



## Behavioural plasticity in the fanning response of bumblebee workers: impact of experience and rate of temperature change

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Flexible division of labour is a key feature of social insects. Our understanding of individual response behaviour and how it is integrated into a functioning colony is still patchy. Most theoretical studies addressing this question are based on the assumption that workers have intrinsic and often fixed response thresholds for task-related stimuli. Here, we investigated the plasticity in worker fanning response behaviour in a bumblebee, *Bombus terrestris*. Using a temperature-controlled brood dummy, we first asked whether the fanning response is modulated by rate of temperature change. Second, we examined to what extent the fanning response is influenced by recent fanning experience. Our results show that the individual fanning response is modulated by both the rate of temperature increase and recent experience. Workers responded at lower temperatures and with a higher probability when the temperature of the brood dummy increased slowly compared with more rapid temperature increases. Workers that repeatedly responded to an increase in brood dummy temperature with fanning showed a significant decrease in their response thresholds, whereas the response thresholds of control workers that experienced the same treatment but did not gather fanning experience remained unchanged. The decrease in response threshold was pronounced when the time interval between two successive fanning events was less than 6 h. When 16 h or more separated fanning events, individual fanning responses returned to higher threshold levels. We suggest that experience-dependent modulation of response thresholds plays an important role in the behavioural differentiation of workers and the flexibility of insect colonies.

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Division of labour is a key property of insect societies. Workers perform different subsets of all tasks necessary for colony functioning and are allocated to those tasks without any central control. It is commonly assumed that division of labour among the workers of a colony is the primary reason for the unsurpassed ecological success of social insects (Oster & Wilson 1978; Hölldobler & Wilson 1990).

One of the most remarkable features of division of labour is that colonies display an amazing degree of plasticity and resiliency. They respond to external changes and internal demands by adjusting the ratios of workers allocated to the various tasks; and they are able to compensate quickly for the removal of a substantial proportion of their workforce by rapid reallocation of workers from other tasks (Theraulaz et al. 1991; Robinson 1992; Gordon 1996). Our understanding of the mechanisms integrating individual

behaviour into these amazingly flexible yet robust colony systems is still limited. What are the mechanisms underlying division of labour, and how is colony flexibility implemented at the level of the individual worker?

The current paradigm for division of labour is the response threshold model. It is built on the simple assumption that workers have intrinsic response thresholds for task-associated stimuli, and that differences in response thresholds between the workers of a colony give rise to division of labour (reviewed in Beshers & Fewell 2001). The majority of models assume individual response thresholds to be fixed. However, individual flexibility through experience and learning is presumably one of the key mechanisms underlying short-term plasticity of colony responses.

Reinforcement models incorporate experienced-based plasticity in response behaviour: performance of a task induces a decrease in the corresponding response threshold of a worker, whereas the lack of opportunity or failure in performance has the opposite effect (Plowright & Plowright 1988; Theraulaz et al. 1998). Other models assume that individual response thresholds are modulated through social interactions (O'Donnell & Bulova 2007).

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Response threshold models have been explored extensively from a theoretical perspective and have provided a much better understanding of the mechanisms underlying colony organization. However, models necessarily make simplifying assumptions concerning behavioural decision rules. The behaviour of workers within a natural colony is bound to be much more complex. In response to encountering a stimulus repeatedly and/or performing the corresponding task repeatedly, individual behaviour may be modified in different ways.

First, almost all behavioural responses are fine-tuned through learning, and experience may modulate task performance itself, i.e. the speed, efficiency, location or precision of a behaviour. Most empirical studies on the effect of experience in social insects have focused on such changes in task performance: for example, in foraging, nest repair, comb building, orientation (reviewed in Chittka & Müller 2009) or recruitment (Franklin et al. 2012).

Second, experience may modulate individual response behaviour towards the stimulus. As assumed in the reinforced threshold models, experienced workers may respond to a stimulus at lower or higher stimulus intensities (change their response threshold). They may also respond with a lower or higher probability (change their response probability). In contrast to response threshold models, individual response threshold and response probability may be two independent parameters (Weidenmüller 2004) and changes in both parameters result in changes of individual responsiveness.

It is important to note that experience-dependent changes in task performance and in task responsiveness may be two independent processes. In ants, task performance may change with increasing task experience, while the responsiveness towards the task-associated stimulus may remain unchanged (Weidenmüller et al. 2009).

Empirical evidence for a direct link between an individual's experience and its responsiveness towards a stimulus is scarce (Weidenmüller 2004; Ravary et al. 2007; Robinson et al. 2012).

Individual response behaviour may be modulated not only through recent experience, but also through characteristics of the stimulus itself. Although some task-related stimuli may signify the necessity of a task simply by being present (e.g. comb damage and resulting nest repair, or alarm pheromone triggering nest defence), others, such as temperature, are continuously present and their variation may contain information that modulates individual responses to them. In the context of the control of nest climate, for instance, individuals may display thermoregulatory behaviours as a direct response to absolute temperatures, or to the rate of thermal change (Yousif 2005). Thus, in contrast to the assumption made in most theoretical models, individual response thresholds may not be fixed to one stimulus intensity. Rather, they may result from modulation through several parameters, one of which could be the rate of stimulus change.

Thermoregulation is an ideal system to study both individual and collective plasticity in response behaviour, as temperature naturally undergoes both daily and seasonal changes and can be easily measured and manipulated, and the corresponding behavioural responses can be observed unambiguously. Like most social insects, bumblebees are able to control their nest temperature. This provides considerable independence from environmental conditions and ensures rapid and safe development of the brood. The two thermoregulatory measures employed are incubation (to increase temperature) and wing fanning (to increase evaporative cooling and thereby cooling). These measures allow colonies to maintain their brood at 28–32 °C, even under strongly fluctuating environmental conditions (Schultze-Motel 1991; Weidenmüller et al. 2002). Workers in a colony differ in their fanning response thresholds (O'Donnell & Foster 2001; Weidenmüller 2004; Gardner et al. 2007). Moreover, a study on *Bombus terrestris* provided

evidence for experience-dependent changes in responsiveness: repeated exposure of colonies to temperature stress led to a decrease in individual temperature response thresholds of the fanning workers (Weidenmüller 2004). These findings support the reinforcement models; but they are in contrast to recent findings in *B. impatiens*, in which no effect of experience on individual fanning response thresholds was observed (Duong & Dornhaus 2012). Thus, at the moment there is conflicting evidence for experience-based modulation of response thresholds in bumblebee workers. Furthermore, to date no empirical study has provided evidence for the proposed 'negative reinforcement' by not performing a task that is assumed in the reinforced threshold model by Theraulaz et al. (1998).

In order to understand how the behaviour of numerous individuals is integrated into a functioning colony, we need a detailed knowledge of individual response decisions and of how individual response behaviour is modulated. In this study, we investigated the plasticity in the fanning response behaviour of *B. terrestris* workers on a temperature-controlled brood dummy. First, we exposed workers to different temperature ramps and addressed the question of whether experiencing a fast versus a more gradual change in brood temperature modulates individual response thresholds associated with fanning behaviour. Second, we repeatedly exposed workers to a fixed increase in brood temperature and asked whether recent experience with performing the task of fanning modulates a worker's responsiveness towards a temperature change.

## METHODS

### Laboratory Colonies

Young *Bombus terrestris* (L.) bumblebee colonies were obtained from a commercial breeder (Koppert B.V., The Netherlands) and consisted of the queen and up to 26 workers at delivery. They were housed in wooden boxes (16 × 28 cm and 10 cm high) with Plexiglas covers inside a climate chamber (21.8 ± 1.4 °C, 12:12 h light:dark cycle). The boxes consisted of a nest chamber and a food chamber and had four screened ventilation holes. Colonies were supplied with ad libitum sucrose solution; defrosted, fresh honeybee-packed pollen was given directly into the nest chambers. Newly emerged workers (identified through their pale coloration, which lasts for approximately 24 h) were individually marked with numbered plastic tags (Opalithplättchen). Over the course of the experiments, colony sizes increased up to 140 workers; colonies were no longer used for experiments once they started producing sexuals.

To ensure that tested workers were naïve to the task of temperature fanning, colonies were kept at 22 °C; no insulation material was supplied and colonies were prevented from covering their nests by regularly removing canopy wax. Colonies were checked twice a day for fanning workers; these were observed only rarely (presumably CO<sub>2</sub> fanners); their identities were noted and they were not used for experiments. Experiments were performed between October 2008 and July 2009 at the University of Würzburg, Germany.

### Experimental Set-up

The set-up consisted of eight circular test arenas (diameter: 7.3 cm, height: 4.9 cm) made of Plexiglas (Fig. 1a). Each test arena had 12 ventilation holes, two indentations where sugar solution could be provided and a central temperature-controlled aluminium pin that served as a brood dummy. The base of each aluminium pin (diameter 1 cm) connected to a water-filled aluminium heating

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