

## Quantification of information processing capacity in living brain as physical reservoir

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### Abstract

The information processing capacity (IPC) measure is gaining traction as a means of characterizing reservoir computing. This measure offers a comprehensive assessment of a dynamical system's linear and non-linear memory of past inputs by breaking down the system states into orthogonal polynomial bases of input series. In this study, we demonstrate that IPCs are experimentally measurable in the auditory cortex in response to a random sequence of clicks. In our experiment, each input series had a constant inter-step interval (ISI), and a click was delivered with a 50% probability at each time step. Click-evoked multi-unit activities in the auditory cortex were used as the state variables. We found that the total IPC was dependent on the test ISI and reached a maximum at around 10- and 18-ms ISI. This suggests that the IPC reaches a peak when the stimulus dynamics and intrinsic dynamics in the brain are matched. Moreover, we found that the auditory cortex exhibited non-linear mapping of past inputs up to the 6<sup>th</sup> degree. This finding indicates that IPCs can predict the performance of a physical reservoir when benchmark tasks are decomposed into orthogonal polynomials. Thus, IPCs can be useful in measuring how the living brain functions as a reservoir. These achievements have opened up future avenues for bridging the gap between theoretical and experimental studies of neural representation. By providing a means of quantifying a dynamical system's memory of past inputs, IPCs offer a powerful tool for understanding the inner workings of the brain.

### Main Text

The brain is commonly regarded as a high-dimensional dynamical system that processes inputs, resulting in a diverse range of spatio-temporal activities driven by external stimuli. Mathematically, such systems are modeled as recurrent neural networks, with the recent development of reservoir computing (1-3). Traditional training of recurrent neural networks adjusts all the weights in the network to obtain target outputs based on inputs, whereas reservoir computing optimizes only the linear outputs of state variables from a fixed system. Therefore, the performance of reservoir computing is determined by a physical system with intrinsic non-linear dynamics, or a physical reservoir (4, 5). Previous studies have demonstrated that the living neuronal system is likely to have a fading memory property (2, 6-9) and an echo-state property (10-12), which are considered prerequisite for a physical reservoir. As a result, recent studies have modeled and interpreted physiological findings in the brain as a reservoir (7, 13-19).

The performance of a reservoir has traditionally been evaluated using benchmark tasks (4) such as memory capacity (20), time-delayed logic operation (21), pattern classification (22, 23), and time series forecasting (1, 24). However, these

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measures are task-specific and cannot predict whether and how a given reservoir can be used in other tasks. An emerging measure called information processing capacity (IPC) offers a comprehensive quantification of a dynamical system's linear and non-linear memory of past inputs. IPC achieves this by decomposing the system states into orthogonal polynomial bases of the input series (25). This measure predicts the system's performance in a given task, with the computation represented by the orthogonal polynomial bases. For example, IPC was used to demonstrate that only 9 specific bases were required to perform a time series forecasting of the nonlinear autoregressive moving average of 10 time series (NARMA10), a typical benchmark task (26). Thus, IPC is a powerful tool for characterizing physical reservoirs both theoretically (26-28) and empirically (26, 29). These pioneering works have opened up avenues for using IPC to quantitatively characterize the living brain as a physical reservoir. By providing a more comprehensive assessment of a dynamical system's memory of past inputs, IPC offers a powerful tool for understanding the inner workings of the brain and how it can be utilized for various tasks.

The present study aims to demonstrate the experimental measurability of IPCs in the living brain. Using click-evoked activities in the auditory cortex of rats, we show that IPCs can reveal both linear and non-linear mappings of past inputs and predict performance in benchmark tasks for physical reservoir computing.

To conduct this study, we measured auditory-evoked multi-unit activities (MUAs) in layer 4 of the right auditory cortex of anesthetized rats. We used a microelectrode array with a grid of 10 x 10 probes in a 4 x 4-mm<sup>2</sup> recording area (ICS-96 Array; Blackrock Microsystems Inc., USA). We utilized 15 male Wistar rats at postnatal weeks 9-13, weighing between 260-450 g in the experiments (Tokyo Laboratory Animals Science Co., Ltd., Japan). The protocol was approved by the Committee on the Ethics of Animal Experiments at the Graduate School of Information Science and Technology, the University of Tokyo (Permit Number: JA19-2) and adhered to previously published procedures (30). We anesthetized the rats with urethane (1.0-1.5 g/kg, i.p.) and immobilized them in a custom head-holding device, minimizing discomfort. We surgically exposed the auditory cortex to place the microelectrode array. At the conclusion of the experiments, we euthanized the rats with an overdose of pentobarbital sodium (160 mg/kg, i.p.).

We delivered test stimuli through a free-field speaker (EAS-10TH800; Panasonic Corp., Japan), placed 15 cm from the left pinna, contralateral to the exposed cortex. Using tone bursts with 5-ms rise/fall ramps, 30-ms duration, frequencies ranging between 1.6-64 kHz, and intensities between 20-80 dB SPL (sound pressure level), we defined the auditory cortex as being tone-responsive, with a post-stimulus latency of 5-55 ms, and having a distinct frequency tuning. On average,  $60.6 \pm 12.8$  (mean  $\pm$  s.d.) recording sites were included in the auditory cortex ( $n = 15$ ), and these sites were used to derive IPCs in the auditory cortex.

To estimate IPC in the auditory cortex, we utilized a series of clicks that followed the Bernoulli distribution, with a constant inter-step interval (ISI) of 7, 10, 18, 32, 56, 100, 178, or 316 ms. At each time step, a click was delivered with a probability of 50%. To ensure accuracy, each ISI condition was tested over a sufficiently long period of 10,000-30,000 time steps. IPC was quantified using the method described in our previous work (26). In brief, we denoted the input at the  $n^{\text{th}}$  time step as

$u_n$  ( $1 \leq n \leq N$ ), and the input series was described as follows:

$$u_n = \begin{cases} 1 & (\text{Click}) \\ -1 & (\text{No Click}) \end{cases}, \mathbf{u} = (u_1, \dots, u_N)^T \in \{-1, 1\}^N.$$

Let the internal state variable at the  $i^{\text{th}}$  recording site at the  $n^{\text{th}}$  time step be  $x_{n,i}$ , the internal state vector  $\mathbf{x}_i$  and matrix  $X$  are described as

$$\begin{aligned} \mathbf{x}_i &= (x_{1,i}, \dots, x_{N,i})^T \in R_{N \times 1}, \\ X &= (\mathbf{x}_1, \dots, \mathbf{x}_L) \in R_{N \times L}, \end{aligned}$$

where  $L$  is the number of recording sites. For the target output  $\mathbf{z} = (z_1, \dots, z_N)^T \in R_{N \times 1}$ ,  $\text{IPC}(X, \mathbf{z})$  ( $0 \leq \text{IPC}(X, \mathbf{z}) \leq 1$ ) is defined below:

$$\text{IPC}(X, \mathbf{z}) = 1 - \frac{\min_w \sum_1^N (z_n - \hat{z}_n)^2}{\sum_1^N z_n^2} = \frac{\mathbf{z}^T X X^+ \mathbf{z}}{\mathbf{z}^T \mathbf{z}},$$

where  $\hat{z}_n = \sum_{n=1}^N \mathbf{w}^T \mathbf{x}_n$  and  $X^+ \in R_{L \times N}$  represents the Moore-Penrose inverse of  $X$ . The target outputs were constructed using arbitrary polynomial chaos expansion, which constitutes a complete orthogonal system with input series of random variables with any probability distribution through the application of the Gram-Schmidt orthogonalization procedure. Specifically, in the case of an input series  $\mathbf{u} \in \{-1, 1\}^N$  following the Bernoulli distribution, the target outputs were defined as follows:

$$z_{s_d, n} = \prod_{s \in S_d} u_{n-s} \text{ for } s_d \in S_d,$$

where  $d$  denotes the degree of the polynomial,  $s$  denotes the delay step of input, and  $S_d$  represents a set of entire combinations of  $s$  at degree  $d$ . In theory, the IPCs quantified comprehensively reveal both linear and non-linear mappings of past inputs in dynamical systems. However, due to the limitations of computation time, we were only able to quantify the 1<sup>st</sup> degree IPCs within 30 steps and the 2<sup>nd</sup> – 7<sup>th</sup> degree IPCs within 10 steps in the present study.

To construct the internal state matrix  $X$ , we used a raster plot of click-evoked MUA in the auditory cortex during the presentation of input series of clicks (Fig. 1a). As the post-stimulus latency of MUA ranged from <10 ms to 300 ms, we defined a time window to select spikes included in the internal state variable  $\mathbf{x}_i$  (Fig. 1b). The optimal onset ( $t_s$ ) and length ( $d$ ) of the time window were determined by maximizing the 1st degree IPC (Supplementary Fig. 1), with  $t_s$  ranging from 0 to 80 ms (at  $t_s=0, 7, 10, 20, 40,$  and  $80$  ms) and  $d$  ranging from 7 to 320 ms (at  $d=7, 10, 20, 40, 80, 160,$  and  $320$  ms). The optimal  $t_s$  was typically 0 ms, and  $d$  increased with the ISI, with a value of 40 ms at 7-, 10-, and 18-ms ISI. Using the number of spikes within the optimized window at each time step, we obtained the internal state variable  $x_{n,i}$  at each recording site (Fig. 1c).

Figure 2a depicts the decay of the 1<sup>st</sup> degree IPC from 1 to 30 time steps of each ISI, which indicates that the auditory cortex can be considered a reservoir with a fading memory typically of 10-15 time steps. Figure 2b shows the 2<sup>nd</sup> degree IPC for  $(s_1, s_2) \in S_2$  of 1-10 steps for each ISI, indicating that the auditory cortex exhibits non-linear mapping of past inputs

in addition to the fading memory. Furthermore, Fig. 2c shows the breakdown of IPC at each degree, indicating that the auditory cortex exhibits non-linear mapping of past inputs up to the 6<sup>th</sup> degree. The total IPC, shown in Fig. 2d, was found to be dependent on the ISI of the input series (Kruskal-Wallis test,  $p = 0.0014$ ), and was maximized around ISIs of 10 and 18 ms, indicating that IPC is maximized when stimulus dynamics and intrinsic dynamics in the brain are matched.

We then tested several benchmark tasks for reservoir computing by using half of  $X$  as training data and the remaining half as test data. In the shift register (SR) task, linear support vector classifiers with stochastic gradient descent learning and L2 penalty were constructed for training data  $\mathbf{x}_n = (x_{1,n}, \dots, x_{L,n}) \in R_L$  with class labels  $u_{n-s}$ . For the output of test data  $\hat{z}_n$  and the correct class label  $z_n$ , the classification accuracy was defined as:

$$ACC = \frac{1}{N} \sum_{n=1}^N (1 - |z_n - \hat{z}_n|),$$

was utilized to quantify the performance of the SR task. The results showed that the ACCs were higher than the chance level for time steps ranging from 5 to 15 (Fig. 3a), suggesting that the cortical activity retained linear memory of past inputs for a certain range of time steps. To perform logic operation tasks, we constructed linear regressors using  $\mathbf{x}_n = (x_{1,n}, \dots, x_{L,n}) \in R_L$  as predictors and the logic operation (either AND, OR, or XOR) of  $u_{n-s_1}$  and  $u_{n-s_2}$  (i.e.,  $z_n = F(u_{n-s_1}, u_{n-s_2})$ ) as responses. For the output of the test data  $\hat{z}_n$  and the correct class label  $z_n$ , we calculated the normalized root mean squared errors, which are defined as:

$$NRMSE = \frac{1}{\sigma(z)} \sqrt{\frac{1}{N} \sum_{n=1}^N (z_n - \hat{z}_n)^2},$$

were derived for the original and surrogate data, and the difference

$$\Delta NRMSE = NRMSE_{surrogate} - NRMSE_{original}$$

was used to quantify the task performance.  $NRMSE_{surrogate}$  was  $z_n$  of randomized  $u_n$ . We found that, for some pairs of  $s_1$  and  $s_2$ ,  $\Delta NRMSE$  was positive, indicating that the auditory cortex had IPC for these time-delay logical operations.

Finally, we investigated the relationship between IPC and benchmark task performances (Table 1). To this end, we performed regression analyses using the 1<sup>st</sup> degree IPC as a predictor for each ISI, subject, and delay  $s$ , and the task performance (ACC or  $\Delta NRMSE$ ) as the response. For the SR task, which is nearly identical to the 1<sup>st</sup> degree IPC, the performance was highly explained by the IPC. For the logic operation tasks, we used multiple regression analyses with both the 1<sup>st</sup> and 2<sup>nd</sup> degree IPCs as predictors for each ISI, subject, and combination of  $(s_1, s_2)$ . We found that the AND and OR task performances were significantly explained by the 1<sup>st</sup> degree IPC of  $s_1$  and  $s_2$ , as well as the 2<sup>nd</sup> degree IPC of  $(s_1, s_2) \in \mathcal{S}_2$ , whereas the XOR performance was significantly explained only by the 2<sup>nd</sup> degree IPC of  $(s_1, s_2) \in \mathcal{S}_2$ . These results are consistent with the notion that the logic operation tasks can be broken down into polynomial representations, as described in Table 2, and suggest that both the 1<sup>st</sup> and 2<sup>nd</sup> degree IPCs are required for the AND and OR tasks, but only the 2<sup>nd</sup> degree IPC is required for the XOR task. In summary, our results indicate that IPCs can predict benchmark task performance by decomposing the task into orthogonal polynomials, and thus are a valuable tool for quantifying the living neuronal system as a reservoir.

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Our study demonstrated that IPC can be quantified in the living brain, and we observed that its magnitude depended on the inter-stimulus interval (ISI), peaking at around 10- and 18-ms ISI. This range of ISIs corresponds to the time window of gamma oscillations (30-90 Hz) in the cortex, which play a critical role in stimulus encoding (31, 32). Interestingly, we observed that IPC abruptly decreased at 7-ms ISI, possibly because the auditory cortex employs a rate coding strategy to encode rapid click sequences instead of click-synchronized coding at larger ISIs (33, 34). In this case, the state variables used in our study were not consistent with the encoding strategy in the auditory cortex, which could explain the drop in IPC. These findings suggest that IPC is closely linked to neural representation observed in physiological experiments, and that its measurement could be a useful tool for studying cortical dynamics. Future studies could investigate the relationship between IPC and other features of auditory processing, such as learning-induced plasticity or cognitive performance.

Although we discovered a noteworthy amount of IPC in the auditory cortex, it was significantly smaller than those identified in previous theoretical studies (26-28). There are several possible factors that could explain this discrepancy. First, non-auditory neural activities could substantially decrease the IPC measured here. In a dynamic system with multiple input series, the IPC to each input is determined by the rank of the state variable matrix  $X$  (25, 26). For instance, spontaneous activities, which serve as non-auditory inputs (35-37) may have a significant impact on IPC quantification. Second, anesthetics can induce correlated neural activity and lead to the degeneracy of the rank of  $X$  (38). Third, anesthetics could also alter neural dynamics and impair our ability to derive IPC. For instance, the anesthetized state is typically characterized by burst activities (39, 40), which erase past memory in the neuronal network (9, 41). Although we used urethane as an anesthetic during neural measurements to avoid bursts, it still causes transitions between upstate and downstate (42-45), that are not accounted for in IPC estimation. Fourth, our recordings were made from a limited part of the auditory system, and thus may have overlooked a significant amount of IPC in the brain. Lastly, the state variables we selected may not be optimal for estimating IPC in response to random click sequences. We showed that IPC depends critically on the definition of state variables (Supplementary Fig. 1). Moreover, the click sequence may not be fully encoded in the state variables defined here; in addition to the number of spikes within a test time window, the brain could encode stimuli in other activity features such as post-stimulus latency, inter-spike intervals, and temporal changes in firing rates (within the time window we used in the present work), etc. (33, 34, 46, 47). Addressing these issues is critical for establishing a reliable IPC estimation in the living brain.

In summary, our study demonstrated that the brain can be characterized as a physical reservoir with a measurable IPC. This finding provides future opportunities to bridge the gap between theoretical and experimental studies in neuroscience. Specifically, we are interested in investigating the relationship between learning-induced plasticity in the brain and changes in IPC, as well as exploring potential correlations between IPC and cognitive performance. These avenues of research could lead to a deeper understanding of the neural mechanisms underlying cognitive processes and potentially inform the development of future therapeutic interventions.

### Figures

Figure 1 Definition of of reservoir state variables. (a) Multi-unit activities (MUAs) in the auditory cortex in response to a click sequence with ISI of 100 ms. Clicks are delivered at red lines. (b) Time stamps of spikes (dots) at each time step in a representative recording site (#46). (c) State variables at each time step ( $n$ ) in a representative recording site (#46), i.e.,  $X_{n,46}$ . The number of spikes within a time window with length  $d$  were derived as a state variable.

Figure 2 IPC estimates in the auditory cortex as a function of ISI. (a) The 1<sup>st</sup> degree IPC calculated for four different ISI of 7, 18, 56, and 178 ms, presented with mean and s.d. and are given. (b) The 2<sup>nd</sup> degree IPC for ISI of 7, 18, 56, and 178 ms. (c) Breakdown of IPC. IPC at each degree was averaged and stacked in a bar. (d) Total IPC. Each dot indicates data from a different rat. On each box, the central mark is the median, the edges of the box are the 25th and 75th percentiles. The whiskers extend to the most extreme data points not considered outliers, which are larger than 75th percentiles or smaller than 25th percentiles by 1.5 times inter-quartile range from the box.

Figure 3 Benchmark tasks. (a) Shift register task. The mean and s.d. of ACC for  $u_{t,s}$  are given. Task performances for ISI of 7, 18, 56, and 178 ms are shown in each column. (b) Logic operation.  $ANRMSE$  of AND (upper), OR (middle) and XOR tasks (lower) with inputs  $u_{t-s_1}$  and  $u_{t-s_2}$  are shown in color.

### Tables

Table 1 Regression analyses of benchmark tasks.

Task	IPC	Coef	$p$	$R_{adj}^2$
SR	$IPC(s)$	0.944	$p < 10^{-40}$	0.890
AND	$IPC(s_1)$	0.517	$p < 10^{-40}$	0.847
	$IPC(s_2)$	0.390	$p < 10^{-40}$	
	$IPC(s_1, s_2)$	0.201	$p < 10^{-40}$	
OR	$IPC(s_1)$	0.269	$p < 10^{-40}$	0.788
	$IPC(s_2)$	0.338	$p < 10^{-40}$	
	$IPC(s_1, s_2)$	0.435	$p < 10^{-40}$	
XOR	$IPC(s_1)$	-0.0192	-	0.930
	$IPC(s_2)$	-0.0026	-	
	$IPC(s_1, s_2)$	0.974	$p < 10^{-40}$	

Coef, regression coefficient;  $p$ , statistical significance of regression coefficient;  $R_{adj}^2$ , adjusted coefficient of determination.

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Table 2 Polynomial representation of logic operation tasks.

$x$	$y$	$AND(x, y)$	$OR(x, y)$	$XOR(x, y)$
1	1	1	1	-1
1	-1	-1	1	1
-1	1	-1	1	1
-1	-1	-1	-1	-1
$u_1$	$u_2$	$(u_1 + u_2 + u_1 u_2 - 1) / 2$	$(u_1 + u_2 - u_1 u_2 + 1) / 2$	$-u_1 u_2$

### Supplementary Material

Supplementary Figure 1 The 1<sup>st</sup> degree IPC as a function of time window ( $t_s$ , and  $d$ ). Asterisks indicate the maximum for a given ISI.

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### Conflict of interest

The authors have no conflicts to disclose.

### Ethics approval

The experimental protocol was approved by the Committee on the Ethics of Animal Experiments at the Graduate School of Information Science and Technology, the University of Tokyo (Permit Number: JA19-2).

### Author Contributions

NI: formal analysis, investigation, software, visualization, writing-original draft

TIS: formal analysis, funding acquisition, methodology

TK: conceptualization, methodology, software

DA: validation, writing-review & editing

HT: conceptualization, funding acquisition, project administration, supervision, writing-review & editing

### Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

### References

1. H. Jaeger, H. Haas, Harnessing nonlinearity: Predicting chaotic systems and saving energy in wireless communication. *Science* **304**, 78-80 (2004).

This is the author's peer reviewed, accepted manuscript. However, the online version of record will be different from this version once it has been copyedited and typeset.

PLEASE CITE THIS ARTICLE AS DOI: 10.1063/5.0152585

2. W. Maass, T. Natschläger, H. Markram, Real-time computing without stable states: a new framework for neural computation based on perturbations. *Neural Comput* **14**, 2531-2560 (2002).
3. D. Verstraeten, B. Schrauwen, M. D'Haene, D. Stroobandt, An experimental unification of reservoir computing methods. *Neural Networks* **20**, 391-403 (2007).
4. G. Tanaka, T. Yamane, J. B. Héroux *et al.*, Recent advances in physical reservoir computing: A review. *Neural Networks* **115**, 100-123 (2019).
5. K. Nakajima, Physical reservoir computing - an introductory perspective. *Jpn J Appl Phys* **59**, 060501 (2020).
6. W. Maass, H. Markram, On the computational power of circuits of spiking neurons. *Journal of Computer and System Sciences* **69**, 593-616 (2004).
7. D. Nikolic, S. Hausler, W. Singer, W. Maass, Distributed fading memory for stimulus properties in the primary visual cortex. *Plos Biol* **7**, e1000260 (2009).
8. S. Klampfl, S. V. David, P. B. Yin, S. A. Shamma, W. Maass, A quantitative analysis of information about past and present stimuli encoded by spikes of A1 neurons. *Journal of neurophysiology* **108**, 1366-1380 (2012).
9. M. R. Dranias, H. Ju, E. Rajaram, A. M. J. VanDongen, Short-Term Memory in Networks of Dissociated Cortical Neurons. *The Journal of Neuroscience* **33**, 1940-1953 (2013).
10. G. Manjunath, H. Jaeger, Echo State Property Linked to an Input: Exploring a Fundamental Characteristic of Recurrent Neural Networks. *Neural Comput* **25**, 671-696 (2013).
11. Z. Mainen, T. Sejnowski, Reliability of spike timing in neocortical neurons. *Science* **268**, 1503-1506 (1995).
12. T. Kubota, K. Nakajima, H. Takahashi, Echo State Property of Neuronal Cell Cultures. *Lecture Notes in Computer Science* **11731**, 137-148 (2019).
13. D. V. Buonomano, W. Maass, State-dependent computations: spatiotemporal processing in cortical networks. *Nat Rev Neurosci* **10**, 113-125 (2009).
14. V. Mante, D. Sussillo, K. V. Shenoy, W. T. Newsome, Context-dependent computation by recurrent dynamics in prefrontal cortex. *Nature* **503**, 78-84 (2013).
15. A. Goel, D. V. Buonomano, Temporal Interval Learning in Cortical Cultures Is Encoded in Intrinsic Network Dynamics. *Neuron* **91**, 320-327 (2016).
16. P. Enel, E. Procyk, R. Quilodran, P. F. Dominey, Reservoir Computing Properties of Neural Dynamics in Prefrontal Cortex. *Plos Comput Biol* **12** (2016).
17. E. D. Remington, D. Narain, E. A. Hosseini, M. Jazayeri, Flexible Sensorimotor Computations through Rapid Reconfiguration of Cortical Dynamics. *Neuron* **98**, 1005-1019.e1005 (2018).
18. Y. Yada, R. Kanzaki, H. Takahashi, State-dependent propagation of neuronal sub-population in spontaneous synchronized bursts. *Frontiers in systems neuroscience* **10**, Art 28 (2016).
19. Y. Yada, S. Yasuda, H. Takahashi, Physical reservoir computing with FORCE learning in a living neuronal culture. *Applied Physics Letters* **119**, 173701 (2021).



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PLEASE CITE THIS ARTICLE AS DOI: 10.1063/5.0152585

20. H. Jaeger, Short term memory in echo state networks. *Technical Report GMD Report 152, German National Research Center for Information Technology* (2001).
21. N. Bertschinger, T. Natschläger, Real-time computation at the edge of chaos in recurrent neural networks. *Neural Comput* **16**, 1413-1436 (2004).
22. D. Verstraeten, B. Schrauwen, D. Stroobandt, J. Van Campenhout, Isolated word recognition with the liquid state machine: a case study. *Information Processing Letters* **95**, 521-528 (2005).
23. Y. Paquot, F. Duport, A. Smerieri *et al.*, Optoelectronic Reservoir Computing. *Sci Rep-Uk* **2**, 287 (2012).
24. H. Jaeger, Adaptive nonlinear system identification with echo state networks. *Advances in neural information processing systems* **15** (2002).
25. J. Dambre, D. Verstraeten, B. Schrauwen, S. Massar, Information Processing Capacity of Dynamical Systems. *Sci Rep-Uk* **2** (2012).
26. T. Kubota, H. Takahashi, K. Nakajima, Unifying framework for information processing in stochastically driven dynamical systems. *Physical Review Research* **3**, 043135 (2021).
27. R. Martínez-Peña, J. Nokkala, G. L. Giorgi, R. Zambrini, M. C. Soriano, Information Processing Capacity of Spin-Based Quantum Reservoir Computing Systems. *Cogn Comput* (2020).
28. N. Akashi, T. Yamaguchi, S. Tsunegi *et al.*, Input-driven bifurcations and information processing capacity in spintronics reservoirs. *Physical Review Research* **2**, 043303 (2020).
29. R. Sakurai, M. Nishida, T. Jo, Y. Wakao, K. Nakajima, Durable Pneumatic Artificial Muscles with Electric Conductivity for Reliable Physical Reservoir Computing. *Journal of Robotics and Mechatronics* **34**, 240-248 (2022).
30. Y. Ito, T. I. Shiramatsu, N. Ishida *et al.*, Spontaneous beat synchronization in rats: Neural dynamics and motor entrainment. *Science Advances* **8**, eabo7019 (2022).
31. P. Fries, D. Nikolić, W. Singer, The gamma cycle. *Trends Neurosci* **30**, 309-316 (2007).
32. G. Buzsáki, X. J. Wang, Mechanisms of Gamma Oscillations. *Annual Review of Neuroscience, Vol 35* **35**, 203-225 (2012).
33. T. Lu, X. Wang, Temporal discharge patterns evoked by rapid sequences of wide- and narrowband clicks in the primary auditory cortex of cat. *Journal of neurophysiology* **84**, 236-246 (2000).
34. T. Lu, L. Liang, X. Wang, Temporal and rate representations of time-varying signals in the auditory cortex of awake primates. *Nat Neurosci* **4**, 1131-1138 (2001).
35. A. Arieli, A. Sterkin, A. Grinvald, A. Aertsen, Dynamics of Ongoing Activity: Explanation of the Large Variability in Evoked Cortical Responses. *Science* **273**, 1868-1871 (1996).
36. A. A. Faisal, L. P. J. Selen, D. M. Wolpert, Noise in the nervous system. *Nat Rev Neurosci* **9**, 292-303 (2008).
37. A. Luczak, P. Bartho, K. D. Harris, Spontaneous events outline the realm of possible sensory responses in neocortical populations. *Neuron* **62**, 413-425 (2009).
38. T. Noda, H. Takahashi, Anesthetic effects of isoflurane on the tonotopic map and neuronal population activity in the rat auditory cortex. *Eur J Neurosci* **42**, 2298-2311 (2015).

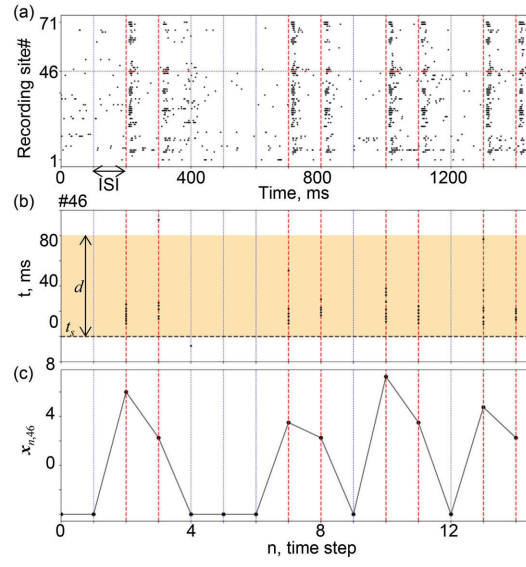
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39. M. Steriade, F. Amzica, D. Contreras, Cortical and Thalamic Cellular Correlates of Electroencephalographic Burst-Suppression. *Electroencephalography and clinical neurophysiology* **90**, 1-16 (1994).
40. M. Steriade, Impact of network activities on neuronal properties in corticothalamic systems. *Journal of neurophysiology* **86**, 1-39 (2001).
41. H. Ju, M. R. Dranias, G. Banumurthy, A. M. J. VanDongen, Spatiotemporal Memory Is an Intrinsic Property of Networks of Dissociated Cortical Neurons. *The Journal of Neuroscience* **35**, 4040-4051 (2015).
42. C. Curto, S. Sakata, S. Marguet, V. Itskov, K. D. Harris, A simple model of cortical dynamics explains variability and state dependence of sensory responses in urethane-anesthetized auditory cortex. *J Neurosci* **29**, 10600-10612 (2009).
43. S. L. Marguet, K. D. Harris, State-dependent representation of amplitude-modulated noise stimuli in rat auditory cortex. *J Neurosci* **31**, 6414-6420 (2011).
44. M. Okun, P. Yger, S. L. Marguet *et al.*, Population Rate Dynamics and Multineuron Firing Patterns in Sensory Cortex. *J Neurosci* **32**, 17108-17119 (2012).
45. E. J. B. Contreras, A. G. P. Schjetnan, A. Muhammad *et al.*, Formation and Reverberation of Sequential Neural Activity Patterns Evoked by Sensory Stimulation Are Enhanced during Cortical Desynchronization. *Neuron* **79**, 555-566 (2013).
46. X. Wang, Neural coding strategies in auditory cortex. *Hear Res* **229**, 81-93 (2007).
47. K. Imaizumi, N. J. Priebe, T. O. Sharpee, S. W. Cheung, C. E. Schreiner, Encoding of temporal information by timing, rate, and place in cat auditory cortex. *Plos One* **5**, e11531 (2010).

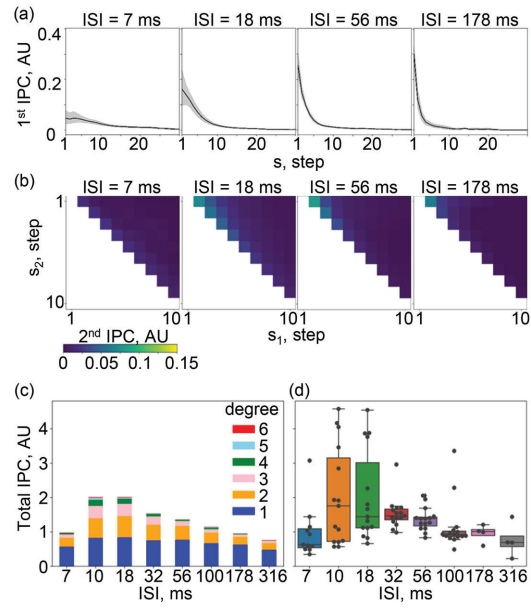
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