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■ *Research Paper*

The Role of Information Acquisition and Processing in Decision-Making by Individual within Insects Colonies

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Insects usually present simple behaviours, but their information processing abilities result in complex collective behaviours, allowing them to perform task allocation and solve difficult problems. Biologists have invested efforts to better understand the mechanisms that govern the behaviour of social insects at the individual level and that allow the emergence of complex behaviours at the colony level. Based on biological researches, we identify the main mechanisms used to acquire different types of information and how this information is processed and used in decision-making. We present Information Acquisition as an essential stage for Information Processing, focusing on external and internal information sources and exploring examples of information processing performed by insects. A better understanding of information processing and collective behavior in nature is the basis for the understanding of how computing is realized in insect societies, as well for new insights to develop more effective computational approaches inspired by social insects.

Keywords social insect; collective behaviour; information processing; decision-making

INTRODUCTION

Social insects, such as ants, bees, wasps and termites, are considered the most socially advanced nonhuman organisms and, in a colony, the insects work together as a functional unit, also known as a superorganism (Hölldobler and Wilson, 2009). Recent researches suggest that social insects display various forms of sophisticated cognition and have the capability of showing vast behavioural repertories (Perry *et al*., 2017). Social insects are complex living beings able to

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adjust their behaviour based on the processing of many input stimuli and constraints. They can make decisions by weighing many factors, sharing information and having cognitive abilities, such as memory, which allow them to hone their decisions (Passino *et al*., 2008; Gadau and Fewell, 2009; Foss, 2017; Perry *et al*., 2017). Furthermore, due, in large part, to behavioural flexibility, social insect colonies are able to respond to changes of internal and external conditions and to adjust the number of insects working in each task. Despite their sophistication at the individual level, a single insect is not able to solve the same complex problems as the entire colony (Feinerman and Korman, 2017).

The collective level and ability to solve problems emerge from the individual behavioural level by self-organizing (SO) phenomena (Camazine *et al*., 2003), where the behaviour of the individuals often rely on relatively simple behavioural rules to guide their actions. The interactions have an important role in SO phenomena since, in nature, insects work with limited information based on their local exploration and the interaction with the environment and other insects. This way, it is usually difficult, if not impossible, for an individual to obtain information about the entire system (Camazine *et al*., 2003; Hölldobler and Wilson, 2009). Despite that, social insects are able to individually evaluate the environmental conditions by processing different types of information and to decide the most suitable action in response. The dynamics of the collective behaviour rely on SO phenomena responsible for a wide range of collective behaviours presented by social animals and insects (Bonabeau *et al*., 1997; Garnier *et al*., 2007). The collective capability is based on the individual cognition of insects and their communication mechanisms that allow them to share and propagate information (Feinerman and Korman, 2017). In a collective level, the insects are able to solve complex problems, such as sorting, reaching consensus and optimizing routes from nest to food sources, what cannot be resolved by an individual insect (Lindauer, 1955; Bonabeau *et al*., 1997; Beshers and Fewell, 2001; Ratnieks *et al*., 2006; Garnier et al., 2007; Franks *et al*., 2015; Feinerman and Korman, 2017).

These characteristics make the collective insect behaviours a rich inspirational source for the design and development of swarm systems and algorithms (Bonabeau *et al*., 2000; Bouffanais, 2016a). Biological researches, especially those from ethology, about collective behaviours, have contributed to improving the understanding of the principles that govern the dynamics of swarms in natural systems. Furthermore, computational models provide a way for researchers to investigate the interactions between different system elements, both in natural and artificial systems, to understand natural phenomena or to solve complex problems (De Castro, 2007; De Castro *et al*., 2011; WayneBrodland, 2015).

The interest of researches in understanding the complex behaviours of social insects is not new. Several researches have been presented with the objective of understanding the physiological, neural and hormonal features of social insects and how they contribute to the formation of complex behavioural patterns (Greene and Gordon, 2003; Gadau and Fewell, 2009; LeBoeuf *et al*., 2013; Gordon, 2016b; Feinerman and Korman, 2017). The main points of these researches are as follows: (i) Understand how the individuals use or combine different types of information (Grüter and Leadbeater, 2014); (ii) Understand how the individual behaviour of a social insect affects the group-level decision-making and; (iii) Understand how the ability of solving complex problems emerges from the individual behaviours (Feinerman and Korman, 2017).

From a computational perspective, the researches focus on the design of new approaches inspired by several collective behaviours and, specially, the improvement of existing ones to solve complex problems in different contexts (Parpinelli and Lopes, 2011; Yang *et al*., 2016). The researches about the collective behaviour of social insects represent an active research field in biology. The current advances in biological researches can contribute for a better understanding of how computing is realized in insect societies and are an important tool for engineers and computer scientists to develop more efficient and robust computational approaches and algorithms.

Syst. Res **36**, 461–475 (2019)
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In this context, this paper aims to present a computational view of the collective behaviour of social insects with focus on the individual decision-making. We present an overview of biological researches about social insect behaviours, identifying information acquisition and individual information processing mechanisms, which are the basis for the emergence of collective behaviour and problem solving abilities in a global level. Based on the mechanisms used to acquire different types of information and how this information is processed and used in decision-making, we propose a taxonomy to the information acquisition process, encompassing how insects acquire information, as well as the types of information acquired. We also present the information sources usually accessed by insects: external and internal. Thus, we provide a computational view of the collective behaviour and decision-making in social insects, focusing on two fundamental processes: the individual information acquisition and processing.

The paper is organized as follows. In Section 2 we describe the general behaviour of social insects, and Section 3 discourses about individual decision-making in insect societies. Section 4 dives into the core of the paper, which is the information acquisition in insect societies, describing the types of information acquired by social insects and the information sources. Section 5 is dedicated to a discussion on information processing in insect societies. The paper is concluded in Section 6 with a general discussion about the proposal and some avenues for future investigation.

SOCIAL INSECTS' BEHAVIOURS

Recent researches suggest that social insects display various forms of sophisticated cognition and have the capability of showing vast behavioural repertories (Perry *et al.*, 2017). They can make decisions by weighing many factors, sharing information, adapting to colony needs and having cognitive abilities, such as memory, which allow them to hone their decisions (Gadau and Fewell, 2009; Feinerman and Korman, 2017; Perry *et al.*, 2017).

An important ability of the colony is the division of labor (Robinson, 1992), also known as task allocation (Gordon, 2016a). According to Robinson (1992), the division of labor in social insects is characterized by different tasks performed simultaneously by groups of individuals. In a general way, two types occur in insect societies: (i) the division of labor between reproductive and non-reproductive tasks; and (ii) the division of labor among the workers for non-reproductive tasks of the colony. The reproductive tasks are exclusive for queens and males, resulting in mating and colony foundation. Queens and males do not present behavioural flexibility, thus performing the same role throughout life. On the other hand, the non-reproductive tasks are performed by other insects of the colony that are sterile females, called insect workers (Grüter and Keller, 2016). The workers have distinct behaviours during their lives, being able to assume several roles and perform different tasks.

The phases of the insect's life are called castes. For example, social bees present two distinct and stable phases of their life (Robinson, 1992): the work performed inside the colony (nurse bees); and the work performed outside the colony (foraging bees). The division of labor between insect workers can occur in two ways:

- *Age polyethism*: the insect changes its role with time, that is, task is allocated based on the age. Age polyethism gives rise to an age or temporal caste;
- *Morphological polyethism*: the insects assume a role based on their individual polymorphism (body structure), generating a physical caste.

Besides that, individual differences among insects within a caste can generate a refined division of labor (Robinson, 1992). Despite the distinct castes, the transition of a task to another is highly flexible and aims to adjust to dynamic environments (Gordon, 2016a).

The communication between and within the different castes is fundamental for colony maintenance. The inter-caste communication can occur in three contexts (Grüter and Keller, 2016): (i) communication between queens and males during mating behaviour; (ii) communication between queens and workers that contribute to

Syst. Res **36,** 461–475 (2019)
DOI: 10.1002/sres.2560

the regulation of reproduction; and (iii) communication between worker castes that regulate the number of workers performing the non-reproductive tasks, such as, foraging, house hunting and defence. Many researches have discussed the importance of inter-caste communication for the colony success and recent advances, such as genomics and epigenetics, aim to reveal how pheromone signals are processed in the insect brain and how internal and external stimuli induce the behavioural modification associated with changes in the gene expression patterns in the brain (Withers *et al*., 1993; Fahrbach, 2006; Robinson *et al*., 2008; Zayed and Robinson, 2012; Yew and Chung, 2015; Kamhi *et al*., 2016).

In a colony level, the insects present collective behaviours, and they are able to solve complex problems that exceed the capacity of the individual insects (Bonabeau *et al*., 1997; Beshers and Fewell, 2001; Feinerman and Korman, 2017). The problem-solving ability in the colony level is a result of the decision-making and information processing by the insects (Garnier *et al*., 2007; Moussaid *et al*., 2009). Hölldobler and Wilson (2009) define the collective behaviour, or social behaviour, as the totality of the relatively sparse and simple individual responses to stimuli and emerge from SO processes.

In this context and based on the biological research of insect behaviour, we present a computational view of the collective behaviour of social insects with focus on the individual decision-making. The individual decision-making is a result of the processing of different information types acquired by insects, as will be described in the following sections.

INDIVIDUAL DECISION-MAKING IN SOCIAL INSECTS

Basically, the individual behaviour of social insects is the result of an insect decision to perform a task or not (e.g. choose a food source (Seeley *et al*., 1991) and perform the waggle dance (Von Frisch, 1967), start forage, etc.). In insect societies, these decisions are the result of a processing of many stimuli, internal and external, by each insect of the colony and are crucial for task allocation and maintaining the colony (Beshers and Fewell, 2001). These stimuli are information sources about the environment, colony, as well as the internal condition of the insect. The individual insect cognition is the combination of the insect's abilities and the current knowledge of the communication network (Feinerman and Korman, 2017). Therefore, the individual decision-making in social insects is a result of the individual information processing performed by insects. The information come from a set of internal and external stimuli perceived by insects, including their cognitive, genetic, metabolic and behavioural abilities, their interaction with the environment and with other insects (Withers *et al*., 1993; Fahrbach, 2006; LeBoeuf *et al*., 2013; Czaczkes *et al*., 2016; Davidson *et al*., 2016).

At the individual level, the behaviour can be characterized by four aspects (Moussaid *et al*., 2009): (i) The individual behaviour in the absence of information; (ii) The kind of information acquired in its neighbourhood; (iii) The individual response for the information acquired; and (iv) How the information is transferred to other individuals. Considering insect societies, initially, the insects move randomly in the environment, acquiring information about their neighbourhood by means of direct or indirect interactions. By processing such information, they produce a response that stimulates or inhibits a particular action and adjust their behaviour. The change of insect behaviour in response to the information results in the local spreading of the information for other insects. Once other insects acquire this information they also adjust their behaviour, propagating it. Then, a positive feedback may be established to amplify or reinforce the behavioural response and, eventually, a negative feedback mechanism acts as a counterbalance. This process is constantly influenced by the individual experience acquired by insect (Bonabeau *et al*., 1997; Moussaid *et al*., 2009; Grüter & Leadbeater, 2014).

In this context, the individual decision-making of an insect is the result of acquiring and processing multiple information types. Thus, the

Syst. Res **36**, 461–475 (2019)
DOI: 10.1002/sres.2560

structure of the decision-making in social insects, presented in Figure 1, relies on two fundamental processes: (i) Information Acquisition; and (ii) Information Processing. In the first process we present the communication mechanisms by which the insects acquire information about the environment and colony, as well the types of information and its sources. And in the second one, we present the processing of the information acquired to understand and analyse the environmental conditions, resources, nest and decision-making processes.

Based on biological researches, especially from ethology, we review the mechanisms used to acquire different types of information and how this information is processed and used in decision-making. First, we present Information Acquisition as an essential stage for information processing, with focus on external and internal information sources. Then, we explore examples of information processing performed by insects.

INFORMATION ACQUISITION IN INSECT SOCIETIES

The decision-making process in social insects is directly influenced by the different types of information acquired by insects. These information come from internal and external sources. Firstly, we describe the types of information acquired by insects. Then, we present the information sources from where the insects are able to obtain each type of information.

Types of Information Acquired by Social Insects

Insects frequently have access to different types of information about the environment (Grüter and Leadbeater, 2014). Several biological researches approach the different types of information and how the insects decide what information type to use (Grüter and Leadbeater, 2014; Burns *et al*., 2016; Czaczkes *et al*., 2016). Gruter and Leadbeater (2014) classify the information acquired by social insects in three types:

- *Private information*: represented by the internal aspects and condition of the insect, such as, information based on the individual experience, cognition and individual aspects, such as physiological and genetic conditions;
- *Public information*: information available in the environment or nest and not yet evaluated or accessed by other insects. This information is accessed by means of individual exploration of the environment;
- *Social information*: information assessed and transmitted by other insects. This information is acquired by means of the observation or interaction with other individuals of the colony.

Thus, the public information is available in the environment, for example, a new food source near the nest. By accessing this new food source, the insects are able to assess the quality of food and then obtain private information. The insect's assessment about the quality of a food source is influenced by its internal state and can be different from the assessment performed by other

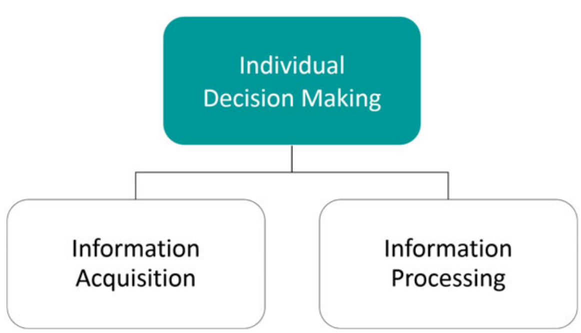

Figure 1 Fundamental decision-making processes in social insects [Colour figure can be viewed at wileyonlinelibrary.com]

Syst. Res **36,** 461–475 (2019)
DOI: 10.1002/sres.2560

insects about the same food source. When the insect transmits the obtained information, the other insects receive this information as a social information. Generally, the private information is prioritized over the public or social information, but, along time, this information can become outdated. In this case, the insects can use the public or social information. Public information can be more up to date; on the other hand, social information tends to be more reliable. The costs and benefits of choosing private, public or social information are highly variable and depend on the context (Grüter and Leadbeater, 2014). Recent researches have attempted to understand how individual features of social insects affect the group-level decision-making and how individuals use combinations of public, private and social information. Czaczes *et al*. (2015) suggest that private and social information complement each other. When these information sources are used complementarily, individuals perform a more efficient exploitation of their environment and, consequently, improve the colony fitness.

Information Sources for Social Insects

In this section, we present the information sources constantly accessed by insects. In nature, the individuals have access to two types of information sources: (1) External Sources; and (2) Internal Sources. The internal sources include genetic, neural and hormonal aspects, as well as the effect of past experience, and the external sources include the interactions between insect workers and between them and the environment (Heisenberg, 1998; Beshers and Fewell, 2001; Burns *et al*., 2016; Czaczkes *et al*., 2016). Both internal and external information sources allow the acquisition of different types of information. In the first case, the insects access the private information. In the second case, they access the social information when interacting with other insects (directly or indirectly), and the public information when interacting with the environment performing an individual exploration. The structure of information sources access by social insects is presented in Figure 2 and detailed in the following.

Internal and external sources are defined from the insect's perspective; thus, the internal is related to internal aspects of the insects and the external is related with the world around the insects. Figure 3 presents the internal and external sources from the insect's perspective. In Figure 3, the insects are represented by grey circles, and the world around them represent their external sources of information, i.e. their interactions with other insects and the interaction with the environment/nest where they live. Figure 3 also shows the structure of the internal source of the insect.

External Information Sources

In nature, the interactions are the communication channel among insects and between them and the environment. The communication by means of interactions allows the insects to acquire information about the environment and the colony and directly influences the individual decision-making. Thus, the external information sources consist of interactions that can occur among insects and between them and the environment. The rules specifying the interactions are performed based on purely local information, without information about the entire colony (Bonabeau, 1998). The interactions allow the insects to share and obtain information about the environment and colony conditions. Interactions among insects can be direct or indirect (Moussaid *et al*., 2009), as presented in Figure 2. Direct and indirect interactions allow the transfer of a variety of olfactory, tactile, visual, vibrational and acoustic messages.

Direct interaction consists of a local communication where no modification of the environment is required. The information exchanged by direct interactions can be of different types, such as physical contact or visual and acoustic signs. Direct interactions among insects can be subdivided in (Feinerman and Korman, 2017): (i) contact-dependent interactions ('one-to-one') and (ii) long-range communication ('multicast' or 'one-to-many'). Contact-dependent interactions require the direct contact between insects and are local, both in space and time, for example, antennation and exchange of fluids or food.

Syst. Res **36**, 461–475 (2019)
DOI: 10.1002/sres.2560

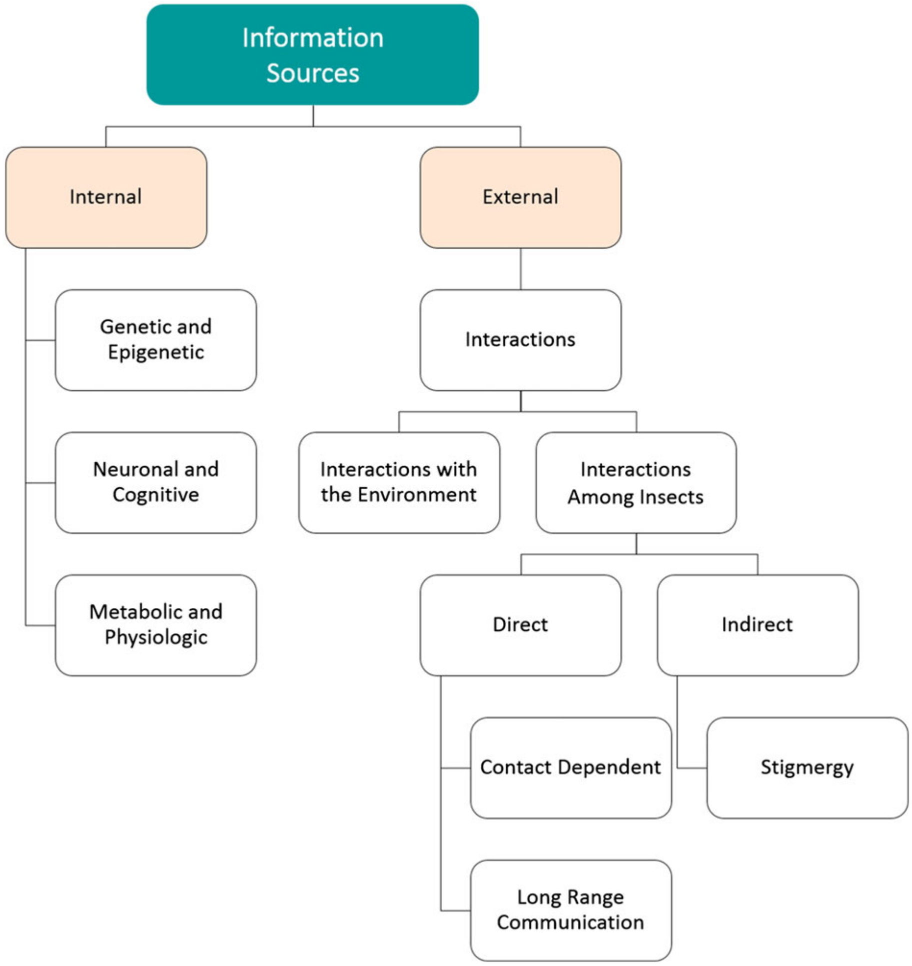

Figure 2 Taxonomy of information sources in insect societies [Colour figure can be viewed at wileyonlinelibrary.com]

The contact-dependent interactions have an important role in the regulation of traffic flows in many activities of the colony (Dussutour *et al.*, 2009; Farji-Brener *et al.*, 2010; Bouchebti *et al.*, 2015). For example, in many species of ants, the contact-dependent interactions by antennation or head-on encounters regulate the flow of insects that go foraging and return to the nest avoiding traffic jams on foraging trails (Dussutour *et al.*, 2009; Bouchebti *et al.*, 2015). Long-range communication consists of the direct interactions between insects that do not require physical contact. In these interactions, the messages can be transmitted to many neighbouring insects at the same time and are considered local in time, but not in space. Examples of long-range communication are pheromone alarm signals (Norman *et al.*, 2017) and acoustic and vibrational signals in waggle dances (Kirchner, 1993).

Indirect interaction is the communication among insects mediated by the environment, known as *stigmergy* (Theraulaz and Bonabeau, 1999). Some individuals modify the environment and others perceive this modification, adjusting their behaviours accordingly (De Castro, 2006). In stigmergic communication, the indirect interactions are established by means of chemical signals (or pheromone) (Yew and Chung, 2015) and the insects interact with their nestmates across both space and time by means of small changes on regions of the environment or nest (Camazine *et al.*, 2003; Grüter and Keller, 2016). The indirect

Syst. Res **36,** 461–475 (2019)
DOI: 10.1002/sres.2560

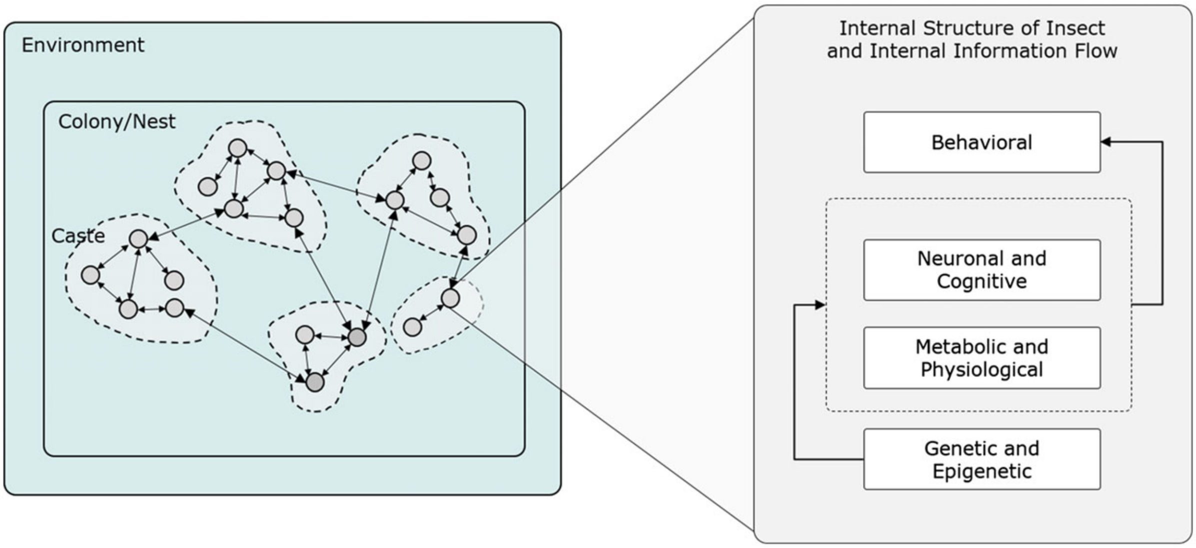

Figure 3 Internal and external information sources in insect societies [Colour figure can be viewed at wileyonlinelibrary.com]

interactions allow insects to share/acquire social information and are important in situations where many insects contribute with an effort to collectively build a structure, such as the pheromone trail in ants (Czaczkes *et al*., 2015b) and the construction of the hexagonal shapes in honeycombs by bees (Nazzi, 2016).

Moreover, another possibility of interaction occurs between the insects and the environment, for example, the insects exploring a region looking for food. In this case, differently from stigmergy, the insects interact directly with the environment (perhaps not explored yet) to acquire new information. In this case public information is accessed (Grüter and Leadbeater, 2014; Grüter & Keller, Inter-caste communication in social insects, 2016). Table 1 presents some examples of interactions, their main characteristics and the types of information exchanged.

Thus, the interactions generate the information flow in insect societies, as presented in Figure 4. The solid arrows indicate the information acquired directly, both from other insects and from the environment. The dotted arrows represent the information flow from indirect interactions by means of environmental modifications. In short, an insect can receive information directly or indirectly. Three interactions are possible: direct interaction among insects; direct interaction between insects and the environment; and indirect interaction among insects mediated by the environment. The *social information* is acquired by direct and indirect interactions, and it is the one responsible for the amplification of fluctuation and reinforcement of an action (*positive feedback*) along multiple interactions. The *public information* is acquired by direct interactions that are the result of the individual exploration and is important for the discovery of novelty and up-to-date information.

Internal Information Sources

The neuronal, physiological and genetic mechanisms by which social insect behaviours are established are poorly understood, but in the last few years many efforts have been made to decipher the basis of social organization in a molecular level. Many biological researches, especially from neurobiology, show that the action performed by social insects is also influenced by neural, physiological, genetic and behavioural aspects of the individual (Heisenberg, 1998; Zayed and Robinson, 2012; LeBoeuf *et al*., 2013). These internal aspects are a rich information source for insects, are crucial to individual behaviours and have direct impact in the decision-making processes:

Syst. Res 36, 461–475 (2019)
DOI: 10.1002/sres.2560

Table 1 Examples of direct and indirect interactions in social insects

Action	Insect	Agents	Interaction type	Information type	Associated task
Waggle dance	Bees	Workers–workers	Direct Long range	Social	Foraging (recruitment)
Pheromone trail	Ants	Workers–environment–workers	Indirect Stigmergy	Social	Foraging (recruitment)
Physical contact	Ants	Workers–workers	Direct Contact dependent	Social	Task allocation, traffic flow and foraging
Flying dance	Bees	Drones–queen	Direct Long range	Social	Mating
Individual exploration	Ants and bees	Workers–environment	Direct with environment	Public	Foraging (searching)
Return to the nest	Ants and bees	Workers–environment	Direct with environment and use of private information	Private and Public	Orientation
Danger alarm	Ants and bees	Workers–workers	Direct Long range	Social	Protection
Evaluate and choose a food source	Ants and bees	Workers–environment	Direct with environment and use of private information	Private and Public	Foraging
Evaluate and choose a new nest's side	Ants and bees	Workers–environment	Direct with environment and use of private information	Private and Public	Search for new nest

Syst. Res **36,** 461–475 (2019)
DOI: 10.1002/sres.2560

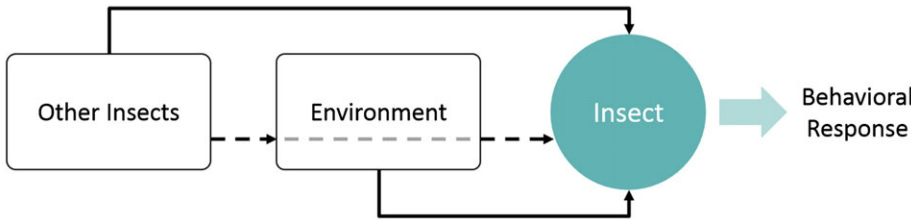

Figure 4 Information flow and individual behaviour response in social insects. Solid arrows represent the information from the environment or other insects to the focal insect directly. The dotted arrows represent the indirect information from other insects [Colour figure can be viewed at wileyonlinelibrary.com]

- *Genetic aspects*: Many genes associated with social behaviour have been co-opted from pathways also presented in primitive species of insects (Leonhardt *et al*., 2016). Genes contribute to the organization and functioning of the neural circuits that express behaviour; thus, genetic aspects have indirect influence in the behaviour and, consequently, the individual decision-making of insects (Robinson *et al*., 2008). The genetic aspects include the parentally inherited factors, such as genotype and maternal factors (Yan *et al*., 2014; Weitekamp *et al*., 2017).
- *Epigenetic aspects*: Epigenetic consists of the chemical modifications to DNA that do not change the DNA sequence. In most cases, the differentiation of castes, for example, between queens and workers insects, is not determined genetically, but by the influence of environmental conditions and colony needs (Weiner and Toth, 2012). Researches about genetics and epigenetics aims to understand how the epigenetic process transform transient environmental conditions into persistent molecular patterns of gene expression in order to modulate the insect behaviour, besides contributing and regulating task allocation (Hölldobler and Wilson, 2009; Weiner and Toth, 2012; Yan *et al*., 2014).
- *Metabolic and physiological aspects*: Researches of social insect physiology have shown that the determination of castes and decision-making about what task to perform is directly influenced by the hormone levels of the insect. Biological experimental researches show that different hormones influence the decision-making in social insects and are related to many activities in the colony (Liang *et al*., 2012; LeBoeuf *et al*., 2013).
- *Neuronal and cognitive aspects*: The structure of the social insect brain associated with learning is known as mushroom bodies (Heisenberg, 1998). In flying insects, like bees, this structure presents a significant anatomical reorganization, which allows plasticity even in adult insects (Withers *et al*., 1993; Fahrbach, 2006). Perturbations in this brain structure can interrupt or disrupt the formation of memory in insects. Experiments have shown that the division of labor in adult bee colonies is associated with substantial changes in specific regions of the brain, including the mushroom bodies (Withers *et al*., 1993; Fahrbach, 2006). In recent years, many efforts have been made to better understand the neurological and cognitive basis of the social complex behaviour of insects, such as task allocation (Kamhi *et al*., 2016).

These aspects are intrinsically related. Some genes underpinning core physiological and neuronal processes can also influence the behavioural aspects of social insects. The relation among genetic, physiological and neuronal aspects and how they influence the insect behaviours is an important open question in biology, more specifically of sociogenomic researches (Amdam *et al*., 2006; Robinson *et al*., 2008; Woodard *et al*., 2011; Mikheyev and Linksvayer, 2015; Kamhi *et al*., 2016). Figure 5 presents the information flow and the structure of internal aspects of social insects presented in this section.

INFORMATION PROCESSING IN INSECT SOCIETIES

According to Bouffanais (2016b), adaptation, collective decision-making and learning are

DOI: 10.1002/sres.2560

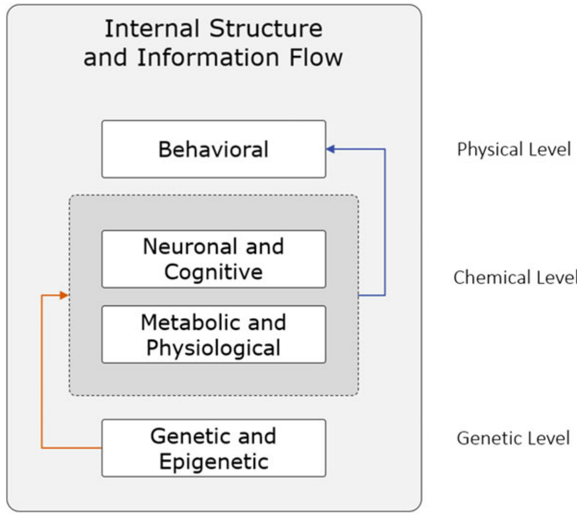

Figure 5 Internal structure and information flow in social insects [Colour figure can be viewed at wileyonlinelibrary.com]

equivalent forms of information processing or computation. In natural systems, information processing can be represented by the decision-making performed by system elements (Xavier and De Castro, 2013). From an information processing perspective, the insects are autonomous information processing units able to store and process information, as well as to give a suitable action in response. A swarm can be defined as a distributed information processing system able to process information and adapt to dynamic environments (Bonabeau *et al.*, 1999; Bouffanais, 2016b). The insects acquire multiple types of information, as discussed previously, including sensory and behavioural stimuli. These information are the input to the system. The outcome of information processing is the way of action. Thus, the decision-making is performed through the processing of multiple information types simultaneously. Through information processing, the insects are able to evaluate the conditions and then take a decision that is expressed in an action, as shown in Figure 6. Thus, the decision-making in social insects is the result of information processing, or computations, performed by insects.

In the information acquisition process, insects have access to public, private and social information. These information allow the insects to evaluate the nest and environmental conditions and to decide the adequate response to the dynamics of the environment and colony needs. Gordon (2016b) defines the collective behaviour as the outcome of a network of local interactions and uses a computational perspective to argue about the evolution of the collective behaviour. According to Gordon (2016b), collective behaviour is a phenotype that evolves to fit the dynamics of a particular environment and three factors are important in the relationship between environment and collective behaviour: (i) *Operating costs*: cost, in terms of energy, to perform a specific task under environmental constraints; (ii) *Stability*: indicates how stable the environment is; and (iii) *Distribution of resources*: indicates the uniformity and concentration of the resources. Thus, the social insects, by means of interactions, perceive the stimuli and are able to evaluate the environmental condition, distribution of resources and cost of operation. An insect obtains and processes this information and then makes a decision, i.e. gives an individual response to the stimuli perceived.

Figure 6 provides a representation of the acquisition and information processing of the collective behaviour and decision-making of social insects, based on the biological researches discussed in this paper. Firstly, in the information acquisition process, social insects acquire information about the environment and colony needs by means of external and internal information sources. By

Syst. Res **36,** 461–475 (2019)
DOI: 10.1002/sres.2560

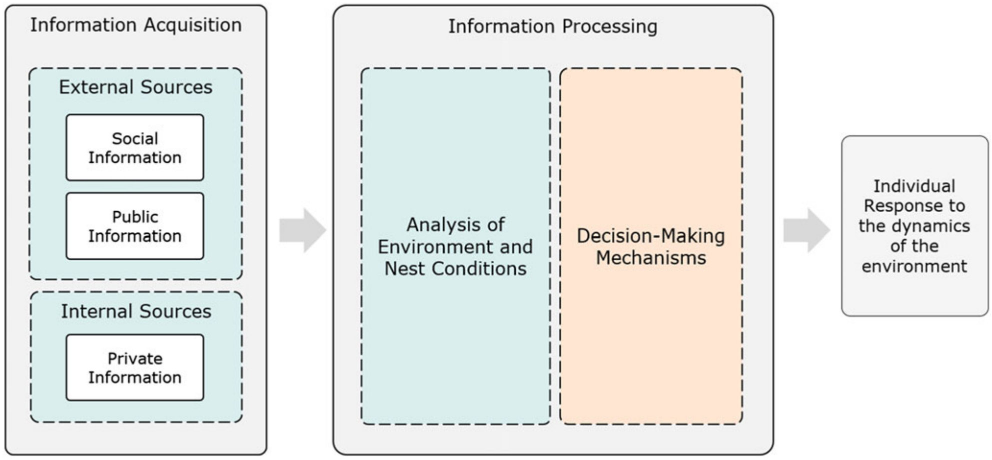

Figure 6 The acquisition and information processing in social insect colonies [Colour figure can be viewed at wileyonlinelibrary.com]

processing these types of information, public, private and social, the insects analyse the environmental conditions and make a suitable individual decision expressed by an action.

Many researches seek to unravel the precise decision-making mechanisms of insects, that is, how insects process the information received and are able to make a decision related to a specific task or action (Beshers and Fewell, 2001; Marshall *et al*., 2009; Mosqueiro and Huerta, 2014; Barron *et al*., 2015).

Decision-making is a central process in the brain enabling the wide range of abilities of insects, such as, to identify objects and scenarios, choose one of many alternatives and decide how and when to perform an action or react to different stimuli. The insect's brain processes the inputs from all sensory organs and is responsible to give a suitable behavioural output, as illustrated in Figure 7.

The processing of information relies on two important processes (Mosqueiro and Huerta,

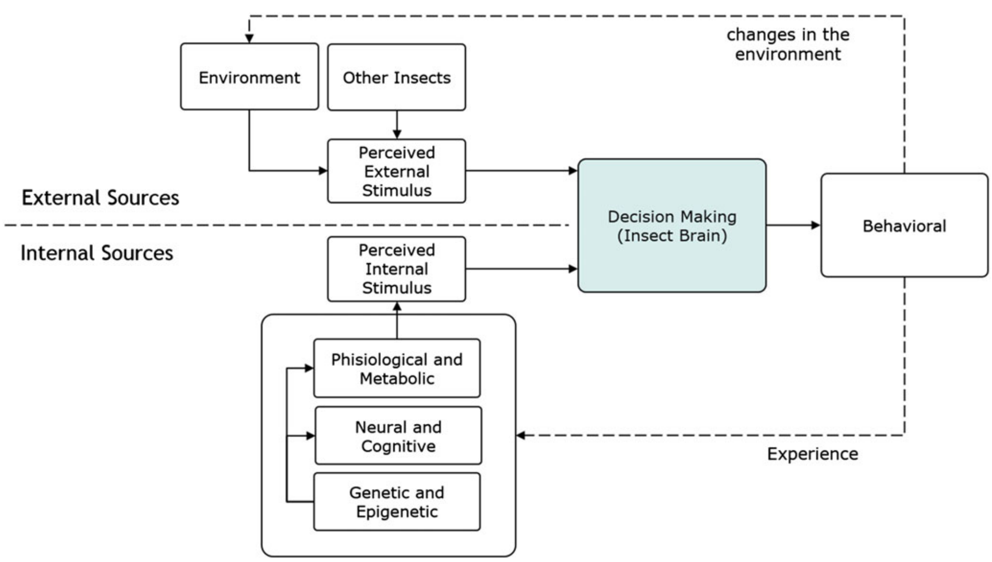

Figure 7 Decision-making in social insect [Colour figure can be viewed at wileyonlinelibrary.com]

Syst. Res **36**, 461–475 (2019)
DOI: 10.1002/sres.2560

2014): the prediction of environmental conditions and changes (regression), and the recognition of patterns to discriminate situations and selection of suitable responses (classification). The information processing and, consequently, the decision-making process, occurs in the insect brain. Many studies point to a region of the insect brain, called mushroom body (Heisenberg, 1998), as being the main responsible for decision-making in social insects, as well as the learning and cognition abilities presented by the insects (Menzel, 2012; Mosqueiro and Huerta, 2014). The understanding of how learning and decision-making processes occur in the insect brain is an important step to uncover the principles of information processing in the brain. Efforts have been made in the search for a better understanding of how the insect brain processes the different stimuli received, especially visual and olfactory stimuli (Beshers and Fewell, 2001; Marshall *et al*., 2009; Chittka and Skorupski, 2011; Mosqueiro and Huerta, 2014; Barron *et al*., 2015).

CONCLUSIONS

This paper discussed the individual decision-making in insect societies relying on the acquisition and information processing mechanisms. We presented the mechanisms by which insects acquire different types of information and a computational view of the collective behaviour of social insects. The information acquisition is a fundamental decision-making stage, having a direct influence in the actions performed by insects and, consequently, influencing the collective behaviour at the colony level.

Researches about the collective behaviour of social insects are very active nowadays. Biologists have invested a great effort to better understand the mechanisms that govern the behaviour of social insects at the individual level and that allow the emergence of complex behaviours at the colony level. On the other hand, computer scientists and engineers have long used the collective behaviour of social insects as inspiration to design algorithms to solve complex problems and currently focus on the use of different biological metaphors as inspiration and the improvement of current approaches to solve several real-world problems (Bonabeau *et al*., 2000; De Castro, 2007; Hussain *et al*., 2018). This must be a two-way street, where both biology and computer science benefit from each other.

The advance of biological researches, especially from entomology, about the basis of social behaviours in insect societies, both at the molecular and behavioural levels, can establish novel perspectives to design new swarm intelligence systems (Bonabeau *et al*., 2000; Fahrbach, 2006; Perry *et al*., 2017) contributing to the natural computing (De Castro, 2007; De Castro *et al*., 2011) research area and the exploration of new frontiers. A better understanding of collective behaviours in nature is the basis for the understanding of how computing is realized in insect societies, as well as for new insights into the development of more robust and effective computational approaches. In this paper we used a computational point of view under the biological researches to answer two questions: 'How does an insect obtain information?' and 'What kind of information an insect has access to?'. The mapping of information sources and information types can provide new insights about how insects process different types of information. The better understanding of the individual decision-making and how social insects individually obtain and process local information about the colony and environment is an important step to understand complex abilities that emerge at the colony level.

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