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COMMENTARY

Within-individual behavioural variability and division of labour in social insects

Raphaël Jeanson*

ABSTRACT

Division of labour, whereby individuals divide the workload in a group, is a recurrent property of social living. The current conceptual framework for division of labour in social insects is provided by the response-threshold model. This model posits that the differences between individuals (i.e. between-individual variability) in responsiveness to task-associated stimuli is a key feature for task specialisation. The consistency of individual behaviours (i.e. within-individual variability) in task performance represents an additional but little-considered component driving robust patterns of division of labour. On the one hand, the presence of workers with a high level of within-individual variability presumably allows colonies to rapidly adapt to external fluctuations. On the other hand, a reduced degree of within-individual variability promotes a stricter specialisation in task performance, thereby limiting the costs of task switching. The ideal balance between flexibility and canalisation probably varies depending on the developmental stage of the colony to satisfy its changing needs. Here, I introduce the main sources of within-individual variability in behaviours in social insects and I review neural correlates accompanying the changes in behavioural flexibility. I propose the hypothesis that the positive scaling between group size and the intensity of task specialisation, a relationship consistently reported both within and between taxa, may rely on reduced within-individual variability via self-organised processes linked to the quality of brood care. Overall, I emphasise the need for a more comprehensive characterisation of the response dynamics of individuals to better understand the mechanisms shaping division of labour in social insects.

KEY WORDS: Ant, Group size, Task specialisation, Ontogeny, Plasticity

Introduction

Across biological scales, variability in phenotypic traits has long been considered as noise, but it is now recognised as beneficial, particularly to produce adaptive responses in fluctuating environments (Kussell and Leibler, 2005). An increasing number of studies are now directed at deciphering the mechanisms that generate and maintain variability in biological systems (Wolf et al., 2015). In social groups, the variability among individuals gives rise to division of labour, which can be broadly defined as the existence of individuals performing different functions from others (Michener, 1974; Jeanne, 2016). This common feature of social living has been documented across many taxa of invertebrates and vertebrates for several activities, such as nest building or hunting (Stander, 1992; Duffy et al., 2002; Holbrook et al., 2014). The highest expression of division of labour is

found in eusocial species where a reproductive caste, the queen(s), monopolises reproduction and is assisted by a caste of sterile workers performing non-reproductive tasks. Division of labour is a colony trait, whereas task specialisation is an individual attribute (Pasquaretta and Jeanson, 2018). The degree of task specialisation shows considerable variation within colonies, as some workers perform one (or a few) task(s) at the exclusion of others, while their nestmates can be engaged in more tasks. The intensity of division of labour also varies greatly both within and across taxa, and group size represents one key component explaining this trend (Jeanson et al., 2007).

The most widely accepted conceptual framework to explain division of labour is provided by the response-threshold model. This model, which was introduced a few decades ago, postulates that workers in a colony differ intrinsically in the stimulus level at which they begin to perform any task (Wilson, 1976; Robinson, 1987; Calabi, 1988; Robinson and Page, 1989; reviewed in Beshers and Fewell, 2001). Individuals with a relatively low threshold for a given task tend to respond to lower stimulus intensities, while individuals with higher thresholds start performing at higher stimulus intensities (Bonabeau et al., 1996). Task allocation based on differences among individuals' response thresholds (i.e. between-individual variability) allows colonies to provide a robust and flexible collective response to handle environmental fluctuations and satisfy colony requirements. In social insects, a worker is usually not committed for life to a given task; workers typically display age polyethism, whereby they progress through a series of different activities, and this is generally accompanied by maturational changes.

Considering only between-individual variability in response thresholds provides an incomplete picture of the ingredients required for the production of robust patterns of task allocation (Jeanson and Weidenmüller, 2014). Variation among group members is a necessary but not sufficient component, and it is also critical that the individuals perform the same activities for a certain amount of time to grant colonies the full benefits of task specialisation. Indeed, a minimal level of behavioural consistency is needed to limit the costs associated with task switching that are possibly detrimental for colony homeostasis (Fig. 1; see also below). Therefore, within-individual variability in behaviours represents another fundamental but still little-explored facet of specialisation and task allocation in social groups.

This Commentary aims first at examining the sources of within-individual behavioural variability in the context of division of labour in social insects, leaving aside the sources of between-individual variation (e.g. genetic, morphological or physiological) that have been reviewed extensively elsewhere (Jandt et al., 2014; Jeanson and Weidenmüller, 2014; Wright et al., 2019). I then ask whether differences in behavioural flexibility can explain, at least partly, the differences in the level of task specialisation. Finally, I propose a testable hypothesis to explain the positive scaling between the intensity of division of labour and group size reported consistently within and across taxa.

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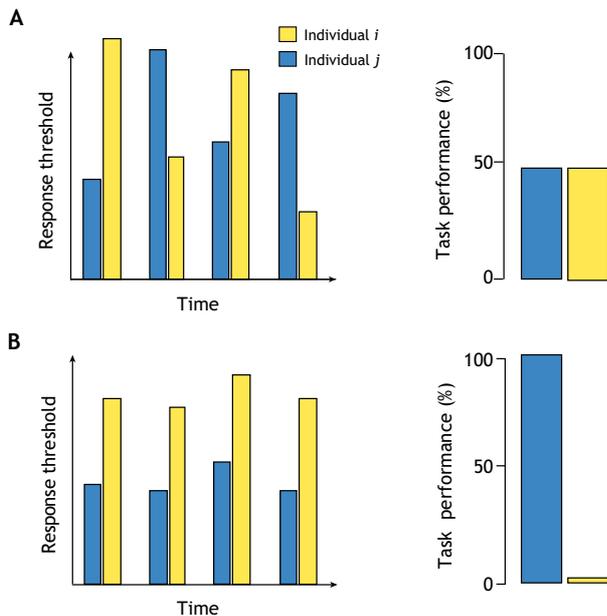


Fig. 1. Within-individual variation in response thresholds. (A) Fluctuating and (B) stable response thresholds over time for a single hypothetical task and two individuals i and j . In A, the range of within-individual variation in response threshold produces no specialisation, the task being performed equally by individuals i and j . In B, the existence of stable response thresholds generates task specialisation, with individual j being the specialist (because of its consistently lower response threshold for the task).

Within-individual versus between-individual behavioural variation

In social groups, the existence of stable patterns of task allocation implies that individuals behave consistently, i.e. that they exhibit a relatively limited within-individual variability. Hereafter, I use the terms ‘within-individual behavioural variability’ and ‘behavioural flexibility’ interchangeably to refer to any behavioural change as function of time. Within-individual variability is preferred over other terms with similar meaning (e.g. temporal plasticity; Stamps, 2016), to echo the classical use of the term ‘between-individual variation’ in the context of division of labour. Also, here, within-individual variability does not imply that observed variations are stochastic or unpredictable (Stamps et al., 2012). Importantly, within-individual variability is not restricted to age polyethism, but also includes any change in behaviour that occurs at shorter time scales (e.g. minutes or hours), the expression of which involves learning or a response to environmental changes, as described below.

The influence of within-individual variability on task allocation needs to be considered with respect to the range of between-individual variability. Indeed, within-individual fluctuations are not necessarily detrimental for the stability of task allocation patterns, provided that there is no overlap in the response thresholds between individuals (Fig. 2). It is important to note that the characterisation of absolute variations in individuals’ response thresholds to understand task allocation is of limited interest if no information is provided on the distribution of response thresholds within colonies.

A trade-off between within-individual variability and consistency

Costs associated with task switching are increasingly recognised as important drivers of division of labour (Goldsby et al., 2012).

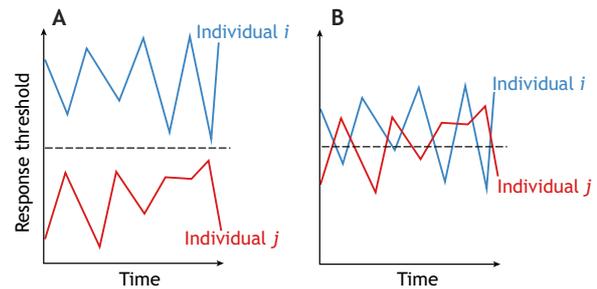


Fig. 2. Within-individual versus between-individual variability. (A,B) Each individual (i or j) shows the same temporal variation in its response threshold in the two panels for a single hypothetical task. The black dashed line represents the stimulus level. In A, the amplitude of within-individual variation in response threshold does not overlap between individuals. In the framework of the response-threshold model, only individual j performs the task in A (because its response threshold is always lower than the stimulus level). In B, the task is performed by both individuals.

Shifting between tasks can generate substantial costs resulting, for example, from transient inefficiency at the new task (Chittka and Muller, 2009), from delays required to change tasks or locations within the nest (Jeanson and Lachaud, 2015; Leighton et al., 2017) or from the time required for relevant physiological adaptations (Johnson, 2005). A low level of behavioural flexibility favours task specialisation, and this possibly improves colony homeostasis via a reduction in task-switching costs and an increase in the efficiency of task performance (e.g. Jeanne, 1986; Trumbo and Robinson, 1997; but see Dornhaus, 2008). By contrast, a high degree of flexibility allows societies to buffer environmental perturbations by reallocating the workforce in response to sudden and unpredictable fluctuations in task needs. Task-switching costs do not necessarily scale linearly with colony size, and the benefits of behavioural flexibility might vary between colonies of different developmental stages (Jeanson and Lachaud, 2015). Colonies thus face a tension between behavioural flexibility and behavioural canalisation, and the optimal trade-off probably differs as a function of life-history traits and ecological constraints.

Different degrees of behavioural flexibility

The main virtue of the response-threshold model is that it explains how colonies can maintain homeostasis by reallocating the workforce as a function of demand. This model posits that if the need for a given task is excessively high, following a major disturbance, for instance, workers are recruited to perform this task as the current level of the stimulus exceeds their threshold. Several studies have manipulated colony demography to determine to what extent colonies show flexibility to maintain homeostasis in response to external perturbations. In the ant *Pogonomyrmex barbatus*, increasing the task need for patrolling or foraging induces workers engaged in nest maintenance to switch tasks (Gordon, 1989). In the ant *Temnothorax rugatulus*, the removal of the most active individuals is compensated for by the recruitment of workers from the reserve pool of inactive individuals (Charbonneau et al., 2007). In species with age polyethism, removing part of the foraging workforce aims at testing the ability of younger workers to accelerate their maturation to take over foraging, whereas a reduction in the number of nurses aims at determining whether foragers can reverse their development to perform brood-tending tasks. Such approaches yield mixed results. In the lower termite *Reticulitermes fukienensis*, young individuals modify their

behaviours to compensate for the absence of larger and older workers (Crosland et al., 1997). In the ant *Temnothorax longispinosus*, old workers can revert to brood care after the removal of younger individuals, but young workers fail to accelerate their development to compensate for the removal of foragers (Kohlmeier et al., 2018). In honeybees, a reduction in the number of foragers induces precocious foraging in young bees, and nurse depletion triggers the behavioural reversion from foraging to brood tending, with the associated physiological changes (e.g. decline in juvenile hormone) (Huang and Robinson, 1996). It was proposed that task switching was more likely to involve tasks that need no physiological differentiation (Johnson, 2005). If task performance is coupled to physiological differentiation, individuals can be locked in a behavioural state until the perception of environmental changes triggers the required endocrinal cascade that accompanies the reversion (Johnson, 2003, 2005).

The reallocation of workers to satisfy colony requirements in response to changes in external conditions does not seem to be a universal rule. In wasps, the removal of water foragers does not increase task switching but rather increases the foraging rate of the remaining water foragers (O'Donnell, 1998). In the seed-harvester ant *Pogonomyrmex badius*, the removal of 50% of foragers is not compensated for by a transition from inside workers to foraging (Kwapich and Tschinkel, 2013). Similarly, the addition of larvae to enhance the workload for brood-tending individuals induces no behavioural reversion from foraging to nursing at the expense of brood survival (Kwapich and Tschinkel, 2016). This suggests that *P. badius* has a unidirectional progression with no possible behavioural reversion. It has been argued that a lack of behavioural flexibility might actually be optimal to allow colonies to cope with environmental seasonality and that the intensity of the experimental demographic disturbance might be of little ecological relevance (Kwapich and Tschinkel, 2016). This nevertheless invites questions about the mechanisms underlying behavioural flexibility.

Sources of within-individual variability in task performance

In the framework of response-threshold models, two categories of mechanisms can explain how individuals switch between tasks. First, the perception of large fluctuations in the intensity of task-associated stimuli can stimulate individuals to change tasks without any (substantial) change in their response threshold. Second, individuals can exhibit internal changes in their responsiveness to stimuli, and these fluctuations can elicit task switching even under stable environmental conditions. In the latter case, the variations in response threshold can operate at time scales differing by orders of magnitude, from minutes to weeks or more. The temporal window over which these behavioural variations occur has potentially important consequences for task allocation: gradual changes in response threshold are less detrimental to the stability of task allocation than sudden deviations.

There are two non-mutually exclusive sources of variation in response threshold that can account for within-individual variability in responsiveness to task-associated stimuli. (1) The variability can arise stochastically through internal noise in sensory perception or motor execution (Faisal et al., 2008). (2) Three main classes of mechanism can contribute to the modulation of individuals' responsiveness: learning, maturation and environmental changes (as outlined below).

Learning

Learning is an important source of within-individual variability (Jeanson and Weidenmüller, 2014). Repeated exposure to a given

stimulus or context can modulate an individual's responsiveness and subsequent behaviours. In the clonal ant *Ooceraea* (formerly *Cerapachys*) *biroi*, for instance, a successful foraging experience increases the likelihood of engaging in that task again (Ravary et al., 2007). Also, bumblebees that repeatedly fan their wings to cool down hives show a reduced response threshold for temperature, but individuals return to higher thresholds after prolonged interruption of their fanning behaviour (Weidenmüller, 2004; Westhus et al., 2013). Interestingly, individual variation in learning ability plays a substantial role in the development of between-individual variability. In honeybees, the responsiveness to sucrose influences the foraging role, with pollen foragers having lower response thresholds than workers collecting nectar (Page et al., 1998). In an appetitive associative learning paradigm, honeybees with high sucrose responsiveness (i.e. low response threshold for sucrose) are better learners than individuals with low sucrose responsiveness, because they give a higher value to the solution used as a reward (Scheiner et al., 2005).

Maturation

Maturation represents a second cause of within-individual variability, with potentially long-lasting effects. In social insects, ageing workers usually move from intranidal duties (typically brood tending) to external tasks (typically foraging) (wasps: Naug and Gadagkar, 1998; honeybees: Seeley, 1995; termites: Hinze and Leuthold, 1999; ants: Hölldobler and Wilson, 1990). When present, age polyethism involves several regulatory networks linked to nutritional and reproductive signalling pathways (Smith et al., 2008). For instance, foragers in social insects typically have lower lipid amounts than nurses, and the depletion of lipids in workers triggers the transition to foraging in honeybees (Toth et al., 2005) and wasps (Daugherty et al., 2011). Foragers also have more elevated levels of circulating juvenile hormones, and topical application of an analogue of juvenile hormone reduces the sucrose response threshold (Pankiw and Page, 2000). The transition from nursing to foraging in honeybees correlates with an upregulation of the *foraging* gene (which codes for a protein kinase) that modulates phototaxis (Ben-Shahar et al., 2003) and gustatory responsiveness (Thamm and Scheiner, 2014). The transition to foraging has also been associated with downregulation of the *vitellogenin* gene (which codes for an egg yolk protein and modulates the response threshold for sucrose) in honeybees (Amdam et al., 2006) or a decrease in the responsiveness to cues emitted by brood in ants (Kohlmeier et al., 2018). A worker's behaviour can also depend on the acquisition or loss of physical abilities. The growth of cephalic musculature influences the likelihood of carrying loads in the ant *Pheidole dentata* (Muscedere et al., 2011), and the perception of mandibular wear presumably prompts workers to shift from cutting to carrying leaves in the leaf-cutter ant *Atta cephalotes* (Schofield et al., 2011).

Environmental changes

The perception of environmental changes, particularly in the social context, can play an additional role in the modulation of individual behaviours. For instance, honeybees exposed to queen mandibular pheromones or brood pheromones show increased responsiveness to sucrose (Pankiw and Page, 2000, 2001). In bumble bees, workers in colonies deprived of a queen show increased ovarian development and a higher sucrose responsiveness than brood-tenders from colonies with a queen (Evans et al., 2016). In halictine bees, individuals have a reduced response threshold for excavation after they experience the presence of nestmates (Jeanson et al.,

2008). In the ant *Temnothorax albipennis*, the removal of diligent workers incites previously indolent individuals to become active, but the removed ants do not resume their prior activity levels when returned to the colony (Pinter-Wollman et al., 2012). This suggests the existence of long-lasting changes in response thresholds following a modification of the social context. The current social context experienced by individuals plays an important role in responsiveness; for example, in honeybees the probability of fanning depends on the composition of the social group (Kaspar et al., 2018). Recently, Garrison et al. (2018) assessed the fanning response of bumblebees tested alone or in groups. Interestingly, they found that the presence of conspecifics reduces the responsiveness to temperature, and that the threshold measured in a non-social context is a poor predictor of the threshold observed in a social context. These results are of particular importance when considering that the vast majority of studies quantifying response thresholds involve workers in a solitary context.

Brain plasticity in social insects

Across taxa, the mechanisms underlying the expression of behavioural plasticity have received considerable attention over recent decades (Kolb and Whishaw, 1998). Brain plasticity plays a crucial role in the ability of organisms to process external cues and to produce adaptive behaviours in a dynamic environment. The modulation of the efficacy of synaptic connections and the rearrangement of neuronal circuits are important mechanisms underlying brain plasticity that accompanies learning, maturation and environmental changes, and that participates in the expression of within-individual behavioural variability. In social insects, developmental variation in biogenic amines (e.g. dopamine, serotonin, octopamine), which act as neurotransmitters or neuromodulators, is involved in the modulation of the responsiveness to task-associated stimuli (Scheiner et al., 2006; Kamhi and Traniello, 2013). For instance, the transition from nursing to foraging is accompanied by an increase in tyramine titre in honeybees, and workers treated with tyramine show increased gustatory responsiveness to sucrose (Scheiner et al., 2017). Several studies in social insects have reported modification of brain connectivity along with behavioural changes. The modifications in brain architecture particularly concern the mushroom bodies, a region involved in multisensory integration and high-order cognitive processing (Menzel, 2014). In social insects, variation in behavioural flexibility is associated with changes in the architecture of mushroom bodies. The expansion of mushroom bodies has two components: one that does not depend on experience but prepares individuals leaving the nest to experience new stimuli (experience-expectant plasticity) and one that does depend on learning (experience-dependent plasticity) (Fahrbach et al., 1998). For example, long-term memories formed after olfactory associative learning are accompanied by structural synaptic rearrangements in the mushroom bodies (Hourcade et al., 2010). The transition from nursing to foraging coincides with an increase in the volume of the mushroom bodies (Withers et al., 1993; Gronenberg et al., 1996). The social environment experienced early in life also affects both the number of synaptic boutons in the mushroom bodies and the ability to learn complex tasks (e.g. olfactory reversal learning) in honeybees (Cabirol et al. 2018). In the ant *Pheidole dentata*, as workers age, they show a substantial expansion of their behavioural repertoire and they experience synaptic remodelling in the mushroom bodies and changes in amine titre (Seid et al., 2005; Seid and Traniello, 2006; Giraldo et al., 2016). This presumably reflects a need for increased sensorial integration and processing as

individuals leave the nest and experience a larger breadth of environmental stimuli (O'Donnell et al., 2004; Muscedere and Traniello, 2012). A comparative study between different species of the ant *Pheidole* reported that workers with the highest degree of specialisation have smaller mushroom bodies than workers with a broader task repertoire and a higher behavioural flexibility (Muscedere and Traniello, 2012). In the *Eciton* army ant, soldiers, which have a narrow task repertoire, show reduced investment in mushroom bodies compared with that of more generalist workers (O'Donnell et al., 2018). It is thus now relatively well documented that differences in behavioural flexibility correlate with changes in brain connectivity, but further efforts are still needed to establish a firm causal relationship.

Increased specialisation with group size

From multicellular organisms to human organisations, a general rule is that the size of the system dictates the degree of specialisation. Such positive scaling has also been found repeatedly both within and between taxa in social insects (Darchen, 1964; Thomas and Elgar 2003; Jeanson et al., 2007; Holbrook et al., 2011; Ulrich et al., 2018). These empirical reports suggest that variations in colony size over ontogeny are associated with changes in the level of within-individual behavioural variability. As colonies grow, individuals tend to be less flexible and more canalised. In the ant *P. barbatus*, workers engaged in nest maintenance switch tasks more easily in small than in large colonies (Gordon, 1989). In the wasp *Polybia occidentalis*, increased specialisation results from a reduction in the frequency of transition between tasks (Jeanne, 1986). From an evolutionary perspective, a lower level of specialisation in small societies is expected to be beneficial, because colonies have to maintain homeostasis with a reduced number of workers that may need to rapidly adapt to environmental changes (Moritz and Page, 1999). We still do not know, however, what mechanisms drive the scaling between individual specialisation and colony size.

One hypothesis is that increased specialisation can arise as a by-product of increased colony size without requiring any change at the individual level. Indeed, group size is a powerful driver of collective dynamics, which can incidentally influence the probabilities of engaging in a subset of tasks. For instance, colony size can modify the rate of workers' interactions or it can impact nest architecture and the spatial distribution of workers, which are then exposed to different stimuli (Buhl et al., 2004; Gordon and Mehdiabadi, 1999). An alternative and non-mutually exclusive hypothesis involves the modulation of developmental and physiological processes in response to variation in colony size. In this case, the expression of a stricter division of labour in larger societies probably relies on a combination of increased between-individual variability and/or reduced within-individual variability in task performance.

Across species, the workforce in large colonies usually shows a greater heterogeneity of response thresholds than that in small societies due to increased genetic diversity (Oldroyd and Fewell, 2007). In many species of ants, individuals in incipient societies are usually similarly sized and only colonies above a critical size produce workers that differ in size or physical attributes and that tend to specialise on different tasks (Tschinkel, 1988; Wetterer, 1994; Fjerdingstad and Crozier, 2006). However, little is known about the neuro-physiological correlates of the observed decline in behavioural variability with colony size, although a comparison between different monomorphic species of fungus-growing ants with different colony sizes at maturity revealed a negative correlation between colony size and brain size (Riveros et al., 2012). Thus far, only one study has investigated the interplay

between colony size and brain changes in the species, thereby limiting the confounding factors inherent to interspecific comparisons. In the ant *Pseudomyrmex spincicola*, it was shown that increased behavioural specialisation in large colonies correlates with a task-dependent reduction in subregions of the mushroom bodies (Amador-Vargas et al., 2015).

Linking colony size, self-organisation and behavioural flexibility

In addition to the study of the neuronal and behavioural correlates of increased canalisation, it is necessary to understand how changes in colony size are perceived and integrated to modulate the expression of behavioural flexibility. I propose that the variations in the range of an individual's behavioural flexibility over a colony lifetime can arise automatically via self-organisation (Fig. 3). Self-organisation is a process in which global patterns emerge from interactions among the lower-level components of the system, using local information with no reference to the global pattern (Camazine et al., 2001). Many collective behaviours in animal groups benefit from self-organisation, including the formation of trail networks, nest construction or decision making. I hypothesise that fluctuations in the social environment experienced during colony ontogeny might shape the extent of behavioural variability at adulthood. Changes in the preimaginal (i.e. prior to the adult stage) environment can affect the developmental trajectories of the brood with important consequences later in life. Such developmental plasticity might be adaptive, as the environment experienced early in life can provide information on future conditions (Nettle and Bateson, 2015).

In social insects, small colonies tend to be less efficient in buffering external fluctuations than large colonies, which offer more stable conditions for the developing brood (e.g. Kleineidam and Roces, 2000). Also, the size of colonies might affect the frequency and stability of brood care. Indeed, the per-capita productivity (defined as the total number of workers and sexuals produced by a colony divided by colony size) in social insects often declines with increases in colony size. In ants, colonies typically display a peak in per-capita productivity, which is followed by a decline at colony sizes much smaller than the species-specific average (Kramer et al., 2014). A major consequence of this relationship is that the brood-to-worker ratio (number of brood items divided by worker number) decreases during colony ontogeny. We can speculate that incipient societies endure more variation in brood care than large colonies and

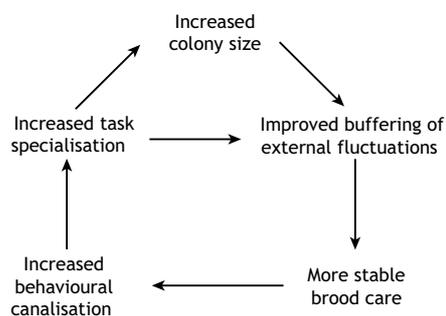


Fig. 3. Hypothetical interactions between colony size, within-individual variability and division of labour. A larger size buffers colonies against external perturbations and offers stable conditions to the brood. This might result in a reduction in within-individual variability and increased behavioural canalisation and task specialisation. Possible negative feedback (e.g. limitation in resource availability, competition) stabilising colony growth is not represented for clarity.

that fluctuations in brood attendance translate into increased within-individual behavioural variability at adulthood. This effect might be further reinforced by the fact that young workers, which are in the majority in incipient colonies, are less efficient brood tenders than old workers (Muscedere et al., 2009).

Despite the massive internal changes accompanying metamorphosis in social insects, preimaginal experience nevertheless has long-lasting consequences for a suite of traits in insects, including habitat choice, host selection or feeding behaviours at adulthood (Amat et al., 2018). For instance, honeybees exposed to a high-aggression environment during early development behave more aggressively in adulthood than bees that experience low-aggression environments (Rittschof et al., 2015). In ants, the temperature experienced by developing pupae affects the thermal response of adult brood-tending workers (Weidenmüller et al., 2009). The hypothesis that fluctuating preimaginal conditions result in increased within-individual variability in behaviours awaits empirical investigation.

In providing more steady conditions, a larger workforce in growing colonies might promote a reduction in behavioural flexibility, thus favouring increased specialisation. An increase in specialisation supports the expression of a more efficient division of labour that further reinforces stability. A reduction in behavioural plasticity in workers reared from large colonies might allow better canalisation, granting colonies the full benefits of specialisation. Moreover, a more optimal pattern of task allocation might promote the existence of a pool of inactive workers acting as a reserve that can be recruited in response to unexpected external perturbations, which further supports colony homeostasis. Therefore, a positive feedback loop involving colony size, behavioural flexibility and colony homeostasis might account for increased division of labour over a colony lifetime. We can speculate that this developmental plasticity is adaptive for incipient colonies in preparing workers to show variability in task performance at adulthood. This idea could also explain differences in the intensity of division of labour documented across species. Evaluating this hypothesis requires us to manipulate the brood-to-worker ratio in experimental colonies and to test adult workers in a series of behavioural assays (e.g. activity test, quantification of response thresholds) to assess their degree of flexibility. In addition, we should determine whether variation in behavioural plasticity translates into differences in specialisation in task performance and how this impacts the patterns of division of labour.

Overall, ontogenetic or seasonal changes in worker-to-brood ratio could represent a simple but efficient mechanism that, without any explicit coding, could shape behavioural diversity and allow colonies to produce optimal patterns of division of labour.

Future research directions

Most of our knowledge on the proximate mechanisms of division of labour in social insects, including its physiological basis, originates from work on honeybees. These studies were of prime importance and opened avenues for research in other taxa. However, we should ask to what extent the mechanisms identified in honeybees are valid in other taxa and in less-derived societies, particularly in the context of the influence of colony size on task specialisation. In honeybees, colony size can vary between 5000 and 50,000 individuals depending on the phase of the colony's annual cycle (Free and Racey, 1968; Russell et al., 2013). Many species of ants, wasps or termites show much more dramatic variations in size during their ontogeny: societies founded by a single queen can comprise hundreds of thousands of workers at maturity. Surprisingly,

however, little is known about how the changes in colony size experienced by workers during colony ontogeny influence division of labour. One reason lies in the technical challenge of monitoring an individual's performance over time, but recent advances in automatic tracking alleviate this concern and offer promising perspectives (Ulrich et al., 2018).

A complete description of division of labour should not only incorporate the values of response thresholds (Weidenmüller, 2004); in this Commentary, I have argued that the contribution of within-individual variability to the expression of division of labour deserves further attention. However, an important question will be to determine which facet(s) of an individual's response can vary. Indeed, we can easily think of individuals that start performing a task at a similar stimulus intensity but that show considerable variation in other components of their response, such as the duration or intensity of behaviours. Considering only individual responsiveness can thus lead to an inaccurate estimation of behavioural consistency. This emphasises the need for a more thorough characterisation of an individual's response, including its efficiency in task completion. In the context of division of labour, what mechanism(s) would support the expression of behavioural consistency: the maintenance of response thresholds over time and/or a longer duration of task performance? Both theoretical and experimental studies should thus now attempt to integrate response dynamics to provide a more comprehensive picture of the variations in behavioural patterns both within and between individuals.

Concluding remarks

The current framework to approach division of labour is provided by the response threshold model, which posits that between-individual variation in responsiveness to stimuli is necessary for task specialisation. In an ecological setting, the heterogeneity in response thresholds among individuals grants colonies both flexibility and robustness when environmental conditions fluctuate. This simple and appealing paradigm has garnered theoretical and empirical support and its explicative potential has largely contributed to its wide acceptance. However, response threshold models may not be sufficient to capture all facets of task allocation in social insects. If we accept the idea that individuals start engaging in a task when the intensity of the associated stimulus exceeds the individual's internal threshold, how can we then justify that, at least in some species, a task can be left unattended after the partial loss of the workforce? In seed-harvester ants, for instance, how can we explain that in-nest workers are not recruited to compensate for the removal of foragers and that this even occurs at the expense of brood survival? Shall we assume that workers have (near-) infinite thresholds for some tasks? If so, this might call into question the significance of the paradigm of response thresholds. At the minimum, this indicates that the flexibility of workers has been exaggerated. This observation also encourages a revision of the overly simplistic view of virtually unlimited behavioural plasticity allowing individuals to shift tasks and colonies to adapt to any changes in their environment. We thus have to develop a more comprehensive approach in which the role of within-individual variability occupies a central position to understand how the balance between flexibility and canalisation can lead to optimal patterns of task allocation.

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Competing interests

The author declares no competing or financial interests.

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