Information socialtaxis and efficient collective behavior emerging in groups of information-seeking agents

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Individual behavior, in biology, economics, and computer science, is often described in terms of balancing exploration and exploitation. Foraging has been a canonical setting for studying reward seeking and information gathering, from bacteria to humans, mostly focusing on individual behavior. Inspired by the gradient-climbing nature of chemotaxis, the infotaxis algorithm showed that locally maximizing the expected information gain leads to efficient and ethological individual foraging. In nature, as well as in theoretical settings, conspecifics can be a valuable source of information about the environment. Whereas the nature and role of interactions between animals have been studied extensively, the design principles of information processing in such groups are mostly unknown. We present an algorithm for group foraging, which we term "socialtaxis," that unifies infotaxis and social interactions, where each individual in the group simultaneously maximizes its own sensory information and a social information term. Surprisingly, we show that when individuals aim to increase their information diversity, efficient collective behavior emerges in groups of opportunistic agents, which is comparable to the optimal group behavior. Importantly, we show the high efficiency of biologically plausible socialtaxis settings, where agents share little or no information and rely on simple computations to infer information from the behavior of their conspecifics. Moreover, socialtaxis does not require parameter tuning and is highly robust to sensory and behavioral noise. We use socialtaxis to predict distinct optimal couplings in groups of selfish vs. altruistic agents, reflecting how it can be naturally extended to study social dynamics and collective computation in general settings.

foraging | information maximization | chemotaxis | exploration | exploitation

Foraging is fundamental for survival and reproduction in numerous species and is often based on sparse and noisy sensory cues in complex environments. Understanding how organisms represent space and navigate and the utility functions and computations that underlie movement patterns and social behavior (1–6) critically depends on characterizing the nature of foraging. Theoretical models of foraging have been pivotal in economics, physics (7, 8), and machine learning (9) as a general framework for decision making, exploration and exploitation, optimization, and learning (10).

Climbing the gradient of a sensory signal is an efficient foraging strategy for finding a strong source in nonturbulent environments or on a microscopic scale, as demonstrated, for example, by theoretical and experimental studies of bacterial chemotaxis (1, 11). However, for weak sources, or on a macroscopic scale that is characterized by turbulent flows, the signal coming from a source is typically broken into random, sparse, and disconnected patches (12). Without a continuous gradient, a different strategy is needed to read and use information from these patches about the location of the source (13). Vergassola et al. (14) presented a foraging algorithm based on maximizing the information that an agent has about the location of a source and showed that it

is highly efficient in finding a sparsely signaling source in a turbulent environment. These infotaxis search trajectories resemble the paths of foraging insects, suggesting a biological implication of this model.

In nature, many species, including bacteria (15), amoebae (16), insects (17, 18), fish (19), birds (3), and mammals (20, 21), display complex group behavior, including foraging. The mechanisms that underlie group behavior have been of great experimental and theoretical interest, focusing on the computation that each individual performs (22–24) and emergent collective behavior (24, 25). In terms of social behavior, such models have been used to describe exploration and exploitation of the environment, finding food or mates, decision making (26–29), and altruistic and opportunistic behavior, as well as the design of systems of conflicting components (30) and distributed algorithms (31).

We present a model of foraging in a group that combines infotaxis and social interactions, using information as a unifying principle. In this socialtaxis model, agents seek a signal-emitting source, using the information they receive through their own "senses" and information they receive from other agents or that they infer from the behavior of their conspecifics. We show that certain forms of socialtaxis allow a collection of opportunistic individuals to find the source considerably faster than a collection of independent agents and comparable to the case of agents sharing all their sensory information and decision making using a centrally managed strategy (which is exponentially more expensive). Moreover, we find that coordinated group behavior emerges in a collection of selfish individuals each maximizing their own goal. We further present biologically plausible versions of socialtaxis,

in which agents share little or no information, and its robustness to various forms of noise. Finally, we show socialtactic optimal behaviors in game theory-like settings of competing and opportunistic agents, suggesting a wide range of applications for this model.

From Individual Infotaxis to Socialtaxis

The infotaxis algorithm (14) describes a strategy for individual foraging in space, where an agent (or animal) moves to maximize the information it has about the location of a stationary source that emits signals (or particles) in random directions at a low rate. In its discretized version, the search space is divided into "cells," and the agent estimates at each time t a probability map of the possible locations ($\mathbf{r}$) of the source $P_t(\mathbf{r})$. The entropy of the map at time t, given by $S[P_t(\mathbf{r})] = -\Sigma_\mathbf{r} P_t(\mathbf{r}) \log_2 P_t(\mathbf{r})$ (32), measures the uncertainty or missing information about the location of the source, in bits. At each time point, the agent may (*i*) find the source, (*ii*) detect a signal from the source ("hit"), or (*iii*) detect nothing. The agent then updates its probability map over the space based on one of these three events and uses the new map to decide whether to move to a neighboring cell or stay still. This decision is based on the expected information it would gain from each possible move, which is given by the expected change in entropy of each of the possible events in that location (finding the source, getting a hit, or not getting a hit), weighted by the probability of occurrence of each event (*Materials and Methods*). Fig. 1*A* shows the trajectories of two agents who are independently searching the source using infotaxis in a 2D arena, completely ignoring one another (Movie S1). The paths of these independent agents are typical of individual infotaxis searches (14), resembling trajectories of insects in nature.

If there are other agents (animals) around, then in addition to its own sensory information about the source, each agent may use information it receives from conspecifics or infers from their behavior. We therefore extended the infotaxis algorithm to consider the behavior of groups of agents. Here, each agent moved to minimize a combination of its own entropy (as in infotaxis) and some function of its relation to other agents. Thus, rather than minimizing entropy, each agent minimized a "free energy," given by

$$F_i = S[P_i] + \beta G_i(\text{group}), \qquad [1]$$

where $S[P_i]$ is the entropy of the probability map P_i of agent i, as in the single-agent infotaxis above, G_i is a social interaction term between agent i and the rest of the group, and β weighs the balance between the individual's information and its coupling to others. The nature of this socialtaxis model is determined by G_i, or how individuals affect one another, and β, the coupling strength or inverse "temperature," which balances individual information and social interactions: $\beta = 0$ reduces socialtaxis to the standard individual infotaxis behavior of each agent, and $\beta \to \infty$ implies pure socially driven behavior.

Following many models of collective behavior, a natural choice for the relation between individuals would be one that is determined by the physical distance between them. We consider here the case where the free energy of agent i is given by

$$F_i^{dist} = S[P_i] + \beta \Sigma_j d_{ij}^\alpha, \qquad [2]$$

where d_{ij} is the Euclidean distance between agents i and j, $\alpha > 1$ is a tunable parameter that determines the scaling of the distance between agents, and the summation goes over all group members. We explored the behavior of groups of 2–20 agents searching for a single sparse source in a 2D arena and found that for each choice of α, there was an optimal β that was always positive and minimized the time needed for the first member of the group to find the source (*Distance-Based Socialtaxis*). However, even for the optimal values, the improvement in search time compared with independent agents was very small (more below). Fig. 1*B* shows an example of the cohesive trajectories of two coupled agents with their optimal β_{opt} (Movie S1).

We then considered a socialtaxis model in which social interactions were based on the information that agents have and not their physical locations. Here each agent aims to minimize the combination of its entropy and the overlap in the information it has in common with the other agents,

$$F_i^{info} = S[P_i] - \beta \Sigma_j D_{KL}[P_i||P_j], \qquad [3]$$

where P_i and P_j are the probability maps of agents i and j, and D_{KL} is the Kullback–Leibler divergence (32) between probability maps, which measures in bits the dissimilarity between the distributions. For positive β this social term would drive agents to make their probability maps different from one another (constrained by the individual infotaxis term), whereas for negative β the social term would drive agents to merge their knowledge and make their individual maps more similar. Fig. 1*C* shows the trajectories of two agents under this model with strong coupling $\beta = 10$, reflecting their seemingly diverging yet highly time-efficient paths toward the source (Movie S1). The agents' trajectories are qualitatively different from the independent or distance-based algorithm and are similar to the trajectories of fully cooperating agents who use a joint probability map based on their joint hits, and individual movements are determined by
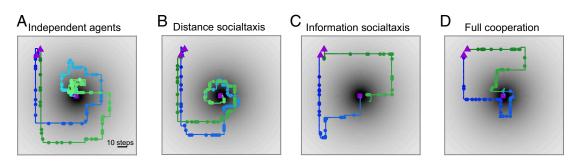

Fig. 1. Characteristic trajectories of pairs of agents searching for a source under different social interaction regimes. Shown are examples of pairs of agents, searching for a source located in the middle of the arena (purple square). Agents begin their search at the top left corner (purple triangles), and their trajectories are marked by blue and green paths, which are becoming lighter with time along the search; the circles on top of the trajectories indicate positions where hits were obtained (main text). The grayscale background represents the mean detection rate, decaying exponentially at large distances. (*A*) Independent agents, each performing infotaxis and ignoring one another. (*B*) Distance-dependent socialtaxis agents (Eq. **2**) remain close to each other and are slightly more efficient than independent agents. (*C*) Information-based socialtaxis agents (Eq. **3**) start off in different directions, seemingly dividing the search space and then quickly converging, resulting in highly efficient searches. (*D*) Fully cooperating pairs, who share their hits and coordinate their movements using a joint infotaxis algorithm (*Materials and Methods*), are highly efficient at finding the source.

a joint infotaxis strategy (Fig. 1D, Movie S1, and *Materials and Methods*).

We simulated the different socialtaxis models, under different parameter values, each with 3,000 randomly chosen initial configurations of the agents and the location of the source (to avoid any effects of specific choice of configuration, see also ref. 33). As the example trajectories in Fig. 1 reflect, the distance-based social-taxis enabled the agents to find the source a little faster than in the case of independent agents, but they were much slower than the fully cooperating agents (Fig. 2A), even with an optimal choice of β_{opt}, which we had to find numerically. A spring-like interaction between agents that drove them toward a nonzero distance gave qualitatively similar results, whereas negative β values, typically resulted in failure to find the source at all.

In clear contrast, the information-based socialtaxis showed a clear and abrupt decrease in search time compared with that of independent agents (Fig. 2A). Importantly, the performance of agents improved monotonically as β increased, and with large β this model was on par with the case of fully cooperating agents. This optimal behavior did not require any tuning of model parameters, which we show analytically (*Analytical Analysis of the Functional Dependence of the Search Times on Coupling Strength*). Notably, negative β values, which intuitively might
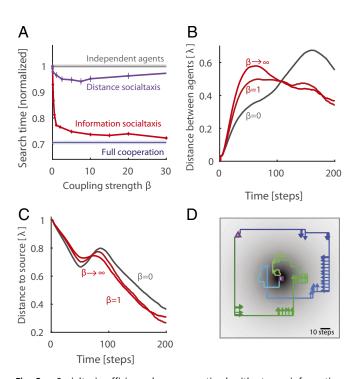
seem to enable agents to average their information and filter noise, resulted in failure to find the source in almost all cases (compare Movie S2 for $\beta > 0$ and Movie S3 for $\beta < 0$).

The nature of trajectories of the agents in the information-based socialtaxis delineates its efficiency: Because of the social information term, agents "repel" each other early on, more strongly as β is increased (Fig. 2B), which leads to an effective division of the search space. Later in the search, the social interaction is constrained by the individual knowledge, which results in faster and more accurate convergence toward the source. Accordingly, information coupling between agents reduced the characteristic long "overshoots" in the initial part of the trajectories seen in standard infotaxis that take them away from the source ($t \in [70, 100]$ in Fig. 2C). This is further reflected by comparing the individual locations along the path, where infotactic and socialtactic agents would move in different directions (Fig. 2D). Notably, information-based socialtaxis is robust to different kinds of variations, such as the starting distances from source, the size and shape of the arena, strength of the source, and decay length of the signal from the source (*Socialtaxis Is Robust to a Multitude of Environments and Wrong Modeling of the Environment* and Fig. S1), as well as different forms of sensory, odometry, or computational noise (Figs. S2 and S3). It was also highly efficient in reducing search times in a 3D space compared with the case of independent agents (Fig. S1E).

Emergent Group Behavior of Opportunistic Socialtaxis Agents Maximizing Their Information Gain

An emerging spatial collective behavior in the information-based socialtaxis becomes apparent when we study the trajectories of agents in larger groups (Fig. 3A and Movie S4). For a given group size N, increasing the weight of the social term β resulted in a faster finding of the source (Fig. 3B). For a given β value, the dependency on group size showed monotonic improvement in search time, hinting at the possibility of a power-law scaling (Fig. 3B, *Inset*). Again, large groups of agents that relied on distance-based socialtaxis showed only a small improvement in search times compared with those of independent agents, even in the best case ($N \approx 15$), and required fine tuning of model parameters (Fig. S4).

The socialtactic agents gain information about the source at a rate that is similar to that of independent agents in the initial parts of their search, but the social interactions boost the rate of information gain significantly later on (Fig. 3C). Consequently, when the first agent finds the source, all other agents have also gathered much more information. The information socialtaxis keeps agents consistently less clustered spatially than independent agents (Fig. 3D), yet when the first agent finds the source (faster), they are all much closer to it than in the case of independent agents (Fig. 3E). Thus, whereas there is no obvious residual N dependence of information sharing in terms of time to source of the first agent, there is clear benefit for the rest of the group: Even if the other agents did not know that the first agent had found the source, they would still find it faster as the coupling becomes stronger (Fig. S5 and *Socialtaxis Is Efficient for the Group, Beyond the First "Finder"*). Consequently, the group demonstrates a spatial "social structure" and coherent movements, despite the lack of an explicit spatial term in the model.

Biologically Plausible Socialtaxis and Optimal Behavior of Selfish, Opportunistic, or Altruistic Agents

How relevant is socialtaxis for real animal groups? First, we considered a more biologically realistic case, where each individual may be coupled differently to its conspecifics—as these couplings may be innate or learned from experience. Focusing on pairs of agents, we find that for a given coupling value of agent 2 to agent 1, $\beta_{2 \rightarrow 1}$, the mean time to find the source decreased

Fig. 2. Socialtaxis efficiency becomes optimal with strong information social coupling. (A) Mean search time vs. coupling strength β for two foraging agents using either information-based socialtaxis (red) or a distance-based one (purple, $\alpha = 4$). Search times are shown for two independent (gray) and fully cooperating agents (blue), with search times rescaled such that the search time of two independent agents is set to 1. Results shown are averaged over 3,000 randomly chosen configurations of the initial positions of the agents and the source; shaded regions and error bars represent SEM. Negative β values led to failed searches. (B) Average distance between agents vs. time for different coupling strengths β. (C) Average distance between the source and the agent that finds it vs. time. Results in B and C are averaged over 1,000 simulations of two agents, with the source in the center and agents starting near one another, close to one of the corners. (D) Trajectories of two independent infotactic agents are overlaid with marking of the points where a socialtaxis agent with the same information would choose a different direction; the direction of the socialtaxis agent is shown by an arrow; other details are as in Fig. 1.
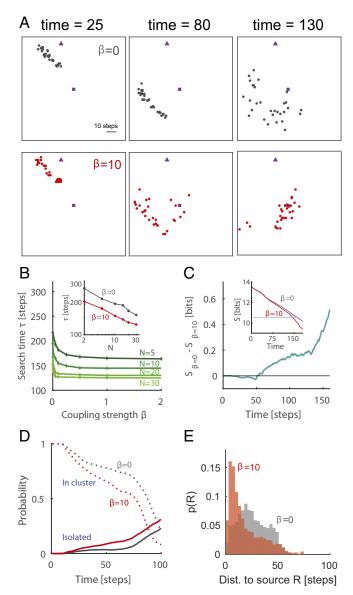
Fig. 3. Information socialtaxis in large groups and the emergence of collective behavior. (*A*) Examples of 30 agents performing infotaxis independently (*Top*) and information-based socialtaxis with $\beta = 10$ (*Bottom*). Each panel shows a snapshot in time of the agents. Starting area of agents is shown by a purple triangle and the source by a purple square. For presentation clarity, source is shown to be larger than its actual size, which is a single lattice site. (*B*) Mean search time for different group sizes *N*, performing information-based socialtaxis. Results are for 250 different groups and error bars show SEM. *B*, *Inset* shows mean search time as a function of group size for two values of β. (*C*) Difference in information gain between agents in information socialtaxis and independent agents as a function of time. *C*, *Inset* shows the average entropy of agents in the two cases as a function of time. Gray line shows the mean residual entropy when the source is found. (*D*) Average probability of an agent to be in a close group (cluster) with other agents (dotted lines) or alone (solid lines) vs. time for infotaxis and socialtaxis (see *Materials and Methods* for details). (*E*) Distribution of distances of agents from the source when the first agent has found it, for independent infotaxis agents and information socialtaxis ones. Groups started from the same initial conditions in both cases, and distributions are averaged over 1,000 random simulations.

monotonically as a function of the reciprocal coupling $\beta_{1 \to 2}$ (Fig. 4*A*). Thus, even when each agent can have an individually chosen coupling to the others, strong couplings are beneficial for the group as a whole. However, the optimal coupling value that

would benefit an individual's chances of finding the source are different from what would be good for the group: For a given value of $\beta_{2 \to 1}$ the optimal $\beta_{1 \to 2}$ that would raise the probability for agent 1 to find the source first has a peak at $\beta_{1 \to 2} \approx 0.5$, regardless of the value of $\beta_{2 \to 1}$ (Fig. 4*B*). Thus, optimizing group success or individual success requires very different coupling values. Still, even the most opportunistic choice of coupling values was more efficient for the group than the case of independent agents and would benefit the group.

The critical question of relevance of the socialtaxis model to real animals is the feasibility of information sharing between agents (34). Surprisingly, we found that even a very limited form of information sharing gives a highly efficient socialtaxis: If instead of sharing their full probability map at each time point (which is obviously biologically unrealistic), agents shared only the location of the peak of a Gaussian that approximates their current probability map, the search time of the group was comparable or even better than the case where the whole map was shared (Fig. 4*C*). Interestingly, the difference between the sharing of just the peak and that of their full maps was most apparent for weak coupling between agents; for strong couplings the
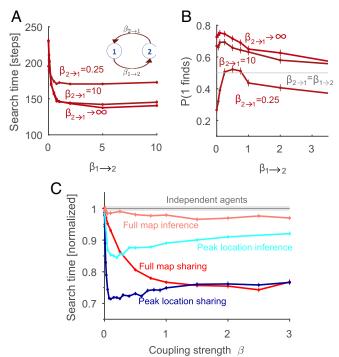

Fig. 4. Biological relevance and extensions of socialtaxis: diverse coupling strength, limited information sharing, and inference. (*A*) Mean search time of pairs of agents for different combinations of individually different couplings between them. Each line shows for a given coupling strength between 2 and 1, $\beta_{2 \to 1}$, the search time as a function of the coupling from 1 to 2, $\beta_{1 \to 2}$. (*B*) The probability that agent 1 would be the first one to find the source is shown as a function of the coupling strength from 1 to 2, $\beta_{1 \to 2}$, whereas $\beta_{2 \to 1}$ is held fixed at different values. Results for *A* and *B* are averaged over 3,000 random starting configurations. (*C*) Mean search time vs. coupling strength for two socialtaxis agents that share their respective maps with one another as above (dark red) and the search time when they share just the peak of a Gaussian fit with a predetermined variance to their map (dark blue). For the normalized mean search time for agents that do not share information, but infer their respective maps from the movement of other agents, inference of the full map based on estimated hits (pink) gives very small improvement compared with the case of independent agents (gray), whereas inferring only the peak location using GLM gives a significant improvement (light blue). Search times are normalized by the search times of two independent agents (set to 1). Error bars shown are SEM.

different models showed stable asymptotic behavior (Fig. S6 and *Exploring the Peak Inference Algorithm*).

Whereas this limited-bandwidth information sharing could be relevant for animals that actively communicate with one another, we further asked whether socialtaxis could work without any form of communication between individuals. We found that even if agents did not share any information, but instead tried to infer information about the source from their conspecifics based only on observing their behavior, they were able to perform a highly beneficial socialtaxis. Here, each of the agents used a simple generalized linear model (GLM) that estimated the peak position of the map of the other agent, based on its trajectory, which led to a substantial decrease in search time. This GLM-based inference model was less efficient than the information-sharing socialtaxis, but was still able to get the agents to find the source in 84% of the time needed by independent agents. We emphasize that this model is only a lower bound on how well inference-based socialtaxis can work, and therefore conclude that such an approach can be highly efficient with low computational cost for individual agents and is biologically feasible, in terms of memory and computational simplicity.

Discussion

We have introduced a model and algorithm for group foraging in complex environments where each agent aims to maximize the information from its own sensory perception and minimize the overlap in information it has with group members. Increasing the information diversity between members made the group highly efficient, similar to fully cooperating, optimally managed agents, in clear contrast to the small improvement achieved by models of group behavior that rely on the physical distance between individuals. Importantly, information socialtaxis did not require parameter tuning and was efficient under various variations of the model and robust to a multitude of noise sources. Most interestingly, biologically plausible versions of the model, based on limited or no information sharing, proved to be similar to or even better than the full model, making it a compelling framework for considering behavior of real animals.

Modeling individual behavior in a group, as an optimization problem combining self-information and group information, unifies the ideas of gradient-based search using sensory signals; social interactions; and game theory notions of opportunism, individualism, and group benefits. The success of our model challenges the commonly used models of group behavior based on distance or explicit spatial organization—suggesting information as key sufficient substance of sensory processing and collective behavior. In addition to being a biologically plausible, robust, and efficient model of group behavior in a variety of settings, socialtaxis suggests a potential design for new algorithms for distributed searching and learning.

Our framework also naturally exemplifies the benefits of diversity in groups and the qualitatively different collective behaviors that may arise from individual traits. Whereas these ideas have obvious parallels in game theory and behavioral economics, we note the relation of information-based socialtaxis to the studies of decorrelation and redundancy reduction as an optimization principle in neural coding (35). We thus suggest that information socialtaxis can be readily extended to explore animal groups; artificial agents; or other systems in which group relations can be learned or dynamically modulated; and groups in which individuals have different innate behaviors, preferences, or motivations.

Materials and Methods

Model of the Environment. A single source at an unknown location $\mathbf{r}_0$ in a finite environment is emitting particles with finite lifetime τ_p at a rate of R particles per second in random directions, advected by a mean wind V and diffusing Brownianly, with diffusivity D; for other conditions, see *Effect of Noise on Independent and Social Agents*. The average concentration field at

position $\mathbf{r}$ is a solution of the advection–diffusion equation, which for a constant diffusion coefficient $\nabla \cdot D = 0$ and incompressible flow $\nabla \cdot \vec{v} = 0$ gives (with advection flowing in the negative y direction) in the two-dimensional case a hit rate of

$$R_{hits}(\mathbf{r}|\mathbf{r}_0) = \frac{R}{\ln\left(\frac{\lambda}{a}\right)} exp\left[-\frac{(y - y_0)V}{2D}\right] K_0\left(\frac{|\mathbf{r} - \mathbf{r}_0|}{\lambda}\right), \quad [4]$$

where K_0 is the monotonically decreasing modified Bessel function of the second kind of order zero, and λ is the correlation length of the source. Here we focus on the case with no wind ($V = 0$), which has been shown to be the most difficult one (14, 36).

Infotaxis. The infotaxis algorithm is described in the main text and in detail in ref. 14. Briefly, an agent searching for the source decides on its move at time t based on the expected change in entropy of the probability distribution over the locations of the source, $p_t(\mathbf{r})$ from each of the possible moves from its location $\mathbf{r}(t)$. This is given by weighting the change of entropy from finding the source, getting a hit or "no hit" by their relative probabilities

$$\langle \triangle S(\mathbf{r}(t) \rightarrow \mathbf{r}') \rangle = p_t(\mathbf{r}')[-S] + (1 - p_t(\mathbf{r}'))[\rho_0(\mathbf{r}')\triangle S_0 \\ + \rho_1(\mathbf{r}')\triangle S_1], \quad [5]$$

where the first term on the right-hand side is the weighted value of the vanishing entropy from finding the source when moving to $\mathbf{r}'$ ("exploitation term"); and the second term is the sum of change in entropy from a hit and a no hit in that location weighted by their probabilities, where $\rho_k(\mathbf{r}')$ is the probability to get k hits at $\mathbf{r}'$. As in ref. 14, we neglect the case of $k > 1$ due to sparseness of the source.

Estimating and Updating the Probability Map of an Agent. At each time point, an agent estimates the expected number of hits at position $\mathbf{r}$ by $h(\mathbf{r}) \equiv \Delta t \int p_t(\mathbf{r}_0)R(\mathbf{r}|\mathbf{r}_0)d\mathbf{r}_0$. Assuming independent hits the probability to obtain k hits is given by a Poisson distribution, and then using the posterior map of a hit trace, the updated map is given by

$$p_{t+1}(\mathbf{r}_0) = \frac{1}{Z}p_t(\mathbf{r}_0) \begin{cases} e^{-R(\mathbf{r}(t)|\mathbf{r}_0)}, & \text{if } k = 0 \\ e^{-R(\mathbf{r}(t)|\mathbf{r}_0)}R(\mathbf{r}(t)|\mathbf{r}_0), & \text{if } k = 1' \end{cases} \quad [6]$$

where $h = 1(0)$ stands for the agent obtaining (not obtaining) a hit during this dt time step, Z is a normalization factor of the posterior probability, and the probability in visited sites is set to zero.

Model of Fully Cooperating Groups. Following Masson et al. (37), we consider the case of fully cooperating groups where agents shared a single probability map, updated at each step based on the hits/no hits of all agents,

$$p_{t+1}^{sh}(\mathbf{r}) = \frac{1}{Z}p_t^{sh}(\mathbf{r}) \cdot$$

$$\Pi_{i=1}^N \begin{cases} e^{-R(\mathbf{r}_i(t)|\mathbf{r}_0)}, & \text{if } k_i = 0 \\ e^{-R(\mathbf{r}_i(t)|\mathbf{r}_0)}R(\mathbf{r}_i(t)|\mathbf{r}_0), & \text{if } k_i = 1' \end{cases} \quad [7]$$

where N denotes the number of agents in the group, $\mathbf{r}_i$ denotes the position of agent i, $h_i = 1(0)$ corresponds to agent i obtaining (not obtaining) a hit during this time step, Z is the normalization factor, and the superscript sh indicates this map is shared by all agents. The decision on where to move is also coordinated as the agents evaluate all of the possible joint moves of the group. We note that the number of possible actions the group can take on a 2D square lattice is 5^N, which limits the size of the group that could use this algorithm due to the exponential growth in computational cost.

Spatial Organization of Groups of Agents. Analyzing behavior of large groups, "in cluster" and "isolated" agents were defined according to the number of conspecifics n_{nbr} inside the neighborhood of an agent, which was defined as a circle of radius d around it. In cluster was defined as $n_{nbr} \geq n_{cluster}$ and $n_{nbr} \leq n_{isolated}$ was defined as isolated. Here we used $d = 10$, $n_{cluster} = 10$, and $n_{isolated} = 3$, but different choices of parameters d, $n_{cluster}$, and $n_{isolated}$ gave qualitatively similar results.

Inference Model of Another Agent's Probability Map Based on Its Trajectory. Two inference models of the map of other agents were used to explore socialtaxis without sharing of information between agents. In the full-map inference model, agent i iteratively used its current model of the map of agent j, $\hat{P}_i^j(t)$, to assess the likelihood that the recent move of j was the result of a hit, and from the inferred hits, it estimated the probability map of the other agent (in the common case where both events would result in the same movement we assumed that i assigned a hit to j with a probability based on the map that i had at that time). Trying to infer hits using longer

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memory of past behavior of the other agents gave a small improvement of performance, but at an exponential computational cost. In the peak inference case, each agent tried to infer the location of the peak of the probability map of other agents, using a GLM. The x and y coordinates of the peak were estimated independently of each other with different models, where the past positions of the other agent were weighted and fed to a nonlinear function, to estimate the x or y location of the peak. We learned a separate model for a different starting region of the agents (space was split into 64 different 7×7 starting regions), and each model was trained using 10^5 simulated trajectories. This procedure was performed separately for every coupling strength β. In that case, the inferred map that i has of j,

$\hat{P}_i^j(t)$, was a Gaussian fit to the estimated peak position at t, with variance predetermined as in the regular Gaussian case described in the main text. To make this algorithm more stable and computationally compact, we used a limited temporal window for the social term, $t \in [50, 150]$, and the estimate of the location of the peak was updated only every five steps.

1. Berg HC, Purcell EM (1977) Physics of chemoreception. *Biophys J* 20:193–219.
2. Barkai N, Leibler S (1997) Robustness in simple biochemical networks. *Nature* 387:913–917.
3. Cavagna A, et al. (2010) Scale-free correlations in starling flocks. *Proc Natl Acad Sci USA* 107:11865–11870.
4. Nagy M, Akos Z, Biro D, Vicsek T (2010) Hierarchical group dynamics in pigeon flocks. *Nature* 464:890–893.
5. McNaughton BL, Battaglia FP, Jensen O, Moser EI, Moser M (2006) Path integration and the neural basis of the cognitive map. *Nature* 7:663–678.
6. Egnor S, Branson K (2016) Computational analysis of behavior. *Annu Rev Neurosci* 39:217–236.
7. Viswanathan G, et al. (1996) Levy flight search patterns of wandering albatrosses. *Nature* 381:413–415.
8. Viswanathan GM, et al. (1999) Levy optimizing the success of random searches search patterns of wandering albatrosses. *Nature* 401:911–914.
9. Pirolli P (2007) *Information Foraging Theory: Adaptive Interaction with Information* (Oxford Univ Press, New York).
10. Bonabeau E, Dorigo M, Theraulaz G (1999) *Swarm Intelligence: From Natural to Artificial Systems* (Oxford Univ Press, New York).
11. Berg HC (1993) *Random Walks in Biology* (Princeton Univ Press, Princeton).
12. Shraiman BI, Siggia ED (2000) Scalar turbulence. *Nature* 405:639–646.
13. Mafra-Neto A, Carde RT (1994) Fine-scale structure of pheromone plumes modulates upwind orientation of flying moths. *Nature* 369:142–144.
14. Vergassola M, Villermaux E, Shraiman BI (2007) Infotaxis as a strategy for searching without gradients. *Nature* 445:406–409.
15. Waters CM, Bassler BL (2005) Quorum sensing: Cell-to-cell communication in bacteria. *Annu Rev Cell Dev Biol* 21:319–346.
16. Gregor T, Fujimoto K, Masaki N, Sawai S (2010) The onset of collective behavior in social amoebae. *Science* 328:1021–1025.
17. Gordon DM (1996) The organization of work in social insect colonies. *Nature* 380:121–124.
18. Gelblum A, et al. (2015) Ant groups optimally amplify the effect of transiently informed individuals. *Nat Commun* 6:7729.
19. Sumpter DJT (2010) *The Principles of Collective Animal Behaviour* (Princeton Univ Press, Princeton).
20. Strandburg-Peshkin A, Farine DR, Couzin ID, Crofoot MC (2015) Shared decision-making drives collective movement in wild baboons. *Science* 348:1358–1361.
21. Shemesh Y, et al. (2013) High-order social interactions in groups of mice. *Elife* 2:e00759.
22. Vicsek T, Czirok A, Ben-Jacob E, Cohen I, Shochet O (1995) Novel type of phase transition in a system of self-driven particles. *Phys Rev Lett* 75:1226–1229.
23. Ballerini M, et al. (2007) Interaction ruling animal collective behavior depends on topological rather than metric distance: Evidence from a field study. *Proc Natl Acad Sci USA* 105:1232–1237.
24. Couzin ID, Krause J, James R, Ruxton GD, Franks NR (2002) Collective memory and spatial sorting in animal groups. *J Theor Biol* 218:1–11.
25. Mora T, Bialek W (2010) Are biological systems poised at criticality? *J Stat Phys* 144:268–302.
26. Couzin ID, Krause J, Franks NR, Levin SA (2005) Effective leadership and decision making in animal groups on the move. *Nature* 433:513–516.
27. Franks NR, Pratt SC, Mallon EB, Britton NF, Sumpter DJT (2002) Information flow and opinion polling and collective intelligence in house-hunting social insects. *Philos Trans R Soc Lond B Biol Sci* 357:1567–1583.
28. Simons AM (2004) Many wrongs: The advantage of group navigation. *Trends Ecol Evol* 19:453–455.
29. List C (2004) Democracy in animal groups: A political science perspective. *Trends Ecol Evol* 19:168–169.
30. Livnat A, Pippenger N (2005) An optimal brain can be composed of conflicting agents. *Proc Natl Acad Sci USA* 102:3198–3202.
31. Passino KM (2002) Biomimicry of bacterial foraging for distributed optimization and control. *IEEE Contr Syst* 22:52–67.
32. MacKay DJC (2003) *Information Theory, Inference and Learning Algorithms* (Cambridge Univ Press, Cambridge, UK).
33. Rodriguez JD, Gomez-Ullate D, Mejia-Monasterio C (2014) Geometry-induced fluctuations of olfactory searches in bounded domains. *Phys Rev E* 89:042145.
34. Korman A, Greenwald E, Feinerman O (2014) Confidence sharing: An economic strategy for efficient information flows in animal groups. *PLoS Comput Biol* 10:e1003862.
35. Barlow H (2001) Redundancy reduction revisited. *Network* 12:241–253.
36. Barbieri C, Cocco S, Monasson R (2011) On the trajectories and performance of infotaxis and an information-based greedy search algorithm. *Europhys Lett* 94:20005.
37. Masson JB Bailly-Bechet M, Vergassola M (2009) Chasing information to search in random environments. *J Phys A Math Theor* 42:434009.

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