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Inhibitory signaling in collective social insect networks, is it indeed uncommon?[☆]

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Individual entities across levels of biological organization interact to reach collective decisions. In centralized neuronal networks, competing neural populations commonly accumulate information over time while increasing their own activity, and cross-inhibiting other populations until one group passes a given threshold. In social insects, there is good evidence for decisions mediated by positive feedbacks, but we found evidence for similar inhibitory signals only in honey bee (*Apis mellifera*) stop signals, and Pharaoh's ant- (*Monomorium pharaonic)* repellent pheromones, with only the former occasionally being used as cross-inhibition. We discuss whether these differences stem from insufficient research effort or represent genuine differences across levels of biological organization.

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Introduction

Animal decisions related to foraging, mating, and finding a place to live, are thought to optimize their fitness [1]. Collective decision-making systems are diverse and range from single-celled organisms [2,3], to social insect colonies [4••], schools of fish [5], and groups of mammals [6], including humans [7]. Central nervous systems within individual animals are themselves a collection of cells, including neurons, that perform collective decision-making via numerous, interconnected circuits [8,9]. Collective behavior in animals has been well-studied and has inspired the engineering of decentralized robotic systems [10,11], path optimization algorithms [12], and computer network resource allocation [13].

Typically, collective decisions are made by individuals reaching a consensus on one of several available options. This is often done by reaching an agreed-upon quorum [2,14,15], after which individuals in the group accept and follow the decision. This type of decision-making can improve accuracy by canceling out individual biases [16], as well as simultaneously increasing decision speed [17]. Alternatively, many systems make decisions regarding resource allocation, such as attention allocation or forager distributions (e.g. [18]), which may differ from consensus decisions while still relying upon estimating the relative values of several options simultaneously and allocating resources according to the perceived values. However, despite some apparent similarities, it is not clear to what extent social and neuronal networks follow the same rules when reaching a decision. Here, we compare one aspect of this process, the use of explicit inhibition, in neurons and social insects.

There are many types of collective actions or decisions that are based on diverse 'decision-making' processes. These include dominance hierarchies, division of labor, colony defense, and nest construction. We focus here on best-of-n-type problems, as these are relatively simple and ubiquitous, and relatively easy to compare to decisions in neuronal networks. In this group of problems, the decision-making system attempts to assess the value of different options and choose the most valuable option or distribution between options — a functionally important collective decision [19]. Best-of-n-type problems are better studied in both neural and social insect networks and are functionally comparable. More complex and lineage-specific decisions, on the other hand, will not be discussed in this work as there is less research regarding them and their direct comparison across levels of biological organization is more difficult or even inappropriate.

[☆] Given his/her role as Guest Editor, Guy Bloch had no involvement in the peer review of the article and has no access to information regarding its peer-review. Full responsibility for the editorial process of this article was delegated to Ricarda Scheiner.

Collective decision-making model of neuronal networks

One of the best-studied collective decision-making processes is found in neural circuits in the mammal brain. Many models for decision-making in the mammalian brain, including perception-based choices, are based on sequential probability ratio tests (SPRT), which work by distinct neural populations continuously accumulating information supporting each alternative hypothesis until a computation of their statistical likelihood ratio for one hypothesis exceeds a predetermined threshold [8,20]. Each population of neurons receives a noisy input signal from sensory processing parts of the central nervous system such that supporting and opposing information temporarily increases or decreases the population's activity. Excitatory neurons in an active population excite others in the population, while inhibitory neurons cross-inhibit other populations proportionally to their own firing rate. Thus, neuronal populations that are highly activated by the incoming input exert stronger inhibition on the firing rate of others until the cumulative firing rate of one population reaches a threshold, triggering the decided-upon action (e.g. motor response toward the chosen stimulus [21], e.g. choosing a preferred flavor of drink at a store). Cross-inhibition has been described in decision-making in diverse neuronal networks and animal species. It is commonly seen as a mechanism that improves the differentiation among discrete options and a means to prevent unresolved decisions [22].

The apparent logic of this mechanism is that the positive feedback acts as a 'race' between populations to accumulate support, whereas the cross-inhibition ensures that a single or a few preferred alternatives are chosen, and reduces the risk of stochastically reaching suboptimal choices [20,23,24]. The inhibition in these decision-making networks is typically explicit, meaning that neurons produce a signal that directly decreases the firing rate in postsynaptic neurons. Mechanistically, the inhibitory signaling is mediated by the release of neurotransmitters such as γ-aminobutyric acid (GABA) or glycine that activate positively charged potassium channels, causing inhibitory postsynaptic potential, and limiting the postsynaptic neuron's receptivity to excitatory signals from anion channels. The negative feedback can also be implicit, by means of the decrease or decay of positive feedback (e.g. the rate of neurotransmitter reuptake from the synaptic cleft). Below, we focus mainly on networks with explicit inhibition as these are primarily active inhibitory signals that are ubiquitous in neuronal networks and are commonly thought to improve their decision-making process.

Collective decision-making in social insects

Insect societies provide excellent model systems to study decision-making and emergent collective cognition ('swarm intelligence') at a higher level of biological organization (multicellular organisms vs. cells). The size of social insect colonies, ranging from dozens to millions [25,26], and emerging colony-level behaviors are commonly supported by high genetic relatedness [27]. Shared genetic makeup is thought to lead to a common fitness interest affecting many actions and decisions unmatched by vertebrate groups. Indeed, their remarkable cooperativity, elaborated communication systems, along with obligate caste differentiation, often lead eusocial insect societies to be referred to as 'superorganisms' [4••,28•]. Individual social insects have cognitive abilities that, though simple relative to primates, far outweigh the processing abilities of individual neurons [29••]. Additionally, analogous to cell differentiation in the brain, only certain individuals in the colony take part in the colony-level decision-making process. For example, foragers or scouts gathering information about the external and in-nest environment can optimally exploit discovered resources without each forager wasting time searching independently [30].

Studies on decision-making in insect societies are diverse and include social foraging [18,31•], nest selection [32,33], group defense [34,35], nest construction [36], and the timing of colony reproduction [37,38]. It appears that similar methods of communication and amplification feedback loops are used to optimize forager allocation to rewarding patches and to discern optimal nest sites, with small differences in application allowing different types of decisions (distribution vs. consensus). Some of the best-studied collective decision-making processes in social insects include the honey bee waggle dance [39,40], pheromone trails used by multiple groups [29••,41], and ant tandem leading [42]. These are used for both foraging and house-hunting and will be further discussed below.

Defense, construction, and reproduction-related decisions will not be discussed in this work because, to our understanding based on the available knowledge, they do not fit well with the basic best-of-n choices problem. Forager allocation to resources and nest site selection are well-studied collective decisions that are initiated by a few informed individuals who typically independently find a desired resource (food sources or potential new homes) and convey information describing their subjective assessment to interested followers. Recruitment to better options is done more effectively or with more enthusiasm (e.g. stronger or longer recruitment periods, shorter recruitment latency), increasing the number of individuals choosing to visit this option, which in turn often return to the colony and recruit additional individuals to the selected site [43]. The resulting positive feedback among hundreds of individuals differing in their response threshold to the relevant signal [44,45•] allows not only optimal utilization of the time of individuals but also reaching a consensus, which is thought to optimize the utilization of the workforce between distinct resources or the choice of the better potential home.

Negative feedback in social insect collective decision-making

Most of the research in social insects focused on positive feedback loops that repeatedly emerge as important in decisions taken by different species. There is also evidence that implicit negative feedback is important in collective decisions taken by social insects. For example, the allocation of a limited workforce to multiple sources or tasks limits the number of available workers that can forage on a previously attractive source [46]. Also, the crowding at, or leading to, food sources [47], food exhaustion [48], or filling of nest reserves can cause foragers to abandon certain sources. Additional examples of implicit negative inhibition include the gradual evaporation of trail or alarm pheromones that cease recruiting additional individuals if not constantly reinforced. By contrast, there is only little evidence for explicit negative feedback in collective decisions in social insects [49••]. Considering the vital importance of cross-inhibition in neuronal networks, the scarcity of evidence for negative feedback in social insects is puzzling.

Honey bee stop signal

Honey bees recruit foragers to a rewarding site, or scouts to putative nests by performing a repeating figure-eight-shaped ‘dance’ on the vertical combs next to their nest entrance. This well-known ‘waggle dance’ is commonly accepted as a form of symbolic communication conveying information about the azimuth and distance to reach the advertised resource, with additional cues on the body of the forager indicating the type and quality of the resource [31•]. Sites that are subjectively assessed as more valuable are recruited for with longer dance sessions and more vivid dances. As recruited workers can become recruiters themselves, the resulting positive feedback loop [18], allows the colony to optimally allocate foragers between sources of different qualities or to choose the best among multiple home sites without any bee needing to be aware of more than a single source or site (although some typically do visit more than a single site) [14,32].

Honey bee workers also produce brief acoustic ‘stop-signals’ by vibrating their wing muscles while butting their head against a dancing bee, or thorax against the adjacent comb, commonly leading to a brief pause of the dancer. Multiple sequential stop signals increased the likelihood of the dancer ceasing dancing [50,51], curbing her recruitment activity. A basal level of stop signaling is typically seen in foraging colonies [52], similar to basal-inhibitory firing rates in neural networks. The stop signal rate is significantly increased when foragers quickly curb recruitment to a food source that has become dangerous, significantly less productive, or is already crowded and cannot be exploited faster by recruiting additional foragers [53,54]. Moreover, in the Asian honey bee *Apis cerana*, the frequency and duration of stop signals elicited when sensing a potential predator appear to encode information about the severity of the threat [55,56••]. It should be noted, however, that the stop signal in the context of social foraging fits a model of self-inhibition within a population of workers foraging from the same site, rather than the cross-inhibition utilized by neuronal networks (i.e. inhibiting a different population of foragers).

Stop signals are also performed during the events leading to colony swarming. In this context, scouts direct stop signals toward workers recruiting for sites different than the one the stop-signaler examined herself [57]. Thus, in the context of nest hunting, explicit signals are used as cross-inhibition between groups of scouts recruiting to different prospective nest sites, similar to the process integral to collective decision-making in neural populations.

Ant pheromone trails

Foragers and scouts of several ant species were shown to lay a volatile scent trail that recruits nestmates to a profitable food source or potential home [58–60]. Reinforcement by additional workers, often only upon their return from a source or nest site independently found to be valuable [61], is required to counteract the gradual evaporation of the trail. This behavior shapes a positive feedback in which trail strength is proportional to the number of foragers using each trail while allowing the colony to transition to more profitable sources if found [62]. Pheromone-based recruitment, which has been well-studied in ants (see [29••,63] for recent reviews), is also known in termites [64], stingless bees [65], and wasps [66], but is less studied in these lineages. To the best of our knowledge, explicit inhibition has not been reported in these lineages.

The only form of explicit inhibition in ants known in the literature is found in Pharaoh’s ants (*Monomorium pharaonic*), which use three types of trail pheromones to mark the path between the nest and food sources: permanent, long-lasting trail pheromone; short-lasting recruitment pheromone; and a negative repellent pheromone. The latter is placed by foragers at trail bifurcations on branches leading to less-rewarding sources and has the effect of turning foragers away from these trails [67]. As in the case of the use of stop signals in the context of honey bee foraging, the inhibitory effect of the repellent trail pheromone is consistent with self- rather than cross-inhibition.

Theoretical models of negative feedback

Decision-making processes in social insects are typically complex, and isolating variables could be hard to achieve in many experimental settings: insect-based networks are numerically and spatially large, mobile and dynamic, and consist of individuals with cognitive and communication abilities far outweighing individual neurons.

Therefore, a supplementary approach has been to mathematically model these systems. Models allow isolating variables, including network structure, signaling strength, and individual thresholds, as well as simplifying environmental contexts such as food source variation and distribution. Additionally, models can quickly assess the effects of multiple variables and conditions that would take a long time to achieve using empirical setups. Another advantage is that models can examine and predict theoretical effects of network motifs that are not known empirically, including explicit and cross-inhibition. However, as many variables cannot be precisely estimated from empirical data, the implications of these models may be limited and require corroboration from further experimental testing. Together, the combination of theoretical and empirical approaches can help articulate predictions and test new hypotheses.

Some models predicting insights on explicit inhibition in social insect networks include:

- Multiple models have simulated honey bee house-hunting [57,68] and foraging [69••] decision processes faced with multiple options of a similar perceived value by calculating the change in the proportion of workers committed to each site over a relatively long period while adjusting the inhibitory strength of cross-inhibiting stop signals between simulations. These models predict that *cross-inhibition* in honey bee collective decisions plays a crucial role in *breaking ties between close options* and preventing split decisions, in a way comparable to perceptual choices in the brain. Not reaching a consensus may be catastrophic for the colony under some circumstances, such as moving a swarm into a new nest.
- A recent model by Reina & Marshall [70••] compared the ability of honey bee forager distribution processes with and without self-inhibition to achieve the mathematically ideal distribution of foragers across food sources of differing values. The simulation results suggest that constant, low levels of *self-inhibition* within populations foraging from a specific site (as reported by [52]) might help colonies achieve the *ideal distribution across rewarding patches*, despite the typical stochastic variation in forager performance. The model predicted that this mechanism allows for greater foraging productivity over time.
- Another model by Robinson et al. [71] simulated the responsiveness of Pharaoh's ant forager populations to changing resource values while using stimulating or inhibitory pheromones of different relative strengths. This model suggests that *self-inhibition* during foraging may help prevent the colony from being locked into *suboptimal decisions*. In this case, informed individuals redirect foragers away from suboptimal food sources to better ones. Furthermore, as inhibiting foragers from taking suboptimal trails prevents them from maintaining the repellant pheromone, periods of strong inhibition are followed by periods of low pheromone levels at bifurcations leading to the suboptimal sites. During these periods, foragers may return to the suboptimal sources and assess their status, allowing them to recruit again to these sites if their profitability is improved.

Why are there only a few examples of negative feedback in social insect networks?

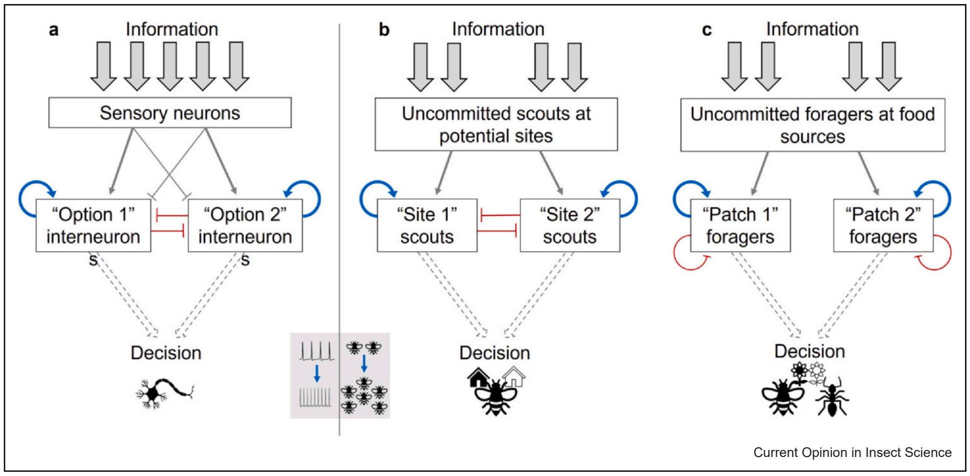
Considering the importance of cross-inhibition in neural networks, and the advantages predicted for this mechanism in collective decision-making, it is puzzling that the only clear evidence for a collective decision using cross-inhibition in social insects is during the process leading to nest site selection in honey bees.

We propose two lines of explanation for this finding. The first is that explicit inhibition is actually more common but has not yet been discovered due to insufficient research effort. The second line assumes that explicit inhibition is indeed scarce in social insect decision-making, and this can be explained by functional differences between decision-making in neuronal and social networks.

The process of decision-making has been rigorously enough studied in only a fraction of social insect species, with the highly studied *A. mellifera* being the sole example of cross-inhibition in insects. Thus, we cannot exclude the possibility that cross-inhibition is more common than currently appreciated. This premise makes more sense if these negative feedback systems are relatively more difficult to discover. Inhibitory signals may be more difficult to observe because inferring the connection of a behavior's absence to a signal is less clear than observing the stimulation of a behavior. Perhaps, inhibitory signals, and cross-inhibition in particular, occur at a lower frequency or salience compared with excitatory ones. Inhibitory signals may also represent a greater level of complexity in decision-making algorithms as they follow and affect positive signals. A historical timeline for the discovery of positive and negative feedback mechanisms in both *A. mellifera* and *M. pharaonic*, although clearly limited in number, may provide some support for this notion. As summarized in Figure 2, positive feedback mechanisms were discovered before negative feedback mechanisms in both systems.

Though the existence of undiscovered examples of explicit inhibition in social insects does not necessitate the

Figure 1



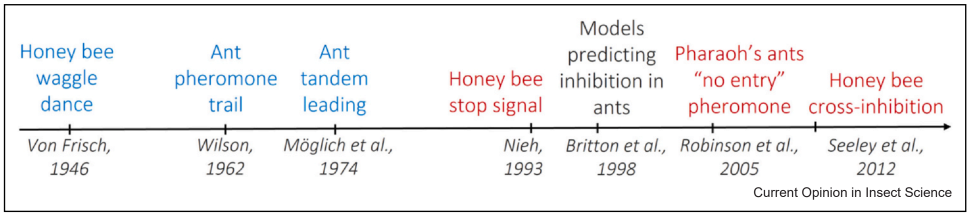
Schematic organization of decision-making processes in neuronal and social insect networks. The main positive and negative feedback mechanisms are depicted in blue and red, respectively. **(a)** Typical decision-making in neuronal networks making perceptual choices. **(b)** Nest site selection by honey bees. **(c)** Allocation of foragers to multiple rewarding patches in honey bees and Pharaoh's ants. In all these systems, external information is perceived by distinct populations, leading to an increase in their own activity (blue feedback loop). The activated population concomitantly inhibits other populations (red whisker lines in **(a)** and **(b)**) or negatively regulates itself (red feedback loop in **(c)**) until one population crosses a threshold (gray box; firing rate in **(a)**, population size in **(b)** and **(c)**), thus reaching a decision. It should be noted that uncommitted scouts (in **(b)**) become committed to a site and begin recruiting while also performing cross-inhibition, which may be analogous to sensory neurons both exciting and inhibiting interneurons.

lack of functional differences between them and neuronal networks, if explicit inhibition is not common, why it is utilized by some but not other species becomes an important question in uncovering universal principles of collective cognition.

One possible functional explanation is that by contrast to neuronal networks, for many decisions, insect colonies do not need to reach a consensus, granting insect colonies the term 'liquid brains' [74••,75•]. For example, given that a single floral patch is typically not sufficient for a large colony, allocating foragers to multiple rewarding patches is probably a better colony-level strategy than recruiting all of the thousands of foragers to a single patch, even if it is the most rewarding one on a given day [70••] (in contrast to [69••]).

Another key difference is that, typically, neurons act as either excitatory or inhibitory nodes (known as 'Dale's law'; [76]), whereas an individual insect can readily produce both positive and negative signals interchangeably. Recent models suggest that systems with separate excitatory and inhibitory populations can make faster decisions but are more prone to stochastic imbalance between inhibitory and excitatory signaling strengths [77•]. The added effect in which smaller networks are already more prone to stochastic variation may help explain why relatively small social insect decision-making networks do not follow Dale's law. Additionally, whereas brains show a strong separation between sensory- and inter- neurons [78], the same honey bee scout discovering a prospective nest site also recruits and inhibits others in the swarm, and therefore can be considered analogous to both sensory- and inter- neurons (Figure 1b).

Figure 2



Historical timeline for the publication of key studies deciphering the positive (blue) and negative (red) feedback mechanisms in *A. mellifera* and *M. pharaonic* decision-making [39,50,57,58,67,72,73].

However, it is currently unclear if and how these two differences between bees and neurons affect the honey bee decision-making process.

From an evolutionary perspective, it is possible that implicit inhibition represents an optimal solution in terms of fitness costs and benefits. According to this logic, explicit inhibition may indeed produce faster and more accurate decisions, but it also comes with higher fitness costs. A system of explicit inhibition may require the development and maintenance of parallel biosynthetic, behavioral, and sensory pathways for excitation and inhibition. Both the development and maintenance of these systems can be assumed to be costly. Thus, to evolve a system based on explicit inhibition, the benefits of this system need to outweigh its costs and overall form a better evolutionary strategy compared with implicit inhibition.

Summary and future directions

Our literature review reveals only a single clear evidence for explicit cross-inhibition as a mechanism for collective decisions in social insects. We find this notable given that cross-inhibition is very common in decision-making by neuronal networks. We point out that this apparent discrepancy between decisions taken by groups of cells and groups of individual insects may point to functional differences between these two systems, or stem from a lack of sufficient research exploring this possibility in social insects. Thus, an obvious future direction is to design research aimed at testing the hypothesis that explicit inhibition, and specifically cross-inhibition, plays a role in communication systems underlying decision-making in as many social insects and ecologically relevant decisions as possible. With more research, we will be in a better position to assess whether there are functional differences between these two types of decision-making networks.

The possibility that decisions in cell and organism-level networks differ is important beyond our focus on negative feedback mechanisms. Networks have many properties that have yet to be analyzed in detail across systems (such as learning and memory, task specialization, and network organization and motifs). From a practical point of view, model systems differ in their advantages and limitations [79•] (e.g. greater experimental manipulability of social insect colonies in which social variables and resources can be manipulated in an ecologically relevant context, more developed paradigms of neurobiology, and novel methods of simulating decision-making processes using new technologies such as robotic swarms and AI). Comparing many aspects of network architecture and properties in diverse systems with complementary advantages may help in comprehending the basic principles of the emergence of collective behavior or ‘swarm intelligence’ from complex interactions of relatively simple entities. Comparative studies across levels of biological organization should also help understanding which network properties are universal at different levels of biological organization, across different ratios of individual-to-collective processing abilities, and in diverse network organizations, thus leading to a more universal understanding of collective cognition.

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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