Neural Networks as Mechanisms to Regulate Division of Labor

Paweł Lichocki,[1,*] Danesh Tarapore,[1,2,*,†] Laurent Keller,[2,‡] and Dario Floreano[1,‡,§]

1. Laboratory of Intelligent Systems, École Polytechnique Fédérale de Lausanne, Station 11, CH-1015 Lausanne, Switzerland;
2. Department of Ecology and Evolution, Biophore, University of Lausanne, Dorigny, CH-1015 Lausanne, Switzerland

ABSTRACT: In social insects, workers perform a multitude of tasks, such as foraging, nest construction, and brood rearing, without central control of how work is allocated among individuals. It has been suggested that workers choose a task by responding to stimuli gathered from the environment. Response-threshold models assume that individuals in a colony vary in the stimulus intensity (response threshold) at which they begin to perform the corresponding task. Here we highlight the limitations of these models with respect to colony performance in task allocation. First, we show with analysis and quantitative simulations that the deterministic response-threshold model constrains the workers' behavioral flexibility under some stimulus conditions. Next, we show that the probabilistic response-threshold model fails to explain precise colony responses to varying stimuli. Both of these limitations would be detrimental to colony performance when dynamic and precise task allocation is needed. To address these problems, we propose extensions of the response-threshold model by adding variables that weigh stimuli. We test the extended response-threshold model in a foraging scenario and show in simulations that it results in an efficient task allocation. Finally, we show that response-threshold models can be formulated as artificial neural networks, which consequently provide a comprehensive framework for modeling task allocation in social insects.

Keywords: task allocation, social insects, division of labor, response thresholds, neural networks.

Introduction

High levels of cooperation are often cited as the primary reason for the ecological success of social insects (Oster and Wilson 1978; Hölldobler and Wilson 1990; Robinson 1992). In social insects, workers perform a multitude of tasks, such as foraging, nest construction, and brood rearing, without central control of how work is allocated among individuals (Wilson and Hölldobler 1988; Seeley

* These authors contributed equally to this work.
† Present address: Institute for Systems and Robotics, Instituto Superior Técnico, 1049-001 Lisboa, Portugal.
‡ These authors contributed equally to this work.
§ Corresponding author; e-mail: dario.floreano@epfl.ch.

1989; Gordon 1996; Pratt 2005). Experimental evidence indicates that individuals in a colony vary in their propensity to perform different tasks (Oldroyd et al. 1993; Julian and Cahan 1999; Kryger et al. 2000; Jones et al. 2004; Robinson et al. 2009). It has been suggested that workers choose a task by responding to stimuli gathered from the environment (e.g., presence or absence of food) or from interactions with other workers (Bonabeau et al. 1996).

Empirical studies have identified a variety of factors affecting the stimulus intensity (response threshold) at which workers begin to perform a given task (Duarte et al. 2011). First, in many species there is a strong division of labor based on the age of workers, a phenomenon designated "age polytheism" (Wilson 1971; Oster and Wilson 1978). Second, size and morphology are also strongly correlated with the likelihood of workers to undertake various tasks in species with distinct morphological castes (Wilson 1980). Third, in species with multiply mated queens or multiple queens per colony, different patrilines and matrilines tend to differ in their tendencies to perform certain tasks, demonstrating a genetic component in response threshold (e.g., Robinson and Page 1988). Finally, individual experience has been shown to influence task preference in the ant *Cerapachys biroi* (Ravary et al. 2007).

The combined effects of age, size, genetic background, and individual experience should lead to substantial intracolony variation in response thresholds. The resulting difference in the responses of workers to a given stimulus intensity leads to individuals with a lower threshold for a given task being more likely to perform that task than individuals with a higher threshold. A variety of models have been proposed to account for the emergence of intracolony division of labor on the basis of variation in response thresholds (Robinson 1987, 1992; Bonabeau et al. 1996; Page and Mitchell 1998; Théraulaz et al. 1998; Graham et al. 2006; Jeanson et al 2007; also see Beshers and Fewell 2001; Smith et al. 2008).

The two most often used models are the deterministic response-threshold model (DTM; Page and Mitchell 1998)

and the probabilistic response-threshold model (PTM; Bonabeau et al. 1996). Both models assume that all workers receive information about colony needs via commonly perceived stimuli. In the DTM, each worker performs the task with the highest positive difference between the stimulus and its own corresponding response threshold. If all the stimuli are lower than the corresponding thresholds, then the worker remains idle. In the PTM, the relation between stimulus and threshold is interpreted as the probability of performing the task. While these response-threshold models are frequently used to explain division of labor in colonies of social insects (Bertram et al. 2003; Graham et al. 2006; Jeanson et al. 2007), no attempts have been made to quantify their efficiency in task allocation. Here, we show with analysis and quantitative simulations that using the DTM (Page and Mitchell 1998) and the PTM (Bonabeau et al. 1996) leads to suboptimal colony performance under some stimulus conditions. To overcome these problems, we propose an extended response-threshold model (ETM) that can result in an efficient task allocation for any stimulus conditions. We experimentally compare all models by means of directed evolution (Nolfi and Floreano 2000; Floreano and Keller 2010) in a foraging scenario that requires a dynamic reallocation of workers to different tasks according to colony needs (Tarapore et al. 2010). Finally, we show that the response-threshold models can be formulated as artificial neural networks (McClelland et al. 1986; Haykin 1998), which consequently constitute a comprehensive framework for modeling task allocation in social insects.

Material and Methods

Task Allocation Mechanism

We assumed that workers receive information about colony needs via commonly perceived stimuli and that workers' thresholds do not vary during their lifetime. We considered a colony composed of 1,000 workers facing two distinct tasks. In the DTM, every worker has two thresholds, corresponding to the two tasks. A worker performs the task with the highest positive difference between the stimulus and its own corresponding response threshold; it remains idle if both of its thresholds are higher than the stimulus (Page and Mitchell 1998; Jeanson et al. 2007). If the difference between the stimulus and the worker's corresponding response thresholds is the same for both tasks, one of them is randomly chosen and performed by the worker. In the PTM, every worker has two thresholds, corresponding to the two tasks, and the difference between the stimulus and the response threshold constitutes the probability that the worker will engage in the corresponding task. In appendix D, available online, we show that

our probabilistic model is very similar to the original probabilistic response-threshold model (Bonabeau et al. 1996), because both models lead to similar colony performance and patterns of division of labor. In the ETM, every worker has two thresholds, corresponding to the two tasks, and two weights, corresponding to the two stimuli. A worker performs the task with the highest positive difference between the weighted stimulus and its own corresponding response threshold; it remains idle if both of its thresholds are higher than the weighted stimuli. If the difference between the weighted stimulus and the worker's corresponding response threshold is the same for both tasks, one of them is randomly chosen and performed by the worker. For formal definitions of all models, see appendix A, available online.

The response-threshold models (DTM and PTM) and the extended response-threshold model (ETM) can all be formulated as a more general class of parallel distributed-processing models known as artificial neural networks (McClelland et al. 1986; Haykin 1998; Lek and Guégan 1999). Artificial neural networks have been successfully used to control the behavior of individuals in a colony (see, e.g., Floreano et al. 2007; Waibel et al. 2009), making it a useful approach to consider in modeling task allocation in social insects. An artificial neural network is a computational model that consists of a set of units (neurons) connected by weighted links, where the response of the output units is the sum of the weighted inputs (McClelland et al. 1986). In the DTM and the PTM, each stimulus constitutes an input, the thresholds are the weights of the additional input constantly set to -1, and the allocated task for the worker is derived from the output neurons (fig. 1*A*, 1*B*). While in the DTM and the PTM the weights for task stimuli are set to 1, in the ETM they can vary between workers (fig. 1*C*). In the DTM and the ETM, a worker performs the task corresponding to the output unit with the highest positive value; it remains idle if both outputs are less than or equal to 0. In the PTM, the values of the output units are interpreted as probabilities of performing the corresponding tasks.

In artificial neural networks with so-called hidden neurons, a nonlinear activation function that transforms the output of the neuron is often used. Because the artificial neural networks used here do not need nonlinear activation functions and do not have hidden units, we do not mention such a function explicitly. Mathematically speaking, we consider the activation function to be the identity function. If the neuronal formalism is extended, one may use the activation function, depending on the needs of the architecture.

A. DTM

B. PTM

C. ETM
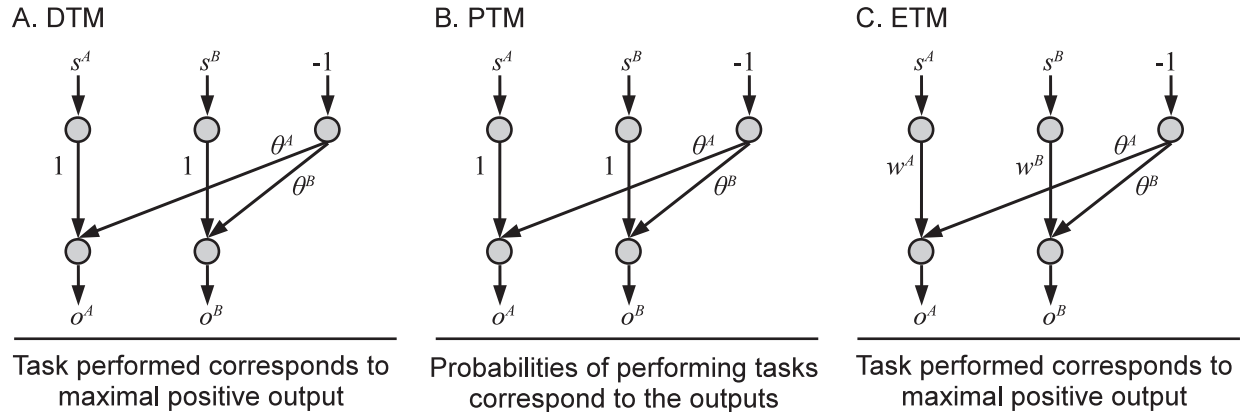
Figure 1: Task allocation mechanisms: *A*, deterministic response-threshold model (DTM); *B*, probabilistic response-threshold model (PTM); *C*, extended response-threshold model (ETM). Consider a colony composed of multiple workers facing two tasks, A and B. s^A stands for the task A stimulus and s^B for the task B stimulus; θ^A and θ^B are the corresponding thresholds. Outputs are the sum of the weighted inputs and are calculated as $o^A = 1 \times s^A - \theta^A$ and $o^B = 1 \times s^B - \theta^B$ for the DTM and the PTM and as $o^A = w^A \times s^A - \theta^A$ and $o^B = w^B \times s^B - \theta^B$ for the ETM. Note that the ETM uses two additional variables, namely, w^A and w^B, which are the weights for the connections between corresponding input and output neurons. In the case of DTM and PTM, these weights are constant and set to 1. In *A* and *C*, each worker collects items of the type corresponding to the output unit with highest positive value or remains idle if both outputs are less than or equal to 0. In *B*, the values of the output units are interpreted as probabilities that the worker chooses the corresponding task. For the sake of simplicity, we considered a situation with only two tasks, but the presented formalism scales to any number of tasks.

Colony Tasks

To quantify the workers' efficiency in task allocation, we used a stochastic agent-based simulation to model a situation in which workers had to perform two distinct tasks (Tarapore et al. 2010). Our aim was to mimic situations with two vital tasks, such as foraging and regulation of nest temperature. If the colony is efficient in foraging but does not regulate nest temperature well, the brood may die. Conversely, if nest temperature is well regulated but little food is collected, then only a few offspring can be reared. A colony consisted of 1,000 workers placed in an environment with an infinite number of two types of items, foraging and regulatory. The colony life span was divided into 100 time steps. At the beginning of each time step, a worker was presented with two task stimuli, one for the foraging items and the other for the regulatory items. If there were no items in the nest, the corresponding stimulus was set to its maximal intensity, which was 1. Otherwise, the intensity of the stimulus for each task was inversely proportional to the number of corresponding items in the nest. At each time step, every worker performed the chosen task (or stayed idle) according to the task-allocation mechanism (DTM, PTM, or ETM) considered in the experiment. At each time step, a worker had a probability of 0.1 of successfully collecting one item corresponding to the task performed, and at each time step the number of foraged and regulated items in the nest was depleted by 10 items, with an expected probability of

0.4. For formal definitions of the stimulus dynamics and the foraging scenario, see appendix C, available online.

Colony performance directly depended on the number of foraging items collected, but these were counted only when the number of regulatory items in the nest was within predefined bounds (140–160 items). At the first time step of a simulation, there were no items of the foraging and regulatory tasks in the nest. The colony performance (fitness) f was calculated by adding the partial performance obtained at each time step, with $f = \sum_{t=1}^{100} f(t)$, where the colony performance at each time step ($f(t)$) was quantified as the number of items of the foraging task collected when the number of items of the regulatory task present in the nest was between 140 and 160: $f(t) = b(t) \times g^F(t)$, where $b(t) = 1$ if $140 \le g^R(i) \le 160$ and $b(t) = 0$ otherwise, $g^F(t)$ represents the number of items foraged at time step t, and $g^R(t)$ represents the number of items being regulated within the nest at time step t. Thus, if colonies performed well in only one of the two tasks, their fitness was low. We normalized the resulting fitness values by 10,000, which is the expected number of foraging items collected if all 1,000 workers were foraging for all 100 time steps with the probability of success equal to 0.1.

In all simulations, the regulatory bounds were constantly fixed to the same values (140–160 items; Tarapore et al. 2010). Changing the regulatory bounds would not qualitatively affect our results. First, the regulatory bounds

have to be narrow for the regulatory task to require a dynamic reallocation of workers. Thus, the difference between the regulatory upper bound and the regulatory lower bound should not be varied. Second, placing the regulatory bounds on a different level (e.g., 100–120 or 200–220 items) would change only the relative lengths of the "initialization" phase (i.e., when the regulatory items are accumulated to reach the lower bound for the first time) and the "control" phase (i.e., when the regulatory items are maintained within the regulatory bounds). Such a change does not qualitatively affect any of the models' properties that we investigated.

The fitness function used here leads to a strong influence of the efficient performance of the regulatory task on the benefits of foraging. It is likely that the efficient performance of two tasks frequently does not interact so strongly under natural conditions. However, we used such a strong on-off transition to get clearer results on the processes regulating the efficient performance of two complementary tasks. In some cases, such a strong on-off transition may also occur in natural situations, for example, as a result of dramatic variation in temperature affecting brood survival or colony response to flooding (which requires rapid movement of all individuals to avoid colony extinction). Note also that, for simplicity, we assume no conflict of interest among colony members about task allocation (i.e., the fitness of all colony members is proportional to overall colony performance). This would, for example, be the case in a species where workers are completely sterile or when task performance does not affect the likelihood that an individual will reproduce in the future.

Genetic Architecture

In experiments with the DTM, each worker had a genome consisting of two thresholds, both ranging from −1 to 1 (8-bit encoding, 256 possible real values, with a resolution of 1/128). In experiments with the PTM, each worker had a genome consisting of two thresholds, both ranging −1 to 1 (8-bit encoding, 256 possible real values, with a resolution of 1/128). In experiments with the ETM, each worker had a genome consisting of two thresholds and two weights, all ranging from −1 to 1 (8-bit encoding, 256 possible real values, with a resolution of 1/128).

Although threshold values are typically expected to be nonnegative (Bonabeau et al. 1996; Page and Mitchell 1998; Graham et al. 2006; Jeanson et al. 2007), we allowed values between −1 and 1 in order to be consistent with the formalism of neural-networks weights. We conducted a control experiment for the DTM with thresholds in the range from 0 to 1 (8-bit encoding, 256 possible values, with a resolution of 1/256) to make sure that our choice

did not significantly affect the result of the experiments. We support this claim in appendix D, showing that the difference in the range of threshold values does not importantly alter the division of labor patterns and colony behavior in the treatments with the DTM.

Reproduction and Selection

Artificial selection was conducted in 30 independent replicates for each of the three treatments. We used populations of 1,000 colonies, each consisting of 1,000 workers. At the first generation of each replicate, the alleles of all million workers were set randomly to one of the 256 values between −1 and 1, with a resolution of 1/128. To construct the 1,000 colonies of the next generation, we selected the 300 colonies with the highest fitness (performance). This selected pool of 300 × 1,000 workers was used to create the next generation of workers by using fitness-proportional selection (i.e., the probability of a worker contributing to the next generation was proportional to its colony's fitness). The million newly created workers were then randomly distributed among the 1,000 new colonies of the following generation. Finally, the alleles of the workers were mutated; that is, with a probability of 0.001, each allele was set randomly to one of the 256 values between −1 and 1, with a resolution of 1/128.

Worker Behavior and Statistical Analysis

To compare the task-allocation efficiency for the DTM, the PTM, and the ETM, we averaged, for each treatment and replicate, the performance of the 1,000 colonies (30 replicates per treatment) at generation 1,000. The same procedure was applied to compare other characteristics of the models. In order to understand the difference in performance between the models, we compared the proportion of workers in each of the three states (foraging, regulating, and idle) averaged over all 100 time steps (fig. 3). We also compared the proportion of workers in each of the three states as a function of the time step (fig. 4). Next, we compared the number of workers' transitions between states summed over all 1,000 workers and all 100 time steps, normalized by the number of all state transitions (separately for each model). Next, we compared the time that the regulatory items were out of the predefined bounds during the entire colony life span (fig. 6A). We also compared the time until the regulatory items were within the predefined bounds (140–160) for the first time (fig. 6B). Finally, we compared the proportion of colonies that kept the regulatory items within the predefined bounds as a function of the time step (fig. 7). In a statistical test, we compared the proportion of colonies that kept the regulatory items within the predefined bounds after they

were within the predefined bounds for the first time (in order to provide a fair comparison, this test was performed at the fiftieth time step for all treatments). Statistical significance within all treatments was determined with the Kruskal-Wallis test (nonparametric one-way analysis of variance) and that between a pair of treatments with the Wilcoxon test (rank-sum test for equal medians). The statistical tests were performed after the thousandth generation.

Results

Theory

The common understanding of the response-threshold models is that a worker's tendency to perform various tasks depends on its thresholds and that by changing its threshold values, the worker can express any behavior, from generalist (switching between tasks) to specialist (dedicated to a specific task; Robinson 1992; Bonabeau et al. 1996; Beshers and Fewell 2001). However, a mathematical analysis of the DTM reveals that a worker's behavioral flexibility depends not only on the its thresholds but also on the difference between stimulus intensities. In particular, a worker can switch from task A to task B only if there is a decrease in the difference between stimulus intensities of task A and task B. A worker can switch back from task B to task A only if there is an increase in that difference (see app. B, available online, for more details). Thus, contrary to the intuition behind response-threshold models (Robinson 1992), the workers' behaviors are influenced not only by the absolute intensities of the stimuli but also by their relative intensities. Consequently, the values of the stimuli constrain the worker's ability to switch tasks, regardless of the values of the individual thresholds. In the PTM, this constraint is less marked, because the workers' responses are stochastic, thus allowing them to switch tasks more easily. However, stochastic individual responses make the response at the colony level more unreliable, even under fixed stimulus conditions (i.e., for the same stimulus intensities, the response of a worker may be different because of its random component). Thus, both the DTM and the PTM have limitations that could be detrimental to colony performance. These problems can be overcome by extending the DTM with additional variables that weigh stimuli (ETM; fig. 1). The weights relax the constraints on the flexibility of task allocation by allowing the workers to scale the stimuli if necessary (see app. B for more details). At the same time, the deterministic decision rules employed in the ETM allow the workers to precisely respond to changing colony needs.

Simulations

To test whether the ETM allows a higher behavioral flexibility of workers and/or more precise responses at the colony level to varying stimuli, hence translating into higher colony performance, we conducted experimental evolution with a stochastic agent-based simulation to model a situation in which workers had to perform two distinct tasks. The first was a regulatory task, where workers had to maintain the amount of a given food item in their colony within predefined bounds. This would, for example, be the case for a honeybee colony maintaining about 1 kg of pollen in the hive or workers regulating within-hive temperature (Seeley 1995). The other was a foraging task, where workers had to collect the highest possible amount of a second type of food item. Consequently, at a given point in time, a worker could be engaged in the regulatory task, engaged in the foraging task (foraging worker), or inactive (idle worker). The fitness of colonies was a function of workers being able to perform both tasks efficiently (Tarapore et al. 2010, see "Material and Methods").

For each of the three models, the performance of the colonies rapidly increased within the first 200 generations of selection and converged within 1,000 generations (fig. 2). However, there were important efficiency differences between the models (Kruskal-Wallis test: $df = 2$, $P < .001$). The highest performance was achieved for the ETM (PTM: -10.3% [i.e., 10.3% worse than that for the ETM]; DTM: -20.4%; all pairwise Wilcoxon tests: $df = 29$, $P < .001$).
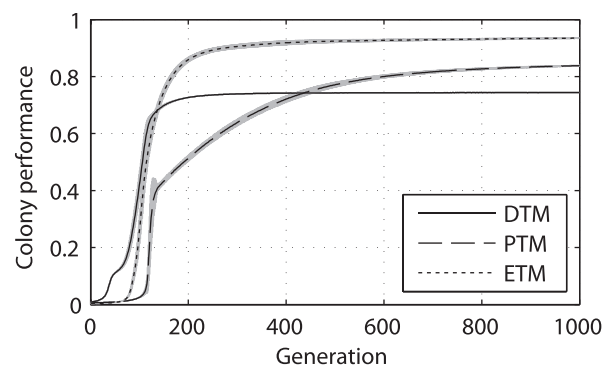

Figure 2: Mean performance (gray indicates SD) of each of the three response-threshold models over 1,000 colonies (30 replicates). The performance directly depended on the number of the collected items of the foraging task, but these were counted only when the number of items of the regulatory task was within predefined bounds. Thus, the performance was high only if the workers efficiently performed both the regulatory and the foraging tasks. See figure 1 for definition of DTM, PTM, and ETM.

The difference in performance between threshold models was associated with differences in the proportion of workers engaged in the foraging task (Kruskal-Wallis test: df = 2, $P < .001$). The proportion of foraging workers was the highest for the ETM (PTM: −1.1%; DTM: −10.5%; all pairwise Wilcoxon tests df = 29, $P < .001$; fig. 3). The proportion of workers staying idle also differed (Kruskal-Wallis test: df = 2, $P < .001$) and was the lowest for the ETM (PTM: +2,293.2%; DTM: +21,907.5%; all pairwise Wilcoxon tests: df = 29, $P < .001$; fig. 3). By contrast, there was only little variation in the proportion of workers engaged in the regulatory task (fig. 3), although the differences among models were significant (Kruskal-Wallis test: df = 2, $P < .001$). Furthermore, with the PTM the proportion of foraging workers was not constant during the entire colony life span and decreased in time, which was not observed for other models (fig. 4).

The differences in workers' distribution among the three threshold models was associated with the differences in the frequency of worker transitions between being engaged in the foraging and regulatory tasks and staying idle (six Kruskal-Wallis tests, one for each type of transition: all df = 2, all $P < .001$; fig. 5). In line with theoretical predictions, the behavioral flexibility between the foraging and regulatory tasks was constrained in the DTM, with the effect that the workers switched much more often between the regulatory task and staying idle than in other models (all pairwise Wilcoxon tests: df = 29, $P < .001$; fig. 5). This lack of flexibility in switching tasks resulted in a high proportion of idle workers in the DTM, so as to enable an efficient response to changes in colony needs (fig. 3). By contrast, with the PTM and the ETM the workers readily switched between the regulatory and foraging tasks (all
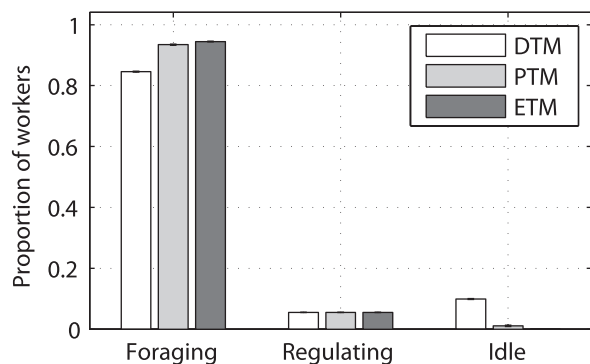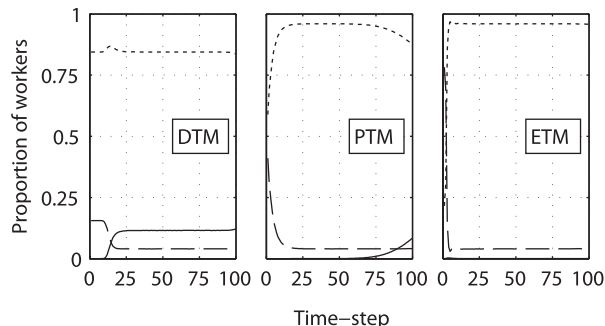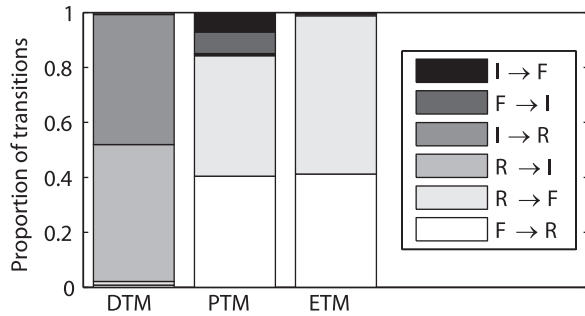

Figure 4: Mean proportion of workers engaged in the foraging task (short-dashed line), engaged in the regulating task (long-dashed line), or staying idle (solid line) as a function of time steps. Results are given for each of the three models over 1,000 colonies of the thousandth generation (30 replicates). See figure 1 for definitions of DTM, PTM, and ETM.

pairwise Wilcoxon tests: df = 29, $P < .001$; fig. 5), thus not requiring the colonies to maintain a high proportion of idle workers (fig. 3).

The difference in foraging strategies induced by the three threshold models translated into variation in the proportion of time during which the regulatory items were out of the predefined bounds during colony life span (Kruskal-Wallis test: df = 3, $P < .001$). The most efficient regulation was with the ETM (all pairwise Wilcoxon tests: df = 29, $P < .001$; fig. 6A). The difference between models in the efficiency of regulation was primarily due to two factors. First, there were differences in the time until the regulatory items were within the predefined bounds for the first time (Kruskal-Wallis test: df = 3, $P < .001$), the most efficient model being the ETM (PTM: +267.5%, DTM: +384.2%; all pairwise Wilcoxon tests: df = 29, $P < .001$; fig. 6B). Second, there were differences in the proportion of colonies that successfully kept the regulatory items within the predefined bounds after they were first within those bounds (Kruskal-Wallis test: df = 3, $P < .001$), the most efficient models being both the DTM and the ETM (PTM: −2.1%; Wilcoxon test between the DTM and the ETM: df = 29, $P = .11$; all other pairwise Wilcoxon tests: df = 29, $P < .001$; fig. 7).

We investigated the sensitivity of our findings to changes in the implementation of mutations and in the population's size. We conducted additional experiments with two alternate mutation implementations (Gaussian mutations and mutations switched off instead of uniform mutations) and two smaller population sizes (100 and 500 colonies instead of 1,000). These experiments showed that the results were robust to changes in both cases (see app. E, available online, for more details).

Figure 3: Mean ± SD proportion of workers engaged in foraging, regulating, or staying idle. Results are given for each of the three models over 100 time steps and 1,000 colonies of the thousandth generation (30 replicates). See figure 1 for definitions of DTM, PTM, and ETM.

Figure 5: Mean proportion of transitions between being engaged in foraging or regulatory tasks and staying idle, summed over 1,000 workers. R stands for the regulatory task, F stands for the foraging task, I stands for idle, and the arrow indicates for the direction of the transition. Results are given for each of the three models over 100 time steps and 1,000 colonies of the thousandth generation (30 replicates), normalized separately for each model by the number of all state transitions (number of all state transitions: DTM: 3,829 ± 147, PTM: 10,926 ± 296, ETM: 4,543 ± 327). See figure 1 for definition of DTM, PTM, and ETM.

Discussion

A comparison of the deterministic (Page and Mitchell 1998), the probabilistic (Bonabeau et al. 1996), and our new extended response-threshold models showed that they affect the workers' responses to varying stimuli and colony performance. As predicted by our formal analysis, the deterministic response-threshold model was found to constrain the workers' ability to switch tasks because workers with a high foraging threshold and a low regulatory threshold became idle when the regulatory items were within bounds and the foraging stimulus was lower than the workers' thresholds. Consequently, colony performance was low in this model when dynamic task allocation was required. In the case of the probabilistic response-threshold model, the workers' behavioral flexibility was less limited, but the colony was unable to respond precisely to changes in the stimuli values by stochastically switching between tasks. This led to relatively low colony performance. In addition, when the stimuli decreased, the probability that a worker performed the corresponding tasks decreased too (even if the stimulus was above the threshold). Thus, when the foraging stimulus was low, workers more often switched between being engaged in the foraging task and staying idle, which also had a detrimental effect on colony performance. The extended model did not suffer from these limitations because the weights of the stimuli allowed the workers to switch tasks while keeping their response deterministic.

We showed that the response-threshold models (Bo-

nabeau et al. 1996; Page and Mitchell 1998) and the extended model proposed in this article could be formulated as artificial neural networks. The neuronal formalism introduced here will be useful for further extension of models, such as changing the threshold values with age or the integration of adaptive learning, where the connection weights of the neural network are updated via experience-based learnings rules (Floreano and Urzelai 2001; Floreano et al. 2008). Furthermore, one could use neural networks with recurrent connections (Mandic and Chambers 2001) to equip the workers with a memory. These and other extensions would facilitate addressing increasingly complex and biologically relevant questions on division of labor in social insects. Of note is that although we considered a situation with only two tasks, the neuronal formalism can be easily scaled for a higher number of tasks.

We focused on a situation with two tasks, one of which is regulatory (the number of items in the nest ought to be kept within boundaries) and the other maximizing (the number of foraged items ought to be maximized). The results allow us to speculate how the models compare in three other situations: (1) with two foraging tasks, (2) with two regulatory tasks, and (3) with more than two tasks. First, with two foraging tasks the simulation is strongly simplified and of little interest, because there is no need to dynamically reallocate the workers between the tasks. Thus, all models should lead to high colony performance. Second, with two regulatory tasks, there could be two outcomes, depending on whether a dynamic reallocation of the workers is required. If not, then the workers could split into two distinct subsets and handle the tasks independently. The workers from the first subset would per-
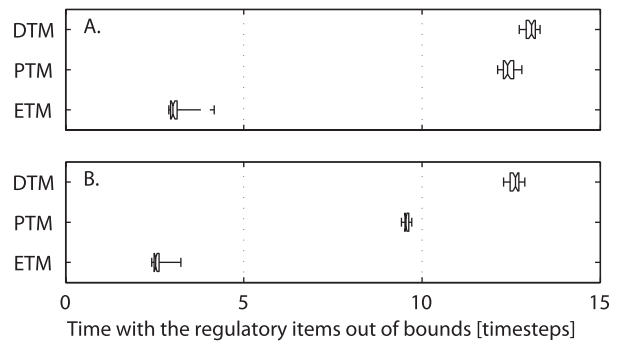
Figure 6: Box-and-whisker plots showing the number of time steps that the regulatory items were out of the predefined bounds during entire colony life span (*A*) and the number of time steps until the regulatory items were within the predefined bounds for the first time (*B*). Results are given for each of the three models over 1,000 colonies of the thousandth generation (30 replicates). See figure 1 for definition of DTM, PTM, and ETM.
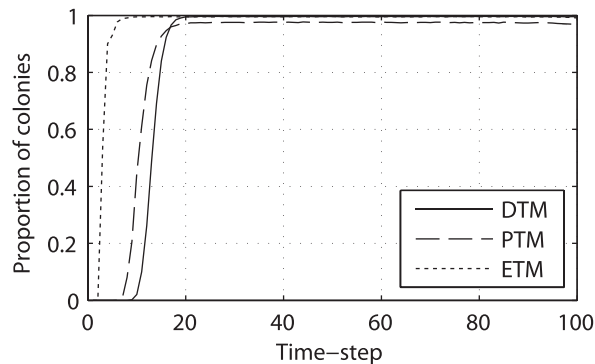
Figure 7: Mean proportion of colonies with regulatory items within the desired bounds as a function of time step. Results are given for each of the three models, over 1,000 colonies of the thousandth generation (30 replicates). See figure 1 for definition of DTM, PTM, and ETM.

form the first task or be idle, and the workers from the second subset would perform the second task or be idle. In such a case, high performance should be obtained under both the deterministic and the extended response-threshold models, while the probabilistic response-threshold model, which is unable to provide a precise colony response to a stimulus change, should lead to a lower performance. By contrast, if the dynamic reallocation of workers is required, the tasks cannot be handled independently by distinct subsets of workers. Consequently, this constitutes a condition similar to that when there is one regulatory task and one foraging task, and thus the colony performance and behavior should not differ from those observed in this study. Finally, if there are more than two tasks, all the limitations of the considered models still hold, and this should not qualitatively affect the results.

Our foraging system implicitly assumed that it was beneficial to minimize the number of idle workers. This might not always be the case in nature, as the presence of idle workers may be beneficial for the colony, for example, because of energy constraints (Gordon 1989; Robinson 1992; Krieger et al. 2000) or to serve as reserve force that can be mobilized when needed (Wilson 1983; Gordon 1989; Robinson 1992). It would be possible to include such effects in more complex foraging scenarios and to study, for example, the expected relationship between the proportion of idle workers and colony size (Jeanson et al. 2007; Dornhaus et al. 2009). Finally, we assumed that the task stimuli are available to all workers in the colony. What happens to the workers' behavioral flexibility and task allocation efficiency in cases when stimuli are available to only a subset of workers or depend on spatial configurations is a question that remains to be investigated.

To further investigate the possible consequences of partial information, we performed a simulation with the version of the deterministic response-threshold model proposed by Jeanson et al. (2007). The stimuli are presented to each worker sequentially in a random order and not all at once, as is assumed by Page and Mitchell (1998). In particular, the workers always perform the first encountered task for which their threshold is lower than the corresponding stimulus. Thus, although the decisions made by the workers are deterministic, the model does not limit the workers' ability to switch tasks, because of the random order of task encounters. The performance and the behavior of the colonies evolved in the deterministic response-threshold model with random task encounters are similar to those obtained for treatments with the extended response-threshold model (app. D). This similarity of the phenotypic traits, evolved using very different mechanisms of task allocation, is interesting and might be a promising direction for further studies.

The main focus of this article was to compare several commonly used models of task allocation. We showed that by not only allowing for variation in stimulus response thresholds but also adding weights to these perceived stimuli, one obtains a much more flexible task-allocation system. In contrast to the original response-threshold models, the extended response-threshold model performs well under a wide range of environmental stimuli. However, it remains to be investigated what rule ants and other social insects use. In particular, it would be interesting to study whether social insects employ rules more sophisticated than a fixed threshold. While evolution is often considered to be an effective optimization process (Parker and Smith 1990), there are many factors, such as stochasticity, genetic drift, insufficient time to reach the optimum, or the existence of local maxima and other developmental and physiological constraints, that may lead to nonoptimal behavior (Pérez-Escudero et al. 2009). With social insects, the question of evolutionary optimality is especially difficult to address, because colonies are complex, multicomponent systems. There are multiple functions on which persistence of a colony depends (e.g., foraging, colony maintenance, and defense) and many constraints that the colony must respect (e.g., spatial and energy). Consequently, one cannot rule out the possibility that the suboptimality of a foraging strategy might be due to increased performance of some other tasks that are also important.

It has recently been suggested that in systems of many components, the largest deviations from optimality are expected in those components with less impact on the indirect measure of fitness (Pérez-Escudero et al. 2009). Applying this idea to social groups leads to some predictions associated with colony-size differences. For example, efficient and flexible task allocation is expected to be par-

ticularly important in small colonies, which typically contain only a few idle workers. By contrast, deviations from optimality in task switching might have a lower impact in large colonies, which usually contain a substantial reserve force that can be mobilized when needed (Wilson 1983; Gordon 1989; Robinson 1992). It would thus be of interest to compare the mechanisms of task allocation among species varying in colony size and also to investigate whether there are differences within species during the ontogeny of the colony.

Overall, our analyses highlight the limitations of the response-threshold models that are currently used in the literature (Robinson 1987, 1992; Bonabeau et al. 1996; Page and Mitchell 1998; Théraulaz et al. 1998; Beshers and Fewell 2001; Bertram et al. 2003; Graham et al. 2006; Jeanson et al. 2007; Smith et al. 2008). We extended these models by weighting the stimuli. We also showed that response-threshold models could be formulated as artificial neural networks, thus providing a solid theoretical framework for further studies. Finally, it is worth mentioning that although threshold models have been developed to explain division of labor in social insects, they may also be used to devise efficient systems of task allocation and dynamic scheduling in engineering (Bonabeau et al. 2000; Campos et al. 2000; Matarić et al. 2003; Berman et al. 2009).

Acknowledgments

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