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The Psychology of Superorganisms: Collective Decision Making by Insect Societies

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Keywords

rationality, cognition, learning, cognitive overload, self-organization, psychophysics

Abstract

Under the superorganism concept, insect societies are so tightly integrated that they possess features analogous to those of single organisms, including collective cognition. If so, colony function might fruitfully be studied using methods developed to understand individual animals. Here, we review research that uses psychological approaches to understand decision making by colonies. The application of neural models to collective choice shows fundamental similarities between how brains and colonies balance speed/accuracy trade-offs in decision making. Experimental analyses have explored collective rationality, cognitive capacity, and perceptual discrimination at both individual and colony levels. A major theme is the emergence of improved colony-level function from interactions among relatively less capable individuals. However, colonies also encounter performance costs due to their reliance on positive feedback, which generates consensus but can also amplify errors. Collective learning is a nascent field for the further application of psychological methods to colonies. The research strategy reviewed here shows how the superorganism concept can serve as more than an illustrative analogy.

INTRODUCTION

Insect societies process information and make decisions as a group, making them leading models of collective cognition (22, 27, 69, 131). Cognition by whole colonies does not depend on knowledgeable leaders but instead emerges from interactions among many insects, each possessing only partial information but acting on it with appropriate rules. Thus, colonies of bees and ants can choose the richest food source, the best nest site, or the shortest travel route even when few if any colony members know about more than one option. Over the past 30 years, an extensive body of work on self-organization has shown how these collective decisions emerge from the behavioral rules, communication pathways, and local cues used by colony members (17, 26, 35, 53, 103, 105, 126). A cornerstone of collective cognition is reliance on large numbers of independent assessments to more precisely characterize an environmental context or group state (17, 125, 128). Colonies also depend on positive feedback to share information rapidly and to amplify weak signals (17, 53, 75). In addition, nonlinear interactions between individuals help drive groups to consensus on a single option (74, 125, 128).

In recent years, researchers have begun to apply concepts and methods from psychology to the collective decisions of insect societies. This application stems from the superorganism concept, which holds that highly integrated societies have evolved group-level phenotypes analogous to those of individual organisms (25, 48, 54, 89). The term superorganism is appropriate for societies in which the fitness of members depends largely or entirely on the success of the group, freeing natural selection to shape elaborate cooperative phenotypes that parallel those of organisms. Thus, concepts and methodologies developed to study organisms might also be fruitfully applied to corresponding aspects of colonies. Psychology is the discipline that aims to understand cognition, the process by which organisms acquire, evaluate, and store information from their environment. If information processing by colonies is analogous to that of individuals, it is reasonable to apply psychological approaches to insect collective behavior.

The psychology of superorganisms can draw on a rich set of experimental paradigms to answer novel questions about collective cognition. For example, do the decision-making strategies of collectives and individual brains share formal similarities despite obvious differences in specific mechanisms? Can the concept of rational choice be applied to collectives as well as individuals? Do colonies learn, and if so, is this a truly emergent property or simply a summing of learning by individual members? Another class of questions takes advantage of the relatively low level of integration in a colony compared to a brain. That is, the workers in a colony, unlike the neurons in a brain, are not only parts of a collective decision-making apparatus but also decision makers in their own right. Their relative independence means that we can present the same tasks to colonies and to isolated individuals to learn how abilities change when many decision makers are combined into one.

In this article, we do not attempt a thorough review of all aspects of collective decision making by social insects. Rather, we focus on emerging efforts to treat the colony as a single cognitive unit and to probe its function using psychology-inspired methods. Our goal is both to highlight this work and to offer a model of how this approach can be broadened to include other species, biological contexts, and cognitive challenges.

PSYCHOLOGICAL MODELS OF SIMPLE DECISIONS

Collective decision making by social insects was pioneered by the study of simple tasks, such as the selection of a richer over a poorer food source. Psychologists have also learned much from simple two-choice tasks, but their insights are augmented by considering not just the accuracy of a choice but also the time taken to make it (87, 119). Here, we consider how formal models

of two-choice response-time tasks shed light on the balance of speed and accuracy in collective decision making.

Sequential-Sampling Models of Two-Choice Tasks

In one well-studied psychological paradigm, a primate subject views a screen full of dots; most of the dots move randomly, but a percentage move coherently in one direction (73, 100, 112). The subject must judge whether motion is to the left or to the right and indicate its choice by looking in that direction. The choice is error prone, and the subject can improve accuracy by gathering more information but only at the cost of taking longer to make up its mind. This simple task thus captures the inherent trade-off between speed and accuracy.

Insight into this trade-off has been aided by the development of sequential-sampling models (12, 13, 87, 88, 119). This is a large and varied class of models, but all of them share common elements. The subject is viewed as receiving streams of noisy sensory evidence for two competing alternatives. The brain integrates these streams over time, arriving at a decision when its accumulated activity level surpasses a threshold. In some models, the streams accumulate independently, and the option that first crosses the threshold is chosen. In others, such as the diffusion model, the brain tracks the difference between activity levels accumulated for each option, and the decision depends on whether the difference first hits an upper or lower threshold (12, 119) (**Figure 1**). In all versions, evidence for correct options accumulates faster, but the presence of noise creates the possibility of error. Integrating over more time improves the ability to distinguish signal from noise, thus capturing the speed/accuracy trade-off seen in behavioral data. Moreover, the models provide a simple mechanism for adjusting this trade-off by changing the threshold required for a decision. This adjustment also accords with experimental data, which shows that subjects take more time and improve their accuracy if a higher cost is imposed for errors.

Certain sequential-sampling models, including the diffusion model, implement the sequential probability ratio test (SPRT), a mechanism that achieves a statistically optimal decision (12). That is, for any given probability of choosing the wrong option, the SPRT will find the solution fastest. A requirement for this to be true is mutual, activity-dependent inhibition by competing options. In other words, it is not enough for evidence to be gathered at a rate that depends on option quality; each option must also inhibit the growth of evidence for the competing option, with an effectiveness that depends on the inhibiting option's quality. Interestingly, neuroscientists in recent years have found anatomical and physiological evidence for structures in the primate brain that can implement each component of the sequential-sampling model, including mutual inhibition (12, 14, 119).

Applying Sequential-Sampling Models to Collective Decisions

Psychological and neural sequential-sampling models have remarkable parallels in the collective decisions of ant and bee colonies choosing between nest sites (67, 78). We focus here on ants of the genus *Temnothorax*, which are also central to other case studies described below. These ants form small colonies that inhabit preformed rock crevices and are adept at moving to a new home when their old one is damaged (66, 72, 79, 82). Colonies readily inhabit artificial nests that mimic natural crevices, allowing emigrations to be induced and closely observed in the laboratory simply by removing the roof of a colony's nest while providing one or more intact empty nests nearby. Colonies show strong preferences for a variety of nest-site features, including adequate cavity size, small entrance size, and low interior light level (39, 66, 79, 95). When presented with two candidate sites that differ in these attributes, colonies can reliably emigrate to the better one within a few
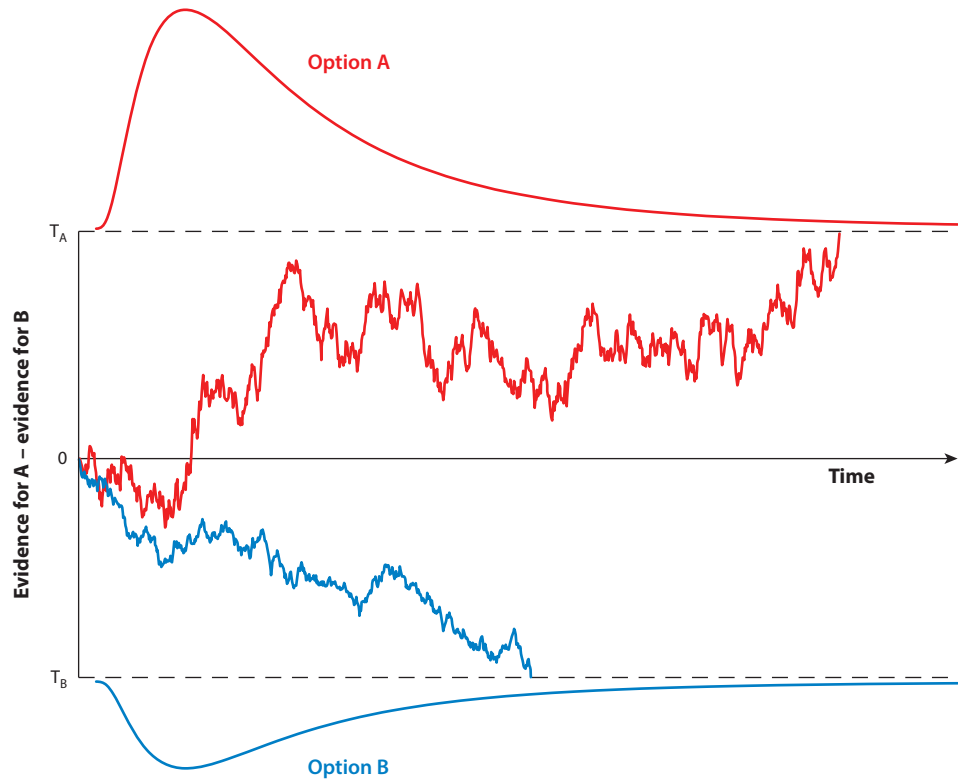
Figure 1

The diffusion model of two-choice decision making. The model tracks the moment-by-moment difference in evidence favoring the competing options A and B. The process starts at zero and accumulates evidence until it reaches one of two thresholds: If the upper threshold (T_A) is reached first, then option A is chosen (*red sample path*). If the lower threshold is reached first, then option B is chosen (*blue sample path*). The direction and magnitude of the rate of accumulation depend on the difference in the options (i.e., the greater the difference, the more rapidly the process moves toward the better option's threshold). However, noise in the process and variability over time in the quality of the evidence allow for incorrect choices and produce distinctive distributions in the response time for correct and incorrect responses (shown by the *top* and *bottom smooth lines*).

hours. They make their choice in a highly decentralized way without reliance on well-informed scouts that have visited both candidates (86, 92, 93). Instead, the choice is made via competition between recruitment efforts at the two sites (66, 79) (**Figure 2**). Better sites have an advantage in this competition because scouts that discover a site initiate recruitment with a probability that depends on site quality. This results in stronger positive feedback, and thus more rapid population growth, at the better site. Once a site's population reaches a threshold, or quorum, its recruiters fully commit to it as the colony's new home, accelerating their recruitment and switching their target from fellow scouts to the passive majority of the colony (80, 83). A move of the entire colony to the chosen site typically follows in short order.

The major components of the ants' decision algorithm map directly onto sequential-sampling models of individual decision making (67). Growing numbers of recruiters at each site correspond to accumulating neural activity in support of each option, and the quorum corresponds to the
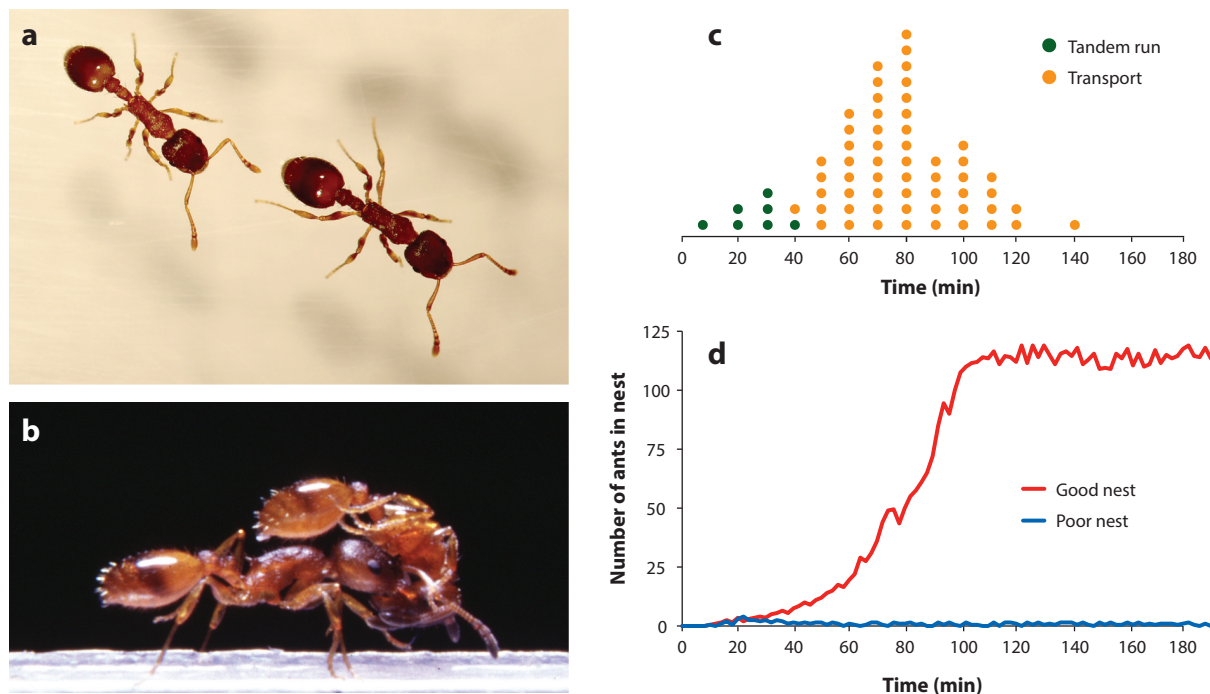
Figure 2

Behavioral elements of collective nest-site selection by *Temnothorax* ants. (*a*) Scout ants responsible for finding and assessing sites recruit one another via tandem runs by which a single nest-mate is led to the new nest. (*b*) Scouts transport the bulk of colony members by physically carrying them to the new nest. Transport is faster and more stable than tandem recruitment. (*c*) Scouts use tandem runs early in the migration, switching to transport once a new site's population surpasses a threshold, or quorum. (*d*) If a colony is choosing between two sites of different quality, the better site's population increases more rapidly because scouts are more likely to initiate recruitment there. The quorum rule amplifies this difference by accelerating recruitment at the better site once its population reaches the threshold. As a result, the passive majority of the colony (queen, nonscouts, and brood) are transported to the better nest. Photo in panel *b* adapted from Reference 40.

activity threshold that marks a decision in the brain. Just as individuals can adjust their sampling behavior to change the balance between speed and accuracy, colonies can tune their search effort, recruitment rate, and quorum size to prioritize speed when the colony is dangerously exposed or prioritize accuracy when it has plenty of time to make a better choice (36, 68, 85).

There is, however, one important gap in the ants' behavior: There is no evidence that recruiters to one site reduce recruitment to a competing site, either by inducing competitors to switch their loyalty or by causing them to cease recruitment altogether. Without such mutual inhibition, the ants cannot be inferred to achieve an optimal speed/accuracy trade-off. Still, the existence of an inhibitory signal cannot be ruled out. Scouts of *Temnothorax albipennis* have been shown to mark inferior sites in a way that makes it less likely the colony will later move into them (described in more detail in the section titled Collective Learning and Memory below) (38, 123). In *T. rugatulus*, ants that have been disturbed within a nest-site release an inhibitory pheromone from their mandibular glands (96). If this site is later pitted against an otherwise identical but unmarked site, colonies show a strong preference for the latter. These observations show that *Temnothorax* ants have the behavioral tools to send mutually inhibitory signals, but it is not yet known whether ants deploy them during normal nest-site selection.

The situation is different for honey bees, cavity nesters that also perform an elaborate decision process when they need to migrate to a new home (77, 105, 108). Indeed, their decision algorithm shows remarkable similarities to that of the ants, despite the large differences in colony size (a few hundred ants versus tens of thousands of bees), communication mechanism (tandem runs versus waggle dances), and means of movement (passive one-by-one transport over land versus self-powered simultaneous flight). Like the ants, bees deploy a minority of scouts to find and assess candidate sites (106). They also advertise these to fellow scouts with an effectiveness that depends on site quality (104, 107, 110). As in the ants, this advertisement uses a relatively slow recruitment mechanism (the waggle dance) that gives way to full commitment and accelerated motion once a quorum of scouts has arrived at a candidate site (109). Unlike the ants, however, the bees possess an activity-dependent, mutually inhibitory signal. Specifically, a scout advertising a given site will sometimes interrupt her waggle dancing to deliver vibratory stop signals to dancers for competing sites (111). These signals increase the likelihood that the recipient will cease dancing. Models show that this inhibitory signaling if practiced by advertisers for each site at rates proportional to the strength of their advertising allows the bees to implement the statistically optimal SPRT (67, 111).

RATIONAL DECISION MAKING BY INDIVIDUALS AND GROUPS

In this section, we turn from the border of psychology and neurobiology to that between psychology and economics to consider the concept of rational choice.

The Application of Economic Rationality to Behavioral Ecology

Classical economic theory assumes that decision makers are rational, meaning that they act to maximize utility, an implicit measure of benefit or value (137). However, behavioral economists, who study the psychological mechanisms behind decision making, have found that humans readily violate the principles that are required for utility maximization. One of these principles is transitivity: This principle holds that a preference for A over B and for B over C implies a preference for A over C (55, 133). Another is independence of irrelevant alternatives (IIA), which holds that the relative preference between two options should not change if a third decoy option is added to the set, especially if the decoy itself is universally rejected (91). For example, consider a wine buyer choosing between bottles A and B, such that A is cheaper but less flavorful than B. Depending on the exact values of the trade-off, the buyer will have some probability of choosing the more expensive wine B. Now imagine that a decoy option is added. Bottle C is just as tasty as wine B but even more expensive. In the jargon of behavioral economics, C is asymmetrically dominated in that it is clearly inferior to B because of its price, but not to A, which has the disadvantage of inferior taste. Experiments on this kind of choice typically find that subjects never choose option C. However, its mere presence increases the popularity of the dominant option (in this example, the expensive wine B) (51). In the most extreme cases, the presence of C completely reverses a preference for A over B. This sensitivity to the decoy is inconsistent with maximization and thus constitutes irrational behavior.

The significance of irrational behavior to psychology lies in its insights about underlying cognitive mechanisms. Irrational choice can be explained by constraints on the brain's computational resources that lead to bounded rationality (117). An ideal decision maker would accurately calculate the utility of each option and then always pick the highest one. In reality, this is very difficult and time consuming, especially for options that vary in multiple attributes. Hence, people instead use heuristics, or shortcuts, such as making pairwise comparisons among the options in a choice set

and favoring any clear winners (130). Such a rule strongly favors the dominant option in the wine shopping scenario described above. Behavioral economists have suggested an array of simple but effective decision rules that can explain common observations of irrational choice (4, 133–136).

Rationality and its violation have also proven relevant to behavioral ecology, which shares with economics an assumption that decision makers are maximizers but of fitness rather than utility (6, 55). There are many experimental demonstrations of animals violating rationality principles when making decisions with clear fitness consequences (6, 8, 9, 61, 97, 113–115, 138). Because these observations challenge the axiom that animals are fitness maximizers, some behavioral ecologists have responded by arguing that apparently irrational behavior can be consistent with fitness maximization when viewed more closely (49, 50, 70, 101, 132, 139). However, more may be learned by taking the approach of behavioral economics and using observed departures to infer something about underlying cognitive mechanisms. In analogy with bounded rationality, animals may be characterized as showing ecological rationality (121). That is, they have evolved not to be universal fitness maximizers but instead to solve specific problems in specific contexts relevant to their survival and reproduction. The mechanisms that meet these needs may nonetheless be susceptible to irrational behavior when presented with particular challenges, such as choice sets with asymmetrically dominated decoys. By identifying circumstances that do and do not lead to irrational behavior, we can infer exactly what heuristics animals use for a given problem.

The Emergence of Collective Rationality from Irrational Individuals

The potential of irrational behavior to shed light on decision mechanisms is particularly clear for the collective choices of social insects. It has long been known that individual social insects are vulnerable to the same irrational errors seen in humans and other animals. Honey bee foragers violate both IIA and transitivity when faced with decisions among sucrose feeders that impose trade-offs between important attributes, such as sucrose concentration and ease of access (113, 114). A similar violation of IIA was found by individual *Temnothorax* ants deciding between nest sites (97). Scouts were separated from their colony and given a choice between two target nests A and B that posed a trade-off between entrance size and interior illumination (**Figure 3**). These attributes are important to *Temnothorax*, with colonies showing a strong preference for smaller entrances and darker interiors (39, 79, 84). In addition to the targets, the option set included a decoy that was asymmetrically dominated either by A (D_A) or by B (D_B). These decoys had the predicted effect: A was preferred to B in the presence of D_A, but B was preferred to A in the presence of D_B. However, when the same option sets were presented to whole colonies, they behaved rationally: The relative preference between A and B was the same regardless of which decoy was present (34, 97).

A plausible explanation of these findings is that lone ants, much like other animals, rely on simplifying heuristics based on pairwise comparisons (7, 116). In a collective setting, however, such comparisons are unnecessary because each ant needs assess only one site. As described above, comparison at the group level emerges from a competition between scouts with information about only one site. This limited perspective imposes the best strategy for consistent choice: Evaluate a given option the same way, regardless of the alternatives. The separate evaluations of many ants are then integrated through a complex behavioral algorithm (85, 86). The result is emergence of a rational group decision from individual ants prone to irrationality.

This is not the only possible explanation for the observed results. In distributed systems that rely on positive feedback, like insect colonies, the probability of choosing the best option depends on the strength of feedback. Furthermore, the optimal strength varies with the number of options (76). Thus, if the strength of a colony's positive feedback is fixed (because it is an inherent property
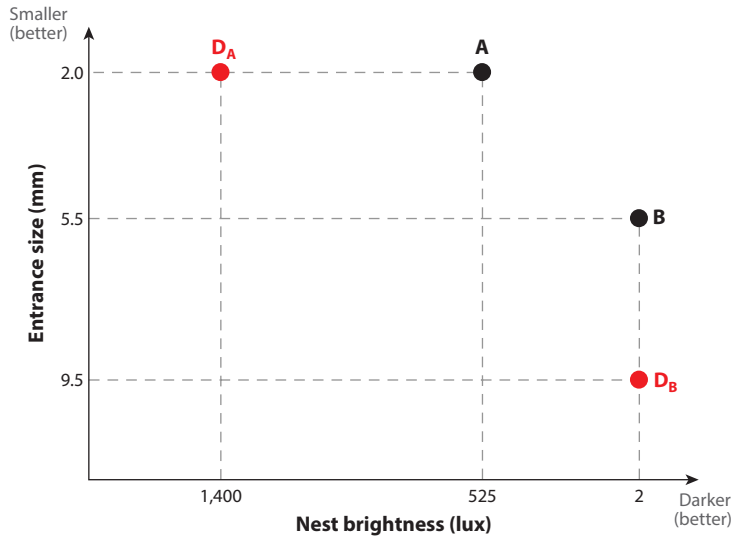
Figure 3

Target options and decoys used to test rational choice in nest-site selection by *Temnothorax* ants (97). Options A and B impose a trade-off between two desirable attributes (small entrance size and dark nest interior). Decoy options D$_A$ and D$_B$ are asymmetrically dominated by A and B, respectively. That is, D$_A$ is clearly worse than A, because A is darker, but not B, because B has a larger entrance. Similarly, D$_B$ is clearly worse than B, because B has a smaller entrance, but not A, because A has a brighter interior. If either decoy is included in the option set, this tends to increase the preference of individual decision makers for the dominating target. This change in preference violates the principle of independence of irrelevant alternatives, which decision makers must follow if they are to consistently maximize fitness, utility, or any other currency. Figure adapted from Reference 97, with permission.

of its recruitment behavior), then adding additional options may reduce the colony's ability to select the best one. Models show that this effect can explain the presence of irrational choice in distributed systems with a strong positive feedback (76). In principle, it might also be consistent with the absence of irrational choice in *Temnothorax* colonies, but this has yet to be rigorously investigated.

ENHANCED COGNITIVE CAPACITY OF DECENTRALIZED GROUPS

The emergence of collective rationality is one way that colonies can improve on the performance of individuals. Another is by increasing the cognitive capacity of the group compared to its component members. This has been shown in *Temnothorax* nest-site choice by studying cognitive overload, the paradoxical deterioration of choice outcomes with increasing option numbers (22, 47, 69, 102). Although more choices might be expected to give a decision maker greater opportunity to find an ideal solution, it can instead lead to worse decisions if it requires the decision maker to digest more information than it can handle. By combining the efforts of many members, insect colonies have the potential to overcome these individual limitations (22, 69, 129).

The greater cognitive capacity of colonies was shown in an experiment that required subjects (either lone ants or whole colonies) to select a new nest in one of two conditions (98). In the simpler condition, they chose between only two nests, one good and one poor. In the more

challenging condition, they chose among eight options, four good and four poor. The results showed that individuals performed significantly worse when the number of options was eight rather than two, indicating that they experienced cognitive overload. Colonies, by contrast, performed equally well with either two or eight options, with at least 90% choosing a good nest in each condition. Thus, colonies achieved a significantly improved decision performance in the face of increased processing load than did individuals.

A more detailed look at individual behavior showed that colonies were better able to share the burden of option assessment (98). In the eight-nest treatment, most lone ants visited five or more sites before making their choice. Their subsequent poor performance can be explained by this effort exceeding the amount of information they could effectively process. Individual scouts within whole colonies, by contrast, rarely visited more than one or two sites. The colony nonetheless assessed all sites because it could deploy different ants to different sites. In this way, the collective gathered thorough information without overtaxing the abilities of its members.

PERCEPTUAL DISCRIMINATION BY GROUPS VERSUS INDIVIDUALS

Collective rationality and enhanced cognitive capacity illustrate the wisdom of crowds—in other words, the improvement of decision making in groups compared to individuals (15, 58, 81, 105). The classic examples of such wisdom attribute it to the power of averaging many noisy independent judgements so that random errors cancel each other out (21, 118, 126). In these cases, a group of independent individual decisions is subjected to some form of centralized tally or average. Although many human examples fit this pattern (41, 58), social insects and other animal groups violate it in an important way. They lack a centralized mechanism for counting or averaging individual inputs and so rely instead on interactions among group members. As discussed above, the key means of interaction for social insects is recruitment communication that generates positive feedback driving the colony to one option among those offered. In the best case, positive feedback improves decisions by amplifying small differences in quality, allowing the group to make finer discriminations than a single animal (11, 18, 24, 28, 45). However, it can also happen that feedback amplifies errors and drives the group to the wrong choice (5, 29, 57, 58, 65).

A study of perceptual discrimination by *T. rugatulus* ants illustrates the double-edged nature of positive feedback (95). Like the cognitive overload and rationality research described above, this study borrowed a classic approach from psychology, in this case psychophysical methods used to study sensory discrimination (20, 30, 31, 43). *Temnothorax* subjects (either lone ants or whole colonies) were given a series of choices between a constant nest, with a very dim interior light level, and a comparison nest. The comparison nest was always brighter than the constant nest, but its exact brightness was varied across tests to provide challenges of varying difficulty. All subjects were expected to prefer the constant nest in every test because these ants have a strong and unambiguous bias toward darker sites (39, 66, 79). Thus, any choice of the comparison nest could be taken as a failure to discriminate the options.

As expected, both individuals and colonies made more accurate decisions as the choice became easier (**Figure 4**). However, the shapes of the discrimination curves were quite different. When the differences were small (i.e., difficult choices), colonies showed collective intelligence, more precisely discriminating options than individuals did. When differences were large, however, colonies did slightly but consistently worse than individuals. This basic pattern could be replicated by a simple mathematical model that incorporated key components of the ants' behavior, namely their quality-dependent recruitment, their reliance on a nonlinear quorum rule, and their limited individual ability to compare sites and choose the better one. A simple interpretation of these results
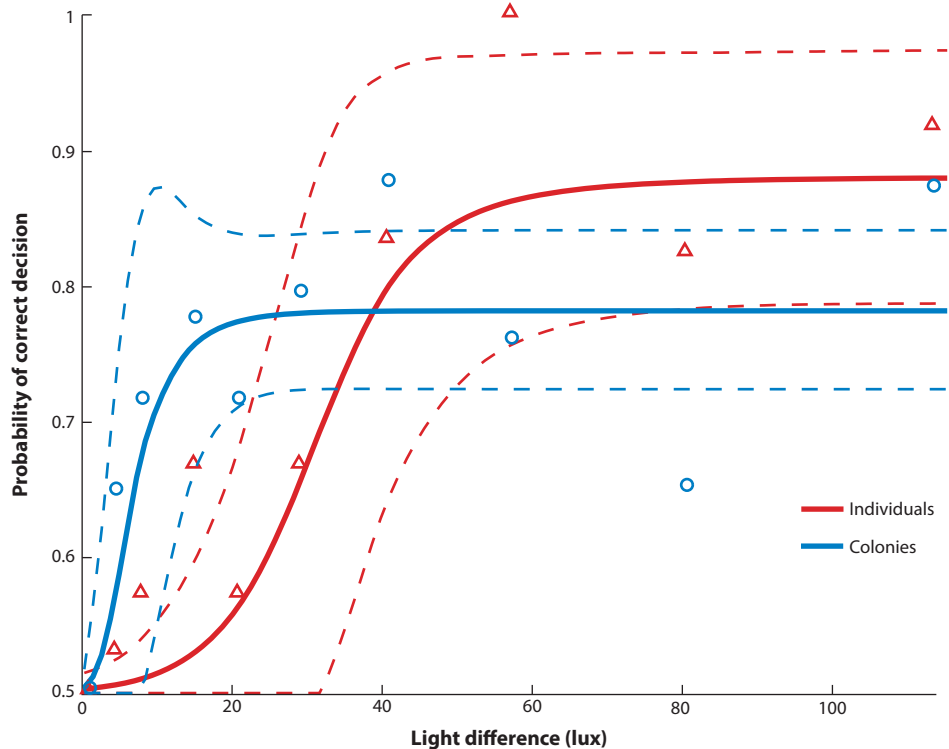
Figure 4

Difference in ability to discriminate nest-site brightness by colonies and individual ants. Colonies (*blue circles*) could detect smaller brightness differences than individuals (*red triangles*). However, individuals performed better for larger illumination differences, meaning that the asymptotic performance for individuals was higher than that for colonies. Separate sigmoidal response functions were fitted to the colony and individual data. The solid blue and red lines are best-fit psychophysical functions to the colony and individual data, respectively. The blue and red dashed lines give 95% confidence intervals for the colony and individual functions, respectively. Figure modified from Reference 95.

is that positive feedback between group members effectively integrates information and sharpens the discrimination of fine differences. When the task was easier, the same positive feedback could occasionally lock the colony into a suboptimal choice. This might happen if a sequence of random individual errors drives the inferior site above the ants' quorum, thus unleashing a positive feedback cascade. Such an outcome cannot happen when one ant works alone, and for easy choices, a lone ant's discrimination abilities are adequate to select the better option.

COLLECTIVE LEARNING AND MEMORY

Last, we consider the role of learning and memory in collective decision making, a subject that remains very little studied despite its central importance to cognition. Although there is ample evidence for sophisticated learning by individual social insects (44, 120), most studies of collective behavior have not considered how it changes over time or is impacted by experience. One exception is colony migration by *Temnothorax* ants, which have been found to increase their migration speed over successive trials (60, 71). In *T. albipennis*, which has received the most study, the effect

disappears after an interval of six full days, but repeated emigrations at one-day intervals yield an improvement that persists, even after a subsequent six-day rest.

In addition to improving the speed of emigration, experience can also influence decision accuracy. When *T. albipennis* colonies were given the opportunity to assess a high-quality nest for one week, and then induced to emigrate, they completed the move more rapidly than did naive colonies, and they were less likely to split between sites if given a choice of potential new homes (122). If exposed to both high- and low-quality nests, colonies moved faster, remained more cohesive, and showed greater likelihood of choosing the better nest (122). Perhaps the most interesting phenomenon is seen in colonies exposed only to a low-quality nest. In this case, colonies are less likely to choose this nest in a subsequent emigration, even if it is pitted against a nest of identical quality (38, 124). Thus, the colony's memories of its environment include both positive and negative ratings of potential homes. This can sometimes lead to suboptimal outcomes, as when a colony learns an aversion to a site and then rejects it in favor of an even worse but unfamiliar site (124).

Learning has the potential to improve collective choice by adjusting decision standards to prevailing conditions. This idea is inspired by many examples of context-dependent mate choice, where animals match their choosiness to the average quality of available mates (1). This helps to optimize the trade-off between settling for an inferior mate and delaying choice too long (142). Collective decision makers may similarly benefit from adjusting their choosiness. For example, in an environment where desirably large cavities are very rare, scouts should highly rate a medium-size cavity that would rate very poorly in an environment where large cavities were abundant. Evidence for such adjustment is mixed. A study of *Temnothorax curvispinosus* found no evidence for adaptive changes in choosiness when colonies were required to emigrate repeatedly in an environment characterized either by very good or very poor nests (46). However, the experimental design was open to confounding influences of colony state at the time of emigration. Somewhat better evidence has been found in *T. albipennis*. The quality of a colony's nest influenced the degree to which it learned an aversion to a reconnoitered nest; that is, there was no effect of familiarity if the familiar nest was no worse than the ants' current nest, but familiarity bred contempt if the familiar nest was worse than the current nest (124).

In addition to affecting the ants' overall choosiness, experience may also influence the weighting that ants give to different site attributes, such as cavity size, entrance size, interior light level, ceiling height, the presence of competitors or predators, and the availability of food, among others (19, 37, 39, 84). There is evidence that *T. albipennis* use a weighted additive strategy to combine these attributes into a single score (39). In *T. rugatulus*, colonies were found to change the relative weighting of different nest-site attributes according to how informative each attribute had been in recent colony migrations (99). Thus, when colonies repeatedly found cavity brightness to be the distinguishing feature in a series of decisions, they increased their weighting of this attribute in subsequent choices.

If colonies learn, where exactly does the learning happen? Is it within the brains of individual insects, as a foraging bee learns the location, color, and odor of a rewarding flower? Or is learning somehow dispersed across the colony and its environment? When a colony of *T. albipennis* retains knowledge of familiar good and poor nests that its scouts have discovered, this could be implemented by the memories of individual scouts. There is evidence for this, in that scouts who visit a site before the emigration memorize its location and later use this information to find the site faster than naive ants. Informed scouts also use their memories to initiate recruitment more rapidly once emigration is underway. By contrast, aversion toward familiar nests is mediated by a chemical signal that scouts apply to sites that are inferior to their current home (123). This signal influences not only the scouts that visited the site but also naive ants that only experience the

marked nest during emigration. In this sense, the signal constitutes a colony-level memory rather than an individual one.

CONCLUSIONS AND PROSPECTS

The application to colonies of concepts and methods from psychology attempts to make the superorganism concept more than a suggestive analogy. In this section, we argue for further application of the approaches reviewed above. Collective cognition has often been assessed using rudimentary tasks; hence the full abilities of colonies may have been overlooked. Methods from psychology can make more probing tests of cognitive ability, such as rational choice, avoidance of cognitive overload, and collective learning. One lesson of this work is that the details of collective mechanisms matter in determining how the group functions. It cannot be assumed, for example, that the combination of multiple individuals always produces group improvement or collective intelligence. As shown with perceptual discrimination by ant colonies, the outcome depends both on how the colony integrates the inputs of its members and exactly what problem is being solved.

The work reviewed here shows the potential for experiments that compare the performance of whole colonies with that of isolated individuals at the same task. There is some risk in drawing inferences from insects isolated from their normal social environment, but this is generally true of any experiment that artificially manipulates behavior. If proper controls are used, the manipulation can reveal novel insights about whether and how collective behavior improves on or detracts from individual performance. This approach can also shed light on the ambiguous relationship between group and individual cognition within insect societies. Colonies possess a broad range of information-processing structures, from highly distributed mechanisms in which cognition is an emergent property to less integrated mechanisms in which the bulk of information processing is done within the brain of a single insect (35). A full understanding of collective cognition requires an appreciation of the degree to which a given task is processed at the individual versus the group level.

A rich array of psychological approaches has potential for application to collective cognition. There is great promise in studying the interaction between collective behavior and learning. Indeed, there may be feedback between the two processes, such that new knowledge emerges during collective action, and this knowledge in turn improves group function in a lasting way (10, 56). These approaches need not be limited to social insects. Collective cognition has been identified across a wide range of taxa, from arthropods (2, 3, 42, 52, 64, 94) to group-living vertebrates (23, 63, 127, 140, 141) to human societies (32, 33, 58, 59). Recent studies have shown that collective decisions are even made by social amoebae that lack nervous systems (61, 62, 90). The psychological study of highly tractable insect societies can thus illuminate cognition in a much broader range of organisms.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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