Insect societies and the social brain
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The 'social brain hypothesis,' the relationship between social behavior and brain size, does not apply to insects. In social insects, especially those of the Order Hymenoptera (ants, bees and wasps), sociality has not always increased individual behavioral repertoires and is associated with only subtle variation in the size of a higher brain center, the mushroom bodies. Rather than sociality, selection for novel visual behavior, perhaps spatial learning, has led to the acquisition of novel visual inputs and profound increases in mushroom body size. This occurred in nonsocial ancestors suggesting that the sensory and cognitive advantages of large mushroom bodies may be preadaptations to sociality. Adaptations of the insect mushroom bodies are more reliably associated with sensory ecology than social behavior.

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Introduction

Does sociality require complex behaviors and large, integrative higher brain centers to support those behaviors? Does the evolution of sociality occur in concert with the evolution of large higher brain centers? When considering primates, and especially humans, the answer to these questions seems quite clearly affirmative. However, a broader consideration of animal sociality has revealed that not all social interactions, and the behaviors they require of individuals, are alike. For example, neocortex size was observed to positively correlate with social group size in anthropoid primates, a relationship that was not preserved in other mammals that live in large groups such as some carnivores, ungulates, and basal primates [1–4]. It is now believed that anthropoid primate social interactions are unique amongst mammals, as their social groups consist of multiple individuals forming tight-knit associations with one another. These relationships are considered the equivalent to pair bonds that typically form only between mated individuals and which are associated with increases in brain size in non-anthropoids [5]. Evolution of such a complicated social network in anthropoids, in which an individual must maintain pair bond-like associations with many individuals rather than a single mate, has necessitated selection for complex behaviors that facilitate and maintain these interactions, and in turn, very large brains to support the necessary computations [6].

The emerging nuances of the 'social brain hypothesis,' as it is termed in the primate literature (as reviewed by [7,8]), are an important reminder of the care that must be taken when considering the overarching generality of associations made in a single clade. But it is tempting, especially when considering our own species' complex sociality and large neocortices capable of seemingly unmatched feats of intellect, to assume that sociality mirrors intelligence, even in species as distantly related to us as insects. Although social insects have long been known to have particularly large higher brain centers relative to many solitary species, a convincing case for an overarching impact of sociality on these neuropils remains to be made. In fact, it appears that other selective pressures drove the evolution of large and structurally complex mushroom bodies in several insect lineages, including those that lack sociality. In those lineages that have social species, the acquisition of large higher brain centers long before this behavioral innovation suggests that they are perhaps a preadaptation, rather than an outcome of sociality.

Eusociality and the mushroom bodies, an insect higher brain center

The insect mushroom bodies are multimodal sensory integration neuropils that are important for a number of cognitive tasks including associative and configural learning and memory, computations suited for more complex types of learning such as feature extraction and identification of salient sensory cues, and attention [9–16,17•,18••,19••,20•,21••]. These functional roles have been uncovered primarily in the fruit fly *Drosophila melanogaster* and the honey bee *Apis mellifera*. The honey bee has a well-characterized behavioral repertoire associated with sociality, navigation and learning [22–25] and is a tractable model for neurophysiology [9,26]. The particularly large and elaborate mushroom bodies of honey bees and other social species of the Order Hymenoptera has also invited the attribution of higher cognitive functions to these brain regions.

The insect mushroom bodies are variable in morphology across species, yet adhere to a common groundplan [27].

Mushroom bodies are composed of thousands to hundreds of thousands of intrinsic neurons (Kenyon cells) [28**]. Their dendrites make up the calyx, an ovoid neuropil in small mushroom bodies that is expanded to form two deep cups subdivided by afferent input (visual, olfactory, etc.) in the largest mushroom bodies [29]. Kenyon cell axon-like processes funnel through a pedunculus beneath the calyx and bifurcate into a pair of lobes where they are both pre- and post-synaptic to extrinsic neurons [30,31]. Small mushroom bodies are characterized by receiving primarily olfactory input to the calyces, and have a single pair of lobes with multiple 'trauben' (spherical bodies containing Kenyon cell axon branches) or a few separate pairs of lobes as observed flies (Diptera) such as *Drosophila melanogaster* [27,32–34]. Additional longitudinal subdivisions are revealed by arborization patterns of extrinsic neurons in the lobes [35]. Large mushroom bodies often have just one large pair of lobes, densely packed with tens of thousands of Kenyon cell axon-like processes subdivided into multiple laminae, each with a characteristic Kenyon cell type and neurotransmitter profile [30,36]. All mushroom body lobes are further segmented into proximal to distal zones by extrinsic neuron processes [35,37]. Large mushroom bodies are exemplified by those of the aculeate Hymenoptera, including social species in the families Formicidae (ants), Vespidae (wasps), and Apidae (bees) (Figures 1 and 2a). Large mushroom bodies have arisen independently in a number of insects outside of the Hymenoptera, including in species that are not social [29].

The earliest insect neuroanatomy studies noted the variability of mushroom body size and morphology across species (reviewed by [38,39]). Dujardin [40] suggested that the 'intelligence' of the apocritan Hymenoptera, perhaps inferred from the social behavior of some species [41], was associated with exceptionally large and folded mushroom body calyces that he likened to the gyri and sulci of the human cerebral cortex. This may mark the beginning of an 'insect social brain hypothesis' the association between large, complex mushroom bodies and social behavior, which remained tacitly accepted in the literature for decades. However, further comparative studies described non-social insects with similarly large mushroom bodies, including cockroaches and some beetles and butterflies [38,42–45]. Furthermore, solitary aculeate Hymenoptera and parasitoid Hymenoptera [42,46–48], the latter of which arose 90 million years before the social hymenopteran lineages [49] have very large mushroom bodies with deep, cup shaped calyces much like those observed in social Hymenoptera (Figures 1 and 2a, b, e). The most basal Hymenoptera lack these features of the mushroom bodies (Figure 2d). A systematic survey of the Hymenoptera finally pinpointed the origin of large, complex mushroom bodies to the base of the parasitoid lineages, long before the evolution of sociality in ants,

bees and wasps [50**] (Figure 2c). While this suggests that large mushroom bodies and social behavior did not evolve concomitantly, it does not preclude additional adaptations to mushroom body structure and function subsequent to the acquisition of sociality in some lineages.

If the acquisition of large mushroom bodies does not coincide with the evolution of sociality in the Hymenoptera, why do both parasitoid and social Hymenoptera (Apocrita) have large mushroom bodies, while the most basal phytophagous Hymenoptera (sawflies) do not (Figure 1)? In the apocritan Hymenoptera, but not the phytophagous species, the calyces are subdivided by sensory input from the olfactory system and a novel source of sensory input from the optic lobes of the visual system [50**,51,52]. Social and solitary Hymenoptera possess a well-characterized ability for spatial learning of visual landmarks in the environment to navigate between learned locations of hosts, food sources and nest sites over time spans ranging from days to months [53–59]. Although visual spatial learning is best studied in social and solitary aculeates, at least one parasitoid, *Hyposoter horticola* (Ichneumonidae), uses learned visual landmarks to repeatedly visit egg clusters deposited by its host [60,61].

Like large mushroom bodies, optic lobe visual input to the calyces are observed sporadically across the insects, even outside of the Hymenoptera [62,63]. Intriguingly, optic lobe visual inputs to the calyces are in many cases found in species that like the apocritan Hymenoptera use visual cues for navigation. For example, diurnal butterflies (Lepidoptera) such as those of the genus *Heliconius* navigate among food sources using learned visual landmarks [45,64]. *Heliconius* species have very large mushroom bodies rivaling those of the social Hymenoptera [45] (SM Farris, personal observations), and optic lobe visual input to the calyces has been observed in species belonging to the lepidopteran Families Pieridae and Papilionidae [65,66]. Cockroaches also have large mushroom bodies, and in at least one species the calyces receive visual input from the optic lobes [67,68]. Urban pest species of cockroach such as *Periplaneta americana* and *Blatella germanica* employ visual landmarks to navigate between shelter areas and food sources [69,70]. Finally, in the aquatic whirligig beetle *Dineutus sublineatus* (Coleoptera: Dytiscidae), which uses its dorsal pair of eyes to monitor visual cues above the water surface [71], olfactory input to the large mushroom bodies appears to have been wholly replaced with optic lobe visual input [72].

A role for the mushroom bodies in visual spatial learning was first suggested by work in the cockroach *Periplaneta americana*, in which mushroom body lesions prevented navigation using learned visual landmarks in a modified Morris water maze assay [73]. *Periplaneta* has large mushroom bodies that receive optic lobe visual inputs to the