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Central processing in the mushroom bodies

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The mushroom bodies in the insect brain serve as a central information processing area. Here, focusing mainly on olfaction, I discuss functionally related roles the mushroom bodies play in signal gain control, response sparsening, the separation of similar signals (decorrelation), and learning and memory. In sum, the mushroom bodies assemble and format a context-appropriate representation of the insect's world.

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Introduction

The mushroom bodies are striking in appearance, resembling bilaterally arranged cups brimming with tiny neurons, supported by stems that bend and branch in several directions dorsally and laterally. The tiny neurons, Kenyon cells, (KCs) send long thin processes down through the stems, which form distinct lobes. These prominent and complex structures, found in all but the earliest insects, are as interesting as they look — they serve a number of functions important for processing sensory information. In many insects, groups of KCs receive sensory information from visual, gustatory, and mechanosensory areas, and, perhaps most often studied, thick tracts of olfactory input from the antennal lobes [1,2]. In honeybees and other insects, different populations of KCs appear to receive direct input from different sensory modalities, although some KCs may also be multimodal. The KCs also receive inhibitory and recurrent input, and neuromodulators such as dopamine that provide reward signals [3]. Together, these inputs endow the mushroom bodies with information processing powers that are gradually coming to light. Here, focusing mainly on olfaction, I discuss functionally related roles the mushroom bodies appear to play in signal gain control, response sparsening, the separation of similar signals (decorrelation), and learning and memory.

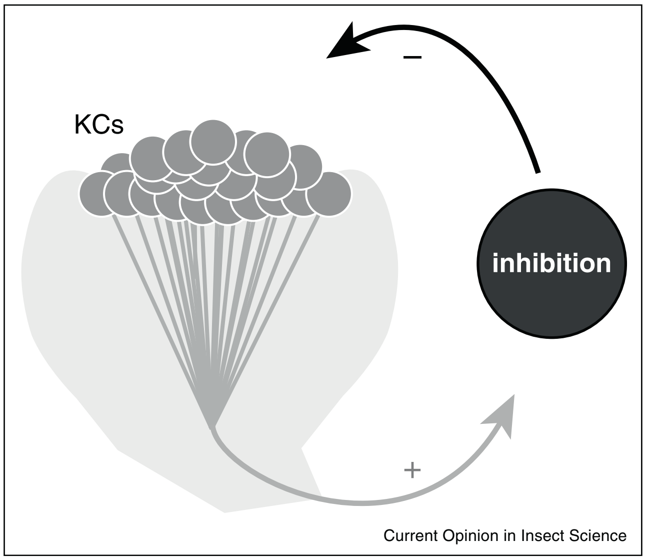
Gain control

Sensory stimuli can be weak or strong, and sensory systems must accommodate this dynamic range. In several insect species the mushroom body's KCs have been found to form feedback connections with powerful inhibitory neurons that may help contain responses to sensory stimulus within limits (Figure 1). The anatomy of feedback connectivity provides a hint that any increase in the output of KCs will be tamped down by inhibition that increases proportionally with the response of the KCs, and is reflected back to them by the inhibitory cells. In fact, in locusts, a singular giant GABAergic neuron (GGN) appears to play precisely this role. GGN is anatomically positioned to receive input from, and provide output to, KCs. Intracellular electrophysiological measurements show GGN depolarizes in response to all tested odors; artificially depolarizing it reduces the responsiveness of every tested KC and effectively silences lobe neurons that receive inputs from KCs [4••]. Thus, GGN appears to receive input from all KCs, and, in turn, provide inhibitory output to all KCs. GGN itself appears to be regulated by another inhibitory neuron, inhibitor of GGN (IG). Other insects also have GABAergic neurons that seem similar to GGN; for example, in *Drosophila*, genetic manipulations of activity and calcium recordings have shown that a neuron called anterior paired lateral neuron (APL) similarly regulates KCs [5••]. The mushroom body circuitry comprising these inhibitory neurons and KCs together regulates the excitability of the KCs, allowing them to respond with appropriate amounts of spiking to a wide dynamic range of sensory signals arriving from the antennal lobe and perhaps elsewhere.

Sparsening and decorrelation

Among the inputs received by KCs are olfactory signals carried by projection neurons from the antennal lobe. Anatomical studies show that each olfactory KC receives input from multiple presynaptic projection neurons [6,7], and electrophysiological recordings show that the projection neurons (PNs), which are spontaneously active in the absence of stimuli [8], respond to odors with voluble bursts of spikes. Given the sheer number of action potentials arriving at KCs, one might predict these neurons would roil with activity before, during, and after any given olfactory stimulation. Yet, KCs are nearly silent at rest [9,7,10•]. Further, any given KC responds only to a narrow range of odors or even particular concentrations of those odors [11,12], and the odor-elicited responses of each KC consist of very few spikes, often only one or two. Thus, the mushroom bodies transform the flood of odor-elicited spikes arriving from PNs into very sparse representations of the odor (Figure 2, top).

Figure 1

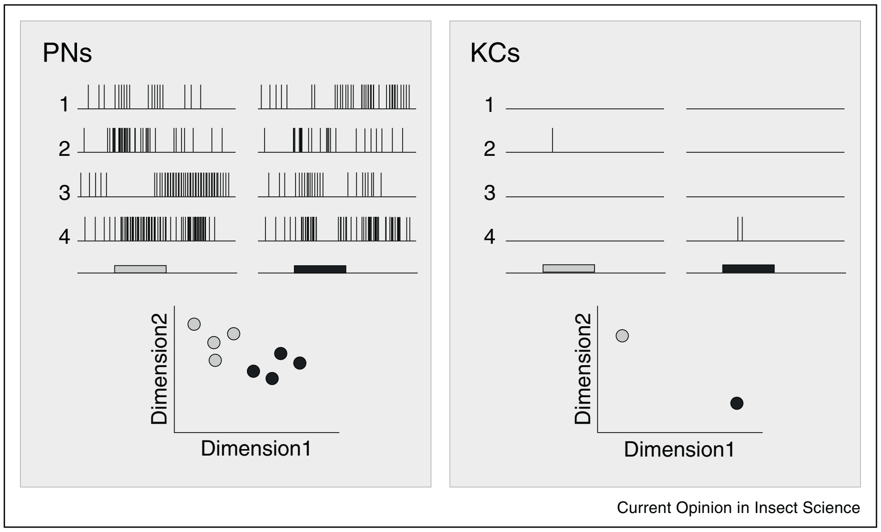


Gain control in the mushroom bodies. In several insect species, singular giant inhibitory neurons, or groups of smaller inhibitory neurons, have been shown to receive output from all Kenyon cells (KCs) and then feed it back as inhibition to all KCs. This mechanism maintains the activity of KCs within a narrow range.

Several mechanisms contribute to this sparsening function. One is the gain control effect exerted by giant inhibitory neurons like GGN and APL, which tamps down the excitability of KCs (see Figure 1). A second mechanism, demonstrated in the cockroach, is GABAergic inhibition that tonically hyperpolarizes the membrane potential [13]; the source of this tonic inhibition is uncertain. A third mechanism is the oscillatory structure of the spikes arriving from PNs. Owing to reciprocal excitatory and inhibitory circuitry in the antennal lobe, PNs are excited by repeatedly-encountered odors to oscillatory synchronization of their spiking (locusts: [14]; bees: [15]; moths: [16]; flies: [17]); each cycle consists of a spiking alternating with a period of relative quiescence. Thus, during each odor-elicited response, KCs receive an extra measure of excitatory input from PNs during a small portion of each cycle. The contribution of feedback inhibition to sparsening is magnified by the oscillatory responses as each pulse of excitation arising from KCs is reflected back after a brief delay as a pulse of inhibition. This leaves KCs free to spike only during the brief depolarized ‘integration window’ occurring between consecutive waves of inhibition. Evidence from physiology experiments in locusts and computational models suggests that the duration of the integration window can vary with the intensity of the input from PNs: more intense input causes GGN to respond earlier in each oscillatory cycle, thus shortening the integration window [18,19]. This mechanism helps maintain the sparseness of responses in KCs regardless of input intensity.

In addition to these circuit mechanisms, intrinsic properties of KCs also favor sparse responses. In cockroaches, whole-cell electrophysiological recordings from KCs have revealed two unusual conductances that promote sparseness: an inward calcium conductance with a very low activation threshold; and an outward potassium

Figure 2



Sparsening and decorrelation. Left: PNs (4 examples shown here) are spontaneously active and respond to odors with bursts of temporally-patterned spikes. Different odors (light gray bar at left, dark gray bar at right) elicit different patterns of activity. The responses of the PN population can be visualized as clouds of points (here, in a 2-dimensional space). Right: KCs, by contrast, are nearly silent at rest and respond to odors with great specificity, and with only a few spikes. Sparsening and decorrelation mechanisms separate the responses of KCs elicited by different odors, making them easy to distinguish.