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Evolution and function of the insect mushroom bodies: contributions from comparative and model systems studies

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Comparative and model systems neurosciences represent complementary approaches to understanding nervous system function. The capacity for experimental manipulation of the *Drosophila* model system eclipses that available for other insect species, but data from a single laboratory model species provides little insight into the function of nervous systems in the natural environments for which they have evolved. Comparative studies can bridge this gap by first identifying conserved and derived aspects of neural circuits in different species, and second, associating features of neural circuits with adaptive behaviors produced in a particular species' natural environment. The insect mushroom bodies provide an exemplary case of the power of the *Drosophila* model system for elucidating the structure and function of a neural circuit, while comparative studies show that these circuits are evolutionarily malleable and capable of different functional roles in other insect species. Although model systems and comparative studies of insect mushroom bodies represent nearly parallel fields, emerging technologies for manipulating gene expression such as CRISPR/Cas9 hold promise as a means to unite both approaches in a complementary manner.

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Model systems and comparative studies in insect neuroscience

In the past 50 years, a handful of insect species have served as model systems for nervous system development, structure, and function. These species represented several taxonomic Orders of insects, often chosen for their tractability in laboratory studies of behavior, development, and neurophysiology. In recent years, the fruit fly *Drosophila melanogaster* has become the juggernaut in the field of insect neuroscience due to the ease and precision with which gene expression can be manipulated. More recent breakthroughs in targeted labeling and activation/deactivation of neurons have allowed circuit architecture and function to be elucidated at nearly the single cell level [1,2•,3–6,7••]. The contribution of *Drosophila* research to cellular and molecular neuroscience has been especially prodigious.

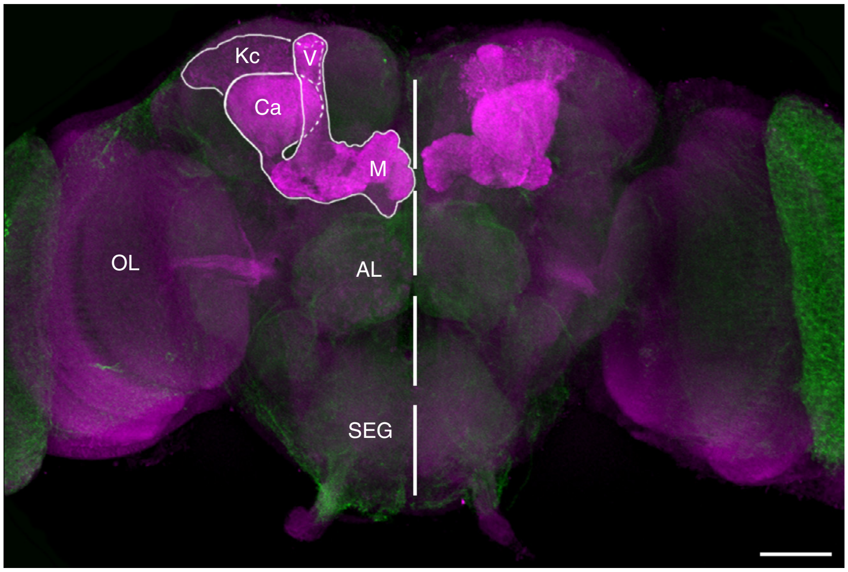
However, insects are tremendously diverse and occupy a wide range of habitats. The evolution of sensory and behavioral adaptations for survival in these habitats is enabled by changes in the structure and function of neural circuits. Insect nervous systems are morphologically and functionally diverse. Comparative studies are essential for differentiating between conserved and divergent attributes of neural circuits so that findings may be extrapolated from a single model system to broader taxa, and can even uncover 'natural experiments' that provide unique and novel insights into nervous system function [8,9••]. In seeking an understanding of how nervous systems are shaped by selection to generate adaptive behaviors, or of general principles of nervous system structure and function that are shared through common ancestry, studies in a single model species represent a sharply focused but narrow perspective.

The insect mushroom bodies: a case study in comparative versus model systems approaches

In the insect nervous system, the potential for conflict and resolution between model system and comparative studies is exemplified by the insect mushroom bodies, integrative centers in the first (protocerebral) segment of the brain in all insects except the basal Archaeognatha [10]. Insect mushroom bodies share an ancestral ground plan characterized by large numbers of tiny, densely packed intrinsic neurons (Kenyon cells) with thin processes forming a dense parallel fiber bundle that branches into a system of lobes. Atop this groundplan organization, the size, morphology and sensory inputs of the mushroom bodies are highly variable and reflect adaptations to different habitats and life histories [11–14] (Figure 1). It is likely that mushroom body function also varies across species that have evolved under different selection pressures.

Early studies in two model species, the honey bee *Apis mellifera* and the fruit fly *Drosophila melanogaster*, were critical for establishing the insect mushroom bodies as

Figure 1



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The brain of *Drosophila melanogaster* illustrated by phalloidin (green) and anti-DC0 (PKA catalytic subunit) immunolabeling (magenta). The mushroom bodies (outlined in left hemisphere and labeled heavily with anti-DC0 antibody) are paired structures on either side of the brain midline (vertical dotted line). Intrinsic neurons of the mushroom bodies called Kenyon cells (Kc) form the calyx (Ca) with their dendrites and the vertical (V) and medial (M) lobes with their bifurcating axons. Although not visible here, different Kenyon cell populations make up separate compartments within the lobes. AL: antennal lobe; OL: optic lobe, SEG: subesophageal ganglion. Scale bar = 50 μm.

centers for olfactory associative learning and memory formation [15–24]. These studies continue today and have made great leaps in elucidating the cellular components of the olfactory associative learning circuit [25•,26••,27••]. It is highly likely that this function is an important one for many insects. Most terrestrial insects, including *Apis* and *Drosophila*, receive olfactory input from first order olfactory neuropils, the antennal lobes, to a dedicated input neuropil of the mushroom bodies called the calyx [11,28,29] (Figure 1). Olfaction is a key sensory modality for many insects, as odor cues provide both aversive and appetitive information about food sources, oviposition sites, and conspecifics [30,31]. However, comparative studies have provided evidence that the mushroom bodies are likely more than olfactory learning centers.

Perhaps the most persuasive evidence for non-olfactory functions of the mushroom bodies is observed in insects in which olfaction is of minimal importance for adult behavior. Aquatic insects, or those that are short-lived and do not feed as adults, often have reduced olfactory systems characterized by short (setaceous) antennae with few olfactory sensillae, small, non-glomerular antennal lobes, and a reduced or absent mushroom body calyx [10,11,32] (Figure 2c–e). These species include aquatic beetles and true bugs, as well as the short-lived terrestrial cicadas and mayflies. All of these insects still possess the mushroom body lobes, which are innervated by both inputs and outputs, suggesting that this circuitry plays an important role in non-olfactory functions as well as in olfactory associative learning [26••,33].

Other non-olfactory sensory inputs to the mushroom bodies have been extensively documented in species representing a wide range of insect Orders. In the apocritan Hymenoptera (Parasitica + Aculeata) and some Lepidoptera, Coleoptera and Dictyoptera, olfactory input to the mushroom body calyces co-occurs with visual input arising from the medulla and/or the lobula of the optic lobes [28,34–38] (Figure 2a–c). Some species with reduced olfactory systems appear to have nearly completely replaced olfactory input to the mushroom bodies with visual input, as in the Odonata and whirligig beetles (Coleoptera: Dytiscidae) [39–41]. Inputs from gustatory centers appear to be even more widespread, co-occurring with olfactory and sometimes visual inputs to the calyces [42–44]. Few studies have investigated the role of non-olfactory modalities in mushroom body function in these species [45–48] much less how these modalities interact to produce behavior. Recent studies in *Drosophila* suggest that gustatory and visual associative learning employs the mushroom bodies [49,50••,51•,52]. *Drosophila* does not receive direct visual input to the calyces [50••,53], but electrophysiological and Ca^{++} imaging studies demonstrate that multimodal sensory information reaches

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