

Synchronization modes in bipartite oscillator networks

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Collective oscillations in neuronal systems often arise from interactions between excitatory and inhibitory populations rather than from recurrent coupling within a single ensemble. Motivated by the coexistence of strongly and partially synchronized regimes in such systems, we study the Kuramoto-Sakaguchi model on a bipartite network. Despite its minimal structure, the model exhibits rich collective dynamics, including both continuous and discontinuous transitions from full synchrony to partial synchrony (PS). In the PS regime, global oscillations fail to entrain one of the two populations, whose oscillators display quasiperiodic dynamics with an average frequency that can significantly deviate from that of the global field, as observed in neuronal networks. We show that this PS state constitutes an example of self-organized quasiperiodicity, arising here in the bimodal Kuramoto-Sakaguchi model despite its purely linear global coupling.

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I. INTRODUCTION

The emergence of coherent oscillations in large networks of self-sustained oscillators is a ubiquitous phenomenon in nature [1–3]. In the seminal theoretical frameworks of Winfree and Kuramoto [4,5], collective synchronization arises from recurrent interactions within a single, globally coupled population. However, global rhythms may originate instead from the crosstalk between distinct populations—often of different types and coupled nonreciprocally [6].

A paradigmatic example is found in neuronal circuits, where oscillations emerge from the interplay between excitatory (E) and inhibitory (I) neurons [7,8]. Models of interacting E and I spiking neurons often exhibit a strongly synchronized (S) regime, where both populations fire at every cycle of the global oscillation [9,10]. This regime is well described by the Kuramoto model on a bipartite network [11]. However, experimental observations frequently reveal a partially synchronized (PS) regime [7,8], where E cells skip cycles of the global rhythm while inhibitory neurons fire more regularly [12].

To investigate the mechanisms underlying these synchronization modes, we analyze an extension of the paradigmatic Kuramoto-Sakaguchi (KS) model [13] in which oscillators in population σ interact only with oscillators in the opposite population σ' :

$$\dot{\theta}_i^\sigma = \omega_\sigma - \frac{K_{\sigma'}}{N} \sum_{j=1}^N \sin(\theta_i^\sigma - \theta_j^{\sigma'} - \alpha_\sigma), \quad i = 1, \dots, N, \quad (1)$$

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where θ_i^σ is the phase of the i th oscillator in population $\sigma \in \{A, B\}$. Here, ω_σ , K_σ , and α_σ are natural frequencies, coupling strengths, and phase-lag parameters, respectively. Equation (1) can be formally derived from an E-I network of *identical* quadratic integrate-and-fire (QIF) neurons with conductance-based synapses [14]. Though QIF neurons have identical intrinsic parameters, the nonreciprocal nature of E-I interactions generically leads to mismatches in frequencies ($\omega_A \neq \omega_B$), coupling strengths ($K_A \neq K_B$), and phase lags ($\alpha_A \neq \alpha_B$) in the reduced equation (1) (see the Supplemental Material [15]).

A substantial body of work has investigated PS states in symmetrically, fully connected two-population KS networks of identical oscillators [16–23]. Most notably, PS states emerging through symmetry breaking and known as *chimera states* have attracted enormous interest; see, e.g., Refs. [24–27] for reviews. In contrast, the bipartite KS model has received little attention. So far, Eq. (1) has been analyzed either for $\alpha_\sigma = 0$ [6,11,28–31] or for $\alpha_\sigma \neq 0$ and $\omega_A = \omega_B$ [32]; in none of these cases have PS states been reported.

In this article, we demonstrate that both S and PS states arise from cross-population interactions in Eq. (1). This simplicity allows for a transparent analysis of the underlying mechanisms leading to PS states. We show that these states represent an example of *self-organized quasiperiodicity* (SOQ) [33,34], which here emerge solely from the bipartite structure of the network and do not require the presence of nonlinear mean-field coupling [33–35].

In what follows, we set $\alpha_A = \alpha_B = \alpha$ without loss of generality [36]. Moreover, we consider the case $K_A = K_B = K > 0$, $\alpha \in [0, \pi/2)$, and $\Delta = \omega_A - \omega_B > 0$ (see the Supplemental Material [37]).

II. NUMERICAL ILLUSTRATION OF S AND PS STATES

The raster plots in Fig. 1 illustrate the two synchronization modes of the KS model [Eq. (1)]. The time points at which the oscillators' phases reach a multiple of 2π are depicted, after a transitory period of 1000 time units—Initial phases

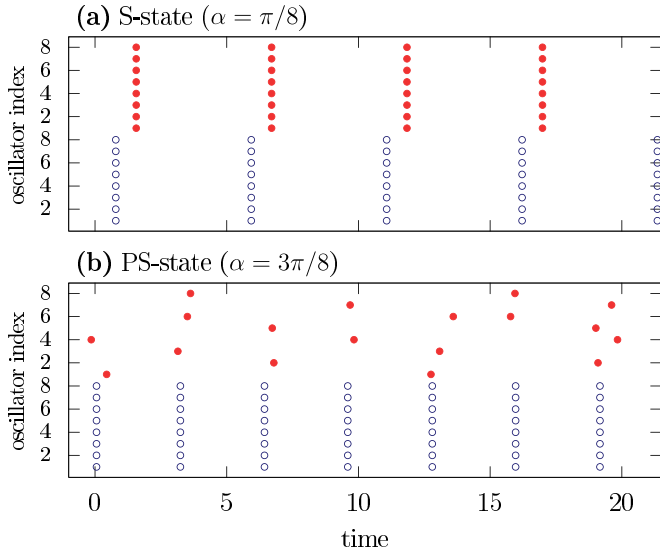


FIG. 1. Synchronization modes of Eq. (1), with $N = 8$. Raster plots of populations A (open circles, blue) and B (closed circles, red) in (a) the S state ($\alpha = \pi/8$) and (b) the PS state ($\alpha = 3\pi/8$). Parameters: $K = 1$, $\omega_A = 1.75$, and $\omega_B = 0.25$ ($\bar{\omega} = 1$, $\Delta = 1.5$).

were randomly drawn from a uniform distribution in $(0, 2\pi]$. In the S regime [panel (a)], oscillators in populations A (blue open dots) and B (red dots) are in-phase synchronized, and the two populations are locked to a common frequency Ω . In this case, the network dynamics reduce to that of two mutually coupled oscillators, with a constant phase mismatch $\phi^* = \theta_i^A - \theta_j^B > 0$, for all i, j . In the PS regime [panel (b)], A oscillators become in-phase synchronized, while B oscillators remain asynchronous. Note that B oscillators rotate nonuniformly with a time-averaged frequency clearly below that of A oscillators, mirroring the PS states observed in E-I neural networks.

III. EXISTENCE OF S STATES

We begin by analyzing Eq. (1) in the case of two coupled nonidentical oscillators, $N = 1$ [5,38]. Two possible regimes exist: an S state with the dynamics shown in Fig. 1(a) and an asynchronous regime where oscillators A and B are not frequency locked but undergo quasiperiodic oscillations. The evolution of their phase difference $\phi = \theta_1^A - \theta_1^B$ obeys the Adler equation $\dot{\theta}_1^A - \dot{\theta}_1^B = \dot{\phi} = \Delta - 2K \cos \alpha \sin \phi$, which has a saddle-node (SN) bifurcation at

$$\alpha_S = \arccos\left(\frac{\Delta}{2K}\right), \quad (2)$$

if $\frac{\Delta}{2K} \in (0, 1)$. For $\alpha \in [0, \alpha_S)$, there is a stable equilibrium (S state)

$$\phi^* = \arcsin[\Delta/(2K \cos \alpha)], \quad (3)$$

with frequency

$$\Omega = \bar{\omega} + \frac{K}{2} \tan \alpha \sqrt{(2 \cos \alpha)^2 - (\Delta/K)^2}, \quad (4)$$

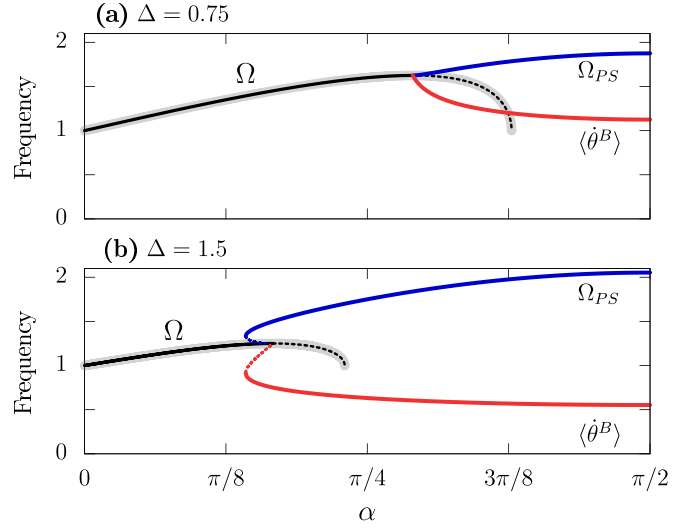


FIG. 2. Frequencies of the mean fields in the S [Ω_S : black lines, Eq. (4)] and PS [Ω_{PS} : blue lines; Eq. (17)] states, and time-averaged frequency of asynchronous oscillators in the PS state [$\langle \dot{\theta}^B \rangle$: red lines, Eq. (18)]. Gray thick line: function $\Omega(\alpha)$, Eq. (4). Solid and dashed lines: stable and unstable states, respectively. Parameters: $K = 1$, $\bar{\omega} = 1$, and (a) $\omega_A = 1.375$, $\omega_B = 0.625$ and (b) $\omega_A = 1.75$, $\omega_B = 0.25$.

for $\bar{\omega} = (\omega_A + \omega_B)/2$. The function $\Omega(\alpha)$ (thick gray lines, Fig. 2) has a maximum, $\Omega_M = \omega_B + K$, at

$$\alpha_M = \arccos \sqrt{\frac{\Delta}{2K}}. \quad (5)$$

At this critical point, Ω maximally deviates from ω_B . Next, we show that S states with $\alpha > \alpha_M$ are inherently unstable in networks with $N > 1$ and lead to the “disintegration” of the in-phase synchronized cluster of B oscillators.

IV. STABILITY OF S STATES

To elucidate the origin of this instability in large networks, we initialize Eq. (1) in an S state for some $\alpha \in (0, \alpha_S)$ such that $\theta_j^{A,B} = \psi_{A,B}$ for all $j = 1, \dots, N$, with a phase difference $\psi_A - \psi_B = \phi^*$ defined by Eq. (3). We then study the dynamics of a single oscillator “ i ” in population B driven by a periodic force of frequency $\Omega(\alpha)$. In the thermodynamic limit ($N \rightarrow \infty$), the relative phase of the oscillator, $\varphi_i = \psi_A - \theta_i^B + \alpha$, evolves according to the Adler equation [39]

$$\dot{\varphi}_i = \Omega(\alpha) - \omega_B - K \sin \varphi_i, \quad (6)$$

where the time-independent frequency $\Omega(\alpha)$ is given by Eq. (4). At the critical value $\Omega(\alpha_M) = \Omega_M$, Eq. (6) possesses a unique fixed point, $\varphi_i^* = \phi^*(\alpha_M) + \alpha_M = \pi/2$, which defines the boundary of the synchronization region (Arnold tongue) for the driven oscillator. Inside the Arnold tongue ($\Omega < \Omega_M$), Eq. (6) yields two equilibria corresponding to frequency entrainment: a stable one at $\varphi_i^* < \pi/2$ and an unstable one at $\varphi_i^* > \pi/2$.

Systems with $\alpha < \alpha_M$ possess an S state that satisfies $\phi^*(\alpha) < \phi^*(\alpha_M)$ because the phase difference in Eq. (3) is a strictly increasing function of α [see Fig. 4, panels (c) and

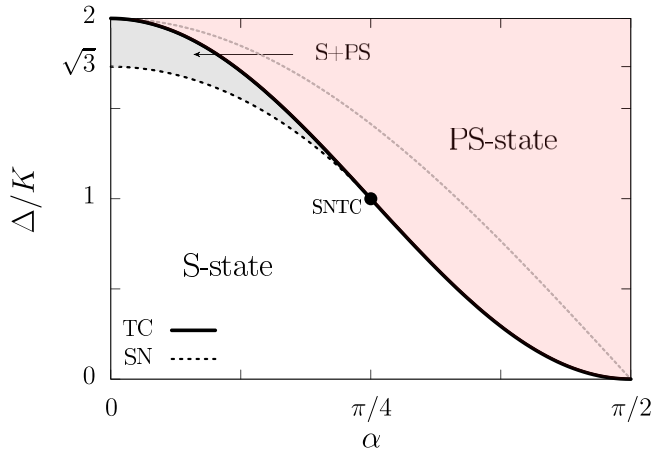


FIG. 3. Phase diagram of the bipartite KS model. Dotted thin line: SN boundary, Eq. (2). Black solid line: instability boundary (TC bifurcation in the OA equations), Eq. (5). Dashed line: SN bifurcation, Eq. (15). Symbol “•”: Saddle-Node-Transcritical (SNTC) point ($\pi/4, 1$). White region (S state): S state is the only stable attractor. Red region (PS state): PS state is the only stable attractor. Gray region (S + P): coexistence of stable S and PS states.

(d)]. This S state corresponds to a fixed point of Eq. (6) where $\varphi_i^* = \phi^*(\alpha) + \alpha < \phi^*(\alpha_M) + \alpha_M = \pi/2$, and is therefore stable. In contrast, systems with $\alpha > \alpha_M$ exhibit an S state with $\phi^*(\alpha) > \phi^*(\alpha_M)$, which corresponds to a fixed point of Eq. (6) with $\varphi_i^* > \pi/2$, and it is unstable.

This asymptotic analysis is corroborated by a full linear stability analysis of Eq. (1), which shows that S states are unstable for $\alpha > \alpha_M$ not only in very large networks, but also in networks of any finite size $N > 1$ [40]. This instability leads to the disintegration of the in-phase synchronized cluster of B oscillators. Its boundary [Eq. (5)] is depicted in the phase diagram in Fig. 3. Additionally, the synchronization frequency Ω is plotted in Fig. 2, where solid and dashed black lines indicate whether the S state is stable or unstable, respectively.

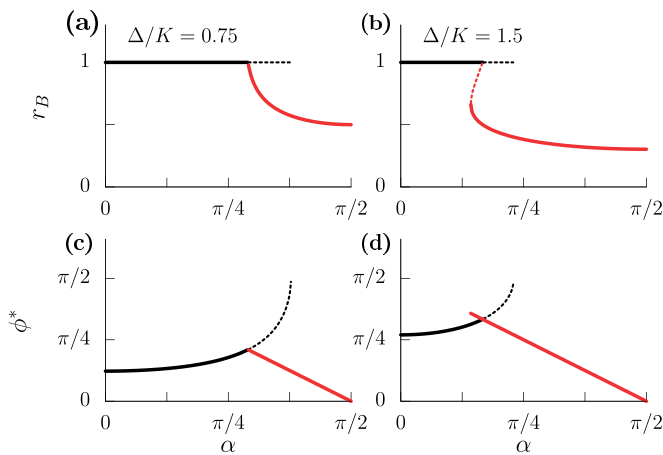


FIG. 4. Bifurcation diagrams of Eqs. (10)–(12), for $r_A = 1$. Black: S state, $r_B = 1$ and ϕ^* given by Eq. (3). Red: PS states, r_B given by Eq. (14), and ϕ^* by Eq. (13). Solid and dashed lines denote stable and unstable states, respectively. Parameters: (a), (c) $\Delta/K = 0.75$; (b), (d) $\Delta/K = 1.5$.

V. OTT-ANTONSEN EQUATIONS

Next, we demonstrate that beyond the critical point $\alpha = \alpha_M$, a stable PS state exists characterized by a mean field of frequency $\Omega_{PS} > \Omega_M$ that does not entrain the oscillators of population B. To investigate PS states, we analyze the thermodynamic limit of Eq. (1) by means of the Ott-Antonsen (OA) ansatz [41]. Here, we succinctly describe the basic steps to obtain low-dimensional equations describing the dynamics of Eq. (1) in the so-called OA manifold [18,42]. Our derivation trivially follows that of Refs. [17,19].

We assume the existence of two probability densities $f_\sigma(\theta_\sigma, t)$ that satisfy continuity equations for each population, where

$$v_\sigma(\theta_\sigma, t) = \omega_\sigma + \frac{K}{2i} [z_{\sigma'} e^{-i(\theta_\sigma - \alpha)} - \bar{z}_{\sigma'} e^{i(\theta_\sigma - \alpha)}]$$

corresponds to the continuum limit of Eq. (1) (the overbar denotes the complex conjugate), and

$$z_\sigma = r_\sigma e^{i\psi_\sigma} = \int_0^{2\pi} e^{i\theta_\sigma} f_\sigma(\theta_\sigma, t) d\theta_\sigma \quad (7)$$

are the complex Kuramoto order parameters. The OA is the expansion of $f_\sigma(\theta_\sigma)$ in the Fourier series [41]

$$f_\sigma(\theta_\sigma, t) = \frac{1}{2\pi} \left(1 + \sum_{n=1}^{\infty} [a_\sigma(t) e^{in\theta_\sigma}]^n + \text{c.c.} \right), \quad (8)$$

where “c.c.” denotes the complex conjugate of the preceding term. Substituting Eq. (8) into the continuity equation, $\partial_t f_\sigma = -\partial_\theta (v_\sigma f_\sigma)$, and using the identity $z_\sigma = \bar{a}_\sigma$ yields a system of ordinary differential equations

$$\dot{z}_\sigma = i\omega_\sigma z_\sigma + \frac{K}{2} [e^{i\alpha} z_{\sigma'} - e^{-i\alpha} \bar{z}_{\sigma'} z_\sigma^2]. \quad (9)$$

In polar coordinates, the system reduces to a three-dimensional system

$$\dot{r}_A = \frac{K}{2} r_B (1 - r_A^2) \cos(\phi - \alpha), \quad (10)$$

$$\dot{r}_B = \frac{K}{2} r_A (1 - r_B^2) \cos(\phi + \alpha), \quad (11)$$

$$\begin{aligned} \dot{\phi} = & \Delta - K r_A \frac{1 + r_B^2}{2 r_B} \sin(\phi + \alpha) \\ & - K r_B \frac{1 + r_A^2}{2 r_A} \sin(\phi - \alpha), \end{aligned} \quad (12)$$

where $\phi = \psi_A - \psi_B$. These equations have a fixed point $r_A = r_B = 1$ and $\phi = \phi^*$, corresponding to the synchronized S state analyzed above. The Jacobian matrix corresponding to the S state is triangular with three real eigenvalues μ, μ_A, μ_B , which coincide with the eigenvalues determining the stability of the S state in the finite-size system (see Ref. [39]).

Equations (10)–(12) have another type of fixed points corresponding to PS states. Setting $r_A = 1$, the fixed point equation $\dot{r}_B = 0$ yields a phase mismatch [43]

$$\phi^* = \pi/2 - \alpha, \quad (13)$$

which depends only on the phase-lag parameter α . Setting $\dot{\phi} = 0$, we find two roots of the order parameter

$$r_B = (\Delta/K \pm \sqrt{(\Delta/K)^2 - 4 \cos^2 \alpha + 1})^{-1}. \quad (14)$$

Note that for $\alpha = \alpha_M$ the order parameter reaches $r_B = 1$. Hence, Eq. (5) is the locus of a TC bifurcation where the S and PS states exchange stability [44]. In addition, Eq. (14) shows that PS states are born with $r_B = K/\Delta \leq 1$ in an SN bifurcation at

$$\alpha_{PS} = \arccos\left(\frac{1}{2}\sqrt{1 + (\Delta/K)^2}\right), \quad (15)$$

for $\Delta/K \in (1, \sqrt{3})$. The SN and TC bifurcations meet at an SNTC bifurcation point when $r_B = K/\Delta = 1$, for $\alpha = \pi/4$. The unfolding of this codimension-2 point reveals two scenarios (see Fig. 3). Specifically, the bifurcation diagrams in Fig. 4 show that for $\Delta/K \in (0, 1)$ the PS state bifurcates continuously from the S state, whereas for $\Delta/K \in (1, \sqrt{3})$ the transitions $S \leftrightarrow PS$ are discontinuous and hysteretic.

VI. SELF-ORGANIZED QUASIPERIODICITY IN KURAMOTO-SAKAGUCHI NETWORKS

Our last result concerns SOQ, a remarkable self-organization mechanism proposed to explain the emergence of partially synchronized states in *single* populations of identical oscillators interacting through *nonlinear* mean-field coupling [33,34].

We now show that the same mechanism operates in the PS states of Eq. (1), despite the fact that the KS model depends only *linearly* on the mean field. To see this, we assume $\theta_i^A = \psi_A$ for all i , and rewrite the evolution equation of the B oscillators in terms of their own mean-field phase ψ_B :

$$\dot{\theta}_i^B = \omega_B - K \sin(\theta_i^B - \psi_B - \beta(\phi)), \quad (16)$$

where $\beta(\phi) = \phi + \alpha$. The stability of the in-phase synchronized state of B oscillators is determined by $d\dot{\theta}_i^B/d\theta_i^B = -K \cos \beta(\phi)$. Notably, using Eq. (13), we find $d\dot{\theta}_i^B/d\theta_i^B = 0$, so that the oscillators are neither attracted to nor repelled from their mean-field phase ψ_B . In other words, the system operates at the critical boundary between synchrony and incoherence by self-adjusting the phase difference between the order parameters [Eq. (13)]. The phase difference ϕ is a degree of freedom that is not available in single populations of identical oscillators, which require additional structure (e.g., nonlinear coupling) to sustain partial synchrony [33,34].

Finally, we evaluate the average frequency of the oscillators in the B population and show that it can be made arbitrarily smaller than that of the mean field, in agreement with E-I neural oscillations. Using Eq. (9), we find the mean-field frequency

$$\Omega_{PS} = \omega_B + K(1 + r_B^2)/(2r_B), \quad (17)$$

where r_B is given by Eq. (14). Note that this frequency coincides with Ω_M for $r_B = 1$ and increases (without bound) as $r_B \rightarrow 0$ (see Figs. 2 and 4). Therefore, $\Omega_{PS} \geq \Omega_M$, so the mean-field frequency cannot entrain the oscillators in population B. Accordingly, these oscillators exhibit quasiperiodic dynamics with time-averaged frequency

$$\langle \dot{\theta}^B \rangle = \Omega_{PS} - \sqrt{(\Omega_{PS} - \omega_B)^2 - K^2}, \quad (18)$$

obtained by integrating Eq. (6) with $\Omega = \Omega_{PS}$ over one rotation period. For $r_B = 1$, $\langle \dot{\theta}^B \rangle = \Omega_{PS}$, while $\langle \dot{\theta}^B \rangle$ decreases as $r_B \rightarrow 0$, asymptotically approaching ω_B (see Figs. 2 and 4). Hence, the mean-field frequency [Eq. (17)] can differ

significantly from that of the B oscillators, in agreement with experimental and computational studies in neuroscience (see, e.g., Refs. [8,45,46] and references therein).

VII. CONCLUSIONS

We investigated the coexistence of full and partial synchrony in E-I neural networks, using the KS model on a bipartite network. This canonical model, which can be formally derived from a network of QIF neurons [15], is highly amenable to analysis. Beyond the expected synchronized state, the bipartite KS model exhibits a partially synchronized state that reproduces key phenomenology observed in E-I networks: namely, fast collective oscillations coexisting with slow, nonperiodic individual oscillator dynamics within one population (typically the excitatory one). However, these dynamics are quasiperiodic and lack the high irregularity characteristic of actual neuronal recordings or models incorporating quenched disorder and stochastic inputs [45–51].

Our analysis reveals two bifurcation scenarios featuring both continuous and discontinuous transitions from full to partial synchrony. Discontinuous transitions are hysteretic and may be relevant for exploring the role of oscillations and synchrony in working memory [46,52–56]. Finally, we found that PS in the bipartite KS model displays a nontrivial self-organizing property: The order parameters of the two populations remain phase locked at a precise phase difference, such that oscillators in one population are neither attracted to nor repelled from their mean-field phase. We showed that this self-organized critical state constitutes a novel form of self-organized quasiperiodicity [33]. Yet, in contrast to the original SOQ mechanism—introduced to explain PS in single populations of identical oscillators—the phenomenon observed here takes place in a system with purely linear coupling and is enabled by the additional degree of freedom provided by the bipartite structure of the network.

Our results suggest that this mechanism may also operate in more general two-population KS networks with recurrent coupling and could underlie the emergence of chimera states in such systems [17–22].

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DATA AVAILABILITY

There are no publicly available research data or software supporting this manuscript. Requests for further information or data should be sent to the authors.

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