

Data-driven inference of coupling functions in oscillatory systems via physics-informed neural networks

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Coupling of oscillators is a universal phenomenon observed across diverse fields, from power grids in engineering to neuronal oscillators and circadian rhythms in biology. Understanding their dynamics requires identifying how individual oscillators interact. Traditionally, inferring the coupling mechanism from observable time series data involves estimating the coupling function—describing the interaction mechanism—using pre-assigned basis functions such as trigonometric polynomials. However, this approach is limited by the lack of a definitive rule for selecting the optimal number of basis functions, relying instead on subjective user choices. Here, we found that no single optimal number of basis functions exists: While using more basis functions helps capture complex coupling mechanisms, it tends to overfit and degrade performance with sparse or noisy data. To overcome these limitations, we developed Inference of Coupling using physics-informed neural networks (IC-PINN). Unlike conventional approaches, IC-PINN can infer diverse coupling functions from sparse and noisy data without requiring manual tuning, making it broadly applicable to various real-world systems of coupled oscillators. IC-PINN successfully identified that the segmentation clock operates via a “Winner-Take-All” synchronization mechanism and accurately inferred the coupling function in the self-assembly of optically interacting nanorotors. By offering a powerful tool for studying coupled oscillators, IC-PINN can provide deeper insights into complex interacting systems across biology, physics, and beyond.

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I. INTRODUCTION

The collective behavior of coupled oscillators is ubiquitous in biology, physics, and engineering [1–3]. In the suprachiasmatic nucleus (SCN), circadian rhythms are synchronized through coupling via vasoactive intestinal peptide [Fig. 1(a)] [4]. The segmentation clock generates synchronized rhythms of presomitic mesoderm (PSM) cells via Notch signaling during vertebrate embryonic development [Fig. 1(b)] [5]. Precise synchronization within the segmentation clock ensures the proper timing and formation of segmented body structures such as vertebrae and ribs. In photonics, quantum dot micro-lasers as optical oscillators exhibit striking differences from their classical counterparts due to the impact of enhanced spontaneous emission noise [6,7]. In a power system, the dynamical behavior of voltage is modeled as a system of coupled oscillators, with the stability and synchronization of the grid being essential for reliable operation [8,9].

These diverse systems of coupled oscillators can be represented via a network, where oscillators are modeled as nodes and their interactions as edges. For instance, macroscopic chimeralike states can emerge in multilayer multiplex networks [10]. Thus, understanding these mechanisms depends critically on knowledge of the underlying network structure. Equivalently, reliable network representations are essential for faithfully encoding such mechanisms.

To uncover the interaction mechanism, network inference (or reconstruction) is typically carried out using two representative approaches: model-free methods, which directly exploit observed data, and model-based methods, which incorporate explicit dynamical models. A representative example of model-free network inference is causality detection. A range of model-free techniques, including Granger causality (GC) [11] and convergent cross mapping [12], have been extensively employed to infer causal relationships from time series data. A variant of GC [13] has been recently introduced to infer networks of various systems, including the Kuramoto network. Although model-free methods are convenient and widely applicable, they fail to capture complex dynamics, such as distinguishing between direct and indirect causation [14].

To capture such complex dynamics, model-based network inference provides a high level of accuracy, despite its computational cost. When the specific model is chosen, network inference is reduced to the problem of estimating the

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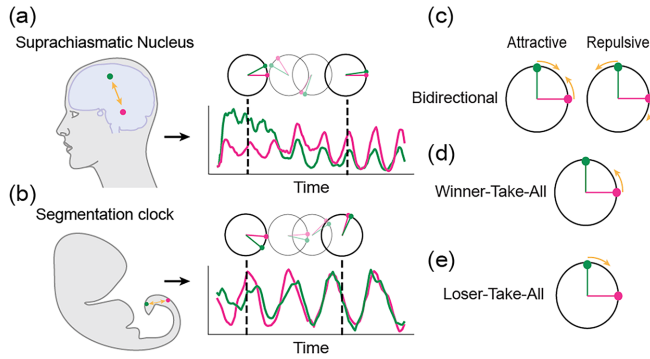


FIG. 1. Coupling of oscillators is a universal phenomenon. When coupling is activated, oscillators begin to synchronize their frequencies or phases [e.g., in panel (a) the suprachiasmatic nucleus and in panel (b) the segmentation clock]. (c)–(e) The coupling mechanisms can vary widely. The coupling can be bidirectional (e.g., mutually attractive and mutually repulsive) (c). The coupling can also be unidirectional, such as (d) “Winner-Take-All” or (e) “Loser-Take-All.”

parameters of a predefined model [15]. Using the model with various predefined coupling functions, Prasse and Van Mieghem [16] predicted network dynamics by fitting a network matrix and constructing a surrogate network. Recently, there has been growing interest in systems exhibiting higher-order interactions. In Ref. [17], the network with higher-order interactions is inferred, which is essentially formulated as an optimization problem to identify a model’s coefficients. However, these model-based inference outcomes are heavily influenced by model selection, and the use of an inappropriate model may produce false positives, thereby restricting their applicability. To overcome this limitation, inference methods using flexible models including inferring oscillatory networks [18] and general ODE-based inference [19,20] have been developed to infer the network among multiple agents. In Ref. [21], network inference is performed using a graph neural network-based deep learning approach with incomplete data. The authors proposed a framework that simultaneously enables both network inference and prediction of future states.

However, network inference alone cannot accomplish the inference of diverse coupling mechanisms. In bidirectional coupling between two oscillators [Fig. 1(c)], the interaction can be either attractive or repulsive, depending on the sign of the coupling function (or coupling strength). For example, in the SCN, attractive coupling among circadian oscillators is crucial for the synchronization of their rhythms [22,23], while repulsive coupling has been shown to be essential for day-length encoding in the SCN network [24]. Coupling can also be unidirectional: the leading oscillator may dominate, resulting in “Winner-Take-All” synchronization [25,26] [Fig. 1(d)], or the lagging oscillator may dominate, producing “Loser-Take-All” synchronization [27] [Fig. 1(e)]. Importantly, these coupling scenarios arise from the form of the coupling function, as well as the network structure. Thus, such diverse coupling behaviors are more accurately characterized by inferring the coupling function of oscillatory systems.

The task of identifying coupling functions in the interacting particle system has been extensively investigated in

previous studies. A fundamental approach relies on basis expansion theory, in which a coupling function is expressed in terms of a linear combination of a predefined set of basis functions. The corresponding coefficients in the combination are then estimated through an optimization procedure. For example, in Ref. [15], the coupling function was first simplified through low-dimensional reduction and mean-field approximation, after which the coefficients were estimated using the sparse identification of nonlinear dynamics [28] framework. Higher-order coupling functions have also been explored [17], but these are still typically approximated using polynomial expansions before coefficient estimation.

In coupled oscillator systems, where the coupling function is periodic, previous studies have commonly employed trigonometric polynomials as the basis for such expansions. The coefficients of the trigonometric polynomials are determined by solving a least-squares problem constructed from observed time series data. In this process, as the coupling function is unknown, a large number of trigonometric polynomials are typically used, which can lead to overparametrization. To address this issue, regularization techniques have been applied. For instance, Panaggio *et al.* [29] employed sparse regression [15,28], while Wang *et al.* [30] used truncated singular value decomposition [31] as a regularization method. However, regularization alone does not completely eliminate overparametrization, highlighting the importance of selecting an appropriate number of basis functions beforehand, which remains unclear.

In this study, we found that there is no single best number of trigonometric polynomial basis functions. Specifically, we observed that using a small number of basis functions made it difficult to accurately infer various coupling functions. Conversely, when a large number of basis functions were employed, the errors increased considerably as the observed data became sparser. To overcome this limitation, we developed IC-PINN (Inference of Coupling using physics-informed neural networks), a PINN-based neural network method [32–34], as neural networks enable function estimation without relying on predefined basis functions. This function estimation problem focuses on identifying an unknown periodic coupling function, rather than estimating states or parameters in a fixed model, which motivates us to adapt the PINN framework by introducing separate networks for phase evolution and interaction dynamics under physical constraints. IC-PINN demonstrated strong performance even without tuning the neural network structure, effectively estimating various coupling functions in cases with a small number of observations, noisy data, or distinct coupling structures. Furthermore, IC-PINN can be extended to simultaneously infer various network structures and the coupling function. When IC-PINN was applied to the experimental data of gene activity oscillations in PSM cells obtained from the mouse embryo tail bud [35], it successfully identified that the segmentation clock synchronizes through a “Winner-Take-All” mechanism. Moreover, IC-PINN successfully inferred the coupling function underlying the self-assembly of optically interacting nanorotors within circularly polarized light. To facilitate the broad applicability of IC-PINN, we have provided a user-friendly package.

II. RESULTS

A. Phase model describing collective behavior of coupled oscillators

In a system of coupled oscillators, their phase dynamics can be described using a system of differential equations [Fig. 2(a)], where θ_1 and θ_2 denote the phases of the oscillators, while ω_1 and ω_2 represent their respective frequencies. In this model, their relative phase difference determines the coupling so that the coupling affects θ_1 and θ_2 via $\Phi(\theta_2 - \theta_1)$ and $\Phi(\theta_1 - \theta_2)$, respectively.

By changing the shape of Φ , the model can illustrate various types of coupling [Fig. 2(b)]. For instance, with a sine-shaped coupling function, bidirectional interactions can be captured [Fig. 2(b), (i)]. Specifically, when θ_1 is leading θ_2 ($\theta_1 - \theta_2 > 0$), the coupling function in θ_1 equation becomes negative ($\Phi(\theta_2 - \theta_1) < 0$) and thus the leading phase θ_1 is decelerated. On the other hand, the coupling function in θ_2 equation is positive ($\Phi(\theta_1 - \theta_2) > 0$) and thus the lagging phase θ_2 is accelerated. Next, when the negative part of the sine-shaped coupling function becomes zero [Fig. 2(b), (ii)], then the coupling function no longer influences the leading phase θ_1 ($\Phi(\theta_2 - \theta_1) = 0$). Thus, it can be used to capture “Winner-Take-All” synchronization: The leading oscillator affects the lagging oscillator but not vice versa. Specifically, from the system [Fig. 2(a)], we see that $\dot{\theta}_2 = \omega_2 + \frac{1}{2}\Phi(\theta_1 - \theta_2) > \omega_2$. Thus, the lagging oscillator θ_2 is accelerated by the coupling. On the other hand, because the negative part of the coupling function is zero ($\Phi(\theta_2 - \theta_1) = 0$), we obtain that $\dot{\theta}_1 = \omega_1 + \frac{1}{2}\Phi(\theta_2 - \theta_1) = \omega_1$. Conversely, if the positive part of the sine-shaped coupling function becomes zero [Fig. 2(b), (iii)], then the coupling function no longer affects the lagging phase θ_2 ($\Phi(\theta_1 - \theta_2) = 0$). This can describe “Loser-Take-All” synchronization: the lagging oscillator influences the leading oscillator but not the other way around.

B. Limitations of the conventional method

Underlying coupling scenarios can be identified by inferring the coupling function Φ in the system [Fig. 2(a)]. One of the most widely used approaches for this inference is based on estimating the coefficients of trigonometric polynomials (e.g., sine and cosine) [29] as a basis that can describe the coupling function, which is periodic. The coefficients of trigonometric polynomials [Fig. 2(c), (ii)] are estimated by fitting the phase model [Fig. 2(a)] to the time series data of oscillator phases [Fig. 2(c), (i)]. Specifically, the total loss function, the sum of the loss and the regularization [Fig. 2(c), (iii)], is minimized to obtain the coefficients ($c, a_1, b_1, \dots, a_N, b_N$), while keeping the number (N) of basis functions fixed (see Sec. IV for details). However, in general, there is no definite rule for selecting the number (N). To investigate whether an optimal number exists, we applied the conventional approach with a small number of basis functions ($N = 2, \Phi_2$) and a larger number ($N = 10, \Phi_{10}$) [Fig. 2(d)] to infer three different types of coupling [Fig. 2(d), (i)–(iii)]. Regardless of the choice of number of basis functions (Φ_2, Φ_{10}), the sine coupling is accurately inferred [Fig. 2(d), (i)] from time series data [(Fig. 2(d), (i), inset)]. However, more complex coupling

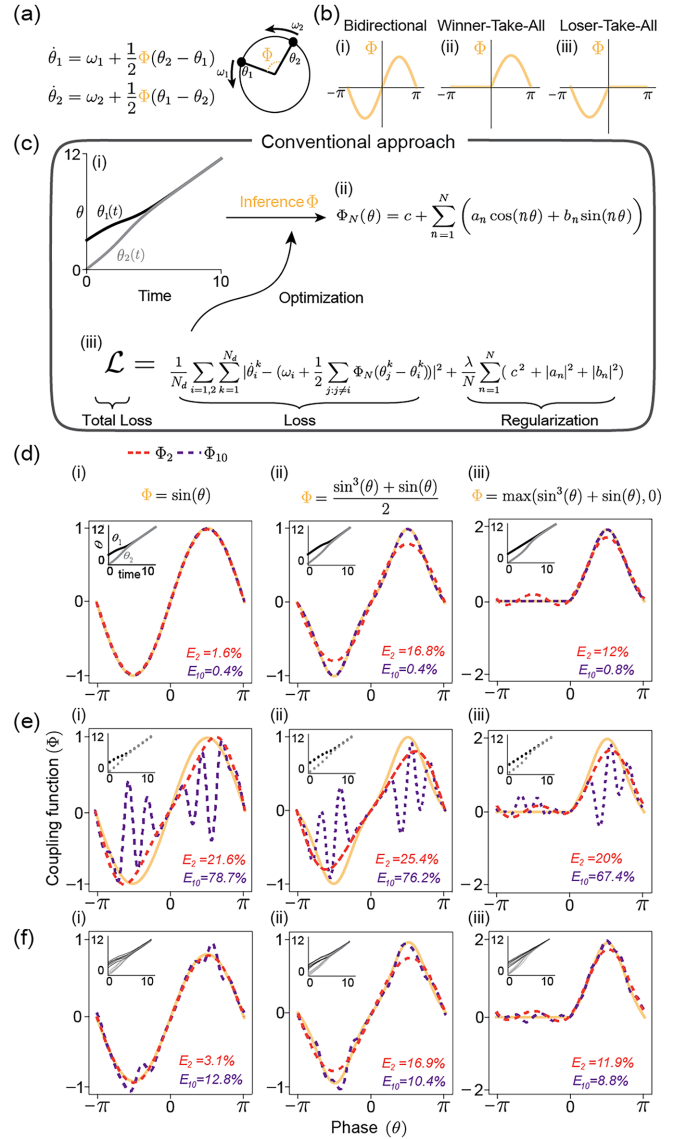


FIG. 2. Inference of coupling function based on basis expansion has limitations. (a) The dynamics of phases (θ_1 and θ_2) of two oscillators with frequencies (ω_1 and ω_2) can be described by differential equations with the coupling function Φ . (b) The shape of a coupling function Φ is different depending on the coupling mechanisms: (i) bidirectional, (ii) “Winner-Take-All,” and (iii) “Loser-Take-All.” (c) The conventional approach infers Φ from time series of θ_1 and θ_2 (i) using trigonometric polynomials Φ_N , where N represents the number of sine and cosine terms included in the summation (ii). Then, the coefficients of Φ_N are estimated, leading to minimizing the total loss: the sum of the loss and the regularization (iii). (d) The conventional method inferred Φ with two different choices of basis numbers ($N = 2$ and $N = 10$) from simulated data (insets) with three different coupling functions: (i) $\sin(\theta)$, (ii) $\frac{\sin^3(\theta) + \sin(\theta)}{2}$, and (iii) $\max(\sin^3(\theta) + \sin(\theta), 0)$. The inferred Φ with $N = 10$ (Φ_{10}) outperformed the inferred Φ with $N = 2$ (Φ_2). (e) However, when data are sparse, Φ_2 outperformed Φ_{10} . (f) When noise is introduced into the data, the estimation error dramatically increases with Φ_{10} but not Φ_2 . Here, E represents the relative L^2 error between Φ and Φ_N (See Sec. IV for details).

functions are accurately inferred with Φ_{10} but not Φ_2 [Fig. 2(d), (ii)–(iii)]. This indicates that to infer various types

of coupling functions, it is advantageous to use many basis functions. A sufficient number of basis functions have also been employed in prior studies. For example, Panaggio *et al.* [29] used $N = 5$ (10 trigonometric polynomials) to estimate coupling functions in a coupled oscillator system. Similarly, Wang *et al.* [30] used 25 basis functions, combining Legendre polynomials, to estimate a coupled system of three agents.

However, using a larger number of basis functions (Φ_{10}) leads to significant errors [Fig. 2(e), (i)–(iii)] when observed time series data are reduced [Fig. 2(e), (i)–(iii), inset]. This results from the lack of time series data relative to a larger number of parameters (N), which can lead to overparametrization. Furthermore, a larger number of basis functions is more sensitive to noise in the data. Specifically, when noise is added to the data [Fig. 2(f), (i)–(iii), inset], the estimation error increases dramatically [Fig. 2(f), (i)–(iii)].

Taken together, while a larger number of basis functions is advantageous for estimating various types of coupling functions, using too many basis functions leads to greater errors when time series data are few or noisy. Consequently, there is no single optimal number of basis functions for accurately estimating the coupling function.

C. Accurate estimation using the PINN-based method

To avoid using basis functions to infer the coupling function, a natural alternative is a neural network. We constructed two neural networks [Fig. 3(a)] as the coupled oscillator model contains two types of functions, the phases (θ_1, θ_2) and the coupling function Φ . To estimate θ_1 and θ_2 , the first neural network takes t as an input to obtain θ_1^{NN} and θ_2^{NN} through three layers. The second neural network consists of four layers where an input θ is mapped to the pair $(\sin(\theta), \cos(\theta))$, enforcing the periodicity. Then, the pair is mapped through the other three hidden layers to output the coupling function Φ^{NN} .

These neural networks are used to infer the coupling function Φ . As the coupling function Φ cannot be directly observed from time series data, it must be indirectly inferred using θ_1 and θ_2 . To achieve this, we develop IC-PINN [Fig. 3(b)]. Specifically, we first construct a data loss [Fig. 3(b)] to ensure that θ_1^{NN} and θ_2^{NN} match the given time series data. Next, along with θ_1^{NN} and θ_2^{NN} , we construct a physics loss [Fig. 3(b)] to ensure that the coupling function Φ^{NN} satisfies the governing equations [Fig. 2(a)]. Then, the total loss, the sum of data loss and the physics loss, is minimized to estimate neural network parameters (see Sec. IV for details).

IC-PINN successfully estimated various coupling functions without tuning the parameters of the neural networks [Fig. 3(c), (i)–(iii)] from the dataset used for the test of the conventional approach [Fig. 2(d), (i)–(iii)]. Furthermore, IC-PINN showed robust estimation even with sparse time series data [Fig. 3(d), (i)–(iii), inset]. Such robustness stems from two features of the neural network we constructed: automatic differentiation and physical constraint. Automatic differentiation eliminates numerical approximation errors, while physical constraints help prevent deviations in the phase trajectories. Moreover, IC-PINN showed robust estimation

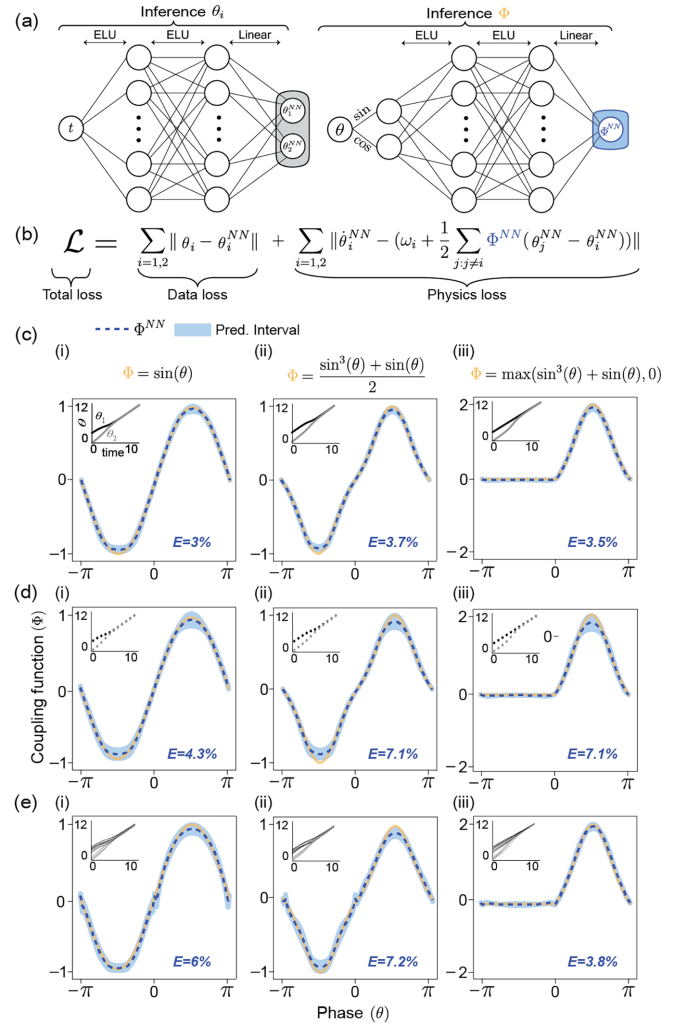


FIG. 3. IC-PINN framework accurately estimates the coupling function. (a) IC-PINN framework consists of two neural networks. The first neural network (NN) assigns the phases of two oscillators (θ_1^{NN} and θ_2^{NN}) for the observed input time t . In the second NN, the input θ is mapped to the pair $(\sin(\theta), \cos(\theta))$ to enforce the periodicity. This pair is then processed through hidden layers whose output becomes the coupling function Φ^{NN} . In both NNs, the exponential linear unit is used as the activation function for fast convergence and improved estimation of smooth functions. (b) IC-PINN identifies θ_1^{NN} , θ_2^{NN} , and Φ^{NN} that minimize the total loss function consisting of the data loss and the physics loss. The data loss measures the discrepancy between the predicted phases (θ_1^{NN} , θ_2^{NN}) and the observed phases (θ_1 , θ_2). The physics loss quantifies how well θ_1^{NN} , θ_2^{NN} , and Φ^{NN} satisfy the governing equations [Fig. 2(a)]. IC-PINN successfully estimates the coupling functions Φ for the full dataset [panel (c)], sparse dataset [panel (d)], and noisy dataset [panel (e)]. Here, Φ^{NN} is the average of 20 inference results, and the prediction interval is given by $\Phi^{NN} \pm 1.96\sigma$, where σ denotes the standard deviation of the 20 inference results.

with noisy data [Fig. 3(e), (i)–(iii)]: the estimation error did not increase significantly compared to the baseline estimation [Fig. 3(c), (i)–(iii)]. Finally, beyond the coupling functions shown in Figs. 2 and 3, IC-PINN was also able to accurately infer more complex coupling functions, including the

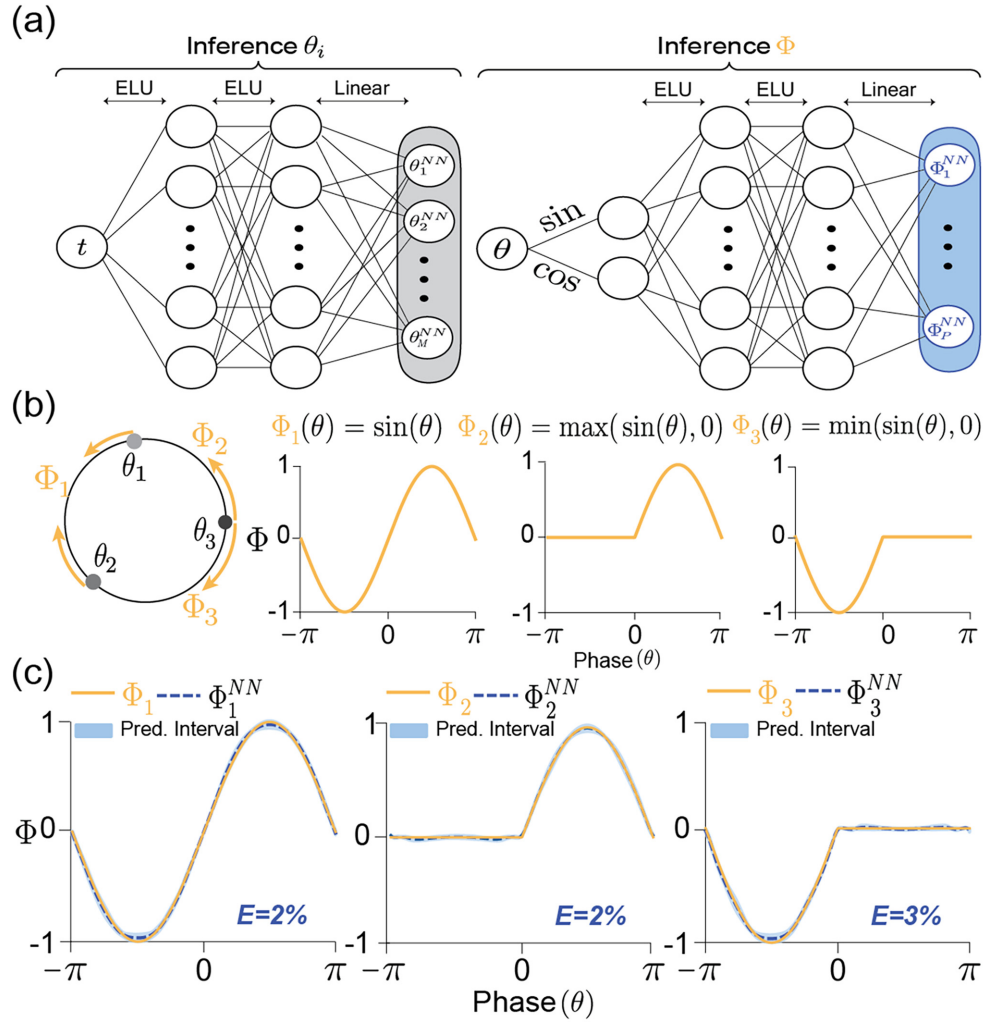


FIG. 4. IC-PINN accurately infers the coupling function of complex coupled oscillators. (a) The IC-PINN framework naturally extends to a system with more than two oscillators with varying coupling functions. The first NN outputs the M phases ($\theta_1^{NN}, \dots, \theta_M^{NN}$), while the second NN is designed to output coupling functions ($\Phi_1^{NN}, \dots, \Phi_P^{NN}$). The structures of both NNs remain the same as in Fig. 3(a), except for the increased number of outputs. (b) The IC-PINN framework was applied to a three-oscillator system with mutually distinct coupling functions $\Phi_1(\theta) = \sin(\theta)$, $\Phi_2(\theta) = \max(\sin(\theta), 0)$, and $\Phi_3(\theta) = \min(\sin(\theta), 0)$ (see Sec. IV for details). (c) Inferred coupling functions (Φ_1^{NN} , Φ_2^{NN} , and Φ_3^{NN}) with IC-PINN from five sets of time series data (see Fig. S2 in the Supplemental Material [36]) are accurate. Here, Φ^{NN} is the average of 20 inference results, and the prediction interval has mean of $\Phi^{NN} \pm 1.96\sigma$.

Kuramoto-Sakaguchi type (see Fig. S6 in the Supplemental Material [36]).

D. Extension of IC-PINN to the general system of coupled oscillators

IC-PINN can be naturally extended to a system of M coupled oscillators [Fig. 4(a)] by increasing the number of outputs in the neural networks [Fig. 3(a)]. Specifically, the first NN outputs phases ($\theta_1^{NN}, \dots, \theta_M^{NN}$) of M oscillators and the second NN outputs distinct coupling functions ($\Phi_1^{NN}, \dots, \Phi_P^{NN}$) as the coupling can vary for each pair of oscillators. The three oscillators [Fig. 4(b)] mutually interact through different coupling functions (Φ_1, Φ_2, Φ_3), each representing bidirectional, “Winner-Take-All,” and “Loser-Take-All” couplings, respectively.

To infer the distinct coupling functions (Φ_1, Φ_2, Φ_3), the loss function is adjusted to incorporate the increased outputs

in IC-PINN (see Sec. IV for details). IC-PINN successfully estimated all different coupling functions [Fig. 4(c)] from five sets of time series data (see Fig. S2 in the Supplemental Material [36]). Additionally, IC-PINN accurately inferred the coupling function in a system of ten coupled oscillators ($M = 10$) (see Fig. S1 in the Supplemental Material [36]). Moreover, when estimating the coupling function in systems with multiple oscillators, the performance of IC-PINN remained robust against variations in frequency distributions, coupling strengths, and order parameters (see Figs. S4 and S5 in the Supplemental Material [36]).

E. Extension of IC-PINN to network inference

We extended our framework beyond the complete networks, where all nodes are connected, to more general network classes that are more representative of real-world systems, including sparse, modular, and heterogeneous

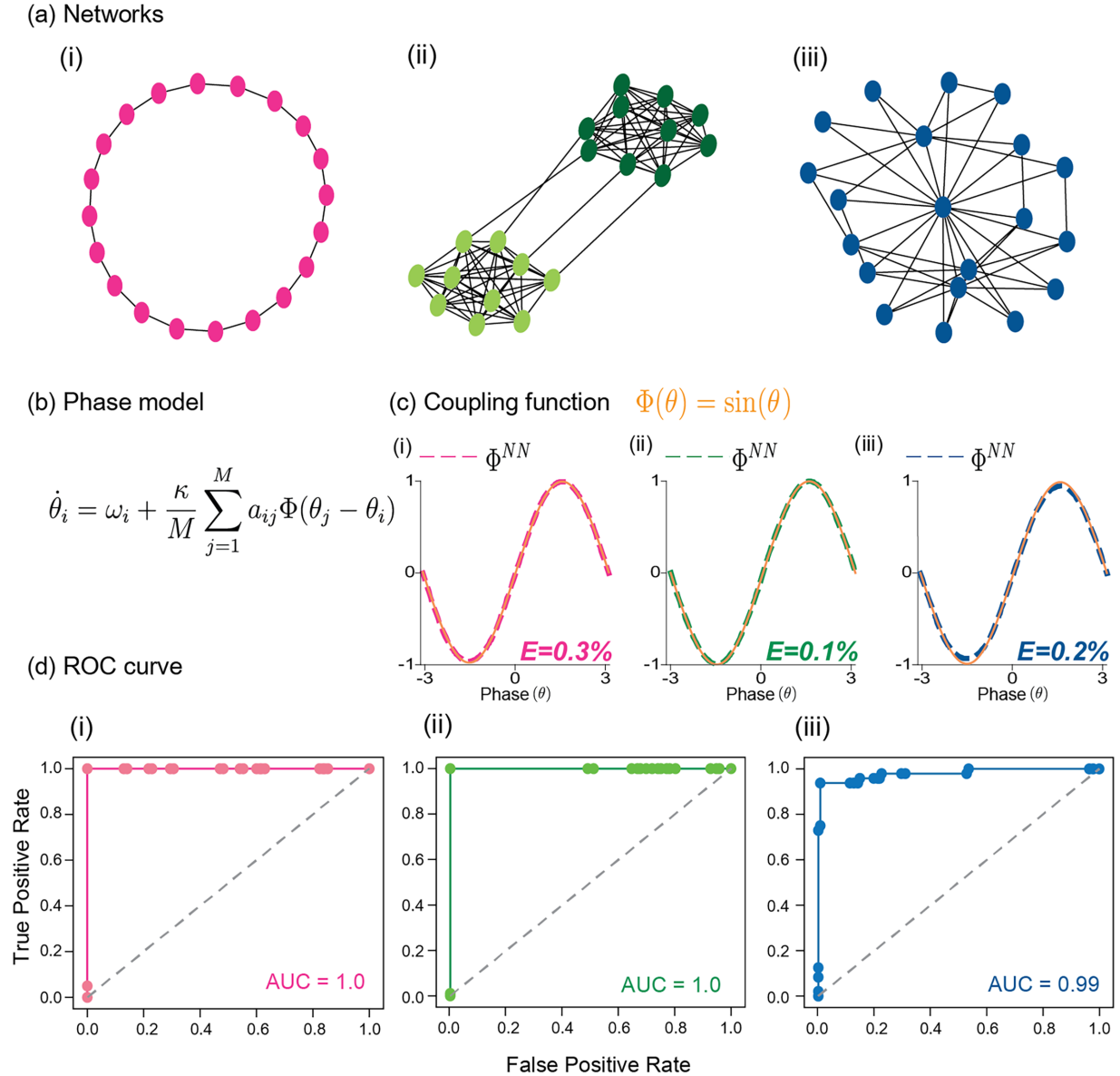


FIG. 5. Inference of diverse network structures along with the coupling function using IC-PINN. (a) Twenty coupled oscillators organized into three types of network structures were used as ground truth: (i) sparse, (ii) modular, and (iii) heterogeneous networks. (b) For each underlying network, time series data were generated by solving the phase model with $\Phi(\theta) = \sin \theta$ and $\kappa = 1$. The coefficients a_{ij} were defined by the adjacency matrix of the network shown in panel (a): $a_{ij} = 1$ if nodes i and j are connected, and $a_{ij} = 0$ otherwise. (c) From the time series corresponding to the three networks [(a)–(i), (ii), (iii)], IC-PINN accurately infers the true coupling function $\Phi(\theta) = \sin \theta$. (d) Along with the coupling function, IC-PINN can also reconstruct the network structure. To infer the network structure a_{ij} , auxiliary parameters w_{ij} were introduced and a sigmoid function σ was applied to map w_{ij} into range $\sigma(w_{ij}) \in [0, 1]$, providing the probability of $a_{ij} = 1$. With the estimated probabilities, ROC curves are computed, achieving AUC values of 1.0, 1.0, and 0.99 for the sparse, modular, and heterogeneous networks, respectively.

structures [Fig. 5(a), (i)–(iii)]. In such networks, the adjacency matrix (a_{ij}), which represents the network structure, takes the value $a_{ij} = 1$ (if nodes i and j are connected) and $a_{ij} = 0$ (otherwise), and must be simultaneously inferred with Φ in the phase model [Fig. 5(b)]. To address this, we extended IC-PINN to infer the adjacency matrix as well as the coupling functions (see Sec. IVE for details). We evaluated this approach on a system of 20 oscillators interacting via a sine coupling function under varying network configurations—sparse, modular, and heterogeneous [Fig. 5(a), (i)–(iii)]. As a result, IC-PINN successfully recovered both the coupling

function [Fig. 5(c), (i)–(iii)] and the underlying network connectivity, yielding AUC [area under ROC (receiver operating characteristic) curve] values of 1.0, 1.0, and 0.99 for the sparse, modular, and heterogeneous networks, respectively [Fig. 5(d), (i)–(iii)].

F. Verification of “Winner-Take-All” coupling in the segmentation clock

In the vertebrate embryo, PSM cells develop into somites, the precursors of the vertebrates. The PSM cells contain the

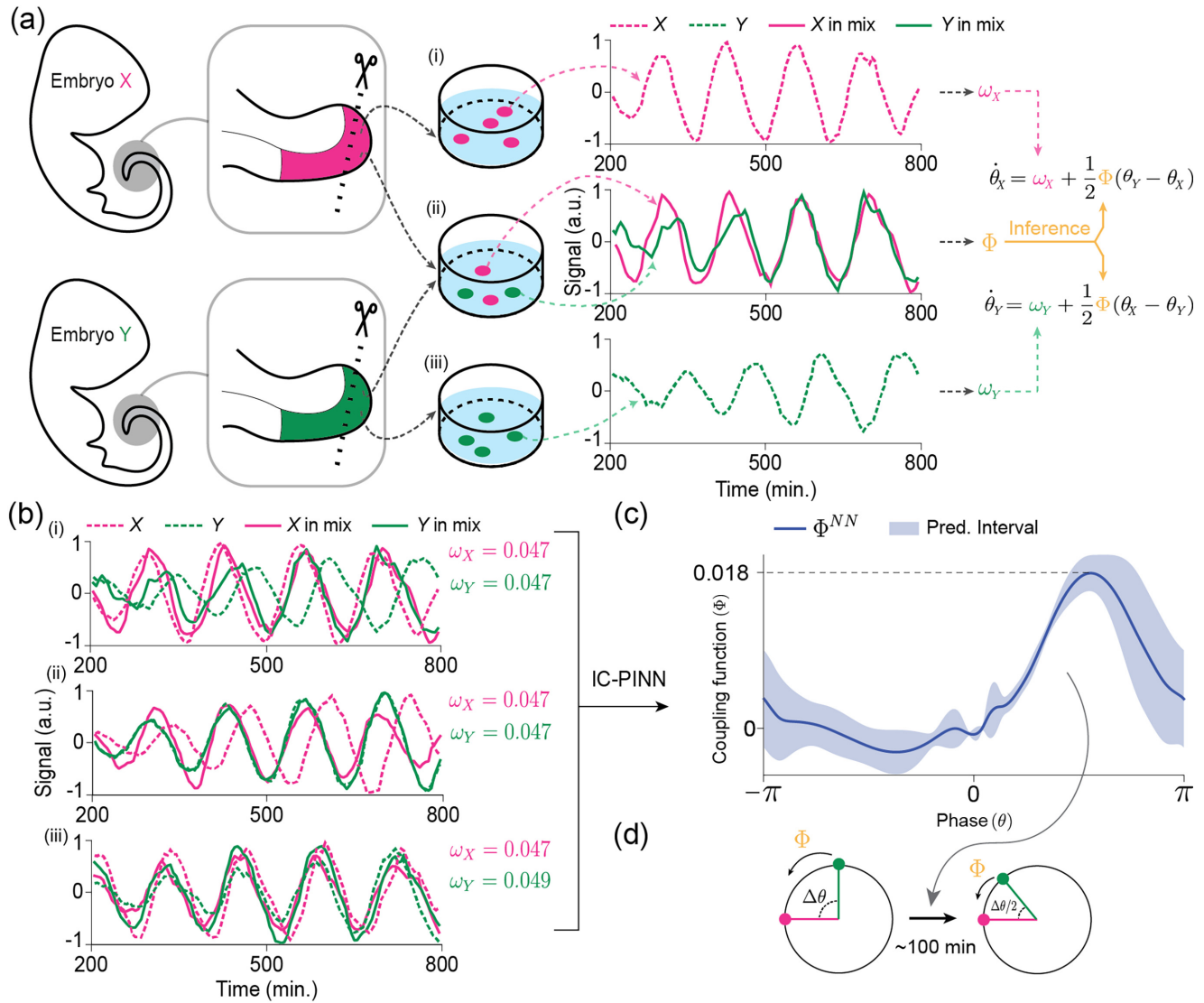


FIG. 6. Successful inference of the coupling mechanism in the segmentation clock with IC-PINN. (a) To study the coupling between oscillations in embryos, PSM cells were extracted in Ref. [35] from tail buds of mouse embryos X and Y. The time series data of HES gene expressions obtained from embryos X (i) and Y (iii) were used to estimate the intrinsic frequencies (ω_X , ω_Y) of PSM cells, as they were not interacting. The time series data of the mixture of embryos X and Y (ii) were used to infer the coupling function. (b) Using the three sets of time series data from Ref. [35], the intrinsic frequencies (ω_X , ω_Y) were estimated: (0.047, 0.047) (i), (0.047, 0.047) (ii), and (0.047, 0.049) (iii). (c) From these data with IC-PINN, the inferred coupling function Φ reveals a “Winner-Take-All” synchronization of PSM cells. (d) According to the inferred Φ , the phase difference ($\Delta\theta$) between two oscillators is expected to be half after about 100 min (see the Supplemental Material [36] for details).

HES gene activity oscillations, referred to as the segmentation clock [35]. PSM cells interact via Notch signaling and become synchronized, critical for robust timing of the segmentation clock.

To investigate the coupling mechanisms, Ho *et al.* [35] extracted PSM cells from the embryo tail buds of mice. Specifically, from two embryos X and Y [Fig. 6(a)], HES gene activity was measured in PSM cells [Fig. 6(a), (i)–(iii)]. As the leading oscillator continued oscillating at the same frequency while the lagging oscillator was accelerated to catch up with the leading oscillator, Ho *et al.* [35] concluded that the segmentation clock follows “Winner-Take-All” synchronization. However, the quantitative characteristics of the coupling remained unknown.

Thus, to infer the coupling function, we applied IC-PINN to the phase time series data [Fig. 6(a)]. Specifically, we first used the time series obtained with noninteracting PSM cells [Fig. 6(a), (i), and (iii)] to estimate the intrinsic frequencies (ω_X and ω_Y) of oscillators (X and Y) [Fig. 6(b)]. Then, we used the time series data obtained with interacting PSM cells [Fig. 6(a), (ii)] to infer the coupling function Φ . Indeed, the inferred coupling function supports the “Winner-Take-All” synchronization among PSM cells [Fig. 6(c)]. Furthermore, from the inferred coupling function, we can predict the speed at which the oscillators synchronize. Specifically, the time required for the phase difference between the two oscillators to reduce to half its initial value is predicted to be about 100 min [Fig. 6(d)] (see the Supplemental Material [36] for details).

G. Inference of coupling mechanisms of optically interacting nanorotors

When light interacts with a small particle, recoil forces emerge from light scattering and absorption, resulting from the conservation of energy and momentum. This light-matter interaction induces an optical binding in a system of particles within the laser field. In a system of anisotropic plasmonic gold nanorods (Au NRs), this optical binding enables their rapid rotation in water under circularly polarized light [37] [Fig. 7(a)]. In this rotation, the phases of the two NRs, θ_1 and θ_2 , are coupled through coherent light scattering, where each phase is defined as the angle between the long axis of the respective NR and the dimer axis. The inertial effects and hydrodynamic coupling are negligible due to the small particle size (length ≈ 166 nm) and the short interparticle distances (< 800 nm) [37]. Then, the spinning dynamics of the NRs is explained by two forces, F and Φ . The force F aligns the long axis orthogonally to the dimer axis and thus phases θ_1 and θ_2 are changed toward $\frac{\pi}{2}$. Furthermore, the coupling Φ synchronizes the phases θ_1 and θ_2 .

Such dynamics of spinning NRs can be formulated by a system of differential equations [37] [Fig. 7(b)]. In this model, F depends on the oscillator's phase, while the coupling function Φ depends on phase differences. Both F and Φ are π periodic as NRs are rectangular-shaped and repeat their orientation for every π rotation. Based on this periodicity, we set $F(\theta) = 0.4 \sin(2\theta)$ and $\Phi(\theta) = 0.4 \sin(2\theta)$ following Cui *et al.* [37].

We simulated a dataset consisting of the phase after synchronization of two oscillators, the initial phases, and their phase difference, ensuring consistency with the experimental data provided in Ref. [37]. From this dataset, we inferred the coupling mechanism of spinning NRs by extending IC-PINN architecture (see the Supplemental Material [36] for details). The inference process was carried out in two sequential steps. First, as the coupling Φ vanishes once the oscillators are synchronized, we applied IC-PINN with the synchronized phase data to infer F [Fig. 7(c)]. Next, we used the accurately inferred F to estimate the coupling function Φ . Specifically, IC-PINN accurately inferred the coupling function Φ [Fig. 7(d)] using the phase difference and initial data $(\theta_1^0, \theta_2^0) = (0, \frac{\pi}{2})$.

In the second step, individual phases (θ_1, θ_2) are unavailable, so the conventional approach cannot infer the coupling function Φ due to the phase-dependent function F . In contrast, IC-PINN overcomes this challenge by estimating (θ_1, θ_2) through the physics loss (see the Supplemental Material [36] for details).

III. DISCUSSION

To infer the coupling mechanism in the coupled oscillator system, we developed IC-PINN. IC-PINN leverages a deep learning architecture specifically designed for oscillatory systems, reducing numerical errors and effectively estimating a wide range of coupling functions [38,39]. Furthermore, training the deep learning architecture with physics-based constraints (physics loss) naturally regularizes the solution, leading to improved robustness against noise and data sparsity.

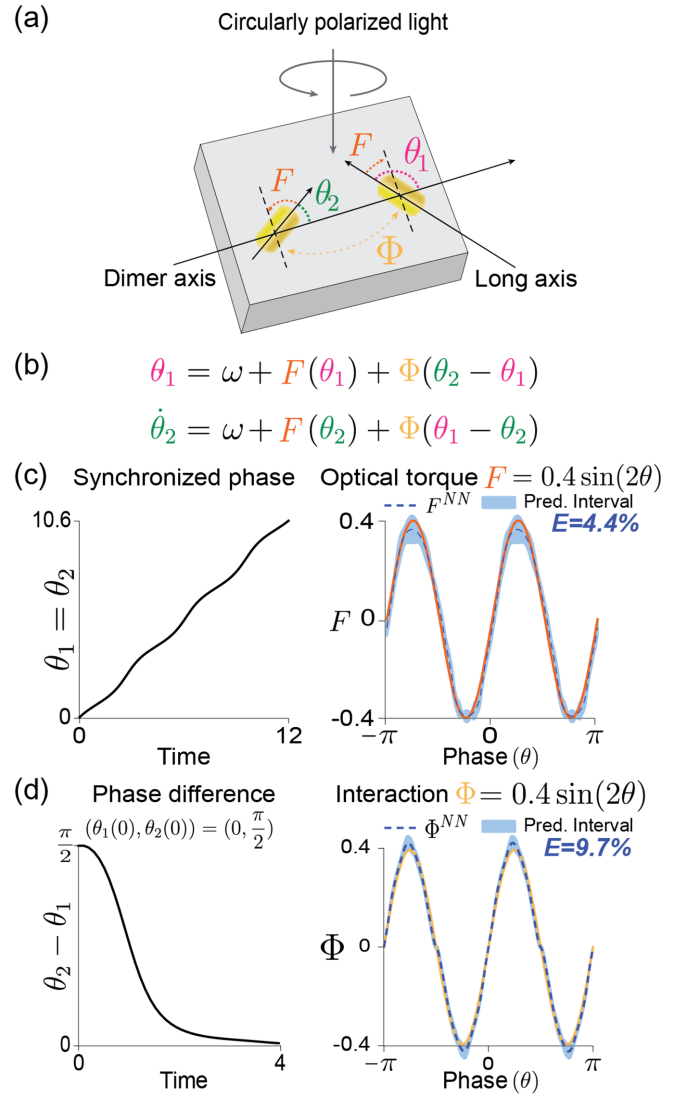


FIG. 7. Successful inference of coupling in self-assembled gold nanorods with IC-PINN. (a) Circularly polarized light induces the rotation of Au NRs, leading to the spin of NRs (green and pink dashed lines). Their angular velocities in the spinning dynamics are governed by the optical torque F , which aligns each NR's long axis orthogonally to the dimer axis (orange arrow), and the coupling Φ , which synchronizes their phases (yellow arrow). (b) This can be described by the phase model with the optical torque F and the coupling function Φ . Note that this model includes a phase-dependent function $F(\theta)$, unlike the phase model shown in Fig. 2(a). (c) From the synchronized phase data, IC-PINN accurately estimated $F(\theta)$. (d) Then, from the phase difference and initial phase data, IC-PINN accurately estimated $\Phi(\theta)$.

As a result, IC-PINN accurately infers the various coupling functions, even when the data are sparse and noisy (Figs. 3 and 4). Thus, IC-PINN is a more suitable choice than conventional methods for experimental data, which often exhibit noise and sparsity. Indeed, IC-PINN successfully inferred the coupling function of the segmentation clock [Fig. 6(c)] and optically bound nanorotors [Fig. 7(d)], which was not possible with conventional methods.

Importantly, IC-PINN is not a direct application of a standard physics-informed neural network, but rather a tailored extension designed specifically for phase-coupled oscillator systems. While physics-informed regularization and PINN-based loss formulations have been widely used in inverse problems, their primary role has typically been to refine unknown parameters within a fixed model structure or a function of state variables [40–44]. In contrast, IC-PINN reformulates the interaction inference problem by explicitly distinguishing between phase dynamics and interaction mechanisms, which possess fundamentally different identifiability properties. By decomposing these components into separate neural networks and coupling them only through governing physical constraints, IC-PINN enables direct identification of coupling functions that are not directly observable yet critically shape system-level dynamics. Crucially, this formulation remains identifiable even in the absence of absolute phase information, allowing physically meaningful coupling functions to be inferred from noisy and partial observations such as phase differences. Moreover, this design mitigates model-selection bias inherent to library-based approaches and facilitates the discovery of nonlinear and asymmetric interaction principles—such as winner-take-all dynamics—without imposing them *a priori*. In this sense, IC-PINN extends the scope of PINNs and positions them as a general inference framework for uncovering hidden interaction structures in complex dynamical systems.

Furthermore, unlike conventional approaches, IC-PINN provides uncertainty quantification (UQ) for the inference (Figs. 3 and 4). Specifically, it inherently incorporates probabilistic elements, such as stochastic optimization and network parameter initialization. As a result, IC-PINN can randomly select the initial parameters and repeat estimations, known as deep ensembles [45], which serves as a method for UQ in this study. More recently, various other techniques have been developed to achieve efficient and accurate UQ directly within deep learning models, such as Monte Carlo dropout layers [46] and Bayesian neural networks [47]. Applying these advanced UQ methods to IC-PINN will be a direction for future research.

Another distinguishing feature of IC-PINN compared to conventional approaches is its flexibility with input data. Conventional approaches require individual phases as input (see the Supplemental Material [36]), but obtaining absolute phase values is often experimentally challenging. Instead, phase differences are measured and used in practice. For example, the Mach-Zehnder interferometer [48] measures phase differences between two light beams. For such data, IC-PINN remains applicable as illustrated with the example of the self-assembly of NRs (Fig. 7).

While we successfully applied IC-PINN to the segmentation clock and nanorotors, it can also be applied to diverse cases. This includes neuronal oscillators [49–51], cardiac pacemaker cells [52,53], and the coupled system of the circadian clock and the cell cycle [54,55]. Outside of biology, the voltage networks in power systems and the interacting electromagnetic waves in coupled laser systems are also coupled oscillator systems [56,57]. Additionally, quantum synchronization of coupled quantum oscillators has been actively studied, with potential applications to quantum communication

and cryptography [58,59]. Such coupled oscillators can be expressed by phase models through phase reduction theory [60]. In particular, a recent study developed phase reduction methods for quantum oscillators [61].

Although we inferred a coupling function from noisy data [Figs. 2(f) and 3(e)], this noise is extrinsic (i.e., errors in the data). However, some studies have considered the presence of intrinsic noise in the system and estimated stochastic systems [62]. For example, Gao *et al.* [63] used a predefined library of functions to infer a governing stochastic differential equation. Similarly, Droin *et al.* [64] used a Hidden Markov Model to estimate the coupling in the stochastic system of a coupled circadian clock and cell cycle. Additionally, Öcal *et al.* [65] developed an inference method using a Hidden Markov Model and UQ of stochastic gene expression. Thus, extension of IC-PINN to stochastic coupled oscillator systems will be a focus of future work. In addition, recent work [21] introduced a method called the “collaborative deep-learning framework for network inference and dynamical prediction” (CoND), which leverages graph neural networks to infer large-scale network structures from partially known node connectivity (i.e., adjacency matrix in Sec. IV E). However, when connectivity information is completely unknown, CoND is less effective than IC-PINN at recovering the full network structure (see Fig. S3 in the Supplemental Material [36]). A promising future direction is to integrate IC-PINN with CoND to enable inference of full network connectivity in large-scale systems without prior knowledge. Moreover, such an integrated framework could also recover the underlying coupling mechanisms, thus advancing our understanding of coupled oscillator systems across scientific disciplines and in real-world applications characterized by complex, large-scale dynamics.

IV. METHODS

A. Description of the coupled oscillator system

The phase dynamics $\theta(t) = (\theta_1(t), \dots, \theta_M(t))$ of M coupled oscillators, interacting through unknown coupling functions $\{\Phi_{(j,i)}\}_{j,i=1}^M$, can be described by the following system of ordinary differential equations [47–49]:

$$\begin{aligned} \dot{\theta}_i &= \omega_i + \frac{1}{M} \sum_{j=1}^M \Phi_{(j,i)}(\theta_j - \theta_i), \\ t &\in [0, T], \quad i \in \{1, \dots, M\}, \end{aligned} \quad (1)$$

where $t \in [0, T]$ denotes continuous time in an observation with the duration T . When all oscillators interact through a common mechanism, we write $\Phi(\theta_j - \theta_i)$ in Eq. (1), omitting the subscripts. In Fig. 4, we consider the symmetric case ($\Phi_{(i,j)} = \Phi_{(j,i)}$) with $M = 3$, where, for simplicity, we write $\Phi_1 = \Phi_{(1,2)}$, $\Phi_2 = \Phi_{(1,3)}$, and $\Phi_3 = \Phi_{(2,3)}$.

B. Data

To evaluate the performance of the conventional approach and IC-PINN, we used the simulation data $\theta^d = (\theta_1^d, \dots, \theta_M^d)$, obtained by solving Eq. (1) ($M = 2$) via the forward Euler method. Specifically, the oscillator frequencies were fixed at $\omega_1 = \omega_2 = 1$, and the initial conditions are set to

$\theta_1^d(0) = 3, \theta_2^d(0) = 0$. The simulation was performed with a time step of $dt = 0.1$ over $T = 10$; i.e., θ^d consists of 100 evenly spaced data points ($N_d = 100$) over the interval $[0, 10]$. A single data pair was used for the noise-free case [Figs. 2(d), 2(e), 3(c), and 3(d)]. For the noisy case [Figs. 2(f) and 3(e)], we generated five data pairs with the identical initial data by adding Gaussian noise $0.02 \times N(0, 1)$.

The simulation data used in Fig. 4 were obtained by solving Eq. (1) ($M = 3$) over the time domain $[0, 10]$ with three distinct coupling functions, $\Phi_1 = \sin \theta$, $\Phi_2 = \max(\sin \theta, 0)$, and $\Phi_3 = \min(\sin \theta, 0)$. The intrinsic frequencies ($\omega_1, \omega_2, \omega_3$) were randomly chosen from $1 + 0.05 \times N(0, 1)$ and then fixed. The five datasets of θ^d with $N_d = 100$ were used for the inference (see Fig. S2 in the Supplemental Material [36]).

The experimental data used to infer the coupling function in the segmentation clock (Fig. 6) were extracted from Fig. 3(c) in Ref. [35]. To obtain the phase information from the raw time series, we applied the pyBOAT wavelet analysis tool kit [66]. Each time series consists of 119 data points ($N_d = 119$). Details of the simulation procedure for the data used in Fig. 7 are provided in Note 4 in the Supplemental Material [36].

C. Conventional method

To infer the coupling function, the conventional approach represents the coupling function as the sum of trigonometric polynomials with coefficients, $(c, a_1, b_1, \dots, a_N, b_N)$ [Fig. 2(c), (ii)]. These coefficients are determined by minimizing a total loss function [Fig. 2(c), (iii)], consisting of the loss function and the regularization term. The loss function is defined as the mean square error which estimates the discrepancy between the left- and right-hand sides of Eq. (1) by substituting the observed data θ_i^o into θ_j and the trigonometric polynomials into $\Phi_{(j,i)}$. The phase velocity $\dot{\theta}_i^n$ in the left-hand side of Eq. (1) is approximated using the forward Euler scheme. To exclude excessively high frequencies, the regularization term $\frac{\lambda}{N} \sum_{k=1}^N (c^2 + |a_k|^2 + |b_k|^2)$ is added to the loss function, with the parameter λ tuned to be 0.01.

D. Training of IC-PINN

We trained our method by minimizing the total loss function:

$$\mathcal{L}(p) = \mathcal{L}_{\text{data}}(p) + \mathcal{L}_{\text{physics}}(p), \quad (2)$$

where $p = (p_\theta, p_\Phi)$ is the set of parameters for the two NNs ($\theta^{\text{NN}} = \{\theta_i\}_{i=1}^M$ and $\Phi^{\text{NN}} = \{\Phi_{(j,i)}^{\text{NN}}\}_{1 \leq i, j \leq M}$) in IC-PINN. The data and physics losses are denoted by $\mathcal{L}_{\text{data}}$ and $\mathcal{L}_{\text{physics}}$, respectively. The data loss function $\mathcal{L}_{\text{data}}$ is used to measure the mean square error between the output of the network θ^{NN} and the observed data $\{\theta^o(t_k)\}_{k=1}^L$, and is defined as

$$\mathcal{L}_{\text{data}} = \frac{1}{L} \sum_{k=1}^L |\theta^{\text{NN}}(t_k) - \theta^o(t_k)|^2. \quad (3)$$

The physics loss is designed to quantify how well the outputs of two networks, θ^{NN} and Φ^{NN} , satisfy the system

in Eq. (1) on the set of collocation points $\{t_l^c\}_{l=1}^{N_c}$ in the time domain $[0, T]$:

$$\mathcal{L}_{\text{physics}} = \frac{1}{N_c} \sum_{l=1}^{N_c} \sum_{i=1}^M |T_i|^2, \quad (4)$$

$$T_i = \dot{\theta}_i^{\text{NN}}(t_l^c) - \left(\omega_i + \frac{1}{M} \sum_{j=1}^M \Phi_{(j,i)}^{\text{NN}}(\theta_j^{\text{NN}}(t_l^c) - \theta_i^{\text{NN}}(t_l^c)) \right),$$

where $\{\Phi_{(j,i)}^{\text{NN}}\}_{1 \leq i, j \leq M} = \{\Phi_l^{\text{NN}}\}_{1 \leq l \leq P}$. In this study, the collocation points $\{t_l^c\}_{l=1}^{N_c}$ were chosen to match the observed data points $\{t_k\}_{k=1}^L$. For sparse observations, we can additionally sample intermediate time points as extra collocation points to strengthen equation satisfaction between measurements without requiring any extra data [33, 67, 68]. For multiple data pairs, the loss functions $\mathcal{L}_{\text{data}}$ and $\mathcal{L}_{\text{physics}}$ are summed accordingly.

To find the optimal p that minimizes $\mathcal{L}(p)$ in Eq. (2), we use the ADAM optimizer for each training iteration with learning rate 10^{-4} . The training is terminated if the difference between consecutive loss values, measured every 2000 epochs, is less than a tolerance of 10^{-6} . In the inference using segmentation clock data, we select results where the data loss is below 10^{-3} .

The error (E) (in Figs. 2, 3, 4, 5, and 7) is computed as the relative L^2 error between the inferred coupling function Ψ and the ground truth Φ , defined as

$$E = \frac{\|\Psi - \Phi\|}{\|\Phi\|}, \quad (5)$$

where $\|f\| = (\int_0^{2\pi} |f(\theta)|^2 dx)^{\frac{1}{2}}$. In practice, we compute the L^2 norm using the mean squared error, as the data are discrete.

In the inference of the coupling function for the nanorotor system (Fig. 7), the data loss based on phase [Eq. (3)] cannot be directly constructed. Thus, to incorporate phase difference data, the data loss function should be modified accordingly. The detailed IC-PINN architecture and simulation data used for the inference of nanorotor system (Fig. 7) can be found in the Supplemental Material [36].

E. Inference of diverse network structures

Beyond complete networks, general network structures are represented by the coupled oscillator system [Eq. (1)] with the adjacency matrix $A = (a_{ij})$:

$$\dot{\theta}_i = \omega_i + \frac{1}{M} \sum_{j \neq i}^M a_{ij} \Phi(\theta_j - \theta_i), \quad (6)$$

$$t \in [0, T], \quad i \in \{1, \dots, M\},$$

where $a_{ij} = 1$ if nodes i and j are connected and 0 otherwise. For the case $i = j$, we assume that oscillators do not self-interact (i.e., $a_{ii} = 0$). To estimate both Φ and (a_{ij}) , we introduce trainable parameters $W = (w_{ij})$ and apply a sigmoid function $\sigma(\cdot)$ to map w_{ij} into range $[0, 1]$, providing the probability of $a_{ij} = 1$. To find the optimal probability values, we first reformulate the original total loss function $\mathcal{L}(p)$ [Eq. (2)] by replacing the coupling function $\Phi_{(j,i)}^{\text{NN}}$ in

Eq. (4) with $\sigma(w_{ij})\Phi$ as follows:

$$L_{\text{physics}}(p, W) = \frac{1}{N_c} \sum_{l=1}^{N_c} \sum_{i=1}^M |T_i|^2,$$

$$T_i = \dot{\theta}_i^{\text{NN}}(t_l^c) - \left(\omega_i + \frac{1}{M} \sum_{j \neq i}^M \sigma(w_{ij}) \Phi^{\text{NN}}(\theta_j^{\text{NN}}(t_l^c) - \theta_i^{\text{NN}}(t_l^c)) \right). \quad (7)$$

After training, we obtain both the optimal parameters $p = \hat{p}$ in Φ^{NN} and $w_{ij} = \hat{w}_{ij}$ that minimize Eq. (7), and hence the corresponding optimal probabilities $\sigma(\hat{w}_{ij})$. From the optimized parameters $\hat{w}_{ij}$ for all $i \neq j$, we infer the adjacency matrix by setting $a_{ii} = 1$ if $\sigma(\hat{w}_{ij}) > \tau$ and 0 otherwise, where $\tau \in (0, 1)$ is a threshold (default = 0.5). As the parameters w_{ii} are not included in Eq. (6) for $i = 1, \dots, n$, we manually

set $\sigma(\hat{w}_{ii}) = 0$ following the assumptions on Eq. (6). For a system of 20 coupled oscillators interacting through a coupling function $\Phi(\theta) = \sin(\theta)$, we inferred different network structures (sparse, modular, and heterogeneous) and evaluated reconstruction performance by plotting the ROC curve across varying thresholds τ (see Fig. 5 for details). Finally, to infer the coupling strengths κ_{ij} that vary across edges, we use Eq. (6) without applying the sigmoid function or any threshold that limits the coefficients to binary values 0 or 1.

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DATA AVAILABILITY

The data are not publicly available. The data are available from the authors upon reasonable request.

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