

Mechanisms of Recruitment and Inhibition on a Time-Dependent Interaction Network



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Objective

The transmission of pheromones that inhibit the maturation of hive bees into foragers regulates task differentiation in honey bee colonies. Significant recruitment of hive bees into foragers occurs in the absence of such transmission. This research aims to develop models of time-dependent social network dynamics, which incorporate key mechanisms of recruitment and inhibition, as well as explain transient and steady-state spatiotemporal variations in the ratio of foragers to hive bees.

Model development

Continuous-in-time and spatially homogenized models (Box 1) of the population dynamics in a honey bee colony assume that the recruitment of hive bees to foragers is governed by the average density of foragers across the entire colony, in analogy to well-stirred chemical reaction kinetics.

Let H and F denote the number of hive bees and foragers, respectively, such that $N = H + F$ is the population size. Then,

$$\begin{aligned} \frac{dH}{dt} &= -R(H, F)H + E(H, F), \\ \frac{dF}{dt} &= R(H, F)H - mF, \end{aligned}$$

where $E(H, F) = LN/(w + N)$ denotes the eclosion rate of hive bees, $R(H, F) = \alpha - \sigma F/N$ denotes the recruitment rate of hive bees into foragers, and m is the death rate of foragers.

Box 1. Model from Khoury, Myerscough, & Barron (2011) PLoS ONE 6(4): e18491.

The low volatility of key signaling pheromones implies that in order to resolve the time-dependent task differentiation in the colony, one must account for interactions between *individual* bees. In an example model (Box 2), the recruitment of hive bees into foragers depends on the local density of foragers, defined in terms of a network neighborhood of interactions.

Consider a time-dependent network of N agents, and associate each agent with a state S , a fraction f of neighboring agents with $S = 1$, and a recruitment rate $r := \alpha - \sigma f$. Then, at each time step, recruitment and inhibition is described by

$$\begin{aligned} S = 0 \text{ and } r > 0 &\xrightarrow{p=r} S = 1 \\ S = 1 \text{ and } r < 0 &\xrightarrow{p=r(1-1/f)} S = 0 \end{aligned}$$

where p denotes the transition probability. Increase the number of agents with $S = 0$ by sampling from a Poisson distribution with expected value $E(\#S = 0, \#S = 1)$. Remove agents with $S = 1$ with probability m . Connect isolated agents to an arbitrary agent of the identical state. Add a connection from each agent to one second-order neighbor. Remove a connection from each agent with sigmoidal probability as function of degree.

Box 2. Stochastic time-dependent network model by Deng & Dankowicz.

Observations

The stochastic model in Box 2 accounts for coupled, time-dependent variations in the agent states *on* the network, as well as in the structure *of* the network. Numerical simulations demonstrate sensitivity, for example, to initial connectivity (Figure 1), as well as to the sigmoidal threshold for forgetting connections (Figure 2).

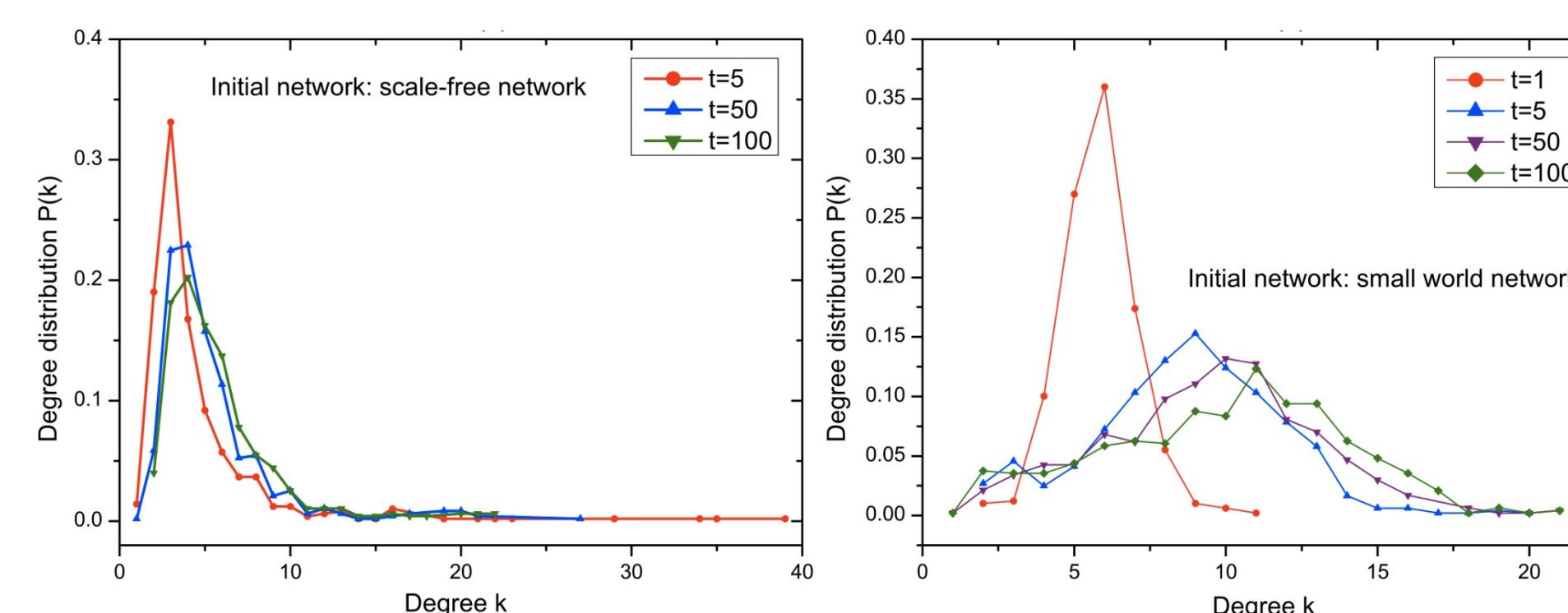


Figure 1. Time-dependent changes in degree distribution following initialization of a scale-free network (left) and a small-world network (right).

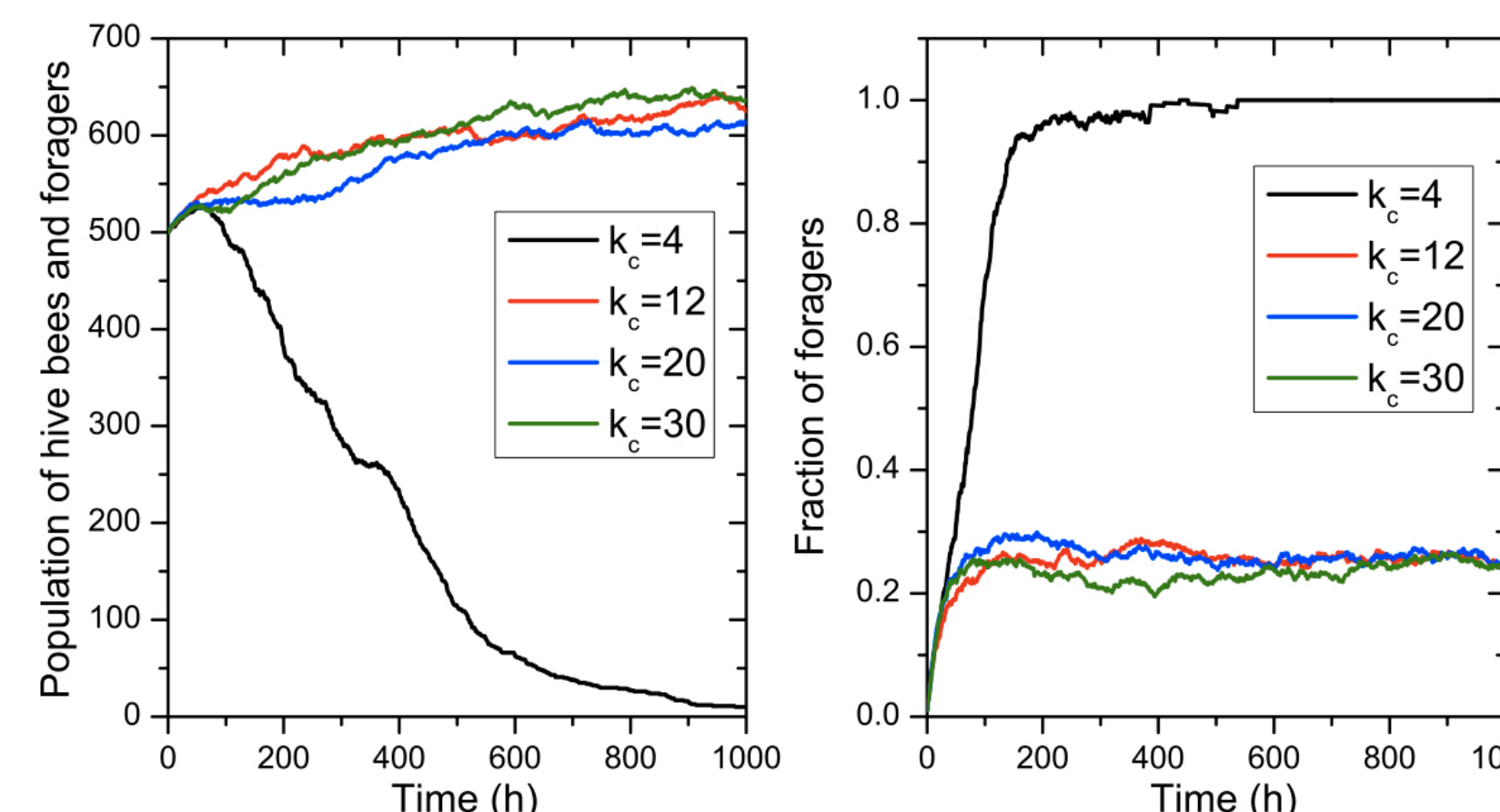


Figure 2. Time-dependent changes in population size (left) and fraction of foragers, i.e., agents with $S = 1$ (right), parameterized by the sigmoidal threshold for forgetting network connections k_c .

As seen in Figure 1, the initial degree distribution is patterned onto the time-dependent network, and sustained by the dynamics in the agent states, even as agents are removed and added to the network.

Similarly, as seen in Figure 2, for low values of the sigmoidal threshold k_c for forgetting network connections, recruitment outpaces inhibition all the way to the collapse of the network. For larger initial populations, changes to k_c also affect the steady-state population size, even in cases where the network persists.

Related trends may also be found in the distribution of ages corresponding to the onset of foraging, i.e., the transition to $S = 1$.

See also

- Poster Session B, #B.21: "Evidence for trophallaxis as a communication channel in honey bees," Tim Gernat, University of Illinois at Urbana-Champaign

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Alternative formulations

In the stochastic model in Box 2, space is represented by network connectivity; physical distance and movement are captured by mechanisms for recruitment and inhibition of connectivity. In an alternative formulation (Figure 3), network connectivity is represented by physical proximity, and network evolution is a passive consequence of a random walk in position and orientation. Foragers leave and return to the colony through the opening.

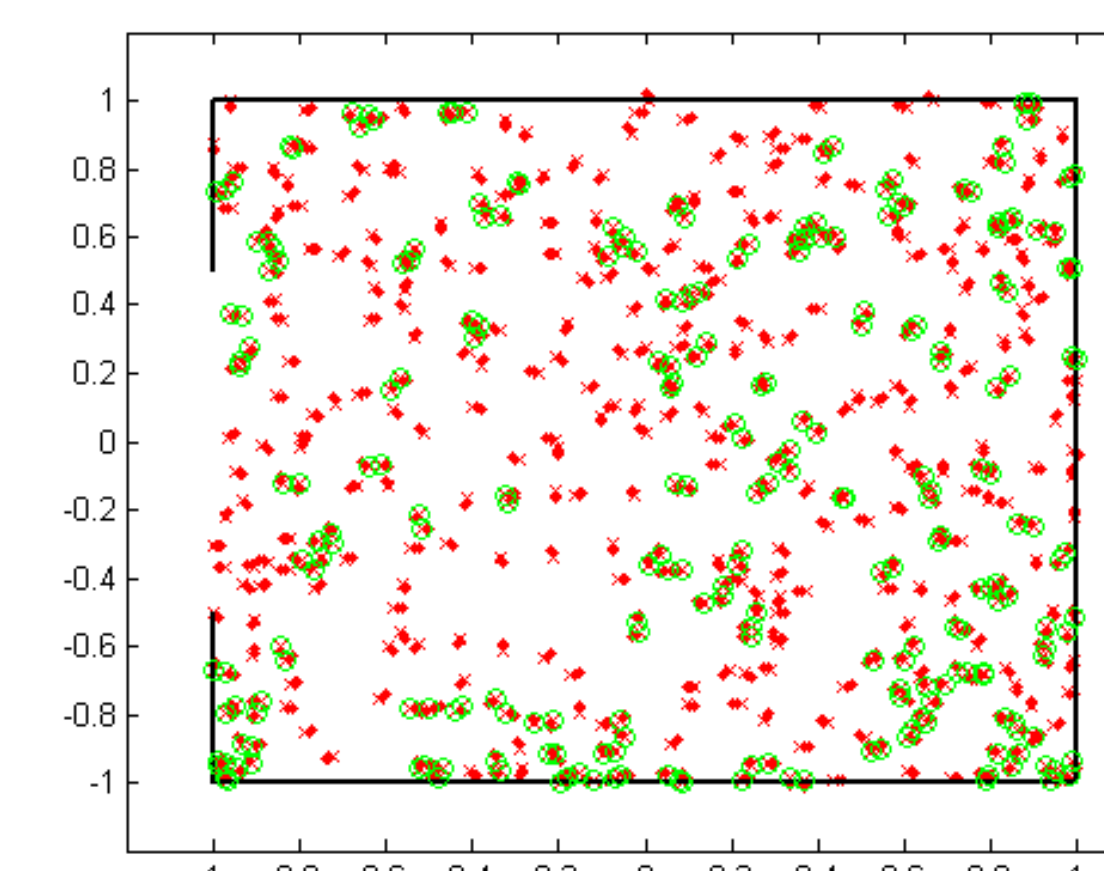


Figure 3. Network connectivity (green) represented by physical proximity of individual agents (red) translating in a bounded domain.

Symmetry breaking

In the stochastic model, no single agent plays a central role in information transmission. The dependence of the future state and connectivity of agents on the network and state time histories is parameterized homogeneously across the population. Ongoing work considers the effects of breaking this symmetry across agents (Figure 4), allowing for variability that may render individual agents more causally central to the effects of recruitment and inhibition on the transient and steady-state nature of the network.

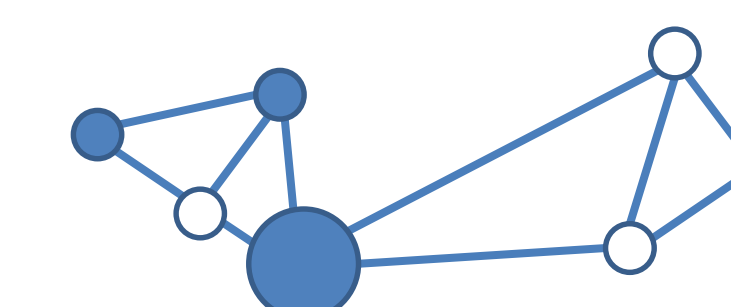


Figure 4. Agents with a higher sigmoidal threshold for forgetting network connections (larger circle) may serve as organizing centers for the signaling of recruitment and inhibition across the network.

Summary

We consider agent-based, stochastic, time-dependent social network models of task differentiation, with emphasis on the dynamics both on and of the network. Of particular interest are effects dependent on network size, the sensitivity to perturbations, and the occurrence of spatiotemporally coherent structures in the network dynamics, for example, persistent or spatially translating patterns of connectivity.

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Emergent Task Differentiation on Network Filters

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Objective

Task differentiation in a complex system affords a mechanism for achieving optimal collective behavior. In a leaderless society, task differentiation is an emergent consequence of the nature and ordering of interactions between individuals. The distribution of tasks exhibits some degree of plasticity to maintain desired function even when environmental conditions change. We analyze the emergence of task differentiation in a model complex system, characterized by an absence of hierarchical control and relying solely on local interactions, yet able to exhibit coordinated behavior and collective function.

Network filters

We consider network filters: collections of coupled, linear, mechanical oscillators with a differentiated, steady-state response to exogenous harmonic excitation. We focus on the near-resonant response of lightly damped filters, characterized by high-gain, long-range signal propagation.

Let $u(t)$ denote the displacement vector for a network of N identical, coupled, single-degree-of-freedom oscillators:

$$\ddot{u}(t) + 2\zeta\Omega\dot{u}(t) + (L + \Omega^2 I)u(t) = f(t)$$

in terms of the network Laplacian L , damping coefficient $\zeta \ll 1$, stiffness Ω^2 , and excitation vector $f(t) = a \cos \omega t$.

With ω far from a natural frequency and large N , we obtain a small-amplitude, spatially concentrated steady-state response.

With ω near a natural frequency Ω_m with mode shape v_m ,

$$u_{ss}(t) = \frac{v_m}{2\Omega\Omega_m\zeta} (v_m \cdot a) \sin \omega t + \mathcal{O}(\zeta)$$

is a large-amplitude, spatially distributed steady-state response.

Box 1. Analysis of the steady-state response of network filters to harmonic excitation.

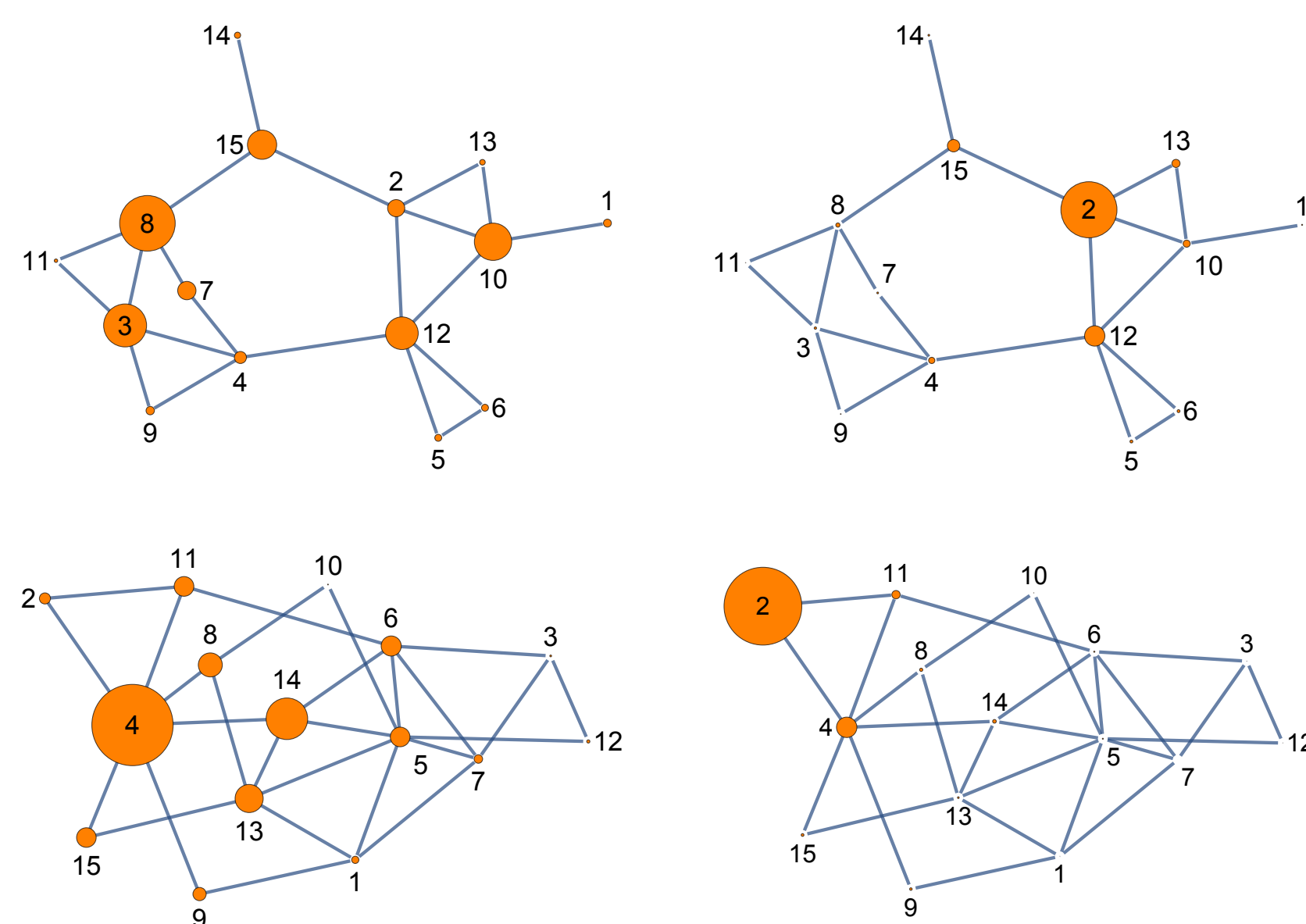


Figure 1. Spatially distributed steady-state oscillations at resonance (left panels) and spatially concentrated steady-state oscillations away from resonance (right panels). In each case, excitation is introduced with unit magnitude at node 2 and the size of the nodes is scaled by the largest response amplitude. The actual amplitudes differ by two orders of magnitude between the left and right panels.

Observations

The amplitude of the steady-state response at resonance is maximized when the vector of excitation sensitivities (a_1, a_2, \dots) is aligned with the mode shape v_m . With $a_i \in [0,1]$, an optimal response is obtained by designating a particular subset \mathcal{S} of *sending nodes* with $a_k = 1$ for $k \in \mathcal{S}$ and $a_k = 0$ for $k \notin \mathcal{S}$ corresponding to a corner of $[0,1]^N$. This assignment of excitation sensitivities imposes a form of task differentiation across the network.

Let P_+ , P_0 , and P_- denote subsets of node indices corresponding to positive, zero, and negative components of v_m , respectively. Then,

$$\sum_{k \in P_+} v_{m,k} \geq - \sum_{k \in P_-} v_{m,k} \Rightarrow \mathcal{S} = P_+$$

is the globally optimal solution.

Box 2. Globally optimal task differentiation across an arbitrary network.

1. Can we design a learning algorithm that converges to the globally optimal assignment of excitation sensitivities based only on local interactions within the network?
2. What conditions ensure such emergent coordination and what conditions prevent coordination?

Learning algorithm

If a node belongs to P_0 , set its sensitivity to 0. If not, look at the node's neighbors. If the node can help by being more sensitive, then increase its sensitivity, otherwise decrease its sensitivity. When in doubt, do nothing!

For $n \notin P_0$, let \mathcal{F}_n denote the neighborhood of the n -th node (excluding the node itself) and let $g_n \triangleq \sum_{k \in \mathcal{F}_n} v_{m,k} a_k$. Then,

$$a_n \mapsto \begin{cases} \rho + (1 - \rho)a_n & \text{if } g_n v_{m,n} > 0 \\ (1 - \rho)a_n & \text{if } g_n v_{m,n} < 0 \\ a_n & \text{if } g_n = 0 \end{cases}, \rho \in [0,1]$$

- The designation of \mathcal{S} as any union of connected components of P_+ or P_- is a fixed point of the learning dynamics.
- The designation of \mathcal{S} as the largest subset of P_+ such that $\mathcal{S} \cap \mathcal{F}_n \neq \emptyset$ for every $n \in \mathcal{S} \cup P_-$ is asymptotically stable if nonempty. Any proper subset of such a set is unstable.
- The globally optimal designation of \mathcal{S} is unstable if $g_n = 0$ for some n , and asymptotically stable if the neighborhood of every node includes nodes in P_+ .

Box 3. Nature of learning dynamics based solely on local interactions.

See also

- Saghafi, M., Dankowicz, H., and Tabor, W. (2017) "Emergent Task Differentiation on Network Filters," *SIAM J. Appl. Dyn. Syst.* 16-3, pp. 1686-1709.
- Gernat, T., Rao, V.D., Middendorf, M., Dankowicz, H., Goldenfeld, N., and Robinson, G.E. (2017) "Automated monitoring of behavior reveals bursty interaction patterns and rapid spreading dynamics in honey bee social networks," in review.

Predictions and numerical verification

For the mode shape in the left panel of Figure 2, $\mathcal{S} = \{1,2,5,9,12,13,15\}$ is asymptotically stable, but suboptimal. Every designation of \mathcal{S} as a subset of P_+ is unstable. Nevertheless, and quite remarkably, $\mathcal{S} = \emptyset$, $\mathcal{S} = \{6,11\}$, $\mathcal{S} = \{8,10,14\}$, and $\mathcal{S} = \{6,8,10,11,14\}$ all attract open sets of initial conditions.

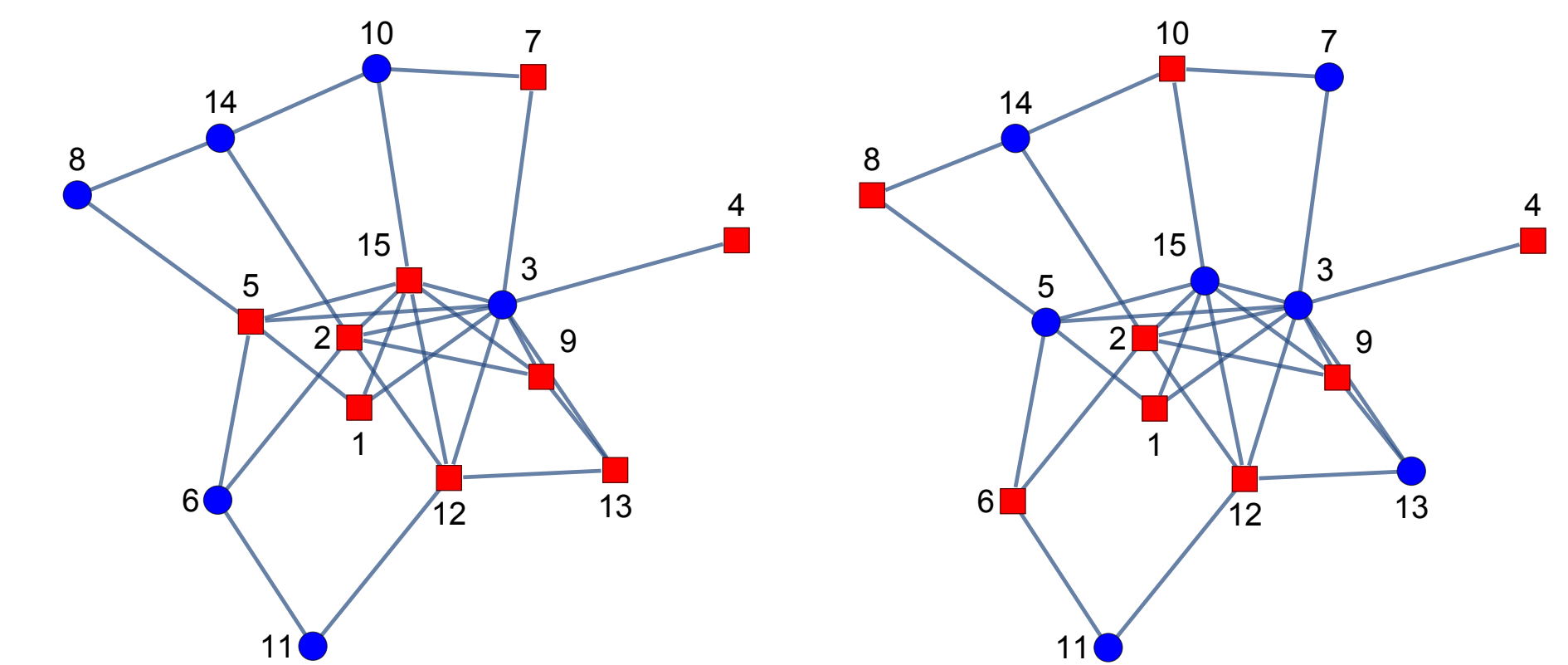


Figure 2. For a given mode shape, the existence and stability of fixed points of the learning dynamics depends on the distribution of nodes belonging to P_+ (blue) and P_- (red).

For the mode shape in the right panel of Figure 2, as suggested in Figure 3, $\mathcal{S} = \{2,6,9,12\}$ is unstable but attracts an open set of initial conditions. On the other hand, $\mathcal{S} = \{3,5,7,13,15\}$ is asymptotically stable, but suboptimal. The globally optimal solution is unstable. Two period-2 attractors exist for $0.772 < \rho < 0.880$. Recurrent transitions between the unstable suboptimal fixed points $\mathcal{S} = \{2,6,9,12\}$ and $\mathcal{S} = \{2,6,7,9,12\}$ may be induced by noise.

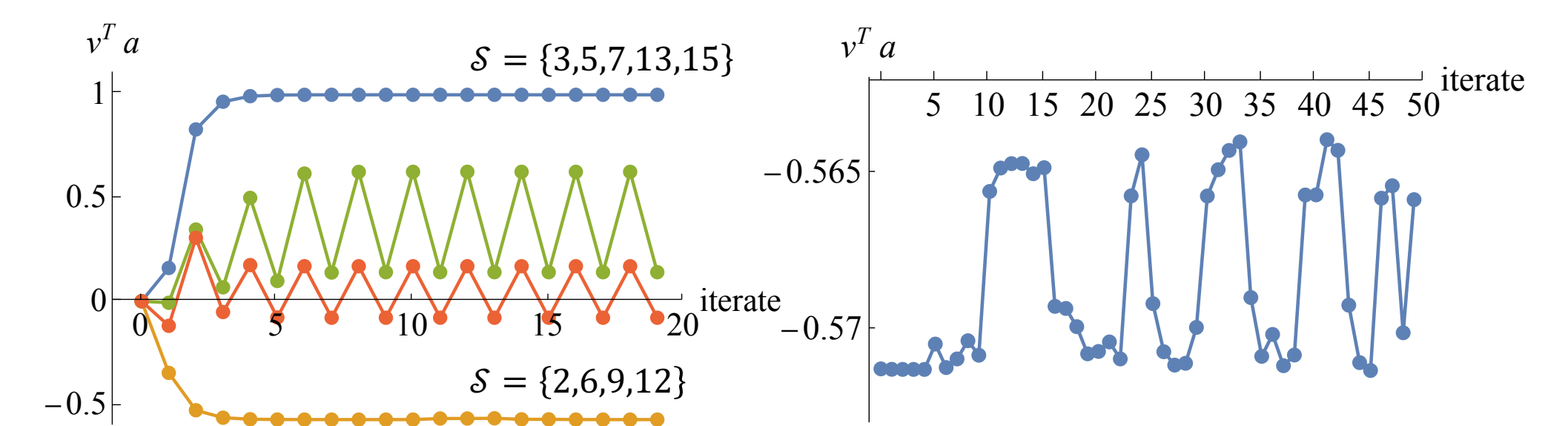


Figure 3. Iterated dynamics of the learning algorithm for $\rho = 0.8$ and initial conditions near the trivial fixed point $\mathcal{S} = \emptyset$ (left) and near a cycle of noise-induced connecting transitions (right).

Discussion

Social insects appear to rely on interaction networks to structure the allocation of tasks across the colony. For example, signaling substances may be exchanged during trophallaxis to regulate the recruitment of hive bees into foragers. The model analysis shows that local interactions that seek to achieve a globally optimal behavior may lead a system to converge to a condition of collapse (here, $\mathcal{S} = \emptyset$), in which negative feedback suppresses the contributions of individual agents toward optimal coordination. Whether this phenomenon explains empirical observations on failures of social insects or other complex systems to coordinate remains an open question.

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