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ORIGINAL PAPER

Swarm cognition in honey bees

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Abstract We synthesize findings from neuroscience, psychology, and behavioral biology to show that some key features of cognition in the neuron-based brains of vertebrates are also present in the insect-based swarm of honey bees. We present our ideas in the context of the cognitive task of nest-site selection by honey bee swarms. After reviewing the mechanisms of distributed evidence gathering and processing that are the basis of decision making in bee swarms, we point out numerous similarities in the functional organization of vertebrate brains and honey bee swarms. These include the existence of interconnected subunits, parallel processing of information, a spatially distributed memory, layered processing of information, lateral inhibition, and mechanisms of focusing attention on critical stimuli. We also review the performance of simulated swarms in standard psychological tests of decision making: tests of discrimination ability and assessments of distractor effects.

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Introduction

The study of group decision making sometimes uses a "collective intelligence" perspective where the group is viewed as a single decision maker (Hölldobler and Wilson 1990; Levine et al. 1993; Franks 1989; Seeley 1989, 1995; Hinsz et al. 1997; Laughlin 1999; Camazine et al. 2001; Surowiecki 2004; Conradt and Roper 2005). Moreover, it has been recognized for some time that the massively parallel animal-to-animal interactions that underlie the cognition processes of integrated groups are functionally similar to the neuron-to-neuron communications that underlie the cognitive abilities of individuals (Markl 1985; Bonner 1988). The primary goal of this paper is to show how several of the key elements underlying cognition in the neuron-based brains of vertebrates are also found in the insect-based swarms of honey bees.

We focus on the group decision-making process whereby a swarm of bees selects its new nest site. honey bee swarms are formed in the spring through a process of colony fission wherein the mother queen and about half the workers in a colony leave their nest and form a cluster on a nearby branch (the biology of swarming is reviewed in Winston 1987). Scout bees fly from the cluster to search the countryside for potential dwelling places, usually cavities in trees. Discovered nest sites of sufficient quality are reported on the cluster via the scouts' waggle dances, which recruit other bees to evaluate the sites. Higher quality sites evoke stronger dancing and hence more recruits. When, via recruitment, 10–20 bees are assembled outside a candidate nest site, a quorum threshold is reached, which triggers choice of the site Seeley and Visscher (2003, 2004a). The scouts from the chosen site return to the cluster, initiate lift off, and the swarm flies as a group to their new home. The study here of what we call "swarm cognition" during this nest-site selection task uses the model in Passino and Seeley (2006) (others are in Britton et al. 2002; Myerscough 2003; Janson et al. 2007). This model was validated using the experiments in Seeley and Buhrman (1999, 2001), Camazine et al. (1999), Seeley (2003), Seeley and Visscher (2003, 2004a). Overviews of the biology of nest-site selection are given in Seeley and Visscher (2004b) and Seeley et al. (2006).

Beginning at the individual bee-level (analogous to the cellular neuron level), we build a detailed explanation of the nest-site selection process to review the key elements and functional organization of swarm cognition. We then show that the swarm has identifiable elements that correspond to neurons, action potentials, interneuron communications, lateral inhibition, short-term memory, neural images, and layers of processing (Kandel et al. 2000). We identify functional similarities to the networks of neurons that perform certain attention, perception, and choice functions in solitary animals (Gazzaniga et al. 1998; Kandel et al. 2000). Using simulations, we show that the swarm's short-term memory (what we call "group memory") is, on average, a representation of the relative quality of the discovered sites that leads to good choice performance. There is a resemblance between the site quality representation in the swarm and the "forage maps" of the hive discussed in Visscher and Seeley (1982).

In choosing a home, a swarm will perform optimally by *quickly* choosing the *best* discovered nest site. The time pressure arises due to energy costs and weather risks that the exposed swarm incurs. The quality pressure arises because the quality of the nest site (protection from weather, predators, etc.) affects colony fitness. Hence, we take the view that the nest-site selection task is a form of the "reaction-time test" studied in psychology (Luce 1986). Such tests have received significant attention in mathematical and cognitive psychology where diffusion (Ratcliff 1978), accumulator (Usher and McClelland 2001), and other mathematical models (Busemeyer and Townsend 1993) have been developed to explain the results of reaction-time tests for humans and other animals (see overviews and applications in Luce 1986; Busemeyer and Townsend 1993; Ratcliff et al. 1999; Roe et al. 2001; Ratcliff and Smith 2004; Smith 2000). One key property of reaction-time tests, the trade-off between speed and accuracy in making a choice, has also been studied for both animal groups (Franks et al. 2003; Passino and Seeley 2006; Marshall et al. 2006) and human groups (Karau and Kelly 1992). In this study, we show that our model of swarm nest-site selection (Passino and Seeley 2006) shares important features with the above-listed models for the decision-making behavior of individual humans, but also that there are key differences. Moreover, we use methods from Gazzaniga et al. (1998), Ratcliff (1978), Roe et al. (2001) to show that, in simulated choice tests, bee-based swarms exhibit several of the same traits, including choice error characteristics, as humans and other animals with neuron-based cognition. First, we show that swarms have discrimination abilities that allow them to distinguish between two nest sites that are relatively close in quality. These discrimination abilities are amplified when comparing low quality sites and are achieved in spite of significant assessment noise at the level of individual bees. Second, we show that swarms can effectively eliminate from consideration many low quality distractor sites. However, if the distractors' qualities are high enough, a swarm can make many errors, as the best site is essentially hidden in a field of adequate-quality sites that compete for the swarm's attention.

Process dynamics of nest-site selection by bee swarms

Review of the model

The model from Passino and Seeley (2006) is summarized via the flow-diagram in Fig. 1. Consider B "scout" bees that take on different roles (explorer, observer, committed, rester, and dead) in the nest-site selection process (we use a fixed value of $B = 100$ and a fixed quorum size for that value). Let k denote time steps in the model; a scout bee can conduct one expedition from the swarm cluster per time step. When a scout, functioning as an "explorer," successfully finds a candidate nest site, it evaluates its attributes to form a quality assessment. We denote the quality of site j as $N^j \in [0, 1]$ with "1" representing a perfect site. We let the position of scout bee i be θ^i, and let $J(\theta)$ denote the "landscape" of site quality, with $\theta = [0, 0]^\top$ the position of the cluster. We have $J(\theta^i) = N^j$ if scout i is at site j, but scout i has assessment noise $w^i(k)$, and a quality threshold $\epsilon_t = 0.2$ below which it will ignore a site. Hence, scout i's assessment of a site for time step k is $S^i(k) = J(\theta^i(k)) + w^i(k)$, if $J(\theta^i(k)) + w^i(k) > \epsilon_t$, and zero otherwise. In this study, $w^i(k)$ is uniformly distributed on $(-0.1, 0.1)$ to represent errors up to ±10% in the scout's assessment of nest-site quality. Any scout bee that finds an above-threshold nest site dances for it

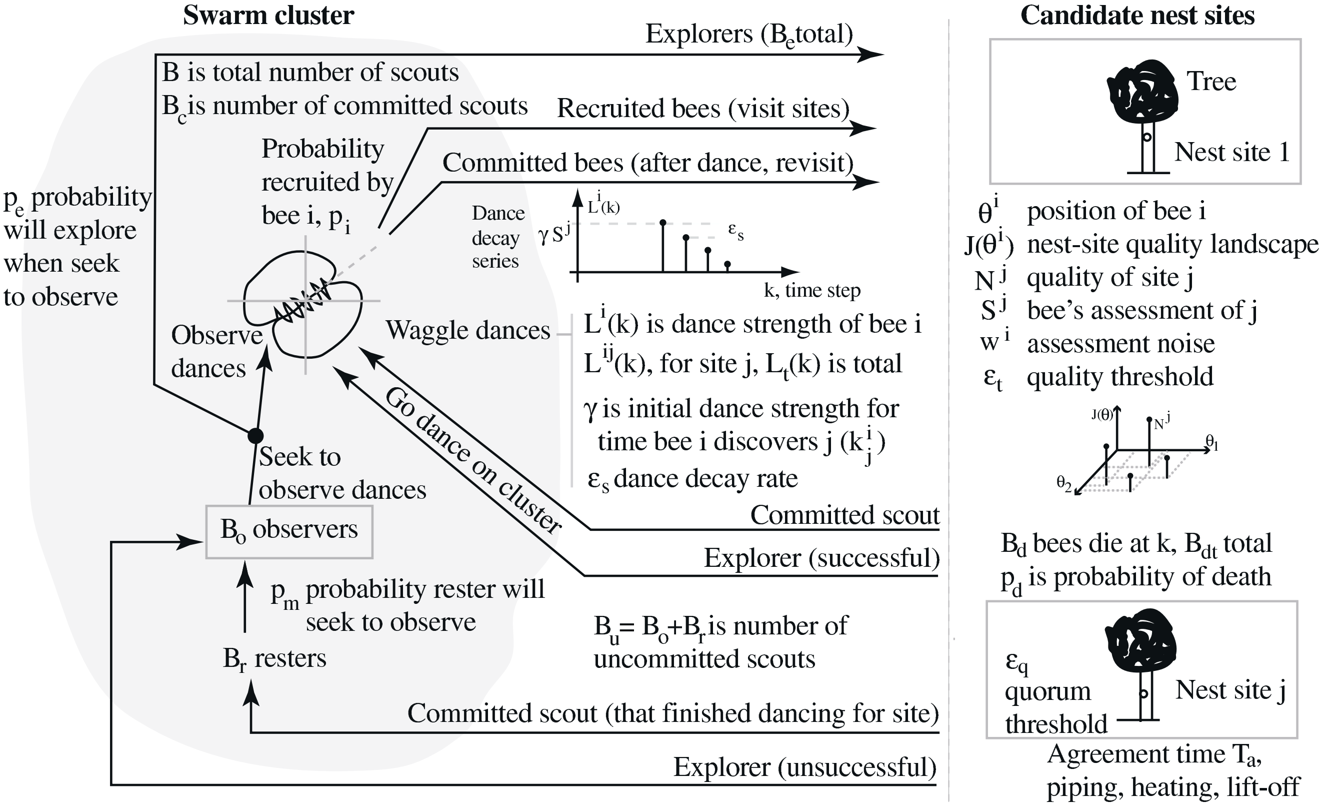

Fig. 1 Flow diagram summarizing the dynamics in the behavior of the scout bees that underlie the nest-site selection process of honey bee swarms

and hence becomes "committed" to that site. Bees die with a small probability $p_d = 0.0016$ on each expedition so that less than 10% die over the whole nest-site selection process.

An unsuccessful explorer returns to the cluster and seeks to observe a dance. The time step that scout bee i first discovers site j is k^i_j, and if the assessed quality of the site is above the quality threshold, this bee returns to the cluster and dances with a strength $L^{ij}(k^i_j) = \gamma S^i(k^i_j)$ waggle runs where $\gamma = 150$. After dancing, this committed bee returns to the site and then back to the cluster, possibly making several such round trips between the swarm cluster and nest site; however, each time it returns to the cluster, it dances $\epsilon_s = 15$ fewer waggle runs than the previous time. The sequence of waggle runs produced by scout bee i over the whole process is L^i, and the total number of waggle runs produced on the cluster for all sites at time step k is $L_t(k)$. We call a sequence of dances by one scout bee for one site, from the time of the initial dance to when the dance strength decays to zero, a "dance decay series." After a committed scout's dance strength has decayed to zero, it rests and rejoins the process (by seeking to observe a dance) at each expedition with a probability $p_m = 0.25$. Scout bees that seek to observe a dance will end up exploring instead with probability $p_e(k) = \exp\left(-\frac{1}{2}\frac{L_t^2(k)}{\sigma^2}\right)$ where $\sigma = 4,000$, representing that when there is not much dancing on the cluster [small $L_t(k)$], then there will be more exploring, and vice versa. There are $B_r(k)$ resters, $B_o(k)$ bees that seek to observe, $B_u(k) = B_o(k) + B_r(k)$ uncommitted bees, and $B_c(k)$ committed bees. With probability $1 - p_e(k)$, observer bees will observe dances, and with probability $p_i(k) = \frac{L^i(k)}{\sum_{i=1}^{B_c(k)} L^i(k)}$, they will be recruited by the i-th committed dancing bee. Bees recruited to site j will visit and dance for it according to their own assessment, as described above.

At any particular time, the set of scout bees is spatially distributed across the environment (explorers), the candidate nest sites, and the cluster, so it is important to think of the process dynamics in terms of the simultaneous activities at all of these places. Key parts of the whole process are occurring simultaneously with the scouts performing and observing dances on the cluster and sensing at each candidate nest site the number of other bees at the site. When the quorum threshold $\epsilon_q = 20$ is reached at one of the sites, the bees there return to the cluster and produce piping signals that elicit heating by the quiescent (non-scout) bees in preparation for flight. Eventually, the entire swarm lifts off and flies to the chosen site, guided by the scout bees. Each expedition by a scout bee is assumed to take 30 min, and the maximum amount of time for the swarm to make its choice is set at 32 h, so there are up to 64 time steps. Due to the possibility of close-quality alternatives, individual bee assessment noise, and random site discovery times, there can be simultaneous quorum achievement at two or more sites resulting in a "split decision." In this case, the process is restarted by having the swarm lift off, fail to fly away, and then reform the cluster. Furthermore, the process can fail to come to agreement before 64 time steps are completed; this is called a "no-decision failure." These failures can arise if a site of sufficient quality, one that will generate a recruitment rate that will assemble the required ϵ_q bees at a nest site, is not discovered early enough.

Distributed evidence gathering and feedback

Within the decision-making process, the evidence of each site's quality takes two forms: dances on the cluster and bees at the site. First, scout bees that are committed to a site perform dances for it on the cluster to advertise it to the observers. The number of observer bees recruited to each site occurs in proportion to the number of waggle runs for each site. If a recruit assesses the site to be of similar quality to what its recruiter found, it will perform a similar series of dances. *Positive* feedback is created, as the number of recruiters and their recruited bees will grow exponentially (assuming an infinite pool of recruits). There are, however, also two types of *negative* feedback, one induced by dance decay rate ϵ_s and the other by scout deaths as defined by p_d. As the probability of death on an expedition is low, its impact on the dynamics is small. However, the impact of the dance decay rate is large. As the decay rate is the same for different quality sites, the dancing for poor sites will fade quickly; hence, there will be few bees recruited to poor sites. This ensures that not too much attention will be dedicated to poor sites.

The second form of evidence of a site's quality is the number of bees assembled at the site. Assuming that the site is not independently discovered by many bees, if several bees are at a site, it is due to recruitment to the site that only occurs if the site is of adequate quality, and if there are many bees at the site, this could only occur if all those bees had judged it to be of good quality. The number of bees visiting each site changes dynamically as new sites are discovered and evidence is gathered by bees. The number of bees visiting the sites drives the recruitment at the cluster, but also the recruitment to each site influences the number of bees visiting the sites. This tight coupling between activities at the cluster and the candidate sites requires us to look broadly at the spatially distributed dynamics of the process, to pay attention to all locations where the bees congregate, not just the cluster.

Mechanisms of selection

A swarm's ability to discriminate between sites of different quality depends on an interplay between positive and negative feedback. We illustrate this via a simple example. Assuming no assessment noise, if two bees are dancing on the cluster for two different above-threshold sites j and j' with qualities $N^j > N^{j'}$, then the difference in the number of recruits for the two cases (and hence strength of positive feedback) is an increasing function of the difference $N^j - N^{j'}$. As an example, first consider two low quality sites $N^j = 0.4$ and $N^{j'} = 0.2$, so $N^j - N^{j'} = 0.2$. A bee that dances for site j' does so with $\gamma N^{j'} = 150(0.2) = 30$ waggle runs in the first visit back to the site and then 15 fewer or 15 waggle runs on the second visit. Then, this bee's dance decay series ends. The total number of runs in this case is 45. In contrast, a bee that dances for site j has a dance strength sequence of 60, 45, 30, 15, and 0 for a total of 150 waggle runs in its dance decay series. The percentage increase when quality increases from 0.2 to 0.4 is $\frac{105}{45} \times 100 = 233\%$. Hence, there are *many* more recruits for the better site compared to the inferior site. Now, if there are two relatively high quality sites $N^j = 1$ and $N^{j'} = 0.8$, again with $N^j - N^{j'} = 0.2$, the total number of waggle runs per dance decay series for qualities of 0.8 and 1 are 540 and 825, respectively. The percentage increase when quality increases from 0.8 to 1 is $\frac{285}{540} \times 100 = 53\%$, much smaller than the above case. Hence, when site qualities are relatively low, a given difference in quality leads to a big percentage difference in the number of dances and the positive feedback gain on recruitment rate to that site. Therefore, the swarm has a very good ability to discriminate between nest-site qualities when they are relatively low quality sites. When site qualities are higher, the same size difference in quality leads to a lower percentage difference in the number of dances and hence recruits. Hence, the swarm's site discrimination ability is poorer for high-quality sites than for low-quality sites.

It should also be stressed that the dynamics in evidence gathering have three features that can make it difficult for a swarm to always succeed in picking the best nest site. First, each bee has a noisy assessment of the quality of any site; hence, the evidence that each bee provides is noisy. The noise is amplified by the nonlinear relationship between differential site quality and the number of recruits, which helps discriminate between sites that differ in quality. However, the quality assessment noise of each individual bee is filtered out at the group level to a significant extent by:

1. *Averaging the effects of multiple bees dancing on the cluster:* Some bees will assess quality as low and some as high, but the relative mean number of dances for a site will closely represent its relative quality.
2. *Quorum threshold effect:* The proportioning of dancing on the cluster results in a proportioning of bees assessing each site in accordance with its relative quality. As the number of bees visiting a site must be above the quorum threshold before it is chosen, a small number of error-prone bees will not cause the swarm to make mistakes.

The second feature that conspires against a swarm always making the best choice is that evidence of site quality, in the form of returning bees that dance, arrives at the cluster *asynchronously*. Evidence arrives randomly in time depending on the time a site is discovered and when the initial discoverer returns to dance for it, and the times of subsequent dances by recruits. Even high quality discoveries near the very end of the process will be unlikely to influence the swarm's choice as many of the scouts are apt to be committed to other sites and hence not available for recruitment. It is possible that a relatively low quality site discovered early in the process will be chosen, especially if no high quality site is found, because then there will be enough time for enough bees to be assembled at the poor site to achieve the quorum threshold.

The third feature that hampers perfect choice is the presence of "distractor" nest sites, ones of sufficient quality to be evaluated, but that should not be chosen, as they are of inferior quality. Strong negative feedback due to dance decay generally enables the swarm to consider each distractor site only briefly. However, if there are *many* distractors, the strength of the positive feedback for the best site is attenuated, perhaps even low enough that a distractor is chosen. Essentially, the swarm is too busy paying attention to many inferior sites to allow it to focus on the assessment and choice of the best site. Noise can amplify this distraction effect, but the averaging discussed above will reduce its effect at the group level.

Search-selection phases and dynamic internal coupling

Nest-site selection has a search phase and a selection phase. Although these two phases are always interleaved and, hence, blend together, it is useful to characterize their general features. The search phase is characterized by a high value of $B_e(k)$, a low value of $B_c(k)$, and a low value of $L_t(k)$, as there is not yet much dancing on the cluster, as not many bees are yet visiting sites. The selection phase is characterized by the exact opposite of this situation so that $L_t(k)$ is higher, $p_e(k)$ is lower (so not as many bees explore), and this raises the positive feedback on recruitment so that a quorum threshold ϵ_q can be quickly reached, resulting in agreement at time T_a.

The feedback processes discussed above are modified by internal coupling (cross-inhibition) between variables associated with different candidate nest sites. Recruitment to one site means that the recruits will not be recruited to other sites until they possibly dance for the site to which they have been recruited, rest, and eventually reenter the process as a new recruit. Hence, if the total strength of dancing for a site and the number of visitors to the site goes up, then bees are inhibited from visiting other sites. The number of visitors at other sites may even *decrease*, because when bees finish dancing for a poor site, they will be likely to be recruited to the better one.

The size of the pool of uncommitted scouts and the phase of the process (search vs. selection) both impact the type of internal coupling. If there is a large amount of dancing on the dance floor, the probability of exploring will go down, the probability to follow dances will go up, which will strengthen the potential for positive feedback due to recruitment. If there are many distractor sites, then probably there will be few uncommitted scouts, but still a relatively low amount of total dancing, so that exploration will stay high if few good sites have been found. If a large number of uncommitted bees is available, then recruiters can achieve their maximum recruitment rate that will tend to focus the swarm on a single great site and inhibit consideration of relatively low quality sites. Hence, in the beginning of the process (during the search phase), there is a type of flexibility in which many alternatives are often considered, but their consideration is coupled in complex ways depending on discovery times and qualities. The nature of the coupling changes as the phase switches from search to selection. Near the end of the process, the coupling is such that there is a strong tendency of the swarm not to consider new evidence. Normally, the relatively low quality alternatives have become significantly less visited due to dance decay, and the best one gets many more recruits, so a crescendo of visits occurs at the chosen site. Hence, the cross-inhibition helps to avoid having oscillations between different alternative choices, at least when there are clear quality differences.

Dynamics create a speed-accuracy trade-off

There is a trade-off between speed and accuracy of choice that is a direct consequence of the process dynamics (Passino and Seeley 2006). Generally, error rate reduction typically costs more agreement time, T_a, or more dances, or both. The time when agreement is reached is a random variable that is affected by the pattern of times of discovery of sites, their qualities, and indeed all aspects of the dynamics described above. Let $\sum L_t$ denote the total amount of dances that have been performed by time T_a. The agreement time is in a sense controlled by the swarm: The swarm will reach agreement when it has evaluated enough alternatives of sufficient quality to make it likely that it picks the best one. Natural selection will favor reducing $\sum L_t$ so that the swarm invests less time and energy in scouting and dancing to achieve a decision. Furthermore, it will favor reducing T_a so that the swarm can lift off, fly to the new nest site, and quickly establish its new home. Generally, choice errors are made in trying to minimize T_a and $\sum L_t$. The main mechanism that tries to make the decision occur quickly is the positive feedback aided by cross-inhibition that forces discrimination and a quick transition from the search to select phases. Correspondingly, the negative feedback tends to slow the process. The balance between the two, mediated by coupling and randomness in assessments and discovery times, leads to the agreement time.

Specific scenarios serve to highlight how the dynamics affect the speed–accuracy trade-off. First, if there are no sites discovered for a period of time or only low quality sites are discovered, then the positive feedback is not strong enough to completely switch from a search to a selection phase, which is good as the swarm needs more time to find a sufficiently high quality site. There can also be an increase in T_a due to the presence of similar quality sites that require more "deliberation time" (coupled dynamic interactions that inhibit each other from achieving a sufficient recruitment rate and hence a quorum), which normally costs more dances (i.e., an increased $\sum L_t$). Such extra deliberation time can even result from the need to distinguish between inferior distractors of different quality. When, luckily, a great nest site is found quickly, both T_a and $\sum L_t$ can be relatively low and the error rate can be low.

Features of swarm cognition

If $N^j \in [0, 1]$ is the quality of site j, its relative quality is $N^j / \sum_j N^j$. For site j, let d_j be the distance from the cluster to site j and let ϕ_j be the angle to site j for a coordinate system with origin at the cluster and the x-axis pointing to an appropriate reference point, the one used in bee dance communication on the cluster. Let $\sum_i L^{ij}(k)$ denote the total number of waggle runs performed by all bees *for site* j at time step k; hence, "$\sum_i$" denotes the sum over all bees dancing with (d_j, ϕ_j). The total number of waggle runs for site j up to T_a is denoted by $\sum_k \sum_i L^{ij}(k)$. Its mean over many nest-site selection processes is $E\big[\sum_k \sum_i L^{ij}(k)\big]$. This expectation is a measure of the total amount of signaling (advertisement) for site j. For plotting purposes, we will consider the *relative* mean total amount of dancing for site j, which is $E\big[\sum_k \sum_i L^{ij}(k)\big] / \big(\sum_j E\big[\sum_k \sum_i L^{ij}(k)\big]\big)$. Let $B(j, k)$ be the number of bees that visit site j at time step k. Then, $\max_k B(j, k)$ denotes the maximum number of bees that visited site j up to T_a. Its mean over many nest-site selection processes is $E[\max_k B(j, k)]$. This expectation is a measure of the maximum number of bees that a site can "attract" before the agreement is reached when the number of bees reaches quorum for some j (the chosen site). For plotting purposes, we use the relative mean $E[\max_k B(j, k)] / \big(\sum_j E[\max_k B(j, k)]\big)$ for each site j.

Interconnected cognition units

An individual scout bee is the fundamental unit of swarm cognition (analogous to a neuron). The unit can change its role and location. It can sense, act, and communicate with other units. The swarm's sensory process is the sum of the sensory processes of all the scout bees. The swarm's spatial "field of view" (Kandel et al. 2000) is dynamically modulated by scout bee choices (e.g., during exploration and site assessment) to appropriately span many square kilometers and many candidate nest sites.

Dances by bee i of strength L^{ij} for site j are analogous to action potentials (Kandel et al. 2000). For this, there is an assessment of quality relative to threshold ϵ_t before such dancing is activated (analogous to activation thresholds in neurons). The dances play a special role in which they act as signals between different units. If we view bees as nodes and bee-to-bee dance communications as directed arcs, a time-varying graph can describe the dynamic interconnection topology of the inter-bee communications on the swarm cluster. The form of the graph is driven by where bees dance on the cluster and which bees happen to be present and observing this dancing. If another graph is used to represent the union of all communications until the agreement time, there would be arcs clustered around bees that discovered relatively high quality sites and arcs pointing from the bee that first discovered each site on a path (of recruits that recruited others) to the last bee recruited for that site. Hence, although it is not a fixed network of communicating units, as is often the case for neural networks, the interconnection topology for bee cognition units has a structure with predictable properties.

Group memory

The group of bees committed to nest site j is a population of units [analogous to a population of neurons (Kandel et al. 2000)] that can accumulate quality evidence for the site. The *set* of such groups for each discovered site serves as a short-term group memory for the swarm. The group memory is an *internal model* of the pattern of nest-site qualities currently in the swarm's field of view [analogous to a neural image (Kandel et al. 2000)]. The group memory is spatially distributed across the cluster and the candidate sites with the distribution defined by the current locations of the committed scouts for each site j:

1. *Group memory at the cluster:* Group memory on the cluster can be decoded from the cluster surface, where dances are performed. For each dancing bee, the value of (d_j, ϕ_j) can be found. Then, the populations of dancing bees can be identified for each nest site j. The dancing on the cluster for any time step $k < T_a$ is a representation of the cluster's current *estimate* of the nest-site quality landscape. Mathematically, when $\sum_j \sum_i L^{ij}(k) > 0$,

$$\frac{\sum_i L^{ij}(k)}{\sum_j \sum_i L^{ij}(k)}$$

   is the relative total number of waggle runs for site j at time step k, the cluster's internal model of $N^j / \sum_j N^j$ at time step k. If a site has not been found, it will not be in the representation. The representation becomes more accurate as more bees visit the site (averaging over numerous bees filters the noise due to individual assessment errors).
2. *Group memory at the candidate sites:* The component of group memory distributed across the sites is composed of the number of bees at each candidate site $B(j,k)$. We call $B(j,k)$ the current "swarm preference" level for each nest site j. When swarm preference for site j reaches the quorum threshold, site j is chosen.

For examples of the time evolution of the cluster's internal model estimate and of the swarm's preference levels, see Passino and Seeley (2006), or for corresponding experimental data, see Seeley et al. (2006).

The swarm's distributed group memory is distinct from the internal neural-based memory of each individual bee. What is known by the swarm is actually *far more* than the sum of what is known by the individual bees, as the swarm's knowledge includes the information stored in the bees' brains *and the information coded in the locations of the bees and their actions.* No bee can know all the locations and activities for all other bees. But this information is coded at the swarm level and, as discussed below, is explicitly used in swarm decision making.

Layered early/late processing at the cluster and nest sites

Group memory is formed in the first (early) layer and sampled and processed in the second (late) layer. Individual bees can sense group memory variables, but with noise, and this provides for layered processing of information via parallel and converging paths as found in neural systems (Kandel et al. 2000; Gazzaniga et al. 1998). There are three forms of sampling of group memory variables:

1. *Allocation to exploration vs. recruitment:* By sensing delays in finding dancers, uncommitted bees can estimate the total number of dancing bees, i.e., a current group memory value. They can use such a value to make decisions about whether to explore or get recruited. The individual decisions can be error prone (e.g., by being unlucky and not seeing any dancers, although there are many), but on average, the *group* of bees that uses this cue (the uncommitted scouts) can make a correct decision. Indeed, as the sizes of groups of committed scouts increase, as is the case for relatively high quality sites, the variance on the groups' sample will *decrease*. Hence, group memory is, in a sense, more accurate for better sites.
2. *Proportionate recruitment:* Although uncommitted scout bees cannot measure the sizes of the different groups dancing for the candidate sites, they can be influenced directly by these values in which they are proportionally recruited according to the proportion of dancing for each site. Hence, cluster-based group memory is used by the swarm to allocate the cognition units among sites. Again, the key is that whereas the individual bee cannot estimate the

proportions of bees dancing for each site, the group of observers effectively does so.

3. *Candidate-site bee assembly:* At each site, the assembly of bees provides a group memory of the number of bees that have assessed (or is assessing) its quality. Via the concurrent and *self-referential* process of quorum sensing, the bees take actions based on this group-level memory, ones that determine when the decision-making process is terminated.

Thus, there is a layering of information processing in the swarm. Bees play roles in the early processing where the information about site quality is acquired and reported. They also have roles in late processing where the overall level of dance activity, the distribution of committed bees among sites, and the numbers of bees assembled at the sites are all used.

Functional relationships to perception, choice, and attention

Several key functionalities of individual cognition—perception, choice, and attention processes (Gazzaniga et al. 1998)—are also found in swarm cognition. Closely analogous to lateral inhibition (Kandel et al. 2000) in neural-based perception and choice systems is what we call cross-inhibition: inhibitory coupling between groups committed to different sites due to the finite size of the pool of potential recruits and sites winning recruits automatically inhibiting other sites from getting recruits. The strength of cross-inhibition is driven by the differences in relative site qualities as relatively high quality sites get more recruits. The result is a type of two-point discrimination process (Kandel et al. 2000) that amplifies site quality differences and allows the swarm to distinguish between sites of similar quality. There is a process of feature detection (Kandel et al. 2000) that occurs in what can be viewed as the later processing by the swarm. The feature that is detected in this late processing is the best of the discovered sites. There is a type of winner-take-all process that emerges via the quorum threshold achievement, agreement, and lift-off, and it is analogous to ones in neural systems (Gazzaniga et al. 1998).

With respect to attention, group memory sets the relative level of attention paid to site j at time step k. More attention will be paid to higher quality sites when they are found. Cross-inhibition between site variables couples focusing dynamics between sites and so concentrates attention on superior sites. Distractor nest sites will enter into a swarm's field of view, but they will be purged from the swarm's attention by low quality assessments and quick dance decay. There is a coupling between early and late attentional processes where, via recruitment, swarm resources are focused on the more interesting (higher quality) points in the spatial field of view of the swarm. Distractors attract some of a swarm's attention and hence can degrade the focusing of attention on the best site. Focusing dynamics are also slowed by a cluttered field of close-quality sites.

Simulation: group memory quality and impact on choice performance

We used 1,000 simulation runs where sites 1–6 have qualities of 0.5, 0.6, 0.7, 0.8, 0.9, and 1, respectively ("case 2" in Passino and Seeley 2006). This is a representative, yet challenging, landscape of site qualities because the sites of low quality will distract the swarm and the sites of high quality will be difficult to choose between.

Consider the top-right plot in Fig. 2. This shows that group memory, as measured by the relative mean total amount of dancing for site j (cluster-portion, white bars) and relative mean of the maximum number of bees visiting site j (site portion, light gray bars), is skewed in comparison with the relative site quality (black bars). The skewing is seen as you scan from site 1 (low quality) to site 6 (high quality), where the white and light gray bars increase more than relative site quality. The swarm's group memory (both at the cluster and at the sites) views low quality sites (e.g., see site 1) as worse than they are. The swarm's group memory views high quality sites (e.g., site 6) as better than they are. The swarm's group memory is used to make choices. The skew indicates that a swarm forms a useful memory for the task at hand; the skew helps the swarm discriminate between sites and favor the choice of a good site. Indeed, the choice distribution (dark gray bars) is strongly skewed in favor of the high quality sites in comparison with the relative site quality distribution (black bars). This shows that, on average, the swarm develops a useful group memory of the quality landscape.

Next, consider the top- and bottom-left plots. The probability distribution of T_a shows that it never decides too fast or too slow (all decisions were made in less than 16 h; there were zero no-decision failures). The distribution is "heavy tailed," which means that long agreement times are not highly unlikely. Early decisions occurred when there was a quick discovery of a great site and few or no other discoveries of good sites, so that a maximum level of positive feedback was achieved and the quorum was reached quickly. Longer T_a times result from slow discoveries and long delib-

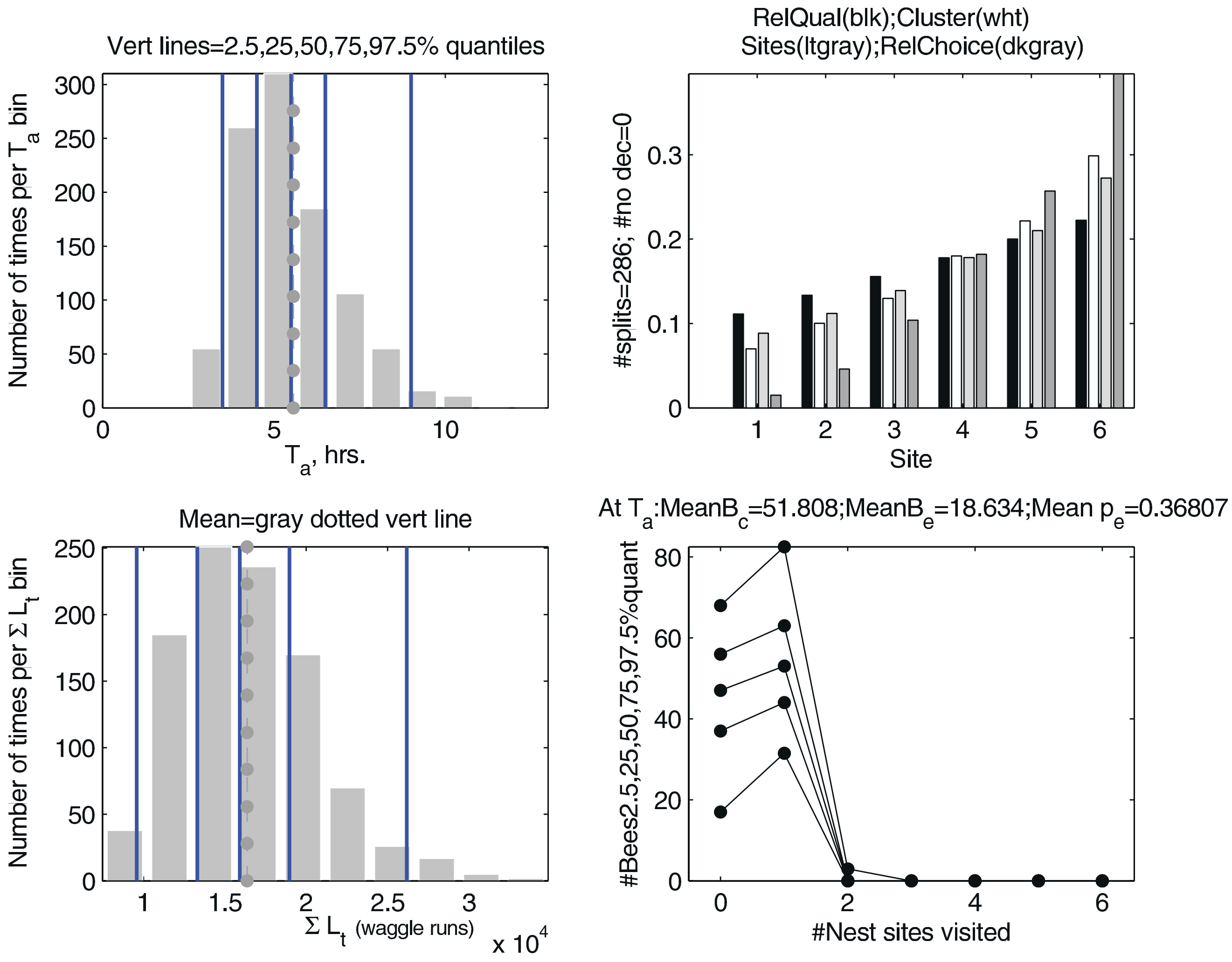

Fig. 2 Simulation results, group memory. *Top-left*: Number of times terminated on or before T_a with the *vertical lines* indicating the quantiles (e.g., 2.5% of the cases terminated with a T_a less than the *leftmost vertical bar*) and the *gray-dotted line* indicating the mean. *Bottom-left*: Similar to *top-left*, but number of times terminated at T_a with $\sum L_t$. *Top-right*: *horizontal* is site number (j), *vertical*: *black* (relative site quality, $N^j/\sum_j N^j$); *white* (relative mean total amount of dancing for site j, $E[\sum_k \sum_i L^{ij}(k)]/(\sum_j E[\sum_k \sum_i L^{ij}(k)])$); *light gray* (relative mean maximum number of bees visiting site j, $E[\max_k B(j,k)]/(\sum_j E[\max_k B(j,k)])$); *dark gray* (proportion times chosen). *Bottom-right* Quantile plot of number of bees that dance for zero, one, two, etc. sites (e.g., 2.5% of the cases terminated with fewer than 18 bees visiting no sites)

eration times in trying to discriminate between sites. The distribution for $\sum L_t$, total waggle runs, has similar characteristics and is also somewhat heavy tailed. Finally, the bottom-right plot shows that almost no bees dance for two or more sites, which shows that a swarm's choice depends little on bees switching from dancing for one site to another. Hence, the comparison process is a group-level, not an individual-level, phenomenon.

Swarm choice tests

Viewing the swarm as a cognitive unit, in this section, we evaluate its choice performance by means of the model of swarm decision making in Passino and Seeley (2006). We consider choice performance of swarms for several landscapes of nest-site quality. For each landscape, we use 100 nest-site selection processes that terminate with a single site chosen.

Discrimination

To test discrimination, let all sites have zero quality, except sites 5 and 6, which both start out at a quality of $N^6 = N^5 = 0.75$ and differentially move to 0.5 and 1. The results are shown in Fig. 3. Before interpreting the results, note that, except for the horizontal axes, the

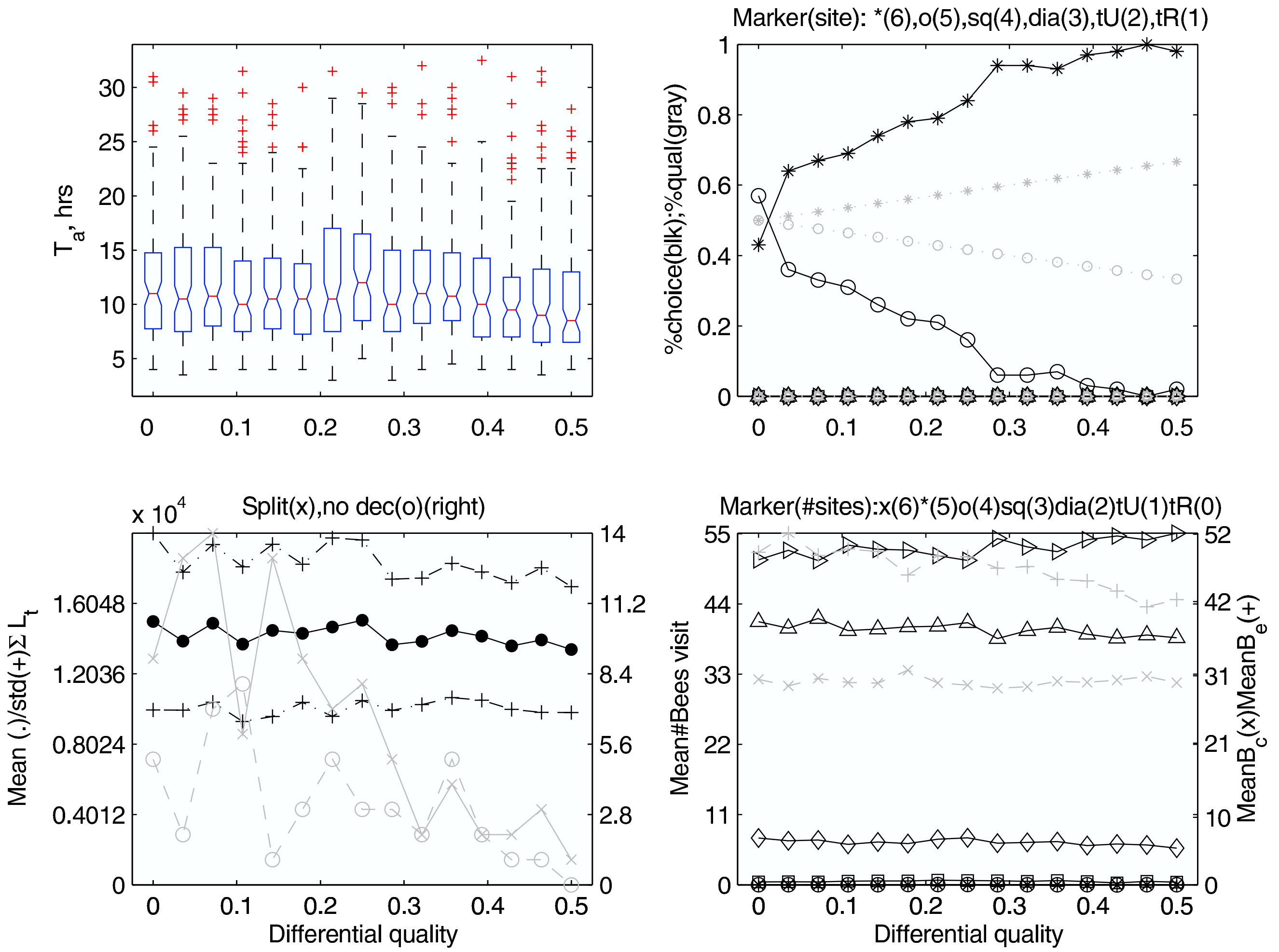

Fig. 3 Discrimination effect, linear differential quality. *Top-left*: *middle line in each box* is the median value of T_a; *boxes with notches that do not overlap* have medians of their data that differ at the 5% significance level, *whiskers (dashed lines)* represent 1.5 times the interquartile range, and outliers are designated with a *plus sign*. *Top-right*: percentage of times each nest site is chosen (*black lines*), with site 1 designated by *triangle right*("tR" represents "triangle right", a right-pointing triangle), site 2 by a *triangle* ("tU" represents "triangle up"), site 3 by a *diamond* ("dia"), site 4 by a *square* ("sq"), site 5 by *circle*, and site 6 by an *asterisk*. The *gray lines with markers* show the relative site qualities, $N^j/\sum_j N^j$. *Bottom-left*: *left-vertical axis and the black lines* show the mean $\sum L_t$ (*solid line*, *dots*), and its standard deviation (*dash-dot line*, *plus marker*), whereas *gray lines and right-vertical axis* show the number of split decision (*multiplication symbol*) and no-decision (*circle*) cases that occur for the 100 nest site selection processes that terminate with a single choice. *Bottom-right*: *left-vertical axis and the black lines* show the mean number of bees out of the 100 total that visit 0 sites (designated with *triangle right*), 1 site (*triangle*), 2 sites (*diamond*), 3 sites (*box*), 4 sites (*circle*), 5 sites (*asterisk*), and 6 sites (*multiplication symbol*), and *right-vertical axis* shows via the *gray lines* the mean number B_c of committed scouts (*multiplication symbol*) and mean number of explorers B_e (*plus sign*) at the agreement time T_a

labeling of all plots in the remainder of this paper is the same.

To interpret the results in Fig. 3, note that, ideally, once the two sites have different qualities, the swarm should always choose the best one. However, the results show that many errors are committed by the swarm, especially for low values of differential quality. The swarm can, however, amplify the quality difference (at a rate of increase higher than that of the relative quality of the two sites) and often makes the correct choice, with choice performance improving markedly as the differential quality increases. The slopes of the curves in the top-right plot are positively correlated with the level of discrimination ability. When the differential site quality is close to zero, the swarm "generalizes" and treats the two sites as having the same quality. Note that there is a uniformly distributed noise in individual bee quality assessments on $(-0.1, 0.1)$; nevertheless, the swarm can often discriminate (due to filtering with multiple bee assessments) between two sites that differ in quality by less than 0.1. There is little change in the median T_a or mean $\sum L_t$ as the differential quality increases. However, for low values of differential quality, there are many split decisions because of a similar build-up of bees at both sites due to their close levels of quality. The number of no-decision cases is higher for lower differential quality because, in this situation, there is no obvious superior site for the swarm to pick. Around half the bees visit no sites; these bees explore or rest. Of the bees that do visit sites, most visit only one. For this case, only a mean number of about six bees visit two sites. This illustrates that there is, at most, a weak coupling between sites by means of scouts quitting one site and then reentering the decision-making process via recruitment to a different site. The mean number of bees that are committed to sites and explore is relatively independent of differential quality.

Distraction avoidance

To examine distraction avoidance, let $N^6 = 1$, $N^1 = 0$, a distractor quality variable $D = N^5 = N^4 = N^3 = N^2$, and consider $D \in [0, 1]$. See Fig. 4. The key result is that the swarm is very effective at evaluating then discarding from consideration distractors so long as they are of a quality $D < 0.4$, as for this range, the swarm always makes the correct choice. As the distractor quality D gets closer to 1, more errors are made. The percentage of correct choices quickly decreases for $D > 0.55$ so that, by about $D = 0.8$, the percentage of times the swarm picks the best site is close to that for the distractors, although the best site is markedly better. The median value of T_a decreases significantly indicating that the errors are made fast, yet the value of the mean of $\sum L_t$ increases as the swarm tries to discriminate between many distractors and the best site and this requires many dancers. When the distractor quality is high, there are many split decisions. In addition, the coupling in the process decreases, which is why the bees lock in on incorrect decisions. The bees are busy discriminating between sites, but this reduces the coupling and so depresses the number of correct decisions.

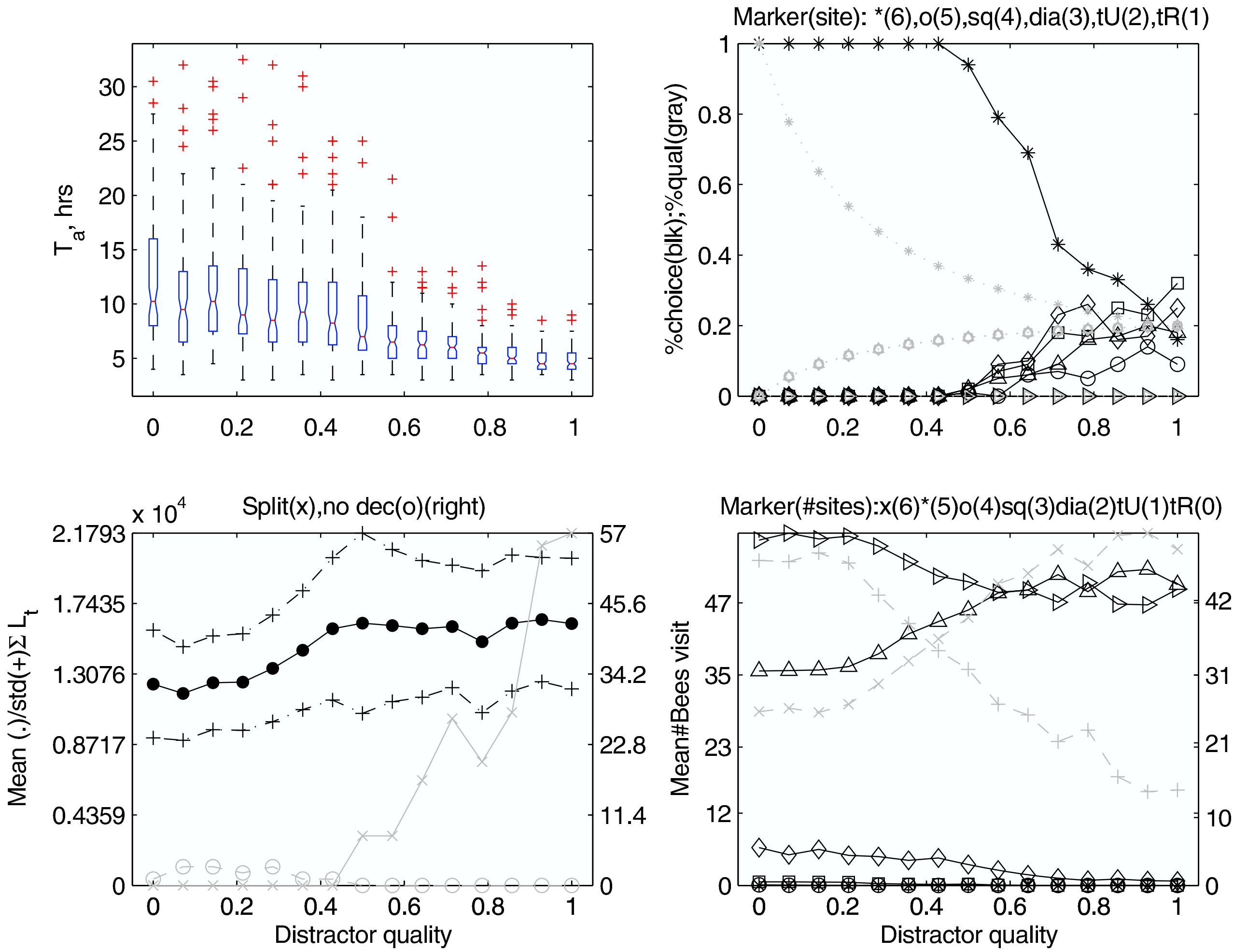

Fig. 4 Distractor effect, four distractors (see Fig. 3 caption for axes explanation)

Indeed, the number of explorers decreases significantly for high distractor quality, as bees quickly find and recruit to all the sites and this leads to a reduction in cross-inhibition between site variables so that there is no clear winner.

Discussion

This paper presents evidence that the insect-based swarms of honey bees have a cognition process that shares several features with the neuron-based brains of vertebrates, both at the level of the neuron/insect and at the level of the brain/swarm.

Relations to neuroscience and psychology

We have noted numerous similarities between swarms and brains in their functional organization for information processing. This entailed showing how key concepts in neuroscience (Kandel et al. 2000; Gazzaniga et al. 1998) are relevant to understanding swarm cognition. These concepts include: early sensory processing (field of view), neurons (bees), activation thresholds (dance thresholds), action potentials (dances), neuron populations (groups of dancing bees), neural network structure and communications (bee-to-bee communications on a random topology), neural image and short-term memory (spatially distributed internal model, group memory), lateral inhibition (cross inhibition), late processing based on memory (go explore/get recruited allocation, proportional allocation of recruits, and quorum sensing), and parallel and converging paths (simultaneous assessment of multiple sites, yet late processing for agreement on the best-of-N). Perhaps most importantly, the study of group memory and choice performance showed that a swarm's group memory on average provides the swarm with a representation of the relative nest-site qualities under consideration that enhances its choice performance. Recognizing these analogies between brains and swarms prompted us to relate swarm cognition to well-studied attention–perception–choice tasks from cognitive neuroscience (Gazzaniga et al. 1998). We noted a surprising similarity in swarms to attentional systems in brains, in which a swarm is able to eliminate distractors from consideration and so focus on the best sites. Similarly, for perception–choice tasks, we noted how a swarm considers its field of view, develops a representation of its problem domain, and then uses that to choose.

The two choice-performance tests we administered with simulated swarms borrowed from ideas in neuroscience and psychology (Gazzaniga et al. 1998; Ratcliff 1978; Roe et al. 2001). First, we performed discrimination tests. We showed that despite significant assessment noise by individual bees, swarms can effectively discriminate between close quality sites. Next, we studied the impact of distractor sites. We showed that swarms can effectively eliminate from consideration multiple distractors provided that their quality is relatively low. However, when distractors are of higher quality, swarms make fast but erroneous choices. It is as if the best site becomes "hidden" by the set of distractors.

Diffusion, accumulator, and other models of reaction-time tests of animals choosing among alternatives (Ratcliff 1978; Luce 1986; Ratcliff et al. 1999; Usher and McClelland 2001; Ratcliff and Smith 2004; Roe et al. 2001; Busemeyer and Townsend 1993; Smith 2000) have a number of similarities to our model of swarms choosing among candidate nest sites (Passino and Seeley 2006). For instance, they all have representations of the time evolution of preference formation based on the probabilistic arrival of evidence regarding multiple alternatives. In addition, in all of them, there is internal coupling between the dynamical formation of the preferences and a preference threshold that triggers choice. Moreover, a range of speed–accuracy trade-offs have been discovered in all these models. In spite of these broad similarities, direct use of these models to represent the nest-site selection process appears inappropriate because: (1) unique nonlinearities exist in the swarm (e.g., due to dance decay and explorer allocation); (2) swarm cognition is a distributed process that leads to a significantly different "information structure" (i.e., when and how variables interact with each other); (3) cross-inhibition is present in the swarm both via dance competition and via the *indirect* path of dance decay and reentry of bees to the recruitment process; and (4) there are (spatially distributed) positive feedback paths in the swarm that *couple* the process of evidence accumulation on the cluster with preference dynamics at the candidate sites (e.g., as the preference for one site increases, the swarm accumulates more evidence on that site by dispatching more assessors).

Recent work from the diffusion model literature, however, does resonate with our approach. Smith and Ratcliff (2004) describe their initiatives to use the diffusion models from psychology to model *neuron-level activity* in a reaction test for monkeys. This innovative work shows that the well-studied behavioral-level diffusion models can actually model the system at the level of neurons. Their descriptions of the dynamics of the neural firing patterns underlying decision making in monkeys are strikingly similar to our description of the dynamics of the bee scouting patterns underlying decision making in swarms Passino and Seeley (2006). The model in Passino and Seeley (2006), however, essentially starts not with the behavior of swarms, but at the "neural-level," the level of individual scout bees. This is possible due the special feature that one can observe how the constituent subunits of a swarm function while the whole swarm is performing a decision-making task. This paper expands on the work in Passino and Seeley (2006) by identifying key features of swarm cognition and adding an assessment of swarm choice performance. Therefore, while we have proceeded in the bottom-up direction and the work in Smith and Ratcliff (2004) rests on a top-down method, we have met in the middle with models of reaction time tests. It will be important to determine if the insights gained from studying decision making in swarms could give useful hints for studying the neural circuit structures and dynamics underlying decision making in brains.

Implications for other species?

It seems likely that elements of the functional organization of swarm cognition in honey bees can be identified in other group living species, including humans. For instance, ant colonies performing nest-site selection (Marshall et al. 2006; Mallon et al. 2001; Pratt et al. 2002, 2005; Franks et al. 2002, 2003; Pratt 2005; Pratt and Sumpter 2006) use quorum sensing in a way similar to honey bees. Hence, the number of tandem runs and quorum levels for these ants may also represent forms of group memory. Similarly, consensus decision making in other species (Conradt and Roper 2005) is likely to involve group memory in the information processing by the group. In honey bees, the physical elements of group memory are built from the *biotic* environment (groups of bees performing activities at various locations). In other species or decision-making processes, however, the *abiotic* environment could also be exploited for building group memory. For instance, it is plausible to view the network of pheromone trails laid by an ant colony's foragers as a type of abiotic group memory. Trails are built in a distributed fashion by individuals and are used to guide foraging activities of the entire group [selecting the richest food sources, choosing the shortest foraging trails, etc. (Jackson and Ratnieks 2006; Camazine et al. 2001)].

With respect to human group decision making, Kerr and Tindale (2004) have stressed the need to better understand how information is dynamically shared and processed in groups. To address this challenge, we suggest that experiments be designed in which human groups perform a time-constrained choice task, one that perhaps also involves searching for the alternatives to be considered. Then, data representing the time histories of individual decision making and individual-to-individual communications should be gathered with the aim of summarizing the group's cognition in a mathematical model [unlike in Kerr 1982; Abelson 1964 and perhaps via extending the models in Ratcliff 1978; Usher and McClelland 2001; or Roe et al. 2001]. Simulations can then be used to evaluate the group's choice dynamics, performance levels, and speed–accuracy trade-offs. This could lead to the identification of key features of the cognition mechanisms of human groups (e.g., group memory). Such discoveries could significantly deepen our understanding of human collective intelligence and enable us to more effectively structure groups to enhance their performance in business, economics, law, and politics (Steiner 1966; Laughlin and Ellis 1986; Laughlin 1999; Kerr and Tindale 2004; Hastie and Kameda 2005; Surowiecki 2004).

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