Approximate information capacity of the perfect integrate-and-fire neuron using the temporal code

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Abstract

The limits on maximum information that can be transferred by single neurons help us to understand how sensory and other information is being processed in the brain. In this paper we approximately calculate the information capacity of the perfect integrate-and-fire neuronal model in dependence on the stimulus range, assuming the simplest form of temporal coding scheme. We couple the information transfer with metabolic cost of neuronal activity and we find that the optimal information per metabolic cost ratios may occur for a relatively small stimulus range.

Keywords: Integrate-and-fire neuron, Information capacity, Temporal coding

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1. Introduction

It is generally accepted that neurons communicate using series of action potentials (spike trains) via chemical and electrical synapses, in a process known as synaptic transmission. One of the fundamental questions in computational neuroscience is the quantification of information transferred and processed by spiking neurons. There are two main hypotheses that describe the representation of information in neuronal output (Kostal et al., 2007; Theunissen and Miller, 1995; Perkel and Bullock, 1968). In the first, denoted as the rate (or frequency) coding hypothesis, information is represented by the neuronal firing rate. The firing rate is defined differently by different authors, e.g., as the number of spikes per fixed time window or as the inverse of the mean interspike interval (ISI), see Lansky et al. (2004)

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for a review. In the second hypothesis, denoted as the temporal coding, features of the spiking activity beyond the firing rate are employed. For example, time to the first spike after the stimulus onset, characteristics based on the second and higher statistical moments of the ISI probability distribution, or precisely timed groups of spikes (temporal patterns) are candidates for temporal codes (Buracas and Albright, 1999; Kostal et al., 2007).

Information theory is a mathematical framework that provides tools for quantification of information content and information transfer in systems defined by probabilistic rules (Gallager, 1968). First studies on information transfer in neurons appeared relatively shortly after Shannon published the theory (Jacobson, 1950; MacKay and McCulloch, 1952; Quastler, 1953). Neuronal information capacities estimated in these studies differ enormously, in the orders of magnitude. The reason lies in employing different coding schemes and also in neglecting the degree of intrinsic ISI variability (Stein, 1967). Probably the first theoretical study of the limits on the information transfer in neuronal models (assuming the rate coding) was done by Stein (1967). Since then, optimality conditions on information transfer in neuronal populations or single neuronal models were analyzed under varying assumptions on the properties of the model, stimulus or the code (e.g., additive Gaussian noise, low- or high-noise limits, etc.), see Brunel and Nadal (1998); Bulsara and Zador (1996); Kostal and Lansky (2010); de Ruyter van Steveninck and Laughlin (1996); Machens et al. (2005); McDonnell and Stocks (2008) for more details. More recently, Ikeda and Manton (2009) numerically calculated the information capacity of both rate and temporal codes in a neuronal model with gamma distribution of ISIs, however, their method is not directly applicable to any neuronal model of choice or stimuli restrictions. Numerical studies with little or no assumptions are rare, mainly due to complicated nature of the involved calculations (Dauwels, 2005; Gallager, 1968).

In this paper, we apply a simple method to calculate information capacity of the the perfect integrate-and-fire model (Tuckwell, 1988) using the temporal coding scheme for a small stimulus range. The trade-off for the approximate nature of our results is, that the method is essentially free of any restrictive assumptions on the neuronal model.

2. Methods

2.1. Information transfer using the temporal code

The ISI lengths in a spike train often vary, apparently randomly at least to some degree, both within and across trials (Shadlen and Newsome, 1998; Stein et al., 2005). Therefore only the probability that a spike occurs can be given, describing the ISI by a random variable T with probability density function (p.d.f.) $f(t)$. Let θ be the stimulus intensity then the p.d.f. of ISIs evoked by this stimulus is denoted as $f(t|\theta)$. The conditional p.d.f. $f(t|\theta)$ fully describes the properties of neuronal model from the temporal coding point of view. During stimulation, stimulus values cannot be known beforehand (from the "point of view" of the neuron), thus the stimulus is described by a random variable Θ with p.d.f. $\pi(\theta)$.

Within the framework of information theory, the information provided about the stimulus $\Theta = \theta$ by observing the response $T = t$ is defined as (Gallager, 1968)

$$I(\theta; t) = \log_2 \frac{\phi(\theta|t)}{\pi(\theta)}, \tag{1}$$

where $\phi(\theta|t)$ is the contitional p.d.f. of Θ given ISI, $T = t$. The most informative stimulus-response pairs are those, where the response t can be used to "identify" θ with high specificity, i.e., with high *a posteriori* to *a priori* probability ratio (Gallager, 1968). The p.d.f. $\phi(\theta|t)$ is usually difficult to calculate, thus the Bayes' law is used to write Eq. (1) equivalently as

$$I(\theta; t) = \log_2 \frac{f(t|\theta)}{f(t)}, \tag{2}$$

where the (unconditional) ISI p.d.f. $p(t)$ is

$$f(t) = \int_\Theta f(t|\theta)\pi(\theta)\, d\theta. \tag{3}$$

The average value of $I(\theta; t)$ taken over all stimulus-response pairs is denoted as the mutual information, $I(\Theta; T)$, between stimuli and responses,

$$I(\Theta; T) = \int_\Theta \int_T I(\theta; t) f(t|\theta)\pi(\theta)\, dt\, d\theta. \tag{4}$$

The value of $I(\Theta; T)$ gives the average number of bits per ISI that can be transmitted reliably by the neuron, represented by $f(t|\theta)$, using the stimulus p.d.f. $\pi(\theta)$. Of particular interest is the maximum rate of reliable information transmission, denoted as information capacity $\mathcal{C}$,

$$\mathcal{C} = \max_{\pi(\theta)} I(\Theta; T), \tag{5}$$

where the maximum is taken over all possible stimulus distributions. Usually, the set of possible stimuli is restricted, e.g., Θ has finite variance or range (Gallager, 1968). In this paper we examine the situation when Θ is known to take values in a given range $[\theta_{\min}, \theta_{\max}]$.

Most often, Eq. (5) cannot be solved in a closed form. Numerical methods must be used, and these can be rather involved unless stimulus is known beforehand to take only finitely many different values (Dauwels, 2005). We employ a simple capacity approximation, which is valid if the neuronal response is weakly tuned to the variation of stimulus over the given range (information transmission under small signal-to-noise ratio, see Fig. 1). In the limit of vanishing stimulus range the capacity-achieving stimulus distribution is binary (Huang and Meyn, 2005; Kostal, 2010), with equiprobable masses located at $\theta_{\min}$ and $\theta_{\max}$. The lower bound on the true capacity, $\mathcal{C} \geq \mathcal{C}_{\text{bin}}$, thus follows

$$\begin{aligned} \mathcal{C}_{\text{bin}} = & \frac{1}{2} \int_T I(\theta_{\min}; t) f(t|\theta_{\min})\, dt + \\ & + \frac{1}{2} \int_T I(\theta_{\max}; t) f(t|\theta_{\max})\, dt, \end{aligned} \tag{6}$$

where $p(t)$ in the definition of $I(\theta; t)$, Eq. (2), is $p(t) = [f(t|\theta_{\min}) + f(t|\theta_{\max})]/2$. Despite the simplicity of the binary approximation, Eq. (6), the difference $\mathcal{C} - \mathcal{C}_{\text{bin}}$ is usually negligible for $\mathcal{C}_{\text{bin}} < 0.8$ bits, see (Forney and Ungerboeck, 1998; Huang and Meyn, 2005; Kostal, 2010) for more details and examples.

2.2. Perfect integrate-and-fire neuronal model

We consider a primitive model of neuronal firing, in which the presynaptic excitatory and inhibitory inputs arrive randomly, according to two independent Poisson processes (Tuckwell, 1988). The value of the membrane depolarization at time t, $V(t)$, satisfies

$$V(t) = a[N_E(t) - N_I(t)], \tag{7}$$

where a is the magnitude of a single inhibitory or excitatory input, $N_E(t)$ and $N_I(t)$ are the counts of excitatory and inhibitory inputs with respective intensities λ and ω, and $V(0) = 0\,\mathrm{mV}$. The action potential is emitted once the depolarization reaches the threshold S, after which the depolarization is reset back to zero. We assume that $\lambda > \omega$ and that S/a is an integer for simplicity.

If the input rates λ and ω are sufficiently high, and the ratio a/S small, the depolarization in Eq. (7) can be approximated by a Wiener process, $\bar{V}(t)$, with drift μ and variance σ^2,

$$\bar{V}(t) = \mu t + \sigma W(t), \tag{8}$$

where $W(t)$ is the standard Wiener process (Tuckwell, 1988). The parameters of the original, Eq. (7), and approximative, Eq. (8), models are related as (Lansky and Sacerdote, 2001; Tuckwell, 1988)

$$\mu = a(\lambda - \omega), \tag{9}$$

$$\sigma = a\sqrt{\lambda + \omega}. \tag{10}$$

The model in Eq. (8) is known as the *diffusion approximation* of the perfect integrate-and-fire (PIF) model given by Eq. (7). Since in this paper we deal with the approximate model only, Eq. (8), we denote it simply as the PIF model. The probability density of ISIs of the PIF model is the inverse Gaussian density (Tuckwell, 1988),

$$f(t|\lambda, \omega) = \frac{S}{\sqrt{2\pi(\lambda + \omega)a^2 t^3}} \exp\left\{ -\frac{[S + (\omega - \lambda)at]^2}{2(\lambda + \omega)a^2 t} \right\}. \tag{11}$$

The ISI density of the PIF model is often given in terms of μ and σ from Eq. (8), however, the parametrization in terms of λ and ω reflects the original model in Eq. (7) better and is often considered as physiological (Lansky and Sacerdote, 2001; Tuckwell, 1988).

2.3. Stimulus parametrization

Three main regimes to stimulate the PIF neuron were proposed in Lansky and Sacerdote (2001):

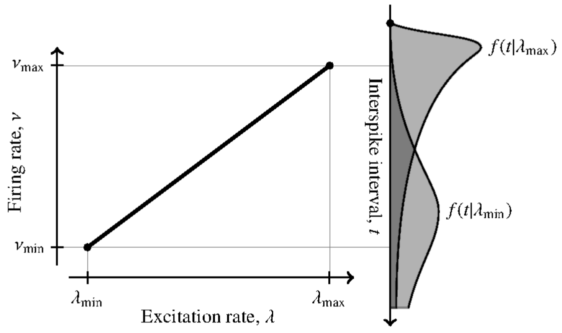

Figure 1: Relationship between the stimulus and the average output firing rate of the perfect integrate-and fire neuronal model. The stimulus is the excitation rate λ (the inhibition rate ω is assumed constant), restricted to the interval $[\lambda_{\min}, \lambda_{\max}]$. Each value of λ evokes a spiking activity with firing rate ν. The evoked activity is not perfectly regular, the lengths of interspike intervals vary according to the probability density function $f(t|\lambda)$, which represents the stimulus-response relationship from the temporal coding point of view. If the stimulus range is small, the two extremal densities $f(t|\lambda_{\min})$ and $f(t|\lambda_{\max})$ overlap significantly, resulting in an information transmission under low signal-to-noise ratio conditions.

1. The excitation rate, λ, is increasing while the inhibition rate $\omega = \omega_0$ is kept constant. In this case $\theta = \lambda$.
2. The excitation rate $\lambda = \lambda_0$ is kept constant while the inhibition rate ω is decreasing, thus $\theta = \omega$.
3. Both rates increase proportionally, $\lambda = q\omega$, with constant $q > 1$. Here we can choose either $\theta = \lambda$ or $\theta = \omega$.

The stimulus, θ, has different interpretation in each of the regimes (excitation or inhibition rate). In order to compare the stimulation regimes meaningfully by using a common scale, we parametrize the stimulus by the (average) neuronal output it evokes (Stein, 1967). We choose the output firing rate, $\nu = 1/\langle T\rangle$, as the stimulus parameter for two reasons, i) the metabolic cost of neuronal activity is directly proportional to ν (see next section), ii) ν is linear in both λ and ω, see Fig. 1, since from Eq. (11) follows

$$\nu = \frac{a(\lambda - \omega)}{S}. \tag{12}$$

The average (unconditional) output firing rate, $\langle\nu\rangle$, is the inverse of the mean ISI of the p.d.f. $f(t)$ from Eq. (3),

$$\langle\nu\rangle = \left[\int_T \int_\Theta t f(t|\theta)\pi(\theta)\, d\theta\, dt\right]^{-1}. \tag{13}$$

Next, we adjust the parameters of each regime above so, that the stimulus range $[\nu_{\min}, \nu_{\max}]$ is equal in all three cases.

1. The range of the excitation rate, $[\lambda_{\min}, \lambda_{\max}]$, and the inhibition rate ω_0 are selected freely, so that $\omega_0 < \lambda_{\min}$. The stimulus is $\theta = \nu = a(\lambda - \omega_0)/S$.
2. The condition on the equality of the stimulus range results in the following equations for the range of the inhibition rate,

$$\omega_{\min} = \lambda_0 - \lambda_{\min} + \omega_0, \tag{14}$$

$$\omega_{\max} = \lambda_0 - \lambda_{\max} + \omega_0, \tag{15}$$

   where the excitation rate λ_0 is selected freely, provided that $\lambda_0 > \omega_{\max}$, thus $\theta = \nu = a(\lambda_0 - \omega)/S$.
3. We set ω as the varying parameter in this case, the equality of the stimulus range gives

$$\omega_{\min} = \frac{\lambda_{\min} - \omega_0}{q-1}, \tag{16}$$

$$\omega_{\max} = \frac{\lambda_{\max} - \omega_0}{q-1}, \tag{17}$$

   where the coefficient of proportionality, $q > 1$, is selected freely, and $\theta = \nu = a\omega(q-1)/S$.

2.4. Metabolic cost of spiking activity

Neurons use significant amount of energy for the spiking activity, thus energy usage is coupled to the effectivity of neuronal information transfer (Laughlin et al., 1998). Theoretical results from biologically relevant single-compartment neuronal models show, that metabolic cost of spiking activity increases linearly over a wide range of firing frequencies (Balasubramanian and Berry II, 2002).

The average metabolic cost W (in ATP molecules per second) of spiking activity resulting from stimulus p.d.f. $\pi(\theta)$ can be thus defined as

$$W = \kappa \langle \nu \rangle \,. \tag{18}$$

The constant of proportionality κ describes the metabolic cost of a single spike, and its value is estimated (for sensory neurons) to lie in the range from 9×10^5 to 9×10^7 ATP molecules (Laughlin et al., 1998). For the purpose of this paper we set $\kappa = 9 \times 10^6$. Alternatively, we consider the quantity

$$W_{\mathrm{add}} = \kappa(\langle \nu \rangle - \nu_{\mathrm{min}}), \tag{19}$$

which describes the additional metabolic cost with respect to the smallest (basal) firing rate, see Fig. 1. In other words, the metabolic cost W_{add} of spiking activity when there is no stimulus, $\langle \nu \rangle = \nu_{\mathrm{min}}$, is zero. We are motivated by the fact, that many neurons show some level of spontaneous activity. Thus W_{add} describes the metabolic cost of actual information transfer.

3. Results

The three stimulation regimes described in Section 2.3 have common output firing rates, but their temporal coding properties are expected to differ. Indication is provided by the ISI coefficient of variation, C_V, the ratio of standard deviation to mean ISI, which is frequently used to describe ISI variability. From Eq. (11) we have

$$C_V = \sqrt{\frac{a(\lambda + \omega)}{S(\lambda - \omega)}}, \tag{20}$$

thus regimes 1 and 2 (increasing λ, decreasing ω) result in a monotonically decreasing C_V (with different values), while regime 3 (proportional increase of λ and ω) results in a constant $C_V = \sqrt{[a(q+1)]/[S(q-1)]}$.

We calculate the approximate capacity by employing Eq. (6) for the three stimulation regimes in dependence on the stimulus range. In other words, we fix ν_{min} while increasing ν_{max}. Two examples are analyzed to demonstrate, that the relative information efficiency of regimes 1, 2 and 3 is not absolute, but depends on how the free parameters are selected. The parameter values are within the physiological range proposed in Lansky and Sacerdote (2001).

In the first example, Fig. 2a–c, the input excitatory rate λ is set large when compared to the inhibitory rate ($\lambda_{\min} = 180 > 150 = \omega_0$). The dependence of C_V of ISIs of the evoked activity on the stimulus value for all three regimes is shown in Fig. 2a. The relatively small range of C_V for regime 1 (from 0.3 to 0.47) indicates small variability of ISIs, thus the ISI length encodes the stimulus value more reliably than in the other regimes. This is confirmed in Fig. 2b, which shows the information capacity per single ISI. The regime 3 has largest overall C_V and correspondingly the poorest information performance. The maximal information transfer per metabolic cost W_{add} is shown in Fig. 2c. Although concerns about precision of the capacity approximation do not allow us to extend the stimulus range, it is likely that the optimal value of information per metabolic cost in regime 1 is reached soon beyond $\nu_{\max} = 2$. Also, note that regime 3 slightly outperforms regime 2 for $\nu_{\max} < 1.1$.

The second example is presented in the Fig. 2d–f. In this case, the inhibitory and excitatory input rates are in their upper range (Lansky and Sacerdote, 2001) and are initially almost balanced ($\lambda_{\min} = 500 > 490 = \omega_0$). The range of C_V over the given stimulus range is quite large for regimes 1 and 2, resulting in both sub-Poisson ($C_V < 1$) and supra-Poisson ($C_V > 1$) ISI variability (Fig. 2d.). Regime 1 has the largest overall C_V and correspondingly its information performance is poorest (Fig. 2e). On the other hand, it is difficult to estimate the relative information performance of regimes 2 and 3 based on C_V only. Fig. 2e shows, that even though C_V of regime 2 is smaller for more than a half of the stimulus range ($\nu > 0.55$) than that of regime 3, its information efficiency is always smaller. The information per additional metabolic cost (Fig. 2f) shows that regime 3 performs significantly better than the other two especially for small stimulus range. Generally, since the C_V of the third regime is constant, its performance improves with smaller C_V. The best performance is obtained in the limit $q \to \infty$, which gives $C_V = \sqrt{a/S}$.

4. Discussion and Conclusions

The presented results give the upper bound on information transfer by the PIF neuronal model using the temporal coding scheme. However, achievability of such information transfer needs to be discussed. First, the temporal coding scheme implicitly assumes that the stimulus value is kept constant until the spike is generated, after which the stimulus changes until the next spike and so on. This is an idealization which requires unrealistic synchronization between stimuli and responses. This problem was also discussed in Ikeda and Manton (2009), but no obvious solution was found. In any case, the true capacity must be lower than that resulting from this idealization. Second, channel capacity gives the upper bound on *reliable* information transfer, e.g., the PIF neuron can be theoretically used, by appropriately changing the stimulus values, to transmit 100 bits of information, at $\mathcal{C}$ bits/ISI on average, and these 100 bits can be recovered exactly from the responses (with arbitrarily small probability of error). Shannon's channel coding theorem ensures that such procedure (coding and decoding operation) exists (Gallager, 1968). However, it is known that the capacity-achieving coding-decoding schemes are incredibly complex and hard to implement practically (Gallager, 1968). The complexity of such operations can be sometimes reduced greatly in the presence of feedback (the dependence of current stimulus on past responses) or by including some fidelity criterion on the approximate reconstruction of the true sensory input (Gallager, 1968; Gastpar et al., 2003). We have not included these possibilities in our current effort. Rather, we take the traditional point of view in computational neuroscience and maximize just the mutual information between stimuli and responses (Atick, 1992; Kostal et al., 2008; Machens et al., 2005; Stein, 1967).

The PIF model employed here was chosen for its analytical tractability (Tuckwell, 1988) and its frequent usage in experimental data analysis (Pouzat and Chaffiol, 2009). The simplicity of the PIF model comes at a price of ignoring the spontaneous decay of membrane potential, so it can be considered as a valid approximation only if the membrane time constant and/or the overall excitation rate are sufficiently large. Furthermore, the PIF model has no memory, the current response does not depend on past stimuli or responses.

In the presence of memory, the capacity approximation presented here is not valid and different methods must be used (Kostal, 2010).

In this paper we have analyzed the upper bound on reliable information transfer in the PIF neuronal model using the temporal code. We employed a binary approximation to channel capacity, valid if the stimulus range is relatively small. Three different stimulation regimes were employed: 1. increasing excitation rate, 2. decreasing inhibition rate and 3. increasing both rates proportionally. These three schemes were mutually compared. Our results show, that the relative efficiency of these three regimes changes depending on the disbalance between overall excitatory and inhibitory rates. We found, that the optimal information transfer per additional metabolic may occur for relatively small input ranges. Although restricted only to relatively small stimuli ranges, the obtained values of capacity per ISI are similar to those obtained by Ikeda and Manton (2009) for the temporal coding scheme of the neuron with gamma distribution of ISIs.

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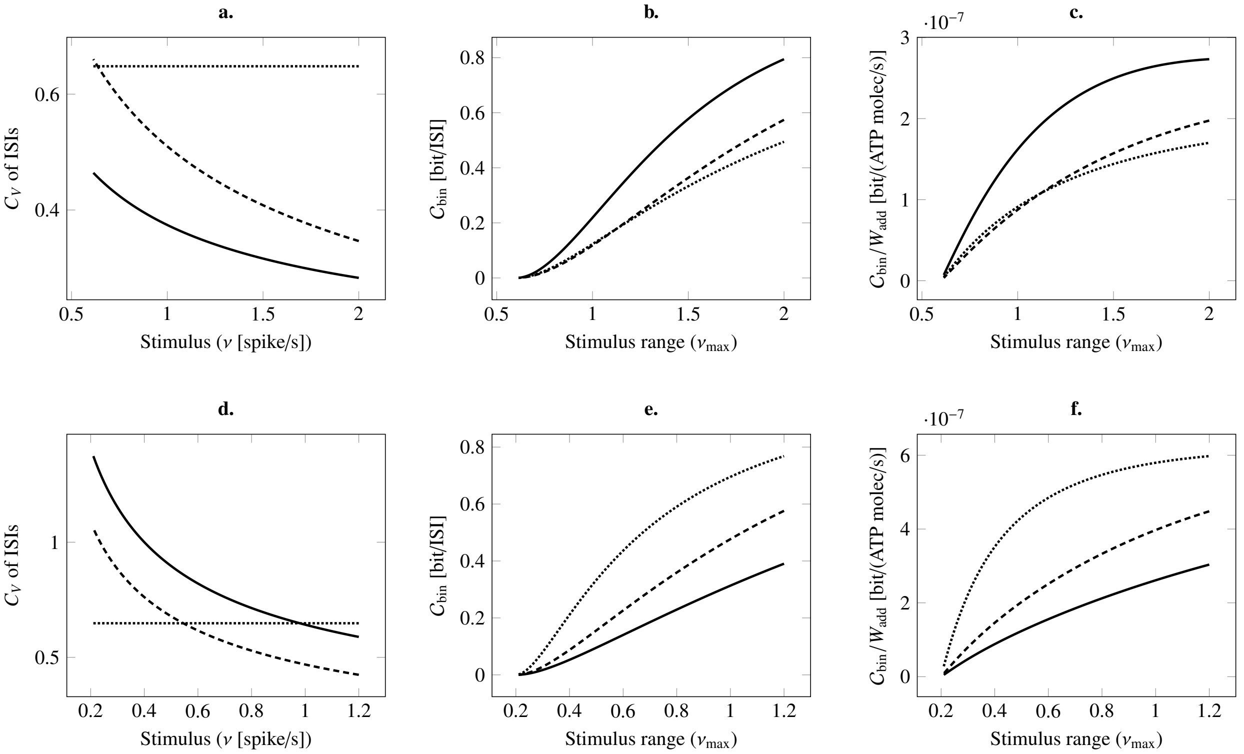

Figure 2: Approximate information capacity of the perfect integrate-and-fire neuronal model using the temporal code. Three stimulation regimes are investigated: 1. increasing excitation rate (solid), 2. decreasing inhibition rate (dashed) and 3. increasing both rates (dotted). Note, that the stimulus is uniquely parameterized by the mean firing rate ν, which provides a common scale for the three regimes, see also Fig. 1. *Parameters (a–c):* $S = 10\,\text{mV}$, $a = 0.2\,\text{mV}$, $\lambda_{\min} = 180$, $\lambda_{\max} = 250$, $\omega_0 = 150$, $\lambda_0 = 350$, $q = 1.1$, $\nu_{\min} = 0.6$. *Parameters (d–f):* $S = 10\,\text{mV}$, $a = 0.2\,\text{mV}$, $\lambda_{\min} = 500$, $\lambda_{\max} = 550$, $\omega_0 = 490$, $\lambda_0 = 300$, $q = 1.1$, $\nu_{\min} = 0.2$. Note, that the relative information efficiency of the regimes in the bottom row is reversed when compared to the top row.