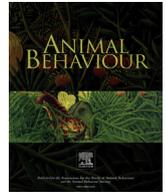




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Communication in social insects and how it is shaped by individual experience

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Communication is the foundation of all social systems, and learning is perhaps the most important cognitive tool. But how do these two critical faculties interact? With social insects being some of the best learners of the invertebrate world, and indisputably the most communicative, we examine the role of learning and experience in social insect communication. Learning plays a major role for both senders and receivers. A sender's experience can modulate what information is available for communication, whether communication is effective and whether individuals are motivated to communicate. Signalling about a resource is often modulated relative to the value of that resource and relative to the value of sharing information about it. The receiver's experience and knowledge can affect which parts of a signal's information content it attends to, how this information is acted on and, indeed, whether it attends to communication at all. Ultimately, while innate responses form the basis of social insect communication, learning is often a critical modulator of communication processes.

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Communication is the foundation of all social systems (Luhmann, 1982) and is at the heart of nearly all social activities in an insect colony. It requires a sender who produces a signal (a trait shaped by natural selection to convey information) and a receiver who responds to the signal (Fig. 1) (Bradbury & Vehrencamp, 1998; Ruxton & Schaefer, 2011; Searcy & Nowicki, 2005). The main purpose of communication in social insects is to provide information that reduces uncertainty about important aspects of colony life (see e.g. Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; Rendall, Owren, & Ryan, 2009; Ruxton & Schaefer, 2011; Searcy & Nowicki, 2005; Seyfarth et al., 2010 for different viewpoints on what the terms information, signal and communication mean), such as the location of resources, the identity of colony members or the nutritional needs of the colony. Unsurprisingly, the study of social insect communication has a long tradition, particularly in ants and bees (von Frisch, 1923, 1967; Hölldobler & Wilson, 1990; Lubbock,

1882; Wilson, 1971). This has led to the discovery of dozens of chemical, tactile and visual signals (von Frisch, 1967; Hölldobler & Wilson, 1990, 2009; Seeley, 1998). Honey bees (*Apis mellifera*), for example, use at least five different signals for the coordination of foraging (Anderson & Ratnieks, 1999; von Frisch, 1967; Nieh, 2010; Seeley, 1998; Thom, Gilley, Hooper, & Esch, 2007). Some of these signals provide specific information about particular food sources (e.g. waggle dance: von Frisch, 1967; stop signal: Nieh, 2010), whereas others have more general effects, such as up- or down-regulating activities involved in foraging (e.g. dance pheromone: Gilley, Kuzora, & Thom, 2012; Thom et al., 2007; foraging pheromone: Leoncini et al., 2004; tremble dance: Seeley, Kühnholz, & Weidenmuller, 1996; vibrational signal: Schneider & Lewis, 2004). The dance and the stop signal are functionally referential signals in the sense that they are produced inside the nest but refer to objects in the outside world (Shettleworth, 2010). They are analogous to having different words for external objects ('resource' at location X, 'danger'). However, unlike in human language, bees use a very small number of specific 'words' and they do not combine signals to create new meaning (see Shettleworth, 2010 for a discussion of differences between human and nonhuman

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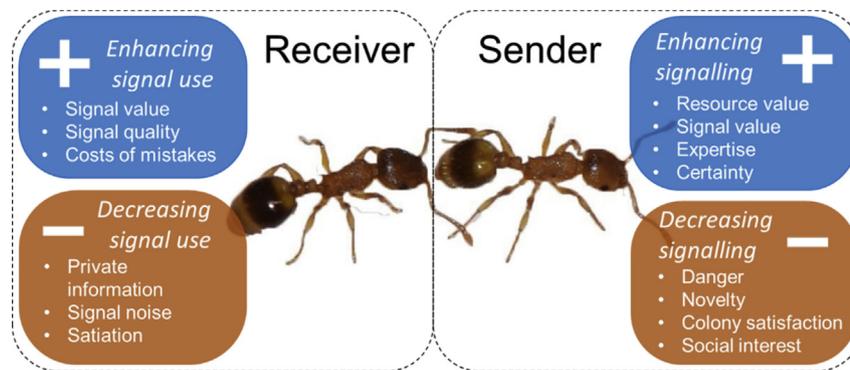


Figure 1. Factors that increase or decrease signalling by potential senders (right box) and the use of signals by potential receivers (left box). The photo shows a *Temnothorax nylanderi* forager (leader) guiding a nestmate (follower) to a new nest site. This form of recruitment is called tandem running (Photo: C. Grüter).

languages). Similarly, some ant species use specific motor displays ('dances') to modify the meaning of a pheromone recruitment trail, with one motor display being used to recruit to enemy incursions into the colony's territory and another used to recruit to newly discovered terrain (Hölldobler & Wilson, 1978).

A fruitful approach to understanding how communication helps colonies to organize their activities has been guided by the idea that simple behavioural rules govern how individuals respond to communication signals (Bonabeau, Theraulaz, Deneubourg, Aron, & Camazine, 1997; Camazine et al., 2001; Deneubourg & Goss, 1989; Detrain & Deneubourg, 2008; Seeley, 1995; Sumpter, 2010). The combination of many individuals following these simple rules leads to the emergence of complex collective behavioural patterns at the colony level. An often repeated example is the response of ants to trail pheromone, which in turn allows colonies to select the shortest routes or the best among several food sources in laboratory settings (Camazine et al., 2001; Czaczkes, Grüter, & Ratnieks, 2015; Deneubourg & Goss, 1989; Detrain & Deneubourg, 2008): if ants returning from a food source deposit an amount of pheromone proportional to the quality of the food source, and ants at a trail bifurcation are more likely to follow stronger trails, then this leads to a positive feedback loop that results in a collective choice of the better food source.

The idea that simple rules underlie collective behaviour is tightly linked to the concept of self-organization (Bonabeau et al., 1997; Camazine et al., 2001; Deneubourg & Goss, 1989; Sumpter, 2010). The success of this approach is evidenced by the fact that theoretical models are often able to predict what we observe in the laboratory (e.g. Deneubourg, Aron, Goss, & Pasteels, 1990; Detrain & Deneubourg, 2008; Grüter et al., 2012; Khuong et al., 2016; Verhaeghe & Deneubourg, 1983) and by its adoption in computer science, e.g. in the form of ant colony optimization algorithms (Dorigo & Stützle, 2004). These algorithms use reiterations of the same simple behavioural rules described above to provide near-optimal solutions to problems that are impractical to solve using conventional means.

On the other hand, it is important to note that, in reality, different workers can use different behavioural rules and particular individuals can change the rules they follow. Furthermore, workers do not always use 'simple' rules when responding to signals. For example, the process of deciding whether to respond to a signal may be fairly complex (see below). Finally, a correspondence between theoretical and empirical results does not imply that models capture the communication rules used by insects in the real world. Real ants might use different behavioural rules than those specified in a model, yet the collective outcome appears similar (e.g. Czaczkes, Salmane, Klampfleuthner, & Heinze, 2016).

Recent research has highlighted that the workers of a colony can differ greatly in both their production and response to particular signals. The aim of this review is to discuss how individual workers show flexibility in the production and response to signals and, in particular, to highlight the role of learning as a major factor shaping the dynamics of communication. We use a broad definition of learning as 'a change in cognitive state due to experience that can affect behaviour' (cognition more generally refers to the sum of processes that allow animals to acquire, store and use information, Menzel & Giufà, 2001; see Shettleworth, 2010 for a discussion). Differences in experience create heterogeneity in the information workers have, which in turn leads to workers having different motivation and fulfilling different functions (e.g. Biesmeijer & de Vries, 2001; von Frisch, 1967; Grüter & Leadbeater, 2014; Stroeymeyt, Franks, & Giufà, 2011). This highlights that learning increases the complexity of communication processes (Janik & Slater, 2000). As we shall see, this learning can be either individual or social learning. The latter refers to learning that is influenced by observation of, or interaction with, another individual or its products (e.g. pheromones) (Heyes, 1994, 2012; Hoppitt & Laland, 2013; Leadbeater & Chittka, 2007; Shettleworth, 2010). Janik and Slater (2000) suggested different types of social learning in communication: in *production learning*, signals and the responses to signals are modified in their form as a result of experience with communication. In *contextual learning*, the context in which signals are produced and/or used changes due to experience with signalling individuals. The latter form of learning is further divided in *usage learning* (signals are produced in new contexts due to experience with communication) and *comprehension learning* (receivers extract new meaning from a signal due to experience with communication). Whereas *production learning* is less likely to be found in social insects, examples of learning that affect the context in which signals are produced and/or used are more common (see below).

We will focus on communication during foraging and colony emigration, because these two situations are particularly well studied. There are several recent reviews on other aspects of communication in social insects (general: Hölldobler & Wilson, 2009; Leonhardt, Menzel, Nehring, & Schmitt, 2016; recruitment communication in ants and bees: Barth, Hrncir, & Jarau, 2008; Beekman & Dussutour, 2009; Czaczkes et al., 2015; Grüter & Farina, 2009a; queen pheromones: Oi et al., 2015; tandem running: Franklin, 2014; inter-caste communication: Grüter & Keller, 2016).

Insect colonies represent a somewhat special case in that the fitness of the mostly sterile workers is primarily achieved via the successful reproduction of a few reproductive relatives (e.g. the

queen). In this respect, they are conceptually similar to multicellular organisms that have a reproductive division of labour among somatic and germline cells (Hölldobler & Wilson, 2009; Wheeler, 1911). This means that communication that aids in the coordination of colony activities can be considered honest because of low levels of conflicts of interest between colony members, e.g. regarding foraging decisions, nest defence or colony emigration. Low levels of conflict may have facilitated the evolution of extensive integration and communicative complexity. Since senders and receivers systematically differ in their information we will discuss them separately.

THE EFFECTS OF EXPERIENCE ON THE SENDER

The context in which signals are produced can be affected by different kinds of experiences. Here we discuss (1) resource-value-dependent signalling, (2) information-value-dependent signalling, (3) expertise-dependent signalling and (4) age-dependent signalling (see Fig. 1 for a summary).

Resource-value-dependent Signalling

Insects searching for a food source or a new nest site will not always communicate what they found to their nestmates. Usually, only resources above a certain profitability threshold elicit the production of a signal. This allows insect colonies to use resources that are above the average available in the environment (Grüter, Leadbeater, & Ratnieks, 2010; Seeley, 1995). For example, honey bees will only perform dances for relatively profitable food sources (von Frisch, 1967). *Temnothorax albipennis* nest-site scouts tune their probability of performing tandem running – a type of recruitment, whereby an informed leader guides a follower to a resource (Fig. 1) – to the suitability of the newly discovered cavity (Mallon, Pratt, & Franks, 2001). Many ant species deposit more pheromone to higher-value resources (Czaczkes et al., 2015; Detrain, Deneubourg, & Pasteels, 1999; Reid, Latty, & Beekman, 2012; Roces, 1993; Roces & Núñez, 1993; Schilman, 2011), or only recruit if food quantity is above a certain threshold (Mailloux, Deneubourg, & Detrain, 2000). Other than its quality, the value of a resource depends on several other factors, such as its distance from the nest, its accessibility or the presence of predators in the vicinity of the resource, and social insects tune their recruitment accordingly (Abbott & Dukas, 2009; von Frisch, 1967; Jack-McCollough & Nieh, 2015; Nieh, 2010; Tan et al., 2016).

The perception of resource value is strongly affected by previous experience. Critically, as in humans (Kahneman & Tversky, 1979), value is often perceived, at least partially, as relative to a reference point – usually an expectation or previous experience. For example, the perception of sucrose rewards changes in response to the quality and quantity of food that is collected by the colony. If large amounts of high-quality food are collected, bees encounter this food in their nest via trophallaxis, and the sucrose response threshold of bees tends to increase (Martinez & Farina, 2008; Pankiw, 2004; Pankiw, Waddington, & Page, 2001), i.e. bees become less responsive to rewards. Thus, the same absolute quality of resource may be perceived as having a lower quality if the sender has previous experience with higher-quality resources, and a higher quality if the sender previously experienced low-quality resources (Bitterman, 1976; Couvillon & Bitterman, 1984; Wendt, Strunk, Heinze, Roider, & Czaczkes, 2018). Such effects, referred to as successive contrasts effects (Flaherty, 1996), have been shown to affect the strength of recruitment in ants (Wendt et al., 2018). Interestingly, perceived reductions in the value of resources often lead to a stronger change in behaviour than an increase in reward (Bitterman, 1996). For example, in the stingless bee *Scaptotrigona*

depilis, food quality per se did not affect recruitment intensity, but lowering the quality caused foragers to stop communicating about the food source whereas an increase in quality had no effect (Schmidt, Zucchi, & Barth, 2006). In honey bees, on the other hand, increases and decreases in food source value affect the motivation to perform dances to a similar degree (De Marco & Farina, 2001).

Contrast effects are expected to be adaptive, especially in variable environments (McNamara, Fawcett, & Houston, 2013). However, perceived value, and thus recruitment strength, can also be influenced in ways that are not necessarily beneficial. Rewards that are received after harder work (due to travelling further, climbing uphill or walking over a rough substrate) are perceived as more valuable by humans, mice and ants (e.g. Clement, Feltus, Kaiser, & Zentall, 2000; Czaczkes, Brandstetter, di Stefano, & Heinze, 2018; Hernandez Lallemand et al., 2013; Johnson & Gallagher, 2011; Kacelnik & Marsh, 2002), with some ants recruiting more strongly to such resources (Czaczkes et al., 2018). This likely arises due to state-dependent learning (Pompilio, Kacelnik, & Behmer, 2006), and specific mechanisms are probably in place to prevent this effect from causing more distant food sources to be more strongly recruited to: in most species, increasing food source distance reduces the motivation to communicate about the resource, most likely because exploiting distant food sources increases the energetic costs (Devigne & Detrain, 2006; Fewell, Harrison, Stiller, & Breed, 1992; Roces, 1990; Taylor, 1977; von Frisch, 1967; but see below for exceptions). The motivation to communicate about food sources can also be affected by encountering novel tastes (Lindauer, 1948; Oberhauser & Czaczkes, 2018) or foraging risks. An interesting example is the interaction between two signals, the waggle dance and the stop signal (a brief vibrational signal that can be perceived as a short sound), in honey bee foraging. If a forager exploiting a food source notices the presence of competitors, e.g. bees from another hive, or predators, e.g. hornets or spiders, then she will often stop performing waggle dances and instead produce stop signals towards other bees dancing for this particular resource. In other words, honey bees respond to perceived risks at food sources not only by stopping their own recruitment but by inhibiting dance communication by others through the production of stop signals (Nieh, 2010). The production of stop signals is tuned to the level of threat, with more dangerous enemies eliciting more stop signals (Tan et al., 2016). This graded production of stop signals suggests that signalling also depends on the value of the information to others.

Information-value-dependent Signalling

Communication among workers is expected to be cooperative; thus, workers should be more likely to provide social information when this information is more valuable for others. For example, as mentioned above, a warning signal is more helpful if a perceived threat is greater (Tan et al., 2016). In the context of foraging, pheromone trails, tandem runs or waggle dances are more helpful when resources are more difficult to find (Beekman & Lew, 2008; l'Anson Price & Grüter, 2015; Pratt, 2008; Schürch & Grüter, 2014), either because they are scarce or because the route leading to them is complex. Consistent with this idea is the finding that *Lasius niger* ants are more likely to lay pheromone trails if they made navigational mistakes during the previous trip to the food source, or upon finding that the food location has changed (Czaczkes & Heinze, 2015; Czaczkes, Grüter, Ellis, Wood, & Ratnieks, 2013), and *Temnothorax* scouts perform more tandem runs when nest sites are more distant (O'Shea-Wheller, Sendova-Franks, & Franks, 2016; but see ; Glaser & Grüter, 2018). In *L. niger*, colonies with a poorer learning performance in a navigational task lay more pheromone, possibly because pheromone

information is more valuable for colonies with poor individual learning (Pasquier & Grüter, 2016). In these cases, pheromone trails can aid nestmates and be a self-help.

Signals advertising a resource are also more valuable the higher the need for the resource. Thus, recruiters from starved colonies might be expected to recruit more strongly to the same resource than recruiters from well-supplied colonies (von Frisch, 1967). For instance, the probability that honey bees perform waggle dances for a given reward changes almost daily, depending on the current supply of food (Lindauer, 1948). Colonies that store sufficient amounts of pollen quickly reduce their pollen foraging, at least partly via reduced waggle dancing to advertise pollen resources (Camazine et al., 1998). Foragers do not need to sample the food stores or explore their foraging environment to gauge the current supply situation (Seeley, 1989). Instead, they can acquire information via trophallaxis, e.g. by responding to how long they have to search for an unloading partner (and the number of unloading partners) inside their nest (Farina, 2000; Grüter & Farina, 2009b; Lindauer, 1948; Seeley & Tovey, 1994). On the other hand, Maillieux, Detrain, and Deneubourg (2006) found that the threshold crop fill for pheromone deposition in an ant increases under starvation, whereas Schorkopf et al. (2016) found that recruitment in the stingless bee *Melipona scutellaris* is unaffected by the amount of food stored.

A signal can also lose its informational value if most nestmates are already informed. For example, if an ant encounters many other ants on a trail to a food source (i.e. many foragers are already informed), then ants reduce their pheromone deposition rate (Czaczkes, Grüter, & Ratnieks, 2013). Similarly, if there is already a lot of information present – i.e. pheromone on the trail – ants in some cases reduce their pheromone deposition (Czaczkes, Grüter, & Ratnieks, 2013).

Expertise-dependent Signalling

Communication can also be affected by the level of certainty or expertise of the signaller. Expertise can arise either from having accumulated a lot of information over time or from having acquired highly accurate information that is easy to retrieve. An observation that is consistent with expertise-dependent signalling is that ants and honey bees that discover a new food source will often not initially recruit, and only start to signal after a few visits, as information about the resource accumulates (Czaczkes, Grüter, Ellis, et al., 2013; Franklin, Robinson, Marshall, Sendova-Franks, & Franks, 2012; Glaser & Grüter, 2018; Schweiger, 1958). Ants also signal less when they have low-accuracy information: outgoing foragers that made an error at a bifurcation when returning to a food source laid less pheromone before making the decision (Czaczkes & Heinze, 2015), perhaps because they can identify that the quality of their information is not very good or they have not yet learned the route sufficiently well. Ants which notice their information if of low accuracy while returning to a food source, for example by straying from a pheromone trail, reduce their own pheromone deposition (Czaczkes, Grüter, Jones, & Ratnieks, 2011). On the other hand, honey bees do not seem to dance less if they can only perform disoriented dances (I'Anson Price, Dulex, Vial, Vincent, & Grüter, 2019). Disoriented dances, i.e. waggle phases in random directions, can be induced experimentally by turning wax combs to a horizontal position and preventing bees from seeing the sun or polarized light (the waggle phase is the part of the dance that contains the information about the distance and direction of the food source) (e.g. Donaldson-Matasci & Dornhaus, 2012; Dornhaus & Chittka, 2004; von Frisch, 1967; Sherman & Visscher, 2002). The observation that bees do not dance less when dances are disoriented suggests that dancers do not know if their dances

provide high-quality spatial information (see also von Frisch, 1967). A reason could be that disoriented dances still provide other useful information, such as the odour of a food source (Grüter & Farina, 2009a).

Having expertise, e.g. in locating a resource, can not only affect the propensity to signal to others, but also the quality of the signal itself. Honey bees with more visits to a feeder perform waggle dances of lower variation, i.e. lower error (Schweiger, 1958). In tandem running, the success rate of tandem runs (Glaser & Grüter, 2018) or the directness of trajectories (Franklin et al., 2012) increase with the number of tandem runs an ant has already performed. This suggests that ants become better tandem leaders with more experience.

Age-dependent Signalling

Insect workers change in physiology as they age (e.g. Margotta et al., 2012; Robinson, 1992) and this could affect their signalling. Sometimes, physiological and behavioural changes are driven by experiences, whereas in other instances age per se affects physiology (reviewed in Giraldo & Traniello, 2014). For example, von Frisch (1967, p.74) describes how honey bee foragers that enter the 'stage of senility' (he described this as the last 2–3 days in the life of a bee) start to perform slower and more erratic dances. This suggests that senescence late in life might affect the ability to provide accurate information (but see Rueppell, Christine, Mulcrone, & Groves, 2007). On the other hand, the probability and quality of tandem runs performed by *T. albipennis* appeared to depend on experience, rather than age (Franklin et al., 2012).

Age-dependent changes in foraging behaviour are often accompanied by changes in gene expression (e.g. Feldmeyer, Elsner, & Foitzik, 2014; Whitfield, Cziko, & Robinson, 2003). For example, expression of the *foraging* gene depends on age in some species and experience in others (Oettler, Nachtigal, & Schrader, 2015). *Foraging* is an important driver of foraging behaviour and reward evaluation (Ben-Shahar, Robichon, Sokolowski, & Robinson, 2002; Thamm & Scheiner, 2014). Likewise, octopamine plays an important role in the perception of rewards and modulates dancing in honey bees (Barron, Maleszka, Vander Meer, & Robinson, 2007). The expression of some octopamine receptors changes with age, whereas in others expression depends on experience (Reim & Scheiner, 2014). Thus, since the physiology of the reward system is affected by age, communication about resources might change accordingly, without this being a result of learning according to our definition.

THE EFFECTS OF EXPERIENCE ON THE RECEIVER

The context in which signals are used is affected by different kinds of experiences. Here we discuss (1) signal-value and signal-quality-dependent use of communication and (2) private-information-dependent use of communication (see Fig. 1 for a summary).

Signal-value- and Signal-quality-dependent Use of Communication

It is useful to distinguish between the value and the quality of communicated information. By signal quality we refer to the accuracy or precision of the communicated information, while signal value refers to how useful the information is to the receiver. For example, extremely precise and accurate information about a resource that is large and nearby may be of high quality but low value because foragers can easily find it without using social information. Receivers should respond to the value of communicated information and rely less on it if communication is of low value. If the quality of a signal is low, the best strategy of receivers is less

easy to predict. Receivers could either ignore the signal or pay closer attention to acquire more information. Honey bees seem to show both responses depending on the amount of noise and ambiguity in the signal. When foragers are exposed to disoriented dances (i.e. waggle dances pointing in random directions during the same dance) for extended periods, they reduce their dance following compared to bees exposed to oriented dances (l'Anson Price et al., 2019). Presumably, they switch to a more solitary foraging strategy if only disoriented dances are available. We would thus expect that honey bees inhabiting environments where waggle dance information is more valuable, e.g. in the tropics (Dornhaus & Chittka, 2004; l'Anson Price & Grüter, 2015) to perform more waggle dances and followers to show more interest in dance information than in environments where dance communication is less valuable, e.g. in temperate human-modified environments (l'Anson Price et al., 2019). Another example of learning is found in *L. niger* ants, which quickly stop following pheromone trails if those trails are uninformative or consistently lead to punishments (Czaczkes & Koch, 2018). However, if the informational noise in the waggle dance is moderate (i.e. waggle phases point approximately in the same direction, but with some angular error), then dance followers increase the time they spend following more noisy waggle dances, but only if the indicated food source is far away (Al Toufailia, Couvillon, Ratnieks, & Grüter, 2013). Thus, bees might be investing more time to decode dances when a failure to acquire precise information is likely to be more costly. In this case, the quality of the signal and the value of the information provided by the signal interact to affect dance follower behaviour.

As mentioned above, the value of a resource greatly depends on the colony's need for that resource. Ants from starved nests are more likely to follow recruitment signals (Cassill, 2003; Maillieux, Devigne, Deneubourg, & Detrain, 2010; von Thienen, Metzler, & Witte, 2016), and indeed recruitment success in *L. niger* ants is mostly driven by colony starvation levels, not by recruiter starvation levels (Maillieux et al., 2010).

Private-information-dependent Use of Communication

The reliance on communicated information has been shown to depend on how well informed the potential audience is. In many, but not all, social insects that have private information regarding the location of a food source or a nest site (i.e. they have visited this location in the past and learned about the value of the resource first-hand) will workers often disregard social information from others, and preferentially follow their own memories (Aron, Beckers, Deneubourg, & Pasteels, 1993; Cronin, 2013; De Almeida, Camargo, Forti, & Lopes, 2018; Elizalde & Farji-Brener, 2012; Grüter, Balbuena, & Farina, 2008; Grüter, Czaczkes, & Ratnieks, 2011; Harrison, Fewell, Stiller, & Breed, 1989; Johnson, 1967). In some cases, the use of private information can be triggered by communication signals. Inactive honey bee foragers, for example, can be reactivated by the waggle dance, but may then ignore the directional component of the signal, preferring again to follow their own memory (Gilley et al., 2012; Grüter et al., 2008). The reason why social insects often ignore communicated information is not yet entirely clear because social information is often of high value as signallers have a tendency to only communicate about high-quality resources (see above), i.e. they filter information for those that are interested in social information (Grüter et al., 2010; Rendell et al., 2010). One reason could be ecological: social insects often exploit food sources that persist for extended periods (Quinet & Pasteels, 1996; Ribbands, 1949), e.g. flower patches, and even if they become unavailable temporarily (e.g. during the night or due to rainfall), they have a high chance of becoming rewarding again. An additional and more general reason might be that the

production and interpretation of signals is not perfect. Indeed, recruitment success rates have been reported as somewhat lower than expected in waggle dance-decoding honey bees (e.g. Esch & Bastian, 1970; Mautz, 1971), tandem-running ants (e.g. Wilson, 1959; but see Kaur, Joseph, Anoop, & Sumana, 2017) and some trail-laying ants (Czaczkes, Castorena, Schürch, & Heinze, 2017; Grüter et al., 2011; Jeanson, Ratnieks, & Deneubourg, 2003). Furthermore, signals often only provide very noisy information about the quality of the resource. Having private information does not always decrease the use of communication. One example showing how learning can increase the use of communicated information is found in honey bees that learn the odour of food shared through mouth-to-mouth feeding (trophallaxis) or through sampling food stored in cells (Farina, Grüter, Acosta, & Mc Cabe, 2007; Farina, Grüter, & Diaz, 2005; Gil & De Marco, 2005; Grüter, Acosta, & Farina, 2006). Subsequently, bees that have these olfactory experiences are more likely to follow waggle dances of bees that collect this type of food (Balbuena, Arenas, & Farina, 2012). This suggests that memorized information about types of rewarding food acquired inside the hive increase the interest in communication about where to find this type of food.

Social insects do not stick blindly to one strategy. If private information about the location of a food source becomes unrewarding because the food no longer exists, or if private information is unreliable, e.g. because experienced rewards were very variable, then insect foragers often increase the use of social information (Grüter & Ratnieks, 2011; Grüter, Segers, & Ratnieks, 2013; Smolla, Alem, Chittka, & Shultz, 2016). These information-use strategies have also been called 'copy-if-dissatisfied' (copy refers to the use of social information) or 'copy-if-uncertain' (Grüter & Leadbeater, 2014; Hoppitt & Laland, 2013; Kendal, Coolen, van Bergen, & Laland, 2005; Laland, 2004). Likewise, when *L. niger* ants acquire reliable social information about a better food source, they will switch from private to social information ('copy-if-better' strategy) (Czaczkes & Beckwith, 2018). However, often foragers will not have reliable information about the alternative options to make such comparisons. Thus, as predicted by 'uncertainty avoidance' theory (Ellsberg, 1961; Kahneman & Tversky, 1979), experienced *L. niger* ants will often ignore pheromone trails as long as the reliability of social information is unclear, but begin following the pheromone trails if they receive reliable information that better food is now available (Czaczkes & Beckwith, 2018).

LEARNING ABOUT THE MEANING AND VALUE OF SIGNALS?

While learning clearly affects whether social insects produce or rely on signals (similar to 'contextual learning' in Janik & Slater, 2000), we currently know little about whether insects learn about the meaning and value of the signal itself. Learning about the meaning of signals is important for how birds or humans acquire a song or language, but do honey bees need to learn about the meaning and value of waggle dances and do ants learn the chemical identity of a pheromone trail before following it? It is usually assumed that this is not the case and that the response to signals is innate and unlearned in social insects. However, there is evidence that learning about the meaning shapes communication in social insects. One indication is the observation that young workers often respond differently or not at all to a signal. This, however, can also be explained without learning, e.g. by younger workers differing in physiology (e.g. juvenile hormone) or functional role (brood care and cleaning versus nest defence and foraging) (Hölldobler & Wilson, 1990; Robinson, 1992). Evidence for learning comes from a study on the stingless bee *Scaptotrigona pectoralis*, where workers seem to learn the identity of their trail pheromone (Reichle, Aguilar, Ayasse, & Jarau, 2011). Similarly, it has been speculated that

Myrmica rubra workers must learn to follow pheromone trails, and do so more rapidly in the presence of older experienced workers (Cammaerts, 2013).

Even if insects innately respond to signals, learning about the value of the signal in a particular environment could be used to modify the reliance on the signal in adaptive ways (similar to *comprehension learning* in Janik & Slater, 2000). The reduction in dance following after prolonged exposure to disoriented dances is consistent with bees learning about the value of the waggle dance (l'Anson Price et al., 2019). For instance, bees following disoriented waggle dances could average several waggle phases (Tanner & Visscher, 2008) and, subsequently, fly to the location of the computed vector. By not finding a food source at the location, bees could learn that following waggle dances does not lead to rewards and reduce their interest in dances (l'Anson Price et al., 2019).

FUTURE DIRECTIONS

Learning the Meaning of Signals

Despite recent progress, more research is needed to better understand the role of learning about the meaning and value of signals. While innate behaviour is likely to be important, we would expect that learning about the value of signals and communicated information can help colonies be more successful in a given environment. Broadly, learning is selected for where short-term predictability within an individual's lifetime intersect with long-term unpredictability between generations (Shettleworth, 2010). This may help point us towards situations where learning is more or less likely to be involved. Learning the meaning of a genetically encoded pheromone thus seems unlikely (and indeed evidence for this sort of learning is very rare), but learning about the reliability of a signal would be unsurprising (l'Anson Price et al., 2019), and we predict that it could be found broadly, if searched for. Communication often provides situations in which associative learning can take place indirectly – such as learning the smell of a profitable food source.

Learning to Eavesdrop

Reports exist of social insects eavesdropping on communications from other species (e.g. Gobin, Peeters, Billen, & Morgan, 1998; Lichtenberg, Graff Zivin, Hrnčir, & Nieh, 2014; Menzel, Pokorný, Blüthgen, & Schmitt, 2010; Nieh, Barreto, Contrera, & Imperatriz-Fonseca, 2004). These interactions are not necessarily mutualistic, and may be costly to one of the species (Lichtenberg et al., 2014; Nieh et al., 2004). Such eavesdropping and mutual signal use are poorly studied. However, it seems likely that they can provide examples of learning to interpret communication signals in social insects, as the individual member species of such interactions are often also found in isolation (Menzel et al., 2010). If interspecific trail following does arise through learning, do such species pairs also learn to interpret other allospecific signals, such as alarm signals?

CONCLUSIONS

Seeing social insects as simple organisms that follow simple behavioural rules during communication processes has been fruitful, and improved our understanding of the collective organization of colony life. However, a closer look reveals that the behavioural strategies of insect workers are far from simple. In fact, they show a diverse range of sophisticated and flexible strategies in how they produce and use signals. The information individuals gain while interacting with their world strongly affects their motivation to communicate and to respond to communicated information, and

indeed what information they attend to. Learning plays a major role in modulating many aspects of communication in social insects: signallers learn what resources are worth advertising, when it is worthwhile to signal, and even learn to signal more accurately. Receivers use acquired information to decide when and whether to follow signals at all, and what type of signaller-provided information to attend to. The integral role of learning in social communication makes their communication more flexible than once thought. Ultimately, while innate responses likely form the basis of social insect communication, learning plays a critical role in increasing communication flexibility, effectiveness and efficiency.

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