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Editorial: Neuroethology of the colonial mind: Ecological and evolutionary context of social brains

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Editorial on the Research Topic
Neuroethology of the colonial mind: Ecological and evolutionary context of social brains

Collective behavior relies on interactions among individuals who have neural substrates supporting the exchange and processing of social information (Gordon, 2021). The collective acquisition and processing of information in animal groups suggest that individuals form a "colonial mind." Over the past decades, studies of individual and collective cognition have received a lot of attention (Couzin, 2009; Simons and Tibbetts, 2019). However, little is known about how the two systems interact. For instance, while collective cognition necessarily emerges from individual cognition, individual cognitive abilities are not correlated to collective cognitive abilities (Feinerman and Korman, 2017). Studying cognitive processes across levels of biological organization thus requires a better understanding of the mechanisms of cognition at each level and within an evolutionary context. This necessitates analyzing how animals use social information in different contexts or understanding the neural adaptations associated with group living and ecological challenges. For this research topic, we brought together researchers in neuroscience and collective animal behavior to further examine these aspects of the colonial mind.

Social information transfer can yield fitness benefits to individuals (Krause et al., 2010). For instance, grouped animals often respond faster and more accurately to changes in environmental or social circumstances than isolated conspecifics (Sumpter, 2010). While these cognitive advantages were long considered exclusive to the most socially advanced animals, recent studies show collective cognition can be beneficial across the animal kingdom, even in loosely social species. For instance, Mörchen et al. demonstrate that organgutans, which are less social than other apes, learn about new environments through social information gathered from local individuals when migrating. Ferreira et al. showed how social information influences individual reactions in gregarious fruit flies under threatening situations.

By contrast, the mechanisms underlying the transition from solitary to group living are much less understood. Several physiological changes may have contributed to division of labor in highly social species. Sasaki et al. provide a comparative perspective to understand how neurotransmitters and hormones evolved to support eusociality. The authors compiled literature from eusocial and non-social insects and provided support for the "ovarian ground plan hypothesis" (Amdam et al., 2004), suggesting ovarian function and behavior is physiologically separated into reproductive and non-reproductive forms. They also provided support for the "split-function hypothesis" (West-Eberhard, 1996), which proposes that juvenile hormone, ancestrally involved in reproduction, evolved to have an additional role in worker division of labor (Sasaki et al.).

Neuroanatomical comparisons can also inform researchers about how animals transitioned from solitary to social life. The "social brain hypothesis" posits that increasing levels of sociality are associated with larger brains to support the processing of more social information (Dunbar, 1998). However, the distributed cognition of highly integrated groups with division of labor may alleviate the cognitive load on the individuals, and potentially reduce their neural requirements (Gronenberg and Riveros, 2009). Testing this hypothesis in eusocial insects has so far produced mixed results (O'Donnell et al., 2015, 2019; Kamhi et al., 2016; Sayol et al., 2020). The variation in behaviors and life histories that characterize sociality may be part of the reason for the inconsistencies observed. For instance, many socio-cognitive behaviors once thought to be specific to social species, such as the recognition of individual identity or social learning, have recently been described in non-social animals and may be primarily related to foraging and mating (Poissonnier et al.). Researchers therefore should be more selective in the behaviors associated with sociality in comparative studies.

Accordingly, several studies began to focus on specific characteristics of sociality to better understand how the brain evolves to support particular social behaviors. For example, Caponera et al. defined five characteristics of sociality (intragroup competition, relationship differentiation, information sharing, dominance hierarchies, and task specialization and redundancy) and included an example of how to apply these criteria in a comparison of social and subsocial spiders. The authors found that task redundancy in social spiders was correlated with a reduction in the arcuate body, a brain region involved in mechanosensory integration (Steinhoff et al., 2017). In a similar analysis, Godfrey et al. showed that differences in olfactory processing regions associated with nestmate recognition are positively correlated with colony size across Leptomyrmecini ant species. As in the social brain hypothesis, the authors proposed that increased colony size is associated with a greater need for nestmate recognition; however, they focused specifically on the circuitry that supports this behavior.

Increased investment in olfactory processing is also associated with nestmate interactions in the social wasp *Polistes dominula* (Gandia et al.). In this species, females have larger antennal lobes, while males have larger optic lobes, the primary olfactory and visual processing regions, respectively (Gronenberg, 2008). These differential neural investments correspond to the importance of social interactions in group living for females and the reliance on vision in mating for males. Similarly, reproductive females may have a greater need for group interactions than female workers that primarily forage, and had larger mushroom bodies, a region involved in higher order sensory integration (Fahrbach, 2006). Thus, it is important to account for variation in behavior within the social group. Brain region size of individuals within groups appears to have adapted to the sensory requirements associated with the individuals' specific behavioral requirements (e.g., Arganda et al., 2020).

While social context undoubtedly shapes cognitive and neural function, sociality exists within a broader context of the environment, which also may affect neural circuitry (Healy, 2021). Non-social behaviors such as navigation (Sayol et al., 2020) and foraging (Farris and Roberts, 2005; Farris, 2008; Sheehan et al., 2019) have been shown to influence neural investment. Azorsa et al. used the "ecological brain hypothesis," which states that the brain evolves to account for the cognitive challenges associated with foraging and processing food (DeCasien et al., 2017; Lihoreau et al., 2019; Simons and Tibbetts, 2019), to discuss how predation foraging ecology may interact with group living to affect the sensory requirements and cognitive processing of the species.

Comparative analyses of brain size in relation to the socio-ecology of social insects can provide insight for findings in other organisms. Through a study of fossil records in early humans, DeSilva et al. suggest that there has been a recent decrease in brain size in humans. Using observations from comparative studies of ant neuroanatomy, these authors propose that the trend they observed may be associated with characteristics of collective behavior such as increased sociality, sharing of information, and group decision-making (but see comment by Villmoare and Grabowski and response by DeSilva et al. about potential issues of using rare fossil records for such analyses).

The studies in this collection seek to understand how behavioral and neural characteristics enable individuals to engage in social behaviors and how social organization, or collective behavior, may alter individual cognition. They take advantage of the approaches previously mentioned to nicely illustrate how research on the evolution of brains and cognition has recently moved from broad correlations between brain sizes and social organization (Dujardin, 1850; Dunbar, 1998) to more detailed considerations of the neuroethology of specific socio-cognitive behaviors (Lihoreau et al., 2012; Godfrey and Gronenberg, 2019). Future research will have to account for variation in cognition across group members (Naug and Tait) and life history strategies that characterize the group.

Recent studies, including those in this collection, have progressed our understanding of the neural underpinnings of collective cognition, but more can still be done. While the diversity of animal models used in collective cognition is increasing (i.e. social insects, *Drosophila*, primates), an important effort should be made to broaden the scope further with species comparisons across the spectrum of social organization. The application and tuning of tools such as statistical brain atlases (Arganda et al.) will make these large-scale comparative studies feasible and accurate. Ultimately, a better understanding of the neurobiology of collective minds across the animal kingdom, including humans, may be useful for developing more efficient collective decisions, more robust artificial systems (e.g., Ebert et al., 2020), and more informed interactions with wildlife.

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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