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Synapsin-based approaches to brain plasticity in adult social insects

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Development of the mushroom bodies continues after adult eclosion in social insects. Synapsins, phosphoproteins abundant in presynaptic boutons, are not required for development of the nervous system but have as their primary function modulation of synaptic transmission. A monoclonal antibody against a conserved region of *Drosophila* synapsin labels synaptic structures called microglomeruli in the mushroom bodies of adult social insects, permitting studies of microglomerular volume, density, and number. The results point to multiple forms of brain plasticity in social insects: age-based and experience-based maturation that results in a decrease in density coupled with an increase in volume of individual microglomeruli in simultaneous operation with shorter term changes in density produced by specific life experiences.

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Introduction: plasticity of the mushroom bodies in adult social insects

The mushroom bodies (MB) of the insect brain are critical structures for learning and memory, from simple associative learning to processing of information related to complex stimuli [1,2••,3•,4,5]. The scaffolding of the MB is provided by the axons and dendrites of intrinsic neurons called Kenyon cells (Figure 1a,b). The brains of all insects contain MB and Kenyon cells, but the MB of social hymenopterans have attracted attention since the mid-19th century because of their relatively large size [6]. Although it is now evident that the MB of many non-social insects are also relatively massive [7•], the well-developed MB of the Euhymenoptera (bees, wasps, and ants) continue to intrigue neurobiologists. The relationship between MB structure and behavior can be analyzed from a perspective of phylogenetic trends [6,7•,8–10] or from the neurobiological perspective of MB development and plasticity during the lives of individual insects [11]. This review focuses on the neurobiological perspective.

Changes in the morphology of Kenyon cell dendritic spines in association with orientation flights and foraging in honey bees (*Apis mellifera*) provided early evidence of MB plasticity [12,13]. In the 1990s, analyses based on the Cavalieri Principle were used to estimate regional brain volumes in honey bees. This method is used by stereologists to estimate volumes of irregularly-shaped objects from cross-sectional areas [14]. When brains of honey bees were compared using Cavalieri-based sampling, the MB neuropils of foragers were found to be larger than those of younger bees [15]; other laboratories confirmed this result [16,17]. Studies based on neuropil volume identified factors associated with MB plasticity in social insects: age [18], foraging experience [19], social aggression [20,21], and muscarinic receptor activation [19].

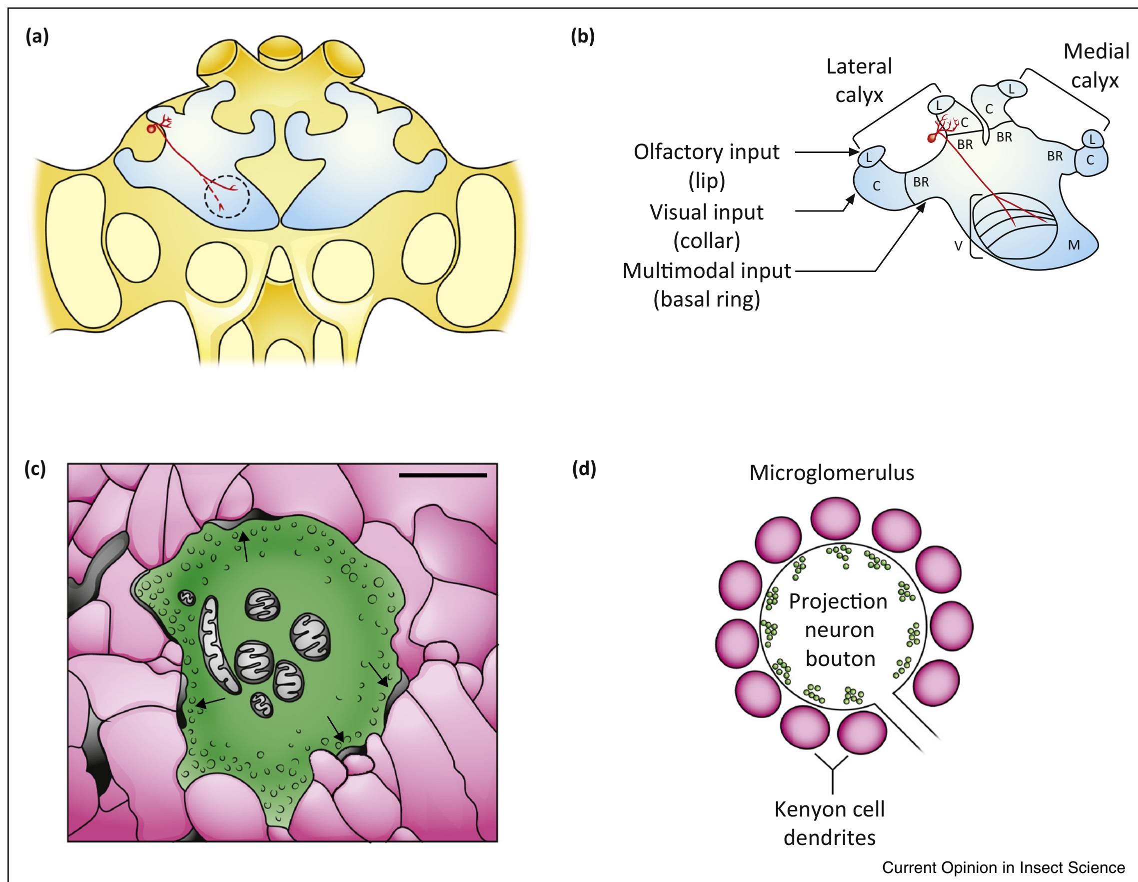
Volume-based approaches suggested that developmental processes remain active in adult social insects. In honey bees, neurogenesis does not occur in the adult MB [22,23]. Golgi studies, however, confirmed that growth of Kenyon cell dendrites occurs in adult honey bees [24,25] and the paper wasp *Polybia aequatorialis* [26]. The dendrites of the Kenyon cells form the calyces of the MB neuropil (singular, calyx). Social hymenopterans have four calyces (Figure 1a). The primary inputs to the calyces are from sensory neuropils (Figure 1b) [11]. The blend of information about the sensory world integrated in the MB varies across taxa: in some, projections arise almost exclusively from the antennal lobes; in others, optic lobe inputs are abundant [6]. Social hymenopterans are notable for having extensive direct visual input to the MB calyces [7•,27]. Each hymenopteran calyx contains lip (antennal lobe inputs), collar (optic lobe inputs), and basal ring (mix of antennal and optic lobe inputs) subdivisions [27]. Insect neuropils are famously complex, and many of the tools used to analyze them — Golgi labeling, electron microscopy — are labor-intensive and difficult to combine with other techniques. After a decade of studies, the study of MB plasticity in social hymenopterans would likely have experienced a lull without the timely introduction of synapsin immunolabeling [28••].

Synapsin

Synapsin immunolabeling is a marker for microglomeruli

Synapsins are phosphoproteins localized in presynaptic boutons. They are substrates for cAMP-dependent

Figure 1



Schematic depictions of the mushroom bodies (MB) and calycal microglomeruli of the honey bee brain. **(a)** Transverse section through the central brain showing the position of the MB (blue). A representative Kenyon cell (red) illustrates the typical location of Kenyon cell somata, dendrites, and bifurcated axons. **(b)** Transverse section showing the major divisions of the MB neuropil, indicating the positions of the lateral and medial calyces and the subdivision of the MB calyces into distinct lip (L), collar (C), and basal ring (BR) regions. The medial (M) and vertical (V) lobes formed by the axon terminals of the Kenyon cells and their synaptic partners are also shown. **(c)** Simplified schematic depiction of a calycal microglomerulus, based upon ultrastructural images of microglomeruli. The central region represents a projection neuron bouton (green). The central region of the bouton is typically occupied by mitochondria (gray). The small circles represent synaptic vesicles. Synapsin protein is abundant in the projection neuron bouton, where it functions to modulate the release of neurotransmitter from synaptic vesicles. The bouton is surrounded by Kenyon cell dendrites (pink), which receives synapses from the projection neuron bouton. The arrows indicate some of the synapses that are present, which are recognizable because of the evident post-synaptic density. Scale bar, 0.5 μm. Drawing based upon a published electron micrograph (Figure 3, Panel F [28••]). **(d)** Highly simplified 2-D representation of a microglomerulus showing a projection neuron bouton containing synaptic vesicles surrounded by Kenyon cell dendrites. At the confocal microscope, synapsin immunolabeling reveals the bouton and phalloidin indicates the presence of f-actin rich dendritic structures. See text for further details.

protein kinases [29] and modulate neurotransmitter release by reversibly attaching synaptic vesicles to actin [30••,31••]. A single gene encoding synapsin is present in all metazoans with a nervous system, with the exception of vertebrates, which have either two or three synapsin genes [30••,32]. Synapsins have multiple phosphorylation sites, and neurotransmitter release is inhibited or facilitated depending on the phosphorylation of specific sites [30••]. The discovery of mammalian synapsins [33] was followed by cloning of the homologous *Drosophila* gene [34••]. In the course of this study, the mouse monoclonal antibody anti-SYNORF1 was generated against a fusion protein. Application of anti-SYNORF1 to *Drosophila* tissues produced immunolabeling of boutons [34••], matching the presynaptic distribution of synapsins in mammals [33]. The SYNORF1 antibody recognizes the sequence LFGGMEVCGL in the conserved C domain of *Drosophila* synapsin found in multiple synapsin isoforms, and produces no signal in null mutants [35].

Function of synapsin in development and plasticity

Triple knockout mice lacking all synapsins displayed normal brain structure and a typical number of synapses, suggesting only a modest role for synapsin in development

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