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 Papillionidae [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

Figure 1
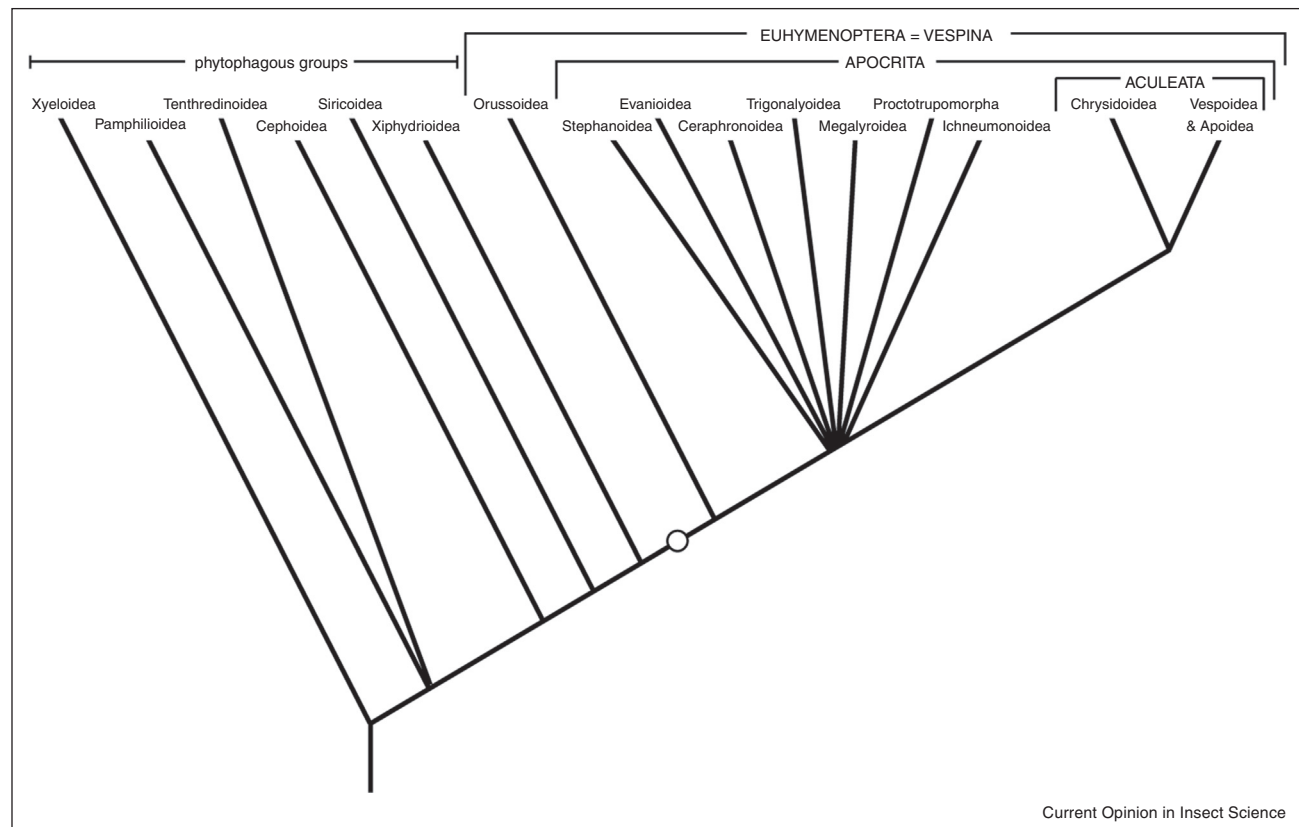
Phylogeny of the Hymenoptera. The Hymenoptera consist of the basal phytophagous families (sawflies) and the Euhymenoptera. Within Euhymenoptera, Apocrita contains all species except the basal parasitoids in the superfamily Orussoidea [89,90]. Monophyly of the Euhymenoptera is supported by both morphological and molecular analyses [91–93]. As indicated by the open circle, all Euhymenoptera have large mushroom bodies with doubled, deeply cup-shaped calyces with direct visual input to the optic lobes unless secondarily eyeless. The Apocrita contain several superfamilies of parasitoid wasps as well as the Aculeata. In the Aculeata, eusociality arose at least four times independently in the Vespoidea and Apoidea [65].
Figure reprinted with permission from [44].

calyces [67,68]. Unfortunately, no further demonstrations of spatial learning functions of the mushroom bodies have been performed in *Periplaneta* or any other insect species with large mushroom bodies receiving optic lobe visual input. In contrast, the fruit fly *Drosophila melanogaster* requires another brain center, the central complex, but not the mushroom bodies for visual spatial learning tasks [74,75]. The small mushroom bodies of *Drosophila* do not receive optic lobe visual input to the calyces [17•,76].

Drosophila species are capable of long distance dispersal but these events are relatively rare [77,78], and there is no evidence that visual spatial learning is employed during this or any other directed movement in wild drosophilids. Together, these findings suggest a hypothesis that visual spatial learning was of particular importance and heavily selected for in some insects, driving the acquisition of optic lobe visual inputs to the mushroom bodies and a concomitant increase in mushroom body size to accommodate a

novel role in visual processing. The independent acquisition of large mushroom bodies with optic lobe visual inputs in non-hymenopteran insects such as cockroaches, butterflies, etc. suggests that convergent evolution of mushroom body structure occurred due to selection for visual spatial learning or some other behavior requiring visual processing.

The evolution of social behavior in Hymenoptera could not have driven the initial acquisition of large mushroom bodies. Could the opposite be true, that large mushroom bodies acquired through selection for another role served as a preadaptation for social behavior? Social hymenopterans typically visit food sources outside of a central nest (central place foraging; [79]). The use of visual and olfactory landmarks for this purpose is well documented in the social Hymenoptera [55,56,59]. Non-social aculeates may provision solitary nest sites, or identify and monitor host nests for parasitoidism or kleptoparasitism

Figure 2
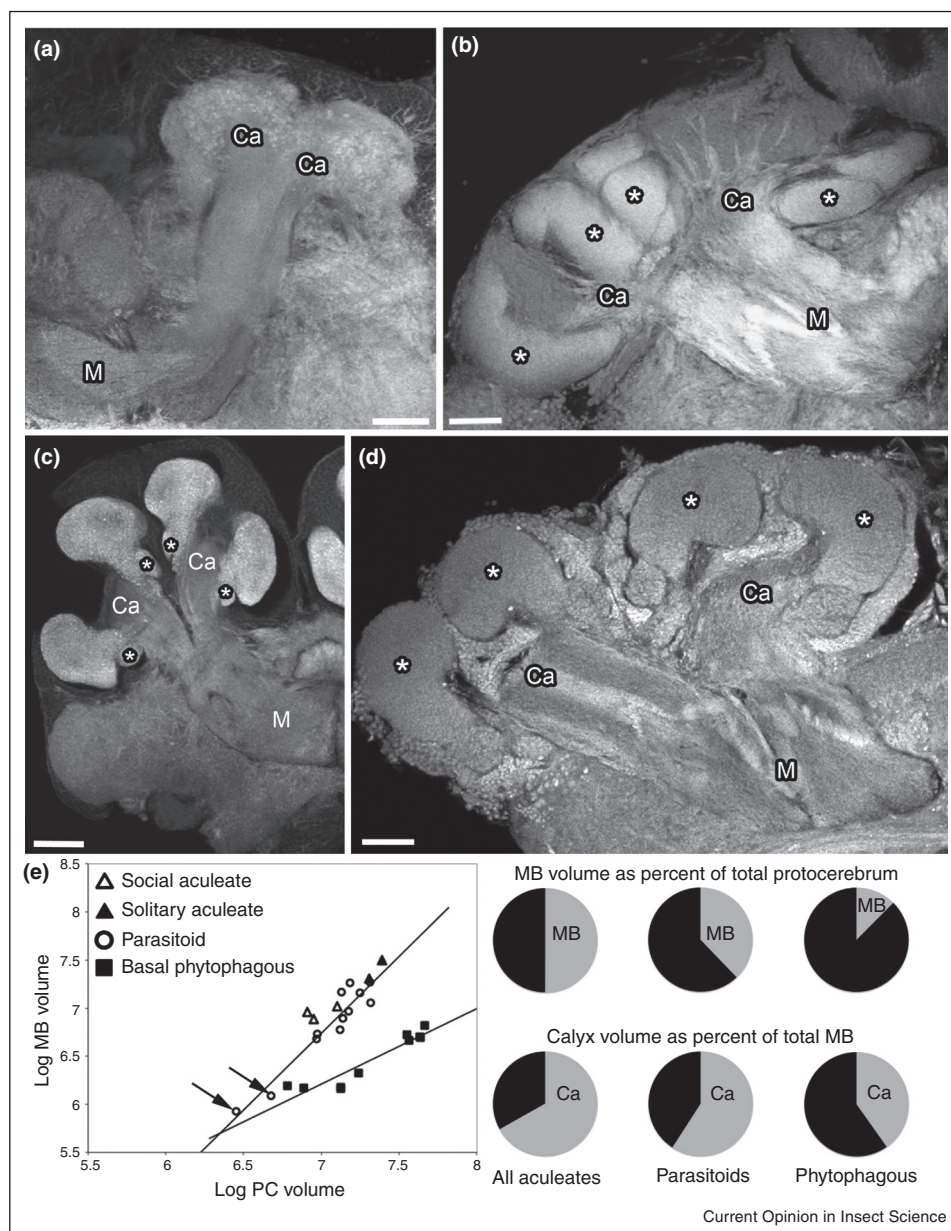
Mushroom bodies of the Hymenoptera. **(a)** Mushroom body of *Dolerus* sp. (Tenthredinoidea), a basal phytophagous sawfly. Calyces are small, ovoid and partially fused. Input to the calyces is predominantly olfactory, with no visual input [44]. **(b)** Mushroom body of *Gasteruption* sp. (Evanioidea), an apocritan parasitoid wasp. Calyces are large, cup-shaped and fully duplicated. Visual input is received by calyx zones indicated by *. **(c)** Mushroom body of *Tetramorium caespitum* (Vespoidea, Formicidae), a eusocial aculeate ant. Calyces are large, cup-shaped and fully duplicated, with visual input to calyx zones indicated by * [44]. Many ants have reduced regions of visual input due relative to other apocritans due to increased reliance on olfactory cues [50**,83]. **(d)** Mushroom body of *Chrysididae* sp. (Chrysidoidea), a solitary aculeate cuckoo wasp. Like other apocritans, the calyces are fully duplicated and increased in size. Visual input areas are greatly enlarged as indicated by * [44], perhaps related to the reliance of these species on spatial learning to monitor host nests [52]. **(e)** Mushroom body (MB) volume relative to the remaining protocerebral brain segment (PC) and calyx (Ca) volume relative to total mushroom body size. The graph shows linear regression of log-transformed mushroom body volumes versus protocerebral volumes for Euhymenoptera (top) and phytophagous Hymenoptera (bottom), adapted with permission from [44]. The equation for the Euhymenoptera regression line is $y = 1.597x - 4.437$ ($R^2 = 0.906$), while that for phytophagous species is $y = 0.785x - 0.716$ ($R^2 = 0.882$). This suggests that the scaling relationship between the mushroom bodies and protocerebrum has changed dramatically between phytophagous and euhymenopteran species. Top row of pie charts shows mushroom body volume as a percent of the total protocerebrum in Aculeates (including social species), parasitoids and phytophagous species. The mushroom bodies of parasitoids are clearly larger than those of phytophagous species but not as large as those of aculeates, perhaps due to two small-brained outlier species with proportionately small mushroom bodies (graph arrows). Bottom row of pie charts shows volume of the calyces relative to total mushroom body volume in the same three groups. Ca = calyx, M = medial lobe. Scale bars = 50 μm.

of larvae using learned visual cues for repeat visits [53,54,57]. In termites, another large and diverse clade of eusocial insects, the crown groups are also central place foragers with very large mushroom bodies [80,81]. As in the Hymenoptera, termites arose from a lineage (the cockroaches) characterized by large mushroom bodies [30,69,73,82]. Perhaps in both the Dictyoptera and Hymenoptera, adaptations acquired by solitary ancestors allowing individuals to learn and remember the locations of resources may have facilitated a transition to central place foraging as is observed in social species.

Mushroom bodies within eusocial insect lineages

Only a handful of studies have considered the mushroom bodies of eusocial termites. Those of basal termites appear similar in size and shape to those of cockroaches, while crown species possess mushroom bodies with very large lobes that curl around the dorsal and lateral protocerebrum [80,83–85]. This latter feature is interesting as the opposite appears true in the Hymenoptera, in which the calyces have become disproportionately large, relative to the lobes, in both parasitoids and aculeates (Figure 2c) [50••]. A more comprehensive survey of the termites will be necessary to determine behavioral and ecological factors associated with the changes observed in the mushroom bodies.

Genomic comparisons in aculeate Hymenopterans have revealed accelerated rates of evolution of genes involved in brain development and function, including the mushroom body-expressed learning and memory gene *dunce*, in primitively eusocial but not highly eusocial species [86•]. Primitively eusocial aculeates live in small, annual colonies and have less strict separation of worker and reproductive castes. While it may seem counterintuitive that rapid evolution of brain-related genes occurred in primitively eusocial rather than highly eusocial species, there is potentially a greater need for behavioral flexibility and general cognitive ability in primitively eusocial individuals. In a small colony in which multiple individuals are capable of reproduction, each may switch between all available worker tasks in addition to reproductive tasks as the need arises [87,88]. Individuals in larger nests, however, tend to settle into loose caste-like repertoires [89]. In contrast, the need for individuals to perform a range of behaviors encompassing reproductive and worker tasks is relaxed in large, eusocial colonies. This is supported by ethograms of eusocial species in which tasks are partitioned across castes, but more equally performed by primitively social individuals [23,90–96]. Neural correlates of differing behavioral repertoires in primitively social and eusocial species are supported by a handful of studies. Primitively social paper wasp queens (Polistinae: Vespidae) in small, independently founded colonies have larger mushroom bodies than workers, perhaps associated with the need to perform reproductive tasks

and maintain dominance in addition to performing worker tasks [97].

In contrast, queens in large honey bee colonies have smaller mushroom bodies than workers, as they perform only reproductive tasks for the majority of their lives [98]. A larger study of 29 species of wasps (Vespidae) ranging from solitary to highly eusocial, showed that the largest mushroom body calyces are found in solitary species [99•]. These studies provide an incomplete picture as they do not provide insight into how increased behavioral repertoire drives changes in mushroom body circuits in particular, or whether certain behaviors may be more cognitively demanding than others and thus have a disproportionate impact on the elaboration of the mushroom body circuit. While these data are in keeping with a decline in individual behavioral complexity with increasing social organization, a great deal more research will be needed to definitively associate individual behavioral repertoires with evolutionary changes in mushroom body structure.

The difficulty of associating behavioral adaptations with adaptations in specific brain loci is well illustrated by the lack of obvious novel neural substrates associated with the most striking social behaviors. For example, some species of primitively eusocial paper wasps (Vespidae) are capable of recognizing the faces of individual colony members, but this capability is not reflected by measurable change in the visual processing region of the mushroom bodies [100–102]. Similarly, there appear to be no novel peripheral sensory circuits associated with the ability of honey bees to perform and interpret the dance language [103]. The lack of definitive neural substrates for these social behaviors, in addition to many other behaviors associated with eusociality, suggests that as striking as they seem, these behaviors may not be so computationally different from 'typical' insect behaviors that they require their own specialized circuitry. To date, the most pronounced differences observed in comparative studies of the hymenopteran mushroom bodies, such as the dramatic reorganization of the lobes in vespid wasps, appear to be associated with phylogeny [104] and/or sensory and behavioral ecology rather than any aspect of social behavior [27,29,41,51,52,62,105].

Conclusion

The 'social brain hypothesis' as articulated for vertebrate mammals does not hold for social insects, perhaps in part because insect sociality (especially eusociality) and the social behaviors of anthropoid primates have selected for very different individual behavioral repertoires [6,94]. In primates, the extension of pair bond-like relationships to multiple individuals appears to have driven the evolution of a large neocortex for keeping track of interactions and generating appropriate social behaviors. In contrast, the decrease in behavioral repertoire of eusocial Hymenoptera

in large colonies has had subtle effects, and in some species appears to have decreased mushroom body size.

The question for insects is thus the nature of the selective pressure for large mushroom bodies with optic lobe visual, if not sociality. The evidence thus far suggests that visual behavior, perhaps spatial learning, has driven the acquisition of visual inputs to the calyces and concomitant increases in mushroom body size [50**,63]. Future studies exploring the functional role of mushroom bodies in visual spatial learning, as well comparing visually guided behavior in insects with and without large mushroom bodies, will help to resolve this decades-old question in insect neurobiology.

Acknowledgements

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