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How Honeybees Break a Decision-Making Deadlock

Jeremy E. Niven

For a honeybee swarm of potentially thousands of individuals, choosing a home is a momentous decision. Failing to choose a single location may cause the swarm to split and the queen to be lost (1); choosing poorly may limit the swarm’s growth or expose it to freezing temperatures during the winter (2). Studies over the past 60 years have shown that honeybee swarms use quorum sensing, a form of decentralized decision-making, to choose a suitable nest site, but many gaps remain in our understanding of this process. On page 108 in this issue, Seeley et al. (3) show that an inhibitory signal between bees advocating different locations allows them to make a decision even when potential nest sites are equally favorable.

Honeybee colonies reproduce through budding, whereby the queen and some workers leave the nest and bivouac on a branch. Some of the most experienced workers leave to locate suitable nest sites (4). Upon their return, these scouts advertise potential locations and their qualities by performing a waggle dance. During the dance, the scout walks straight across the bivouacking bees, making side-to-side waggles of her body. She then stops, turns left or right, and walks a semicircular return path to her starting point. The waggle run’s duration and orientation encode the length and the angle of the outward flight, respectively, whereas the number of dance circuits encodes the quality of the potential nest site (5). Waggle dances recruit additional scouts to a site until a quorum number is reached and the swarm prepares to move to its new home (2).

Scouts advocating less attractive sites produce fewer dance circuits and make fewer trips to the site (6). Along with the recruitment of uncommitted scouts to more attractive sites, this was assumed to be sufficient to enable the bees to reach a quorum, thereby deciding which site to choose (2). However, foraging workers use an additional type of signal to communicate with other bees. Upon returning from a feeder that is crowded or where a predator is present, forager bees produce a brief vibrational signal that discourages other bees from producing waggle dances that advertise the location of that feeder (7). Hypothesizing that a similar signal may be used by house-hunting bees, Seeley et al. set out to observe scout behavior. They found that scouts received “stop” signals—head butts mainly to their head and thorax—from other bees during the return run of the waggle dance (see the figure). These stop signals occurred more frequently just before a scout stopped dancing.

The authors next established swarms on Appledore Island (Maine), which lacks natural nest sites, and gave them a choice of two identical nest boxes. Scouts visiting one box were marked with yellow paint; those visiting the other were marked with pink paint. Most of the bees giving “stop” signals had paint marks, showing they were scouts. During the decision phase of the nest-site selection process, dancing scouts with yellow paint received many more stop signals from scouts with pink paint and vice versa, showing that scouts from one site preferentially inhibit the dances of those advertising a competing site (see the figure, panel A). Once the scouts started implementing the decision, dancing scouts received stop signals from scouts that had visited either site. When swarms were given only one nest box, scouts received few stop signals during the decision phase but many during the implementation phase. This general inhibition of dancing during the implementation phase presumably ensures that all the bees are present when the swarm takes flight.

To demonstrate a role for the observed cross inhibition between scouts advertising competing sites, Seeley et al. constructed a series of computational models of the collective decision-making process, based on the interaction rules they had observed among the scouts. Models that incorporated no or indiscriminate stop signaling predicted that the scouts would reach a stable deadlock, failing to choose between two

Cease and desist. (A) Seeley et al. have found that during house hunting, scouts advertising one nest site preferentially inhibit scouts advertising another site during the decision-making process. Inhibition is conveyed by a “stop” signal, given mainly to the head and thorax of a scout during the return phase of the waggle dance. (B) Stop signals from scout bees inhibit other scouts, discouraging them from advertising a potential site. These inhibitory stop signals combine with recruitment of neutral scouts to produce a winning site.
equally suitable nest sites. Only a model incorporating sufficiently high levels of cross inhibition predicted that the scouts would converge rapidly upon a decision.

The authors compare the interactions among scouts with those among neurons in primate decision-making networks, which can be modeled with similar interactions (8). They argue that populations of bees and neurons can be considered to be mutually inhibitory, leaky integrators of sensory evidence that lead to a choice when they exceed a threshold (see the figure, panel B). These features are not restricted to neural circuits but underpin decisions in many biological processes, such as pattern formation (9, 10).

Although Seeley et al. gave the bees a choice between two identical nest sites, house-hunting swarms typically evaluate many sites of differing quality. This may require scouts to distinguish waggle dances advertising several other sites from their own, possibly through forming categories of “same” and “different,” or more likely through odor cues. In this situation, scouts may produce stop signals in proportion to the quality of the site they have located, which would produce effects similar to lateral inhibition in neural circuits and cell fate decisions (9–12). By averaging surrounding activity, lateral inhibition can reduce the effects of intrinsic noise and maintain sensitivity over a wide range of stimulus intensities (11, 12). Thus, as well as reinforcing asymmetries vital for resolving deadlocks, inhibitory signals of scouts may be important for reducing noise at the beginning of the decision-making process and for rescaling the process when there are many good alternatives.

The findings of Seeley et al. emphasize the computational value of signals involved in decision-making in house-hunting honeybees. The stop signal has either been co-opted to or from foraging, but in doing so its use has switched: scouts use the stop signal to inhibit bees advertising different sites rather than the same site, and they do so because of the high, rather than low, quality of the site they have visited. Thus, inhibitory (vibratory head butt) and excitatory (waggle run) signals can be used to form behavioral circuits (foraging, house-hunting), just as they are in the nervous system to form neural circuits. Future research stands to benefit from this computational approach, incorporating behavioral analysis with concepts and ideas from neuroscience and developmental biology.

References

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GENETICS

Variable Outcome of Mutations

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Why do some mutations produce a particular trait or disease, whereas others only increase the likelihood of such an outcome? One explanation is that other variants in the DNA sequence strengthen or weaken the effect of a given mutation, although environmental factors may also have an impact. On page 82 of this issue, Casanueva et al. (1) show that in the nematode Caenorhabditis elegans, stochastic differences in the amount of a protective chaperone protein, after exposure of the worms to mild stress, influence the effect of mutations.

In some cases, the link between an individual’s genotype (DNA code) and phenotype (traits, diseases) is straightforward. For example, individuals with more than 41 cytosine-adenine-guanine repeats in the Huntingtin gene will invariably develop Huntington’s disease. However, many variations in the DNA sequence do not always produce a certain trait or illness. Women carrying the BRCA1 mutation have about a 65% chance of developing breast or ovarian cancer before the age of 70 (2). Why don’t all women carrying the mutant allele develop these cancers? One reason is that other genomic variation may influence the effect of a given mutation (3). For example, certain alleles of the TNRC9 gene increase the effect of having the mutant BRCA1 allele (2, 4). However, when a large number of loci show genetic interactions, it becomes difficult to predict the importance of a given variation (3), much less an individual outcome.

Environmental factors may also influence the effect of a mutation (3), but their functional consequences can be difficult to unravel. Casanueva et al. show that C. elegans worms with a potentially deadly mutation in the transcription factor–encoding gene lin-29 have a 35% better chance of surviving if they receive a mild heat stress at an early developmental stage (see the figure). The authors reason that heat stress induces the expression of molecular chaperones that protect cells by preventing misfolding and aggregation of other proteins. However, chaperones can also protect against harmful effects of some mutations, possibly by reducing the chance that a mutation leads to protein misfolding (6). Indeed, worms exhibiting a stronger stress response (as measured by gene expression) to heat exposure had reduced mortality, and those with a constitutively activated stress response also showed better survival, even in the absence of any stress stimuli.

Individually not only differ in their DNA code and environment, but also exhibit seemingly random (stochastic) differences in the transcription of some genes (7, 8). Casanueva et al. found that stochastic differences in the expression of protective chaperone genes (in the absence of a stress treatment) also reduced the effect of mutations; indi-