

## Limitations of response thresholds models of division of labor

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### Extended Abstract

High levels of cooperation are often cited as the primary reasons for the ecological success of social insects (Oster and Wilson, 1978; Hölldobler and Wilson, 1990). 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 (Gordon, 1996). It has been suggested that workers choose a task by responding to stimuli gathered from the environment (Robinson, 1992). 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 (see Beshers and Fewell (2001)). In (Lichocki et al., 2012), we investigated the limitations of the models of division of labor that base on the response thresholds. This abstract is meant to convey a brief summary of the points we raised in that study.

The two most often used models of division of labor are the deterministic response threshold model (DTM; Page Jr and Mitchell (1998)), and the probabilistic response threshold model (PTM; Bonabeau et al. (1996)). Both models assume that all workers receive information of the colony needs via commonly perceived stimuli. With 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 the worker remains idle. With the PTM the relation between stimulus and threshold is interpreted as a probability to perform 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. In (Lichocki et al., 2012), we showed with formal analysis and quantitative simulations that DTM (Page Jr and Mitchell, 1998) and PTM (Bonabeau et al., 1996) lead to sub-optimal colony performance under some stimulus conditions. To overcome these problems we proposed an extended response threshold model (ETM) that can result in an efficient task allocation for any stimulus conditions. We experimentally compared all models by means of directed

evolution (see, e.g., Floreano and Keller (2010)) in a foraging scenario that required a dynamic re-allocation of workers to different tasks according to colony needs (Tarapore et al., 2010).

The common understanding of the response threshold models is that the workers' tendency to perform various tasks depends on its thresholds and that, by changing the 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 the worker's behavioral flexibility depends not only on the worker's 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 of the aforementioned difference. Thus, contrary to the intuition standing behind the 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 stimuli conditions (i.e., for the same stimuli intensities the response of a worker may be different, due to its random component). Thus, both the DTM and the PTM have limitations, which could be detrimental to colony performance (Fig. 1). These problems can be overcome by extending the DTM with additional variables that weigh stimuli (ETM). The weights relax the constraints on the flexibility of task allocation by allowing the workers to scale the stimuli if needed. At the same time, the deterministic decision rules employed in the ETM allow the workers to precisely respond to changing colony needs.

Overall, our analyses highlighted the limitations of the re-

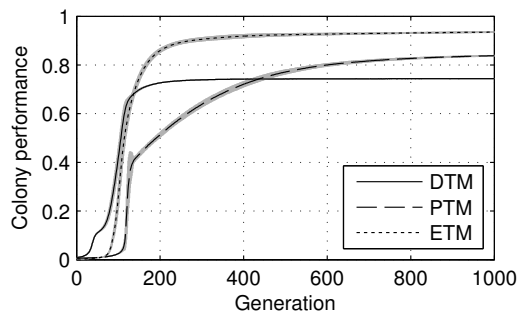


Figure 1: Mean  $\pm$  s.d. (in grey) performance with the deterministic (DTM), probabilistic (PTM), and extended (ETM) response threshold models over 1000 colonies (30 replicates). To quantify the workers' performance in task allocation we used a stochastic agent-based simulation to model a situation in which workers had to perform two distinct tasks. 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, only few offspring can be reared. Thus, the performance was high only if the workers efficiently performed both the regulatory and foraging tasks.

response threshold models that are currently used in the literature (see, e.g., Bonabeau et al. (1996); Page Jr and Mitchell (1998); Bertram et al. (2003); Graham et al. (2006); Jeanson et al. (2007)). We extended these models by weighting the stimuli. In (Lichocki et al., 2012), we also showed that the response threshold models can be formulated as artificial neural networks (see, e.g., (Haykin, 1998)). Artificial neural networks have been successfully used to control the behaviour 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. The neuronal formalism will be useful for further extension of models, e.g., changing the threshold values with age or the integration of adaptive learning. Consequently, it constitutes a comprehensive framework for modeling task allocation in social insects. Finally, it is worth mentioning that although threshold models have been developed to explain division of labor in social insect, they may also be used to devise efficient systems of task allocation and dynamic scheduling in engineering (see, e.g., Campos et al. (2000); Bonabeau et al. (2000)).

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