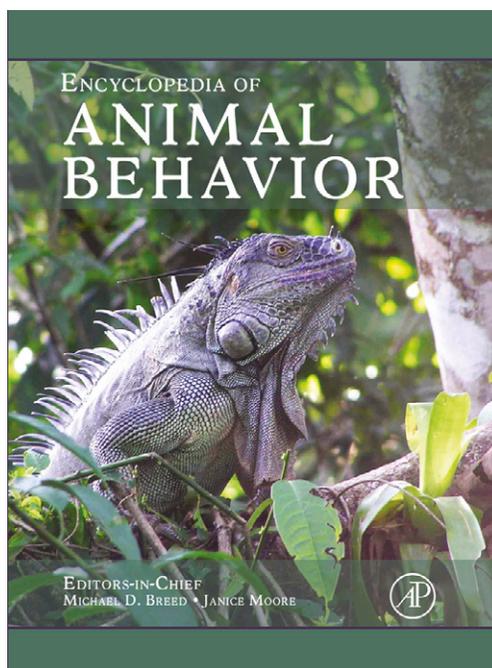


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## Collective Intelligence

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### Introduction

A collective intelligence is a group of agents that together act as a single cognitive unit. The iconic example is a swarm of honeybees cooperating to make decisions, build complex nest structures, allocate labor, and solve a host of other complex problems. Its defining characteristic is coordination without central control. Intelligence does not belong to a single knowledgeable leader, but instead is distributed across the entire group. Adaptive collective behavior emerges from interactions among a large number of individuals, each applying appropriate decisions rules to strictly local information. Although especially well-described in the social insects, collective intelligence is found in many systems, from the complex behavior of bacterial communities to the coordinated motion of fish schools and bird flocks. These examples have in turn inspired the development of artificial approaches to collective robotics and decentralized computational algorithms. This article reviews the major characteristics that allow collective intelligence to emerge from individual behavior, using both illustrative examples from well-studied cases and models that reveal the basic principles.

### Self-Organization and Positive Feedback

A revealing example of collective intelligence is the forging of consensus decisions by colonies of the ant *Lasius niger*. These ants exploit sugary food using chemical trails that recruit nest-mates to rich sources. If a colony is presented with two artificial feeders filled with sugar water of different concentrations, it will soon develop a busy trail to the better one, largely ignoring the other (Figure 1(a)). This collective decision can be explained by a very simple model that does not require any ant to visit both feeders and determine which is better. Instead, the colony's choice emerges from the dynamics of recruitment behavior at each site. An ant that finds a feeder deposits a trail to it with a probability that depends on its richness. The trail summons nest-mates who reinforce it based on their own assessment, making it still more attractive to further recruits. Although recruitment happens at both feeders, quality-dependent reinforcement means faster growth for the trail to the better one. The difference is amplified as the stronger trail outcompetes the weaker one in attracting and retaining foragers. Eventually, the weaker trail dies out altogether, starved

of the reinforcement needed to overcome evaporation of the volatile trail pheromone.

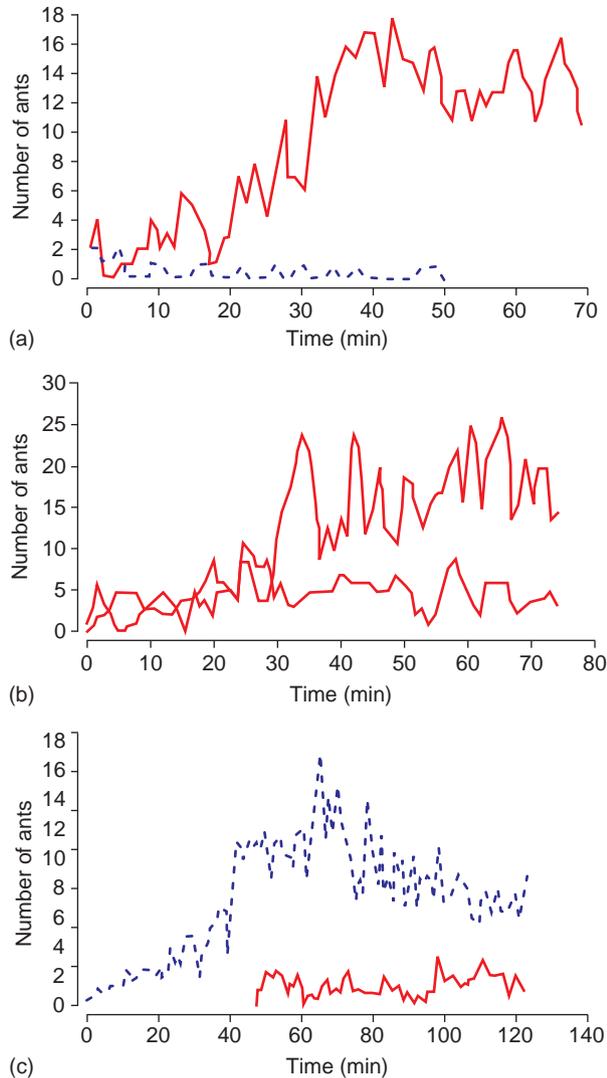
This process illustrates several principles of collective intelligence. First, group-level order self-organizes from a large number of purely local interactions. Each ant applies appropriate decision rules to limited information about a single feeder or trail, and none has a synoptic picture of the whole problem. Second, control of foraging is highly decentralized, with no leader or hierarchy to guide the group's behavior. All ants are essentially identical in their behavioral rules and in their capacity to affect the behavior of others. Third, and most important, coordination depends on positive feedback. Small initial differences in trail strength are strongly amplified as each ant's reinforcement makes further reinforcement more likely. In this way, many small actions grow into a major group accomplishment.

Similar positive feedback underlies a broad range of complex collective behavior. Ants use pheromone trails to choose not only the better of two feeders, but also the shorter of two routes to the same feeder. Honeybees use another method of recruitment the dance language to allocate foragers among food sources or to choose a new home. For ants of the genus *Temnothorax*, tandem runs and social transports provide the recruitment needed for collective nest site selection. Positive feedback can also emerge without explicit signaling. It is sufficient for one animal to imitate the actions of another, thus becoming a model for still more imitators. In this way, a group of cockroaches can settle on a common aggregation site using only simple rules that make joining an aggregation more likely (and leaving it less likely) as its size increases.

### Nonlinearity and Consensus

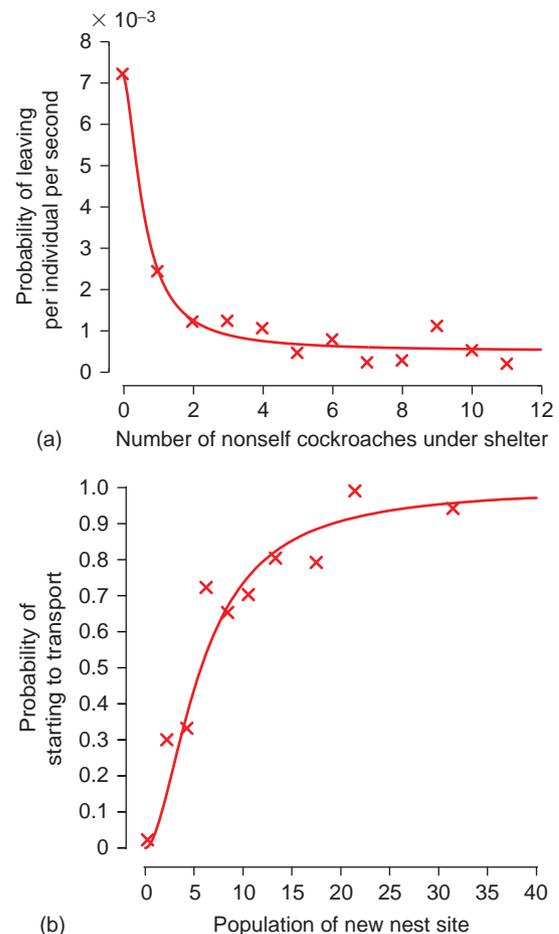
Although positive feedback is central to group coordination, mathematical models suggest that it is not enough for the clear decision-making shown by *L. niger* colonies. These models predict that consensus on a single option will happen only when feedback is highly nonlinear. That is, doubling a pheromone trail's strength must lead to more than a doubling of the rate at which it attracts recruits. Only then will differences between options be amplified sufficiently to eliminate all but a single trail. If the growth in trail attractiveness is linear, the best site will still be favored, but weaker recruitment will persist at lesser sites.

The consensus-building power of nonlinear responses shows very clearly when a colony of *L. niger* is presented with two identical feeders. The ants randomly choose one feeder and exploit it heavily while largely ignoring the other one (Figure 1(b)). The key to this consensus is amplification of random variation. If one feeder happens to be found first and thus gains a small advantage in number of visitors, nonlinear positive feedback will rapidly amplify this difference, allowing the early leader to monopolize the colony's foragers.



**Figure 1** Collective decision-making by colonies of *Lasius niger* ants. (a) Change over time in the number of workers visiting two feeders, one with 1 M sucrose solution (solid line) and the other with 0.1 M solution (dashed line). (b) When presented with two identical 1-M feeders, the ants randomly choose one, largely ignoring the other. (c) If the 1-M feeder is presented after a trail is already established to a weaker feeder, the ants cannot switch their efforts to the better source. Adapted from Camazine S, Deneubourg JL, Franks NR, Sneyd J, Theraulaz G, and Bonabeau E (2001) *Self-Organization in Biological Systems*. Princeton, NJ: Princeton University Press.

Nonlinear responses are called for whenever groups value consensus. Cockroaches, for example, may benefit from better predator defense and environmental homeostasis when they form a single large aggregation (Figure 2(a)). For *L. niger*, the benefit may be better defense of the honeydew-secreting homopterans that are a common natural sugar source. In other cases consensus is not ideal, and groups may do better with linear responses that produce split decisions. The honeybee's waggle dance is rather linear: if a bee doubles her dance effort, she



**Figure 2** Nonlinear responses underlying collective behavior. (a) A cockroach's probability of leaving a shelter declines sharply as the number of roaches there increases. This nonlinear response helps a group of roaches reach consensus on one of two available shelters. Reproduced from Ame JM (2006) Collegial decision making based on social amplification leads to optimal group formation. *Proceedings of the National Academy of Sciences USA* 103: 5835–5840. (b) Nest site scouts of *Temnothorax curvispinosus* use a quorum rule when deciding whether to fully commit to a candidate site as their colony's new home. Crosses show the proportion of ants deciding to transport, rather than lead a tandem run, as a function of the population of the site being recruited to. Line shows a nonlinear function fit to these data. Reproduced from Pratt SC (2005) Behavioral mechanisms of collective nest-site choice by the ant *Temnothorax curvispinosus*. *Insectes Sociaux* 52: 383–392.

approximately doubles the number of recruits that she summons. Accordingly, a colony presented with two feeders exploits each at a level roughly proportional to its quality. This may allow colonies to respond more quickly if relative quality changes, a likely event for the ephemeral nectar flows on which bees depend.

On the other hand, consensus is critical for nest site selection by social insects, lest part of the sterile work force become separated from the reproductive queen. Interestingly, the two best-studied cases rely on linear forms of recruitment: honeybees use waggle dances and *Temnothorax* ants use tandem runs, in which recruits are led singly to a candidate site. Both groups are quite adept at reaching consensus on the best of several candidates, but how do they do so with these linear responses? The key appears to be re-introduction of nonlinearity in the form of a quorum rule (Figure 2(b)). Emigrations begin with a deliberative phase characterized by slow recruitment of scouts to multiple candidate sites. This gives way to rapid movement of the bulk of the colony to the first site whose population reaches a threshold. Models show that this nonlinear change in recruitment effectiveness increases the colony's likelihood of unanimously moving into the best nest, rather than splitting among several.

## The Wisdom of Crowds

So far we have considered sociality as a constraint on intelligence: the group must reach a common solution despite its members' limited knowledge and influence. Theoretically, group living can offer a cognitive advantage, allowing many poor decision-makers to achieve greater accuracy than a well-informed individual. The basic insight was had by the Marquis de Condorcet in the eighteenth century. He described a jury of  $n$  members deciding between two options, each individual having probability  $p$  of making the correct decision. If each votes independently, with the group selection going to the option getting a majority of votes, then the probability that the jury's decision is correct rises with jury size, provided that  $p > 0.5$ . In other words, if everyone meets the rather low standard of exceeding a chance probability of being correct, the group as a whole can approach a 100% chance of making the right choice.

This 'wisdom of crowds' has many applications in human society, from democratic voting systems and jury trials, to prediction markets and internet search engines (Surowiecki, 2004). Similar advantages have been posited for animal groups, but few studies have been made. The best evidence is from experiments on different size groups of stickleback fish making movement decisions. Larger groups were better at choosing to follow the more attractive of two leaders.

Social enhancement of decision-making poses something of a paradox: it requires that group members influence each other, but also that each choice be independent. If individuals simply copy one another, then their mistakes become correlated rather than cancelling each other out. In humans, this is the problem of 'groupthink.' On the other hand, if everyone relies only on his own knowledge, then no one gains the benefit of others' wisdom. The solution lies in finding the proper balance of personal and social information. Foraging ants, for example, receive social information in the form of recruitment signals that bring them to options that others have found valuable. Once there, however, each one makes her own independent assessment before herself recruiting.

A simple model of collective choice suggests that striking the right balance is aided by the nonlinear responses described above. Consider a group in which each member chooses an option with a probability that depends both on its intrinsic quality and on the number of other group members that have already selected it. Inclusion of a social influence improves performance compared to purely independent decision-making, but this effect is much greater when the response to others is highly nonlinear. That is, accuracy increases if individuals follow the example of others only when their number exceeds a threshold. In this way, the group gains the advantage of pooled opinions without being misled by individual errors.

There are costs as well as benefits to the integrating power of nonlinearity. In a small proportion of cases, nearly all group members choose the wrong option, due to chance amplification of a few early mistakes. Experiments also indicate that very nonlinear recruitment systems restrict decision-making flexibility. When a colony of *L. niger* is given a high quality feeder after first developing a trail to a mediocre feeder, it is unable to switch its foraging to the better target (Figure 1(c)). The attractive power of the established trail is simply too great for a nascent trail to overcome. Honeybees faced with the same challenge can nimbly shift their foraging effort due to their more linear recruitment response.

## Collective Motion

Some of the more spectacular examples of collective intelligence are seen in the acrobatic motions of fish schools and bird flocks, in which thousands of individuals execute rapid and near-simultaneous turns. The collective structures they form – parallel streams, spinning balls, toruses – may contribute to foraging efficiency or predator avoidance, or they may simply ensure that the group remains cohesive as it moves. Much of this coordinated behavior can be reproduced by self-propelled particle (SPP) models. In these models each animal chooses its direction and speed of motion based on two sources of

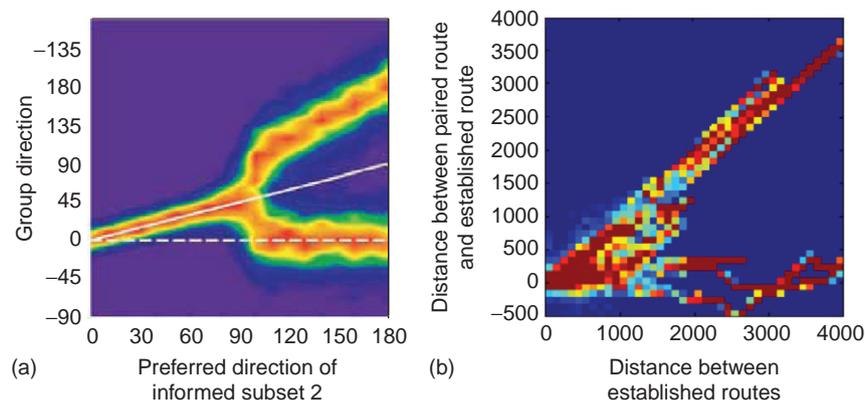
information: (1) its own desired heading, perhaps guided by direct knowledge of the location of a food source, predator, or migration destination, and (2) the position and headings of its neighbors within the group. Cohesion is maintained by a policy of attraction to more distant group members, while collisions are avoided by turning away from neighbors who get too close. Common direction depends on alignment to others within a certain radius. Models of this type can account not only for cohesive movement, but also for the rapid transmission of changes in direction. The imitative behavior in these models plays the same role as recruitment in social foraging: it creates a positive feedback cascade that quickly spreads new information through the group.

Similar mechanisms may explain how a group can find its way to a destination known to only a few of its members. A honeybee swarm flies unerringly to its new home even though only 5% of its several thousand members know the location. Scouts appear to guide the ignorant majority by flying through the swarm at high velocity in the direction of the target site. An SPP model shows how these streakers could plausibly guide the swarm, if uninformed bees follow simple rules for avoidance at close distances and attraction and alignment at longer distances. A more general model of this type was developed by Couzin and colleagues. It shows that guidance is possible even when knowledgeable individuals fly at the same velocity as others and balance their directed flight with the same kind of social information used by uninformed bees. This model does not assume that group members can tell who is informed, but nonetheless predicts effective navigation toward the goal.

## Decision-Making on the Move

What if the group contains two kinds of knowledgeable individuals, each with a different preferred heading? Models suggest that the outcome depends on the number favoring each direction, with even a small majority able to win over the whole group. If numbers are similar and desired headings are not too different, the group is expected to compromise on an intermediate direction. Above a critical difference in headings, the group either splits in two or reaches consensus on one of the two preferred directions (Figure 3(a)). In case of consensus, the choice of heading is random, unless there is a difference in how much each group weighs its preferred direction relative to social information. Even a small advantage in motivation will increase a subgroup's power to win over the whole group. This result suggests that leadership by a small number of individuals can have major influences on the behavior of otherwise self-organized groups.

Some support for these models is found in the observed behavior of homing pigeons traveling either alone or in pairs from a common release site (Figure 3(b)). After multiple solo flights, each pigeon develops an idiosyncratic route. When traveling together, pairs show three possible outcomes: they separate and follow their individual routes, they compromise on an average route, or they both adopt the preferred route of one bird. Pairs that stay together show the distance dependency predicted in the model: compromise at short distances and selection of one bird's preference at larger ones. Leadership was also evident, with some birds consistently more likely than others to prevail, perhaps on the basis of their higher social status.



**Figure 3** Guidance and decision-making in collective motion. (a) Results of a model showing that a small number of informed individuals can guide a large group. The model assumes two subsets of five informed group members with different desired headings, plus 90 uninformed members. When the difference in headings is small, the whole group adopts the average heading. Above a critical difference, the group reaches consensus on one heading or the other, with equal probability. Reproduced from Couzin ID, Krause J, Franks NR, and Levin SA (2005) Effective leadership and decision-making in animal groups on the move. *Nature* 433: 513–516. (b) Pairs of homing pigeons show a similar switch from compromise to leadership. When the difference between their preferred routes is small, the birds take an intermediate route. When the difference surpasses a threshold, the chosen route is nearly identical to that of one bird, and very different from that of the other. Reproduced from Biro D, Sumpter DJT, Meade J, and Guilford T (2006) From compromise to leadership in pigeon homing. *Current Biology* 16: 2123–2128. In each graph, color indicates the probability  $p$  of each group direction as a function of the difference in subset headings, ranging from blue ( $p = 0.0$ ) to red ( $p = 1.0$ ).

Pairs of pigeons also took shorter paths home than did solo birds, providing some evidence for the 'many wrongs' hypothesis. This idea holds that many individuals, each with a noisy estimate of the heading to a common destination, can average out their independent errors to find a much more precise group heading. In addition to improving navigation, models suggest that this kind of process can help animals follow subtle gradients toward food concentrations or better physical environments.

## Phase Transitions

The switch from compromise to consensus in collective motion is one example of a phase transition, a central feature of nonlinear collective systems. Phase transitions are dramatic changes in behavior in response to continuous variation of a single key feature. Another example is seen in the trail-laying ant *Monomorium pharaonis*. Below a critical number of foragers, a colony cannot sustain a trail; above this number the positive feedback of trail reinforcement is strong enough to overcome evaporative losses. Thus, a group switches suddenly from solitary to group foraging as its size increases.

Similar sensitivity to group size is seen in the collective movements of gregarious locusts. Massive flying swarms of adult locusts are preceded by the assembly of younger insects into ordered marching bands. An SPP model shows how these bands can self-organize from each individual's tendency to align with nearby members, combined with a competing tendency to maintain its current heading. As their density increases, the locusts undergo a phase transition from random movement to ordered motion at a common direction and speed. For intermediate densities, direction frequently changes, but at higher densities it remains constant for long periods. Very similar phase transitions are in fact observed in groups of walking locusts confined to a ring-shaped arena.

Phase transitions may have significant impacts on a group's ability to match group behavior to changing circumstances. Near a phase transition, nonlinear systems have multiple stable states and can shift relatively easily from one to another, as demonstrated by the locusts' directional changes. This implies that adaptive selection of the best behavior may be easiest near the transition. For example, a single individual that detects a predator can more easily lead the group away from danger if it is near a phase transition.

## Hysteresis and Group Memory

The existence of multiple stable states makes collective behavior dependent on a group's recent history. This characteristic of nonlinear systems is known as hysteresis.

Medium-sized groups of the ant *M. pharaonis*, for example, can forage either solitarily or with trails, depending on how the colony reached its current size. If reduced from a size at which a trail formation is easy, then the medium-sized group can maintain a trail already formed. If expanded from a size at which trail formation is impossible, the medium-sized group will not be able to build one from scratch. Thus, two otherwise identical groups can show very different behavior, based on their different histories.

Hysteresis creates a kind of group memory. Fish schools, for example, can form a remarkable variety of collective structures, ranging from disordered swarms, to parallel revolution about a central point, to cohesive directed motion. Mathematical models show that transitions from one structure to another can be achieved by simply changing the spatial range over which individual fish attempt to align themselves with their neighbors. For any given range, however, more than one structure may be stable. When fish in a disordered swarm increase their zone of alignment to a moderate value, they begin to swim in an orderly torus. When fish in a mobile, directed group decrease their zone of alignment to the same moderate value, they remain in their directed structure. Thus, the group's 'memory' of its former state determines its behavior. It is important to note that this is not an individual memory. Each fish follows precisely the same rules in the two conditions, and the difference in group behavior is an emergent property of the whole group.

## Comparison to Neural Systems

The idea of collective intelligence is born from a fundamental analogy between societies and brains. Similar principles of feedback, nonlinearity, and multistability apply in both cases. Although the mechanistic details are vastly different, the structural similarity is sometimes very striking. For example, the house-hunting algorithms of ants and bees have great similarity to models of decision-making in the primate brain. Both assume competing streams of noisy evidence for different options borne either by sensory neurons or the recruitment behavior of scouts. This evidence accumulates, either as activity within a particular neural center or as a population of scouts advertising and visiting a nest site. A decision is made when the activity or population for one option surpasses a threshold, marking it as the chosen option.

Marshall and his colleagues made this loose analogy more rigorous by expressing both systems in the same modeling framework. Their results suggest at least one important functional difference: the neural system can achieve a statistically optimal tradeoff between decision speed and accuracy, because it includes mutually inhibitory connections between competing centers. No such connections are currently known for the ants or bees. However, the

honeybee stop signal is an inhibitory behavior that conceivably plays such a role, leaving open the possibility that bees too can achieve statistical optimality.

Comparison to neural models underscores an important common feature of brains and societies: the role of forgetting. Neural decision systems depend on a steady loss of activity in the absence of new external input. This improves sensitivity to changes in the strength of a stimulus. In the same way, a honeybee scout eventually stops dancing for a candidate nest site that she has found, no matter how good it is. This helps the colony to avoid stalemates in which bees obstinately advertise more than one site. It also allows the colony to switch its attention from an early mediocre discovery to a better site found later.

## Rationality

One might expect that an intelligent decision-maker would also be a rational one, but this is not always the case. When faced with certain kinds of challenging decision problem, animals and humans are likely to make errors that can prevent them from consistently maximizing their fitness. For example, decision-makers will change their preference between two options if a third, less attractive distracter option is also presented. These errors often occur when options vary in multiple attributes, such that no option is clearly superior in all attributes. This makes determining which is best a computationally challenging task. Individuals can deal with this by using simple rules of thumb based on local comparisons among options. Thus, if it is hard to say whether A or B is better, A may be chosen over B if it more clearly exceeds a distracter C than does B. Such rules may work well most of the time, but fail for particularly challenging cases.

Rationality has only begun to be addressed for collective decision-makers, but early work by Pratt and his colleagues suggests that collectives may be less prone to this kind of comparative error. They presented *Temnothorax* ant colonies with a choice that required them to trade off two prized features of nest sites – entrance size and light level. Colonies did not show the irrational changes in preference commonly seen when individual animals face a similar choice. An intriguing possibility is that the ants' highly distributed decision-making filters out irrational errors. Few individual ants know of all the options under consideration by the colony, and thus do not have the opportunity to make the comparisons that bring about irrationality. Thus, an apparent constraint – the relative ignorance of individual ants – may help the colony as a whole to perform better.

## Applications

In recent years, swarm intelligence has proven a fertile source of inspiration for the design of artificial systems. In

computer science, 'ant algorithms' provide an effective means of solving the hardest kind of optimization problems, where the total number of possible solutions is far too great for all to be tested. The basic idea, inspired by ant foraging, is to let distinct computational agents ('ants') sample the solution space, score the quality of each sample, and 'recruit' other agents to test variations of promising leads. This general approach has been used to design telecommunication networks and to schedule complex transportation routes. In robotics, ongoing research aims to design swarms of robots that can inspect dangerous and inaccessible places, efficiently monitor large areas, or build structures in remote and dangerous locations.

Engineers are attracted to several advantages of natural collectives. They are highly robust, working well if individual members are lost or if communication channels are broken. Cognitive sophistication is a feature of the whole group, not each member, so individual agents can be simple and cheap. Collectives work well at different population sizes without requiring wholly different control algorithms. They are also effective in the variable environments typical of real-world problems. In fact, randomness is an important component of natural collective intelligence, as when ant trails amplify random variation to select a single food source. Finally, swarms do not require unwieldy central control networks that can be extremely difficult to design and manage for large and complex systems.

In designing artificial systems, engineers often stray far from the original biological inspiration, as their goal is to solve a problem, not to mimic a natural system. Nonetheless, natural models are still crucial to the process, if only as a proof that solutions to certain difficult problems are attainable. In addition, the work of engineers and computer scientists can enhance the study of natural collectives, by providing useful analytical tools and concepts. Indeed, much of the work described in this article is a kind of reverse engineering, looking for the hidden mechanisms that explain complex collective behavior. Future discoveries will depend on the exchange of insights between engineers and biologists about both natural and artificial collective intelligence.

*See also:* Communication Networks; Consensus Decisions; Decision-Making: Foraging; Distributed Cognition; Group Movement; Honeybees; Insect Social Learning; Nest Site Choice in Social Insects; Rational Choice Behavior: Definitions and Evidence; Social Information Use.

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