

bation, the keratinocytes were assayed for DNA damage by γ H2AX staining. Because keratinocytes were grown in different media (EpiLife) than LCs [tryptophan-deficient RPMI: RPMI^{W(-)}], controls included each medium cultured with DMBA for 24 hours (but without LCs or keratinocytes present). The supernatants from DMBA-treated LCs, but not those from identically treated keratinocytes, provoked a significant increase in DNA damage above baseline (Fig. 4, I and J). Hence, although DNA damage can result from the cell-autonomous breakdown of DMBA by keratinocytes, it is substantially increased by the actions in trans of human LCs.

LCs survey the epidermis via both locomotion and repetitive extension/contraction of their dendritic processes and migrate to draining lymph nodes where their main function has been viewed as initiating and/or regulating adaptive immune responses (28). Here, however, a major pathophysiologic role for LCs is described that is independent of adaptive immunity. Instead, it highlights the tissue-scavenging functions of LCs, by which they take up and metabolize chemical contaminants of the epidermis. Although this capability may powerfully attenuate the potency of natural toxins, it may be confounded by industrial PAHs such as DMBA where the detoxified metabolites that are released are more mutagenic than the starting compound. Thus, this innate action of LCs increases DNA damage and specific *Hras* mutations in neighboring keratinocytes. Although further studies are necessary to determine the precise mechanism by which LCs transfer DMBA metabolites to keratinocytes, the proximity of LCs to basal keratinocytes is evident. Given that PAHs are highly prevalent in industrial pollution and that extracts of airborne particles topically applied to mouse skin results in SCC development that is *Ahr* dependent (29), PAH-containing particulate matter might represent an underappreciated environmental factor in human skin cancer. Activating *Ras* mutations are found in ~50% of human epidermal SCCs (30), and in xenografting experiments, the activation of *Hras* signaling (plus inhibition of NF- κ B) was entirely sufficient to transform primary human keratinocytes into SCCs (31).

Although the capacity of keratinocytes to metabolize DMBA (32) and express CYP1A1, CYP1B1, and EPXH1 enzymes (33) has clearly been demonstrated previously, this is nonetheless insufficient to induce substantial tumor formation in the absence of LCs. Others have revealed the potential for nonepithelial stromal cells to activate PAH mutagens (34). The marked resistance of LC-deficient skin to chemical carcinogenesis, in an experimental system optimized for tumor formation, markedly establishes the capacity of LCs to substantially enhance the toxicity of environmental agents. Collectively, our data are consistent with a cooperative carcinogenicity scenario in which LC CYP1B1 and EPXH1 preferentially metabolize DMBA to DMBA-t-3,4-diol, which is subsequently delivered to adjacent keratinocytes wherein CYP1A1 converts the DMBA-t-3,4-diol

to mutagenic DMBAD (fig. S2). Furthermore, our findings also provoke the possibility that locally resident DC populations may enhance PAH-induced mutations and tumor development within other epithelial tissues, contributing to the risk of lung, colon, and genitourinary carcinomas.

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Supporting Online Material

www.sciencemag.org/cgi/content/full/335/6064/104/DC1
Materials and Methods
Figs. S1 to S4
References (35–37)
Movie S1

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Stop Signals Provide Cross Inhibition in Collective Decision-Making by Honeybee Swarms

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Honeybee swarms and complex brains show many parallels in how they make decisions. In both, separate populations of units (bees or neurons) integrate noisy evidence for alternatives, and, when one population exceeds a threshold, the alternative it represents is chosen. We show that a key feature of a brain—cross inhibition between the evidence-accumulating populations—also exists in a swarm as it chooses its nesting site. Nest-site scouts send inhibitory stop signals to other scouts producing waggle dances, causing them to cease dancing, and each scout targets scouts' reporting sites other than her own. An analytic model shows that cross inhibition between populations of scout bees increases the reliability of swarm decision-making by solving the problem of deadlock over equal sites.

The decision-making mechanisms in nervous systems and insect societies are quite similar (1–3). In both types of systems, the decision-making process is a competition

between mutually interacting populations of excitable units (neurons or individuals) that accumulate noisy evidence for alternatives, and, when one population exceeds a threshold level of activ-

ity, the corresponding alternative is chosen (4–7). An important feature of many of the models of neural decision-making is that each population of integrator neurons inhibits the activation of the others to a degree proportional to its own activation (8–10). These inhibitory connections help ensure that only one of the alternatives is chosen and may enable statistically optimal decision-making (3, 10). Given the importance of cross inhibition in neural decision-making circuits, we looked for cross inhibition in the social decision-making process of a honeybee swarm choosing a nest site.

Honeybee swarms are produced in the spring when several thousand worker bees leave their hive with their mother queen to establish a new colony. The swarming bees cluster near the parental hive for a few days while several hundred of the oldest bees in the swarm, the scout bees, find prospective nest sites and choose the best one (11, 12). We began our study with the finding that scout bees use a signal for the inhibition of waggle dances—the stop signal—during the process of choosing their swarm’s future home. We then observed swarms choosing between two nest boxes and found that the scout bees committed to each box directed their stop signals mainly toward scouts promoting the other box; this created cross inhibition between the two populations of scout bees. Lastly, we explored the functional implications of this cross-inhibitory signaling by modeling the bees’ collective decision-making process.

Honeybees possess an inhibitory signal, the stop signal, that is known to reduce waggle dancing and recruitment of foragers to food sources (13–15). Bees that have been attacked while foraging produce stop signals upon return to the hive, preferentially targeting nestmates visiting the same food source (16). The stop signal is a vibrational signal that lasts about 150 ms, has a fundamental frequency around 350 Hz (17), and is typically delivered by the sender butting her head against the dancer (13). Dancers usually do not show an immediate response to a stop signal. Rather, an accumulation of stop signals increases the probability that a bee will cease dancing. The stop signal enables a colony to reduce its recruitment to food sources that are perilous (16).

Knowing that foraging bees use the stop signal to inhibit waggle dances advertising food sources, we explored whether house-hunting bees use this signal to inhibit dances advertising nest sites. We began by making video and sound recordings of nest-site scouts performing waggle dances on five swarms (18). Close-up recordings of 40 dancers on two of these swarms (20 dancers

per swarm) revealed the use of stop signals. These bees produced dances that lasted 74 ± 54 s (mean \pm SD) and contained 24 ± 20 dance circuits, and 23 of these dancing bees received a total of 109 stop signals [(Fig. 1); 4.7 ± 4.3 signals per signaled bee] that were produced by 40 different bees. Each bee that produced a stop signal followed a dancer for 3.0 ± 1.5 dance circuits before lunging toward the dancer, contacting her with head (98%) or thorax (2%) for 0.25 ± 0.44 s, and delivering 2.4 ± 1.9 stop signals, each of which lasted 0.21 ± 0.10 s. Senders disproportionately contacted dancers during the return phase of the dance (96 contacts) rather than the waggle phase (13 contacts) [if delivered in proportion to the lengths of these phases, 73.0 and 36.0 contacts would be expected; chi-squared test, $\chi^2(1, 109) = 21.9, P < 0.0001$]. Dancing bees that received stop signals ceased dancing shortly (36 ± 22 s) after they began to receive the signals. After ceasing to dance, 17 of the 23 bees walked quietly over the swarm cluster, 3 started to produce piping signals to stimulate others to warm up for departure (19), and 3 flew off.

To clarify the relation between receiving stop signals and stopping dancing, we recorded 109 dances on three more swarms and determined the distribution of the 525 stop signals received during these dances. Stop signals occurred more toward the ends of dances than expected if these signals had been given at random [(Fig. 1C); chi-squared test, $\chi^2(9, 525) = 234, P < 0.0001$ (all dances); $\chi^2(9, 358) = 58, P < 0.0001$ (long dances)]. Evidently, the stop signals caused the cessation of dancing. If the relation were not causal but instead were a result of stop signals and ends-of-dances both becoming more likely as dances progress, then longer dances should have begun receiving many stop signals midway through. Yet even in the long dances the stop signals were strongly overrepresented in the last circuits. It is likely that dances ended because

stop-signal inhibition exceeded some threshold in the final circuits.

We next conducted an experimental study to determine how bees use the stop signal throughout a swarm’s process of choosing its nest site. We set up two swarms, one at a time, on an island devoid of natural nesting cavities and provided them with a choice of two identical nest boxes. Scout bees visiting the nest boxes were labeled with nest-box-specific paint marks (pink or yellow). We recorded video of the scouts producing waggle dances and tracked them (one at a time) with a microphone to know when they received stop signals. In most cases (98.4%, $n = 1379$), we could identify which bee produced a given stop signal; each time we heard one, we noted which bee standing near the dancer lunged toward and pressed against her. Nearly every stop signal (94.5%, $n = 1357$) was produced by a bee bearing a paint mark, hence, by a nest-site scout.

There were notable differences in the colors of the paint marks of the scout bees delivering stop signals toward the dancers for the two nest boxes during the decision phase of the nest-site selection process, that is, when a swarm is choosing among possible nest sites. In both swarms, the pink and yellow dancers both received many more signals from different-colored bees (“contra signals”) than from same-colored bees (“ipsi signals”): contra signals, 213, from at least 46 bees; ipsi signals, 24, from at least 14 bees. Moreover, both pink and yellow dancers received disproportionately more contra signals than would be expected if the signals had been delivered in proportion to the number of scouts of each color marked at the times of their dances [Fig. 2; chi-squared test, $\chi^2(1, 237) = 114.55, P < 0.0001$ (analysis of signals); $\chi^2(1, 60) = 16.18, P < 0.0001$ (analysis of minimum signalers); see (18) for explanation of the two statistical analyses]. How the scout bees discriminated the two types of dancers is not known. They may have decoded the location of

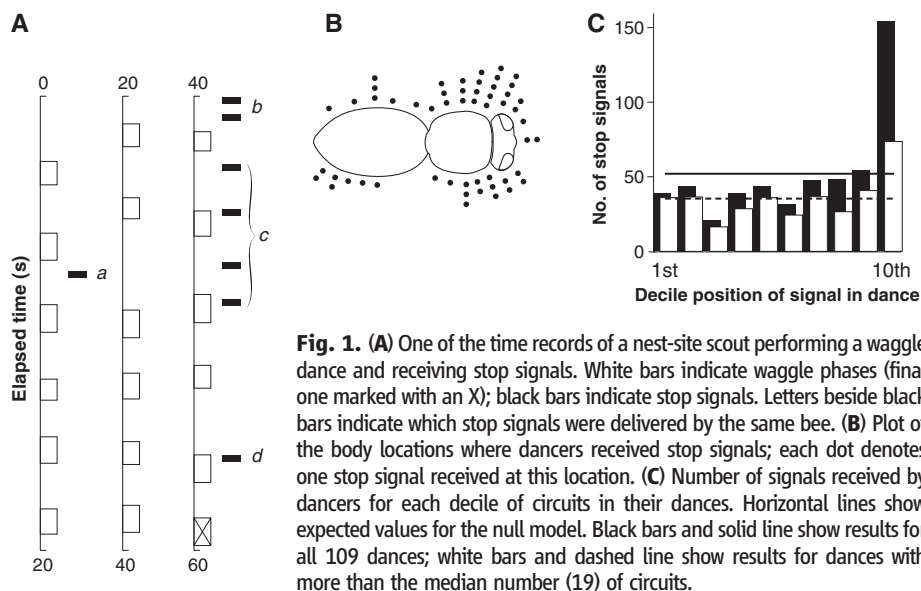


Fig. 1. (A) One of the time records of a nest-site scout performing a waggle dance and receiving stop signals. White bars indicate waggle phases (final one marked with an X); black bars indicate stop signals. Letters beside black bars indicate which stop signals were delivered by the same bee. (B) Plot of the body locations where dancers received stop signals; each dot denotes one stop signal received at this location. (C) Number of signals received by dancers for each decile of circuits in their dances. Horizontal lines show expected values for the null model. Black bars and solid line show results for all 109 dances; white bars and dashed line show results for dances with more than the median number (19) of circuits.

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each dance or—as is the case for stop-signaling bees in the context of foraging (13)—they may have used odor differences. Because stop signals were delivered to unmarked bees in the first five swarms studied, visual cues from the paint marks were most likely not involved.

During the implementation phase, that is, when a swarm has finished choosing its nest site and is preparing to move there, the scout bees no longer directed their stop signals primarily at dancers advertising the other site. In both swarms, pink and yellow dancers received contra signals (185 from at least 70 signalers) and ipsi signals (210 from at least 79 signalers) in proportion to the number of different-colored scouts and same-colored scouts marked at the time of their dances [chi-squared test, $\chi^2(1, 395) = 1.49$, $P < 0.23$ (analysis of signals); $\chi^2(1, 149) = 0.34$, $P < 0.56$ (analysis of minimum signalers)].

Thus, in both swarms there was evidence of cross inhibition between the two groups of scout bees when these groups were competing to reach a threshold (quorum). Once one group did so, indicated by the onset of worker piping (19), there was a general inhibition of waggle dancing. Shutting down recruitment during the implementation phase through stop signaling helps ensure that all the scout bees will be present on the cluster when the swarm flies to the chosen site.

This interpretation of the results of the two-nest-boxes trials is confirmed by the results from two additional swarms that made a “choice” with only one nest box under consideration. If stop signals function mainly for cross inhibition of waggle dances in the decision phase and for general inhibition of dances in the implementation phase, then in the decision phase the proportion of dancers receiving stop signals should be smaller in the one-nest-box trials than in the two-nest-boxes trials. In the implementation phase, however, the proportion should not be smaller in the one-nest-box trials. These are precisely the patterns that we found. In the decision phase, only 26% of dancers ($n = 38$) received stop signals when one nest box was under consideration, whereas 66% ($n = 74$) did so when two boxes were [Fig. 2; chi-squared test, $\chi^2(1, 112) = 16.03$, $P < 0.0001$]. In the implementation phase, the respective percentages are 86% ($n = 148$) and 77% ($n = 133$) (chi-squared test, $\chi^2(1, 281) = 3.92$, $P = 0.05$).

We have demonstrated that the stop signal is an integral part of the decision-making process used by a honeybee swarm to choose its nest site. During the initial phase of the process, when the choice is being made, this signal creates cross inhibition between populations of scout bees representing different sites. This cross inhibition curtails the production of waggle dances for, and thus the recruitment of bees to, a competing site. Because we know from previous studies (20, 21) that when a scout bee stops producing waggle dances for a site she soon stops making visits to the site, we can be confident that the cross inhibition created with the stop signal also inhibits

the number of bees visiting a competing site. Thus, it appears that the stop signals in bee swarms serve the same purpose as the inhibitory connections in models of decision-making in primate brains, such as the Usher-McClelland (U-M) model: to suppress the activity levels of integrators representing different alternatives (3, 8).

The similarities between the decision-making processes in honeybee swarms and in the U-M model are notable. In both, there are populations of units (bees or neurons) that act as mutually inhibitory, leaky integrators of incoming evidence, and in both the choice is made when the integrated evidence supporting one of the alternatives exceeds a threshold (12). To understand the implications of the observed stop-signaling behavior, we have modeled the collective decision-making process of the bees by using ordinary differential equations rigorously derived from the individual-

level interaction rules that we have determined through empirical observations (18). These equations enabled us to analytically describe the average population-level behavior of the scout bees over time. The models of decision-making that we analyzed in this manner were (i) a model proposed to enable statistically optimal collective decision-making through individual bees inducing each other to directly change their commitment (3), (ii) a model based on the observed stop-signaling behavior of honeybees but assuming that stop signals are delivered indiscriminately to all bees encountered, and (iii) a model based on the observed stop-signaling behavior but including the observation that stop signals are largely delivered to bees dancing for a site that differs from the one the signaler has encountered.

The results of this modeling work, illustrated in Fig. 3 and presented in detail in (18), are

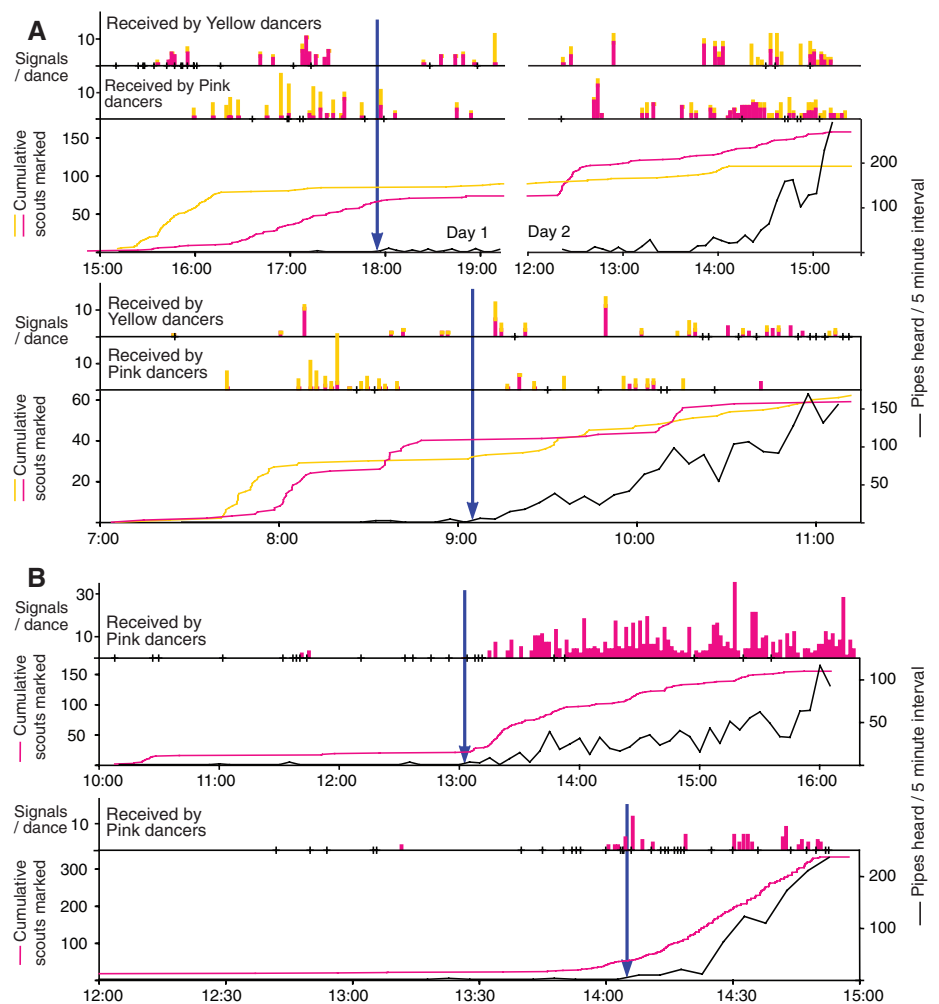


Fig. 2. Patterns of stop signaling and of growth in the populations of scout bees with paint marks throughout the nest-site selection processes of four swarms. In the upper portion of each graph, each dance observed is represented by a tic if it received no stop signals or a colored bar indicating the number of stop signals received from scouts marked with each color (rare unmarked signalers are not shown). A vertical arrow indicates the onset of worker piping, the acoustic signal produced by scouts to stimulate the nonscouts in a swarm to prepare to fly to the chosen site (19). Hence, each vertical arrow marks the transition from making to implementing the swarm’s choice. (A and B) Results for trials with two nest boxes or one nest box, respectively.

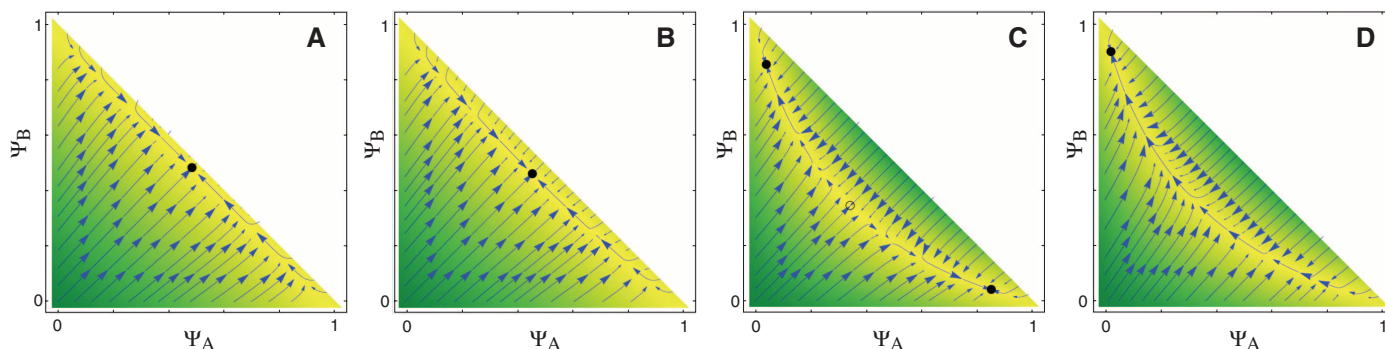


Fig. 3. Dynamical behavior of the different models described in the text, demonstrating how discriminate cross inhibition enhances the decision-making reliability of a honeybee swarm. The two axes show the proportions of a swarm's scout bees, Ψ_A and Ψ_B , that are committed to two alternative nest sites, A and B, respectively. The directions and lengths of arrows illustrate net change in these proportions over a fixed time interval and so represent the dynamical behavior of the models. Stable and unstable fixed points are shown as solid and open black circles, respectively. (A) The direct-switching model of (3) with finite decay and equal alternatives, showing convergence to stable

deadlock between the available sites. (B) The discriminate stop-signaling model with equal alternatives but with incidence of stop signaling below the critical threshold, so that the stable deadlock seen in (A) persists. (C) The model shown in (B), but with the incidence of stop signaling above the critical threshold; as a result, the swarm randomly achieves a consensus for one of the two equal alternatives. (D) The model shown in (B) and (C), but with the difference in the qualities of the two alternatives exceeding a critical threshold; as a result, the swarm is expected to converge on a consensus for the superior alternative.

conclusive. They show that, for the first model (i), given just the tiniest amount of decay from the integrating populations of scouts (probably inescapable in a real biological system), a decision between two equal alternatives (as studied empirically in this paper) inevitably results in a stable deadlock with equal numbers of scouts committed to the two alternatives. When one site gains a majority of scouts, the switching of scouts from it to the other site increases, forcing the system back to a state of equal commitment [Fig. 3A and (18)]. Such stable deadlock is clearly sub-optimal, because it will result in the swarm never achieving a consensus; this could mean the swarm never lifts off. If it does, the equal numbers of scouts committed to two different sites will cause problems for the swarm's cohesiveness as it attempts to fly to its new home (22, 23). The same situation occurs for the indiscriminate stop-signal model (ii) when the alternatives are equal (18). Stable deadlock is also observed for the discriminate stop-signaling model (iii) when the incidence of stop signaling is below a critical threshold (Fig. 3B). Once that threshold is exceeded, however, two stable attractors appear, one for each nest site, and the swarm chooses at random between the two equal alternatives [Fig. 3C and (18)]. Such signaling behavior thus breaks the deadlock of the previous models and allows the swarm to quickly converge on a consensus decision. Importantly, this discriminate stop-signaling model is in accordance with experimental observations (Fig. 2). Intriguingly, when the difference in the qualities of the two alternatives exceeds a critical

threshold, the swarm is expected to converge on the better of the two options [Fig. 3D and (18)].

For neural models of decision-making, cross inhibition between integrating populations is crucial for effective decision-making and has been shown to allow optimal decisions under some circumstances (10, 24). As we have shown here, cross inhibition between integrating populations is also present in honeybee swarms and is very important for their success when making decisions. It is tempting to think that the ability to implement a highly reliable strategy of decision-making is what underlies the astonishing convergence in the functional organization of these two distinct forms of decision-making system: a brain built of neurons and a swarm built of bees.

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Supporting Online Material

www.sciencemag.org/cgi/content/full/science.1210361/DC1
Materials and Methods
SOM Text
Figs. S1 to S4
Tables S1 and S2
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Stop Signals Provide Cross Inhibition in Collective Decision-Making by Honeybee Swarms

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Stop, Don't Go There

Decision-making in complex brains requires the reaching of a consensus based on information relayed by multiple neurons. A similar situation occurs in the decision-making process of swarming bees, where multiple individuals relay information about suitable hive sites, but a single site is chosen by the swarm. **Seeley et al.** (p. 108, published online 8 December; see the Perspective by **Niven**) show that consensus in this system is reached as information from scouting bees accumulates within the hive. Stop signals were given by scout bees from a particular site to those scout bees signaling from other sites. As the signals accumulate, scouting ceases and the bees prepare to swarm to the site that was best represented among the scouts. When this process was simulated, the results indicated that cross-inhibition among the bees functions similarly to that which occurs among neurons within complex brains. In both cases, such cross-inhibition prevents the overall system from coming to an impasse.

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