

Social complexity and brain evolution: insights from ant neuroarchitecture and genomics

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Brain evolution is hypothesized to be driven by requirements to adaptively respond to environmental cues and social signals. Diverse models describe how sociality may have influenced eusocial insect-brain evolution, but specific impacts of social organization and other selective forces on brain architecture have been difficult to distinguish. Here, we evaluate predictions derived from and/or inferences made by models of social organization concerning the effects of individual and collective behavior on brain size, structure, and function using results of neuroanatomical and genomic studies. In contrast to the predictions of some models, we find that worker brains in socially complex species have great behavioral and cognitive capacity. We also find that colony size, the evolution of worker physical castes, and task specialization affect brain size and mosaicism, supporting the idea that sensory, processing and motor requirements for behavioral performance select for adaptive allometries of functionally specialized brain centers. We review available transcriptomic and comparative genomic studies seeking to elucidate the molecular pathways functionally associated with social life and the genetic changes that occurred during the evolution of social complexity. We discuss ways forward, using comparative neuroanatomy, transcriptomics, and comparative genomics, to distinguish among multiple alternative explanations for the relationship between the evolution of neural systems and social complexity.

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Perhaps, a brain is best described not as an actual physical object, but as an emergent process whose individual structural components are subject to biological evolution and may possess physical independence in order to collectively generate aspects of behaviour. In other words, the brain can be seen as a rather fluid or liquid entity. There is little doubt that much more work is necessary to begin to understand and apply these new concepts.

Pagan, 2019 [•1]

Introduction

Our understanding of the impact of group living and its complexities on brain evolution remains incomplete after extensive theoretical development and empirical research. The social brain hypothesis states that increased requirements to monitor complex relationships in large groups selected for larger brains capable of advanced behavioral calculus to promote fitness [2,3]. This begs the broader question of the role of brain size in behavioral performance [4,••5] and the application of the social brain hypothesis to eusocial insects, which have miniature brains, has indeed been explored ([6–8], and references therein). Additionally, questions concerning regulatory mechanisms of colony-level behavior and how neural systems may be targeted by selection related to emergent group properties remain unanswered — as suggested by Pagan [•1]. Individual members of societies vary in their capacity to behave autonomously and/or engage in group decision-making and collective problem-solving [9–12]. In ants, workers are often facultatively or obligatorily sterile and their size and morphology may correlate with task repertoires, in turn affecting variation in demands for behavioral performance and/or cognition that can influence brain evolution [13,14]. Furthermore, colony-level collective intelligence can be assembled — without central control — from local interactions and communication. Our understanding of how elements of social organization such as division of labor and emergent colony properties influence brain size and structure is incomplete.

Here, we integrate sociobiological, neuroanatomical, genetic, and -omic analyses to examine how social organization, behavior, and brain size and structure may be evolutionarily coupled. We associate mechanistic underpinnings of worker behavioral performance at the

individual and colony level with predictions or inferences generated by models of social organization.

Ant evolutionary neurobiology: social organization and brain evolution

Ants exhibit an extraordinary richness of social systems to examine how the behavioral/cognitive challenges of individuals and colonies affect brain size, structure, and function [6,13,15–19]. Worker brains scale in size to body size, follow Haller's rule (brains are relatively larger in small workers [20]), and show adaptive allometry in patterns of brain-compartment investment ([13], and references therein). Increased worker-task diversity appears to correlate with larger brains, including larger mushroom bodies (MB), centers of higher-order processing, learning, and memory [21]. Ant brains also show age-related volumetric and synaptic changes that correlate with task diversity, the development of behavioral efficiency, and plasticity [14,22–24].

Our knowledge of social organization and its mechanistic basis in ants is framed in colony ergonomics [25], task allocation and worker interaction [26,27], principles of self-organization (e.g. [28–31]), and the superorganism concept [32]. These models, and those drawing parallels between decision-making processes in neural systems and colony decision-making [33–35], differ in perspective. Their predictions concerning brain evolution are not often clearly defined.

It is also unclear how emergent group behavior (e.g. [36]) affects brain evolution. Pagan [1] noted eusocial insects have 'traditional' nervous systems as well as the ability to generate adaptive responses through worker interaction, and thus have 'brains within brains'. The regulation of social insect worker behavior therefore involves neural networks within tissue ('physical brains') as well as social networks — aneural systems or 'liquid brains' [1,37–39]. Worker interactions generate collective intelligence. We expect macroscopic and cellular architectures of physical brains will reveal imprints of either selective force (Table 1), and will be identifiable in molecular signatures underlying social evolution (e.g. [40]).

The neuroanatomical basis of social organization

Social insect-brain evolution reflects the importance of various selective forces acting through colony-level design on worker behavioral and neural phenotypes (Table 1). Complexity in eusocial insect-colony organization may involve either selection for smaller, neurally differentiated worker brains [8,41–43], larger brains [44], or allometrically large brain centers [13] that may metabolically offset costs of increased size [45]. The social brain hypothesis [2] is broadly supported by studies of brain evolution in the ant genus *Cataglyphis*: workers of

species that form large colonies have larger brains [44]. However, the social brain hypothesis does not imply the existence of an emergent 'social group brain' and the *Cataglyphis* comparative study does not involve reproductive competition, but rather suggests a role for colony size, which affects the number and complexity of worker interactions. We therefore distinguish between the predictions of the social brain hypothesis and influences of colony size in Table 1. In contrast, distinct neural phenotypes in social insects may be adapted to narrowly circumscribed worker-task repertoires and thus more specialized demands for task performance. This distributed cognition model, derived from Jaffe and Perez [46], predicts reduced brain size or brain-compartment sizes in species with worker size-based division of labor.

Models of self-organization and the emergence of colony-level behavior from local worker interactions and collective intelligence are 'liquid brain' models that indirectly address questions of social insect-brain evolution. The association of group problem-solving properties and the behavioral capabilities of individual workers has been summarized as "*the more complex a society, the more simple the individual*", and the cognition of individual workers has been described as 'fairly limited' [47]. Although the notion of complexity in social systems is debated [48], there does not appear to be a similar questioning of the meaning of behavioral 'simplicity' or its involvement in brain evolution. Yet, concepts of simplicity and complexity are both significant to understand selection for brain design. Self-organization predicts workers will perform innate task routines supported by minimal neuropil investment that constrains behavioral sophistication and flexibility. However, it is clear that this is not the case in honeybees, which have a high degree of collective intelligence (e.g. an aneural colony-level brain) as well as extraordinary individual cognitive abilities [49] based in a physical brain [50]. Individual simplicity does not appear to be the case in ants as well [51].

Self-organization implies that workers in complex ant societies are deficient behaviorally in comparison to those living in small, more socially basic small colonies, the likely ancestral state. In contrast, large, socially complex colonies may have polymorphic workers that vary in task performance. Alternatively, large colonies may have monomorphic workers showing flexible colony need-dependent task allocation [27]. Concerning division of labor by physical castes, socioecological forces influence the evolution of morphologically and behaviorally differentiated workers. Polymorphism, task specialization, and brain size and structure are linked in the leafcutter ant *Atta cephalotes*, in which minor, media, and major workers perform fungal care and nursing, leaf harvesting, and defense, respectively. Their brains show

Table 1

Influences of task-performance requirements on ant-brain evolution under the conditions described or inferred in models of social organization. Self-organization and collective intelligence involve aneural or superorganism brains. Predictions concerning brain size and structure, primarily in workers, are inferred from task-associated behavioral and/or cognitive demands. The influence of social conflict is presented as the social brain hypothesis [2] for ant species characterized by reproductive competition.

Model	Behavioral requirements	Brain size/structure
Self-organization [28,47]	'Simple' workers follow basic behavioral algorithms and interact locally to assemble complex actions, decreasing performance demands on individuals	Worker brains will be relatively small and mosaically differentiated to process mostly olfactory signals
Collective intelligence [33,34,45]	Group decision-making efficacy exceeds that of individual workers, reducing worker performance demands	Altered demand for worker processing ability may reduce or increase brain or brain-center size, depending on context of group cognition
Social brain hypothesis [2]: 'social challenge' [••19,42]	Reproductive conflict increases requirement for information processing	Brain size increases or decreases, depending on fertility, dominance order, and processing needs of workers or gamergates
Colony size/social interaction [44]	Increased interindividual interaction in large colonies requires greater social information processing	Brain size increases with colony size/ interaction rates independent of foraging and navigational needs
Task allocation [27]	Flexible behavior enables task switching to meet fluid colony demands	Brains increase in size to process more diverse social cues and signals associated with diverse tasks and assessment of colony needs
Task specialization (monomorphic workers) [53]	Task-dependent relationship between colony size and brain and/or mushroom body size	Brain compartments supporting behavior will be allometrically large in large colonies
Distributed cognition (polymorphic worker-task specialization) [13,17,42,46]	Worker size- and/or age-related task specializations correlate with behavioral demand variation in task repertoires	Brain size/structure reflect diversity and complexity of task repertoire and processing needs

significantly different patterns of size-scaling and allometries in functionally specialized brain compartments that correlate with behavioral/cognitive demands of task performance [13]. MBs are disproportionately large in media workers, which have the highest task diversity and demands for behavioral performance and (likely) cognition. Although leafcutter ants represent a pinnacle of biological complexity, workers do not seem to have cognitive deficits [52].

Greater task specialization and MB scaling in worker brains may be a consequence of large colony size in the acacia ant *Pseudomyrmex spinicola*, which has monomorphic workers. The relative size of MBs increases in workers that forage on the surfaces of host-plant leaves, but is smaller in defense specialists [53]. In large colonies of monomorphic workers, collective organization is in part evident in pheromone-mediated foraging decisions in which information is exchanged between groups of workers [54]. Relatively narrow requirements for chemical information processing could underlie simple behavioral algorithms governing pheromone responses. Small brains characterized by low investment in the optic and antennal lobes and MBs would be predicted to operate within an aneural brain framework.

Ant brains may be influenced by selective forces associated with registering social encounters and group computation. Task allocation [27] is a system of dynamic worker responsiveness to changing colony needs. Requirements for this social fluidity — monitoring

conditions through worker exchanges and storage and recall of information rather than morphological or neural phenotypes dedicated to performing a given task — may be extensive. Increased brain or MB size may allow workers to more efficiently process context-dependent social information, such as interaction rates in varying environmental contexts, to quickly pivot to immediate task needs. Alternatively, simple rules for task-switching could pose low behavioral/cognitive demands that select for reduced brain investment.

In sum, diverse models of insect social organization — some involving aneural systems of decision-making — make different predictions whether explicitly stated or implied about ant-brain-size evolution. In respect to how striking the differences are, the social brain hypothesis generally predicts brain size will be larger in species characterized by larger societies, whereas self-organization theory assumes worker behavioral simplicity and thus decreased brain investment. Considering other concepts such as distributed cognition, it appears there is no overarching theory to explain brain evolution in ants and we are thus challenged to understand increases or decreases in brain size, in particular, sociobiological contexts.

The molecular basis of neural development, function, and evolution

Studies of the molecular mechanisms influencing individual behavior and social organization, together with studies of the genetic changes underpinning the evolution of individual behavior and social organization, can

complement the studies linking neuroanatomy and social organization described above. Since the honey bee genome was first sequenced and the advent of sociogenomics, transcriptomic studies have attempted to identify genes that are functionally important for individual and group-level traits such as individual behavior and group-level social organization. Many studies demonstrate that genes are differentially expressed in the tissues of colony members, depending on their caste, behavior, age, and the social environment they experience (e.g. [40,55–58]). Additional studies have used a comparative transcriptomic approach and have quantified the degree of shared versus lineage-specific patterns of gene expression associated with social behavior (e.g. [59,60]). Many studies have emphasized specific conserved genes and pathways that likely play important roles in regulating individual behavior as well as colony social organization. For example, functionally important genes differentially expressed in the brains of colony members include the neuropeptide corazonin [61] that suppresses expression of vitellogenin (implicated in regulating worker behavior, for example [56,62]), inotocin, the insect ortholog of oxytocin/vasopressin [63,64], the transcriptional repressor Kr-h1 that is regulated by ecdysone and juvenile hormone [65], transcripts related to biogenic amine and neurohormonal signaling [40], and insulin-like peptide 2 [66]. These studies are increasingly focused at finer scales in terms of specific brain regions and single cells [67], and will further elucidate genes and molecular pathways important for regulating division of labor and social function within colonies. Such transcriptomic studies provide a convenient means to quantify variation in neurogenomic state and function, which may help to distinguish among the hypotheses described above. For example, according to some models of social organization, workers will show little variation in neural state and function between individuals, while others specifically assume variation between individuals associated with task specialization.

In addition to studies seeking to elucidate which genes and molecular pathways are important for individual behavior, neural function, and colony-level social regulation, comparative genomic and population-genomic approaches have been used to identify *genetic changes* in protein-coding genes, regulatory elements, and gene families associated with the evolution of social behavior and eusociality (e.g. [68–70]). These studies have identified genetic changes associated with neurogenesis and neural function [71–73], providing initial evidence that the evolutionary origin and elaboration of sociality involves changes in genes with neurobiological importance. Larger-scale studies with the genomes of dozens to hundreds of species with varying degrees of social complexity can further characterize the degree to

which changes in genes associated with neural development and function are important for the evolution of social organization and the origin and elaboration of social complexity. Specifically, these comparative genomic studies can characterize which genes have experienced intensified or relaxed selection during the transition from relatively simple to relatively complex societies and the emergence of aneural brains. Complex societies may evolve via increased neural complexity within and between workers. This would represent an application of the colony-size model in respect to how computational demands of living in large societies may have selected for large physical brains in the absence of reproductive conflict. We would thus expect to see signatures of intensified positive and purifying selection shaping genes and regulatory elements associated with neural development, regulation, and function. In contrast, if social complexity evolves via emergent interactions among individuals with neural function that is decreased relative to the ancestral state (e.g., consistent with self-organization and an aneural brain), we would expect to see signatures of relaxed selection for these genes and regulatory elements.

Conclusions

Models of social organization converge and diverge in their perspectives of the evolution of the size and neuroarchitecture of ant brains, which may adaptively increase or decrease in size and structure according to social context. The impact of collective intelligence and aneural brains, and other aspects of group decision-making, requires further research. Division of labor has selected for morphological and behavioral differentiation among sterile workers to maximize the efficiency of task performance, which correlates with brain size and/or compartmental allometries. Task performance has social influences in respect to colony size and dynamic allocation of worker labor involving discretized sensory physiology and biomechanical adaptations, factors related to selection pressures associated with functional ecology.

It is challenging to distinguish among selective forces of brain evolution predicted or implied by historical and current thought in insect sociobiology. In addition to whole-brain and neuropil volumes, cellular analyses (neuronal densities, for example [18], identity, and structure of individual neurons) may enable such discrimination. Comparing neural phenotypes across species in phylogenetic context may identify their relationships to social complexity across ant phylogeny, and how they have changed when compared with the inferred ancestral state. For example, we can test whether relative MB size (e.g. [74]) has coevolved with aspects of social complexity such as group decision-making.

Models of social organization do not make explicit predictions about the genes involved in neural development, function, and evolution or how physical brains and their genetic underpinnings change in association with social systems that concern collective intelligence. However, comparative transcriptomic studies, including single-cell transcriptomics, can help identify the number and diversity of genes associated with behavioral variation within colonies, and whether evolutionary changes in gene regulation are associated with the evolution of social complexity, including emergent behavior. Furthermore, comparative genomics and population genomics can be used to determine which genes have experienced shifts in patterns of molecular evolution. Overall, these approaches can help refine existing models to focus on specific molecular pathways underlying evolutionary changes in neural phenotypes and social organization.

Conflict of interest statement

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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