# Ant Colonies as a Model of Human Computation

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Organisms process information in order to survive and reproduce. Biological computation is often distributed across multiple interacting agents, and is more adaptive, robust and scalable than traditional computation that relies on a central processing unit to schedule and allocate resources. In this chapter we highlight key features of computation in living systems, particularly focusing on the distributed computation of ant colonies as a model for collaborative human computation.

Natural computation is necessarily robust because sensory inputs are noisy and error prone, and appropriate behavioral responses are contingent on dynamic and unpredictable environments. For example, plant and animal cells extract information from the dynamic chemical soup in which they exist and convert that information into actions. Cells transmit information from the cell membrane via signal transduction pathways throughout the cell. These signals interact with molecules and structures built by the cell according to instructions encoded in DNA. Cellular computation is distributed across a Byzantine set of chemical reactions that are robust to individual component failures (Bray 1990, 1995). There is no central controller in the cell; instead myriad processes act in parallel and the interaction among processes give rise to behavior.

The immune system is another information storage and computational system in multi-cellular animals. The cells that comprise the immune system collectively distinguish self from other and remember previously encountered pathogens (Von Boehmer 1990). Immune cells respond only to local information but collectively mount a coherent global response to infection. The tolerance of T cells to "self" proteins exemplifies this process: T cells that bind to an animal's own healthy cells are eliminated in the thymus, thus all remaining T cells can safely attack cells to which they bind without checking any central authority. Immune cells release and respond to chemical signals such as chemokines that direct cell movement in space

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and cytokines that regulate cellular activity (Rossi and Zlotnik 2000). Cells move and react based on random sampling combined with positive and negative reinforcement from chemical intermediaries, enabling the immune system to self-regulate without central control (Moses and Banerjee 2011).

The brain is a more obvious computing machine than a cell or an immune system, but similar computation occurs through the interaction of billions of individual neurons each responding to thousands of inputs using a redundant and distributed network of neural pathways. Animals are computing systems that integrate immune systems, brains, sensory input and other organ systems, each made up of individual cells carrying out local tasks.

Superorganisms, such as ants, and bees are groups of individual organisms in which natural selection acts primarily on a colony's collective behavior. The computational capabilities of colonies emerge from interactions among individuals (Greene and Gordon 2003). These interactions range from direct antennal contacts between ants to communication via stigmergy, such as laying chemical pheromones in the environment where they are sensed, responded to, and sometimes reinforced by other ants. Colonies demonstrate how cooperative computation can be organized among autonomous agents, each individually capable of its own local computation.

Each of these biological systems—cells, brains, and ant colonies have inspired successful computational algorithms and heuristics. The behavior of cells inspired the development of cellular automata (Von Neumann and Burks 1966) and more recently, membrane computing (Berry and Boudol 1992; Cardelli 2005). Neural networks, first developed as models of the neuron, were quickly incorporated into the first computers (McCulloch and Pitts 1943), and have since become ubiquitous tools for solving classification problems which require generalization and plasticity. Artificial immune systems are algorithms and architectures that mimic biological immune systems in order to secure computers (Bersini and Varela 1991; Forrest and Perelson 1991). The recognition that evolution itself is a powerful computational process led to the field of Genetic Algorithms (Holland 1975; Mitchell 2006; Schwefel 1965), which have taken a central place along with neural networks to solve a vast array of optimization problems. The collective computational abilities of ants inspired Ant Colony Optimization (ACO) algorithms that mimic ant chemical communication via pheromones to focus computational resources on successful partial problem solutions (Dorigo 1992). ACO have been successful in a wide variety of problem domains, particularly in scheduling and routing tasks (Dorigo and Stützle 2010). ACO are also a key component of the field of Swarm Intelligence, which examines how collective computation can emerge from interactions among local agents, for example in swarm robotics (Hecker et al. 2012; Brambilla et al. 2012).

A recent response to the need for scalable, adaptable and robust computing that more closely mimics natural systems is the Movable Feast Machine (MFM, Ackley et al. 2013). A MFM is composed of relatively simple computational modules containing a processor, memory, and input/output ports; the computational power of the MFM comes from spatial interactions among the components that maintain a sort of computational homeostasis that is resilient to disturbance from hardware failure or malicious attack. In much the same way that multiple ants in a colony contribute to a collective goal while minimizing the propagation of individual mistakes, the MFM combines multiple processors into a distributed scalable system in which the computation of the system is more robust than that of its individual components.

In this chapter we transcend specific classes of algorithms like ACO and explore ant colonies more generally as complex systems capable of computation. We describe the manner in which ants, seen as simple agents, are able to use local information and behavior to produce colony wide behavior that is robust and adaptive. Ant colonies are particularly suitable models for distributed human computation because they demonstrate how individuals can collaborate in order to perform qualitatively different computations from those any individual agent could perform in isolation. This feature of ant colonies has led them to become extraordinarily successful foragers, dominating ecosystems across the globe for tens of millions of years. While there are key differences between ant colonies and collections of human agents, the nascent field of human computation can learn from the myriad strategies that ants have evolved for successful cooperation.

## Colony Computation

Colony computation is distributed, adaptive, robust and scalable to large numbers of ants. Colony computation includes, for example, processes of collective decision-making (Franks et al. 2006; Marshall et al. 2009), task allocation (Gordon 2002; Pacala et al. 1996), and regulation of activities such as selecting new nest sites and foraging (Beverly et al. 2009; Franks and Deneubourg 1997; Gordon 2010; Mailleux et al. 2003). Here we focus on foraging behavior as a collective process in which individual ants react to local environmental conditions and information, including information produced by other ants, without central control (Bonabeau et al. 1999, 1997; Camazine et al. 2001).

Foraging ants exploit spatial information without building maps, balance exploration and exploitation without explicit planning or centrally directed task assignments, and leverage noise and stochasticity to improve search. Communication among ants is embodied in physical signals that are inherently local, decentralized, and used only when needed. Foraging is achieved without centralized coordination. Ant behavioral responses to local information regulate colony behavior; thus, the collective behavior of the colony emerges from local interactions (Gordon 2010; Pinter-Wollman et al. 2011; Prabhakar et al. 2012). The resulting colony dynamics are adaptive, robust and scalable, similar to other complex distributed biological systems such as immune systems (Moses and Banerjee 2011).

*Colony computation is adaptive:* Ant colonies adapt their foraging strategy as they sense features of the surrounding environment. For example, foraging behaviors change in response to incoming cues that reduce uncertainty about the location and availability of food. Pheromones, direct physical contact between ants, and food sharing are all examples of interactions that communicate information about food locations. Cues can be conveyed to the colony with the discovery of each food source, and the colony can respond with a strategy appropriate to the average availability and distribution of food in that species' environment (Flanagan et al. 2011).

Ants adjust collective and individual behaviors in response to the availability and distribution of food. Colonies increase activity when resources are more abundant (Crist and MacMahon 1992; Davidson 1997). Group foragers tend to focus on high-density resources, with distinct trails forming to rich resource patches (Davidson 1977), which become increasingly longer with decreasing resource density in the environment (Bernstein, 1975), providing an efficient search strategy for dispersed resources and greater energetic return for the colony. Ants can communicate food locations by laying chemical pheromone trails that other ants follow and reinforce if they successfully lead to food (Wilson 1965). Pheromones exemplify how colonies incorporate the physical environment (in this case, the ground) and stochastic interactions into their computation. In this system, the chance encounters of foragers with physically embodied pheromone signals balances exploration with exploitation: ants that happen not to encounter pheromones will explore for other resource locations, while ants that follow pheromones reinforce exploitation of known resources. Trails allow the colony to adjust the number of foragers to form stronger trails towards more abundant food (Detrain et al. 1999). The Argentine ant *Iridomyrmex humilis* makes extensive use of pheromone trails to recruit other ants to newly discovered food sources (Aron et al. 1989). New World leafcutter ants (*Atta* and *Acromyrmex* spp.) create large visible trunk trails in order to harvest massive quantities of leaves clumped on individual trees (Wilson and Osborne 1971).

Pheromones are not the only form of communication. For example, in *Pogonomyrmex* seed harvesters, foragers are stimulated to leave the nest by the return of successful foragers: the probability of beginning a new foraging trip increases as the encounter rate with foragers returning with seeds increases. This positive feedback mediated by the simple encounter rate among ants enables the colony to increase foraging activity in response to currently available food (Schafer et al. 2006).

*Colony computation is robust*: Workers of ant colonies face a variety of predators, parasites (Whitford and Bryant 1979) and adverse environmental conditions that impose mortality risks (Whitford and Ettershank 1975). Sometimes, whole-colony disturbances can disrupt colony tasks (Backen et al. 2000). Two particular features of colonies lead to robustness: the absence of central control or communication prevents single points of failure, and the ability of many individuals to perform the same task provides the flexibility necessary to tolerate disturbances and loss of colony members. While the redundancy required to respond to changing needs may appear inefficient, when integrated over long time periods and dynamic and unpredictable environments, such robustness may actually optimize performance of tasks such as food collection. For example, in a redundant work-force, individual ants are able to take risks because similar ants are available to compensate for mistakes.

Additionally, small individual differences among ants may cause slight variations in foraging behaviours which may be useful in unpredictable and dynamic environments. Successful behaviours can be reinforced through recruitment.

While some colonies have a few morphologically distinct castes, most ants are arranged in much more flexible task groups, often with individuals cycling through different tasks as they age (Gordon 1999). Ants respond to changes in demand for a particular task by reacting to local cues and switching to a task when that task is completed at a slower rate compared to other tasks. For example, in *Leptothorax* ant colonies, after a disturbance, each individual reacts independently, returning quickly to its work zone and resuming the disrupted task (Backen et al. 2000). This decentralized task allocation provides the colony flexibility and responsiveness to internal and external changes without reliance on any centralized authority (Bourke and Franks 1995). Thus, robustness arises from this independent action of individuals combined with the redundancy of individuals that can tackle a task concurrently or easily switch tasks. Similar to the “c-factor” which predicts success at collective tasks in groups with high social sensitivity and equity (Woolley et al. 2010), the ability of ants to simultaneously communicate effectively and substitute the actions of one ant for another may contribute to colony success.

*Colony computation is scalable:* Colonies range in size from dozens to millions of ants (Beckers et al. 1989). Distributed communication and lack of central control lead to colony computation being highly scalable. When communication and actions are executed locally, each ant can respond quickly regardless of the size of the colony.

However, foraging presents a particular challenge to scalability. Central place foraging may incur substantial travel costs for each ant when the foraging area is large. As ants transport resources between a central place and the space of the territory, the work a colony must do to acquire food increases faster than the number of foragers (Moses 2005). Thus, colonies experience diminishing returns as the individual cost of transport increases with colony size.

To achieve efficiency at scale, each forager can react to local cues and interact within a small local range with others, forming large information-sharing networks linked by individual interactions and pheromone trails (Holldobler and Wilson 1990). These structures particularly improve foraging efficiency in large colonies that have more workers to acquire information to make effective group decisions and mobilize a large, fast response (Anderson and McShea 2001; Aron et al. 1989).

Polydomous ant colonies have evolved multiple interconnected nests which decentralize foraging in space and increase scalability. In *Myrmicaria opaciventris* (Kenne and Dejean 1999) and the invasive Argentine ant, Linepith the exploitation of a foraging area is transformed into an additional nest site, enabling reduction of the transport cost in colonies with a large number of foragers (Debout et al. 2007). The wide-ranging trail and dispersed nest system of the polydomous Argentine ant includes dynamic, flexible foraging trails (Fig. 1a) that grow and contract seasonally (Heller and Gordon 2006) and in synchrony with the availability of food sources. Dynamic local recruitment of ants from trails rather than from more distant nests further reduces individual travel costs (Fig. 1b) (Flanagan et al. 2013).

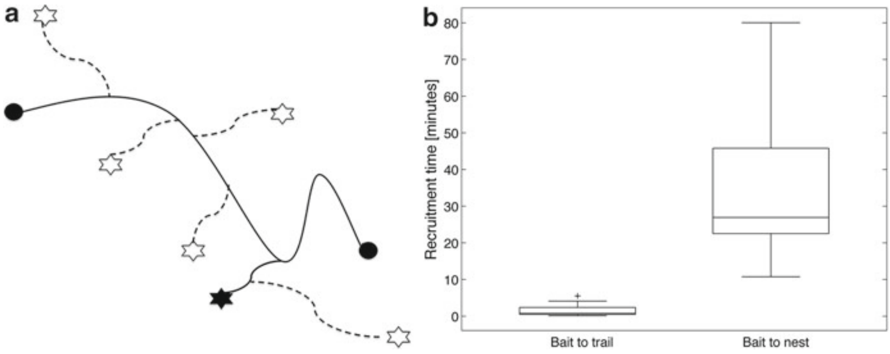

**Fig. 1** (**a**) Argentine ants form dynamic trail and nest systems that grow and contract according to availability of food sources. Trails to ephemeral food sources are short-lived, disappearing once the food is no longer available. Trails to stable food sources become more permanent and may give way to other branches. Circles are nests, solid lines are permanent trails to permanent food sources (*blue stars*). Dotted lines are transient trails to ephemeral food sources (*orange stars*) (**b**) the box-plot shows round trip transport time from bait to the trail versus the round trip time from the bait to the closest nest. Mean travel time is significantly reduced ($p<0.001$) by recruiting from the nearest trail instead of the nest (Data from Flanagan et al. 2013)

The Argentine ant strategy of recruitment from trails suggests a solution to a common engineering problem, that of collecting or distributing resources in “the last mile” where infrastructure networks connect to individual consumers. In biological and engineered networks, the dynamics in the last mile can set the pace of the entire system (Banavar et al. 2010). The last mile presents a challenge, because if a network delivers or collects resources in a large area, the majority of the network wires may be in the many short-distance low-capacity links that fill the last mile.

Wireless networks make coverage of the last mile less difficult. Just as cell phone towers maintain links only when a phone is active, the ephemeral recruitment trails of invasive Argentine ants appear and disappear as needed, allowing ants to gather dispersed resources without the infrastructure costs of permanant trails. Ants that discover new food, and go to the trail to communicate that discovery to nearby ants, act as relays that efficiently route ants to ephemeral food. The network exists only when it is needed—when the resource is exhausted, the network can disappear so that effort can be invested elsewhere. The ability of Argentine ants to cover the last mile with ephemeral trails is yet another example of a solution to a search and communication problem evolved by ants that mirror or inspire approaches used by engineers (Dorigo et al. 2006; Prabhakar et al. 2012).

There are tradeoffs inherent in the adaptive, robust and scalable computing strategies used by ants. For example, ant colonies balance the costs and benefits of private individual information versus communicated social information. The location of food may be stored in individual memory (Czaczkes et al. 2011) or communicated via pheromone trails (MacGregor 1947; Wilson and Osborne 1971). An individual ant can forage efficiently by making repeated trips from the nest to a known foraging site, without recruiting other foragers to the effort (Letendre and Moses 2013), a behavior known as site fidelity (Holldobler 1976). If a forager discovers a particularly good foraging site, whole-colony foraging success may be improved by communicating the location to its nestmates. However, too much communication can reduce foraging success if too many foragers are recruited to a site; that overshoot leaves foragers searching an area depleted of seeds (Wilson 1962). Thus, ants must balance the use of private and social information in their foraging (Grüter et al. 2011; Letendre and Moses 2013).

In order to gain insights into how ants make this trade-off, we have used genetic algorithms (GAs) to find the optimal balance of site fidelity and recruitment to maximize seed collection rates by colonies of simulated ants (Flanagan et al. 2011, 2012; Letendre and Moses 2013). We select for solutions that maximize food collection at the level of the colony, even though simulated ants can only perceive and communicate locally. The GA selects individual behaviors that are adaptive in obtaining a whole colony solution.

Ants make decisions based on local knowledge of a foraging site: when to recruit other ants to the site; when to continue foraging at the known site; or when to abandon a known site and instead follow recruitment trails to a new site. Because an individual ant knows food availability on only a small portion of the colony's territory, it cannot know with certainty if other ants have discovered better foraging sites than its own. The group level selection in our model results in ants with behavioral responses to local conditions which produce, on average, optimal colony-level responses to a particular food distribution, and the repeated interaction of the ants and repeated sampling of the environment tends to overcome individual errors in decision-making. In colonies evolved by GAs, ants recruit to sites where the availability of food outweighs the problem of overshoot and ants continue to forage at sites until the availability of food is reduced to the point that, on average, it would be more beneficial to follow a pheromone trail to a new site. We hypothesize that natural selection acts similarly, balancing an individual's reliance on its own computation (its own local sensory information or memory) and communicated information (by pheromones, interaction rates or other forms of communication). Thus, each individual's behavior improves collective function on average for that species and its particular foraging ecology.

We have illustrated the potential benefits of individual memory and social information in simulations in which ants may use site fidelity or recruitment alone, or both together, and compared their performance at food collection to models in which ant use no information and search at random (Letendre and Moses 2013). We found that in an environment which food is power-law distributed spatially—a random scattering of seeds, many small piles, and a few large, dense piles of seeds—site fidelity and recruitment increase foraging rate by 35 % and 19 % respectively (Fig. 2). For these simulated ants, individual memory appears to be generally of more benefit than social information when the two are isolated. However, combining the two forms of information further increases foraging rate to 48 % over colonies of ants that use no information. Differences in foraging success are even more pronounced when ants are foraging on foods more patchily distributed in the environment.

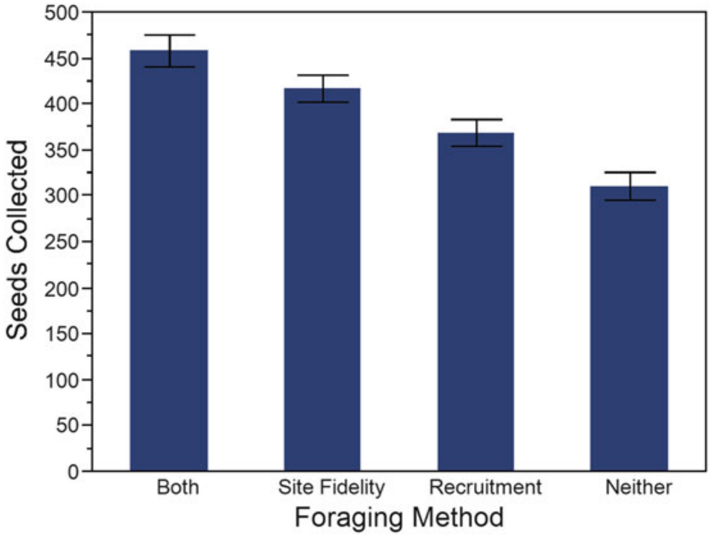

**Fig. 2** Foraging success of simulated ants selected by a genetic algorithm to maximize collective foraging success. Colonies of 100 ants forage for power-law distributed seeds using site fidelity, recruitment, both together, or neither, for 10,000 time steps (Letendre and Moses 2013, in press)

Our analysis illustrates a synergy between private and social information. This synergy is especially remarkable in light of the fact that after the optimal balance is struck by the GA between site fidelity and recruitment, 98 % of foraging trips begin with site fidelity compared with only 2 % that begin by following a recruitment trail to a foraging site. The small number of trips that begin following a recruitment trail provide an out-sized benefit by bringing ants to new foraging sites where thereafter they can return to the site using individual memory. The two behaviors are also synergistic in the sense that ants foraging with site fidelity are more successful if they are foraging at a high quality patch to which they have previously been recruited. Additionally, pheromone trails are more useful when they can be limited to very high quality sites because seeds from smaller patches can be collected using site fidelity (Fig. 3). Thus site fidelity can allow recruitment to work more effectively and vice versa.

The combination of individual memory and local computation with communication expands the behavioral repertoire of responses to varying quality of foraging sites. Ants can use site fidelity to effectively collect seeds from small patches and pheromones to collect seeds from large patches. Optimization schemes might similarly be applied in human computation to balance the use of communication versus independent action.

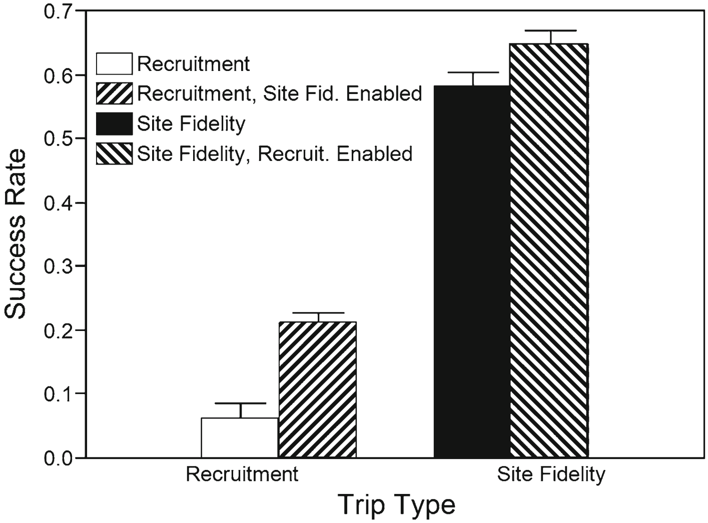

**Fig. 3** Frequency that simulated ants using recruitment successfully find a seed at the site to which they have been recruited, and frequency that ants using site fidelity successfully find a seed at a site to which they have returned based on individual memory. The addition of site fidelity to recruitment improves the success rate of recruitment trips; and the addition of recruitment to site fidelity improves the success rate of trips based on site fidelity

## Conclusions

The adaptive, robust and scalable computation achieved by ant colonies serves as a model for human computation. The features of social computing in ants have been tuned by natural selection for millions of years to accomplish a wide variety of tasks in a wide variety of environments. Social computing in ants demonstrates that individual behaviors can be selected to maximize collective performance, even when the individuals are unaware of the global goal. Ants act locally, but colonies act globally.

Ant colonies offer several suggestions for how human computation can strive for more than connecting many humans together to gain additive benefit from each human. Ultimately, as in the emergent computation of ant colonies, the sum of human computation should be greater than the individual contributions of each individual. Ants demonstrate the feasibility of collective coherent behavior, even when individuals have only a narrow local perspective. By tuning the rules of interaction, individual behaviors can be rewarded to maximize collective benefit.

It is worth contrasting colony computation with market economies, another complex system in which collective function emerges from interactions among individual agents. While economies and colonies are collective entities whose properties emerge from the interactions of individual agents, colonies largely avoid a pitfall of market economies—the tragedy of the commons in which individuals acting in their own short term best interests deplete shared resources, diminishing the long term interests of the group. While ants in a colony and humans in an economy both respond to locally perceived information, human agents in an economy are rewarded based on their own self-interest; in contrast, ants are rewarded based on collective colony interests. Colonies demonstrate how interaction rules can be designed to maximize collective performance rather than individual performance, even when individuals respond only to local information.

The mechanisms by which cooperation emerges in colonies are in some sense unique to the particular physiology of ants. Pheromone communication is useful for animals with highly sensitive smell; ants may react to encounter rates with other ants simply because they are incapable of integrating more complex information. Humans are obviously capable of vastly more sophisticated computation, learning and innovation. Technology allows humans to communicate at any distance. Further, humans can, potentially, choose among numerous biological behaviors to imitate and adapt to their own needs.

Regardless of whether the actual mechanisms for cooperation are the same, successful cooperation in both systems may rest on similar principles. The cooperative behaviors of ants reflect not just the particular physiology of these insects, but also more general principles for cooperative computation that form a foundation for human computation. Like ant colonies, human computational systems should:

- Balance reliance on local verses communicated information
- Decide when successful individuals should guide others and when individuals should explore independently
- Trade-off an individual's attention to a task with the cost of switching to new tasks
- Reinforce good solutions while being robust to local errors

The proper balance of these tradeoffs in individuals results in a synergy at the collective level that balances exploitation of what is already known with exploration for novel solutions. In ants, natural selection has developed an incentive structure that rewards individuals who balance this tradeoff to maximize contributions to global rather than individual goals. Human computational systems will have to engineer incentives to individuals to create the right balance of behaviors for collective computational goals.

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