JOURNAL OF THE ROYAL SOCIETY Interface

On optimal decision-making in brains and social insect colonies

James A.R Marshall, Rafal Bogacz, Anna Dornhaus, Robert Planqué, Tim Kovacs and Nigel R Franks

Supplementary data	"Data Supplement" http://rsif.royalsocietypublishing.org/content/suppl/2009/02/20/rsif.2008.0511.DC1.html
References	This article cites 61 articles, 7 of which can be accessed free http://rsif.royalsocietypublishing.org/content/early/2009/02/22/rsif.2008.0511.full.html#ref-list-1
P<P	Published online 25 February 2009 in advance of the print journal.
Subject collections	Articles on similar topics can be found in the following collections biocomplexity (6 articles) biomathematics (39 articles) computational biology (33 articles)
Email alerting service	Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click **here**

To subscribe to *J. R. Soc. Interface* go to: **http://rsif.royalsocietypublishing.org/subscriptions**

On optimal decision-making in brains and social insect colonies

James A. R. Marshall[1],*, **Rafal Bogacz[1]**, **Anna Dornhaus[2]**, **Robert Planqué[3]**,
Tim Kovacs[1] and Nigel R. Franks[4]

[1]*Department of Computer Science, University of Bristol, Woodland Road,
Bristol BS8 1UB, UK*
[2]*Department of Ecology and Evolutionary Biology, University of Arizona,
PO Box 210088, Tucson, AZ 85721, USA*
[3]*Department of Mathematics, VU University Amsterdam, De Boelelaan 1081a,
1081 HV Amsterdam, The Netherlands*
[4]*School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK*

The problem of how to compromise between speed and accuracy in decision-making faces organisms at many levels of biological complexity. Striking parallels are evident between decision-making in primate brains and collective decision-making in social insect colonies: in both systems, separate populations accumulate evidence for alternative choices; when one population reaches a threshold, a decision is made for the corresponding alternative, and this threshold may be varied to compromise between the speed and the accuracy of decision-making. In primate decision-making, simple models of these processes have been shown, under certain parametrizations, to implement the statistically optimal procedure that minimizes decision time for any given error rate. In this paper, we adapt these same analysis techniques and apply them to new models of collective decision-making in social insect colonies. We show that social insect colonies may also be able to achieve statistically optimal collective decision-making in a very similar way to primate brains, via direct competition between evidence-accumulating populations. This optimality result makes testable predictions for how collective decision-making in social insects should be organized. Our approach also represents the first attempt to identify a common theoretical framework for the study of decision-making in diverse biological systems.

**Keywords: decision-making; diffusion model; optimality; neurons; social insects;
sequential probability ratio test**

1. INTRODUCTION

Animals constantly make decisions. Habitat selection, mate selection and foraging require investigation of, and choice between, alternatives that may determine an animal's reproductive success. For example, many animals invest considerable time and energy in finding a safe home (Hazlett 1981; Seeley 1982; Hansell 1984; Franks *et al.* 2002). Similarly, an animal may frequently have to deal with ambiguous sensory information in deciding whether a predator is present or not (Trimmer *et al.* 2008).

There has been ongoing speculation as to whether decision-making mechanisms in brains and in colonies of social insects might be closely related to each other, beginning at least with Hofstadter (1979) and generating continued interest (Seeley & Buhrman 2001; Visscher 2007; Passino *et al.* 2008). In this paper, we examine a model of decision-making in the primate

brain (Usher & McClelland 2001) and compare it with three new models of collective decision-making during house-hunting by social insect colonies. These models are based on a proposed model for emigration in the rock ant *Temnothorax albipennis* (Pratt *et al.* 2002), and two models proposed for nest-site selection in the honeybee *Apis mellifera* (Britton *et al.* 2002). The similarities are striking: both systems are modelled with mutually interacting populations; in both systems, a decision is made when one population exceeds some threshold; and in both systems, this threshold can be varied to mediate between the speed and the accuracy of the decision-making process. As well as examining the structural similarities and differences between the neuron model and social insect models, we examine optimality criteria for decision-making in the social insect models. Bogacz *et al.* (2006) showed how the model of decision-making in the brain proposed by Usher & McClelland (2001) can be parametrized to implement the statistically optimal strategy for choosing between two alternatives. Here, we analyse to what extent each of the social insect models can implement or

*Author for correspondence (James.Marshall@bristol.ac.uk).

approximate this statistically optimal strategy. This gives testable predictions for how social insects should behave when house-hunting in order to optimize their decision-making. The analysis we present represents the first step in establishing a common theoretical framework for the study of decision-making in biological systems, i.e. based on the interactions between their components rather than the details of the components themselves. Hence, this framework should prove applicable to diverse biological systems at many levels of biological complexity.

2. OPTIMAL DECISION-MAKING

Decision-making is a process in which uncertain information must be processed in order to make a choice between two or more alternatives. We can illustrate decision-making with a simple perceptual choice task, in which a primate subject is presented with a display filled with moving dots. The subject is required to decide whether the majority of dots move to the left or the right and to make an eye movement in the same direction. The proportion of the displayed dots that move in a coherent direction can be varied to make the decision task easier or harder, and the rewards for correct choices can be modified to vary the optimal compromise between the speed and the accuracy of the decision.

The above description is just one example of a decision-making problem, but diverse organisms face a wide variety of decision problems exhibiting the key features of variable difficulty, and a dynamic tension between the speed and the accuracy of the decision-making process (Edwards 1965; Chittka *et al.* 2003). Based on the analysis of human reaction-time distributions in decision tasks, psychologists proposed the 'diffusion model' of decision-making (Stone 1960; Ratcliff 1978), which represents the process abstractly as Brownian motion on a line representing relative evidence for the two alternatives, with constant drift towards the correct hypothesis (figure 1).

The diffusion model of decision-making is, in fact, a special case of the more general sequential probability ratio test (SPRT).[1] The SPRT provably achieves optimal decision-making over two alternatives (Wald & Wolfowitz 1948), as it makes use of the Neyman–Pearson (1933) lemma familiar to statisticians and scientists. The SPRT works by continuing to gather evidence for the two alternative hypotheses until the log of their likelihood ratio exceeds a positive or negative threshold; this is the test that, among all possible tests, minimizes decision time for any desired decision error rate. Through an adjustment of this threshold, the test can achieve the optimal trade-off between decision accuracy and decision speed.

The diffusion model of decision-making has recently been shown to fit reaction-time data better than the models that do not implement statistically optimal decision-making (Ratcliff & Smith 2004). Moreover,

[1]This special case is obtained when information gain over time becomes continuous: the standard SPRT works with discrete evidence samples.
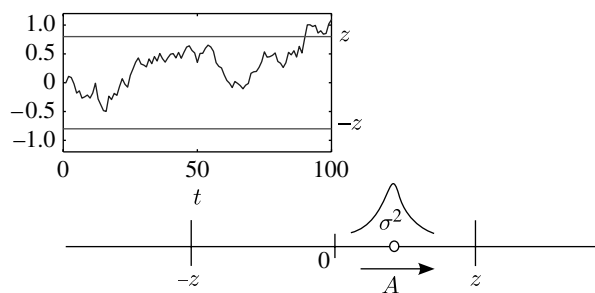

Figure 1. The diffusion model of decision-making can be thought of as a random walk with normally distributed step size (Wiener process or Brownian motion) along a line where the positive direction corresponds to increasing evidence for one of the available alternatives, and the negative direction to increasing evidence for the other alternative. The random walk is subject to a constant drift A, a tendency to move along the line towards the better alternative, whose strength is the difference between the expectations of the incoming data on the available alternatives. The variance in the random walk (proportional to σ^2) represents the uncertainty in these incoming data. The diffusion model of decision-making implements the statistically optimal sequential probability ratio test, and by varying the decision threshold z can compromise between speed and accuracy of decision-making. *Inset.* A sample trace of the diffusion model: at time $t=0$ when decision-making starts, there is no evidence in favour of either alternative. As time passes evidence accumulated so far varies stochastically, but consistently tends to increase in favour of one of the two alternatives. At approximately time $t=90$, the positive decision threshold is reached and the corresponding alternative is chosen.

neural recordings from cortical regions in monkeys undertaking the moving-dots decision task are better described by the diffusion model than by other, non-optimal models (Ratcliff *et al.* 2003). This suggests that neural decision networks can be parametrized in a way that allows optimal decision-making, as we shall discuss in §§3 and 4.

3. DECISION-MAKING IN THE CORTEX

The neural bases of decision-making are typically studied in the context of the moving-dots experiment described in §2. Neuronal activity recordings from single cells in the monkey cortex suggest that decision-making during this task involves two main brain areas.

First, the neurons in the medial temporal (MT) area process the motion present in the visual field. Each of the MT neurons responds proportionally to the magnitude of motion in a particular direction (Britten *et al.* 1993). Hence, the neurons in the MT area that are selective for motion in different directions provide sensory evidence supporting the corresponding alternatives. However, this sensory evidence is uncertain owing to the noise present in the stimulus and the neural representation itself.

Second, the neurons in the lateral intraparietal (LIP) area and the frontal eye field are concerned with controlling eye movement. These neurons are selective for the direction of eye movement. During the motion discrimination task, it has been observed that the neurons corresponding to the correct alternative

gradually increase their firing rate (Schall 2001; Shadlen & Newsome 2001; Roitman & Shadlen 2002). Detailed studies of their activity provide strong evidence that the LIP neurons integrate input from the corresponding MT neurons over time (Huk & Shadlen 2005; Hanks *et al.* 2006). Hence, as time progresses in the task, the sensory evidence accumulated in the LIP neurons becomes more and more accurate.

It has been observed that when the activity of the LIP neurons exceeds a certain threshold, the decision is made and an eye movement in the corresponding direction is initiated (Schall 2001; Shadlen & Newsome 2001; Roitman & Shadlen 2002). This arrangement of neural populations with decision thresholds lends itself to representation through a simple model, as described in §4.

4. THE USHER–McCLELLAND MODEL

The Usher–McClelland model represents decision-making using neural populations that act as mutually inhibitory, leaky integrators of incoming evidence (figure 2). In the moving-dots decision task described above, these integrator populations would represent the LIP neural populations corresponding to the different possible eye movement decisions. Each population of integrator neurons receives a noisy input signal that it integrates, subject to some constant loss. Each population also inhibits the activation of the other to a degree proportional to its own activation. So, as one population becomes highly activated, the suppression it exerts on the activation of the other grows stronger. For a binary choice, the linearized version of the system is formally described as a pair of coupled stochastic ordinary differential equations

$$\begin{cases} \dot{y}_1 = I_1 + c\eta_1 - y_1 k - y_2 w, \\ \dot{y}_2 = I_2 + c\eta_2 - y_2 k - y_1 w, \end{cases} \tag{4.1}$$

where y_i is the activity of population i; $\dot{y}_1$ is the change in that activity over time; I_i is the strength of the input signal for alternative i; $c\eta_i$ is the noise in that input signal described as a Wiener process with mean zero and standard deviation proportional to c; w is the rate at which one population inhibits the activation of the other; and k is the rate at which a population's activation level decays. The decision is made by the model if the activity of either of the populations reaches a threshold value.

Choosing different coordinates, $x_1 = (y_1 - y_2)/\sqrt{2}$ and $x_2 = (y_1 + y_2)/\sqrt{2}$, the model can be decoupled into two independent random processes

$$\begin{cases} \dot{x}_1 = (w - k)x_1 + \dfrac{I_1 - I_2}{\sqrt{2}} + c\eta_{1'}, \\ \dot{x}_2 = (-k - w)x_2 + \dfrac{I_1 + I_2}{\sqrt{2}} + c\eta_{2'}, \end{cases} \tag{4.2}$$

where $\eta_{1'} = (c\eta_1 - c\eta_2)/\sqrt{2}$, and similarly for $c\eta_{2'}$. If $w = k$, then x_1 simply undergoes a biased random walk. Moreover, taking both these parameters to be large, x_2 quickly converges to a limiting value (figure 3).
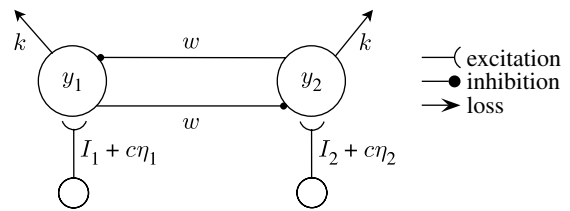

Figure 2. In the Usher–McClelland model of decision-making in the primate visual cortex, neural populations represent accumulated evidence for each of the alternatives. These populations y_1 and y_2 integrate noisy inputs I_1 and I_2, but leak accumulated evidence at rate k. Each population also inhibits the other in proportion to its own activation level, at rate w. When $w = k$ and both are large, the Usher–McClelland model reduces to the diffusion model of decision-making (figure 3).
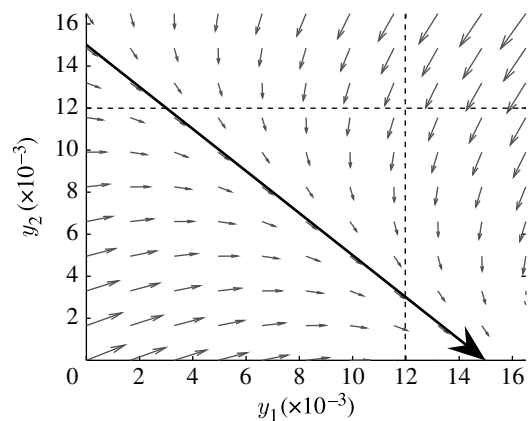

Figure 3. The expected dynamics of the Usher–McClelland model, plotted as the activation of population y_1 against the activation of population y_2. When decay equals inhibition ($w = k$), the system converges to a line (bold arrow) and diffuses along it, until a movable decision threshold is reached (dashed lines). Along the attracting line, the Usher–McClelland model is equivalent to the optimal diffusion model of decision-making (figure 1).

Since x_2 quickly converges, the decision is made when the difference between integrated evidence, x_1, exceeds a positive or negative threshold (Bogacz *et al.* 2006). This corresponds to the statistically optimal diffusion model of decision-making (figure 1). Thus, when $w = k$ and both of these parameters are relatively high, the Usher–McClelland model approximates optimal decision-making.

5. DECISION-MAKING IN SOCIAL INSECT COLONIES

The rock ant *T. albipennis* lives in colonies of up to a few hundred individuals, inhabiting small enclosed cavities such as rock crevices, which break down over time. Colonies of the honeybee *A. mellifera* are substantially larger, often comprising more than 50 000 workers nesting in large cavities in hollow trees. For both species, the need to hunt for a new nest site arises when the nest degrades or is destroyed, or when the colony propagates. To minimize exposure, colonies must minimize the duration of the emigration, while still gathering substantial information about potential nest sites. 'Scout' individuals leave the old

nest (or the bee swarm) to search for new suitable sites. When an individual has located a new site, this is thoroughly inspected according to multiple criteria (Mallon & Franks 2000; Franks *et al.* 2003*b*, 2005, 2006*b*, 2007*a*).

A unanimous decision among the discovered nest sites is required, and the highest quality site should be identified to maximize future success. To achieve all of this, both rock ants and honeybees use a process of quality-dependent recruitment to nest sites, causing positive feedback, coupled with quorum sensing, ultimately leading to a collective decision.

In *T. albipennis*, scouts recruit nest-mates to a site they have discovered by tandem running, teaching others the route (Möglich & Hölldobler 1974; Möglich 1978; Franks & Richardson 2006; Richardson *et al.* 2007). The recruiters pause for longer before recruiting to poor nests than they do for good nests (Mallon *et al.* 2001). Recruits inspect the new nest and also start recruiting, leading to a positive feedback, with more ants arriving faster at higher quality nest sites. When a certain number of ants, a quorum, have accumulated in the new site, all ants that are committed to it switch from tandem running to carrying nest-mates. This represents a switch to decision implementation, as brood items and passive ants are carried to the chosen nest site. The colony's collective decision for a new nest is thus usually for the site that first attracts the quorum number of ants. By adjusting this number, the ants opt for a quick but error-prone, or a slower but more accurate decision, depending on their group size and external conditions (Franks *et al.* 2003*a*; Dornhaus *et al.* 2004; Dornhaus & Franks 2006).

In *A. mellifera*, scouts similarly start recruiting to discovered nest sites, here using the honeybee waggle dance (Lindauer 1955; von Frisch 1967; Seeley 1982). The probability of performing waggle dances, as well as their duration, depends on the quality of the discovered site. Positive feedback thus arises only if recruits become recruiters, which happens only for superior sites (Seeley & Buhrman 1999, 2001). Eventually all recruitment is for a single site, which is then chosen by the honeybee swarm (Seeley 2003). Honeybees may also use a quorum at the new site to determine whether this decision has been made (Seeley & Visscher 2004*b*).

Both of these decision-making mechanisms operate without central control, and individuals use only local information (Mallon *et al.* 2001). Both species can select the best nest site even if news of it arrives late in the decision-making process (Britton *et al.* 2002; Franks *et al.* 2007*b*). However, there are some differences between the two collective decision-making systems. In the bees, the decision-making process is separated from the execution of the decision: the flight of the swarm to the new site occurs after the decision has been made, and is guided by a small number of informed individuals (Beekman *et al.* 2006; see also Couzin *et al.* 2005). In the ants, these processes are integrated, introducing a logistics problem into the decision problem (Planqué *et al.* 2007). Note that the decision problem solved by colonies during emigration is one of optimal consensus decision-making, and thus differs
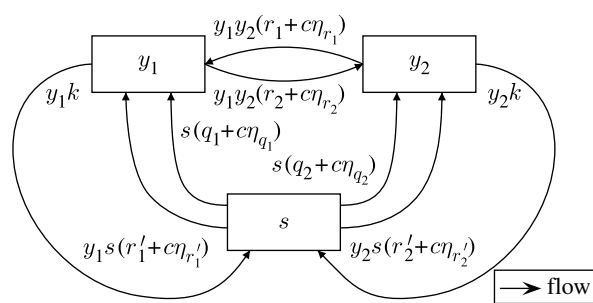

Figure 4. In the direct-switching model of decision-making during emigration by the honeybee *A. mellifera*, populations of scouts y_1 and y_2 discover two alternative potential sites and compete with each other to recruit uncommitted scouts s and scouts committed to the other alternative. If there is no decay from commitment ($k=0$), then once all scouts are committed to one alternative or the other subsequent decision-making is exactly equivalent to the statistically optimal diffusion model of decision-making (based on a model by Britton *et al.* (2002)).

from the problem of distributed resource intake maximization that colonies tackle during foraging (e.g. Seeley 1995).

6. MODELS OF HOUSE-HUNTING BY SOCIAL INSECT COLONIES

In this section and §7, we will examine how social insect colonies might implement optimal decision-making, through formal analysis and numerical simulations of mathematical models. We propose three new models based on one published model of house-hunting by *T. albipennis* (Pratt *et al.* 2002) and two published models of house-hunting by *A. mellifera* (Britton *et al.* 2002). Our aim is to examine which model or models can implement optimal decision-making, and use this to generate testable hypotheses about how social insects should behave if they are to decide optimally.

To understand how collective decision-making may be optimized in situations characterized by uncertainty, our models are stochastic differential equations, as in the neural case. This departs from previous modelling efforts using deterministic differential equations (Britton *et al.* 2002; Pratt *et al.* 2002), population matrix models (Myerscough 2003) or individual-based models (Pratt *et al.* 2005; Marshall *et al.* 2006). All the models represent flows between populations of individuals having different behavioural states. The structure of all of these models is very similar, and one such model is presented by way of illustration in figure 4; the models differ however in the details of the rates at which individuals flow between these populations.

6.1. House-hunting in *T. albipennis*

We begin with the model of emigration by *T. albipennis* (Pratt *et al.* 2002). The full model considers the complete emigration process both before and after the quorum threshold is satisfied at a potential site: thus the model includes both tandem-running behaviour and carrying. In accordance with current biological understanding, we model only the decision-making process up to quorum satisfaction, considering that after this

point a collective decision has been made and all that remains is its implementation (Pratt *et al.* 2002). This view is not without its problems (Franks *et al.* 2007*b*; Planqué *et al.* 2007), but is an acceptable simplification for our purposes. We further simplify the original model by removing the intermediate class of assessor ants: ants thus switch directly from uncommitted to committed.

Our simplified version of the Pratt *et al.* (2002) model thus considers only ants discovering nest sites and recruiting to them through tandem running. Ants leave the class of uncommitted scouting ants s, discover and become recruiters y_i for nest site i at rate q_i: this rate is proportional to the nest site's quality and ease of discovery, and is subject to noise $c\eta_{qi}$. Recruiters for a site recruit uncommitted scouts in class s at noisy, quality-dependent rate $r_i'(s)$ where

$$r_i'(s) = \begin{cases} r_i' + c\eta_{r_i'}, & \text{if } s > 0, \\ 0, & \text{otherwise.} \end{cases} \quad (6.1)$$

Finally, recruiters for a site spontaneously switch to recruiting for the other site at rate r_i, or switch to being uncommitted to any site at rate k_i. These rates are subject to noise $c\eta_{ri}$ and $c\eta_{ki}$, respectively. In this model, as in the other stochastic models below, we consider only stochasticity in any process related to quality assessment of the available alternatives. This enables our analysis to concentrate on how this relevant noise is processed by the system. This strategy has already been used implicitly in the Usher–McClelland model: there decay and inhibition are modelled deterministically, yet corresponding neural processes in the real world will of course be noisy.

Thus the ants' decision-making process is described by the following equations:

$$\begin{cases} \dot{y}_1 = (n - y_1 - y_2)(q_1 + c\eta_{q1}) + y_1 r_1'(s) \\ \quad + y_2(r_2 + c\eta_{r2}) - y_1(r_1 + c\eta_{r1}) - y_1(k_1 + c\eta_{k1}), \\ \dot{y}_2 = (n - y_1 - y_2)(q_2 + c\eta_{q2}) + y_2 r_2'(s) + y_1(r_1 + c\eta_{r1}) \\ \quad - y_2(r_2 + c\eta_{r2}) - y_2(k_2 + c\eta_{k2}), \end{cases} \quad (6.2)$$

where as population size is constant $s = n - y_1 - y_2$, and hence the equation for $\dot{s}$ is redundant.

In the (x_1, x_2) variables, we seek to parametrize the model so that the random process $\dot{x}_1$ is independent of the random process $\dot{x}_2$, and is identical to the diffusion model of decision-making. It can easily be shown that this paramerization requires the decay parameters and switching rate parameters to be set according to the qualities of both the alternative nest sites under consideration (see the electronic supplementary material). In other words, optimal decision-making can only be achieved under this model if individuals have global knowledge about the alternatives available. Given our understanding of social insects' house-hunting mechanisms, we do not expect all committed individuals to have quantitative knowledge of the qualities of both alternatives. Hence, optimal parametrization of our model of house-hunting in *T. albipennis* seems biologically unrealistic.

6.2. House-hunting with indirect switching in **A.** mellifera

In this section and §6.3, we now consider two models of house-hunting in *A. mellifera* due to Britton *et al.* (2002). These models differ only in whether or not they allow scouts committed to one site to switch directly to commitment to the alternative site. First, we consider the case in which scouts cannot directly switch: that is, they can only change their commitment by first becoming completely uncommitted.

We adapt the model of Britton *et al.* (2002) so that, as in the Pratt *et al.* model, we have one population of uncommitted scouts, s, and two populations of recruiters, y_1 and y_2, for the two alternative sites under consideration. This is a simplification of the full Britton *et al.* model, in that we dispense with their populations of committed but inactive recruiters. We make a further small modification to the Britton *et al.* model by adding spontaneous discovery of alternative sites by uncommitted scouts at rates q_1 and q_2. We make these rates independent of site quality, to agree with the modelling approach of Britton *et al.* and with the current biological understanding of *A. mellifera* (Seeley 2003); however, they may vary according to how distant, or how hard to discover, a potential nest site is.

Using the same notation as in equations (6.2), our indirect-switching model of house-hunting by *A. mellifera* is described by the following equations:

$$\begin{cases} \dot{y}_1 = (n - y_1 - y_2)(q_1 + c\eta_{q1}) - y_1(k_1 + c\eta_{k_1}) \\ \quad + y_1(n - y_1 - y_2)(r_1' + c\eta_{r_1'}), \\ \dot{y}_2 = (n - y_1 - y_2)(q_2 + c\eta_{q2}) - y_2(k_2 + c\eta_{k_2}) \\ \quad + y_2(n - y_1 - y_2)(r_2' + c\eta_{r_2'}). \end{cases} \quad (6.3)$$

It is easy to show that the indirect-switching model can neither be reduced to two independent random processes, nor does it asymptotically converge to the diffusion model of decision-making (see the electronic supplementary material). Thus, the indirect-switching model of decision-making in *A. mellifera* cannot be (asymptotically) reduced to one dimension and therefore cannot be made exactly or approximately equivalent to the diffusion model of decision-making. This does not rule out the possibility that indirect switching may be an effective decision-making strategy, but it does rule out it being a statistically optimal decision-making strategy.

6.3. House-hunting with direct switching in **A.** mellifera

We now consider the Britton *et al.* model in which the scouts can directly switch their commitment between alternative sites (figure 4). The equations for this decision-making system are

$$\begin{cases} \dot{y}_1 = (n - y_1 - y_2)(q_1 + c\eta_{q1}) + y_1(n - y_1 - y_2) \\ \quad \times (r_1' + c\eta_{r_1'}) - y_1 k + y_1 y_2(r_1 - r_2 + c\eta_{r1} - c\eta_{r2}), \\ \dot{y}_2 = (n - y_1 - y_2)(q_2 + c\eta_{q2}) + y_2(n - y_1 - y_2) \\ \quad \times (r_2' + c\eta_{r_2'}) - y_2 k - y_1 y_2(r_1 - r_2 + c\eta_{r1} - c\eta_{r2}). \end{cases} \quad (6.4)$$

The key differences between the model described above for *A. mellifera* and the *T. albipennis* model of equations (6.2) are in the nature of the recruitment mechanism. In the *T. albipennis* model of §6.1, the number of ants recruited per unit time is a linear function of the number of recruiters (as long as recruits are still available). In the honeybee, recruitment occurs through waggle dancing, which is a process in which both parties meet (von Frisch 1967); thus in the *A. mellifera* model, the number of bees recruited per unit time depends on the numbers of both recruiters and potential uninformed recruits. If either is small, the growth of new recruiter numbers is limited.

Unlike the *T. albipennis* model, it is not possible to make the random process $\dot{x}_1$ independent of the random process $\dot{x}_2$. However, we can analyse how $\dot{x}_1$ behaves in the limit when x_2 converges. By setting the decay rate $k=0$, all scouts will become recruiters over time so x_2 approaches $n/\sqrt{2}$. In this limit, the dynamics of $\dot{x}_1$ are described as

$$\dot{x}_1 = \left(\frac{n^2}{2} - x_1^2\right)\left(\frac{r_1 - r_2}{\sqrt{2}} + c\eta_r\right). \quad (6.5)$$

In this random process, both noise and strength of drift vary quadratically with x_1. Choosing an appropriate nonlinear coordinate transformation to x (see the electronic supplementary material), we find by the chain rule that the random process can be expressed as

$$\dot{x} = \frac{\mathrm{d}x}{\mathrm{d}x_1}\frac{\mathrm{d}x_1}{\mathrm{d}t} = A + c\eta, \quad (6.6)$$

where $A = (r_1 - r_2)/\sqrt{2}$.

Thus when $k=0$, decision-making asymptotically converges to the diffusion model (figure 1), a decision-making process that is exactly equivalent to the statistically optimal strategy. We therefore describe the direct-switching model without decay as *asymptotically optimal*.

Optimal decision-making in the model occurs when no uncommitted scouts remain in the colony. For honeybees, we presume that this usually occurs, as swarms typically take hours or days to reach a decision. As the emigration progresses more and more honeybees enter the decision-making process, and the number of sites considered by the colony reduces as known alternatives are eliminated and new alternatives are discovered less and less frequently (Seeley & Buhrman 1999; Visscher & Camazine 1999b). Before this full-commitment stage is reached, decision-making will be governed by differences in discovery (q_i) and recruitment rates (r_i') for the available alternatives, and by the availability of information on the alternatives. These rates can depend not only on the quality of the available sites, but also on their distance, or the difficulty of their discovery. Thus an easy to discover, close but inferior site may attract more recruitment effort early on owing to positive feedback than a more distant, hard to discover but superior site. Once all scouts are committed, however, no new information on other alternatives can arrive (as there are no scouts searching), and decision-making between the available alternatives is made optimally, solely on the basis of their relative quality. The only deviation from purely optimal diffusion decision-making will be
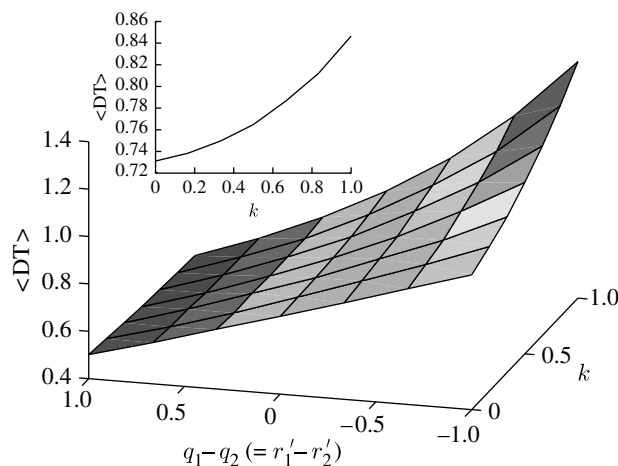

Figure 5. Results from numerical simulation of the *A. mellifera* direct-switching model. When decay $k>0$, decision-making is more strongly affected by the difference in discovery rates and recruitment rates from the home nest ($q_1 - q_2$ and $r_1' - r_2'$); if these differences are in favour of the superior alternative site (site 1), then decision time (DT) can be reduced by increasing k; however, if the differences favour the inferior alternative, then increasing k increases decision time. *Inset.* If all differences are equally likely, then mean decision time (y-axis) is minimized when k (x-axis) equals zero.

bias in the starting point of the decision-making process on the line $x_2 = n/\sqrt{2}$, resulting as just described. This will either tend to favour or disfavour selection of the best available alternative, depending on the relative ease of discovery, and distance, of the available alternatives. Nevertheless, we expect that setting decay $k=0$ will lead robustly to faster, more accurate decision-making, regardless of how easy or hard nest sites are to find and recruit to. In §7, we undertake numerical simulation of the model to test this optimality hypothesis.

7. NUMERICAL SIMULATION

To test whether decision-making in the *A. mellifera* direct-switching model is optimized by setting decay $k=0$, we conducted a numerical sensitivity test of the model (see the electronic supplementary material): we simultaneously varied the differences in the initial discovery and recruitment rates, $q_1 - q_2$ and $r_1' - r_2'$, respectively, so that they either favoured or disfavoured the selection of the superior nest site (site 1). The difference in the recruitment rates between the two populations of committed scouts, $r_1 - r_2 = 2$, reflects the true relative qualities of the two alternatives. We then simulated the model with decay k varying between 0 and 1. The results (figure 5) show that, although the benefit or cost of increasing k for decision time varies according to whether the superior site is easier or harder to find than its inferior alternative, setting $k=0$ is robustly optimal as it minimizes expected decision time across all scenarios considered.

8. DISCUSSION

We have presented the first optimality hypothesis for collective decision-making during emigration for social insect colonies. We have also presented the first formal

investigation of similarities between certain neural decision-making processes, and collective decision-making in social insect colonies, similarities which others have previously discussed (Hofstadter 1979; Seeley & Buhrman 2001; Visscher 2007; Passino *et al.* 2008). In both brains and social insect colonies, mutually interacting populations must reach an activation threshold to precipitate a decision. We argue that the interaction patterns between populations are the crucial part of the decision-making process at both these levels of biological complexity, organismal and super-organismal. Notwithstanding their impressive individual abilities (Koch 1999), neurons are simple in comparison with individually sophisticated social insects (Giurfa *et al.* 2001; Chittka *et al.* 2003; Franks *et al.* 2003*b*; Franks & Richardson 2006; Richardson *et al.* 2007). Simple interaction patterns in both these systems, however, may implement robust, efficient decision-making regardless of how sophisticated their individual components are.

Of the models presented here, only one approximates statistically optimal decision-making in a biologically plausible manner. This is the direct-switching model of house-hunting by the honeybee *A. mellifera*, based on a model proposed by Britton *et al.* (2002) in which scouts switch their commitment between alternatives owing to direct recruitment by others. Thus, our optimality hypothesis is that such direct switching through recruitment should occur in social insect colonies if they are to implement optimal decision-making. Lack of direct switching does not imply ineffective decision-making, but does imply departure from statistical optimality, and also weakens the analogy between cross-inhibition in neural decision-making circuits and in social insect colonies. We do not expect natural selection necessarily to result in optimal behaviour, but we do expect natural selection to achieve the optimal compromise between benefits of optimal behaviour, and costs of overcoming developmental or other constraints on that behaviour. Of course our optimality hypothesis remains useful in this case, by providing a gold standard of optimal behaviour that we can use to quantify theoretically the cost a real biological system incurs by deviating from optimality, and set against this the cost of overcoming any constraints on that system (Parker & Maynard Smith 1990).

Considerable discussion has focused on whether direct recruited switching, or indirect switching via decay to being uncommitted, is more biologically plausible, both for *A. mellifera* and *T. albipennis*. In both species, significant numbers of scouts have been observed to visit more than one alternative site (Seeley & Buhrman 1999; Mallon *et al.* 2001), yet experimentation and argument have suggested that direct comparison is not necessary (Visscher & Camazine 1999*a*; Britton *et al.* 2002; Pratt *et al.* 2002). More recently, further evidence on the ability of *T. albipennis* scouts to directly switch commitment has been presented (Franks *et al.* 2007*b*). While the optimal direct-switching model of equations (6.4) was proposed by Britton *et al.* (2002) as a model of honeybee decision-making, experimental evidence now suggests that honeybees may not be influenced in their switching

by the activities of recruiters for other alternatives (Seeley 2003), but may simply decay from their commitment to a site over time as in the indirect-switching models of Britton *et al.* (2002) and this paper. However, researchers have recently observed the production of the 'stop signal' during decision-making by honeybee swarms (Seeley & Visscher 2004*a*). This signal inhibits the production of waggle dances (Nieh 1993), and it has been suggested that this could serve the same purpose as the inhibitory connections stated by the Usher–McClelland neuronal model (Visscher 2007). Inhibition followed by recruitment is functionally similar to direct recruited switching. This hypothesis may be tested empirically by observing whether the targets of stop signals subsequently might follow dances for, and become committed to, alternative sites. The direct-switching nonlinear model also seems to be a plausible description of pre-quorum decision-making in *T. albipennis*. We reanalysed the experimental data of Pratt *et al.* (2002) from a binary emigration experiment with *T. albipennis*, and found that 14 per cent of commitment switches from poor to good nest occurred through recruitment, compared with 3.8 per cent of switches from good to poor nest.[2] Such relative levels of switching are consistent with the optimal parametrization of our direct-switching model presented here in that, while switching occurs in both directions, more individuals switch from poor to good sites, as they would if the colony were implementing a diffusion process in reaching its decision. In general, for both species the data available on direct switching are sparse yet very interesting, and deserve closer examination supplemented by additional experiments investigating mechanisms such as the honeybee's stop signal. If such an examination conclusively shows that direct switching does occur in either species, then our optimality hypothesis will be supported. If, however, direct switching is shown definitely not to occur, then our optimality hypothesis will enable us to quantify theoretically the cost of deviation from optimality, in terms of speed and accuracy of decision-making.

In this paper, we have considered only the binary decision case, for which the SPRT is provably optimal. Much experimental work undertaken with social insect colonies involves binary choice experiments. However, in the real world, it seems unlikely that a colony will ever be faced with a choice between only two alternatives. Optimal decision-making becomes more difficult in the presence of more than two alternatives, and a provably optimal strategy is not known. However, a decision-making strategy that is asymptotically optimal (as required error rate goes to zero) is known in the form of the multihypothesis SPRT (Veeravalli & Baum 1995), and it has recently been proposed that the vertebrate basal ganglia could implement this test (Bogacz & Gurney 2007). Other work has shown that the simple SPRT applied to multiple alternatives can be very effective when some of the alternatives are much better than the others

---

[2]These rates were despite the physical proximity of the nests (10 cm apart), which reduces the need for recruitment processes to augment independent discovery and switching (Pratt 2008).

(Bogacz *et al.* 2007), a scenario that may be common in nature, and under which both *T. albipennis* (Franks *et al.* 2003*b*, 2006*a*) and *A. mellifera* (Seeley & Buhrman 2001) colonies have been experimentally demonstrated to perform well.

One complicating factor for our analysis is that in social insect colonies, decision-making is conflated with decision implementation. In *T. albipennis* colonies, once the quorum is satisfied, only those scouts that know the location of the new site will be able to undertake the transportation of the remainder of the colony: ants transported by carrying are carried in a pose unsuitable for learning the route. Hence, the quorum threshold must be optimized not just for optimality of decision-making, but for the efficiency of decision implementation (Planqué *et al.* 2007). This may account for other authors' observations of a reduced effect of quorum threshold on emigration time during computer simulations of *Temnothorax* emigrations (Pratt & Sumpter 2006). A similar, but arguably less acute, situation occurs in *A. mellifera* colonies, where a sufficiently large minority of informed scouts must guide the entire swarm to the new nest site (Couzin *et al.* 2005). To increase confidence in the theoretical predictions from our models, which are necessarily simplified for analytical tractability, it could be interesting to attempt to validate these predictions using more biologically plausible individual-based models, such as those of Pratt *et al.* (2005), Marshall *et al.* (2006) and Passino & Seeley (2006).

An additional complication arises because, in real emigrations, news about all the alternatives is not available to the colony from the beginning: discovery of potential nest sites by scouts is a stochastic process, and the best available alternative may not be discovered until quite late in the decision-making process. Experimental (Franks *et al.* 2007*b*) and theoretical (Britton *et al.* 2002) work has examined the robustness of social insects' collective decision-making to this kind of late information. Our analysis shows how such robustness might be understood because under the direct-switching model, once all scouts are committed and no further information on new alternatives can arrive, decision-making proceeds optimally between the available alternatives based on their quality: the only departure from optimality is the bias in the starting point of the decision process based on the relative discovery times of the alternatives.

The previous point brings us to one final observation, that social insect colonies may face a subtly different decision problem to neural circuits in the vertebrate brain. A social insect colony must actively acquire information from its environment, whereas in the visual decision-making task considered in this paper information on both alternatives arrives at an equal and unvarying rate. Scouts stochastically discover alternative sites, but once some potential sites are known the colony is faced with the traditional explore/exploit dilemma: should the colony send more scouts to assess the known alternatives and gain a better estimate of their quality, or should it allocate scouts to attempt the discovery of unknown, potentially better, alternatives? As previously noted (Marshall *et al.* 2006), the colony is thus faced with a decision problem that is a hybrid of the 'bandit' problem, in which trials must be allocated across noisy alternatives of unknown quality in order to maximize long-term gain, and the minimal decision time problem that the SPRT addresses. To our knowledge, no attempt has previously been made to formalize or analyse such a problem. We believe that analysis of the social insects' behaviour, and models thereof, could provide a fruitful avenue for tackling this new decision problem. We expect that this problem will also reveal further similarities between collective and neural decision-making processes, leading to further extension of the general decision-making framework outlined here.

REFERENCES

Beekman, M., Fathke, R. & Seeley, T. 2006 How does an informed minority of scouts guide a honeybee swarm as it flies to its new home? *Anim. Behav.* **71**, 161–171. (doi:10.1016/j.anbehav.2005.04.009)

Bogacz, R. & Gurney, K. 2007 The basal ganglia and cortex implement optimal decision making between alternative actions. *Neural Comput.* **19**, 442. (doi:10.1162/neco.2007.19.2.442)

Bogacz, R., Brown, E., Moehlis, J., Holmes, P. & Cohen, J. D. 2006 The physics of optimal decision making: a formal analysis of models of performance in two-alternative forced choice tasks. *Psychol. Rev.* **113**, 700–765. (doi:10.1037/0033-295X.113.4.700)

Bogacz, R., Usher, M., Zhang, J. & McClelland, J. L. 2007 Extending a biologically inspired model of choice: multi-alternatives, nonlinearity and value-based multidimensional choice. *Phil. Trans. R. Soc. B* **362**, 1655–1670. (doi:10.1098/rstb.2007.2059)

Britten, K. H., Shadlen, M. N., Newsome, W. T. & Movshon, J. A. 1993 Responses of neurons in macaque MT to stochastic motion signals. *Visual Neurosci.* **10**, 1157–1169.

Britton, N. F., Franks, N. R., Pratt, S. C. & Seeley, T. D. 2002 Deciding on a new home: how do honeybees agree? *Proc. R. Soc. B* **269**, 1383–1388. (doi:10.1098/rspb.2002.2001)

Chittka, L., Dyer, A. G., Bock, F. & Dornhaus, A. 2003 Bees trade off foraging speed for accuracy. *Nature* **424**, 388. (doi:10.1038/424388a)

Couzin, I. D., Krause, J., Franks, N. R. & Levin, S. A. 2005 Effective leadership and decision-making in animal groups on the move. *Nature* **433**, 513–516. (doi:10.1038/nature03236)

Dornhaus, A. & Franks, N. 2006 Colony size affects collective decision-making in the ant *Temnothorax albipennis*. *Insectes Soc.* **53**, 420–427. (doi:10.1007/s00040-006-0887-4)

Dornhaus, A., Franks, N. R., Hawkins, R. M. & Shere, H. N. S. 2004 Ants move to improve: colonies of *Leptothorax albipennis* emigrate whenever they find a superior nest site. *Anim. Behav.* **67**, 959–963. (doi:10.1016/j.anbehav.2003.09.004)

Edwards, W. 1965 Optimal strategies for seeking information: models for statistics, choice reaction times, and human information processing. *J. Math. Psychol.* **2**, 312–329. (doi:10.1016/0022-2496(65)90007-6)

Franks, N. R. & Richardson, T. 2006 Teaching in tandem-running ants. *Nature* **439**, 153. (doi:10.1038/439153a)

Franks, N. R., Pratt, S. C., Mallon, E. B., Britton, N. F. & Sumpter, D. J. T. 2002 Information flow, opinion polling and collective intelligence in house-hunting social insects. *Phil. Trans. R. Soc. B* **357**, 1567–1583. (doi:10.1098/rstb.2002.1066)

Franks, N. R., Dornhaus, A., Fitzsimmons, J. P. & Stevens, M. 2003*a* Speed versus accuracy in collective decision making. *Proc. R. Soc. B* **270**, 2457–2463. (doi:10.1098/rspb.2003.2527)

Franks, N. R., Mallon, E. B., Bray, H. E., Hamilton, M. J. & Mischler, T. C. 2003*b* Strategies for choosing between alternatives with different attributes: exemplified by house-hunting ants. *Anim. Behav.* **65**, 215–223. (doi:10.1006/anbe.2002.2032)

Franks, N. R., Hooper, J., Webb, C. & Dornhaus, A. 2005 Tomb evaders: house-hunting hygiene in ants. *Biol. Lett.* **1**, 190–192. (doi:10.1098/rsbl.2005.0302)

Franks, N. R., Dornhaus, A., Best, C. & Jones, E. 2006*a* Decision making by small and large house-hunting ant colonies: one size fits all. *Anim. Behav.* **72**, 611–616. (doi:10.1016/j.anbehav.2005.11.019)

Franks, N. R., Dornhaus, A., Metherell, B. G., Nelson, T. R., Lanfear, S. A. J. & Symes, W. S. 2006*b* Not everything that counts can be counted: ants use multiple metrics for a single nests. *Proc. R. Soc. B* **273**, 165–169. (doi:10.1098/rspb.2005.3312)

Franks, N. R., Dornhaus, A., Hitchcock, G., Guillem, R., Hooper, J. & Webb, C. 2007*a* Avoidance of conspecific colonies during nest choice by ants. *Anim. Behav.* **73**, 525–534. (doi:10.1016/j.anbehav.2006.05.020)

Franks, N. R., Hooper, J. W., Gumn, M., Bridger, T. H., Marshall, J. A. R., Gross, R. & Dornhaus, A. 2007*b* Moving targets: collective decisions and flexible choices in house-hunting ants. *Swarm Intell.* **1**, 81–94. (doi:10.1007/s11721-007-0007-8)

Giurfa, M., Zhang, S., Jenett, A., Menzel, R. & Srinivasan, M. V. 2001 The concepts of 'sameness' and 'difference' in an insect. *Nature* **410**, 930–933. (doi:10.1038/35073582)

Hanks, T. D., Ditterich, J. & Shadlen, M. N. 2006 Microstimulation of macaque area lip affects decision-making in a motion discrimination task. *Nat. Neurosci.* **9**, 682–689. (doi:10.1038/nn1683)

Hansell, M. H. 1984 *Animal architecture and building behaviour.* London, UK: Longman.

Hazlett, B. A. 1981 The behavioral ecology of hermit crabs. *Annu. Rev. Ecol. Syst.* **12**, 1–22. (doi:10.1146/annurev.es.12.110181.000245)

Hofstadter, D. R. 1979 *Gödel Escher Bach: an eternal golden braid.* New York, NY: Basic Books.

Huk, A. C. & Shadlen, M. N. 2005 Neural activity in macaque parietal cortex reflects temporal integration of visual motion signals during perceptual decision making. *J. Neurosci.* **25**, 10 420–10 436. (doi:10.1523/JNEUROSCI.4684-04.2005)

Koch, C. 1999 *Biophysics of computation: information processing in single neurons.* New York, NY: Oxford University Press.

Lindauer, M. 1955 Schwarmbienen auf wohnungssuche. *J. Comp. Physiol. A: Sensory Neural Behav. Physiol.* **37**, 263–324. (doi:10.1007/BF00303153)

Mallon, E. B. & Franks, N. R. 2000 Ants estimate area using Buffon's needle. *Proc. R. Soc. B* **267**, 765–770. (doi:10.1098/rspb.2000.1069)

Mallon, E. B., Pratt, S. C. & Franks, N. R. 2001 Individual and collective decision-making during nest site selection by the ant *Leptothorax albipennis. Behav. Ecol. Sociobiol.* **50**, 352–359. (doi:10.1007/s002650100377)

Marshall, J. A. R., Dornhaus, A., Franks, N. R. & Kovacs, T. 2006 Noise, cost and speed–accuracy trade-offs: decision-making in a decentralized system. *J. R. Soc. Interface* **3**, 243–254. (doi:10.1098/rsif.2005.0075)

Möglich, M. 1978 Social organization of nest emigration in *Leptothorax* (Hym., Form.). *Insectes Soc.* **25**, 205–225. (doi:10.1007/BF02224742)

Möglich, M. & Hölldobler, B. 1974 Social carrying behavior and division of labor during nest moving in ants. *Psyche* **81**, 219–236. (doi:10.1155/1974/25763)

Myerscough, M. R. 2003 Dancing for a decision: a matrix model for nest-site choice by honeybees. *Proc. R. Soc. B* **270**, 577–582. (doi:10.1098/rspb.2002.2293)

Neyman, J. & Pearson, E. 1933 On the problem of the most efficient tests of statistical hypotheses. *Phil. Trans. R. Soc. A* **231**, 289–337. (doi:10.1098/rsta.1933.0009)

Nieh, J. C. 1993 The stop signal of honey bees: reconsidering its message. *Behav. Ecol. Sociobiol.* **33**, 51–56. (doi:10.1007/BF00164346)

Parker, G. A. & MaynardSmith, J. 1990 Optimality theory in evolutionary biology. *Nature* **348**, 27–33. (doi:10.1038/348027a0)

Passino, K. M. & Seeley, T. 2006 Modeling and analysis of nest-site selection by honeybee swarms: the speed and accuracy trade-off. *Behav. Ecol. Sociobiol.* **59**, 427–442. (doi:10.1007/s00265-005-0067-y)

Passino, K. M., Seeley, T. D. & Visscher, P. K. 2008 Swarm cognition in honeybees. *Behav. Ecol. Sociobiol.* **62**, 401–414. (doi:10.1007/s00265-007-0468-1)

Planqué, R., Dechaume-Moncharmont, F. X., Franks, N. R., Kovacs, T. & Marshall, J. A. R. 2007 Why do house-hunting ants recruit in both directions? *Naturwissenschaften* **94**, 911–918. (doi:10.1007/s00114-007-0273-8)

Pratt, S. C. 2008 Efficiency and regulation of recruitment during colony emigration by the ant *Temnothorax curvispinosus. Behav. Ecol. Sociobiol.* **62**, 1369–1376. (doi:10.1007/s00265-008-0565-9)

Pratt, S. C. & Sumpter, D. J. T. 2006 A tunable algorithm for collective decision-making. *Proc. Natl Acad. Sci. USA* **103**, 15 906–15 910. (doi:10.1073/pnas.0604801103)

Pratt, S. C., Mallon, E. B., Sumpter, D. J. T. & Franks, N. R. 2002 Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis. Behav. Ecol. Sociobiol.* **52**, 117–127. (doi:10.1007/s00265-002-0487-x)

Pratt, S. C., Sumpter, D. J. T., Mallon, E. B. & Franks, N. R. 2005 An agent-based model of collective nest choice by the ant *Temnothorax albipennis. Anim. Behav.* **70**, 1023–1036. (doi:10.1016/j.anbehav.2005.01.022)

Ratcliff, R. 1978 A theory of memory retrieval. *Psychol. Rev.* **85**, 59–108. (doi:10.1037/0033-295X.85.2.59)

Ratcliff, R. & Smith, P. L. 2004 A comparison of sequential sampling models for two-choice reaction time. *Psychol. Rev.* **111**, 333–367. (doi:10.1037/0033-295X.111.2.333)

Ratcliff, R., Cherian, A. & Segraves, M. A. 2003 A comparison of macaque behavior and superior colliculus neuronal activity to predictions from models of two choice decisions. *J. Neurophysiol.* **90**, 1392–1407. (doi:10.1152/jn.01049.2002)

Richardson, T., Sleeman, P., McNamara, J., Houston, A. I. & Franks, N. R. 2007 Teaching with evaluation in ants. *Curr. Biol.* **17**, 1520–1526. (doi:10.1016/j.cub.2007.08.032)

Roitman, J. D. & Shadlen, M. N. 2002 Response of neurons in the lateral intraparietal area during a combined visual discrimination reaction time task. *J. Neurosci.* **22**, 9475–9489.

Schall, J. D. 2001 Neural basis of deciding choosing and acting. *Nat. Rev. Neurosci.* **2**, 33–42. (doi:10.1038/35049054)

Seeley, T. D. 1982 How honeybees find a home. *Sci. Am.* **247**, 158–169.

Seeley, T. D. 1995 *The wisdom of the hive: the social physiology of honey bee colonies.* Cambridge, MA: Harvard University Press.

Seeley, T. D. 2003 Consensus building during nest-site selection in honey bee swarms: the expiration of dissent. *Behav. Ecol. Sociobiol.* **53**, 417–424.

Seeley, T. D. & Buhrman, S. C. 1999 Group decision making in swarms of honey bees. *Behav. Ecol. Sociobiol.* **45**, 19–31. (doi:10.1007/s002650050536)

Seeley, T. D. & Buhrman, S. C. 2001 Nest-site selection in honey bees: how well do swarms implement the 'best-of-N' decision rule? *Behav. Ecol. Sociobiol.* **49**, 416–427. (doi:10.1007/s002650000299)

Seeley, T. D. & Visscher, P. K. 2004a Group decision making in nest-site selection by honey bees. *Apidologie* **35**, 101–116. (doi:10.1051/apido:2004004)

Seeley, T. D. & Visscher, P. K. 2004b Quorum sensing during nest-site selection by honeybee swarms. *Behav. Ecol. Sociobiol.* **56**, 594–601. (doi:10.1007/s00265-004-0814-5)

Shadlen, M. N. & Newsome, W. T. 2001 Neural basis of a perceptual decision in the parietal cortex (area lip) of the rhesus monkey. *J. Neurophysiol.* **86**, 1916–1936.

Stone, M. 1960 Models for choice reaction time. *Psychometrika* **25**, 251–260. (doi:10.1007/BF02289729)

Trimmer, P., Bogacz, R., Houston, A. I., Marshall, J. A. R., McNamara, J., Mendl, M. & Paul, E. 2008 Mammalian choices: combining fast-but-inaccurate and slow-but-accurate decision-making systems. *Proc. R. Soc. B* **275**, 2353–2361. (doi:10.1098/rspb.2008.0417)

Usher, M. & McClelland, J. L. 2001 The time course of perceptual choice: the leaky, competing accumulator model. *Psychol. Rev.* **108**, 550–592. (doi:10.1037/0033-295X.108.3.550)

Veeravalli, V. V. & Baum, C. W. 1995 Asymptotic efficiency of a sequential multihypothesis test. *IEEE Trans. Inf. Theory* **41**, 1994–1997. (doi:10.1109/18.476323)

Visscher, P. K. 2007 Group decision making in nest-site selection among social insects. *Annu. Rev. Entomol.* **52**, 255–275. (doi:10.1146/annurev.ento.51.110104.151025)

Visscher, P. K. & Camazine, S. 1999a Collective decisions and cognition in honeybees. *Nature* **397**, 400. (doi:10.1038/17047)

Visscher, P. K. & Camazine, S. 1999b The mystery of swarming honeybees: from individual behaviours to collective decisions. In *Information processing in social insects*, pp. 355–378. Basel, Switzerland: Birkhäuser.

von Frisch, K. 1967 *The dance language and orientation of bees.* Cambridge, MA: Belknap Press.

Wald, A. & Wolfowitz, J. 1948 Optimum character of the sequential probability ratio test. *Ann. Math. Stat.* **19**, 326–339. (doi:10.1214/aoms/1177730197)