PHYSICAL REVIEW RESEARCH **6**, L012009 (2024)

Letter

# Inherent trade-off in noisy neural communication with rank-order coding

Ibrahim Alsolami[*] and Tomoki Fukai
*Neural Coding and Brain Computing Unit, Okinawa Institute of Science and Technology (OIST) Graduate University, Onna, Okinawa 904-0495, Japan*

(Received 13 August 2023; accepted 14 December 2023; published 16 January 2024)

Rank-order coding, a form of temporal coding, has emerged as a promising scheme to explain the rapid ability of the mammalian brain. Owing to its speed as well as efficiency, rank-order coding is increasingly gaining interest in diverse research areas beyond neuroscience. However, much uncertainty still exists about the performance of rank-order coding under noise. Herein we show what information rates are fundamentally possible and what trade-offs are at stake. An unexpected finding in this Letter is the emergence of a special class of errors that, in a regime, increase with less noise.

DOI: 10.1103/PhysRevResearch.6.L012009

*Introduction.* Currently, there is growing interest in spiking neural networks in physics and engineering [1,2], mainly because of their potential to improve power efficiency, which, to a great extent, depends on the coding scheme employed. For spiking neural networks, a variety of coding schemes are available. Chief among them is rank-order coding; this coding scheme offers a fundamentally different approach for neural information transmission. In rank-order coding, information is encoded in the order of neural spikes; utilizing this degree of freedom can substantially boost communication speeds and efficiency.

Rank-order coding has been proposed as a faster alternative to the traditional rate coding scheme [3]. While rate coding is the most widely accepted coding scheme in neuroscience, it has a subtle problem: Some experimental observations are hard to reconcile with it because it is slow. For example, primates can respond selectively to the presentation of three-dimensional (3D) objects as quickly as 100–150 ms after the onset of a stimulus [4,5]. This response is too fast to be explained with rate coding as it needs, for a reasonable degree of accuracy, to accumulate spikes over periods much longer than 150 ms.

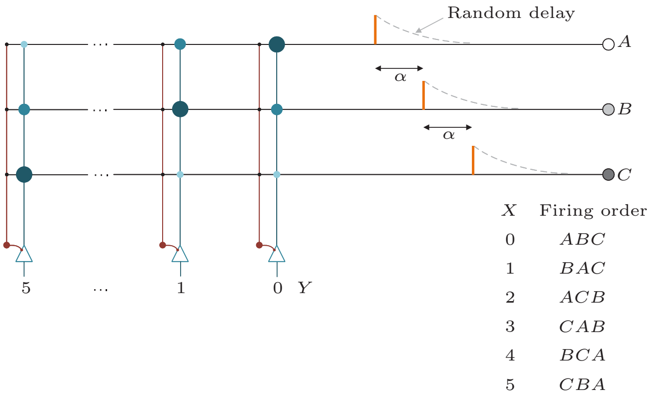
One could, of course, argue that rate coding across a reasonably large number of neurons could provide speed (in terms of bits/s). In such an approach, we would have $n$ neurons firing in parallel, and one counts the number of spikes generated within a relatively short time window. This population rate coding approach can certainly provide speed as we would need a longer time window to accumulate $n$ spikes from a single neuron than $n$ neurons firing in parallel. However, one must contend with the fact that such an approach is inefficient in terms of bits/neurons [6]. For instance, in an extreme case, we may consider a short time window in which a neuron would fire at most once. In this time window, the number of spike counts can range from 0 to $n$ (no neuron fires to all neurons fire)—collected by a set $\mathcal{S} = \{0, 1, \dots, n\}$. If a postsynaptic neuron cannot distinguish which presynaptic neurons fires, then the total number of possible symbols of this rate coding approach is $n + 1$ (the number of elements in $\mathcal{S}$), which encodes a maximum of $\log_2(n + 1)$ bits. As such, the efficiency of this population rate coding approach is upper bounded by $\frac{\log_2(n+1)}{n}$ (bits/neuron)—that is, the more neurons, the less the efficiency. Additionally, the rapid speed of visual processing is likely to be accomplished with very few spikes [5], and this would require a neural coding scheme whereby a few neurons can communicate efficiently.

Rank-order coding can offer both speed and efficiency. With $n$ neurons, rank-order coding can encode $\log_2 n!$ bits per transmission compared to $\log_2(n + 1)$ bits per transmission for rate coding (because with $n$ neurons, there are $n!$ different ways in which neurons can fire after each other, which is utilized by rank-order coding to encode information, $\log_2 n!$). The encoding ability of rank-order coding is vast. Take, for instance, a setting with ten presynaptic neurons. With these neurons, rank-order coding can in principle form $10! = 3\,628\,800$ symbols, that is, firing orders of neurons (Fig. 1). As $n$ increases, the encoding ability of rank-order coding rapidly accelerates. This vast amount of information available in the arrival order of spikes is often forgotten, and studying neural codes that utilize such an arrival order could provide clues on how neurons can transmit information rapidly and efficiently across brain regions.

Converging evidence suggests that the relative timing, or rank, of neuronal firing plays an important part in encoding information. In retinal ganglion cells of salamanders, the rapid transmission of visual scenes is likely accomplished by encoding information in the relative timing of spikes [7]. It was shown later in a population of retinal ganglion cells of mice that the content of a visual stimulus could be

---

[*] ibrahim.alsolami@oist.jp



| $X$ | Firing order |
|---|---|
| 0 | $ABC$ |
| 1 | $BAC$ |
| 2 | $ACB$ |
| 3 | $CAB$ |
| 4 | $BCA$ |
| 5 | $CBA$ |

FIG. 1. Rank-order coding with temporal noise (random delay). Here, $\alpha$ is the spacing between successive spikes before noise is introduced. In this illustration, the magnitude of synaptic weights is represented by the size of the depicted circles. Here, postsynaptic neurons integrate and fire and are progressively desensitized by shunting inhibition circuits (red). With shunting inhibition, the sensitivity of a neuron progressively decreases as $\beta^k$, where $k$ is the arrival order of a spike, and $\beta$ is a constant that takes values in the range $0 < \beta < 1$. A postsynaptic neuron is maximally activated if spikes arrive in the order of its synaptic weights; by setting the firing threshold to this maximum excitation/activation level, a postsynaptic neuron becomes selective to a particular temporal pattern.

accurately inferred from the wave of the first stimulus-evoked spikes, indicating the importance of the relative timing of spikes to encode sensory information [8]. An analysis of the odor-evoked responses of olfactory neurons of *Xenopus laevis* (African clawed frogs) demonstrated that the rank of spike latencies is a reliable predictor of odor identity [9]. It was also shown that synchronized firing among motor cortex neurons of macaque monkeys performing a pointing task is associated with movement planning, highlighting the importance of precise spike timing in decision making [10].

In addition to its biological applicability, rank-order coding is gaining attention in the field of artificial spiking neural networks, which are becoming popular as they hold great potential in energy-efficient computing [11]. It was shown that spiking neural networks with rank-order coding can achieve a high image-classification accuracy with a relatively small number of spikes in multilayer feed-forward networks [12] as well as in recurrent networks [13]. Rank-order coding is also finding favor in hardware implementations of spiking neuromorphic processors; it was demonstrated that rank-order coding can enhance power efficiency [14] and provide a favorable trade-off between energy consumption and classification accuracy [15]. Recently, it was shown that rank-order coding successfully reduced the on-chip inference latency in neuromorphic devices [16].

Despite increasing interest in the use of rank-order coding, far too little attention has been paid to the effect of noise on its performance. Our goal here is to analytically understand the impact of noise on the performance of rank-order coding, as noise is unavoidable in any physical system. In rank-order coding, noise can cause spikes to be swapped with each other, giving rise to errors. Contrary to intuition, reducing noise does not necessarily reduce all types of errors. Moreover, we show that information rate and communication efficiency cannot be simultaneously maximized due to an intrinsic trade-off between them.

*Methods.* We consider a noise model in which the spike times of presynaptic neurons exhibit random delays (Fig. 1) characterized by an exponential probability density, and is given by

$$f_i(z) = \begin{cases} \lambda\, e^{-\lambda[z-(i-1)\alpha]}, & \text{if } z \geqslant (i-1)\alpha, \\ 0, & \text{otherwise.} \end{cases} \tag{1}$$

Here, $f_i(z)$ is the probability density function (pdf) of the $i$th presynaptic neuron, $i \in \{1, 2, \dots, n\}$. This pdf describes the likelihood of observing a randomly delayed spike, by noise, at time $z$. Such noise may arise when neurons do not respond instantly to a stimulus, at an expected time, but rather with a random delay (Fig. 1).

Without loss of generality, we hypothesize that a postsynaptic neuron responds selectively and reliably to a particular order of presynaptic spikes. A feed-forward shunting inhibition circuit was suggested as the underlying mechanism of this precise decoding of temporal patterns [6,17]. However, exploring the detailed decoding mechanisms is beyond the scope of this Letter.

The channel capacity enables us to compute the maximum amount of information postsynaptic neurons can receive and is defined as [18,19]

$$C = \max_{p(x)} I(X;Y) \quad \text{(bits/symbol)}, \tag{2}$$

where $I(X;Y)$ is the mutual information between random variable $X$ (input symbol) and $Y$ (output symbol), and is given by

$$I(X;Y) = H(Y) - H(Y|X) \quad \text{(bits/symbol)}. \tag{3}$$

Here, $H(Y)$ is the entropy of $Y$, and $H(Y|X)$ is the conditional entropy of $Y$ given $X$.

In Fig. 1, we have $(n!)^2$ possible combinations of input and output symbols, where a symbol is defined as a particular order of neural spikes (e.g., the sequence ABC). Here, $n$ is the number of presynaptic neurons. The probability of sending symbol $x$ and, because of noise, receiving symbol $y$ is given by the transition probability $p(y|x)$. The following probability transition matrix describes such a communication channel:

$$\boldsymbol{p(y|x)} = \begin{pmatrix} p(0|0) & p(1|0) & \cdots & p(n!-1|0) \\ p(0|1) & p(1|1) & \cdots & p(n!-1|1) \\ \vdots & \vdots & \ddots & \vdots \\ p(0|n!-1) & p(1|n!-1) & \cdots & p(n!-1|n!-1) \end{pmatrix}_{n!\times n!} = \begin{pmatrix} p_0 & p_1 & \cdots & p_{n!-1} \\ p_1 & p_0 & \cdots & p_{n!-2} \\ \vdots & \vdots & \ddots & \vdots \\ p_{n!-1} & p_{n!-2} & \cdots & p_0 \end{pmatrix}_{n!\times n!}. \tag{4}$$

This communication channel is symmetric because rows of the transition matrix are permutations of each other, and so are the columns. The capacity of this channel is achieved by a uniform distribution on the input $X$ [19] [$p(x) = \frac{1}{n!}$], which results in a uniform distribution on the output $Y$ [$p(y) = \frac{1}{n!}$], and is given by

$$\begin{aligned} C &= \max_{p(x)}[H(Y) - H(Y|X)] \\ &= \log_2 n! - H(\boldsymbol{r}) \quad \text{(bits/symbol)}, \end{aligned} \tag{5}$$

where $H(\boldsymbol{r}) = -\sum_{j=0}^{n!-1} p_j \log_2 p_j$ is the entropy of a row of matrix $\boldsymbol{p(y|x)}$.

*Results.*

*Transition probabilities.* Here, we determine the transition probabilities to find the channel capacity in Eq. (5). These probabilities are the likelihood that a particular neural spike sequence is received under the perturbation of noise (random delay, Fig. 1). For instance, for three neurons, $p(CBA|ABC)$ is the probability that the sequence CBA ($y = 5$) is erroneously received due to noise, given that the original noise-free sequence is ABC ($x = 0$). It suffices to compute the transition probability of any row of $\boldsymbol{p(y|x)}$ because the channel is symmetric [19]. Calculations of the transition probabilities are straightforward but tedious. Therefore, we only determine these probabilities when the number of presynaptic neurons is relatively small (see Supplemental Material for a derivation [20]).

We can obtain

$$\begin{aligned} p_0 &= p(AB|AB) = 1 - \tfrac{1}{2}e^{-\lambda\alpha}, \\ p_1 &= p(BA|AB) = \tfrac{1}{2}e^{-\lambda\alpha}, \end{aligned} \tag{6}$$

for two presynaptic neurons and

$$\begin{aligned} p_0 &= p(ABC|ABC) = 1 - e^{-\lambda\alpha} + \tfrac{1}{6}e^{-3\lambda\alpha}, \\ p_1 &= p(BAC|ABC) = \tfrac{1}{2}e^{-\lambda\alpha} - \tfrac{1}{2}e^{-2\lambda\alpha} + \tfrac{1}{6}e^{-3\lambda\alpha}, \\ p_2 &= p(ACB|ABC) = \tfrac{1}{2}e^{-\lambda\alpha} - \tfrac{1}{3}e^{-3\lambda\alpha}, \\ p_3 &= p(CAB|ABC) = \tfrac{1}{6}e^{-3\lambda\alpha}, \\ p_4 &= p(BCA|ABC) = \tfrac{1}{2}e^{-2\lambda\alpha} - \tfrac{1}{3}e^{-3\lambda\alpha}, \\ p_5 &= p(CBA|ABC) = \tfrac{1}{6}e^{-3\lambda\alpha}, \end{aligned} \tag{7}$$

for three presynaptic neurons. In the above expressions, $\alpha$ is the spacing between successive spikes before noise is introduced, and $\lambda$ is the rate parameter of the exponential distribution of the noise. Results with four presynaptic neurons are shown in the Supplemental Material [20].

As expected, when $\lambda\alpha$ increases, error probabilities decrease [Fig. 3(a)]. There is a notable exception, however. In the range $0 \leqslant \lambda\alpha \leqslant \ln\sqrt{2}$, the error probability $p(ACB|ABC)$ increases. This can be viewed in two different ways: (1) For a fixed value of $\alpha$, as the noise decreases (that is, $\lambda$ increases), the probability of this type of error increases [Fig. 3(b)]. (2) For a fixed value of $\lambda$, as the spacing between spikes ($\alpha$) increases, the error probability increases as well. A similar phenomenon is also observed when we have four ($n = 4$) presynaptic neurons (see Supplemental Material [20]). This error probability momentarily increases with less noise, which is counterintuitive: Errors typically decrease with less noise—not the opposite (see the Appendix for an explanation as to why they emerge). Throughout this Letter, we shall refer to this class of probabilities as *atypical probabilities*. This type

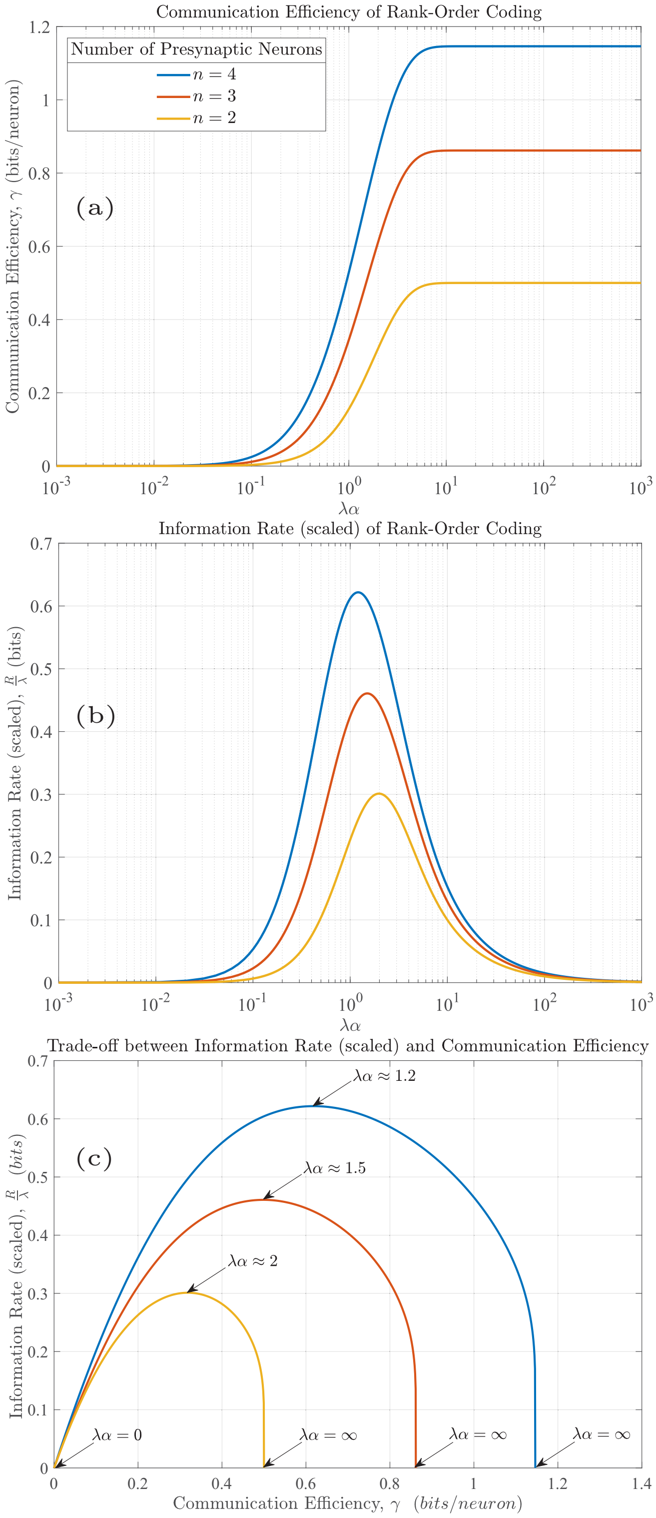


FIG. 2. Performance of rank-order coding. (a) Communication efficiency. (b) Information rates. Here, we plot the scaled version of $R$ (that is, $\frac{R}{\lambda}$) rather than $R$ as it eliminates the need to display $R$ for various combinations of $\lambda$ and $\alpha$. (c) The trade-off between information rates and efficiency.

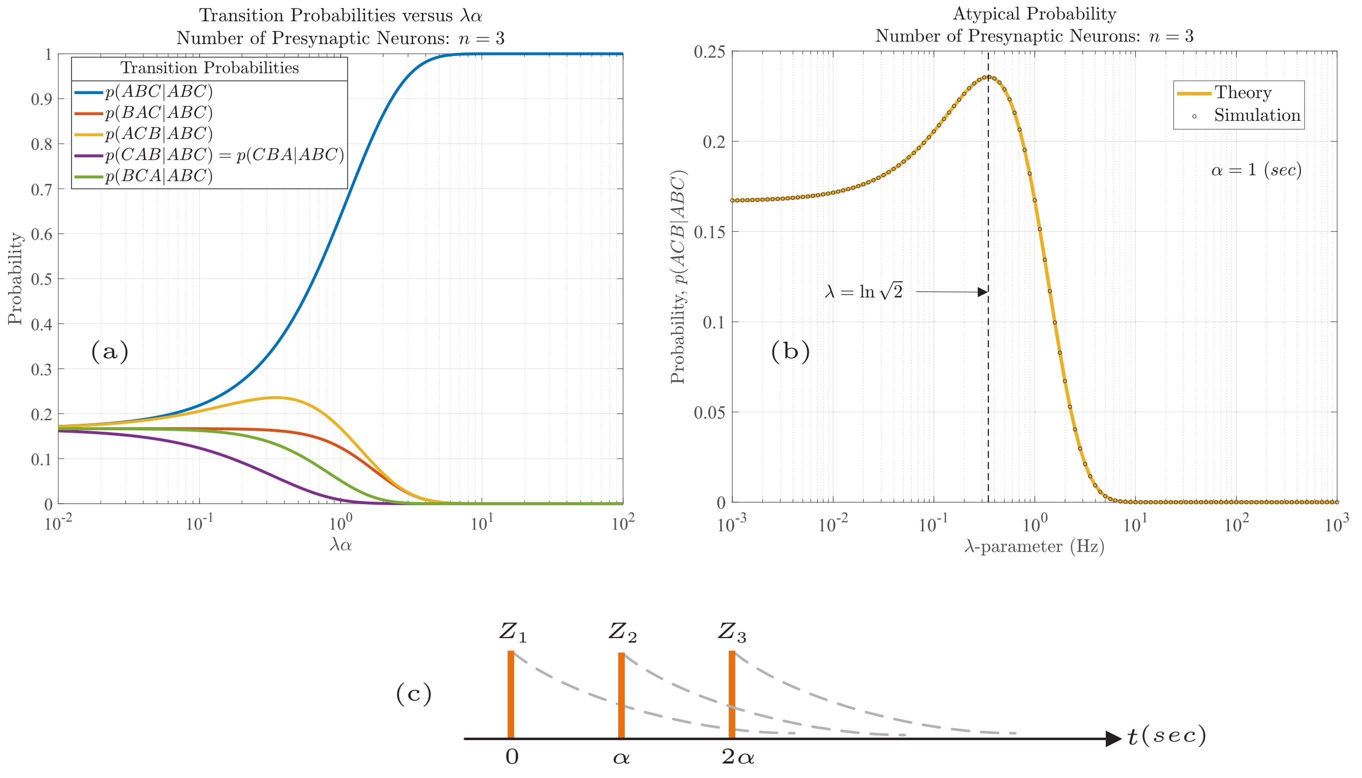


FIG. 3. Transition probabilities and spikes of rank-order coding with temporal noise. (a) Transition probabilities for three presynaptic neurons ($n = 3$). (b) Atypical probability $p(ACB|ABC)$. Here, $\alpha$ is arbitrarily set to 1 (second), and the number of samples per point used in the simulation is $10^9$. (c) Spikes of rank-order coding with temporal noise (random delay).

of error is not limited to exponential noise; it can also be observed, for example, with Gaussian noise (see Supplemental Figs. 6 and 7 [20]).

*Communication efficiency and information rate.* Figure 2(a) shows the performance of rank-order coding in terms of communication efficiency, which is defined as

$$\gamma = \frac{C}{n} \quad \text{(bits/neuron)}, \tag{8}$$

where $C$ can be calculated by using Eq. (5). The communication efficiency increases monotonically with $\lambda\alpha$. This increase in efficiency eventually plateaus and is asymptotically bounded by $\gamma^* = \lim_{\lambda\alpha\to\infty} \frac{C}{n} = \frac{\log_2(n!)}{n}$ (bits/neuron). Moreover, the higher the value of $n$, the more efficient is the communication.

We can further evaluate the performance of rank-order coding in terms of information rate, which is defined as

$$R = \frac{C}{\bar{T}} \quad \text{(bits/s)}. \tag{9}$$

In the absence of noise, the average symbol duration $\bar{T}$ (that is, the time difference between the first and last spikes of a rank-order coding symbol) is $(n-1)\alpha$. However, with noise, the average symbol duration increases and is given by

$$\bar{T} = \alpha + \frac{1}{\lambda}e^{-\lambda\alpha} \quad \text{(s/symbol)} \tag{10}$$

for two presynaptic neurons ($n = 2$),

$$\bar{T} = 2\alpha + \frac{1}{\lambda}e^{-\lambda\alpha} + \frac{1}{2\lambda}e^{-2\lambda\alpha} \quad \text{(s/symbol)} \tag{11}$$

for three presynaptic neurons ($n = 3$), and

$$\bar{T} = 3\alpha + \frac{1}{\lambda}e^{-\lambda\alpha} + \frac{1}{2\lambda}e^{-2\lambda\alpha} + \frac{1}{2\lambda}e^{-3\lambda\alpha} - \frac{1}{6\lambda}e^{-4\lambda\alpha} - \frac{1}{6\lambda}e^{-5\lambda\alpha} + \frac{1}{6\lambda}e^{-6\lambda\alpha} \quad \text{(s/symbol)} \tag{12}$$

for four presynaptic neurons ($n = 4$) (see Supplemental Material for a derivation [20]).

In Fig. 2(b), we display the (scaled) information rate as a function of $\lambda\alpha$. The information rate is a nonmonotonic function of $\lambda\alpha$ and increases with $n$. Moreover, there is an optimal operating point at which the information rate is maximized; beyond this critical point, the information rate rapidly diminishes.

In a noisy environment, there exists an inherent trade-off between the communication efficiency of rank-order coding and its information rate. The communication efficiency continuously increases with $\lambda\alpha$ [Fig. 2(a)], but this gain in efficiency comes at the cost of a loss in the information rate once $\lambda\alpha$ is beyond a critical value [Fig. 2(b)]. A range of trade-offs is shown in Fig. 2(c), in which the value of $\lambda\alpha$ is varied and the pair $(\gamma, \frac{R}{\lambda})$ is displayed.

*Discussion.* This Letter set out to study the impact of noise on the performance of rank-order coding. The communication speed and efficiency of rank-order coding come from its ability to utilize the order of neural spikes. This coding scheme is advantageous as it allows for a multitude of symbols ($n!$) to be constructed using a few spikes. A disadvantage, however, is that it is susceptible to temporal noise, which can swap spikes with each other, causing errors at postsynaptic neurons.

In noisy environments, the information rate and communication efficiency depend at least on three factors: The spacing between spikes $\alpha$, the rate parameter $\lambda$, and the number of presynaptic neurons $n$. The higher the value of $\lambda\alpha$, the more efficient is the communication. However, increasing $\lambda\alpha$ beyond an optimal operating point has the adverse effect of reducing the information rate. Additionally, we found a class of error probabilities that increase with less noise. This result is counterintuitive because errors commonly decrease with less noise—not the opposite. The presence of such error probabilities raises a need for special care in designing error correction schemes for neuromorphic devices that employ rank-order coding.

We revealed that rank-order coding has an inherent trade-off between information rate and communication efficiency. This result could provide insights to better understand what trade-offs neurons make in different brain regions (under the rank-order coding hypothesis) between the conflicting needs to be fast and, at the same time, efficient. The trade-off result also offers a realistic picture of neuromorphic computing with rank-order coding: Information rate and communication efficiency cannot be simultaneously maximized—a compromising trade-off between them needs to be made [Fig. 2(c)].

In the present Letter, we assumed that postsynaptic neurons respond selectively to a particular order of spikes (temporal pattern). Studies have shown that cortical neurons exhibit such selectivity to temporal input sequences [21]. Various biological mechanisms of temporal pattern detection have been proposed (e.g., Ref. [22]). A feed-forward shunting inhibition circuit, which progressively desensitizes a postsynaptic neuron as spikes arrive (see Fig. 1), may accomplish selectivity to a particular temporal pattern of rank-order coding [6,17]. In such a setting, a postsynaptic neuron would be maximally activated (and fire only) if spikes arrive in the order of its synaptic weights. A small portion of extremely strong synapses observed in log-normally distributed synaptic weights [23] may enhance this progressive desensitization. Moreover, a belief-voting decoder may provide a robust means for decoding the order of neural spikes [24].

To conclude, rank-order coding can provide speed and efficiency, but noise imposes a trade-off between them. The results of this Letter offer insight into the performance of rank-order coding.

*Acknowledgments*. The authors would like to thank B. Chockalingam and T. Burns for their suggestions and comments. We are grateful for the help and support provided by the Scientific Computing and Data Analysis section of the Research Support Division at OIST. T.F. acknowledges support from JSPS KAKENHI (Grants No. JP18H05213 and No. JP19H04994).

*Appendix: Atypical probabilities. Why do errors increase when we have less noise?* The emergence of atypical probabilities can be explained as follows. Let the probability $P(ACB|ABC)$ serve as an example [Fig. 3]. Moreover, let random variables $Z_i$ $(i = 1, 2, 3)$ represent a spike's latency after the perturbation of noise; here, $i$ denotes the index of the $i$th presynaptic neuron. These random variables are independent. For the event $Z_1 < Z_3 < Z_2$, or equivalently the sequence $ACB$, to occur, the following two conditions should be simultaneously satisfied: (i) Random variable $Z_2$ needs to be the largest value and (ii) random variable $Z_1$ needs to be the smallest value.

(i) The probability of $Z_2$ being the largest value (i.e., $Z_2 > Z_3$) decreases with $\lambda$ (the larger the value of $\lambda$, the less the noise) because the amount of overlap between the distributions of $Z_2$ and $Z_3$ decreases as $\lambda$ increases.

(ii) In contrast, the probability of $Z_1$ being the smallest value increases with $\lambda$ in the interval $(0, 2\alpha)$ for the following reason. The event $Z_2 > Z_3$ implies that $Z_2 > 2\alpha$ [Fig. 3(c) and Eq. (1)]. Thus, when $Z_2 > Z_3$, more space (from $\alpha$ to $2\alpha$) for $Z_1$ has been made to take the position of the smallest value in the interval $(0, 2\alpha)$, thereby increasing the likelihood of the neural order $ACB$ $(Z_1 < Z_3 < Z_2)$.

Factor (i) causes $P(ACB|ABC)$ to decrease, whereas factor (ii) causes $P(ACB|ABC)$ to increase. The net effect of factors (i) and (ii) is $P(Z_1 < 2\alpha < Z_3 < Z_2)$, which is a concave function. This component brings about a rare regime in which errors increase with $\lambda$ (or, equivalently, with $\alpha$). Mathematically, the probability $P(Z_1 < 2\alpha < Z_3 < Z_2)$ can be obtained by splitting the integration region of $P(ACB|ABC)$ into two parts:

$$
\begin{aligned}
P(ACB|ABC) &= P(Z_1 < Z_3 < Z_2|ABC) = \int_{2\alpha}^{\infty}\int_{2\alpha}^{z_2}\int_{0}^{z_3} f_1(z_1)f_3(z_3)f_2(z_2),\, dz_1\, dz_3\, dz_2 \\
&= \underbrace{\left(\int_{2\alpha}^{\infty}\int_{2\alpha}^{z_2}\int_{0}^{2\alpha} f_1(z_1)f_3(z_3)f_2(z_2),\, dz_1\, dz_3\, dz_2\right)}_{\text{Concave: } P(Z_1 < 2\alpha < Z_3 < Z_2)} + \underbrace{\left(\int_{2\alpha}^{\infty}\int_{2\alpha}^{z_2}\int_{2\alpha}^{z_3} f_1(z_1)f_3(z_3)f_2(z_2),\, dz_1\, dz_3\, dz_2\right)}_{\text{Convex: } P(2\alpha < Z_1 < Z_3 < Z_2)} \\
&= \underbrace{\left(\underbrace{\frac{1}{2}e^{-\lambda\alpha}}_{\text{Factor (i): } P(2\alpha < Z_3 < Z_2)} \times \underbrace{(1 - e^{-2\lambda\alpha})}_{\text{Factor (ii): } P(Z_1 < 2\alpha)}\right)}_{\text{Concave: } P(Z_1 < 2\alpha < Z_3 < Z_2) = P(Z_1 < 2\alpha) \times P(2\alpha < Z_3 < Z_2)} + \underbrace{\left(\frac{1}{6}e^{-3\lambda\alpha}\right)}_{\text{Convex: } P(2\alpha < Z_1 < Z_3 < Z_2)} \\
&= \frac{1}{2}e^{-\lambda\alpha} - \frac{1}{3}e^{-3\lambda\alpha}. \qquad \text{(A1)}
\end{aligned}
$$

[1] D. Marković, A. Mizrahi, D. Querlioz, and J. Grollier, Physics for neuromorphic computing, Nat. Rev. Phys. **2**, 499 (2020).

[2] G. V. Vinci, R. Benzi, and M. Mattia, Self-consistent stochastic dynamics for finite-size networks of spiking neurons, Phys. Rev. Lett. **130**, 097402 (2023).

[3] R. VanRullen, R. Guyonneau, and S. J. Thorpe, Spike times make sense, Trends Neurosci. **28**, 1 (2005).

[4] S. Thorpe, A. Delorme, and R. Van Rullen, Spike-based strategies for rapid processing, Neural Networks **14**, 715 (2001).

[5] S. J. Thorpe and M. Imbert, Biological constraints on connectionist modelling, in *Connectionism in Perspective*, edited by R. Pfeifer, Z. Schreter, and F. Fogelman-Soulié (Elsevier, Amsterdam, 1989), pp. 63–92.

[6] L. Bonilla, J. Gautrais, S. Thorpe, and T. Masquelier, Analyzing time-to-first-spike coding schemes, Front. Neurosci. **16**, 971937 (2022).

[7] T. Gollisch and M. Meister, Rapid neural coding in the retina with relative spike latencies, Science **319**, 1108 (2008).

[8] G. Portelli, J. M. Barrett, G. Hilgen, T. Masquelier, A. Maccione, S. Di Marco, L. Berdondini, P. Kornprobst, and E. Sernagor, Rank order coding: a retinal information decoding strategy revealed by large-scale multielectrode array retinal recordings, eNeuro **3**, ENEURO.0134-15.2016 (2016).

[9] S. Junek, E. Kludt, F. Wolf, and D. Schild, Olfactory coding with patterns of response latencies, Neuron **67**, 872 (2010).

[10] A. Riehle, S. Grun, M. Diesmann, and A. Aertsen, Spike synchronization and rate modulation differentially involved in motor cortical function, Science **278**, 1950 (1997).

[11] E. Lemaire, L. Cordone, A. Castagnetti, P.-E. Novac, J. Courtois, and B. Miramond, An analytical estimation of spiking neural networks energy efficiency, in *International Conference on Neural Information Processing* (Springer, Berlin, 2022), pp. 574–587.

[12] S. R. Kheradpisheh, M. Ganjtabesh, S. J. Thorpe, and T. Masquelier, STDP-based spiking deep convolutional neural networks for object recognition, Neural Networks **99**, 56 (2018).

[13] Y. Yan, H. Chu, X. Chen, Y. Jin, Y. Huan, L. Zheng, and Z. Zou, Graph-based spatio-temporal backpropagation for training spiking neural networks, in *2021 IEEE 3rd International Conference on Artificial Intelligence Circuits and Systems (AICAS)* (IEEE, New York, 2021), pp. 1–4.

[14] C. Frenkel, M. Lefebvre, J.-D. Legat, and D. Bol, A 0.086-mm$^2$ 12.7-pJ/SOP 64k-synapse 256-neuron online-learning digital spiking neuromorphic processor in 28-nm CMOS, IEEE Trans. Biomed. Circuits Syst. **13**, 145 (2018).

[15] C. Frenkel, J.-D. Legat, and D. Bol, MorphIC: A 65-nm 738k-synapse/mm$^2$ quad-core binary-weight digital neuromorphic processor with stochastic spike-driven online learning, IEEE Trans. Biomed. Circuits Syst. **13**, 999 (2019).

[16] Y. Wu, R. Zhao, J. Zhu, F. Chen, M. Xu, G. Li, S. Song, L. Deng, G. Wang, H. Zheng *et al.*, Brain-inspired global-local learning incorporated with neuromorphic computing, Nat. Commun. **13**, 65 (2022).

[17] S. Thorpe and J. Gautrais, Rank order coding, in *Computational Neuroscience: Trends in Research, 1998* (Springer, Berlin, 1998), pp. 113–118.

[18] C. E. Shannon, A mathematical theory of communication, Bell Syst. Tech. J. **27**, 379 (1948).

[19] T. Cover and J. Thomas, *Elements of Information Theory* (Wiley, Hoboken, NJ, 2012).

[20] See Supplemental Material at http://link.aps.org/supplemental/10.1103/PhysRevResearch.6.L012009 for derivation of equations and simulation results.

[21] T. Branco, B. A. Clark, and M. Häusser, Dendritic discrimination of temporal input sequences in cortical neurons, Science **329**, 1671 (2010).

[22] R. Gütig and H. Sompolinsky, The tempotron: a neuron that learns spike timing-based decisions, Nat. Neurosci. **9**, 420 (2006).

[23] G. Buzsáki and K. Mizuseki, The log-dynamic brain: how skewed distributions affect network operations, Nat. Rev. Neurosci. **15**, 264 (2014).

[24] A. Pitti, C. Weidmann, and M. Quoy, Digital computing through randomness and order in neural networks, Proc. Natl. Acad. Sci. USA **119**, e2115335119 (2022).