



# Response threshold reinforcement and division of labour in insect societies

Guy Theraulaz<sup>1</sup>, Eric Bonabeau<sup>2</sup> and Jean-Louis Deneubourg<sup>3</sup>

<sup>1</sup>Laboratoire d'Ethologie et de Psychologie Animale, CNRS-UMR 5550, Université Paul Sabatier, 118 route de Narbonne, 31062 Toulouse Cédex, France

<sup>2</sup>Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA

<sup>3</sup>Unit of Theoretical Behavioural Ecology, Service de Chimie-Physique, CP231, Université Libre de Bruxelles, Boulevard du triomphe, 1050 Brussels, Belgium

A model of division of labour in insect societies, based on variable response thresholds is introduced. Response thresholds refer to the likelihood of reacting to task-associated stimuli. Low-threshold individuals perform tasks at a lower level of stimulus than high-threshold individuals. Within individual workers, performing a given task induces a decrease in the corresponding threshold, and not performing the task induces an increase in the threshold. This combined reinforcement process leads to the emergence of specialized workers, i.e. workers that are more responsive to stimuli associated with particular task requirements, from a group of initially identical individuals. Predictions of the dynamics of task specialization resulting from this model are presented. Predictions are also made as to what should be observed when specialists of a given task are removed from the colony and reintroduced after a varying amount of time: the colony does not recover the same state as that prior to the perturbation, and the difference between before and after the perturbation is more strongly marked as the time between separation and reintroduction increases.

**Keywords:** division of labour; learning; response thresholds

## 1. INTRODUCTION

Colony-level flexibility in response to external challenges and internal perturbations is an essential feature of division of labour in social insects (Calabi 1988; Robinson 1992). Simple response threshold models, which assume that each worker responds to a given stimulus when stimulus intensity exceeds the worker's threshold, can explain how flexibility at the colony level results from the workers' behavioural flexibility (Bonabeau *et al.* 1996). Empirical evidence for response thresholds has been found in ants and honeybees (Robinson 1987, 1992; Detrain & Pasteels 1991, 1992; Seeley 1989, 1992; Schatz 1997). Previous threshold models have several limitations, because they assume that workers' thresholds are fixed over the studied time-scale. (1) Such models cannot account for the genesis of task allocation, including temporal polyethism, for they assume that individuals are differentiated and roles preassigned; (2) they cannot account for *robust* task specialization within (physical or temporal) castes; (3) they are valid only over sufficiently short time-scales, where thresholds can be considered constant; (4) They are not consistent with recent experiments on honeybees (Robinson *et al.* 1994; Calderone & Page 1996), showing that ageing and/or learning play a role in task allocation.

The foraging-for-work model (FFW) (Tofts & Franks 1992), in which individuals actively seek work and continue to perform a given task as long as they are stimu-

lated to do so, can, under specific conditions, account for sociogenesis, weak temporal polyethism, and within-caste task specialization (Tofts 1993). FFW, however, is still limited by point (4), and is not robust enough to explain strong temporal polyethism (Bonabeau *et al.* 1998), as is observed, for example, in honeybees (Robinson 1992) or *Polybia* wasps (O'Donnell & Jeanne 1993). FFW shares some similarities with the fixed-threshold model, of which it can be seen as a particular case, where individuals all have *fixed, identical, very low* response thresholds. Here, we extend the fixed-threshold model (and, therefore, the FFW model as well) by allowing thresholds to vary in time, following a simple reinforcement process: a threshold decreases when the corresponding task is performed, and increases when the corresponding task is not performed. Deneubourg *et al.* (1987), Plowright & Plowright (1988) and Theraulaz *et al.* (1991) introduced this idea (see also Oster 1976), but did not attempt to explore its consequences in detail, especially when several tasks need to be performed. Moreover, our formulation of the reinforcement is based on a threshold model which was previously shown to be in excellent quantitative agreement with experiments (Bonabeau *et al.* 1996; Wilson 1984). The main competing hypothesis to overcome limitations (1)–(4) is absolute ageing or, within the present context, deterministic age-based changes in response thresholds. Although ageing may have some importance (Robinson *et al.* 1994), the reinforcement hypothesis is fully consistent with experiments, and can overcome limitations (1)–(4):

it is therefore worth undertaking a detailed study of a threshold model based on this hypothesis.

Several experiments suggest the existence of a reinforcement process or support the reinforcement hypothesis. Deneubourg *et al.* (1987) proposed that such a hypothesis would be consistent with experimental observations of foraging in ants. Sendova-Franks & Franks (1994) suggested that reinforcement learning plays a role in the ability of *Leptothorax* ant colonies to quickly reassemble after dissociation. Withers *et al.* (1993) observed that important changes in some regions of the brain are associated with ageing in honeybees: the brain of a forager (more than 20 days old) is significantly different from that of a one-day-old bee. While their observations could result from absolute ageing, further experiments, where worker bees were forced to start foraging early, showed that precocious foragers were similar in brain organization to normal, older foragers. This suggests that behaviour influences brain organization, which in turn certainly influences under what conditions tasks are performed. Other experiments, which have been interpreted as suggesting ageing as the main factor, can be reinterpreted along the same lines. For example, the probability of behavioural reversion from foraging to nursing in honeybees (Seeley 1982) is a decreasing function of the time spent foraging, which suggests that some kind of learning may occur. Another example is the recent study of Calderone & Page (1996), who showed that deprived bees (raised in isolation in wire cages with a queen) exhibit precocious foraging, suggesting that the lack of certain stimuli may influence the rate of behavioural ontogeny (a possibility that Calderone & Page (1996) did not rule out; see also Huang & Robinson 1992). More generally, relative age (that is, age relative to the rest of the colony and to the individual's own experience) is often a more relevant parameter than absolute age (Lenoir 1979; Jaisson *et al.* 1988; Calabi 1988; Van der Blom 1993; Sendova-Franks & Franks 1994), which means that stimuli provided by the environment and other colony members, as well as individual history, are likely to play an important role in shaping behavioural ontogeny. These studies suggest that individual experience shapes behavioural ontogeny, and that response thresholds may be dynamic, rather than static.

**2. THE MODEL**

Assume that  $m$  tasks need to be performed. These tasks are associated with stimuli or demands, the levels of which increase if they are not satisfied (because the tasks are not performed by enough individuals, or at high enough rates). Let us assume that there are  $N$  workers, denoted by  $i$ , with response thresholds  $\theta_{ij}$  ( $i=1, \dots, N$  and  $j=1, \dots, m$ ) with respect to task  $j$ -associated stimuli. Let  $s_j$  denote the intensity of task  $j$ -associated stimuli. In the fixed-threshold model (Bonabeau *et al.* 1996), individual  $i$  engages in task  $j$  with probability

$$T_{\theta_{ij}}(s_j) = \frac{s_j^2}{s_j^2 + \theta_{ij}^2} \tag{1}$$

For  $s_j \ll \theta_{ij}$ ,  $T_{\theta_{ij}}(s_j)$  is close to 0, and  $s_j \gg \theta_{ij}$ ,  $T_{\theta_{ij}}(s_j)$  is close to 1; at  $s_j = \theta_{ij}$ ,  $T_{\theta_{ij}}(s_j) = 0.5$ . Therefore, individuals with a

lower  $\theta_{ij}$  are more likely to respond at a lower level of stimulus. In addition,  $\theta_{ij}$  is updated in a self-reinforcing way (Theraulaz *et al.* 1991). The more individual  $i$  performs task  $j$ , the lower  $\theta_{ij}$ , and vice versa. Let  $\xi$  and  $\varphi$  be the coefficients that describe learning and forgetting, respectively. In this time-incremental model, individual  $i$  becomes more (respectively less) sensitive by an amount  $\xi\Delta t$  (respectively  $\varphi\Delta t$ ) to task  $j$ -associated stimuli when performing (respectively not performing) task  $j$  during a time period of duration  $\Delta t$ :

$$\theta_{ij} \rightarrow \theta_{ij} - \xi\Delta t \tag{2a}$$

if  $i$  performs task  $j$  within  $\Delta t$ , and

$$\theta_{ij} \rightarrow \theta_{ij} + \varphi\Delta t \tag{2b}$$

if  $i$  does not perform the task within  $\Delta t$ . Let  $x_{ij}$  be the fraction of time spent by individual  $i$  in task  $j$  performance: within  $\Delta t$ , individual  $i$  performs task  $j$  during  $x_{ij}\Delta t$ , and other tasks during  $(1-x_{ij})\Delta t$ . The resulting change in  $\theta_{ij}$  within  $\Delta t$  is therefore given by

$$\theta_{ij} \rightarrow \theta_{ij} - x_{ij}\xi\Delta t + (1-x_{ij})\varphi\Delta t, \tag{3}$$

which combines equations (2a) and (2b).  $\xi$  and  $\varphi$  are assumed to be identical for all tasks, and the dynamics of  $\theta_{ij}$  is restricted to an interval  $[\theta_{\min}, \theta_{\max}]$ . The decision to engage in task  $j$  performance is still given by  $T_{ij}$  (equation (1)), but  $\theta_{ij}$  now varies in time according to equations (2) and (3). The continuous-time formulation of equation (3) is given by

$$\partial_t \theta_{ij} = [(1-x_{ij})\varphi - x_{ij}\xi]\Theta(\theta_{ij} - \theta_{\min})\Theta(\theta_{\max} - \theta_{ij}), \tag{4}$$

where  $\partial_t$  denotes the time derivative and  $\Theta$  is a step function ( $\Theta(y) = 0$  if  $y \leq 0$ ,  $\Theta(y) = 1$  if  $y > 0$ ).  $\Theta$  is used to maintain  $\theta$  within bounds in the model. The average temporal dynamics of  $x_{ij}$  is given by:

$$\partial_t x_{ij} = T_{\theta_{ij}}(s_j) \left( 1 - \sum_{k=1}^m x_{ik} \right) - p x_{ij} + \psi(i, j, t). \tag{5}$$

The first term on the right hand side (rhs) of equation (5) describes how the  $1 - \sum_{k=1}^m x_{ik}$  fraction of time potentially available for task performance is actually allocated to task  $j$  performance. The second rhs term in equation (5) expresses the assumption that an active individual gives up performing the task and becomes inactive with probability  $p$  per unit time (that we take to be identical for all workers and all tasks). The average time spent by an individual in performing task  $j$  before giving up this task is  $1/p$ . It is assumed that  $p$  is fixed, identical for all tasks and individuals, and independent of stimulus. Individuals give up task performance after  $1/p$ , but may engage in it again immediately if stimulus intensity is still large.  $\Psi(i, j, t)$  is a centred gaussian stochastic process of variance  $\sigma^2$ , uncorrelated in time, and uncorrelated among individuals and among tasks:

$$\forall i, j, t \langle \Psi(i, j, t) \rangle = 0, \tag{6a}$$

and

$$\forall i, j, h, k, t, t' \langle \Psi(i, j, t) \Psi(h, k, t') \rangle = \sigma^2 \delta_0(i-h) \delta_0(j-k) \delta_0(t-t'), \tag{6b}$$

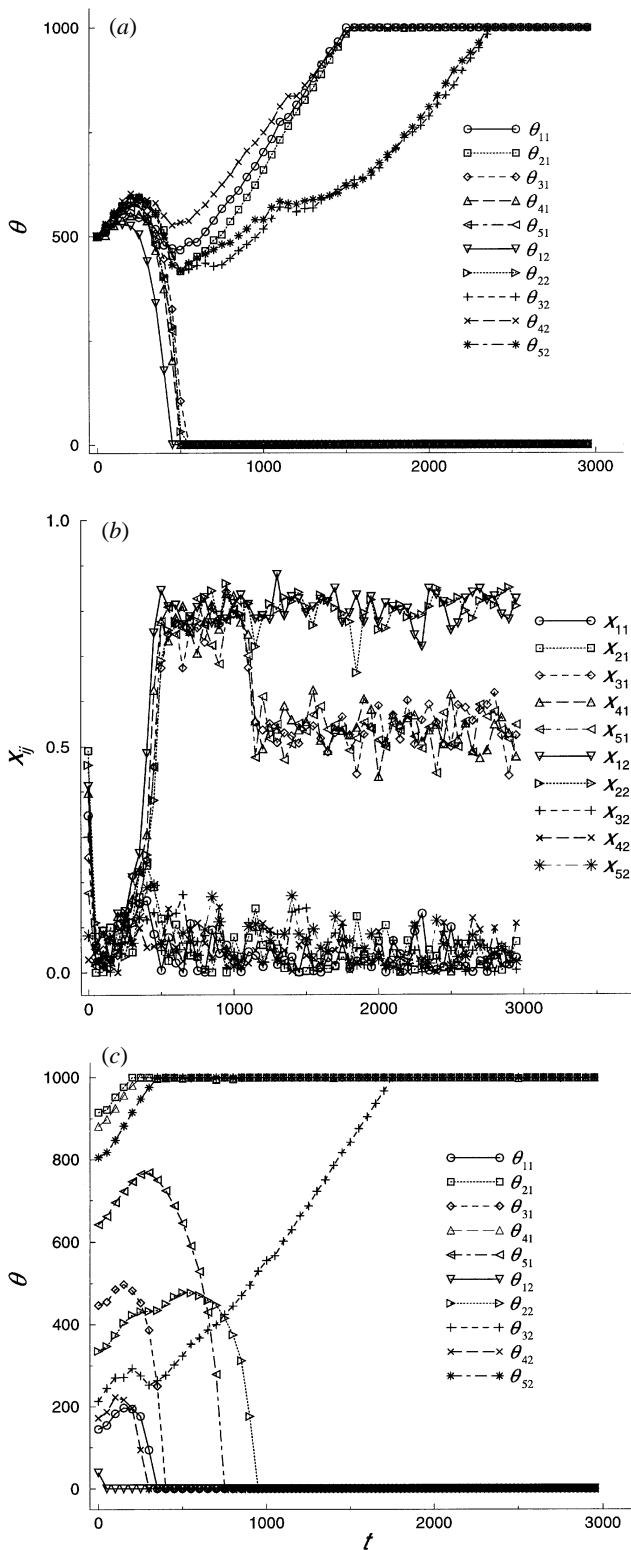


Figure 1. (a) Dynamics of response thresholds  $\theta_{ij}$  for  $N=5$  individuals and  $m=2$  tasks.  $\alpha=3$ ,  $\delta=1$ ,  $p=0.2$ ,  $\xi=10$ ,  $\varphi=1$ ,  $\sigma=0.1$ . Initial conditions:  $\forall i \in \{1, \dots, N\}$ ,  $\forall j \in \{1, \dots, m\}$ ,  $\theta_{ij}(t=0)=500$  and  $x_{ij}(t=0)=0.1$ .  $x_{ij}$  is the response threshold of individual  $i$  to task  $j$ ; for example,  $\theta_{21}$  is the response threshold of individual 2 to task 1. A low value of  $\theta_{ij}$  indicates that individual  $i$  is highly sensitive to task  $j$ -associated stimuli and is therefore a specialist of task  $j$ . Individuals 3, 4 and 5 are task 1 specialists, and individuals 1 and 2 are task 2 specialists. (b) Dynamics of the fractions of time spent in task performance  $x_{ij}$  for the same parameter values as in (a)  $x_{ij}$  is the fraction of time spent by individual  $i$  in performing task  $j$ ; for example,  $x_{42}$  is the

where  $\delta$  is the Dirac distribution.  $\Psi(i, j, t)$  is a stochastic term that simulates the fact that individuals encounter slightly different local conditions. Assuming for simplicity that the demand for each task increases at a fixed rate per unit time, the dynamics of  $s_j$  the intensity of task  $j$ -associated stimuli, is described by

$$\partial_t s_j = \delta - \frac{\alpha}{N} \left( \sum_{i=1}^N x_{ij} \right), \quad (7)$$

where  $\delta$  is the increase in stimulus intensity per unit time, and  $\alpha$  is a scale factor measuring the efficiency of task performance. It is assumed that both factors are identical for both tasks, and that  $\alpha$  is fixed over time and identical for all individuals. In reality, however,  $\alpha$  can vary as a result of specialization (Dukas & Visscher 1994; Johnson 1991). The amount of work performed by active individuals is scaled by the number of individuals  $N$ , as can be seen in equation (7), to reflect the idea that demand is an increasing function of  $N$ , that we take to be linear here. For example, the brood should be divided by 2 when colony size is divided by 2 (Wilson 1984).

### 3. RESULTS

The dynamics of the model, described by equations (1)–(7), can lead to specialization. Individual  $i$  is considered a specialist of task  $j$  if  $\theta_{ij}$  is small. Figure 1a shows an example of specialization: thresholds are represented as a function of time for five individuals and two tasks ( $N=5$ ,  $m=2$ ) (initially,  $\forall i \in \{1, \dots, 5\}$ ,  $\forall j \in \{1, 2\}$ ,  $\theta_{ij}=500$ ,  $x_{ij}=0.1$ ,  $\alpha=3$ ,  $\delta=1$ ,  $p=0.2$ ,  $\xi=10$ ,  $\varphi=1$ ,  $\sigma=0.1$ ). Some of these individuals become highly responsive to stimuli associated with task 1, but not to those associated with task 2, and others exhibit the opposite behaviour. Individuals 1 and 2 are task 2 specialists, while individuals 3, 4 and 5 are task 1 specialists. Figure 1b shows the frequencies  $x_{i1}$  and  $x_{i2}$  of task performance for all individuals as a function of time. Individuals with small  $\theta_{ij}$  (respectively large) tend to have large (respectively small)  $x_{ij}$ . Individuals adjust their levels of activity to maintain stimulus intensity below the threshold, so that the three individuals 3, 4 and 5, who all perform mostly task 1, are less active ( $x_{i1} \approx 0.55$ ,  $x_{i2} \approx 0.05$ ) than individuals 1 and 2, who perform mostly task 2 ( $x_{i1} \approx 0.05$ ,  $x_{i2} \approx 0.8$ ). This specialization seems to well describe what is observed in the primitively eusocial wasp *Polistes dominulus*, where a clear division of labour, including reproductive division of labour, emerges after a few days (Theraulaz *et al.* 1992) despite the lack of initial individual differentiation.

When, instead of initially being all identical, thresholds are initially randomly distributed in  $[\theta_{\min}, \theta_{\max}]$ , indi-

fraction of time spent by individual 4 performing task 2. When  $x_{ij}$  is close to 1, individual  $i$  spends most of its time performing task  $j$ . Individuals 3, 4 and 5, who all perform mostly task 1, are less active ( $x_{i1} \approx 0.55$ ,  $x_{i2} \approx 0.05$ ) than individuals 1 and 2, who perform mostly task 2 ( $x_{i1} \approx 0.05$ ,  $x_{i2} \approx 0.8$ ). (c) The same as in (a), except that the initial distribution of thresholds is uniform over  $[\theta_{\min}=1, \theta_{\max}=1000]$ . Individuals 1, 3 and 5 are task 1 specialists, and individuals 1, 2 and 4 are task 2 specialists (individual 1 is a specialist of both tasks).

duals with an initially small  $\theta_{ij}$  are more likely to become task  $j$  specialists (figure 1c): in a genetically diverse colony, individuals with close genotypic characteristics (for example, belonging to the same patriline) may have similar response thresholds and are therefore predisposed to perform the same tasks (Breed *et al.* 1990; Calderone & Page 1988; Frumhoff & Baker 1988; Page & Robinson 1991; Robinson & Page 1988) (genes might also influence  $\alpha$ ,  $p$ ,  $\xi$ ,  $\varphi$ ,  $\theta_{\min}$  and  $\theta_{\max}$ ). On figure 1c, individuals 1, 3 and 5 are task 1 specialists, and individuals 1, 2 and 4 are task 2 specialists; individual 1 is a specialist of both tasks.

Specialization can be observed over a certain portion of parameter space. Let  $T_c$  be the convergence time, i.e. the time it takes for all individuals to become either specialists or non-specialists of both tasks (the criterion is:  $\forall i \in \{1, \dots, N\}, \forall j \in \{1, \dots, m\}, \theta_{ij} > 900$  or  $\theta_{ij} < 100$ ), and let  $N_1$  and  $N_2$  be the number of specialists after convergence of tasks 1 and 2, respectively. Figure 2a shows  $T_c$ ,  $N_1$  and  $N_2$  as a function of  $\varphi$  (forgetting rate) for  $N=100$  and  $m=2$ , assuming that  $\varphi + \xi = 11$  (where  $\xi$  is the learning rate). When  $\varphi < 0.4$ , all individuals are specialists because the forgetting rate is small.  $T_c$  becomes large as  $\varphi$  approaches 0.4:  $s_j$  always being very low thanks to the large number of specialists, individuals are not easily stimulated to engage in task performance, so that their thresholds fluctuate a lot. For  $0.4 < \varphi < 2$ , the number of specialists for each task decreases, and so does  $T_c$ : differentiation is observed in this region. For  $\varphi > 2$ , forgetting is quick and no specialization is observed. A different pattern is observed when  $T_c$ ,  $N_1$  and  $N_2$  are plotted as a function of  $p$  (probability per unit time of becoming inactive) (figure 2b). All individuals are specialists for  $p < 0.04$  because they spend much time in task performance each time they engage. For the same reason as above,  $T_c$  becomes large as  $p$  approaches 0.04. The number of specialists for each task drops dramatically just after  $p=0.04$ . For  $0.04 < p < 0.42$ ,  $T_c$  decreases and the number of specialists increases with  $p$ , until all individuals become specialists, for  $p > 0.42$ , because they spend so little time in task performance that it requires a lot of specialists to maintain stimulus intensity at a low level.

The model generates several testable predictions. One experiment which can help test our hypotheses involves the removal of, say, task 1 specialists for a variable amount of time  $T_r$  before their reintroduction into the colony. When individuals with low  $\theta_{i1}$  are removed, individuals with previously high  $\theta_{i1}$  lower their  $\theta_{i1}$  and become more responsive to task 1-associated stimuli. Let  $N_n$  be the number of individuals characterized by a large  $\theta_{i1}$  ( $>900$ ) before removal and a low  $\theta_{i1}$  ( $<100$ ) at the time of reintroduction, and  $N_f$  the number of *these* individuals who remain task 1 specialists ( $\theta_{i1} < 100$ ) long after the reintroduction. Both  $N_n$  and  $N_f$  are expected to depend on  $T_r$ . If  $T_r$  is too small, few or none of the remaining individuals will have time to specialize in task 1:  $N_n$  and  $N_f$  should be close to 0. As  $T_r$  exceeds some value,  $N_n$  should increase, but not necessarily  $N_f$ , as the reintegration of previous task 1 specialists prevents newly promoted task 1 specialists from performing task 1. For example, O'Donnell (1998) observes a time lag between the artificial removal of water foragers and the activation of replacement water foragers in the wasp *Polistes instabilis*: this time lag might be the equivalent of the first threshold value of  $T_r$ , but it is not possible to determine, on the sole basis of this obser-

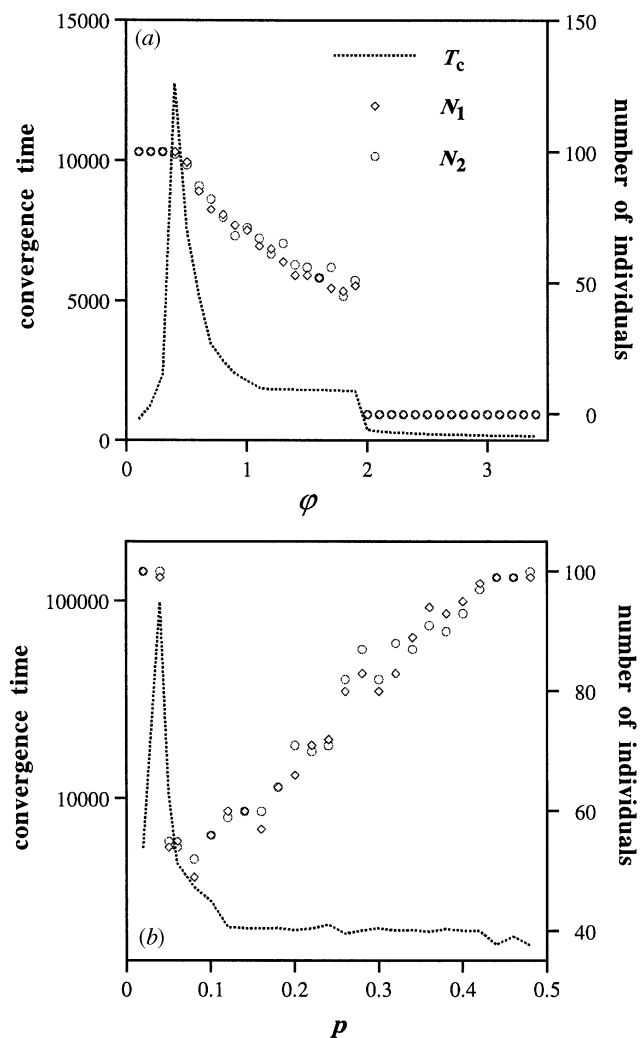


Figure 2. (a) Convergence time  $T_c$  (the time it takes for the following condition to be satisfied:  $\forall i \in \{1, \dots, N\}, \forall j \in \{1, \dots, m\}, \theta_{ij} > 900$  or  $\theta_{ij} < 100$ ), and  $N_1$  and  $N_2$  (the number of specialists of tasks 1 and 2, respectively) as a function of  $\varphi$  (forgetting rate) for  $N=100$  and  $m=2$ , assuming that  $\varphi + \xi = 11$  (where  $\xi$  is the learning rate),  $\alpha=3$ ,  $\delta=1$ ,  $p=0.2$ ,  $\sigma=0.1$ .  $\forall i \in \{1, \dots, N\}, \forall j \in \{1, \dots, m\}, \theta_{ij}(t=0) = 500$  and  $x_{ij}(t=0) = 0.1$ . (b) Convergence time  $T_c$ ,  $N_1$  and  $N_2$  as a function of  $p$  (probability per unit time of becoming inactive) for  $N=100$ ,  $m=2$ ,  $\alpha=3$ ,  $\delta=1$ ,  $\xi=10$ ,  $\varphi=1$ ,  $\sigma=0.1$ .  $\forall i \in \{1, \dots, N\}, \forall j \in \{1, \dots, m\}, \theta_{ij} = 500$  and  $x_{ij}(t=0) = 0.1$ .

vation, whether thresholds are fixed or variable; what it suggests, however, is that different individuals in the colony have different response thresholds with respect to water needs. As  $T_r$  exceeds another threshold,  $N_f$  should also increase because task fixation of newly promoted task 1 specialists has become strong and reintroduced individuals have forgotten their previous roles. In O'Donnell's (1998) experiments on *P. instabilis*, the observation of this second threshold value of  $T_r$  would be proof that the thresholds vary, otherwise only one threshold value of  $T_r$  would be observed. More experiments are required, but O'Donnell's (1998) work shows that testing the model is possible. This behaviour is shown in figure 3 ( $N=100$ ,  $m=2$ ), where the 50 task 1 specialists of the colony are removed and reintroduced after  $T_r$ ; the 50 remaining

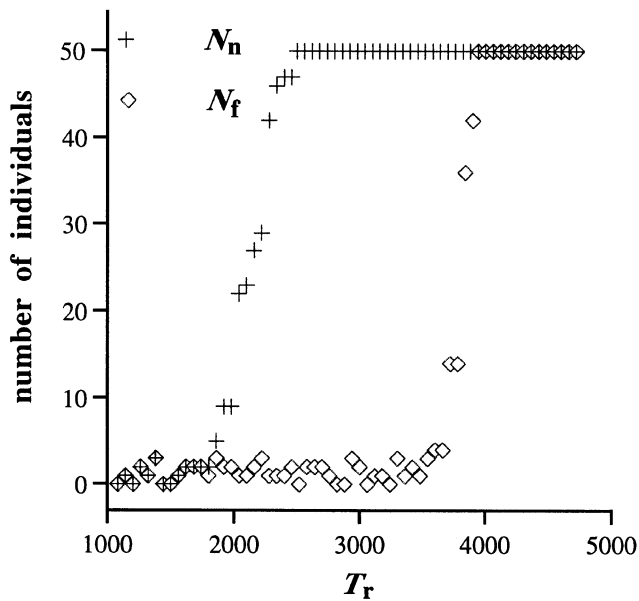


Figure 3.  $N_n$  (number of individuals characterized by a large  $\theta_{11}$  ( $>900$ ) before removal and a low  $\theta_{11}$  ( $<100$ ) at the time of reintroduction) and  $N_f$  (number of these individuals who remain task 1 specialists ( $\theta_{11} < 100$ ) long after the reintroduction of initial task 1 specialists) as a function of  $T_r$  (removal time).  $N=100$ ,  $m=2$ ,  $\alpha=3$ ,  $\delta=1$ ,  $p=0.2$ ,  $\xi=10$ ,  $\varphi=1$ ,  $\sigma=0.1$ . Fifty task 1 specialists of the colony are removed and reintroduced after  $T_r$ .

individuals start to take over task 1 performance as  $T_r$  exceeds 1700, and tend to remain task 1 specialists after reintroduction as  $T_r$  exceeds 3700. This result is the main prediction of the model, and can be tested empirically. It provides an unambiguous way of testing the learning hypothesis when, for example, task 1 is usually performed by younger individuals and task 2 by older individuals. In such a situation, removing younger individuals should induce behavioural reversion in older workers, and task 1 fixation of these older workers would be a strong indicator in favour of the reinforcement model, as such a behaviour cannot be explained by ageing.

#### 4. DISCUSSION

In conclusion, we extended response threshold models for the regulation of division of labour in social insect colonies (Bonabeau *et al.* 1996) to include learning in the form of a reinforcement process. We have shown that this extended model could account for the genesis of task allocation and within-caste specialization. If genes determine initial response thresholds, an initially low threshold favours task performance, and task performance further lowers the threshold, leading to a stabilization of the individual so that it performs the tasks for which it had low thresholds. We have also shown how the learning and task-switching rates are expected to affect specialization. For the sake of simplicity and clarity, we have not discussed temporal polyethism in this article, but the reinforcement mechanism that was described can certainly lead to stable patterns of temporal polyethism. More generally, the formulation of the model lends itself to

many modifications, and, we believe, sets the stage for a global picture of division of labour in social insects. Finally, while our model suggests that absolute age need not be invoked to explain temporal division of labour, the testable predictions made in this article with respect to the removal experiment can serve as a basis for experimental investigation of the respective weights of ageing and learning in behavioural ontogeny.

E.B. is supported by the Interval Research Fellowship at the Santa Fe Institute. G.T. is supported in part by a grant from the Conseil Régional Midi-Pyrénées. E.B. and G.T. acknowledge partial support from a grant of the Groupement d'Intérêt Scientifique (GIS) Sciences de la Cognition.

#### REFERENCES

- Bonabeau, E., Theraulaz, G. & Deneubourg, J.-L. 1996 Quantitative study of the fixed threshold model for the regulation of division of labour in insect societies. *Proc. R. Soc. Lond. B* **263**, 1565–1569.
- Bonabeau, E., Theraulaz, G. & Deneubourg, J.-L. 1998 Fixed response thresholds and the regulation of division of labour in insect societies. *Bull. Math. Biol.* (In the press.)
- Breed, M. D., Robinson, G. E. & Page, R. E. 1990 Division of labor during honeybee colony defense. *Behav. Ecol. Sociobiol.* **27**, 395–401.
- Calabi, P. 1988 Behavioral flexibility in Hymenoptera: a re-examination of the concept of caste. In *Advances in myrmecology* (ed. J. C. Trager), pp. 237–258. Leiden: Brill Press.
- Calderone, N. W. & Page, R. E. 1988 Genotypic variability in age polyethism and task specialization in the honeybee *Apis mellifera* (Hymenoptera: Apidae). *Behav. Ecol. Sociobiol.* **22**, 17–25.
- Calderone, N. W. & Page, R. E. 1996 Temporal polyethism and behavioural canalization in the honeybee, *Apis mellifera*. *Anim. Behav.* **51**, 631–643.
- Deneubourg, J.-L., Goss, S., Pasteels, J. M., Fresneau, D. & Lachaud, J.-P. 1987 Self-organization mechanisms in ant societies (II): learning in foraging and division of labour. *Experientia Suppl.* **54**, 177–196.
- Detrain, C. & Pasteels, J. M. 1991 Caste differences in behavioral thresholds as a basis for polyethism during food recruitment in the ant *Pheidole pallidula* (Nyl.) (Hymenoptera: Myrmicinae). *J. Insect Behav.* **4**, 157–176.
- Detrain, C. & Pasteels, J. M. 1992 Caste polyethism and collective defense in the ant *Pheidole pallidula*: the outcome of quantitative differences in recruitment. *Behav. Ecol. Sociobiol.* **29**, 405–412.
- Dukas, R. & Visscher, P. K. 1994 Lifetime learning by foraging honeybees. *Anim. Behav.* **48**, 1007–1012.
- Frumhoff, P. C. & Baker, J. 1988 A genetic component to division of labour within honeybee colonies. *Nature* **333**, 358–361.
- Huang, Z. Y. & Robinson, G. E. 1992 Honeybee colony integration: worker–worker interactions mediate hormonally regulated plasticity. *Proc. Natn. Acad. Sci. USA* **89**, 11 726–11 729.
- Jaisson, P., Fresneau, D. & Lachaud, J.-P. 1988 Individual traits of social behaviour in ants. In *Interindividual behavioral variability in social insects* (ed. R. L. Jeanne), pp. 1–51. Boulder, CO: Westview Press.
- Johnson, R. A. 1991 Learning, memory, and foraging efficiency in two species of desert seed-harvester ants. *Ecology* **72**, 1408–1419.
- Lenoir, A. 1979 Le comportement alimentaire et la division du travail chez la fourmi *Lasius niger*. *Bull. Biol. France Belgique* **113**, 79–314.
- O'Donnell, S. 1998 Effects of experimental forager removals on division of labour in the primitively eusocial wasp *Polistes instabilis* (Hymenoptera: Vespidae). *Behaviour* (In the press.)

- O'Donnell, S. & Jeanne, R. L. 1993 Methoprene accelerates age polyethism in workers of a social wasp (*Polybia occidentalis*). *Physiol. Entomol.* **18**, 189–194.
- Oster, G. F. 1976 Modeling social insect populations. I. Ergonomics of foraging and population growth in bumblebees. *Am. Nat.* **110**, 215–245.
- Page, R. E. & Robinson, G. E. 1991 The genetics of division of labour in honeybee colonies. *Adv. Insect Physiol.* **23**, 117–169.
- Plowright, R. C. & Plowright, C. M. S. 1988 Elitism in social insects: a positive feedback model. In *Interindividual behavioral variability in social insects* (ed. R. L. Jeanne), pp. 419–431. Boulder, CO: Westview Press.
- Robinson, G. E. 1987 Modulation of alarm pheromone perception in the honeybee: evidence for division of labor based on hormonally regulated response thresholds. *J. Comp. Physiol. A* **160**, 613–619.
- Robinson, G. E. 1992 Regulation of division of labor in insect societies. *A. Rev. Entomol.* **37**, 637–665.
- Robinson, G. E. & Page, R. E. 1988 Genetic determination of guarding and undertaking in honeybee colonies. *Nature* **333**, 356–358.
- Robinson, G. E., Page, R. E. & Huang, Z.-Y. 1994 Temporal polyethism in social insects is a developmental process. *Anim. Behav.* **48**, 467–469.
- Schatz, B. 1997 Modalités de la recherche et de la récolte alimentaire chez la fourmi *Ectatomma ruidum* Roger: flexibilités individuelle et collective. Ph.D. thesis, Université Paul Sabatier, Toulouse, France.
- Seeley, T. D. 1982 Adaptive significance of the age polyethism schedule in honeybee colonies. *Behav. Ecol. Sociobiol.* **11**, 287–293.
- Seeley, T. D. 1989 Social foraging in honeybees: how nectar foragers assess their colony's nutritional status. *Behav. Ecol. Sociobiol.* **24**, 181–199.
- Seeley, T. D. 1992 The tremble dance of the honeybee: message and meanings. *Behav. Ecol. Sociobiol.* **31**, 375–383.
- Sendova-Franks, A. B. & Franks, N. R. 1994 Social resilience in individual worker ants and its role in division of labour. *Proc. R. Soc. Lond. B* **256**, 305–309.
- Theraulaz, G., Goss S., Gervet, J. & Deneubourg J.-L. 1991 Task differentiation in *Polistes* wasp colonies: a model for self-organizing groups of robots. In *From animals to animats* (eds J.-A. Meyer & S. W. Wilson), pp. 346–355. Proceedings of the First International Conference on Simulation of Adaptive Behavior, Cambridge, MA: MIT Press/Bradford Books.
- Theraulaz, G., Gervet, J., Thon, B., Pratte, M. & Semenov-Tian-Chansky, S. 1992 The dynamics of colony organization in the primitively eusocial wasp *Polistes dominulus* (Christ). *Ethology* **91**, 177–202.
- Tofts, C. & Franks, N. R. 1992 Doing the right thing: ants, honeybees and naked mole-rats. *Trends Ecol. Evol.* **7**, 346–349.
- Tofts, C. 1993 Algorithms for task allocation in ants. A study of temporal polyethism: theory. *Bull. Math. Biol.* **55**, 891–918.
- Van der Blom, J. 1993 Individual differentiation in behaviour of honeybee workers (*Apis mellifera* L.). *Insectes Sociaux* **40**, 345–361.
- Wilson, E. O. 1984 The relation between caste ratios and division of labor in the ant genus *Pheidole* (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* **16**, 89–98.
- Withers, G. S., Fahrbach, S. E. & Robinson, G. E. 1993 Selective neuroanatomical plasticity and division of labour in the honeybee. *Nature* **364**, 238–240.