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Is consensus-seeking unique to humans? A selective review of animal group decision-making and its implications for (human) social psychology

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Abstract

Recent research on animal behavior suggests that group decision-making may not be uniquely human. Based on Tinbergen's (1963) "four questions," this paper proposes that linking biological- and socialscience approaches is important to a better understanding of human group decisions. Toward this end, we first review some recent findings on collective behavior by social insects (ants and honeybees in particular). We then argue that several fundamental processes (e.g., positive feedback, nonlinear responses to social frequency information, and use of quorums) commonly underlie human and non-human group decision-making under uncertainty, while key prerequisites for the emergence of collective intelligence may be more vulnerable to social nuances in human contexts. We sketch some future research directions to promote cross-fertilizations between the two fields.

Keywords



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Human societies fundamentally rely on group decision-making. Committees and panels are everywhere, ranging from community-level town meetings, executive committees in firms, review panels in science, juries and examination boards in legal domains, to prefectural, national, and global political assemblies. The heavy use of committees is observed not only in modern societies (Hastie, Penrod, & Pennington, 1983; Kameda, Tindale, & Davis, 2003; Witte & Davis,

1996) but in more traditional societies as well. For example, by reviewing ethnographic data about tribal societies, Boehm (1996) showed that tribes

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usually hold meetings composed of adult men when making important, emergency decisions, such as whether to raid an adjacent tribe to solve land disputes. "Big man," the most powerful man in the tribe, typically serves only as a chairperson of the meeting rather than a dictatorial authority (see also Kameda & Tindale, 2006; Wilson, 1997).

Along with our highly sophisticated faculty for language, the ubiquity of group decision-making across many societies may seem to suggest that group decisions are uniquely human. However, recent research on animal behavior suggests that this is not the case. Group decision-making seems to be common in the animal kingdom as well, including social insects (e.g., ants, termites, honeybees), fish, and some mammals (Conradt & Roper, 2003, 2005; Seeley, 2010; Sumpter, Krause, James, Couzin, & Ward, 2008). Recently, Larissa Conradt and Christian List edited a special issue on "group decision making in humans and animals" in a prestigious biology journal, in which they wrote:

Although cross-referencing of natural science publications by social scientists (e.g. List 2004; Hastie & Kameda 2005), and vice versa (e.g. Conradt & Roper 2005), has already begun, indicating the mutual interest in interdisciplinary exchange, the language and thinking in the social and natural sciences are disparate enough to hamper communication. (Conradt & List, 2009, p. 720)

This paper thus reviews some of recent findings about animal group decision-making and explores their implications for research on human group behaviors. This paper is structured as follows. In the first section, we delineate why linking the knowledge of biological and social sciences is important to understanding human group decisionmaking. Specifically, we base our arguments on Nikolaas Tinbergen's (1963) famous distinctions of "the four questions" (especially the ultimatelevel and proximate-level questions) that should be asked of any animal behavior, including humans (van Vugt & Kameda, in press). In the second section, we selectively review some of the recent findings on group decision-making by non-human animals (social insects in particular), and explore their relevance to human endeavors. In the final section, we sketch future research directions in this field to facilitate the joint enterprise on group decision-making and to overcome the terminological and conceptual barriers between the biological and social-scientific approaches.

Why should social scientists care about "animal group decision-making" (and vice versa)?

What is meant by "animal group decision-making"? This concept may seem mysterious or perhaps simply metaphorical to many social scientists—other animals do not have the sophisticated language capacity of humans, nor can they deliberate over choices or cast votes. How can they make group decisions?

However, as we review below, recent research on animal behavior suggests that, in some nonhuman social animals, specific body postures, ritualized movements or specific vocalizations indeed function as 'votes' (see Conradt & Roper, 2003). Furthermore, such voting signals can be integrated in various ways, including by a majority rule (e.g., Byrne, 2000; Stewart & Harcourt, 1994), accumulating until an intensity threshold (quorum) is reached (e.g., Pratt, Mallon, Sumpter, & Franks, 2002; Seeley & Buhrman, 1999), and averaging over all votes (e.g., Oldroyd, Gloag, Even, Wattanachaiyingcharoen, & Beekman, 2008). Thus, the language faculty, though undoubtedly highly beneficial, does not seem to be the prerequisite for group decision-making in general.

Nikolaas Tinbergen, a Dutch ethologist who won the 1973 Nobel Prize in Physiology or Medicine, proposed that four questions are fundamental to understanding any animal behavior (Tinbergen, 1963)—Questions about (1) mechanism (causation); (2) development (ontogeny); (3) evolutionary history (phylogeny); and (4) function (adaptation) of the focal behavior. The first question concerns the proximate mechanism underlying the behavior, including what stimuli elicit the response, and how the process is regulated at the molecular, physiological, neural, cognitive, or social level. (Most social psychologists are mainly interested in this level of analysis.) The second question concerns the development of the behavior within individuals, including how the behavior changes with age and what early experiences are necessary for the behavior to emerge. The third question concerns the phylogeny of the behavior, or how the behavior compares with behaviors in related species. Finally, the fourth question asks the behavior's ultimate functions, i.e., how the behavior helps the agent's survival and reproduction. Tinbergen (1963) argued that failure to distinguish between the four questions, all of which are essential for a comprehensive understanding of the behavior, could (and did) lead to conceptual confusions.

It is thus important to specify that we will be focusing on the first (proximate mechanism) and fourth (ultimate function) questions, in order to find parallels between seemingly disparate species, which nonetheless have important problems and capabilities in common. As we will review later, group decision-making is most typically evinced when non-human animals engage in foraging for food or other key resources, or when some urgent collective move is needed (e.g., moving to a new nest site when the old nest has been damaged or overcrowded). Interestingly, human group decisionmaking also seems to revolve around the same two themes. In many modern organizations, examples of resource-foraging groups are abundant (e.g., investment committees), as well as task forces to manage urgent risks that demand swift collective action (Reason, 1997). In reviews of ethnographic records of tribal societies, Boehm (1996) also documented various emergency situations (e.g., heightened conflicts with an adjacent tribe, ecological crises caused by natural disasters), where consensus was actively sought through group decision-making to mobilize all band members. Thus, from Tinbergen's fourth, ultimate function-level perspective, group decision-making may be seen as a common solution to common adaptive problems for human and non-human animals, namely, foraging and urgent mobilization

of group members among behavioral-choice options in which uncertainties abound (see Kameda & Tindale, 2006). One function served by group decision-making in such contexts is to improve the accuracy or quality of a behavioral choice beyond other decision mechanisms (e.g., despotism), under constraints of time and effort (e.g., Gigerenzer, Todd, & the ABC Research Group, 1999; Hastie & Kameda, 2005; Kameda, Tsukasaki, Hastie, & Berg, 2011). Another function of group decision-making is to maintain the unity of the group. If the group is spatially or behaviorally divided in emergency situations (e.g., split between different destinations), then members can become more vulnerable to predators or rival groups, as well as losing economies of scale and specialization in their common efforts. It is thus often important to align members toward the same direction and maintain group-based advantages (Conradt & Roper, 2005; Sumpter, 2010).

The third, phylogenic-level perspective suggests that, to understand human group decisionmaking, we should be most concerned with collective behavior by primates, our closest relatives in the animal kingdom. However, we do not take this strategy in this paper; the focus of our review is not on primates but on social insects (ants and honeybees in particular). These animals are certainly quite distant from humans in the phylogenetic tree, yet they display an impressive array of group performances as collectives, sometimes referred to as "swarm intelligence" (Beni & Wang, 1989), despite their limited cognitive capacity as individuals. Related to this phylogenetic distance, the developmental processes of humans and social insects are disparate enough to make Tinbergen's second question (ontogeny) outside the scope of this paper as well. In the next section, we will review how these animals can achieve high-level group performances as collectives by focusing on algorithms of individual agent's choice behaviors (the first mechanismlevel question).

So, using the first and last of Tinbergen's (1963) "four questions," it seems plausible to say that group decision-making is a common but separately evolved set of mechanisms used by

some gregarious species (e.g., humans, ants, termites, honeybees) to perform shared adaptive functions efficiently, i.e., solving problems revolving around foraging and urgent group moves under uncertainty. Given this, we believe that linking the knowledge of biological and social sciences is important to a better understanding of group decision-making under a common theoretical umbrella.

How social insects make group decisions: A selective review

Conradt and Roper (2005) proposed a useful conceptual distinction to classify animal group decisionmaking-combined vs. consensus decisions. Combined decision-making refers to cases where animals decide individually, without requiring a consensus but in a manner that is somehow dependent on the behavior of other group members; the aggregate results of these individual decisions critically affect the group as a whole. Many foraging decisions fall into this category, where foragers seek resources (e.g., nectar, prey) individually but under social influence (e.g., using social-frequency information) from other foragers. As we will examine in the final section, various consumer decisions in humans also fall into this category. Consensus decision making, on the other hand, concerns cases in which group members make decisions together with the requirement of reaching a consensus, i.e., all members abiding by the decision outcome. Moving decisions, including decisions about where and when to migrate to a new nest site, fall into this category. Some foraging decisions (e.g., cooperative hunting by both humans and non-humans) are also in this category. In the following sections, we will review group decision-making by ants and honeybees respectively, according to these categories.¹

Ants

Ants communicate with each other using pheromones. While searching in its environment, a worker ant will often pause briefly to deposit a small amount of pheromone along its route. Others are attracted to these pheromone markings, and will often reinforce them while following the trail. As we will see below, this seemingly simple mechanism provides a foundation for a complex array of coordinated behaviors and patterns, including the formation of trails to food resources and new nest sites, and optimization of these behaviors according to adaptive principles (Hölldobler & Wilson, 1990; Wilson & Hölldobler, 2005).

Combined decisions

Deneubourg and colleagues conducted a series of experiments to examine how ants, which have only a limited individual capacity for orientation, were able to locate food resources efficiently as collectives. In one experiment, Goss, Aron, Deneubourg, and Pasteels (1989) placed a bridge between a nest of ants (Iridomyrmex humilis) and a food source. The bridge had a skewed figure-8 shape. Starting from the nest end, it split into two branches of different lengths at two different points, which eventually merged to the same destination where the food was placed. A forager going in either direction (leaving the nest or leaving the food) had to choose between two paths at two choice points, which yielded four routes in total. Results showed that, 5-10 min after placement of the bridge, explorers crossed it and discovered the food. A few minutes later, the shortest path between the nest and the food source was followed by a large majority of the ants. The ants solved the route-finding problem correctly as a collective.

How could this happen? This occurred because ants traveling the shorter path returned home faster and thus reinforced the pheromone markings on the path more frequently (i.e., a path whose length is half of the other's is marked twice while an ant travels to and from the food source, as compared to the other path that could be marked only once in the same time period), and because others were nonlinearly attracted to the higher pheromone concentration.

In another experiment, Beckers, Deneurourg, and Goss (1993) presented ants (Lasius niger) with two food sources of different quality, which were connected to the nest by a Y-shaped bridge. One end of the bridge always had a 1 M (mol/L) sugar source, while the other end had either 1, 0.5, 0.1, or 0.05 M. Results showed that proportions of the ants visiting the richer source increased rapidly as the difference in concentration between the two sources increased, with 86% of the ants visiting the 1 M source over the 0.1 M source and 100% over the 0.05 M source. This occurred because each ant laid pheromone trail markings in proportion to the concentration of sugar solution found (the richer the source, the more pheromone), and because others were nonlinearly drawn to stronger pheromone markings between the two ends.

We have summarized other examples of research on ants' collective foraging behavior in Table 1.

Consensus decisions

Nest migration requires not only individual search behaviors as we have seen above, but also some mechanisms to aggregate individual judgments into a consensus. In gregarious species such as ants, all members must abide by the consensus outcome whether or not they contributed to it, in order to maintain group cohesion against predation and other risks (Conradt & Roper, 2005; Sumpter, 2010). As we see below, "quorum rules" are usually used in these situations to yield the group consensus.

Franks, Mallon, Bray, Hamilton, and Mischler (2003) conducted a series of experiments to examine how ants (*Leptothorax albipennis*) choose a new nest from among several options, which had different values on three attribute dimensions (darkness, height, width). Results showed that an ant colony whose nest had been damaged was able to aggregate the attribute information coherently, choosing the best nest site in terms of overall quality from among as many as five options. The colony also completed migration (i.e. all individuals transferred) to the new nest site within a couple of hours.

Using an agent-based computer simulation, Pratt, Sumpter, Mallon, and Franks (2005) showed that such collective intelligence in a colony's migration can be understood by the following process model. The model assumes that migration proceeds by four different phases, in which ants gradually develop commitment to a particular nest site. When nest damage is initially detected, a subset of workers (about 30% of the colony) starts an exploration phase, individually searching for candidate sites. Upon finding a candidate site, an individual ant enters an examination phase, carrying out an independent quality evaluation of the site, whose duration is inversely proportional to the site's quality (less time for higher-quality sites). Once the individual has accepted the site in terms of quality, she enters a canvassing phase, returning to the old nest to recruit another ant to the new site (via "tandem-run"). Each of the recruited ants then makes her own independent examinations of the new nest, proceeding to further tandem-run canvassing if warranted. Because ants take less time to accept higher-quality sites, overall recruitment is faster to such sites. Finally, once the population in the new nest exceeds some "quorum threshold," a recruiting ant enters a *committed phase*. The recruiters stop the relatively slow tandem-runs, and accelerate the migration process by carrying passive nestmates and brood to the new nest site. This quorum threshold marks a key feature of ants' migration as a consensus (and not combined) decision. (See Table 1 for recent work about how ants can sense such quorums in the population during nest migration.)

Honeybees

As opposed to the use of pheromones by ants, honeybees communicate with each other about movement decisions primarily through a "waggle dance" with a figure-8 pattern. Waggle dances are performed by foragers that have located food resources (nectar, pollen), water resources, or new nest sites. The direction and duration of the waggle dances are known to be related to the direction and distance from the hive to the

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Study	Animals, task situation, and methods	Summary of findings
Beckers, Deneubourg, Goss, & Pasteels (1990) Nicolis &	Ants; foraging; experiments and simulations Ants; foraging; model	Presented with two food sources of equal quality, a group of workers settled on one of them rather than exploiting both equally, owing to an initial random imbalance between the two which was magnified through the positive feedback of pheromone attraction. If a low-quality food source had been settled on first, a newly-introduced high-quality food source was discovered, but the group did not switch to exploit it instead. If multiple sources of food are available, a group of ants generally choose just one to exploit. However,
Deneubourg (1999)	analysis	if the colony is relatively small or the number of sources is very large, multiple sources may be exploited equally.
Detrain & Deneubourg (2002)	Ants; foraging; review	Ants' simple individual-level food recruitment rules lead to a variety of adaptive group-level behavioral patterns according to differences in individual characteristics and environmental factors. For prey scavenging, the strength of an individual's recruitment pheromone trail is inversely proportional to ability to move the
		prey. This rule effectively encodes information about prey size, shape, and weight, as well as environmental features that hinder retrieval and the presence of sufficient helpers. Simple iteration and feedback leads
		to appropriate recruitment and colony-tever responses for smarter prey (e.g., retrieval by a contingent of small workers) or immobile large prey (e.g., recruitment of larger workers for on-site processing and consumption). A similar rule applies for recruitment in exploitation of liquid nutritional resources: A return trail is only laid if a forager is able to ingest a "desired volume," whose value varies across individuals. This
		rule flexibly tunes the colony's response according to resource size, renewal or depletion, crowding at the food site, and colony nutritional needs.
Pratt (2005)	Ants; nest migration; experiments	In order to switch to the final stage of nest site migration, individual workers detect the quorum threshold density at the site simply via the rate of direct physical encounters with nestmates at the site. This threshold
Pratt &	Ants; nest migration;	varies across individuals, but the intertation appears rough to this variation. Ants seem to use a single decision algorithm to respond adaptively to two different problems: Quickly
Sumpter (2006)	simulations	finding a new nest in a crisis and deliberatively selecting the best available new home. By varying the rates at which they (a) leave the nest to search for new nests and (b) begin recruiting others to an acceptable nest, the colony-level response adaptively favors either speed or accuracy. Varying the quorum threshold primarily affects the probability of solitting the colony among multiple nests, but does not affect the speed.
Camazine & Sneyd (1991)	Honeybees; foraging; model analysis	A non-linear differential equation model describes the activity of foraging bees. Using parameter estimates based on previously published data, the modeling results agreed closely with experimental observations. Selective exploitation of the most profitable nectar sources occurs through an autocatalytic, self-organizing
Visscher & Seeley (2007)	Honeybees; nest migration; experiments	process. Shortly before takeoff, bees emit a crescendo of a high-pitched mechanical signal, called worker piping. Only scouts that have visited the swarm's chosen nest site produce piping signals.

resource (Lindauer, 1961; Seeley, 1995, 2010; von Frisch, 1967).

Combined decisions

Seeley, Camazine, and Sneyd (1991) conducted a series of field experiments to test how efficiently a colony of honey bees (Apis mellifera ligustica) could exploit nectar sources. These researchers placed two feeders (one feeder contained more concentrated sugar than the other) in opposite directions (with each being 400 m away) from the hive, and altered the location of the richer feeder after 4 h. The bees were able to track this change, and consistently focused their foraging efforts as a colony on the more profitable feeder. Seeley and colleagues then examined how the colonylevel ability emerged from the behavior of individual bees through a series of ingenious manipulations. Results showed that the honeybees finely adjusted several components of their foraging behavior in accordance with nectar source profitability. When the quality was higher than some threshold, the bees foraged more quickly and danced more vigorously, thereby recruiting other bees to exploit the richer source. Furthermore, virtually all foragers (e.g., 115 of 117 bees) visited only one of the two feeders during their foraging. This means that the bees achieved high colony-level performance using only individual-level calculations of absolute profitability rather than relative comparison of multiple sources. In other words, this process is based on a decentralized control, whereby a coherent colony-level response to different food sources emerges from local interactions without overall consensus being explicitly sought. (Camazine & Sneyd, 1991, developed a mathematical model for this process; see Table 1.)

Consensus decisions

In late spring to early summer, as a large hive outgrows its nest, a colony of honey bees often divides itself. The queen leaves with about twothirds of the worker bees to create a new colony, and a daughter queen stays in the old nest with the rest of the worker bees. The swarm leaving the colony must find a new home in a short time, which is critical to their survival. The departing swarm, which is composed of 10,000 or so bees, typically clusters on a tree branch, while several hundred scout bees search the neighborhood for a new home. These scout bees fly out to inspect potential nest sites, and, upon returning to the colony, perform waggle dances to advertise any good sites they have discovered (Seeley, 2010).

In an experiment, Seeley and Buhrman (2001) presented honeybees with an array of five nest boxes, only one of which was a high-quality nest site while the other four were of medium-quality. The honeybee swarms chose the best nest site 80% of the time. As in the foraging case, this swarm-level performance in nest search was modulated by a scout bee's adjustment of waggle dances in accordance with nest site quality: The better the site, the stronger the dance. Other scout bees that have not flown out yet, as well as those that have stopped dancing, observed these dances and decided where to visit. In these decisions, the bees were more likely to visit and inspect the sites which have been advertised strongly by many predecessors. This process constitutes a positive feedback loop, yielding the swarm intelligence displayed in locating the best nest site.

Different from the foraging case, however, the scout bees must terminate the search phase at some point and mobilize the entire swarm to the new nest. Seeley and Visscher (2003) examined how such consensus decisions, which all members must abide by, were made. Results from a series of experiments showed that the honeybees used a quorum rule, where they began preparations for liftoff as soon as enough of the scout bees (not necessarily all of them, nor in fact any of the non-scout bees) have approved of one of the potential nest sites. When the quorum was reached, the scout bees used special wing-beat signals, known as "piping," to alert other nonscout bees in the swarm to warm up their muscles in preparation for the entire swarm to lift off and fly to the new nest (Visscher & Seeley, 2007 examined this process in detail; see Table 1).

What have we learned from group decision-making by social insects? Implications for human group decisionmaking

We have reviewed selectively some of the recent findings on group decision-making by ants and honeybees, focusing on proximate mechanisms by which these animals achieve high-level performances as collectives (for a comprehensive expert review, see e.g., Detrain & Deneubourg, 2008). As social scientists concerned with human group decision-making, what have we learned from these animals' behavior?

Key mechanisms underlying swarm intelligence

Taken together, the combined or consensus decisions of ants and honeybees when foraging for food or when migrating to a new nest site, have several key elements in common to yield their highly impressive group-level performances. The key factors include positive feedback along with nonlinear responses to social frequency information (e.g., trail markings by pheromones; the number of bees engaging in waggle dances). In the foraging case (combined decisions: Conradt & Roper, 2005), the process is started by one forager that finds a food source first, which is followed by more and more foragers over time (positive feedback). As more foragers are recruited, the rate of recruitment accelerates further, because foragers react to the social-frequency information in a nonlinear manner (i.e., more accentuated than proportional responses). Small initial differences in social frequency between options are thus amplified, so that the option favored by the greatest frequency is eventually taken by most foragers in the colony. In the case of nest migration where mobilization of the entire group is critical (consensus decisions: Conradt & Roper, 2005), this process is further accelerated and cemented by a quorum rule. The probability of performing an action increases sharply when a certain social frequency, or quorum, is reached. Such a quorum

threshold marks a critical point whereby the entire colony shifts from an exploration phase to a commitment/action phase.

Equivalent mechanisms in human group decision-making

These mechanisms have remarkable similarities in human group decision-making. As repeatedly shown since the original classic studies in social psychology (Asch, 1951; Davis, 1969, 1973; Festinger, 1954; Latané & Wolf, 1981; Sherif, 1932), humans are highly sensitive to social frequency information. Furthermore, human responses to social frequency information are nonlinear. In criminal juries for example, an undecided juror who has just realized that two others are endorsing Guilty and six others are endorsing Not Guilty (the remaining four jurors including self are silent) is likely to join the Not Guilty faction in due course, with a probability greater than 75% (= 6/8; e.g., Hastie et al., 1983). Theoretical analysis has also shown that such disproportionate "conformity bias" in copying is often functionally adaptive under uncertainty (e.g., Boyd & Richerson, 1985; Henrich & Boyd, 1998; Kameda & Nakanishi, 2002, 2003; but see also Kameda, Inukai, Wisdom, & Toyokawa, 2012; Kerr & Tindale, 2011 for maladaptive examples). As in the animal cases we have reviewed, this process often causes positive feedback loops in human groups as well, ranging from spread of happiness (Fowler & Christakis, 2008) and obesity (Christakis & Fowler, 2007) across a social network, through proliferation of crimes in communities (Glaeser, Sacerdote, & Scheinkman, 1997), emergence of a voting trend in the conclave for election of the Pope (Allen, 2002), to "herd behavior" in financial markets and the Internet (Akerlof & Shiller, 2009; Raafat, Chater, & Frith, 2009).

When official consensus is required, human groups often rely on some aggregation rule, which is functionally equivalent to the "quorum rule" in animal consensus-decisions (Conradt & Roper, 2005).² The aggregation rules in use (e.g., unanimity, super-majority, or simple majority)

depend on the importance of the problem, history, conventions, and other social/political factors, which have been a focus of voting theory in social sciences (Arrow, 1963; Black, 1958; see, e.g., Laughlin, 2011a; Mueller, 2003; for a general overview). For instance, the constitutionality of less-than-unanimous jury convictions in criminal cases was disputed in the 1970s at the US Supreme Court (Apodaca v Oregon, 1972; Johnson v Louisiana, 1972), and many jurisdictions in the US today require the jury to reach a unanimous verdict in criminal cases. Interestingly, however, Davis, Kerr, Atkin, Holt, and Meek (1975), who compared mock jury deliberation processes under unanimous or two-thirds majority rules, found almost no differences in verdict patterns between the two official rules; overall verdict distributions in the experiment were best predicted by a two-thirds majority (hung otherwise) modeli.e., the group verdict is predicted to be the alternative favored by at least two-thirds of the jurors at the outset of deliberations; if there is no such majority, the jury ends hung. This finding, along with similar results in mock jury and other group decision-making studies (see Kerr & Tindale, 2004, for a comprehensive review), suggests that behavioral "unanimity" in human groups is often achieved by majority/plurality aggregation (see Davis, 1973; Hastie et al., 1983; MacCoun, 1989), as "consensus" in animal groups is guided by implicit quorum rules. Hastie and Kameda (2005) argued that the majority/plurality aggregation often functions as a heuristic under uncertainty (Gigerenzer et al., 1999), which can solve the speed-accuracy tradeoff in consensus decisions efficiently if several key conditions, as we will discuss below, are met (Pratt & Sumpter, 2006; see also Regenwetter, Ho, & Tsetlin, 2007; Sorkin, Hays, & West, 2001).

The wisdom of crowds, the Condorcet Jury Theorem, and the law of large numbers

The majority/plurality aggregation in human as well as animal group decision-making, as we have

observed above, exaggerates any dominant tendency in individual responses at the collective level (Davis, 1973; Kameda et al., 2003; Kerr, Stasser, & Davis, 1979). By the multinomial theorem in elementary algebra, it can easily be shown that such mechanism yields a macro phenomenon known as group polarization in social psychology (Myers & Lamm, 1976), in which a dominant option at the individual level becomes more dominant at the group level, whereas the non-dominant options become even weaker (Davis, 1973; Kameda & Sugimori, 1995; Kerr, Davis, Meek, & Rissman, 1975; Smoke & Zajonc, 1962). When the number of options in a choice set is two (e.g., to migrate or not), this process can be described by the Condorcet Jury Theorem, formalized by the Marquis de Condorcet, a French social philosopher of the 18th century (Condorcet, 1785/1994). To illustrate, suppose that a group with 2m + 1 members works on some problem with an objectively true (but unknown) solution.³ The choice set is thus classifiable into binary behavioral categories, the one correct option vs. the other incorrect options. Assuming that each individual makes a decision independently from each other, the probability, G that the group reaches the correct choice by the majority rule is given by:

$$P_{G} = \sum_{n=n}^{2m+1} \binom{2m+1}{n} p^{n} (1-p)^{2m-n+1},$$

where p is the (average) probability that each individual endorses the correct option personally. And if individual accuracy (p) is greater than .5, the group accuracy under the majority rule is enhanced above p (i.e., p > .5), a phenomenon known as "the wisdom of crowds" (Surowiecki, 2004). Such a group-level improvement becomes even larger (i.e., P poproaches nearly 100% accuracy) with an increase in group size (e.g., Kameda, 1991; Kerr, MacCoun, & Kramer, 1996; Kerr & Tindale, 2004). When group aggregation is done by averaging (e.g., Larrick & Soll, 2006; Oldroyd et al., 2008), a similar group-level improvement is achieved by the law of large numbers in statistics (Galton, 1907). In either case, even if each group member is not very competent ("many wrongs": Simons, 2004), these simple aggregation mechanisms (majority rule, averaging) can cancel out individual errors and thus yield more accurate decisions in groups as compared to isolated individuals (Hastie, 1986; Hastie & Kameda, 2005; Laughlin, 201

Prerequisites for swarm intelligence

However, this reasoning simultaneously implies that there are at least three prerequisites for the simple aggregation properties (majority rule, averaging) to yield good collective results: (a) a moderate level of individual accuracy (e.g., p > .5above), (b) statistical independence in individual judgments/evaluations, and (c) mechanisms that motivate contributions to the collective decision while discouraging free-riding (Hardin, 1982). For the first condition (moderate competence of members), group aggregation yields lower-quality outcomes than the average performance of isolated individuals if group members' average accuracy is low (e.g., p < .5; Kerr et al., 1996); group decision-making is dysfunctional in these cases. Likewise, if members' judgments or evaluations of choice alternatives are constructed under strong mutual influences (violation of the statisticalindependence condition), errors in their judgments will be highly correlated with each other, and mechanisms that would otherwise enhance group-level performance over the individual level, as expected from the Condorcet Jury Theorem or error cancellation via averaging, will not be effective (Anderson & Holt, 1997; Banerjee, 1992; Bikhchandani, Hirshleifer, & Welch, 1992). Finally, if members free-ride on the outcome of others' efforts without incurring personal costs to improve the collective endeavor (violation of the contribution condition), average individual accuracy is lowered and the benefits of grouping may not materialize (Kameda et al., 2011).

Ants and honeybees seem to be able to solve these potential problems in collective actions. For example, as we have seen, ants lay pheromone trail markings in proportion to the concentration of sugar solution found (the richer the source, the more pheromone: Beckers et al., 1993); for prey scavenging, the strength of an individual's recruitment pheromone trail is inversely proportional to ability to move the prey (Detrain & Deneubourg, 2002). Honeybees also adjust finely several components of their foraging behavior in accordance with nectar source profitability: When the quality is higher than some individual thresholds, the bees forage more quickly and dance more vigorously (Seeley et al., 1991). These finetuned (and genetically acquired) mechanisms seem to assure that ant/honeybee foragers have at least moderate individual accuracies (i.e., p > .5) in most natural cases (though of course sudden changes in their adaptive environments can work against such fine-tuned mechanisms).

It should also be noted that ant/honeybee foragers evaluate the quality of food resources or nest sites *independently* from others. They are certainly affected by other foragers' actions (pheromone trail makings, waggle dances) in their decisions about where to visit. But, simultaneously, they are independent in assessing the quality of the visited site. For example, the duration of the scout bee's dance, which indexes the strength of the bee's preference for the site, is *not* affected by others' waggle dances but determined *solely* by her own perception of the site's quality (List, Elsholtz, & Seeley, 2009; Seeley, 2010).

Finally, free-riding in collective action is not problematic in most social insects, as their colonies are largely composed of kin. Helping biological relatives carrying the same genes can increase inclusive fitness, even if an animal incurs a cost to own survival and/or reproduction. Thus, free-riding is much less common in colonies of social insects than in human societies (Hamilton, 1964).

Some future research directions in human group decision-making

So how do the three prerequisites for swarm intelligence fare in human activities? This question seems to warrant serious theoretical and empirical attention in future research on human group decision-making. Here, we consider some future research directions among the three prerequisites for collective intelligence.

Average individual accuracy in natural contexts

Compared to the fixed, genetically-determined algorithms of ants and honeybees, human cognitive faculties are far more flexible, enabling us to inhabit a wide range of natural environments (from the Arctic to the Gobi Desert), through the use of material and social devices to cope with various adaptive challenges (Gibbons, 1998). Along with our unique language faculty, such flexible cognitive capacity allows us to be far better individual learners (and problem solvers) in much broader contexts than any other species on earth (Mithen, 1996). Given this, it seems rather implausible that average human individuals are incompetent in ecologically representative (natural) task settings (though of course average performance could be poor in evolutionarily novel contexts, such as when learning mathematics; Gigerenzer et al., 1999; Kameda & Hastie, 2004; Krueger & Funder, 2004). This reasoning suggests that, in some natural cases where average individuals may indeed perform badly, the inaccuracies are unlikely to be attributable to cognitive limitations as individual learners per se. Instead, we believe that such decreased individual accuracies are most likely to emerge from the "docility" of our minds (Simon, 1983, 1990), which makes us highly sensitive to social nuances (Kameda & Tindale, 2006). In other words, whether or not a moderate level of individual accuracy (the first condition for collective intelligence) is sustained seems to be largely determined by the other two conditions pertaining to our highly social minds. We will examine this point below.

Independence in evaluations

Herbert Simon introduced the term "docility", meaning a "propensity to behave in socially approved ways and to refrain from behaving in ways that are disapproved" (Simon, 1983, p. 65), which stems from our fundamental motivation to obtain information from social channels. Classic studies in social psychology (Asch, 1951; Sherif, 1936) have documented that such tendencies are particularly pronounced in consensus-seeking situations, in which everyone in a group is susceptible to the same perceptual or cognitive errors, yielding high interdependencies in members' judgments. In addition, members' responses to conformity pressure depend on specific social/ cultural contexts (e.g., leadership styles or corporate cultures; Janis, 1972, 1982), and are also vulnerable to subtle normative cues and nuances (e.g., Bateson, Nettle, & Roberts, 2006).

All these observations seem to suggest that humans may be in some ways even more social than social insects, that is, even more susceptible to influences emitted from others. Then the focal question is whether humans can remain only *selectively* influenced by others, like honeybees that combine dependence (in search) and independence (in evaluation) properly to achieve collective intelligence in foraging (List et al., 2009). Can humans show "swarm intelligence" in combineddecision cases as do social insects? This question is central to many modern mass-behavior contexts (e.g., financial markets, internet shopping) that structurally correspond to *combined* decision cases in animals (Conradt & Roper, 2005).

Two recent experiments shed some light on this question. Salganik, Dodds, and Watts (2006) conducted a large-scale Internet experiment on a "cultural market", whereby people downloaded songs from an artificial music site. In the site, participants were provided social frequency information about how others had decided, while they could also listen to and examine each song individually. The results showed that people's preferences for music might not reflect a song's inherent quality but were strongly affected by others' preferences. As a result, the overall popularity rankings of the songs in the market were susceptible to random fluctuations and were often highly path-dependent. Toyokawa, Kameda, and Kim (2011) extended Salganik et al. (2006) into a situation where the quality of choice options could be defined objectively. These researchers used a "multi-armed bandit" task (e.g., McElreath et al., 2008; Schlag, 1998), where participants had to make choices individually between six "slot machines" whose expected values were different from each other but unknown to participants. Participants played this game repeatedly in groups of five, and the reward for each participant was determined solely by his/her individual choices; thus this was a case of combined decision as in Salganik et al. (2006). Besides the payoff feedback from their own individual choices, participants could also view social frequency information about how many individuals in the group chose each option in the preceding round, along with averages of ratings that each participant gave to his/her chosen option on a 5-point scale (as those found in Amazon or Yelp). Extrapolating from the honeybee's behavioral algorithms (List et al., 2009), the availability of the rating opportunity along with social frequency information could have potentially allowed the human participants to balance dependence (in choice) and independence (in evaluation) properly to yield "swarm intelligence" collectively. Results, however, showed that average performances in the group condition were no better than those in the isolated individual condition; participants in the group condition failed to use the rating capability productively.

Salganik et al. (2008) and Toyokawa et al. (2011) suggest that, even in commercial situations where conformity pressure toward consensus is much weaker, maintaining independence in individual evaluations and choices may not be easy. Future research that delineates conditions in which human individuals can separate out independence in evaluation from dependence in search will be important both theoretically and practically (see Kameda et al., 2012, for further discussions).

Free-riding in collective action

In contrast to most social insects, human groups often contain non-kin members, which makes the issue of free-riding central in any collective action in our societies. Theoretical and empirical research have repeatedly shown that maintaining high-level cooperation poses major challenges in human groups (e.g., Hardin, 1982; Ostrom, 1990). How does the free-riding problem interfere with feasibility of the wisdom of crowds in human groups in particular (Surowiecki, 2004)? This constitutes a core problem for human collective intelligence. Conventional mechanisms that have been proposed to deal with free-riding in a group include sanctions against norm-violating freeriders (e.g., Fehr & Fischbacher, 2004a, 2004b), and reputation systems that promote members' cooperation (e.g., Nowak & Sigmund, 2005). Yet, how these conventional mechanisms are applicable to consensus-seeking situations in relation to emergence of collective intelligence in groups remains unclear.

Recently, Kameda et al. (2011) approached the free-rider problem from an unconventional perspective. The task situation they studied was parallel to animal consensus decision cases (Conradt & Roper, 2005), in which six-person groups had to reach a binding group decision under uncertainty (as in the aforementioned multi-armed bandit situation: Schlag, 1998). Examining incentive (game) structures of the group task, Kameda et al. (2011) argued that many natural groupdecision tasks are not necessarily social dilemmas (as assumed in the previous literature: Kerr, 1983; Ledyard, 1995) where free-riding is a dominant strategy. Instead, they argued that most decision situations can be understood as a "producerscrounger game" (Giraldeau & Caraco, 2000) where cooperators and defectors coexist in a group in a stable manner. That is, some individuals remain cooperative in contributing to the group endeavor (e.g., engaging in costly information search, bearing voting costs) for selfish (rational) reasons, while others loaf; neither cooperation nor free-riding is dominant in the producerscrounger game, yielding a mixed equilibrium in a group (see Foster, 2004; Motro, 1991 for analytic details). Kameda et al. (2011) then argued that, even if no sanctioning or reputation systems exist (Fehr & Fischbacher, 2004a, 2004b; Nowak &

Sigmund, 2005), thanks to those rational cooperators, group decision-making can outperform other decision mechanisms (e.g., despotism where the best and brightest individual makes a decision for the group, or decision-making by isolated individuals) under uncertainty. They tested this prediction by a series of computer simulations and a behavioral experiment. Results supprediction, ported their indicating that majoritarian decision-making can beat other decision mechanisms in a broad parametric range under uncertainty. Kameda et al. (2011) called such superb performances of majoritarian group decision-making "democracy under uncertainty."

These results are suggestive, yet are silent about how conventional control mechanisms (e.g., sanction or reputation systems) may function in human group decision-making in relation to collective intelligence. Future research addressing these questions seems to be promising, which highlights one of the key differences of human groups from groups of social insects which are largely composed of kin.

Research on groups in social psychology has vielded many key insights about human collective behavior. Simultaneously, as we have reviewed in this paper, interests in animal collective behavior are rapidly growing in biology and related disciplines including information sciences, complex systems, and so on (Sumpter, 2010). Yet, the language and thinking in the social and biological sciences are still disparate enough to hamper fruitful communication (Conradt & List, 2009). This state is unfortunate, and it is time for us social scientists to think about how our knowledge about human collective behavior may be linked to developments in research on animal collective behavior. Such cross-fertilizations have great potential for addressing various urgent problems in our societies, where inaccuracy, interdependence, and free-riding among agents are leading to new crises and dilemmas (e.g., Akerlof & Shiller, 2009).

Notes

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- 1 Conradt and Roper (2005) defined group decision broadly as "a decision made by the animals within a group" (p. 449, emphasis added), and then proposed the conceptual distinction, combined versus consensus decision, as described above. Notice that such conceptual distinction along with the broad definition of group decisions has some parallels in social sciences, particularly in the public choice literature (e.g., Mueller, 2003). In this literature, the former are often described as interactive decisions in which people make social decisions (i.e., decisions that affect welfares of others as well as self) in an interactive manner but with no explicit binding mechanism. These cases are often the subject of game theory and have been conceptualized with specific game structures (e.g., public goods, prisoner's dilemmas, chicken, stag hunt game). In contrast, the latter are described as aggregate decisions, which have been the subject of social choice theory (Arrow, 1963) and of group decision making research in social psychology (Davis, 1973). In these cases, members' preferences are aggregated into group decisions explicitly by some institutional mechanism (e.g., elections, jury deliberation), and members must abide by the outcomes even if their preferences are not consistent with them; behavioral unity as a group is enforced.
 - In law and other social sciences, a "quorum" refers to the minimum number of members of a deliberative body necessary to conduct the business of the group. If the quorum is not reached, the meeting is not official; when the quorum is present, decision of the meeting, be it reached unanimously, through voting by a 2/3 majority rule, or by a simple majority/plurality rule among members at the meeting, becomes the official decision of the entire, deliberative body. It seems that some usages of the term "quorum rule" in the animal group decision-making literature (e.g., Sumpter, 2010) may be closer to the aggregation rule rather than to the quorum rule in the legal sense. For example, in cases where nest sites endorsed by smaller factions of scout bees are "outvoted" while the nest site with the greatest majority of scout bees is chosen as the next home for the entire swarm (Seeley, 2010), "aggregation

rule" seems to better describe the decision situation than does "quorum rule" in the social scientific usage.

3 In the case where a group has 2*m* members, we also have to assume that, if there is an equal split, the group decision is made randomly between the correct and incorrect options. This additional assumption, however, does not change the general conclusion to be described in the text.

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