

Evolution of Complex Higher Brain Centers and Behaviors: Behavioral Correlates of Mushroom Body Elaboration in Insects

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Mushroom bodies · Higher brain center · Behavior · Evolution · Insect

Abstract

Large, complex higher brain centers have evolved many times independently within the vertebrates, but the selective pressures driving these acquisitions have been difficult to pinpoint. It is well established that sensory brain centers become larger and more structurally complex to accommodate processing of a particularly important sensory modality. When higher brain centers such as the cerebral cortex become greatly expanded in a particular lineage, it is likely to support the coordination and execution of more complex behaviors, such as those that require flexibility, learning, and social interaction, in response to selective pressures that made these new behaviors advantageous. Vertebrate studies have established a link between complex behaviors, particularly those associated with sociality, and evolutionary expansions of telencephalic higher brain centers. Enlarged higher brain centers have convergently evolved in groups such as the insects, in which multimodal integration and learning and memory centers called the mushroom bodies have become greatly elaborated in at least four independent lineages. Is it possible that similar selective pressures acting on equivalent behavioral outputs drove the evolution of

large higher brain centers in all bilaterians? Sociality has greatly impacted brain evolution in vertebrates such as primates, but it has not been a major driver of higher brain center enlargement in insects. However, feeding behaviors requiring flexibility and learning are associated with large higher brain centers in both phyla. Selection for the ability to support behavioral flexibility appears to be a common thread underlying the evolution of large higher brain centers, but the precise nature of these computations and behaviors may vary.

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What Is Complex Behavior?

Enlarged and structurally complex higher brain centers, such as the cerebral cortex in mammals and the mushroom bodies in insects, have arisen convergently both within and across phyla. These brain regions are involved in higher processing functions such as multimodal sensory integration, learning and memory, attention, and decision-making, as opposed to simpler sensory processing and reflexive motor tasks. Thus, the evolutionary enlargement of higher brain centers is often thought to be a result of selective pressure exerted by niches requiring behaviors supported by these higher processing functions. Such behaviors may be referred to as ‘complex’ and

include sociality, communication, and a 'general intelligence' that provides flexibility and innovation in colonizing new niches and locating and handling unpredictable resources [Lefebvre and Sol, 2008]. This review considers the independent evolution of large and elaborate mushroom bodies in four groups of insects, and the shared structural and developmental features of these mushroom bodies with enlarged cerebral cortices in vertebrates. The behavioral repertoires associated with enlarged mushroom bodies are also considered in light of similar selective pressures upon complex behavioral capabilities that have acted to drive large higher brain center evolution in both vertebrates and invertebrates.

Conservation and Divergence in the Bilaterian Nervous System

Numerous recent review articles have considered the evolutionary heritage of metazoan nervous systems [Reichert and Simeone, 2001; Sprecher and Reichert, 2003; Arendt et al., 2008; Hirth, 2010; Northcutt, 2012]. A great deal of evidence supports the hypothesis that the common ancestor of all bilaterally symmetrical animals possessed a centralized nervous system built using a substantial toolkit of developmental patterning and cell identity genes and perhaps containing rudimentary versions of sensory receptors, modulatory and secretory cells, and other cell types found in animal nervous systems. According to this hypothesis, all bilaterian nervous systems are constructed from homologous cells (neurons) and organized according to a framework of homologous regulatory genes. While enormous diversification has accompanied the evolution of bilaterian nervous systems, they have also been shaped in independent lineages by selective pressures arising from common sensory and functional demands. As a result, convergence at many levels of brain organization and behavioral output is widespread, even across high-level taxa separated by hundreds of millions of years of evolutionary time. As a result, similar external factors acting upon a common toolkit of genes, cells, and perhaps even basic circuits have driven the emergence of complexity in nervous systems and behaviors multiple times in the Bilateria, within both protostomes and deuterostomes. Despite the deep divergence of these groups, complexity in the nervous system may be observed to arise using similar developmental mechanisms and sharing similar organizational and functional features.

Insect Nervous Systems and Higher Brain Centers

Insects are one of several protostome groups that possess centralized nervous systems. Their nervous systems are segmented and cephalized, consisting of a ganglionic ventral nerve cord and a brain (supraesophageal ganglion) subdivided into distinct functional regions. The ventral nerve cord in ancestral species is likely to have been made up of a separate ganglion for each body segment, each linked along the anterior-posterior axis by axon connectives. In modern insects, however, fusion of ganglia in the ventral nerve cord, particularly in locomotor segments (those containing legs and wings), has occurred in many lineages [Niven et al., 2008]. The brain is made up of 3 fused supraesophageal segments and 3 fused subesophageal segments that contain sensory and motor centers for head appendages and sensory organs as well as integrative centers for ascending sensory information and descending motor output [Strausfeld, 1976; Hartenstein, 1993]. The most anterior segment, the protocerebrum, contains visual neuropils called the optic lobes and 'higher' brain centers for sensory integration, locomotor coordination, and learning and memory. One of these centers, the mushroom bodies, has been extensively studied from many perspectives, including development, evolution, and function. While the mushroom bodies are best known for their roles in olfactory learning and memory [Busto et al., 2010; Kahsai and Zars, 2011], comparative studies suggest that this is not the entire story [Strausfeld et al., 2009]. In particular, olfactory processing is not a fundamental function of all insect mushroom bodies, as these structures are not lost in anosmic insects, and have been modified to primarily visual processing centers in at least two groups of insects (Odonata, the damselflies and dragonflies, and whirligig beetles of the coleopteran family Gyrinidae) [Svidersky and Plotnikova, 2004; Strausfeld et al., 2009; Lin and Strausfeld, 2012]. The mushroom bodies have also become greatly enlarged and more complex in at least four divergent insect lineages: the Dictyoptera (cockroaches and termites), some Coleoptera (the herbivorous scarab beetles), some Lepidoptera (the heliconid butterflies), and some Hymenoptera (the Euhymenoptera, encompassing parasitoid, solitary and social ants, bees and wasps). Increased size is associated with the addition of large numbers of intrinsic neurons composed of novel neuronal subtypes [Strausfeld et al., 2000; Strausfeld, 2002], often divided into subcompartments providing novel visual processing functions [Gronenberg, 2001; Farris, 2008a; Farris and Schulmeister, 2011], reminiscent of how the increased size of the mammalian cerebral cor-

tex is accompanied by the acquisition of new functional subdivisions [Kaas, 1995]. Comparative studies have shed light upon the selective pressures that might have driven mushroom body expansion, and the computational roles and behavioral outputs that may have emerged. Fascinating parallels between enlarged and structurally complex higher brain centers in invertebrates and vertebrates have been described, that provide a substrate for novel behaviors that might be together defined as complex, but which differ according to the particular taxon.

The Evolution of Large, Complex Mushroom Bodies in Insects

Since their first description, the insect mushroom bodies have attracted attention due to their large size and complexity in social species of Hymenoptera (ants, bees, and wasps) [Dujardin, 1850]. The social brain hypothesis first emerged as an explanation for the evolution of large higher brain centers in primates, which may have been driven by the computational demands of participating in the complex social systems that characterize these animals [Dunbar, 1998]. Given the presence of large mushroom bodies in the social ants, bees, and wasps, it seemed likely that a similar relationship existed in insects, although until recently this was not explicitly tested [Lihoreau et al., 2012]. Further study in vertebrates, however, has shown that complex higher brain centers do not always accompany the capacity for complex social behavior in some lineages, and the influence of ‘general intelligence’, the ability to be behaviorally flexible, has been difficult to separate from the impact of sociality in other groups [van Schaik et al., 2012]. In insects as well, the association between large higher brain centers and sociality now appears to be less likely than was originally thought.

The honey bee *Apis mellifera* is a prominent insect model organism, and it possesses mushroom bodies that well illustrate the size and complexity characteristic of social species of the order Hymenoptera (fig. 1a). This is most obvious from the elaborate structure of the calyces, which are doubled and cup shaped, enclosing and surrounded by the soma of approximately 170,000 intrinsic neurons called Kenyon cells [Kenyon, 1896; Witthöft, 1967; Mobbs, 1982, 1984]. One mushroom body resides in each brain hemisphere, for a total of 340,000 intrinsic neurons that account for approximately one third of the total number of neurons in the brain [Menzel, 2012]. In contrast, each mushroom body of another important insect model, the solitary fruit fly *Drosophila melanogaster*,

contains just 2,500 Kenyon cells, comprising just 2% of the total neurons in the brain, and the calyces are single and ovoid in shape (fig. 1b, c). This mushroom body morphology is characteristic of that of the majority of insect species, ranging from primitively wingless firebrats (*Thysanura*) to most hemi- and holometabolous insects [Farris, 2005].

Development has been dramatically modified to produce the *Apis* mushroom bodies. The large number of intrinsic neurons in *Apis* arises during development from 4 neuroblast clusters (2 per hemisphere) containing 500 neuroblasts each at the peak of neurogenesis [Panov, 1957; Farris et al., 1999], while in *Drosophila* intrinsic neurons are produced by just 8 individual neuroblasts (4 per hemisphere) [Truman and Bate, 1988; Ito and Hotta, 1992]. Neurogenesis via neuroblast clusters rather than single neuroblasts appears typical of many insects with large mushroom bodies [Urbach and Technau, 2003; Farris, 2008a]; in vertebrates, evolutionarily enlarged cortices are also associated with a dramatic expansion of neural precursors during development [Kriegstein et al., 2006; Rakic, 2009]. Enlargement of the precursor pool thus seems to be a common factor in the evolution of large higher brain centers, although whether this is accomplished by similar molecular mechanisms (such as through regulation of mitotic spindle orientation; for a review, see Gotz and Huttner [2005]) is not known.

In most insects, the mushroom body calyces are made up of the dendrites of Kenyon cells and receive sensory, modulatory, and feedback inputs [Grunewald, 1999; Li and Strausfeld, 1999; Gronenberg, 2001; Sinakevitch et al., 2008]. Olfaction is typically the predominant input modality, arising from projection neurons of the antennal lobes in the deutocerebral segment of the brain [Mobbs, 1982; Homberg et al., 1988]. Mushroom body output neurons respond to many types of mechanosensory information, which may be carried through bimodal antennal lobe projection neurons to the calyces or through additional inputs to the mushroom body pedunculus and lobes [Homberg, 1984; Schildberger, 1984; Li and Strausfeld, 1997, 1999; Mizunami et al., 1998a; Okada et al., 1999]. Gustatory inputs also appear to be common to most insect mushroom bodies but comprise a smaller proportion of total inputs than those from the antennal lobes [Farris, 2008b]. Visual inputs from the optic lobes to the calyces are observed in only a few species, including *Apis* [Gronenberg, 2001; Farris and Schulmeister, 2011]. In *Apis*, the calyces are structurally subdivided by source of sensory input, such that populations of intrinsic neurons are divided into distinct subdomains for processing

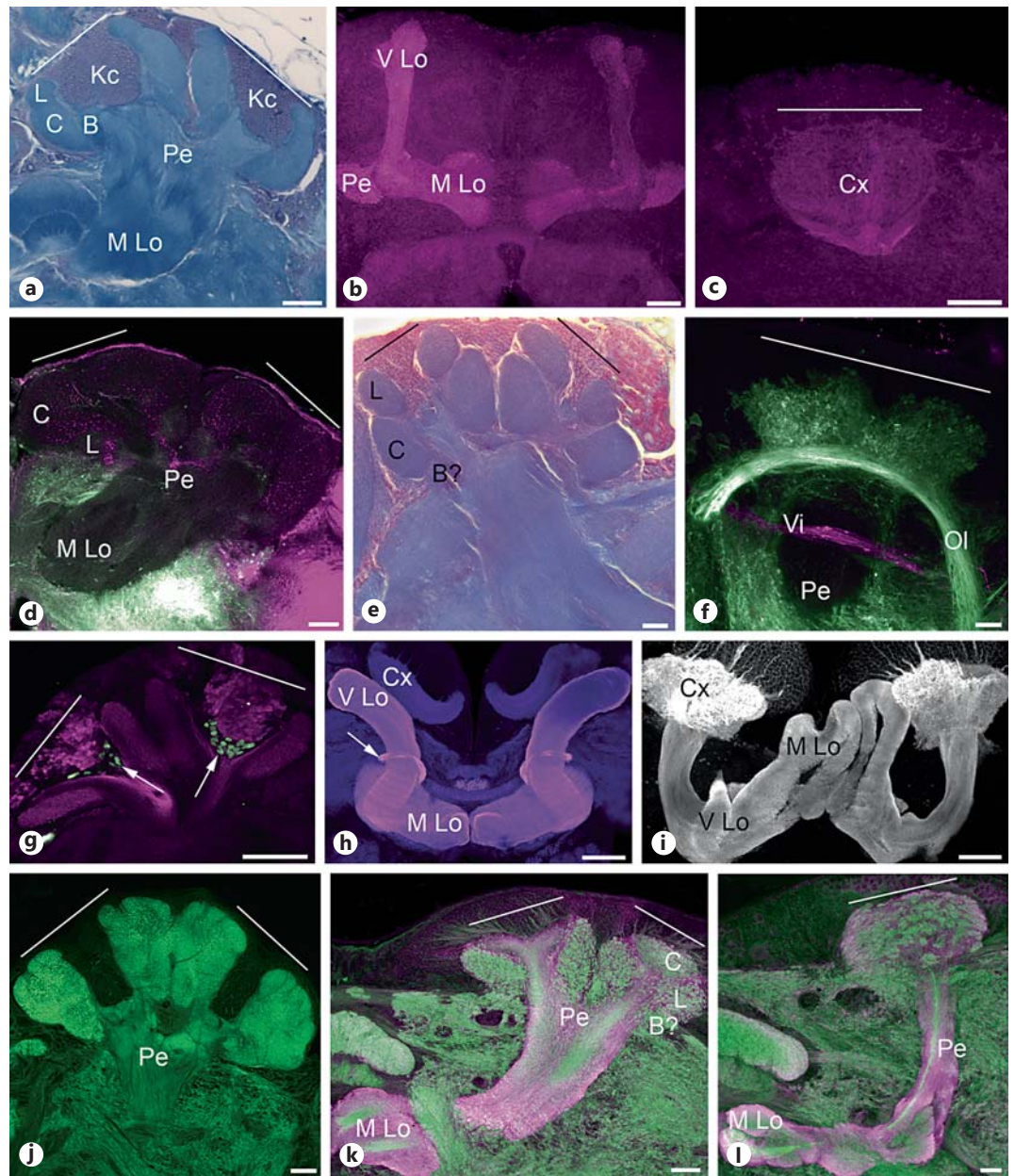


Fig. 1. **a** Mushroom body of *A. mellifera* (Apidae, Hymenoptera) stained with Cason's trichrome stain. **b, c** Mushroom bodies of *D. melanogaster* (Drosophilidae, Diptera) stained with anti-DC0 antibody. **b** Lobes of both mushroom bodies. **c** Calyx of one mushroom body. **d** Mushroom body of Chrysidae sp. (Hymenoptera). Optic lobe inputs labeled with Texas red-conjugated dextran. Antennal lobe inputs labeled with Alexa 488-conjugated dextran. **e** Mushroom body of *Ophion* sp. (Ichneumonidae, Hymenoptera) stained with Cason's trichrome stain. **f** Mushroom body of *Dolerus* sp. (Tenthredinidae, Hymenoptera). Optic lobe tracts bypassing calyx labeled with Texas red-conjugated dextran. Antennal lobe inputs labeled with Alexa 488-conjugated dextran. **g, h** Mushroom body calyxes of *P. americana* (Blattidae, Dictyoptera) labeled with anti-taurine antibody and neuroblasts labeled with BrdU (**g**). Lobes labeled with anti-DC0 antibody. **i** Mushroom bodies of *Gnathami-*

termes plexipus (Termitidae, Dictyoptera) labeled with anti-DC0 antibody. **j** Mushroom body calyxes of *Heliconius charitonius* (Nymphalidae, Lepidoptera) labeled with Alexa 488-conjugated phalloidin. **k** Mushroom body of *C. mutabilis* (Scarabaeidae, Coleoptera) labeled with anti-DC0 antibody and Alexa 488-conjugated phalloidin. **l** Mushroom body of *Onthophagus hecate* (Scarabaeidae, Coleoptera) labeled with anti-DC0 antibody and Alexa 488-conjugated phalloidin. **a, c–g, j–l** Lines indicate calyces. B = Basal ring of calyx; C = collar of calyx; Cx = calyx; Kc = kenyon cells; L = lip of calyx; M Lo = medial lobe; OI = olfactory projection neurons; Pe = pedunculus; Vi = visual projection neurons; V Lo = vertical lobe. Scale bars = 100 μ m (**a, g, h**), 50 μ m (**d, i–k**), and 20 μ m (**b, c, e, f, l**). **a** From Farris et al. [2001]. **f** From Farris and Schulmeister [2011]. **g** From Farris and Strausfeld [2001]. **h, i** From Farris and Strausfeld [2003]. **k** From Strausfeld et al. [2009]. **b–e, j, l** From unpublished data.

olfaction, vision, and gustation [Gronenberg, 2001; Schröter and Menzel, 2003]. Such functional subdivision is less apparent in the *Drosophila* mushroom bodies, where projection neurons from the antennal lobes show only a rough zonal bias to their inputs in the calyx [Tanaka et al., 2004; Jefferis et al., 2007; Lin et al., 2007]. Direct visual inputs from the optic lobes to the calyx have not been observed in *Drosophila* [Tanaka et al., 2008]. Thus, the mushroom bodies of *Apis* and other higher Hymenoptera are not only structurally larger and more complex than those of *Drosophila*, but they have acquired at least one new function employing visual input to the calyx.

A. mellifera and other social bees, ants, and wasps are part of the Aculeata, a monophyletic group within the order Hymenoptera in which sociality is believed to have arisen independently at least four times [Hunt, 1999]. All social species studied to date have mushroom bodies like those of *Apis*. However, so do all of the solitary species of the Aculeata (fig. 1d) [Withers et al., 2008; Farris and Schulmeister, 2011]. This suggests that large complex mushroom bodies arose in the common ancestor of the aculeates prior to the acquisition of sociality, making it unlikely for social behavior to have served as the primary driving force behind the evolutionary enlargement and increased complexity of the mushroom bodies that is typified by those of *Apis*. Further evidence for this hypothesis is provided by studies of mushroom body morphology spanning the entirety of the order Hymenoptera. Large mushroom bodies arose far before the first aculeates, coincident with the acquisition of the parasitoid lifestyle at the split between the Euhymenoptera (parasitoid wasps + the Aculeata) and the basalmost phytophagous families (sometimes referred to as the Symphyta) [Jawłowski, 1959, 1960; Farris and Schulmeister, 2011] (fig. 2). Mushroom bodies of parasitoid wasps are large with doubled, expanded calyces that are functionally subdivided and receive visual input from the optic lobes, more like those of social species like *Apis* than like the simple mushroom bodies of the most basal species (fig. 1e).

Large, complex mushroom bodies with novel visual processing functions seem to have appeared rather suddenly, with all basal phytophagous species possessing small mushroom bodies with ovoid calyces (fig. 1f), while even the most basal group of the Euhymenoptera, the Orussidae, has enormous mushroom bodies with convoluted calyces that take up most of the dorsal and anterior volume of the brain [Farris and Schulmeister, 2011]. The Orussidae and other early parasitic wasps are believed to have evolved, along with their large, complex mushroom

bodies, approximately 90 million years before the first acquisition of sociality in the Hymenoptera [Grimaldi and Engel, 2005]. Sociality is unlikely to have been a factor in the initial acquisition of elaborate mushroom bodies in the Hymenoptera.

Cockroaches belong to the order Dictyoptera and are distantly related to the Hymenoptera but have long been known to also be in possession of large, complex mushroom bodies [Newton, 1879]. The common model species *Periplaneta americana* has approximately 175,000 Kenyon cells per hemisphere, slightly greater than that of *Apis* [Neder, 1959]. With the recent inclusion of the termites within the Dictyoptera, this order, like the Hymenoptera, contains a large group of insects with elaborated mushroom bodies, within which a subgroup has evolved sociality more recently (fig. 1g, h) [Inward et al., 2007]. The pattern in insects concerning the influence of social behavior on the evolution of complex higher brain centers seems to be that, rather than the demands of social behavior driving the evolution of large mushroom bodies, these modified brain structures were present first, driven by some other behavioral demands, and they were perhaps then preadapted for the subsequent evolution of sociality [Farris and Schulmeister, 2011].

The last two groups of insects with large mushroom bodies do not contain social species at all, ruling out a role for social behavior in the evolution of complex mushroom bodies in these species. Scarab beetles (family Scarabaeidae, order Coleoptera) may be divided into two groups based on feeding ecology: specialist dung and carrion feeders, and generalist plant feeders. Only the plant feeders possess greatly enlarged mushroom bodies, which, like those of the Hymenoptera, contain doubled calyces with functional subdivisions according to sensory input, one of which receives novel visual inputs from the optic lobes [Farris and Roberts, 2005; Farris, 2008a]. One species of herbivorous scarab, the green June beetle *Cotinus mutabilis*, has the largest number of mushroom body intrinsic neurons recorded, with over 300,000 Kenyon cells per hemisphere (fig. 1k, l). Similarly, some butterflies of the nymphalid subfamily Heliconiinae possess enormous mushroom bodies [Sivinski, 1989] (fig. 1j). Other butterfly species are known to have acquired visual input to the calyces [Snell-Rood et al., 2009], although this has not been specifically investigated for species of the Heliconiinae.

Sociality has therefore not had a significant impact on the evolution of large, complex mushroom bodies in at least four insect lineages. In fact, it has been hypothesized that in the most advanced social insects individual behav-



Fig. 2. Phylogeny of the Hymenoptera, illustrating the acquisition of large, complex mushroom bodies at the base of the Euhymenoptera (circle), 50 million years prior to the evolution of sociality in the Vespoidea and Apoidea of the Aculeata. From Farris and Schulmeister [2011].

ioral repertoires may be less complex than those of solitary species [Lihoreau et al., 2012]. Social systems in which individuals take on simpler rather than more complex behavioral roles would not be predicted to drive the evolution of larger neural substrates to handle these computational tasks and may even result in a decrease in higher brain center complexity. In insects at least, other selective pressures must have favored the evolution of novel complex behaviors and the neural substrates capable of supporting these behaviors.

What Constitutes Complex Behavior for an Insect?

Large, complex mushroom bodies in four distantly related insect groups share many structural similarities: large numbers of intrinsic neurons, doubled calyces, and functional subdivisions with the novel acquisition of vi-

sual input. Are there any similarities in the behaviors supported by these complex mushroom bodies, suggesting a common selective pressure driving the evolution of large higher brain centers in insects? In vertebrates, it appears likely that multiple factors have played a role in the evolution of brain complexity, especially in integrative regions of the telencephalon such as the cerebral cortex. These include some aspects of sociality, the acquisition of novel food gathering behaviors (especially those involving multiple and/or patchy food sources), greater reliance upon vision (perhaps also as part of food acquisition and social behavior), and a general capacity for learning, innovation, and behavioral flexibility [Kirk, 2006; Lefebvre et al., 2006; Dunbar and Shultz, 2007; Lefebvre and Sol, 2008].

As in vertebrates, it is likely that some insects have more capacity for behavioral flexibility than others, especially with regard to food acquisition, and that this might be linked to morphological complexity in the nervous

system. For example, in scarab beetles, complex mushroom bodies are found only in herbivorous species that are also feeding generalists, indicating a need to locate and handle a variety of different food sources [Farris, 2005]. Many aculeate Hymenoptera are also generalists, although individual bees of species such as *Apis* may show floral constancy at a particular foraging site [Winston, 1987]. Many cockroaches are notorious feeding generalists as well [Bell et al., 2007]. All insects with large mushroom bodies are also relatively long-lived, such that novel foraging and food handling strategies once acquired might be remembered for future use, perhaps requiring larger higher brain centers simply to facilitate a greater need for information storage. However, not all insects with large brains are generalists; for example, some heliconid butterflies are extremely specialized upon a single plant species [Sivinski, 1989]. What behavior might these butterflies have in common with other species with large mushroom bodies?

One clue may be provided by the association of novel visual inputs with large mushroom bodies in all insect groups. This suggests that the morphological complexity of the mushroom bodies may arise as part of the acquisition of new functions in visual processing. In the aculeate Hymenoptera, proficiency with landmark learning and visual cognition, in the form of elemental and nonelemental learning using visual cues, is well documented [Collett and Collett, 2007; Avarguès-Weber et al., 2010]. Unfortunately, the specific role of the mushroom bodies in these behaviors has not yet been tested in the Hymenoptera. The fruit fly *Drosophila* has not been demonstrated to have the ability to perform far-field spatial learning and nonelemental visual learning tasks that aculeate hymenopterans excel at, but it is capable of near-field spatial learning and visual associative learning. In *Drosophila*, however, these functions require another protocerebral center, the central complex, rather than the mushroom bodies [Wolf et al., 1998; Neuser et al., 2008; Zars, 2009; Ofstad et al., 2011]. Perhaps this is related to the fact that, unlike the mushroom bodies of hymenopterans like *Apis*, the *Drosophila* mushroom bodies are small and do not receive direct visual input from the optic lobes [Ito et al., 1998; Tanaka et al., 2008]. It is therefore possible that selection for more complex visual cognitive and landmark learning abilities may underlie mushroom body expansion and the acquisition of visual inputs to the calyces, providing a new substrate for utilizing visual stimuli for these more complex forms of learning.

A direct link between spatial learning and mushroom body function has been shown for one species with large

mushroom bodies, the cockroach *P. americana* of the order Dictyoptera. *Periplaneta* are excellent spatial learners in laboratory assays using both near- and far-field visual cues, the latter behavior being specifically impaired by lesions to the mushroom bodies [Mizunami et al., 1998b; Kwon et al., 2004; Lent and Kwon, 2004; Brown and Strausfeld, 2009]. Many cockroaches are gregarious and employ a loose central place foraging strategy, bringing food items to a concealed location for later feeding [Bell et al., 2007]. A capacity for spatial learning would be well suited to this lifestyle. *Periplaneta* mushroom bodies also receive direct visual inputs to the calyces from the optic lobes like those of social hymenopterans that are also central place foragers [Strausfeld and Li, 1999]. Termites, the eusocial clade of the Dictyoptera, may have extensive foraging ranges from a central location and have very large mushroom bodies [Shellman-Reeve, 1997; Farris and Strausfeld, 2003]. However, many termites lack eyes [Eggleton, 2011] and are thus unlikely to employ visual cues during navigation, and they are unlikely to have visual inputs to the mushroom bodies. It is not clear what advantageous behaviors large mushroom bodies might support in these insects, although a tantalizing clue comes from a recent review of potential ancestral roles of the vertebrate hippocampus in navigation using olfactory cues [Jacobs, 2012]. It would be interesting to test specifically whether termites employ olfactory or perhaps mechanosensory 'landmarks' during foraging, and whether the mushroom bodies might be necessary for this behavior.

Insects do not have to be central place foragers to be capable of or to benefit from far-field spatial learning. Both solitary aculeate and parasitoid Hymenoptera have been shown to employ landmark learning during host location, in which potential hosts are identified and then visited at a later time for egg laying [Rosenheim, 1987; van Nouhuys and Ehrnsten, 2004; Vandersal, 2008; van Nouhuys and Kaartinen, 2008]. Heliconid butterflies are trapline foragers, in which the locations of foraging sites are learned and repeatedly visited in a specific order each day, presumably through use of landmark cues [Sivinski, 1989]. Other butterflies with visual input to the mushroom bodies have also been demonstrated to be capable of learning visual cues associated with food source location [Snell-Rood et al., 2009].

Two groups of insects are known in which the mushroom bodies appear to be almost entirely dedicated to visual processing: the aquatic whirligig beetles (Gyrinidae, Coleoptera) and the dragonflies and damselflies (Odonata). In whirligig beetles, the eyes are split into

above- and below-water components, and only the above-water components provide inputs to the mushroom bodies [Lin and Strausfeld, 2012]. Little is known about visual behavior in these beetles, but they appear to form stable aggregations in bodies of water perhaps through use of above-water landmarks [Brown and Hatch, 1929]. Dragonflies and damselflies are well known as active visual predators that make repeated visits to numerous breeding, foraging, and other sites each day [Eason and Switzer, 2006], and they possess mushroom bodies containing a massively expanded ‘protocalyx’ that receives visual input from the optic lobes [Svidersky and Plotnikova, 2004; Strausfeld et al., 2009]. In arthropods outside of the insects in which vision plays a primary role in orientation and predation, as in stomatopod crustaceans and spiders, higher brain centers that are likely homologues of the insect mushroom bodies are heavily innervated by projections from visual processing centers [Strausfeld, 2012]. Across the phylum Arthropoda, lifestyles that would appear to benefit from complex visual learning abilities are accompanied by enlarged higher brain centers receiving visual inputs.

Conclusions

The capacities for spatial learning, visual cognition, and behavioral flexibility (generalism) in feeding preferences have been directly and indirectly correlated with the evolution of large complex mushroom bodies receiving direct visual input from the optic lobes in insects. Complex visual processing, visual learning, and behavioral flexibility have also been implicated as drivers of tel-

encephalon expansion in vertebrates [Kirk, 2006; Lefebvre et al., 2006; Dunbar and Shultz, 2007; Lefebvre and Sol, 2008; Roth et al., 2010]. In contrast, some forms of sociality appear to underlie the evolution of large higher brain centers in vertebrates, while no such role is thus far apparent in insects. Thus, the links between certain behaviors and their neural substrates span the protostome-deuterostome boundary, representing the crossing of a complexity threshold that requires the additional processing power provided by large higher brain centers regardless of whether the animal is a primate or an insect. Other behaviors appear to drive the evolution of higher brain center enlargement and complexity only in certain lineages, possibly reflecting a fundamental difference in those behaviors across lineages. For example, sociality in vertebrates, especially primates, is very different from that in insects. Primate sociality requires complex behavioral repertoires and increased neural circuitry to produce them, while insect sociality is associated with a decrease in complexity of behavioral repertoires [Dunbar, 1998; Lihoreau et al., 2012]. Although there are many similarities between the selective pressures driving higher brain center expansion in distantly related animals, and the morphological features of these brain centers, all hypotheses on the links between complex higher brain centers and behaviors must ultimately consider the wide variation in computational capabilities and behavioral needs of distantly related animal lineages.

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