



Hierarchical Approach for Comparing Collective Behavior Across Scales: Cellular Systems to Honey Bee Colonies

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How individuals in a group lead to collective behavior is a fundamental question across biological systems, from cellular systems, to animal groups, to human organizations. Recent technological advancements have enabled an unprecedented increase in our ability to collect, quantify, and analyze how individual responses lead to group behavior. However, despite a wealth of data demonstrating that collective behavior exists across biological scales, it is difficult to make general statements that apply in different systems. In this perspective, we present a cohesive framework for comparing groups across different levels of biological organization, using an intermediate link of “collective mechanisms” that connects individual responses to group behavior. Using this approach we demonstrate that an effective way of comparing different groups is with an analysis hierarchy that asks complementary questions, including how individuals in a group implement various collective mechanisms, and how these various mechanisms are used to achieve group function. We apply this framework to compare two collective systems—cellular systems and honey bee colonies. Using a case study of a response to a disturbance, we compare and contrast collective mechanisms used in each system. We then discuss how inherent differences in group structure and physical constraints lead to different combinations of collective mechanisms to solve a particular problem. Together, we demonstrate how a hierarchical approach can be used to compare and contrast different systems, lead to new hypotheses in each system, and form a basis for common research questions in collective behavior.

Keywords: multi-scale, systems theory, honey bees, cellular systems, group behavior, mechanisms

1. COLLECTIVE BEHAVIOR: FROM CELLS TO SOCIETIES

Collective behavior spans across levels of biological organization, from cellular systems, to multi-cellular organisms, to animal and human societies. Even though such systems are wildly different, the fundamental challenges that they face can be strikingly similar: maintaining homeostasis, allocating resources, and coordinating group responses. Depending upon the available resources and the constraints on a system, the processes and solutions for a given challenge can be similar in some cases, but different in others. For example, similar effective forces of repulsion, alignment, and

attraction describe basic motion characteristics in cell colonies (Bi et al., 2016; Camley and Rappel, 2017), schooling fish (Couzin et al., 2002), human pedestrians (Helbing and Molnár, 1995), and social insects (Janson et al., 2005; Diwold et al., 2011). Conversely, while the coordinated response of an insect colony is due to distributed processing, the coordinated response of the organ systems within a single insect comes from centralized control of the central nervous system. How, then, do different types of collectives deal with similar problems?

Although biological systems have many parameters governing behavior, all of the finer-scale details may not matter at a larger scale; because of this property, simplified models are a useful tool for understanding general system function (Machta et al., 2013; Transtrum et al., 2015). A hierarchical approach asks questions at different levels of organization, and then further asks how these levels connect. A common example of such an approach is Marr's three analysis levels of implementation, algorithm, and computation (Marr, 1982; Krakauer et al., 2017). Building on this, Carandini (2012) discusses the need for an analysis hierarchy by demonstrating the limitations of seeking connections between individual neurons and overall behavior without considering computational algorithms; using the analogy of brain as computer, this is likened to seeking correlations between individual transistors and computer

function without considering the operating system. Recently, Hein et al. (2020) adopted Marr's approach to understand pursuit and evasion behavior in animal groups and demonstrated how separating analysis levels highlights the key details that enable a correspondence between experiment and theory. To fully understand a biological system, Tinbergen's four questions describe how both proximate and ultimate mechanisms need to be addressed (Tinbergen, 1963; Taborsky, 2014). By looking at different systems, we see that constraints and selection pressures may lead individuals of different systems to use different approaches to solve the same problem (Gordon, 2016), and that certain algorithms or mechanisms appear repeatedly even though systems may differ widely (Adams et al., 2012).

In this perspective we present a cohesive analysis framework with question levels that can be applied to collective behavior. This framework uses the term "collective mechanisms" to describe the intermediate link between individuals and overall group behavior (Figure 1). To analyze a collective system, we summarize this approach by asking the following questions:

1. Group description: Who is included in the group, and what is the group structure?
2. Implementation: How is individual behavior used to implement a certain collective mechanism?

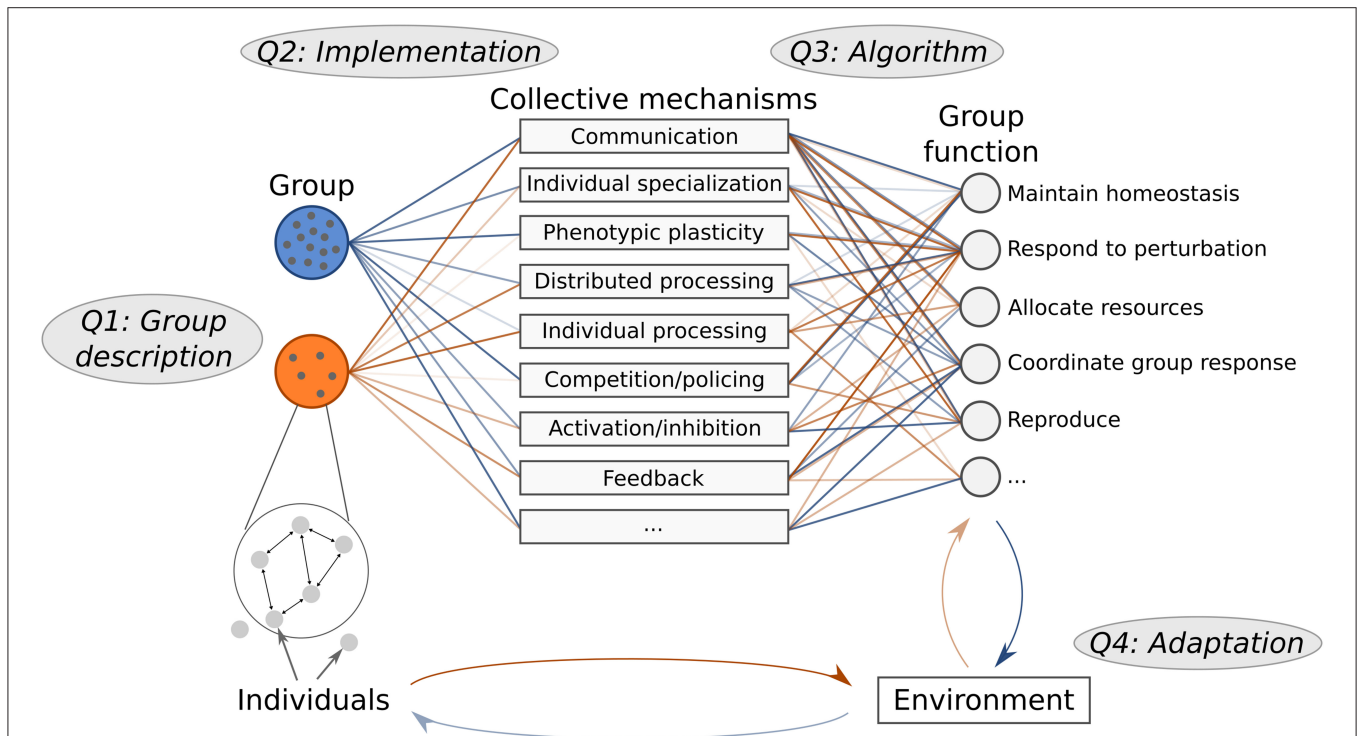


FIGURE 1 | Collective mechanisms link individual to group function. Different groups have different structures, and may use a different set of mechanisms to perform similar functions. The way mechanisms are implemented depends on the constraints and structure of the individuals in a particular group, and thus some groups may be more effective than others at implementing certain mechanisms. Differences between groups are illustrated by the connections and the transparency of the lines linking groups to each collective mechanism. To compare collective behavior in different systems, we use complementary questions: how groups are structured (Q1), how individual behavior is used to implement certain collective mechanisms (Q2), how multiple collective mechanisms contribute to group function (Q3), and how both individual and group behavioral algorithms are adapted to the particular environment (Q4).

3. Algorithm: How do various collective mechanisms contribute to overall group function?
4. Adaptation: How are behavioral algorithms and group function adapted to the surrounding environment?

To make these questions precise, we must first define what we mean by mechanism and function. We refer to a “collective mechanism” as any process that links individual behavior to group function (Table 1). Building on a previous framework (Craver, 2007; Glennan, 2017), we specify that a behavioral algorithm consists of individuals using various collective mechanisms to enact a particular group function. With “group function,” we refer to the mechanistic description of *what* the group does, not the evolutionary explanation of *why* a particular task is performed by the group (Craver, 2007; Keeling et al., 2019). Note that collective systems vary in how much the individual vs. the group may be adapted to a particular function in the environment (Figure 1); this depends on whether selection occurs at the level of individuals or at the level of groups.

In this article we apply this framework with a focus on comparing two systems—groups of cells and honey bee colonies—which exist at different scales, but are similar in how individuals contribute to group function (Yang, 2007). In forming the comparison, we follow the four questions listed above and shown in Figure 1. We first describe the group and an associated division into functional subgroups. Then, using a case-study (response to a perturbation), we compare how various collective mechanisms contribute to the group’s response, and how function is tied to environmental characteristics. While we focus on cellular systems and honey bees, in each part we also discuss similarities and differences with vertebrate animal groups and human organizations.

2. GROUP DESCRIPTION

A group is made up of multiple individuals, with inclusions defined by genetic, reproductive, spatial, or functional factors. Both cellular systems and social insects have further levels of organization, where task- or function-specific subgroups coordinate activity for the maintenance and survival of the group as a whole (Figures 2A–C).

2.1. Cellular Systems

Cellular systems have a multi-level organization: Cells of a certain type group together to form specific tissues, tissues perform distinct tasks relevant to the function of the organ or organ system, and together these systems make up the organism (Saxén and Lehtonen, 1986). For instance, connective tissue provides cohesion and internal support to the organs, muscle tissue enables movement, nervous tissue regulates and controls bodily functions, and epithelial tissue acts as a barrier to prevent invasions of pathogens as well as helping to absorb nutrients from food. Multiple tissue types can be found within a single organ (Figure 2B). Cell type differentiation is settled during morphogenesis, which is the beginning of shape and pattern formation during development. Because of the multi-level organization, the specification of who is included in a “group”

depends on the group function that is being analyzed. For the purpose of understanding a particular function, we include individuals that contribute to that function. For a complex task such as reproduction, this includes multiple different organ systems or even the entire organism. Considering epithelial cells and the specific task of wound healing (Figure 2D) the group includes only the subset of cells involved in healing the wound, most of which belong to a single tissue type.

2.2. Social Insects: Honey Bees

Insect societies are champions of individual specialization (Michener, 1969; Wilson, 1971). As “superorganisms” (Wheeler, 1928; Hölldobler and Wilson, 2009), colonies display physiological features that are typically attributed to organisms, such as gas exchange, nest homeostasis, and nutritional targets (Kleineidam et al., 2001; Dussutour and Simpson, 2009; Ostwald et al., 2016). A honey bee colony is made up of thousands of workers and a single queen (Smith et al., 2016). The workers can be divided into functional subgroups of those caring for brood, processing honey, or foraging (Figure 2C). Unlike other social insect systems, where a worker’s tasks can be distinguished by their physical appearance (e.g., workers vs. soldiers in the army ant *Eciton burchellii*), workers in a honey bee colony organize tasks using a system of temporal polyethism. Generally, young bees care for brood, middle-aged bees work in the nest, and old bees forage outside (Seeley, 1982). A worker may also partition its time between several tasks, which together describe its “task repertoire” (Lindauer, 1952; Seeley, 1982). Changes between tasks are not purely age-driven; they are also mediated by interactions with other individuals, such that task allocation responds to the needs of the colony (Beshers et al., 2001; Johnson, 2010). In addition to age, definitions of subgroups may include interaction networks (Wild et al., 2020) or task-specific spatial localization (Mersch et al., 2013; Modlmeier et al., 2019).

2.3. Comparing Systems

Although in both cellular systems and honey bee colonies there is a clear division into functional subgroups (Figures 2A–C), there are differences in how individual function changes over time, how the “group” is defined for the purpose of analyzing a particular function, and in the overall structure of the organizational levels. In cellular systems, functional groupings are settled during morphogenesis, while the functional subgroup of a worker bee is flexible, depending on changes with age, glandular development, hormone titers such as juvenile hormone, colony requirements, and social interactions (Seeley, 1982; Huang and Robinson, 1992, 1996; Sullivan et al., 2000; Beshers et al., 2001; Grozinger et al., 2003; Wild et al., 2020). Note that here we refer to subgroups among workers, not the reproductive castes that distinguish workers, drones, and the queen (Winston, 1991). The definition of group depends on the function in cellular systems, which can range from the whole organism for complex tasks to only localized cells of a particular tissue for specific functions. For honey bees, the group includes the whole colony for most functions. In addition to these factors, within the multi-level organization of cellular systems the overall activity of multiple organ systems is often coordinated by a

TABLE 1 | Examples of collective mechanisms for cellular systems and honey bees.

Mechanism	Cellular systems	Honey bees
Communication	<ul style="list-style-type: none"> • Chemical: Chemotaxis during organogenesis (Barton et al., 2016) and wound healing (Vishwakarma et al., 2018). • Behavioral: mechanical interactions during wound healing (Vishwakarma et al., 2018). 	<ul style="list-style-type: none"> • Chemical: pheromonal communication, reviewed in Slessor et al. (2005). • Behavioral: waggle dance, shaking signal, stop signal (von Frisch, 1967; Nieh, 1993; Seeley et al., 1998).
Individual specialization/individual differences	<ul style="list-style-type: none"> • Cell type differentiation (Lander, 2011). • Heterogeneity in adult tissues due to accumulation of small mutations (De, 2011). • Dynamic specialization, e.g., tip-stalk cells during cell migration (Weijer, 2009), tumor-cell specialization in cancer (Nowell, 1976). 	<ul style="list-style-type: none"> • Workers specializing in brood care, honey processing, or foraging (Beshers et al., 2001; Johnson, 2010). • Individual differences in temperature response (Jones et al., 2004) or to resources of different quality (Seeley, 1994).
Phenotypic plasticity	<ul style="list-style-type: none"> • Adaptation of metastatic tumor cells to their environment by changing their phenotype from epithelial to mesenchymal cells (Mittal, 2018). 	<ul style="list-style-type: none"> • Adapting to a rise in temperature in the nest, worker bees start fanning and foragers switch collect water (Robinson et al., 1984; Jones et al., 2004; Ostwald et al., 2016). • Following the loss of the queen, worker bees switch to build exclusively specialized cells for direct reproduction (Smith, 2018).
Distributed processing (interactions drive function)	<ul style="list-style-type: none"> • Emergence of leading cells during wound-healing based on mechanical interactions (Vishwakarma et al., 2018). 	<ul style="list-style-type: none"> • Interaction-mediated change to forager (Huang and Robinson, 1992).
Individual processing (intrinsic properties drive function)	<ul style="list-style-type: none"> • Cell type determined by differential gene expression (Wu, 2014). 	<ul style="list-style-type: none"> • Age and development-driven task changes. • Individuals have different response thresholds (e.g., fanning threshold; Jones et al., 2004).
Within-group competition/policing	<ul style="list-style-type: none"> • Cell-competition acts as a surveillance mechanism to measure individual fitness. Aged and less-fit cells are removed to maintain a healthy tissue state (Di Gregorio et al., 2016). 	<ul style="list-style-type: none"> • Working policing: workers eat eggs of other workers, ensuring that only the queen egg's are raised (Ratnieks and Visscher, 1989).
Activation	<ul style="list-style-type: none"> • Chemoattractant cues activate cellular polarization during migration (Weijer, 2009). 	<ul style="list-style-type: none"> • Tremble dance recruits more bees to receive nectar (Seeley, 1992; Seeley et al., 1996). • Shaking signals convey the meaning "prepare for greater activity" (Nieh, 1998; Seeley et al., 1998; Koenig et al., 2020)
Inhibition	<ul style="list-style-type: none"> • Leader cells inhibit formation of other leader cells (Vishwakarma et al., 2018). • Contact inhibition of motion enhances coordinated movement and the guidance of the group by cells at the leading edge (Mayor and Carmona-Fontaine, 2010). 	<ul style="list-style-type: none"> • Queen advertises her fertility; workers do not develop ovaries when a viable queen is present (Keller and Nonacs, 1993; Duncan et al., 2016). • Stop signals used during nest-site selection (and dance-imbalance) (Nieh, 1993; Seeley et al., 2012).
Feedback	<ul style="list-style-type: none"> • Directional cell migration is controlled by a negative feedback loop through regulation of the concentration of attractants during germ cell migration (Lau et al., 2020). • During wound healing, a double negative feedback loop controls cell polarization (Das et al., 2015). • Maintenance of homeostasis in epithelial tissues uses feedback loops (Georgopoulos et al., 2014). 	<ul style="list-style-type: none"> • Foraging uses multiple feedback processes, including waggle dance paired with stop signal (Kietzman and Visscher, 2015). • Nest site selection uses positive feedback to amplify recruitment to a site (Passino and Seeley, 2006) combined with stop signals as cross inhibition between sites (Seeley et al., 2012).

Examples and/or implementation details are listed for each mechanism for cellular systems and honey bees. See also **Figure 1**.

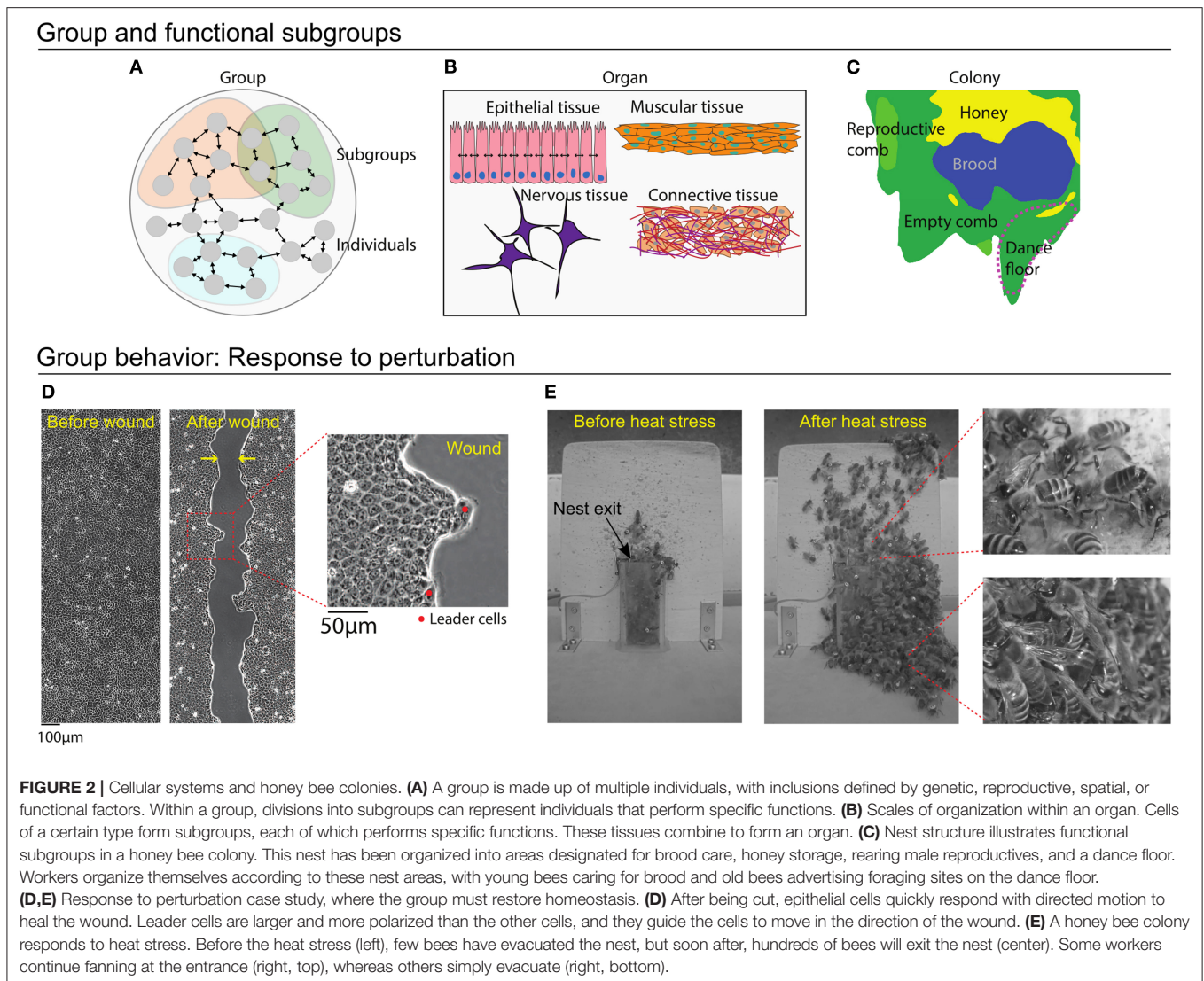
central nervous system (CNS). Thus, even at the lower level of individual cells, there may be some degree of centralized control from the CNS. In contrast, there are no centralized control structures in social insects.

In fission-fusion groups of fish, birds, or ungulates, the overall group function, such as migration, foraging, or avoiding predation, should be considered when defining and describing the group. In these cases there is no division into functional subgroups, but other structural elements may be used to describe the group. For example, faster fish tend to be near the front of the school and thus act as leaders (Jolles et al., 2017); "leader" vs. "follower" birds differ in their flapping ability and position in the group (Flack et al., 2018).

For other vertebrate groups that display a multi-level structure including up to hundreds of individuals (Schreier and Swedell,

2009; Papageorgiou et al., 2019), it can be useful to define the "group" in terms of specific functions. For example, baboons troops of up to approximately 50 individuals forage together, and thus can be considered a group with respect to the function of locating food resources (Strandburg-Peshkin et al., 2015). Many of these groups show consistent membership which is often defined by a dominance hierarchy (Noble, 1939; Schreier and Swedell, 2009; Maruska and Fernald, 2013).

Clear functional subgroups can also be observed in human organizations such as businesses, universities, or government entities. For example, a business may have functional divisions of marketing, research and development, manufacturing, finance, and human resources. While traditional organizational structures are hierarchical, some modern companies instead use a flat or "holocratic" structure that emphasizes distributed



decision-making but retains functional distinctions among working groups (Robertson, 2015). While decision making in groups of honey bees and cellular societies follow entirely different processes, the structure seems to be similar to a holocracy, with functional distinctions yet distributed decision-making. In animal groups with hierarchical dominance structures, decision-making structures may not follow the same hierarchies, as demonstrated in the case of baboon movement decisions which can be initiated by any group member (Strandburg-Peshkin et al., 2015).

Overall, key differences in group structure in all of these different systems can be summarized by the degree of differentiation among group members (or lack thereof), whether individuals take on a consistent role or change over time, and the connectivity or communication structure among individuals in the group with respect to achieving a certain function.

3. IMPLEMENTATION AND ALGORITHM: COLLECTIVE MECHANISMS

Collective mechanisms act as building blocks that link individual behavior to group function. These building blocks are used and adapted by a given system in order to solve a variety of problems. Some collective mechanisms used in both cellular systems and honey bees include communication, individual specialization, distributed processing (or, conversely, “individual processing”), within-group competition, activation, inhibition, and feedback (Figure 1, Table 1). Note that this is not an exhaustive list; other mechanisms may be defined and used to describe collective behavior of other systems, or to form a comparison between systems. For example, Sumpter (2006) uses the terminology of “collective principles” to refer to the same concept, describing mechanisms of integrity/variability, positive feedback, negative feedback, response thresholds, leadership,

inhibition, redundancy, synchronization, and selfishness; further mechanisms could include group-level selective attention, short-term memory/hysteresis, and stigmergy (Couzin, 2009). We note that to compare systems, it is important that collective mechanisms describe a process that links individual to group behavior in a way that does not depend on precise implementation details. While both cellular systems and honey bees systems can implement all of the collective mechanisms in **Table 1**, differences in the nature of the individuals means that the effectiveness of a particular collective mechanism may not be the same in each system. We use a case study to compare and contrast collective mechanisms that contribute to how a group responds to a particular perturbation.

3.1. Epithelial Cell Wound Healing

As the outermost tissue layer, epithelial tissue needs to be able to respond quickly to changes in the surrounding environment. At homeostasis, cells of epithelial tissues are typically jammed and any activity within the epithelia stem mainly from cell maintenance, i.e., the continuous replenishment of aged/damaged cells with healthy individuals (Macara et al., 2014). When homeostasis is perturbed by a wound trauma, cells must move quickly to close the wound in order to protect the underlying organ. Studies have demonstrated that wound healing relies on coordination between cells in order to migrate efficiently toward the exposed area (Poujade et al., 2007; Park et al., 2017). The collective sensing and response during wound healing includes a complex interplay of chemical and physical signals between individuals and with the extra-cellular environment (Ladoux and Mège, 2017). Cells at the wound edge sense a chemical change in their environment due to the mitogens released by wounded cells and due to the cell-free region created by the wound (Ganapathy et al., 2012). In addition, some edge cells specialize into “leader cells,” which have a strong polarization in the direction of the wound (Omelchenko et al., 2003). Leader cells mediate the coordinated motion of the group by using cell-cell contacts to transfer mechanical forces to follower cells (**Figure 2D**; Vishwakarma et al., 2018).

3.2. Honey Bee Heat Stress

Honey bee colonies respond to environmental conditions to maintain nest homeostasis. The brood nest, for example, is carefully regulated between 33 and 35°C; temperatures outside this range are potentially lethal for the developing brood (Lindauer, 1954; Becher et al., 2009). When ambient temperatures rise, honey bee colonies have a series of graded responses to thermoregulate. Workers begin by fanning their wings to increase air circulation within the nest, and foragers switch from collecting nectar to water. These water deliveries are passed to younger receiver bees, who spread the water throughout the nest for evaporative cooling. If the nest temperature continues to rise, hundreds to thousands of workers will evacuate the nest, thereby reducing the number of heat-generating individuals in the nest, and providing additional space for air to circulate (**Figure 2E**; Lindauer, 1954; Robinson et al., 1984; Kühnholz and Seeley, 1997; Cook and Breed, 2013; Ostwald et al., 2016). As long as honey bees have access to water, workers

can maintain broodnest homeostasis, even when faced with ambient temperatures as high as 60°C (Lindauer, 1954). When colonies are subjected to repeated days of heat stress, workers will even begin to store water in their stomachs, and in the honeycomb, to use overnight when foragers cannot fly to collect water (Ostwald et al., 2016).

3.3. Comparing Systems

In both cases, the group must respond to a perturbation—a wound or a temperature change—in order to maintain and restore overall function. How do these different systems solve a similar problem? Both rely on specialists taking on specific roles as part of the group-level response: Leader cells specialize by coordinating the movement to close the wound, and water collector bees specialize on water to initiate evaporative cooling in the nest. The systems, however, differ in their use of individual processing (behavior determined by intrinsic properties) vs. distributed processing (behavior determined by interactions with other individuals, see **Table 1**). Distributed processing is dominant in the case of cellular wound healing; interactions mediate the switch to leader cells (Vishwakarma et al., 2018). A bee colony’s response to heat stress is a mix of individual and distributed processing. A distributed algorithm determines the number of workers collecting vs. spreading water throughout the nest, while individual processing describes how individual workers have different heat thresholds to initiate fanning. In the case of wound healing, we do not know if such individual processing plays a role, e.g., if differences between individual cells at the wound site could be a factor in determining the selection of leader cells. While honey bees adapt their behavior in the case of repeated days of heat stress, there is no evidence that epithelial cells adapt their behavior to facilitate healing after multiple wounds.

How does this compare to the perturbation response of vertebrate animal groups? One example is the response of a school of fish to a predator. Fish release a chemical called “Schreckstoff” that conveys danger to others. When exposed to this chemical, group members will come closer to one another and make the overall size of the group smaller (Sosna et al., 2019). In this tightened configuration, the group is able to spread information more quickly and respond to future threats (Rosenthal et al., 2015). Interestingly, experiments demonstrate that exposure to Schreckstoff does not change individual response thresholds; rather, structural reorganization is the major determinant of the observed changes in the group response (Sosna et al., 2019), making this an example of distributed processing. In contrast, honey bee defense provides a clear example where individual response thresholds do change with exposure: after one bee stings, the tendency for subsequent individuals to sting increases (Millor et al., 1999).

A natural disaster is an example of a perturbation that a human organization must respond to. During a fire, the goal of the fire department is to create a quick and targeted response in order to facilitate a return to homeostasis. Since natural disasters are occasional events but require coordination between people for an effective response, fire departments or other humanitarian organizations rely on a mix of volunteer and

paid employees to meet demand. Similar to honey bees and the cellular system described above, optimizing the problem of task allocation requires components of both individual and distributed processing. Task allocation that considers both organizational needs and individual preferences (Falasca and Zobel, 2012) can be considered a form of individual processing, since allocation is linked to intrinsic preferences, not an emergent outcome of interactions. The alternative, fully distributed processing, would represent an *ad hoc* approach where individuals determine their role based on their interactions with other individuals, and modify according to the need of the collective.

4. ADAPTATION: CONNECTING GROUP BEHAVIOR TO ENVIRONMENT

By comparing collective behavior across different systems we can begin to answer question four, which asks how functional mechanisms and behavioral algorithms are adapted to their environment. The characteristics of the environment can specify the types of problems organisms typically encounter, as well as the effectiveness of different solutions. Given a similar problem, the use of different collective mechanisms may reflect adaptations to specific environmental characteristics, different biological constraints, or a combination of both (Gordon, 2016). Within our analysis framework, biological constraints determine the implementation details of different collective mechanisms, as well as the suite of available collective mechanisms. For honey bees and epithelial cells, the constraints on movement, sensory input/output, and information processing abilities are very different, and thus the implementation details and possible application extent of certain collective mechanisms are different. For example, individual epithelial cells have less individual processing ability than individual bees (and also less than other cell types such as neurons). By using a distributed algorithm, the group has more processing ability than individuals (Levin, 2019). While this is true in both systems, the lesser processing abilities of cells may be one reason that they rely more on a distributed algorithm compared to honey bees in our example of the perturbation response. Nonetheless, as the cases of heat stress and wound healing illustrate, the environmental characteristics of both honey bees and epithelial cells have similarities: both systems need to be able to respond rapidly to changes in the surrounding environment.

Other social insects interact with different environmental conditions. For example, desert harvester ants forage for seeds that are randomly scattered, but the overall supply is relatively constant over time. Gordon (2016) discusses how this difference can affect behavioral algorithms, noting that because of the scattered distribution of resources in their environment, harvester ants do not exchange spatial information when they recruit additional ants to forage. Conversely, for honey bees, the patchy and ephemeral nature of nectar resources makes it essential to share spatial information among foragers. Nonetheless, because they are both social insects, we may still expect similarities between harvester ants and honey bees in

their implementation and use of collective mechanisms, such as the ability of individuals to change task specialization over time. A hierarchical approach provides a natural way to compare collective systems with similar implementation details or available mechanisms but different environmental characteristics (e.g., harvester ants and honey bees), or with different implementations but similar environmental characteristics (e.g., honey bees and epithelial cells).

Human organizations also differ in the types of problems they need to solve. Many human organizations, including businesses, exist in a relatively stable environment; indeed, a stable political and economic environment may be considered a requirement for the advanced specialization and optimization that exemplify modern economies (Acemoglu and Robinson, 2012). Analogous to the environmental differences faced by honey bees and harvester ants, humanitarian logistics for disaster response differs from business logistics because of the unpredictability of the response, and thus needs to be organized differently (Kovacs and Spens, 2007). To this end, human organizations can learn from biological systems in employing mechanisms that are appropriate to address a certain problem (Levin and Lo, 2015).

A key difference between social insects and vertebrate groups or human organizations is the consideration of individual vs. group interests. For honey bees, since reproduction is at the level of the colony, individual, and group interests align. Thus, while a distributed algorithm can contribute to a flexible yet robust group response for honey bees, it could lead to discontent and ineffective group function among human volunteers who each have distinct individual preferences. A distributed process describes the overall decision-making structure of social insect societies, and human organizations with a flat or holocratic organizational structure have similarities in terms of distributed decision processes. However, there are again key distinctions due to individual vs. group interests. While individuals in social insect societies work for the overall function of the group in a structure without dominance hierarchies, a common complaint of human organizations with distributed decision-making structures is that even though it may not be explicitly acknowledged, individual interests cause hierarchy to persist (Freeman, 2013; Bernstein et al., 2016).

5. APPLICATIONS AND FUTURE RESEARCH DIRECTIONS

A comparative approach allows one to ask if a particular mechanism is used in another system, as well as how it is used (Adams et al., 2012). An example of this is the “individual processing” mechanism of having a distribution of individual response thresholds among group members. For honey bees, this contributes to a colony’s ability to maintain stable temperatures inside the nest, as well as enabling a colony’s foragers to produce a graded response to resources of different quality. Using a similar mechanism, recent work has used a distribution of individual response thresholds to model how a population of neurons can represent the probability distribution of future rewards by implementing a form of distributional

reinforcement learning (Dabney et al., 2020). Collective decision-making processes in animal groups have many similarities to neural systems, including for example the speed-accuracy trade-off during decision-making (Couzin, 2009). A further example of comparing mechanisms across systems is the observed use of cross-inhibition in cellular systems, which led to the hypothesis that similar inhibitory signals should be present between groups during house hunting in honey bees (Seeley et al., 2012).

There are multiple areas for interesting future research, including for example how the use of different behavioral algorithms reflect both individual constraints and environmental conditions. Parallel or convergent evolution refers to when similar phenotypes evolve in similar environments (Langerhans and DeWitt, 2004; Losos, 2011). Examining parallel evolution of collective behavior, e.g., in cichlid fish (Turner, 2007), can reveal the role of the environment in shaping the success of certain collective mechanisms. One could also ask what individual capabilities, collective mechanisms, and/or environmental characteristics are associated with successful adaptations of animal groups. For example, Barrett et al. (2019) describe instances of human-induced environmental change where the use of social learning in a group led to either an adaptive (e.g., Teitelbaum et al., 2016) or maladaptive (e.g., Sigaud et al., 2017) group response.

A comparative approach could furthermore be applied to tumorigenesis, and how a group deals with oncogenic cells. For a tumor to metastasize, tumor cells must pass through the constraints and ecology of the tissue and circulatory system, while avoiding detection and death. To do so, tumor cells change their phenotype by undergoing an epithelial to mesenchymal transition, (EMT), break off from the group, and migrate one cell at a time (Mittal, 2018). In honey bees, worker ovary activation provides an analogy for how an individual can change its phenotype in an attempt to reproduce. Workers typically do not lay reproductive eggs as long as a reproductive queen is present (but see Goudie and Oldroyd, 2018), and workers with fully activated ovaries risk aggression from nest mates (Visscher and Dukas, 1995; Smith et al., 2009). Still, partial ovary activation

is widespread in colonies (Smith et al., 2013), even though partial activation incurs costs to the colony (Mattila et al., 2012). Is partial ovary activation permitted because workers lack the ability to detect low-level ovarian development (Q2), because they lack an effective mechanism to form a collective response (Q3), or because there is a functional advantage to having partially-developed workers (Q4)? These questions parallel current cancer research, which asks why some oncogenic cells turn into super-competitors that manifest into tumors, while other mutants are effectively contained and stopped by the epithelial defense against cancer (Vishwakarma and Piddini, 2020). We hope this article inspires further comparisons of collective systems that build on the framework and examples described here.

DATA AVAILABILITY STATEMENT

The raw videos associated with **Figures 2D,E** are available upon request.

AUTHOR CONTRIBUTIONS

JD, MV, and MS conceived of the study, performed research, and wrote the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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