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Collective cognition in animal groups

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The remarkable collective action of organisms such as swarming ants, schooling fish and flocking birds has long captivated the attention of artists, naturalists, philosophers and scientists. Despite a long history of scientific investigation, only now are we beginning to decipher the relationship between individuals and group-level properties. This interdisciplinary effort is beginning to reveal the underlying principles of collective decision-making in animal groups, demonstrating how social interactions, individual state, environmental modification and processes of informational amplification and decay can all play a part in tuning adaptive response. It is proposed that important commonalities exist with the understanding of neuronal processes and that much could be learned by considering collective animal behavior in the framework of cognitive science.

Introduction

It is little wonder that the behavior of animal groups, such as schools of fish, flocks of birds or swarms of insects has been associated with the concept of having a ‘collective mind’ [1]. Grouping individuals often have to make rapid decisions about where to move or what behavior to perform, in uncertain and dangerous environments. Decision-making by individuals within such aggregates is so synchronized and intimately coordinated that it has previously been considered to require telepathic communication among group members or the synchronized response to commands given, somehow, by a leader [2,3].

In fact, individuals base their movement decisions on locally acquired cues such as the positions, motion, or change in motion, of others [2], making the collective response all the more remarkable. Each organism typically has only relatively local sensing ability (further limited in large aggregates by crowding). Groups are, therefore, often composed of individuals that differ with respect to their informational status and individuals are usually not aware of the informational state of others, such as whether they are knowledgeable about a pertinent resource, or of a threat [1,2,4,5].

Recent studies have begun to elucidate how the repeated interactions among grouping animals scale to collective behavior, and have revealed, remarkably, that collective decision-making mechanisms across a wide range of animal group types, from insects to birds (and even among humans in certain circumstances) seem to share similar functional characteristics [2,4,5]. Furthermore, at a certain level of description, collective decision-making by organisms shares essential common features

with mechanisms of decision-making within the brain [1,6]. Although many details differ, there is good reason for increased communication between researchers interested in collective animal behavior and those in cognitive science.

Collective motion

It is usually not possible to scale reliably from individual to group behavior through verbal argument alone. Consequently, considerable progress in revealing the principles of collective behavior has been made using mathematical modeling techniques, such as computer simulation (Box 1). Some of the earliest theoretical approaches were inspired by particle physics [2,7]. These introduced the influential concept of using equations to characterize individual movements and interactions (as ‘social forces’), the aim being to explore whether (and if so, how) individual behaviors can scale to the coherent collective motion exhibited by fish schools or bird flocks.

Valuable insight was gained using such model descriptions. First, it was realized that collective behavior can arise from repeated and local interactions and need not be explicitly coded as a global blueprint or template [2,8–10]. In addition, biologically plausible local interactions can account for the typical group structures found in nature (Box 1). Because of the nature of these local interactions, behavioral control is typically distributed, as opposed to control being hierarchical with one (or a few) leader(s) controlling group-members’ actions.

Because distributed coordination does not depend on a specific subset of individuals, groups are inherently robust to perturbation. Analogous decentralized principles govern the coordination of many neuronal assemblies, enabling robust encoding of information across a wide range of spatial and temporal scales [11–22]. Information from multiple distributed sources can be acquired and processed simultaneously, thus allowing individual (cells or organisms) access to computational capabilities not possible in isolation.

A further principle revealed by computational modeling of grouping, as outlined in Box 1, is that multiple stable modes of collective behavior can co-exist for exactly the same individual interactions [10]. This is directly analogous to multistability in neural systems, in which multiple collective states (attractors) co-exist at the same value of the system’s parameters both within neurons themselves and in neural networks [20]. Multistability in neural systems has been suggested as an important mechanism for memory storage and temporal pattern recognition [20], and an intriguing (but currently untested) possibility is that similar functional benefits might exist for animal groups.

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Amplification and damping of collective response

Feedback processes

The social context created by highly integrated behavior strongly affects the way information is acquired, transmitted and processed by group members. Specifically, it can facilitate the collective amplification and damping of information and, thus, the adaptive tuning of collective behavior in response to external stimuli and/or internal state.

Alignment among individuals (a tendency to move in the same direction as near-neighbors, **Box 1**), for example, can enable information about a change in direction to be transmitted as a rapid wave of turning, over long distances [23,24]. Amplifying local fluctuations through positive feedback is important when threats, such as predators, are detected because it creates an 'effective' sensory range much greater than that of individual perception [1,2]. For example, the change of direction of only a few individuals that initially detect a cryptic predator can be amplified rapidly, as a propagating wave of turning, resulting in a much larger number of individuals, or even a whole group, turning away from the threat [1,2,23,24].

Similar amplification processes are a fundamental component of neural information-processing. They facilitate the translation of local stimuli to response both within the cell (the conversion of localized ion fluxes to action potentials) and to intensification of propagating electrical and chemical activity across networks of cells, such as the traveling waves of activity seen in the vertebrate cortex [13,17,20–22].

A further commonality with neural signal propagation and information encoding is that it is difficult for animals in groups to tune collective response with positive feedback alone. Damping, or negative feedback, is often an important regulator of group response. Tuning, adaptively, collective response through regulation of the relative influence of positive and negative feedback is the essence of decision-making in many neuronal [20–22] and animal systems [2,5,25,26]. In certain ant species, the analogy with neural systems becomes particularly intimate, as outlined in **Box 2**.

Feedback and the speed–accuracy trade-off

Decisions based on uncertain information often benefit from an accumulation of information over time. A very fast decision, in which positive feedback dominates, is typically compromised with respect to accuracy because the choice

made can often be the result of amplification of random fluctuations or stochastic initial conditions. This can result in 'informational cascades' in which arbitrary choices are made [2,5,27]. Incorporating negative feedback can prevent such over-sensitivity of collective response to individual error or environmental noise and can enable long-range patterns to be detected in the face of distracting local fluctuations [28]. Typically, however, this ability comes at a cost as the time taken to make a decision is increased (a speed–accuracy trade-off).

Little is currently known about how vertebrate groups, such as fish, birds or herding quadrupeds actually balance the trade-off between speed and accuracy during collective decision-making. A clue comes from an experimental study by Ward *et al.* [25] on schooling stickleback fish (*Gasterosteus aculeatus*). Individuals were shown to exhibit a highly non-linear response to near-neighbors; they largely disregard the movement decisions of a single neighbor, but strongly increase their probability of copying as more neighbors (a 'quorum') commit to a given direction of travel. This functional response was found to improve the accuracy of individual decision-making by enabling fish to integrate their own estimation with that of others, while not incurring much cost in terms of the time taken to make a movement decision.

This form of non-linear response represents a common theme among many decision-making systems that face speed–accuracy tradeoffs (see later discussions on social insects). An initial slow phase enables appropriate information to be accumulated before a transition to a higher commitment to one option, among alternatives.

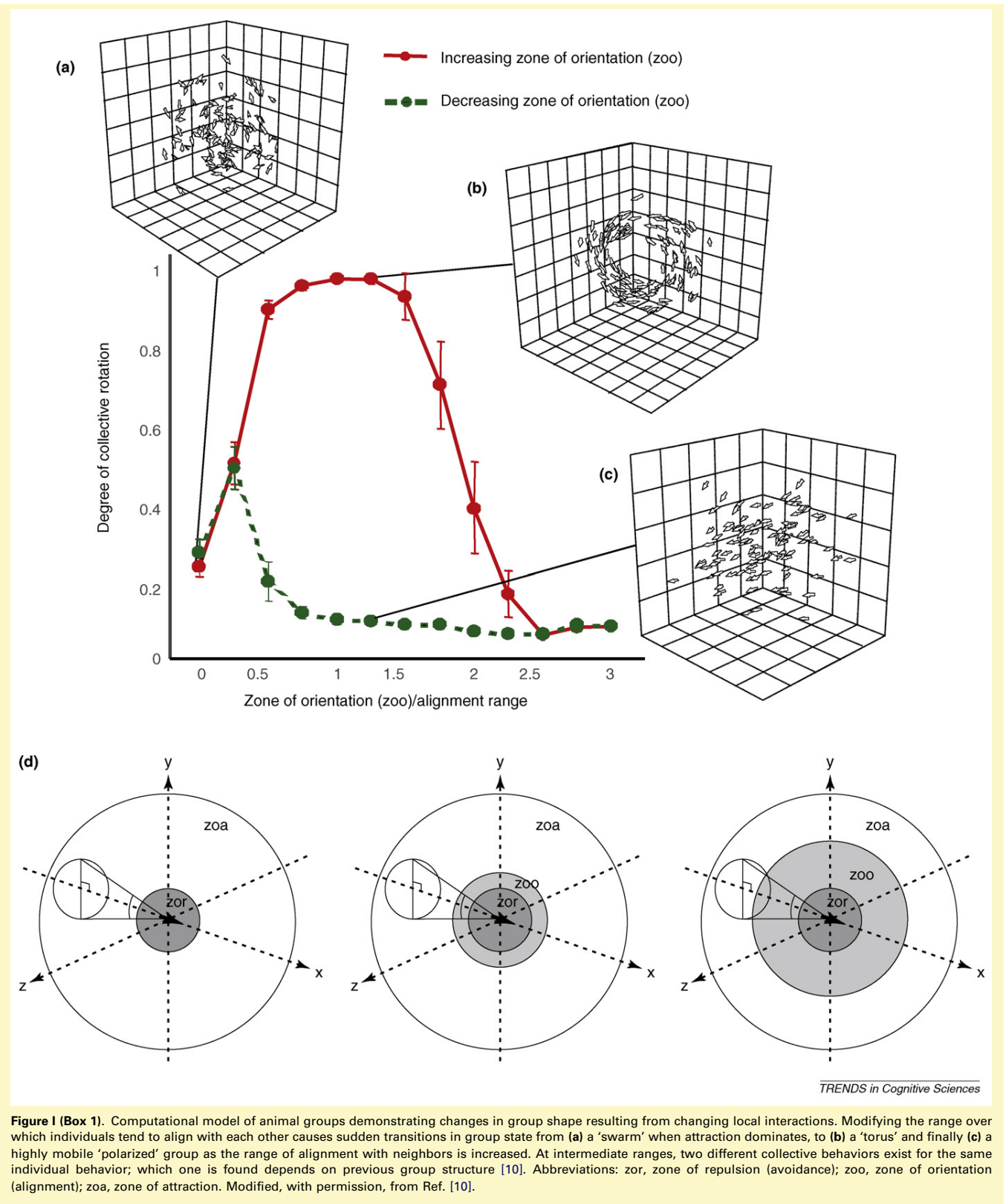
A similar challenge faces the brain when presented with ambiguous conflicting sensory stimuli. Within the primate brain, for example, sensory evidence for different stimuli is encoded as firing rate within separate, competing neural groups [11,12,14–16,18,19]. This evidence is noisy, however, and to appropriately weigh evidence it must be integrated over time. Thus, neuronal decision-making also faces the challenge of when to commit to a decision. If a choice is made too early in the integration process it is too error-prone. If made too late, much valuable time can be lost. In fact, decisions made in brain circuits have been shown to optimize the speed and accuracy of choices, and their trade-off [19]. Although the mechanism determining decision-making is currently unclear, a threshold process has been

Box 1. Scaling from individual to collective behavior

Mathematical modeling proves to be indispensable when investigating many aspects of collective behavior. Spatial features of interactions are typically incorporated by modifying the strength, or type, of interaction as a function of spatial [10] or topological [69] distance to neighbors. For example, behavioral tendencies can be restricted within specified 'zones' around each individual as represented in **Figure 1d** (see next page). Near-range repulsion from others enables collision-avoidance and maintains individual personal space (**Figure 1d**, 'zor'). A relatively long-range attraction maintains group cohesion, minimizing potentially dangerous isolation [2,23,24] (**Figure 1d**, 'zoa'). Furthermore, individuals often exhibit a tendency to align their direction of travel with others (**Figure 1a**, 'zoo').

Despite the continuously varying parameters, only a few types of stable collective-behavior typically emerge. For example, loose, disordered 'swarms' form when individuals exhibit only repulsion

and attraction (**Figure 1a**). Introducing a relatively restricted alignment tendency causes individuals to form a 'torus' in which they perpetually rotate around an empty core (**Figure 1b**), a pattern exhibited by fish species such as barracuda, jack and tuna [2,5,10]. Slowly increasing the range of alignment further, however, results in a transition to a cohesive and 'polarized' (well-aligned) group, much like typical mobile bird flocks and fish schools (**Figure 1c**). The transitions between these collective behaviors are very sudden, even if individual behavior changes only slowly. Multiple stable collective states can exist for the exactly the same individual behavior, and be dependent on the previous history of group structure, such as whether behavioral parameters are increasing or decreasing (see the graph in **Figure 1**), despite no individual having memory of that structure. This demonstrates that animal groups can exhibit a form of hysteresis, or 'collective memory'.



proposed whereby a decision is made once one integrating neural group reaches a certain threshold-level of activity [11,14,19]. Unlike in animal groups, however, this assessment is likely to be made by a higher-level circuit, rather than being arrived at by the integrating units themselves [19].

Group size and collective decision-making

Group size can also have an important role in decision-making. If individuals have access to the same information, but it is inaccurately represented or processed, then averaging response with others (as is inherent in many schooling or flocking strategies; **Box 1**), will improve

Box 2. Ants as mobile neural networks

Ant colonies are parallel information-processing systems capable of intricate collective decision-making during essential tasks such as foraging, moving home or constructing a nest (see main text). If one looks within the nest of several species [72], further similarities to neuronal systems become apparent. Many neuronal cell types are not intrinsically rhythmic and yet together form synchronously firing assemblies as a result of mutual excitation [17,20]. Similarly, ants in isolation display short and temporally erratic bouts of activity [73]. When within the colony, however, a regular rhythm of activity is generated spontaneously (Figure 1).

Analysis of this process indicates a common mechanism [71–74]. Ants seem to exhibit a very ‘neuron-like’ behavior in which inactive ants exhibit a low propensity to become spontaneously active (analogous to spontaneous firing of a neuron). Moving ants can excite individuals with whom they come into contact and ants seem to temporally integrate these inputs. If an inactive ant is excited above a threshold (equivalent to beyond-threshold depolarization of a neuron), they change state and start moving, thus becoming

excitatory themselves. Activity, therefore, can spread across the colony. Insufficient reinforcement of excitatory activity, however, results in active ants tending to become inactive again. Like their neuronal counterparts, once they change to an inactivated state they exhibit a short refractory period during which they have a very low probability of being re-activated. This latter property prevents the system locking into an excitatory state and facilitates the repeated propagation of coordinated waves of activity, similar to those seen in the developing retina [13] and vertebrate cortex [17,21,22].

A functional parallel could exist with input selection in oscillating neuronal systems [17,20]. Rhythmical neuronal network activity is an energy-efficient way to periodically elevate the system close to threshold, thus providing discrete windows of high responsiveness to external stimuli [17]. Similarly, it has been hypothesized that synchrony among ants provides discrete windows of opportunity to detect, and respond to, external foraging opportunities or to efficiently allocate workers to required tasks within the nest, such as brood care [75].

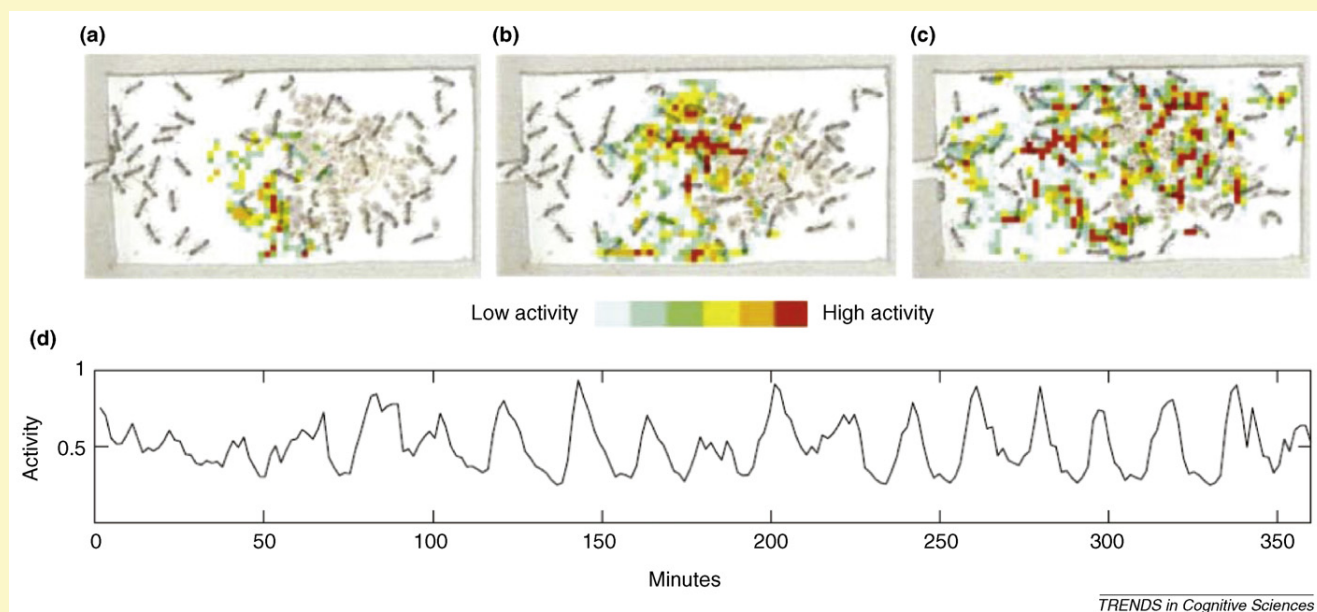


Figure 1. Computer vision techniques reveal the spontaneous generation and spread of rhythmic activity within ant nests superimposed onto images of the nest at the end of each time period; (a) 0–6 min, (b) 6–12 min and (c) 12–18 min. (d) A typical time-series of activity showing a periodicity of ~20 min (0 = no activity, 1 = all ants active). Note that ants spend ~70% of their time inactive. Modified, with permission, from [71].

the decisions of the group-members. This can enable individuals to avoid the time costs associated with temporal integration and has sometimes been referred to as ‘the many-wrongs hypothesis’ [29] or ‘the wisdom of the crowd’ [30]. Note that this argument assumes that individuals have access to the same noisy information and, thus, averaging among an increasing number of individuals inevitably improves accuracy (analogous to convergence under the central limit theorem). In many cases, however, information is not distributed in this way and individuals differ with respect to informational status or motivation [25,26,31]. Increasing group size can still benefit individual-level decision-making under conditions of conflicting information, however. It was recently demonstrated (again using schooling stickleback fish) that increasing group size also gives individuals the opportunity to integrate disparate information more effectively and, thus, reach a more accurate consensus decision [26].

Leadership and coming to a consensus decision

Although leadership is not a pre-condition for group coordination it does frequently emerge in animal groups [2,4,31] such as when only relatively few ‘informed’ individuals have salient information [31]. Using computational modeling, Couzin *et al.* [31] revealed that information transfer within groups requires neither individual recognition nor signaling. If relatively few informed individuals bias grouping tendency with a desired direction of travel (such as towards a resource or away from a threat [31,32]) they can accurately guide other, naïve, group members. Furthermore, as group size increases, the proportion of informed individuals needed to guide the group, for a given accuracy, actually decreases [31].

Following these simple rules, in the face of conflict (disagreement) among informed individuals, groups can also accurately, and quickly, come to a consensus and travel in the direction preferred by the majority. This is

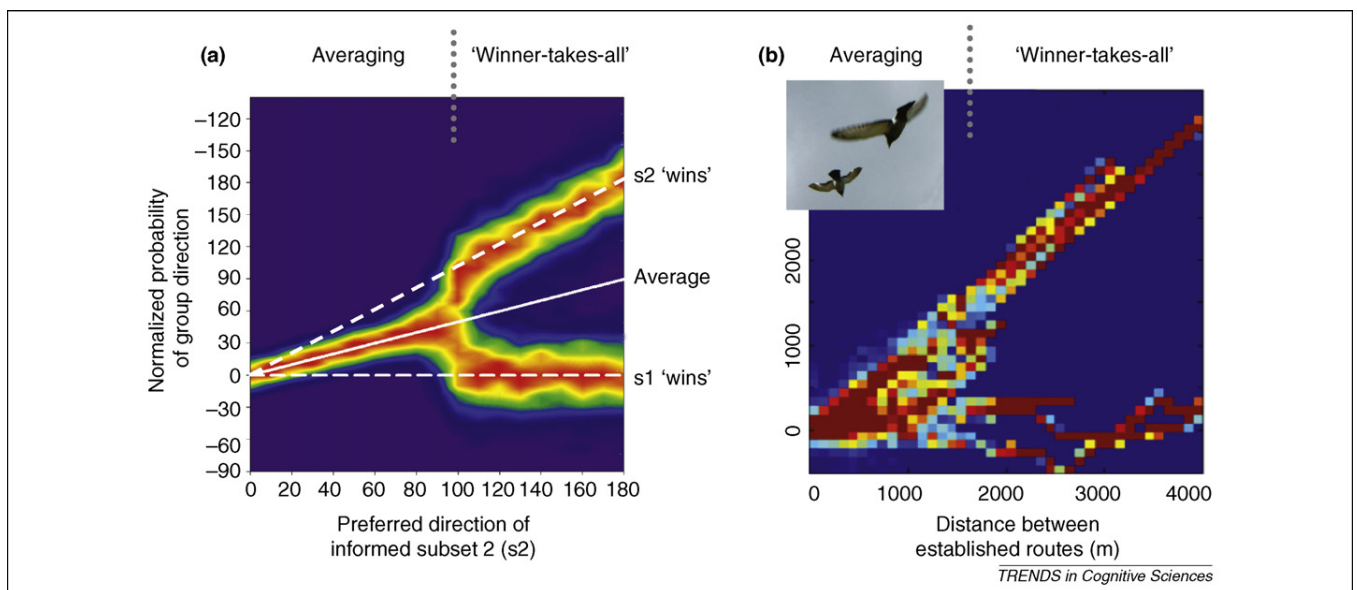


Figure 1. (a) Simulation models have revealed insights into how only a few 'informed' individuals with a biased direction of travel can guide groups with high accuracy, without requiring individual recognition or signaling. Where there are two conflicting subsets of informed individual (s1 and s2; here five individuals in each subset), the whole group adopts the average preferred direction below a critical difference in opinion. Above this, the group enters a consensus phase in which, given a symmetrical conflict, the whole group goes in one preferred direction or the other with equal probability (here group size was 100). In cases of an asymmetry, such that s1 does not equal s2, the group will select, collectively, the majority direction with high probability (see Ref. [31] for details). (b) When faced with a similar conflict, pairs of homing pigeons also tend to compromise when the difference in preferred route is small, but do tend to select one direction or other when this becomes large [33]. (a) Modified, with permission, from Ref. [31]. (b) Modified, with permission, from Ref. [33].

despite the fact that individuals are likely to have no explicit knowledge of whether they are in the majority or minority, or even if there are any other informed individuals at all. Considering the case of two conflicting directions of travel (see Ref. [31]), the type of consensus achieved is predicted to depend on the degree to which the informed individuals within a group disagree. Below a crucial difference in opinion (in this case the angle between the preferred directions of travel) groups adopt the average of informed opinions. Above that difference a consensus is adopted and the group travels in one, or other, preferred direction (Figure 1a).

Recent experiments by Biro *et al.* [33] using homing pigeons have provided support for the existence of such a transition. When released in pairs, pigeons trained to take different routes will tend to take an average course when the distance between routes is not great, but select collectively one, or other, route as the difference increases (Figure 1b). Studies of human crowds have also supported the basic principles of this collective decision-making process [34].

It can be informative to note that, at a certain level of description, the collective selection of direction in animal groups exhibit commonalities with visual choice tasks in humans and primates [11,12,14–16,18,19]. Competition among groups of direction-sensitive neurones enables information from visual scenes to be integrated and a collective decision about motion properties to be made. By artificially stimulating the middle temporal visual area of monkeys to create competing directional visual stimuli, Nichols and Newsome [35] also report a sudden transition between vector averaging to consensus decision-making (winner-takes-all) as the angular difference between conflicting motion vectors increases (Figure 1).

Collective cognition through environmental modification: foraging ants

In highly related grouping organisms, such as the social insects (e.g. ants, bees, wasps etc.), collective cognition can be particularly sophisticated because individual behavior and interactions have evolved to benefit the colony reproductive success (thus reducing inter-individual conflict), a functional integration so tight that they have been termed 'super-organisms' [36]. This is exemplified by ant species that use chemical pheromone trails to coordinate foraging activities [36].

By depositing and responding to trails, ants facilitate spontaneous and indirect coordination of each others' activity by modifying the environment, a process termed 'stigmergy' [37]. Similar indirect feedback principles are thought to facilitate the remarkable nest construction capability of many social insects [37,38]. When foraging, this process enables information about environmental conditions to be built up over time, permitting colonies to more efficiently allocate foragers to food sources and also to provide a means by which colonies can select the closer [36,39,40], or the most profitable [41–44], among multiple available food sources.

In the case of finding the shortest foraging route, it is the fact that ants traverse shorter distances more quickly that means, probabilistically, shorter paths will be more rapidly reinforced with trail pheromone [39,40]. The more concentrated a trail, the more likely it is to be followed than are less concentrated alternatives [36,39–44]. Thus, the ants effectively create a competition (lateral inhibition) among trails. Competition among alternative options is also common to many neuronal decision-making processes such as during intercircuit coordination and spatially selective attention tasks [11,12,14–20]. The strengthening of fre-

quently used trails is also reminiscent of Hebbian reinforcement of active neuronal pathways through long-term potentiation [17,20]. The relative rates of positive feedback (here chemical reinforcement) and negative feedback (evaporative decay of existing trails) largely determine the dynamics, imposing an inevitable trade-off between the speed and accuracy of decision-making. In addition, because ants tend to deposit more pheromone and/or recruit more individuals from the nest in response to higher quality resources, colonies can also focus their workforce ('attention') on the best among available food sources [39–44]. Importantly, such collective decision-making is not reliant on individual ants making direct comparison of the options themselves.

Many ant species employ multiple pheromones during foraging [36,45–50]. This can serve as an important role in enabling lower volatility chemicals (which evaporate more slowly) to be used to store relatively long-term information about the environment, such as providing an extensive network connecting both existing and previous known resources. Simultaneous use of, and response to, a pheromone with higher volatility can enable exploitation of previously undiscovered resources, and in addition, can facilitate rapid re-deployment of ants to areas of the existing long-term trail network if previously depleted resources become available again. The separation of time-scales afforded by employing chemicals with different volatilities enables a form of 'working memory' (encoded using slowly decaying chemicals, which if not reinforced, is eventually lost) and also a 'selective attention' (through the deployment of short-lived, but behaviorally dominant chemicals) in which relevant events, such as exploitable resources, become the focus of foraging activity [44–50].

Finding a new home

In addition to selecting among potential food sources, social insects need to choose where to live. This process has been studied extensively in two, apparently very different, organisms; a species of small ant, *Temnothorax albipennis*, which lives in colonies of between ~50 to 200 individuals in naturally weathered cracks in rocks (these ants are similar to those shown in Box 2, Figure I), and the honeybee, *Apis mellifera*, which typically lives in colonies of tens of thousands of individuals nesting in hollow trees.

T. albipennis colonies move sites relatively frequently because of the inherently transient nature of their nests. These are very small colonies and they cannot effectively employ collective communication using pheromones because of insufficient capacity for trail reinforcement [51,52]. How then, can they come to a consensus when faced with multiple options? Approximately 30% of the colony scouts for new nests using visual cues to navigate [53]. Upon finding a potential site each scout independently assesses it, the time taken being inversely proportional to perceived site quality [54]. If she accepts the nest, based on relatively fixed internal criteria that relate to, among other properties, its size, the size of the nest entrance and brightness [55], her search is discontinued and she begins to actively canvas other ants to also visit and assess the site. This she does by returning to the nest and recruiting a single individual who follows closely

behind as she walks back. During this process the follower can learn the route [56]. Upon reaching the nest she also assesses it, independently [55], and if it is accepted she too becomes a recruiter [54,55,57].

Leading ants to the site is slow, however. If recruiting ants detect a threshold quorum (density) of ants already present in the nest to which they are recruiting [53,58] they begin to physically carry others from the old nest, rather than to lead them [53]. This recruitment is approximately three times faster [53] and represents a higher commitment to a given nest [53,59,60].

This function of this graded recruitment is similar to that described in groups of stickleback fish [25,26]; it enables a relatively slow, but more accurate, phase of decision-making to begin with and, later, a fast committed phase to decrease the overall time taken to make the decision (emigration) [59,60]. Amplification of recruitment to one site inhibits transport to others because of there being a limited pool of potential scouts. The ants tune recruitment speed (positive feedback) according to urgency. Accuracy is compromised for increased speed if their nest is suddenly destroyed; more ants participate in searching, the rate at which they begin recruiting to new sites is increased and they decrease the required density (quorum) needed to switch to fast transport [60].

Honeybees also need to choose among available new nests when moving home. Like ants, the decision is mediated by local interactions occurring in parallel and Passino *et al.* [6] have recently noted similarities with functional organization in the vertebrate brain. Recruitment does not involve individuals directly leading others, like the ants do. Instead, scouts use the famous waggle dance to inform others of the direction of their find [61]. Because dance length is proportional to perceived site quality, probabilistically more bees will be recruited to better sites, creating a positive feedback loop [61–63]. Negative feedback is encoded in the form of a constant dance decay rate resulting in less persistent dancing for poor sites [63]. Like the ants, once a threshold quorum of individuals is found within a site it is used to indicate that it is indeed of adequate quality (many individuals having considered it so) and recruitment to that site then becomes very rapid [6,62,63].

Conclusions and future research

Through collective action, animals of many species can enhance their capacity to detect and respond to salient features of the environment. Interactions with others can enable individuals to circumvent their own cognitive limitations, giving them access to context-dependent and spatially and temporally integrated information. This can result in more accurate decision-making even in the face of distractions and uncertainty. Collective behavior allows access to important higher-order information-processing capabilities that are very difficult, or impossible, to achieve in isolation. Very similar informational benefits exist for neural and other cell assemblages, such as bacterial swarms [64], and perhaps even cell populations within malignant tumors [65].

Distributed feedback processes are the hallmark of collective decision-making. This enables information to

Box 3. Questions for future research

- To what extent can effective collective decision-making result from competitive interactions among selfish individuals? Under what conditions do unrelated individuals adopt cooperative strategies?
- How well do abstract mathematical models of collective behavior capture the dynamics of real biological systems? Currently there is almost no kinematic data on how real organisms move or interact within groups. This presents a key challenge to future researchers.
- How common is multistability of collective state in animal groups? Does it encode information in an analogous way to coexistence of stable modes of collective behavior in neuronal networks?
- How important is complexity at the level of individuals to collective animal behavior? In other words, how does individual cognition relate to group cognition? If collective behavior in animals can be seen as an adaptation to compensate for individual cognitive limitations, then does enhancing collective cognition (which relies on relatively simple reiterative interactions) relax selection pressure on individuals' general cognitive ability?
- How do individuals within coordinated animal groups know what rules to adopt, and when? Do individuals use local proxy measures (such as changes in density or alignment) to infer 'collective state'?
- There has been a tendency in previous research on animal grouping to assume, often implicitly, and sometimes explicitly, that similar types of pattern such as the collective motion exhibited by insects birds and fish, result from commonality of function. In reality, these systems often have very different operational demands and selection pressures. To what extent can common collective behaviors be driven by completely different underlying mechanisms?
- Organismal and neuronal aggregates frequently have to face two opposing survival conditions: to adapt quickly in the face of changing environmental conditions and yet to remain robust and organized even under noisy conditions. How is this conflict resolved?
- How does spatial position within groups reflect informational status, or information-processing capability, of individuals? Which positions maximize individuals' ability to acquire relevant information from the motion of others? How does heterogeneity among group members' behavior affect collective information-processing?
- The feedback processes that tune adaptively collective decision-making could be implemented explicitly in individual rules and/or in dynamical collective properties that emerge from interactions. The relationship between these processes is not yet understood and deserves further study.

be integrated simultaneously, over multiple timescales, and facilitates a self-referential process of quorum sensing, enabling individuals within groups or whole societies to balance appropriately the inevitable trade-off between speed and accuracy of collective decision-making. Group members are typically error-prone and unaware of available options, and yet the collective behavior exhibited is efficient over many scales. This ability is important and bears close comparison with distributed processing of information within and among neural assemblies. Distributed control, in general, is probably a consequence of a common evolutionary pressure to find solutions that are robust and do not fail catastrophically as parameters change.

The study of animal groups presents an opportunity to reveal, in unparalleled detail, how the behavior of individual components scales to that at higher organizational levels. This is a fundamental problem in a wide range of biological disciplines [66], not least the cognitive sciences. Furthermore, evolved coordinated behavior serves as direct inspiration for designed systems such as autonom-

ous robot groups and computational search algorithms [67]. Computer vision technology is now available for vastly improved data collection [68–70], and there holds great promise in the near future of integrated research that implements concepts and analytical tools from cognitive science. In return, this could offer us a more comprehensive view of the extent and role of collective cognition in the natural world (Box 3).

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