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REVIEW

Individual and collective cognition in social insects: what's in a name?

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Abstract

Descriptions of types of intelligence or cognition that conceptualize and categorize behavioral capabilities of workers and cooperative groups of eusocial insects have proliferated. Individual workers are described as having cognition, or less frequently, intelligence, and emergent colony-level behavior is typically described as collective intelligence, swarm intelligence, and distributed intelligence (or cognition). These concepts and terms have historical roots in psychology, education, economics, politics, computer science, artificial intelligence, and robotics, and have varied connotations and denotations that often are inconsistent with their initial context of use. Although integration and hybridization among disciplines can be productive, imprecise and potentially misleading applications may limit the ability to accurately describe or conceptualize social insect behavioral phenomena, generate testable hypotheses, and communicate accurately and broadly within the scientific community and with the media and public. Here, we aim to clarify the origins, meanings, and relevance of terms associated with social insect intelligence and cognition. An historical, semantic, and mechanistic analysis suggests that terms may lack relevant conceptual significance and should be carefully evaluated before applying them free-hand to attempt to inform our understanding of social insect cognition at multiple levels. We provide rationale and recommendations for retaining or discontinuing the use of terms.

Keywords Cognition · Learning · Intelligence · Collective mind · Swarm behavior · Task performance

Introduction

> "What is instinct? What is intelligence? These words have been the subject of hundreds of definitions and have been given innumerable varieties of meaning. Some definitions are so technical as to be unintelligible; others are demonstrably inexact. Certainly many good definitions have been given, yet not one of them is entirely satisfactory."
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> Hingston, *Instinct and Intelligence* (Hingston 1929)

> "Does 'cognition' have a single, stable, well-behaved meaning? That seems doubtful."
>
> Bayne et al. (2019)

The remarkable behavior of eusocial insect workers as individuals, cooperative groups, and societies has for centuries attracted the attention of naturalists and researchers across diverse disciplines. Individuals and colonies often exhibit sophisticated information-processing capacities, behavioral plasticity, learning, and coordinated actions that seem unexpectedly advanced in light of the minute brains of workers (Chittka and Niven 2009; Avarguès-Weber et al. 2011, 2018; Perry et al. 2017; Chittka 2022; Chittka and Rossi 2022; Czaczkes 2022; Fig. 1). It is intuitive that different seemingly "intelligent" behaviors in social insects do not require similar levels of mental capacity and consequently, it is important to use appropriate terms to describe, interpret, and thus understand individual worker and colony-level behavior. The terms *cognition* and *intelligence* are commonly applied. Intelligence—a more casual term often used in public communication and media outreach—is not

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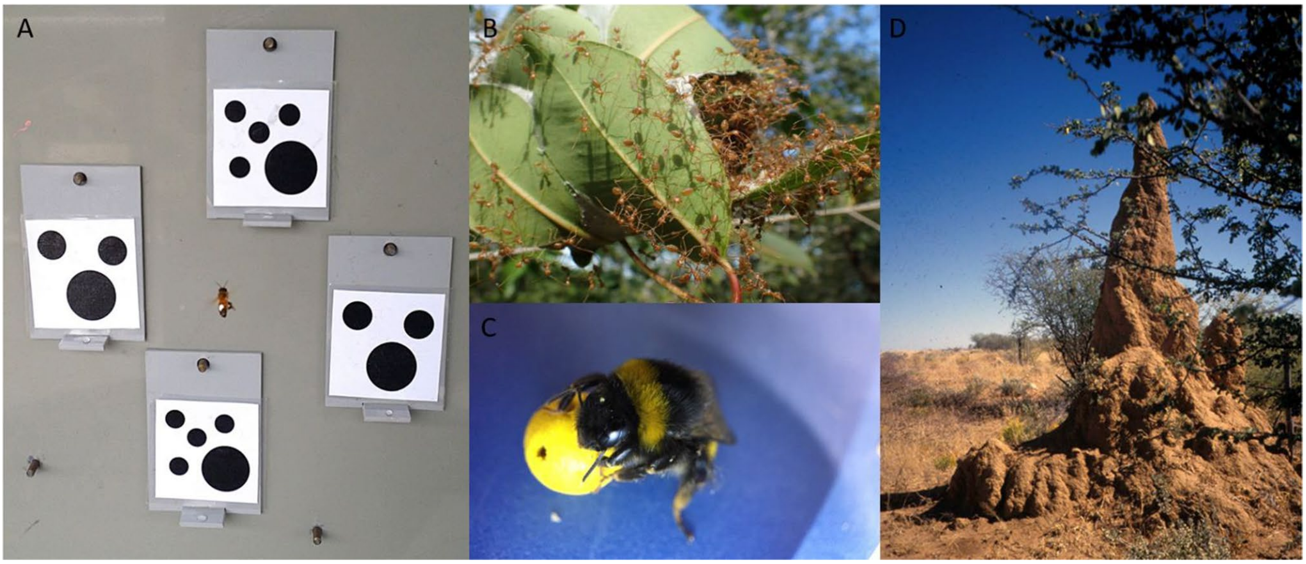

Fig. 1 Examples of "intelligent" behaviors in social insects. **A** Honeybees can count up to five items, order them linearly, and have a notion of zero. Here, the bee has to choose the image presenting the lower number of dots to collect a sucrose reward on the platform. Photo credit: Dr. Scarlett Howard. **B** Weaver ants, *Oecophylla smaragdina*, show remarkable coordination to construct arboreal nests from tree leaves, forming living chains to pull and anchor leaves in position while larvae secrete silk to hold them in place. Photo credit: Dr. Simon Robson. **C** Bumblebees can be taught to play football (soccer) by rolling a ball to a goal to receive a sucrose reward. Observer bees learn to imitate this unnatural behavior. Photo credit: Dr. Lida Loukola. **D** *Macrotermes* mound-building termites build giant air-conditioned nests without centralized control. Photo credit: Dr. Gillian Ashworth

well-defined but understood to imply non-instinctive behavior. Cognition is the scientific counterpart of intelligence that has proper definition through referenced literature and is used by experts. This general term includes all mental processes, from perception, sensory integration, learning, and reasoning to decision-making. It is divisible into subcategories such as social cognition, spatial cognition, numerical cognition, and meta-cognition, among others. Continual debate in diverse disciplines across a wide range of taxa reflect controversy over the use of terms such as intelligence and cognition and their specific meanings. The introductory quotes of Hingston (1929) and Bayne et al. (2019) span 90 years and both suggest controversy and a lack of resolution. Legg and Hutter (2007) report 70 definitions of intelligence, concluding that no single definition may be adequate (see also Barron et al. 2015). Bechtel and Bich (2021) note the difficulty in discriminating between cognitive and non-cognitive actions and these authors, Ginsburg and Jablonka (2021), and Levin et al. (2021) raise the question of the requirement of a nervous system for cognition. Most literature on cognition addresses questions of interindividual differences in human intellectual ability and skills (Deary 2012), the nature of general intelligence (reasoned, flexible behavior), and its distribution across clades (Burkart et al. 2017). Abramson and Wells (2018) caution that the measurement of intelligence is problematic, and hybridizing studies of invertebrate learning with concepts of human psychology requires terminological consistency. Logan et al. (2018) state that humans may not be suitable as a standard for evaluating the behavioral capabilities of other animals.

Theoretical and empirical studies of social insect worker cognition have been based on or have produced multidisciplinary conceptual frameworks. Today, numerous descriptive terms for such behavior are part of the vocabulary of insect sociobiology. Emergent group behavior and decision-making across diverse clades and contexts are often described as "collective intelligence," "distributed intelligence," "collective cognition," "distributed cognition," and "swarm intelligence," augmented with additional detail in variants such as "situated cognition" (Cheng 2018a). Terms such as "social cognition", "teaching", and "emotion" used to describe individual behaviors originate in human psychology. Interdisciplinary approaches and promiscuous hybrid thinking can be innovative and heuristically valuable in the analysis of complex systems by self-organization theory (Camazine et al. 2001; Favela 2020), which is derived from physicochemistry (Nicolis and Prigogine 1977) and can identify global rules of decision-making. Nevertheless, a proliferation of terms raises the question of whether concepts have been developed to maximize the benefits of integrating distantly related ideas or may generate confusion.

Here, we highlight the importance of understanding the origin, history, and application of terms used to describe individual and group-level behavior in social insects, assess their value, and suggest which terms should be retained or discontinued. Our position is that analyzing the language and concepts of intelligence and cognition will improve our knowledge of social insect behavior both by avoiding misinterpretation of the underlying processes of cognition and by generating testable hypotheses of its mechanisms. Although the literature on intelligence encompasses philosophy, psychology, and sociology with a strong human bias and thus is too broad, detailed, and complex to be considered here, understanding the contexts and original use of terms can offer insight into how concepts in different disciplines have been coopted in social insect science and whether they should be continued to be used.

Intelligence of individual workers and worker groups

In *The Insect Societies* (Wilson 1971), intelligence is mentioned once while comparing ant and honey bee behaviors with those of mammals, but is virtually absent from other discussions of the mental capabilities of social insects that include multiple sensory modality learning, sequential task performance, maze learning, memory duration and transference, and play. Worker intelligence is “variously measured as the diversity, precision, and persistence of the separate acts of learning, most particularly the ability to perform rational operations, that is, to generalize learned information by transferring it from one set of circumstances to another” (Wilson 1971, p. 197). Intelligence, cognition, collective intelligence, and related terms and concepts are absent in *The Ants* (Hölldobler and Wilson 1990). Cognition most often describes individual performance, but intelligence does not appear in much current work (e.g., Avarguès-Weber and Giurfa 2013; Caron and Abbott 2017; Cheng 2018a; Howard et al. 2018). The broad use of the term cognition has itself generated significant debate (Bayne et al. 2019), yet contextual frameworks involving cognition have multiplied. Indeed, the “cognitive revolution” in the 1950s guided the emergence of cognitive science to study at first human capacities, their development, and associated pathologies. Replicable experimental tests and a glossary of terms representing cognitive functions with well-defined and clear criteria were developed. The methodology and vocabulary of this novel field were then transposed to animal studies with the main goal of deciphering human cognitive specificities and their evolutionary history. Although non-human primate studies were dominant, additional animal models (pigeons, corvids, parrots, dogs, rats, mice, and dolphins) represented most research effort. Consequently, a novel cognitive revolution occurred during the last 2 decades, with an exponential increase in studies of animal cognition based on the definition, criteria, and testing procedures developed for primates. The cognitive capacities of a yet larger diversity of species (fish, bears, salamanders, chickens)—now including insects (ants, bees in particular)—were explored.

In this historical context, it is clear and not surprising that cognition in individual social insect workers began to be described and evaluated through a vocabulary developed and defined for studies of vertebrate taxa. Research on bees and ants encompassed concept learning (Avarguès-Weber and Giurfa 2013), categorization, counting (Giurfa 2019), emotion (Baracchi et al. 2017; Perry and Baciadonna 2017), social learning (Loukola et al. 2017), teaching (Franks and Richardson 2006), empathy, meta-cognition (Perry and Barron 2013), and play behavior (Dona et al. 2022). The same set of criteria defined in human psychology were applied to and fulfilled by insects, thus justifying the use of those terms. Admittedly, sharing terms facilitated broad media interest in most studies demonstrating unexpected cognitive performances in insects despite their miniature brains and short lifespans. Such discoveries revolutionized our conceptualization of intelligence and its relationship to brain size.

Although applying concepts developed in the field of experimental psychology has been fruitful to adjust the definition of intelligence and its link with brain size, it unfortunately did not lead to the genesis of testable hypotheses concerning neurobiological mechanisms. Indeed, in most cases, the neural substrates of cognitive functions are still not well-defined and those that have been identified in mammalian or avian brains are not easily transposable to the highly divergent insect brain. Interestingly, this challenge has been at the origin of an ever-growing number of computational neuroscience studies that reconsider the actual complexity of cognitive skills such as abstraction, counting or face recognition, by developing very simple models or artificial neural networks capable of solving these tasks.

Colony-level intelligence or cognition

Group decision-making by social insect workers is frequently termed collective intelligence, a concept rooted in disciplines remote from sociobiology (Yu et al. 2017). Although he did not coin the term *collective intelligence*, the “wisdom of crowds” concept in social insect behavior (e.g., Seeley 2010; Sasaki and Pratt 2018) can be traced to Galton (1907), who examined the trustworthiness of democratic processes in a study of a competition among attendees at a livestock exhibition to estimate the dressed weight of an ox. The median estimate of the group was within 1% of the actual weight and more accurate than the value estimated by any individual participant. The phenomenon is not described by Galton as collective intelligence, although this study is often cited as a premier example. Prior to Galton and in a similar political science framework, Condorcet’s

(1785) juror theorem mathematically concluded a majority of jurors is more likely to arrive at a correct decision than a single individual. In addition to its deep origins in political science and sociology, collective intelligence has a history of usage in education, for example, in "collective intelligence tests" for student evaluation (Muller 1970; Moore and Rocklin 1998) of component language, mathematics, and science skill assessments for grade-level advancement. More recent studies (Surowiecki 2004; Sumpter 2006; Sasaki and Pratt 2018; Almaatouq et al. 2020) have distant foundations in this work terminologically but not conceptually, and extend it to collective animal behavior. The term enters the biological literature in statistical measurements of collective intelligence in humans (Szuba 2001) but is not clearly defined. *Collective cognition* was premiered in Gibson (2001) to develop strategies that improve human workplace performance and is commonly used today in studies of social insect emergent actions, such as successful navigation in complex environment or groups of ants cooperatively transporting large food items (e.g., Feinerman and Korman 2017; Gelblum et al. 2020). Collective cognition seems to be used interchangeably with collective intelligence (e.g., Couzin 2009) and colony-level cognition (Marshall and Franks 2009; Marshall et al. 2009).

Distributed intelligence appears to have first been used by Dickinson (1971) in reference to computer terminal systems and applied in computer science, artificial intelligence, and robotics such that its meaning lost precise definition. Parker (2008), for example, described the association of distributed intelligence with "bioinspirational" emergent swarms, without social insect or other specified biological models, "organizational, social, and knowledge-based, ontological paradigms," and how they are applied to meet the challenges of task allocation in multi-robot systems. Members of groups interact and have awareness of the actions of others, and reason about actions and intentions of "teammates" to achieve group goals. Agents may have adversarial or common individual aims. In any case, the computational science literatures on distributed intelligence and distributed cognition appear to be parallel to those on social insects, with occasional non-specific reference.

In computer science and related disciplines, concepts of distributed cognition (and/or distributed intelligence) were originally developed to understand how problems can be solved globally through the interactions of individuals that have access only to local information and differ in performance, sharing capabilities to successfully complete a task (Hendtlass 2004). They also concern how systems are able to learn to improve the outcomes of collaboration by recognizing faults (Parker 2008). This computational work, based in algorithms/software, is broadly translated to social insect behavioral biology through self-organization theory (Bonabeau et al. 1997, 1999; Camazine et al. 2001). The disciplines have the common goal of illuminating how entities using only local information can achieve global goals. A well-known example involves termites constructing the complex architecture of ventilated mount nests without global supervision (Heyde et al. 2021).

Hutchins (1991) described *distributed cognition* in respect to agricultural division of labor in humans, noting that group properties differ from those of individuals and that cognition operates at two levels, reflecting differences among individuals as well as a requirement for supervisory cognition ("subordination to directing authority"). The latter process would disqualify its application to social insects, which lack centralized control. Hutchins (1995) later applied the concept to group problem-solving in humans noting that cognition is not the product of a single mind. Lestel (1993), citing Hutchins (1991), used distributed cognition in reference to Hutchins's (1991) coupling of the concept with human division of labor. Lestel (1993) later discusses ant foraging from the perspective of self-organization. Moore and Rocklin (1998) critically evaluated the use of the term in the educational literature and raise concerns over its imprecise individual and social definitions. Distributed cognition and related terms were subsequently presented as elements of cognitive ecosystem analysis (Hutchins 2010). O'Donnell et al. (2015) presented a distributed cognition model as an alternative to the social brain hypothesis developed for primates (Dunbar 1998). The distributed cognition model predicts a reduction rather than increase in individual brain investment. Cheng (2018b) considered collective intelligence to be a form of distributed cognition associated with brain reduction, as did Theiner (2017, 2018) in reference to "socially distributed cognition." Amon and Favela (2019) express a need for a more rigorous definition of distributed cognition and apply the concept to human/dog cooperation.

The first conceptualization of distributed cognition (Hutchins 1991) references division of labor, which in social insects often reflect functional morphological traits and their contributions to task efficacy. Behavioral and/or cognitive requirements of task performance may vary among workers due to task-associated morphological, sensory, and motor demands (Muratore and Traniello 2020; Muratore et al. 2022, 2023a, 2023b). Nevertheless, one concern in applying the concept of distributed cognition to social insects is whether the implied behaviors represent innate behavioral routines rather than cognitive processes such as attention, initiative, goal recognition, decision-making, learning, and memory (Perry and Chittka 2019). The question of whether selection has favored hardwired sensorimotor circuits that program efficacious task performance but lack flexibility and/or novelty in problem-solving cognitive ability is rarely addressed. Therefore, using the term "cognition" to describe such behavior—and thus the reference to distributed cognition—may be premature. Moreover, the meaning of distributed cognition is controversial among cognitive scientists (Favela and Martin 2017; reviewed in Amon and Favela 2019) and in the field of education (Moore and Rocklin 1998). Extending its application would unproductively embroil researchers in insect sociobiology in these debates.

In a Linnaean-like classification, Cheng (2018a) listed embodied cognition, extended cognition, and enacted cognition as "species" nested within situated cognition, a "variety" of distributed cognition. *Extended cognition* involves the causal coupling of external structures, such as the web of a spider, during web building. In *enactive cognition* (play in dogs, e.g.), cognition follows from action. For *embodied cognition*, peripheral organs rather than the brain perform computational functions, as in octopuses. It could be tempting to apply these concepts to social insect behavior: extended cognition might be represented by cooperative nest construction by weaver ant workers using larval silk to thread leaves together. The concept of embodied cognition may have application in social insect behavior in light of the superorganism nature of colonies, although each computational unit has its own nervous system, and the "colony brain" is a non-neuronal emergent property of worker interactions (Pagán 2019; Traniello et al. 2022).

Swarm intelligence originated in the artificial intelligence literature in descriptions of cellular robotic systems (Beni and Wang 1989; defined in Sadiku et al. 2018) and has since been given biological applications in social insects (Bonabeau et al. 1999), vertebrates, and humans (e.g., Krause et al. 2010; Woolley et al. 2010). It appears to be more frequently used in the computational modelling of collection behavior such as group motion than in ecological or evolutionary accounts of group action.

Semantics of social insect cognition and brain evolution

The study of cognitive phenomena begs questions concerning their mechanistic basis. Do the terms used to describe social insect cognition generate viable hypotheses to identify mechanisms? While neuroanatomical research can test the predictions of models of social organization that may involve cognitive functions (Godfrey and Gronenberg 2019; Traniello et al. 2022), details of the neural circuitry, neuropharmacology, and patterns of brain areas activation or genes expression associated with social insect intelligence have not really tackled yet sophisticated forms of cognition beyond associative learning (Denker et al. 2010; Devaud et al. 2015; Li et al. 2018; Bestea et al. 2022; Geng et al. 2022). Analyses of the association of neuroarchitecture and connectivity, behavioral repertoire size, and cognition can inform our understanding of the relationship of brain size and structure to behavioral performance and cognition. However, given the present stage of development of socio-neuroethological research, it is unclear how the various categories of cognition described in the literature could be distinguished and supported by neurobiological and/or —omic studies, as discussed below.

"Social intelligence" enables coping with the challenges of group living; related selective forces may favor increased brain size and dedicated neuroarchitectures to monitor, store, and respond adaptively to information in contexts of social bonding and reproductive conflict. As predicted by the social brain hypothesis (Dunbar 1998) originally formulated for primates, group size and concomitant selection for greater cognitive skills needed to manage more numerous and complex social relationships drive the evolution of a larger brain. The application of this hypothesis to social insects has been questioned and empirical support has been inconsistent. The fact that social bees, ants, and wasps demonstrate sophisticated cognition in comparison to other insect clades and generally possess enlarged mushroom bodies, a brain compartment often linked to insect "intelligence," seems to broadly support the social brain hypothesis. However, the evolution of mushroom body elaboration occurred prior to the emergence of sociality (Lihoreau et al. 2012; Farris 2016; Traniello et al. 2022).

Cheng (2018a) considers the social brain hypothesis as the "opposite" of distributed cognition, and tests of the latter concern neuroanatomy rather than the nature of the cognition demands involved in task performance. The distributed cognition model predicts social complexity (larger group size and/or level of organization/division of labor in insect societies) involves selection favoring reduction in the cognitive needs of individual workers. Theiner (2017) and Cheng (2018a) noted reduced cognitive capacities resulting from cooperative "team work" in social groups. Used in this context, it should be clarified that the "reduction" in cognition represents more of a specificity of behavioral performance, if in fact cognitive, rather than loss of broader abilities. Additionally, "team work," a controversial topic in social insect biology, is likely to mean division of labor. The notion of reduced cognitive ability among colony members due to increased social complexity was first described for eusocial insects by Jaffe and Perez (1989), who identified a trend toward reduction in capabilities of polymorphic workers in socially complex ants, and that species with highly evolved morphological caste systems show a decrease in brain size relative to body size are "generally less developed neurally," less able to learn, and show "differences in neural specialization among castes." These authors were among the first to conceptually frame brain evolution in terms of social complexity, followed by Gronenberg and Riveros (2009), Muscedere and Traniello (2012), Riveros et al. (2012); Godfrey and Gronenberg (2019), and Traniello et al. (2022).

The hypothesis that brain investment would be reduced by sharing tasks and decision-making between workers was supported by the finding of significantly reduced mushroom body investment in social vespid wasps compared to solitary species (O'Donnell et al. 2015). Variation in social organization among the sampled eusocial species, however, did not significantly affect brain investment patterns. How the social variables assessed (colony foundation, colony size and differentiation of queens) vary in specific behavioral and/or cognitive demands other than those related to reproductive conflict and social hierarchies, along with the role of "social communication," should be clarified. Muratore et al. (2022) demonstrated that estimated variation in sensory and motor demands of task performance among strongly polymorphic workers of the leafcutter ant *Atta cephalotes* correlate with the volume of the mushroom body. Mushroom bodies are disproportionally large in size in media workers, which have the most diverse task repertories, but the extent to which their behavioral performance involves cognition is unknown.

Alternative competing hypotheses on the causal relationship between complex (advanced) sociality, its associated cognitive underpinnings, and brain evolution have been proposed. Importantly, while the possibility that eusociality per se favor mushroom body enlargement is not supported (Farris and Schulmeister 2011; Lihoreau et al. 2012), it remains possible that prior development of integrative brain structures to allow solving challenging foraging and navigational tasks served as preadaptations for eusociality. It is also likely that mushroom body size is evolutionarily labile and responsive to diverse behavioral and/or cognitive demands. The evolution of advanced division of labor with discrete individual specialization could subsequently have resulted in saving energy due to a reduction in brain investment and individual cognition and flexibility or molecular mechanisms that reduce neurometabolic costs (Kamhi et al. 2016). We note that discrete specialization is absent in eusocial bee or wasp species, which potentially explains why the reduction of individual cognitive demand due to eusociality does not seem to apply in these species. Studies of brain evolution present examples of how the term "cognition" could lead to completely opposite interpretations of underlying individual brain resources when used to describe individual or collective "intelligent" behaviors. Social factors may select for either increased or decreased brain size (DeSilva et al. 2021) even under conditions of reproductive conflict (Penick et al. 2021). Gross neuroanatomy may therefore not be able to distinguish among types of cognition and, in any case, could obscure the fine structure of neural networks that underpin cognitive capability.

Consequences of terminological inaccuracy and ambiguity

Although the consequences of using terms and concepts inaccurately are difficult to measure, the uncritical use of diverse terms for cognition in insect sociobiology can negatively impact the scientific record and research. It can compromise publishing ethics by introducing terms without appropriate author credit, even naively. This could be construed as plagiarism or negligence in scholarship; the latter may result in "reinventing the wheel" conceptually. Furthermore, inappropriate terminology can impede communication in behavioral science and across diverse disciplines that analyze cognition. Study aims can be clarified and findings better interpreted if terminology is historically sourced, defined, and refined to improve accuracy. This will minimize the accumulation of semantic "baggage" that can occur if terms are borrowed from the literature on humans (Bell 2017). Research questions and approaches can change depending on how terms are understood; some terms continue to be debated even in their field of origin, while others are ambiguous when applied outside of the discipline in which they were generated. Moore and Rocklin (1998) note new terms should not "merely sanction existing research … without affecting its implementation or interpretation." Since terms may be applied with implied meaning but lack of definition, a broad benefit of consistent, defined terminology would ensure research is focused on the same phenomena. Otherwise, in the absence of agreed-upon meaning, terms can create a "fuzzy generality of reference" (Nash 1993).

A summary of terms used in social insect colony-level behavior illustrates vagueness of definition and multiple unrelated contexts of application during decades of use (Table 1). The uncritical growth of terminology may deter understanding (West et al. 2007; Beekman and Jordan 2017), as terms used to describe behavior may become irrelevant or scientifically meaningless jargon (Gowaty 1982, 1984; Elgar et al. 2013). In social insects, for example, the concept of task allocation, developed to model behavioral responsiveness and collective worker behavior (Beshers and Fewell 2001; Kang and Theraulaz 2016), seems to be more frequently and freely used in disciplines outside of insect sociobiology. Gordon (2019) remarked: "a recent literature search for 'task allocation' led me to more articles about computer science, robotics, and operations research than to studies of social insects."

Terminology should be carefully selected for its epistemological value, and it should not be assumed that what appear to be novel descriptors necessarily provide new insights. Behaviorally differentiated workers, for example, could be described as varying in cognitive bandwidth,

Table 1 Definitions or contexts of application of terms and phenomena used to describe group-level cognition. References credit original usage or later appearance of definition

Collective intelligence

Muller (1970)

“Nous nous proposons ici (…) d’étudier la valeur respective des diverse prédicteurs utilisés dans la sélection scolaire, et plus particulièrement, le role des tests d’intelligence collectifs.”

[We suggest here (…) to study the respective value of the various predicting factors used in pupil selection, a more specifically, the impact of collective intelligence tests.]

Wechsler (1971)

“A group of individuals working together may … through concerted thinking, come up with a better solution (or for that matter a poorer one) but whether in doing so the individuals composing the group may not have acquired or made use of perceptions or insights not experienced or available to them when working or cogitating alone.”

Hiltz and Turoff (1978)

“A collective decision capability (that is) at least as good as or better than any single member of the group.”

Franks (1989)

“Intelligence, natural or artificial, is an emergent property of collective communication.”

Levy (1997)

“.... a form of universally distributed intelligence, constantly enhanced, coordinated in real time, and resulting in the effective mobilization of skills.”

Szuba (2001)

“…collective intelligence emerges because of cooperation or coexistence if at least one problem can be pointed to, such that it can be solved by a lone individual but supported by the group, or by some individuals working together.”

Woolley et al. (2010)

“…the general ability of the group to perform a wide variety of tasks.”

Yu et al. (2017)

“The group can be of more power and better wisdom than the sum of the individuals.”

Malone and Bernstein (2022)

“Groups of individuals acting collectively in ways that seem intelligent.”

Collective cognition

Gibson (2001)

“Collective cognition can be defined as the group processes involved in the acquisition, storage, transmission, and use of information.”

“Collective cognition does not reside in individuals taken separately, though each contributes to it. Nor does it reside outside them. It is present in the interrelations between of group members.”

Distributed cognition

Jaffe and Perez (1989)

“Individual mental capacity seems to be diminished in (highly complex social species), probably as a consequence of a sophisticated polymorphism in which individuals are specialized morphologically (and physiologically) but at the expense of the general capacities of the individual.”

Hutchins (1991)

“All divisions of labor require some distributed cognition in order to coordinate the activities of the participants. When the labor that is distributed is cognitive labor, the system involves the distribution of two kinds of cognitive labor: the cognition that is the task, and the cognition that governs the coordination of the elements of the task. In such a case, the group performing the cognitive task may have cognitive properties that differ from the cognitive properties of any individual.”

“Pour Hutchins (1991) le concept de cognition distribuée est plus important pour l’anthropologie cognitive que celui de division du travail.”

[According to Hutchins 1991, the distributed cognition concept is more important for cognitive anthropology than the concept of division of labor.]

Michaelian and Sutton (2013)

“According to the hypotheses of distributed and extended cognition, remembering does not always occur entirely inside the brain but is often distributed across heterogeneous systems combining neural, bodily, social, and technological resources.”

“Cognition might thus be multiply distributed, both within neural networks and across bodies, artifacts, and social groups.”

O’Donnell et al. (2015)

“Distributed cognition models assume group members can rely on social communication instead of individual cognition.”

“If cooperative information sharing among individuals takes precedence …. selection for individual cognitive abilities can be relaxed (and) …. brain investment will decrease, rather than increase, with increases in sociality.”

Cheng (2018a)

“Distributed cognition (a type of situated cognition) is often used as another term for situated cognition. But behavioral biologists have used the term in another sense, to mean the reduction of cognitive capacities arising from team work in cooperative societies.”

“The term *distributed cognition* …. takes on a different sense at the species level, in which cognition is spread among different animals. Eusocial insects, especially hymenopterans, provide case studies here. If the cognition required for different tasks is spread among different animals, each can be less brainy in both cognitive and anatomical senses.”

Table 1 (continued)

Amon and Favela (2019)

"Distributed cognition refers to situations in which task requirements are shared among multiple agents or, potentially, off-loaded onto the environment."

Distributed intelligence

Dickinson (1971)

"One trend is … the increasing tendency to distribute intelligence throughout a terminal system rather than concentrating it at its center. This can be done through the use of small stored program processors as front end communication processors and remote concentrators and the use of stored program controllers within the terminals themselves. The arguments for distributing intelligence include reduction of traffic due to distributed processing, increased flexibility, increased reliability, and increased cost effectiveness."

Swarm intelligence

Sadiku et al. (2018)

"Swarm intelligence is the emergent collective intelligence of groups of simple agents. It belongs to the emerging field of bio-inspired soft computing. It is inspired from the biological entities such as birds, fish, ants, wasps, termites, and bees."

and emergent problem-solving actions might be described as a "pooling of brain power" (Hays 2020), "hive mind" (Check 2006), global brain, or cloud intelligence. Similarly, distributed brain and distributed mind (Dunbar et al. 2010; Gamble et al. 2014; Gintis 2014) have been used to describe the emergence of a collective human mind that has broad capacities assembled from the contributions of cognitively variable individuals. These concepts may serve a role in science journalism because they are able to attract attention, but such vernacular language is likely too ethereal to drive research agendas.

Recommendations for term use

It is challenging to reconcile the diverse applications of these terms due to their derivation from disciplines ranging from philosophy to robotics. Terms should be discarded if their use is largely rhetorical and it is possible to replace them. Accordingly, we suggest terms to retain or eliminate, beginning with anthropomorphisms.

Despite the effort to provide clear and testable criteria, the use of human-based terminology often implies a certain level of consciousness—the black box of the field of animal cognition (e.g., Barron and Klein 2016). This is due to the quasi-impossibility to test consciousness in the absence of language, despite the importance of assessing the sophistication of animal mental experiences in terms of human representation, as well as for the advent of animal rights legislation (Baracchi and Baciadonna 2020). For example, evidence of behaviors that fulfill the criteria for "teaching," "emotion," or "empathy" are difficult to attribute to an insect. One solution to this definitional problem is to develop a "cognitive-like" terminology using simile (e.g., "emotion-like," "attentional-like"). This convenient solution has an important advantage: it avoids direct comparison with human faculties while building on sets of criteria associated with those terms that, importantly, still remain to be fulfilled when using cognition-like terminology to avoid intellectually dishonest use for sensationalism. Furthermore, borrowing classical terms from psychology heuristically accentuates the fact that insects have evolved elaborate cognitive capacities to integrate information and use them selectively to make flexible and adaptive decisions, acknowledging that the underlying complexity of the neurobiological mechanisms and consciousness levels diverge. This appropriately emphasizes, therefore, that insects are far from simple "reflex machines."

Phenomena such as emotion or attention are not readily or easily measured and representations of these behaviors in insects may not be either homologous or analogous to behaviors in vertebrates, including humans. As Bell (2017) notes "As observers of nonhuman animal behavior, we have little access to our subjects' thoughts and feelings." Consequentially, we believe that anthropomorphisms are inappropriate. Moreover, inventing novel terminology to describe similar functions in social insects would be inaccurate and unproductive, particularly in relation to definitions and protocols first developed in humans. We therefore support the use of "x-like" terminology, which reflects the similarity of function of a given behavioral phenomenon to a potential human "equivalent," recognizing that such terms do not fully identify behavioral processes or their mechanisms. This approach, however, clearly acknowledges the important divergences in underlying physiological, neurobiological or cognitive mechanisms across diverse clades. Indeed, due to the great evolutionary distance and associated divergence in, for example, perception and brain size, structure, and organization, we cannot expect to find pure emotion or attention in social insects because such terms convey significantly more than a function: they also convey a series of underlying processes and often subjective experience impossible to directly assess in non-human animals.

Additionally, we advocate for a parsimonious approach to refining the current terminologically excessive categorization of cognition. Terms such as distributed cognition and distributed intelligence seem attractive and meaningful but are rhetorical and appear referential mostly to brain evolution. Given their origin and lack of definition in current application to social insect behavior, we suggest that these terms should not be used. Few if any of the behaviors referred to in descriptions of distributed cognition actually represent cognitive processes rather than innate behavioral routines. We therefore suggest describing variation among workers in task specialization requiring differentiation of abilities as *behavioral performance polyphenisms.* In respect to the relationship of behavior to brain evolution, Kuebler et al. (2010) introduced the concept of *neuroanatomical polyphenism* to describe variation in brain organization among leafcutter ant polymorphic workers. These terms are more appropriate than distributed cognition, as they carry no ambiguity or controversy from prior use in other disciplines and do not require the demonstration of cognition.

Collective intelligence has had an unusual history of usage due to its association with Galton (1907), whose concern was human sociopolitics, but the concept was not formally defined therein. Collective intelligence has also been applied in education (Wechsler 1971). Origins of the term would thus seem to argue against its continued use. However, the concept of collective intelligence is deeply embedded in the social insect literature and has a meaning sufficiently agreed upon so as to be widely understood. It can be defined as the ability of a group through emergent information-processing capabilities to complete tasks more efficiently and accurately than any individual group member. Collective cognition can be used interchangeably with collective intelligence as the original application of the former term by Gibson (2001) is similar in meaning and definition to correspond to current usage describing group-level processes. We recommend that other terms, such as distributed intelligence and swarm intelligence, be discarded. These terms have limited utility in insect sociobiology as they convey less information than behavioral performance polyphenism or neuroanatomical polyphenism.

Conclusions

The nomenclature used to describe individual and collective cognitive processes is important, and in insect sociobiology could benefit from refinement and clarification is respect to relevance in behavioral ecology. There are theoretical and methodological components to social insect research, and terms should accurately reflect the concepts they denote to better comprehend behavior in the context of evolution and ecology (Rowe and Healy 2014; Lihoreau et al. 2019; Simons and Tibbetts 2019). Multiple terms of varying origin, casually and interchangeably applied, have been incorporated into a vernacular of social insect behavioral biology. We question the accuracy and necessity of the use of this language, and whether it is productive. Because the terms intelligence and cognition may themselves be difficult to define and related concepts have been acquired from several established or newly founded disciplines apart from insect behavior, there has been a lack of clarity in definition and/or meaning, and several terms may vaguely describe what may essentially be the same behavioral phenomena or do not biologically distinguish among them. Computer science-based notions of distributed cognition or distributed intelligence may have general meaning but should have sufficient definition to improve our understanding of the evolution, organization, and mechanisms of behavior. Moreover, concepts of cognition in computer science appear to imply that cognition is monolithic and quantized as an absolute entity and ignore selection for adaptive modes of information-processing requirements within or across species, or consider developmental plasticity. Behavioral processes and their complexities should be discussed in reference to underlying neural systems' needs for sensory perception and information processing, integrative higher-order functions, and motor output. Integration of levels of analyses that are often separated in different cultures of science to describe group-level decisions will benefit from considering individuals not only as agents but as cognitive entities, while studies on individual behavioral and/or cognitive performances would be more impactful by studying the social context and fitness consequences of cognitive processes and inter-individual variability, and if the terms facilitate mechanistic research.

In the absence of direct assessment, behavior should only be hypothesized to be cognitive. Social insect task routines, even if complex, may be instinctive and sensory-driven. Similarly, it should not be assumed that what appear to be simple behaviors performed in response to environmental or social stimuli are hard-wired and inflexible. Cognitive processes in social insects can be defined and higher cognitive problem-solving ability can be explored in relation to clear and specific phenomena. Learned abstract number representation, for example, is simply and appropriately described as numerical cognition (e.g., Bortot et al. 2019; Howard et al. 2019a, b). Social insect behavior does not need to be descriptively subdivided and categorized, potentially producing unnecessary terminology that may force behavior into a particular framework. A common language of cognition would facilitate comprehension, mechanistic, comparative, and phylogenetic study. Our recommendations are not prescriptive but rather intended to encourage discourse.

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