

# A comparative approach to study collective behavior across biological scales

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## Abstract

The study of collective behavior asks how individual actions combine to produce a group response. Research questions encompassing self-organization, collective motion, and decision-making apply to study systems ranging from cellular systems to animal groups and human organizations. Recently, technological advancements have enabled an unprecedented increase in our ability to measure, quantify, and analyze collective behavior. However, despite similar inquiries and the wealth of data available, it is difficult to make general statements about principles of collective behavior that apply across scales. Here we describe a hierarchical approach for comparing collective systems that uses the intermediate link of “mechanisms” to connect individual to group behavior. With this, we argue that an effective way to understand collective behavior across different systems is to ask the complementary questions of how individual behavior implements certain mechanisms, and how various mechanisms contribute to overall function of the group. We apply this framework to compare two systems at very different scales - honey bee colonies and cells of the body - to show how a hierarchical approach can be used to compare and contrast different systems, and lead to new hypotheses forming a basis for common research questions of collective behavior.

## Introduction: collective behavior from cells to organisms

Collective behavior spans across levels of biological organization, from cellular systems, to multicellular organisms, to 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 interactions between individuals and the resources available, 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 in a single insect comes from control of the central nervous system. How do different types of collectives deal with similar problems?

We adopt a hierarchical approach to compare the collective behavior of different systems. With this, instead of seeking unifying principles or common rules that explain how individuals contribute to the overall function of the collective system, we consider an intermediate link that connects between individuals and group. The concept of hierarchical levels of abstraction is well known in complex systems theory (Anderson 1972), and is used in other fields of study. For example, in computational neuroscience, this is reflected in Marr’s three levels of analysis (computation, algorithm, and implementation), and subsequent interpretations such as the levels of neural circuits, computations, and behavior (Marr 1982; Carandini 2012; Krakauer et al. 2017). The key points to apply a similar approach to collective behavior are (1) Considering abstraction in the form of multiple analysis levels is useful to link individuals to overall group function (Carandini 2012), (2) Although systems may differ widely, certain algorithms or mechanisms appear repeatedly (Adams et al. 2012), and (3) System constraints and selection pressures may lead different systems to use dif-

ferent approaches to solve the same problem (Gordon 2016). Applied to collective behavior, we refer to the intermediate link between individuals and overall group behavior as “mechanisms” (Fig 1). To analyze a collective system, we summarize this hierarchical approach by asking the following questions:

1. Who is included in the group, and what is the group structure?
2. How is individual behavior used to implement a certain mechanism?
3. How do various mechanisms contribute to overall function?
4. How is function adapted to the surrounding environment?

In this article we describe this framework and apply it to compare two different systems - groups of cells and social insects - which exist at very different scales yet have commonalities in how individuals contribute to group function (Yang 2007). To explore both the similarities and differences, we first define the parts of each collective, including the group and functional subgroups. We then ask how each system draws from a shared set of mechanisms in order to solve a problem at hand.

## **Cellular systems and social insects: group structure**

A group is made up of multiple individuals, with inclusions defined by genetic, reproductive, spatial, or functional factors. Within a group, multiple factors may be used to form a division into functional subgroups. A key aspect of both cellular systems and social insects is the organization into task- or function-specific subgroups that coordinate activity for the maintenance and survival of the group as a whole (Fig 2).

A division into subgroups describes the multi-level organization of cells, tissues, organs, and organ systems. Task differentiation within these functional subgroups is settled during morphogenesis, which is the beginning of shape and pattern formation when an organism develops. Similar cells of a certain type group together to form specific tissues, and each tissue performs distinct tasks relevant to the function of the organ or organ system; together these systems makes up the organism (Saxén

and Lehtonen 1986). For instance, epithelial tissue functions as a barrier to prevent invasions of pathogens in addition to helping absorb nutrients from food, connective tissue provide cohesion and internal support to the organs, muscle tissue enables movement, and nervous tissue regulates and controls bodily functions (Fig 2b).

Insect societies use individual specialization in the form of cooperative brood care and division of labor (Michener 1969; Wilson 1971). As “superorganisms” (Wheeler 1928; Hölldobler and Wilson 2009), they display physiological features that typically would be found only in organisms, such as gas exchange, nest homeostasis, and nutritional targets (Kleineidam et al. 2001; Ostwald et al. 2016; Dussutour and Simpson 2009). A honey bee colony is made up of thousands of workers, a single queen, and occasionally, several hundred male reproductives (Smith et al. 2016). While the group is defined as the colony, we can also define functional subgroups: workers caring for brood, processing honey, or foraging, each of which use a different nest area (Fig 2c). Unlike other social insect systems, where a worker’s tasks can be distinguished by their physical appearance (e.g. workers versus soldiers in *Eciton burchellii*), workers in a honey bee colony organize tasks using a system of age-based temporal polyethism. Generally, young bees care for brood, middle-aged bees work in the nest, and old bees forage outside the nest (Seeley 1982). A worker may also partition its time between several tasks, which combined describe its “task repertoire” (Lindauer 1952; Seeley 1982). However, 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). Therefore, definitions beyond age have been proposed to define functional subgroups, such as interaction networks or task-specific spatial localization (Mersch et al. 2013; Modlmeier et al. 2019).

Although in both cases there is a division into functional subgroups, a key difference is in how individual function changes over time. For cells, functional groupings are settled during morphogenesis, following which an individual cell continues to remain in the same subgroup. In contrast, for bees an individual’s function changes with age.

## Mechanisms link individuals to group function

Group-level functions that both social insects and cellular systems perform include reproduction, metabolism, collective-sensing, decision-making, and migration. Although the scale and the nature of the individuals in each system are very different, the mechanisms underlying behavior are often similar. We consider behavioral mechanisms as “building blocks” linking individual behavior to group function. These building blocks can then be used and adapted by a given system in order to solve a variety of problems. Some behavioral mechanisms include communication among individuals, individual specialization, distributed processing (or, conversely, “individual processing”), within-group competition, activation, inhibition, and feedback loops (Fig 1; Table 1). Note that our definitions of mechanisms are not mutually exclusive; for example, communication is part of nearly all mechanisms in Table 1. The use of different mechanisms to solve a similar problem may reflect physical constraints or adaptations to specific environmental characteristics (Gordon 2016). We will use two example cases where the group faces a similar problem - responding to a perturbation and coordinating among group members to move to a new location - to compare and contrast how various mechanisms contribute to function in honey bees and epithelial cells.

### Group response to perturbation

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 towards 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’, polarize to migrate towards the wound and use physical force and cell-cell contacts to pull the followers in the direction of migration (Omelchenko et al. 2003). Leader cells mediate the coordinated motion of the group by transferring mechanical forces to follower cells (Fig 3a; Vishwakarma et al. (2018)) .

Honey bee colonies respond to environmental stressors to maintain conditions that allow for brood-rearing. In particular, brood nest temperatures are carefully maintained between 33-35°C; temperatures outside of this 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 keep their brood at temperatures within this range. Workers begin by fanning their wings to increase air circulation within the nest. If ambient air is too hot, foragers switch from collecting nectar to collecting loads of 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 for evaporative cooling (Fig 2b; 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 the homeostasis of their broodnest, 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 the honey comb, and in worker’s crops, to use overnight when foragers cannot fly to collect water (Ostwald et al. 2016).

In both cases, the group must respond to a perturbation - a wound or a tem-

perature change - in order to maintain and restore overall function. How do these radically 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 initiating 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) versus 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 and enable coordinated movement among 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 water versus 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 individuals at the wound site could be a factor in determining selection of leader cells.

## **Coordinated group movement**

Germ cells are cells that create reproductive cells, i.e. eggs or sperm. In the developing embryo, germ cells are specified at one location and must migrate to the gonads, which in females are found in the ovaries and males in the testes (Fig 2c). After crossing this distance, which is more of 100s of cell body lengths, germ cells live and undergo cell division in the somatic gonad. How do germ cells navigate and coordinate migration towards their target gonads? Studies have shown that their guidance mechanism is mediated by a chemical gradient: a chemokine released by the attracting somatic cells activates the germ cells by binding to a specific guidance-receptor and polarizing them to migrate (Barton et al. 2016). Attracted germ cells subsequently move through the gradient towards a higher concentration of the chemokine (Doitsidou et al. 2002; Barton et al. 2016). In order to achieve a strong directional



signal, the chemokine is maintained with concentrations around the dissociation constant ( $K_d$ ) of the guidance-receptor, such that small changes will be amplified and propagated with a high signal-to-noise ratio. This regulation of chemokine concentration is attained through a negative feedback loop with a clearance-receptor such that if concentration is higher than  $K_d$ , the clearance-receptor activates and clears the excess chemokine (Lau et al. 2020). Studies also suggest that only a small number of cells at the front express the guidance-receptor and can process the information of the chemokine gradient (Haas and Gilmour 2006). These informed cells (leading cells) guide the trailing-cells using a combination of physical and chemical signaling. Cells such as germ cells and neural crest cells, migrating *in vivo* must maintain close proximity and move cohesively as a group. This is suggested to be achieved by the inhibition of cell protrusions between individual cells, a phenomena known as contact inhibition of locomotion (CIL) (Carmona-Fontaine et al. 2008). For the group, contact inhibition of locomotion enhances coordinated movement and the guidance of the group by cells at the leading edge (Mayor and Carmona-Fontaine 2010).

When a honey bee colony casts a reproductive swarm, thousands of workers and a single queen gather in a bivouac while scouts search for the colony’s new home (Seeley 2010). This “democratic” process of choosing a new home, however, only involves a subset of workers, so once the scouts have selected a new home, only 5 percent of the workers in the swarm will have already visited the location (Seeley et al. 1979). How do the knowledgeable bees guide a 95-percent naive swarm, and especially their precious queen, to a location that may be up to 4 km away? The guidance mechanism in this case is visual: “streakers” fly quickly atop the airborne swarm in the direction of the new home (Lindauer 1955; Seeley and Morse 1977). Once they reach the front of the flying swarm, they slow down and descend, allowing the swarm to pass. Once at the back-end of the swarm, they can again rise to streak atop the swarm, guiding the naive individuals below (Greggers et al. 2013). The naive workers need only to follow the average movement vector of bees above them to move in the direction of their new home. Surprisingly, this process does not appear to be chemically mediated;

when scouts have their nasonov glands sealed, the swarm is still capable of arriving to the new nest site as quickly as when workers are free to release assembly pheromone (Beekman et al. 2006). This, however, is just for getting the flying swarm from the starting point to within a few meters of their new home. The naive workers must still find the entrance to their new nest-site cavity, which may be a small 2-cm knothole in a dense forest. Both chemical and visual signaling plays a role in guiding worker bees to move together into the entry hole of the new home (Fig 2d). Although they have no trouble reaching the site, swarms of workers with sealed nasonov glands take twice as long to enter their new home than swarms of untreated workers (Beekman et al. 2006).

In both of these cases the group must move towards a target, of which only a few individuals have the directions of where to go. We compare how the mechanisms of communication, inhibition, and feedback are used in each case. Communication among individuals enables coordinated motion of the group, but the means by which information is shared is different in each system: chemical and mechanical signaling are used in the cellular system, while vision is predominant for the coordinated navigation of the swarm of bees. In the cellular system, geometrical and packing constraints are higher, and individuals have low degrees of freedom in possible movement. Interestingly, once the swarm of bees approaches the new nest and must move together over a constrained space into the entrance (Fig 2d), chemical signaling becomes more important. For bees, the use of different sensing modalities thus appears to be related to the density of the population and the degrees of freedom of individual movement. The inhibitory mechanism of contact inhibition of locomotion facilitates cohesive migratory motion of a group of cells. For bees, there is also evidence that flying in a group “inhibits” the average speed of the informed bees. While individual foragers fly between 6 and 9 m/s (depending on inbound vs outbound flight (Seeley 1994)), and streakers have been estimated to fly at over 9 m/s, the overall speed of a swarm is much lower, approx. 3 m/s or less (Beekman et al. 2006). Therefore, while the informed bees could fly quickly to the new nest site, they reduce their average

speed to keep the group together. A feedback system regulates the chemokine gradient during germ cell migration, and if this gradient is disrupted, cell migration may fail, leading to sterility of the animal (Barton et al. 2016). For honey bee swarms, the presence of other fast moving forager bees (from different colonies) can disrupt the motion of the swarm towards the new nest (Latty et al. 2009). It is not known if or to what extent streaker bees use feedback from the movement of the uninformed bees in the swarm in order to modulate the frequency of streaking flights.

## Discussion

Although collective behavior occurs across biological scales, different systems have many of the same core functional requirements and draw from a set of common mechanisms to perform these functions. We explored similarities between two systems - groups of cells and honey bees - where individual specialization in functional subgroups is key to system function. We used the cases of a collective response to perturbation and coordinated group movement (Fig 2) to illustrate how various mechanisms (Table 1) enable effective function of the group.

Honey bees and epithelial cells both must respond rapidly to changes in the surrounding environment. However, other types of cells, and other species of social insects live in different environments. For example, leaf cutter ants and desert harvester ants forage for food sources (leaves and seeds, respectively) that are relatively constant in time, and neural cells exist in the locally stable environment of the brain. By comparing collective behavior across the different systems we can ask how functional mechanisms and behavioral algorithms are adapted to their environment (Gordon 2016). Our comparison shows that cellular systems and honey bees in general employ many of the same mechanisms (Table 1), but that the implementation details and the use of specific mechanisms differs.

Heterogeneity is widespread in biological systems and can be adaptive for group function. Generally, in cellular systems and honey bees, this is evidenced by the over-

all organization into functional subgroups (Fig 2). For honey bees, heterogeneity is important to maintain diverse responses to biotic and abiotic stressors, such as disease resistance (Mattila and Seeley 2007; Seeley and Tarpy 2007), foraging (Mattila et al. 2012), and nest homeostasis (Jones et al. 2004). In cells of epithelial tissues, heterogeneity is revealed by a stochastic landscape of inter-cellular forces across the tissue with peaks and basins revealing regions of high and low cell-cell forces (Vishwakarma and Di Russo 2019; Tambe et al. 2011). During wound healing, the switch to leader cells is mediated by interactions with other cells, but appears to be facilitated by heterogeneities in cell shape, mobility, and inter-cellular forces (Vishwakarma et al. 2018).

The presence of multiple cell clones within a single cell population in adult tissue is linked to epigenetic events (Muller-Sieburg et al. 2012; Altschuler and Wu 2010). Other work shows that gene expression levels vary in different cell populations which have different specialized cell types (Shekhar et al. 2016). In honey bees, genetics determines an individual’s temperature response threshold (Jones et al. 2004), and gene expression levels relate to changes in tasks with age (Grozingier et al. 2003; Alaux et al. 2009). Even the nature of social interactions in honeybees has a genetic component (Linksvayer et al. 2009). A key challenge of future work is to connect genetic or other mechanistic drivers of heterogeneity with the overall functional consequences for the group.

Phenotypic plasticity is the ability of one genotype to produce more than one phenotype when exposed to different environment (Pigliucci 2005; Kelly et al. 2012). Although often used to describe phenotypic differences between organisms, this concept also can be used at smaller scales. For instance, tumor cells display phenotypic plasticity in order to adapt to the constraints and the ecology of the tissue and of the circulatory system in order to metastasise from one organ to the other (Mittal 2018). For social insects, phenotypic plasticity is an important behavioral characteristic and individuals often retain flexibility throughout life, i.e. even though the tasks are distributed according to age, honey bees can respond to changes in their environment

by switching tasks as needed for the colony (Huang and Robinson 1996).

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 honeybees, this contributes to a colony’s ability to maintain a 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). Are there other cases where individual processing contributes to group function in cellular systems?

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). Building on this we can ask, are there other situations in collective animal behavior where inhibitory signaling plays a prominent role? To answer such questions it is key to first ask how the collective system implements a certain mechanism (e.g. inhibition is implemented using stop signals), and then subsequently how it links to group function (e.g. cross-inhibition facilitates consensus decision on a new home site). In future work we hope this article inspires further comparisons of collective systems that build on the framework and mechanisms described here.

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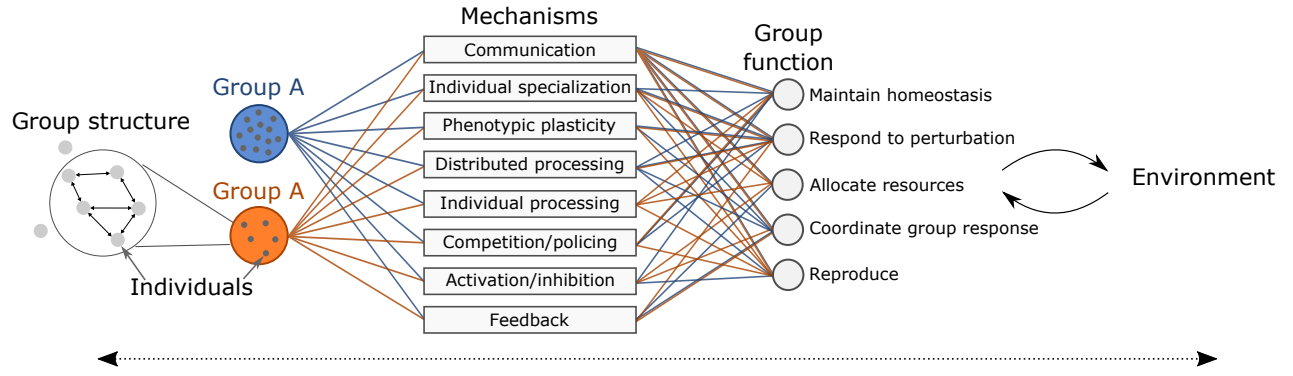


Figure 1: **Mechanisms link individual to group function.** Different groups may use a different set of mechanisms to perform similar functions. The way mechanisms are implemented depends on the constraints and structure of the individuals in a particular group. To compare collective behavior in different systems, we use complementary questions: how groups are structured, how individual behavior is used to implement certain mechanisms, and how multiple mechanisms contribute to group function. A further link can ask how function is adapted to the particular environment.

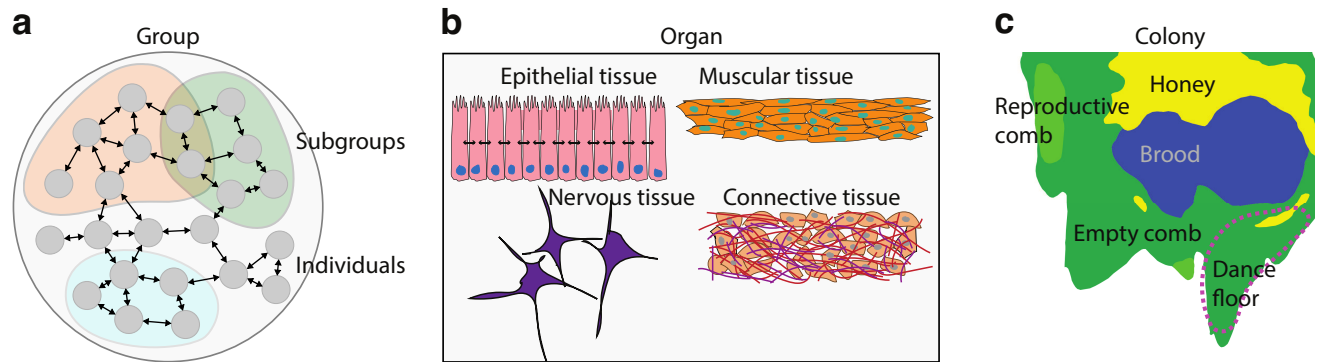
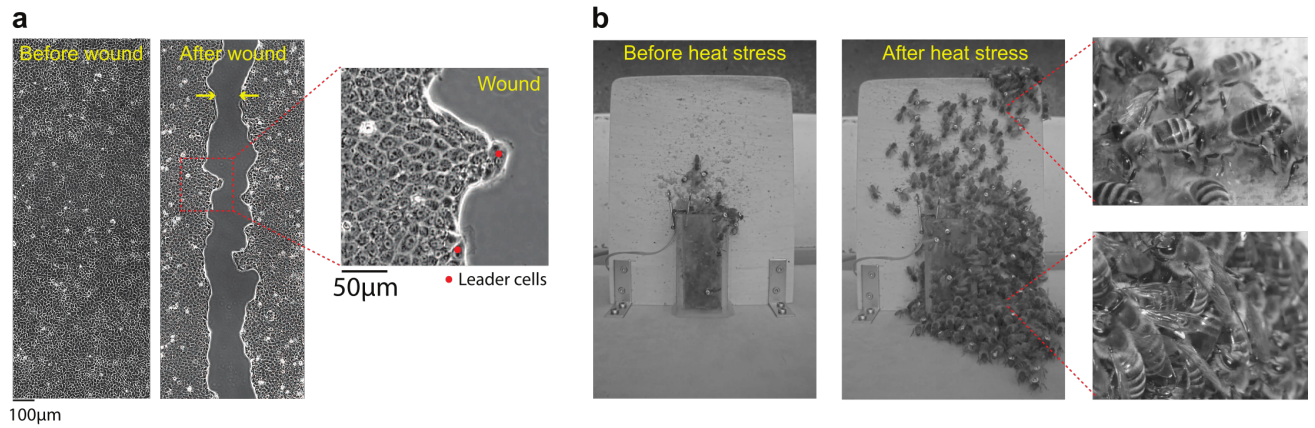


Figure 2: **Subgroup structures in cellular systems and honey bee colonies.** (a) A group is made up of multiple individuals, with inclusions defined by genetic, reproductive, spatial, or functional factors. Within a group, divisions into subgroups reflect individuals that perform specific functions. (b) Multiple scales of organization from cells to organs. Cells of a certain type form subgroups as tissues, each of which performs specific functions. Tissues combine together to make up an organ. (c) Nest structure illustrates functional subgroups in a honey bee colony. The nest is organized into areas designated for brood care, honey storage, rearing male reproductives, and a dance floor. Workers organize themselves according to these nest areas, such as young bees tending to brood and old bees advertising foraging sites on the dance floor.

### Case 1: Response to perturbation



### Case 2: Coordinated group movement

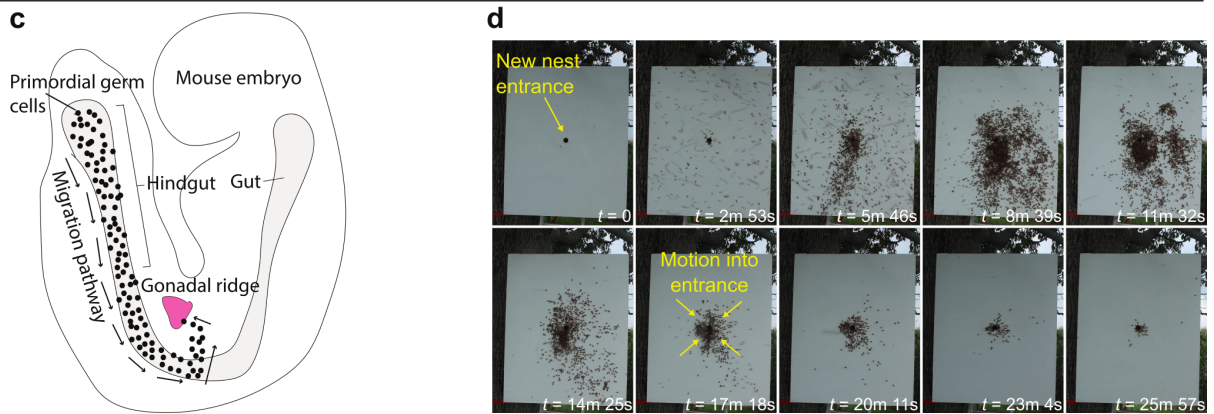


Figure 3: **Cases of similar group function for cellular systems and honey bees.** (a) Epithelial cells respond to a disturbance by a quick directed motion to heal the wound. Leader cells are larger and more polarized than the other cells, and they guide the cells to move in the direction of the wound. (b) A honey bee colony responds to heat stress. Before the heat stress (left), few bees have evacuated the nest, but soon after, hundreds of bees will exit the nest (center). Some workers continue fanning at the entrance (right, top), whereas others simply evacuate (right, bottom) (c) Following specification, germ cells migrate towards the somatic gonads in a developing embryo. A group of germ cells employs mechanisms such as chemotaxis and contact inhibition of locomotion to coordinate movement towards the target gonads. (d) A swarm of honey bees arrives at their new home. Only a subset of the bees had visited before leading the entire group of 10000+ bees into the 3.5cm nest entrance.

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

Table 1: **Mechanisms and associated examples for cellular systems and honey bees.** See also Fig 1. We use mechanisms as an intermediate link that connects individuals to overall group function.