) \geq \frac{1}{[(\varphi^{-1})'(\lambda)]^2 J(\varphi^{-1}(\lambda))}, \quad (3)$$

where $J(\cdot)$ is given by Eq. (2) and the denominator on the right-hand side of Eq (3) plays the role of Fisher information about λ .

RESULTS AND DISCUSSION

The main message of this paper stems from the fact that Fisher information depends on the parameterization of the problem, as seen from Eq. (3). Usually, results obtained under different coordinate or physical unit systems are expected to be identical (invariant). We show that the dependence in Eq. (3) is not benign and affects the interpretation of coding accuracy greatly. The implied consequences are of broad validity and the actual physiological identity of the neuronal model is of lesser importance here.

In the classical study, Winslow and Sachs [17] investigated the response of cat auditory nerve fibers to a varying sound pressure level of a pure tone. Ensembles of fibers best responding to 8 kHz sound frequency were chosen. The rate-level function of the fiber type considered here was determined by Winslow and Sachs [17, Eq. (A7)] as

$$\mu(\theta) = \frac{10^{c\theta/20} r_m}{10^{t_E/20} (1 + 10^{-t_I/20} 10^{\theta/10})^{c/3} + 10^{c\theta/20}} + r_{sp}, \quad (4)$$

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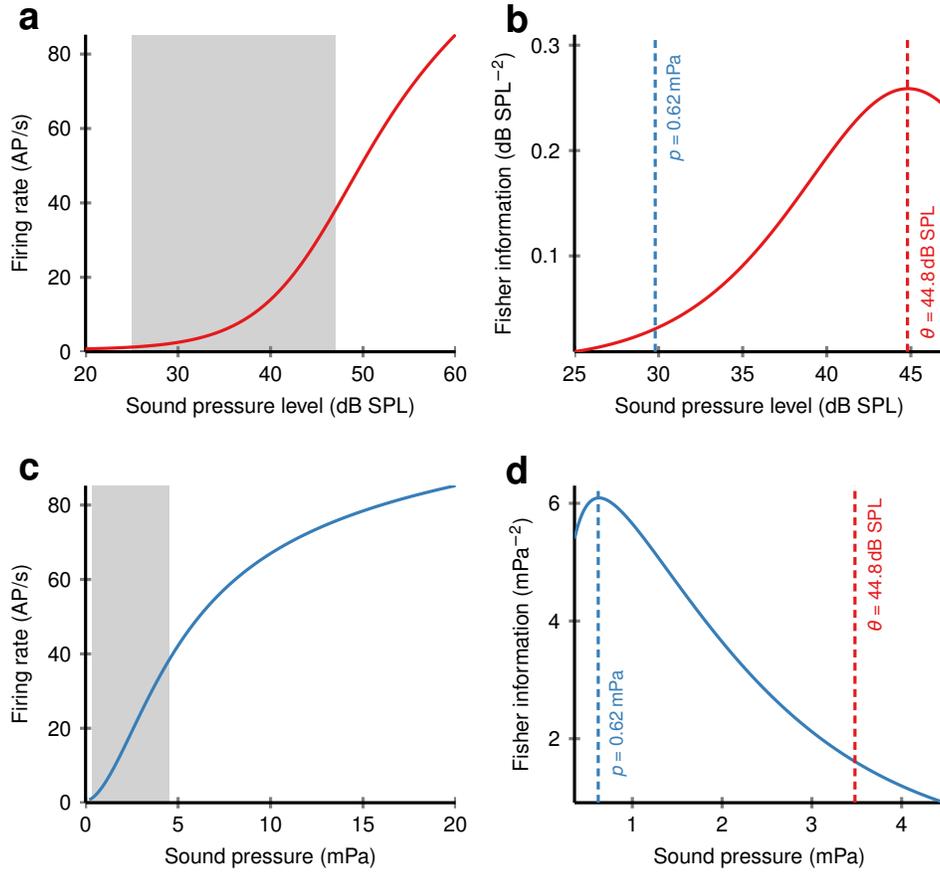


Figure 1. Choice of stimulus units affects the coding accuracy (Fisher information). **(a)** Rate-level function of cat auditory nerve fiber best responding to 8 kHz sound frequency in dependence on the sound pressure level (loudness) in dB. The stimulus range yielding Poissonian statistics of spike counts is marked. **(b)** Fisher information about the sound pressure level. **(c)** The same neuronal model as in **(a)**, the stimulus is equivalently expressed as the sound pressure in Pascals. **(d)** Fisher information about the sound pressure for the same stimulus range as in **(b)**. It is not obvious whether quiet or loud tones are better identified by the system unless the stimulus units are specified. The optimal stimulus intensity (maximal Fisher information) depends on the unit choice and occurs at inconsistent values **(b, d)**: $J(\theta)$ is maximized at $\theta \doteq 44.8$ dB SPL ($p \doteq 3.48$ mPa), while $J(p)$ is maximized at $p \doteq 0.62$ mPa ($\theta \doteq 29.8$ dB SPL).

where the stimulus θ is the sound pressure level expressed in decibels (dB SPL) and the mean response $\mu(\theta)$ is given in spikes per second (AP/s). The parameter $t_E = 89.4$ dB SPL determines the response threshold, $t_I = 100$ dB SPL is a parameter related to the two-tone suppression model [18], $r_m = 135.1$ AP/s is the maximum rate change which can be observed in response to a pure tone stimulus, $r_{sp} = 0.5$ AP/s is the spontaneous discharge rate and $c = 1.77$ is a model constant. The rate-level function is shown in Fig. 1a.

The response spike-count distribution in auditory nerve fibers is reported to be close to Poisson [17, 19], especially if the mean response frequency is below 40 AP/s [20] (marked in Fig. 1a), above that level the effect of maximum physiological firing rate becomes apparent. The probability of observing n spikes during time window Δ is therefore

$$\Pr(N = n; \theta) = e^{-\mu(\theta)\Delta} \mu(\theta)^n \Delta^n / n!, \quad n = 0, 1, \dots \quad (5)$$

The Eq. (5) represents the stochastic model of the fiber since the response (in AP/s) is simply $r = n/\Delta$. The actual value

of Δ depends on the experimental protocol; in accord with Winslow and Sachs [17] we set $\Delta = 500$ ms. Fisher information for the model in Eq. (5) is shown in Fig. 1b for the range of 25–47 dB SPL.

So far, the stimulus intensity was expressed in dB SPL. Equivalently, the tone loudness is expressed in Pascals (Pa) by the effective sound pressure, p , as

$$p = 10^{\theta/20} p_{\text{ref}}, \quad (6)$$

where $p_{\text{ref}} = 20 \mu\text{Pa}$ [21]. The relationship between θ and p is one-to-one and monotonic so that louder tones correspond to higher pressures and larger values of dB SPL. The tuning curve in Eq. (4) parameterized by the sound pressure is shown in Fig. 1c (p spans the same range as θ in Fig. 1a) and the gray region 0.3–4.5 mPa corresponds to 25–47 dB SPL. Qualitatively, Fisher information $J(p)$ (Fig. 1d) is strikingly distinct from $J(\theta)$ (Fig. 1b). Loud tones result either into higher (b) or lower (d) Fisher information values when compared to quiet tones. The maximum of $J(\theta)$, corresponding to the best iden-

tifiable (optimal) stimulus, occurs at $\theta \doteq 44.8$ dB SPL, yielding $p \doteq 3.48$ mPa (Fig. 1d) due to Eq. (6). On the other hand, the maximum of $J(p)$ occurs at $p \doteq 0.62$ mPa, corresponding to $\theta \doteq 29.8$ dB SPL (Fig. 1b). The choice between Pascals or decibels is *arbitrary* and therefore the conclusions on stimulus optimality above are ambiguous. More precisely, the conclusions are inseparable from the particular choice of units.

The dependence of Fisher information on the stimulus scale must be taken into account and requires an appropriate interpretation. A minute difference in values of p close to zero transforms due to Eq. (6) into a substantial numerical difference in θ . Similarly, if a large decoding error is made for high p the corresponding error on the log-scale may be marginal. Thus the maximum-likelihood decoding follows the Cramér-Rao bound in both cases, and from this point of view there is no contradiction. Also note that maximum of the likelihood function is invariant with respect to stimulus re-parameterization. If for some observed response $\hat{\theta}$ and \hat{p} are the solutions to the maximum-likelihood problem in the respective parameterizations, then these solutions are related by Eq. (6). However, the decoding precision depends on the “concentration” of these maxima and therefore it is critically affected by the re-scaling of the parameter. The usage of dB SPL units in auditory neuroscience is at least partially motivated by the well-known Weber’s law. However, the law is known to be neither universal across different sensory modalities nor exact [22, 23].

In situations where the response variability is independent of the stimulus intensity, or when the response variability is not considered, the maximal slope of the monotonous rate-intensity function is considered as the most sensitive or optimal stimulation point [3, 24]. This can also be seen as a special case of the inference based on maximal Fisher information [25]. For example, olfactory receptor neurons exhibit

sigmoidal (Hill-type) tuning curves with respect to the log-concentration of the odorant [26]. The maximal slope occurs at the inflection point of the sigmoid and thus at non-zero concentrations. However, the same system exhibits the point of maximal slope precisely at the zero concentration, whenever decadic concentrations are employed. It is also worth noting, that the position of the highest slope depends on the parameterization of both stimulus and response, while Fisher information is invariant under response re-parameterizations.

In addition, according to the efficient-coding hypothesis [27], sensory neurons are adapted to the statistical properties of the signals to which they are naturally exposed. We thus expect a correspondence between the theoretically optimal stimulation (based on the model inference) and natural signals. Since the theoretical optimum is arbitrary (affected by the stimulus scale), we need to know what is the coordinate system that actually matters to sensory neurons. We find it quite unlikely that it would correspond precisely to, e.g., the units given by the standard SI system. Unless the mapping from the convenient physical units to the units of neuronal “interest” is known, Fisher information must be considered carefully as the criterion of stimulation optimality.

Finally, we note that the non-invariance of $J(\theta)$ might be of no importance when employed in a different context. For example, both the *low-noise* [8, 10] and the *high-noise* [28] approximations to the Shannon’s mutual information include $J(\theta)$ inside their equations. However, the transformation factor $[(\varphi^{-1})'(\cdot)]^2$ in Eq. (3) cancels out and hence these approximations are also invariant with respect to coordinate transforms.

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