lottery, where the jackpot is a huge, often human-made resource. And it is not clear whether there are any specific themes that characterize the evolutionary trajectory towards 'pestness', other than the size of that jackpot. What is clear is that for a species to become a pest certain preconditions need to be met, in the case of *Drosophila* flies their association with fruits and especially their high reproductive output. On this evolutionary substrate then fairly small behavioral changes can lead to vast ecological gains for the species. Just as it happened for this planet's mightiest pest of all: humans.

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Neuroscience: Intelligence in the Honeybee Mushroom Body

Sophie Caron[1] and Larry F. Abbott[2]
[1]Department of Biology, University of Utah, Salt Lake City, UT 84112, USA
[2]Department of Neuroscience, Zuckerman Mind Brain Behavior Institute, Columbia University, New York, NY 10027, USA
Correspondence: sophie.caron@utah.edu (S.C.), lfabbott@columbia.edu (L.F.A.)
http://dx.doi.org/10.1016/j.cub.2017.02.011

Intelligence, in most people's conception, involves combining pieces of evidence to reach non-obvious conclusions. A recent theoretical study shows that intelligence-like brain functions can emerge from simple neural circuits, in this case the honeybee mushroom body.

The mushroom body, a conspicuous structure in the brain of insects, was first described by the French biologist Felix Dujardin in 1850 [1]. When examining the brains of various insects, Dujardin observed that social insects, such as honeybees, have a bigger and more complex mushroom body than their less social relatives, solitary bees, for instance. This observation inspired Dujardin to propose that the mushroom body was the seat of intelligence in the insect brain. Dujardin was remarkably insightful: after more than 150 years of research, a large body of evidence demonstrates that the mushroom body is a multisensory brain center required for the formation, storage and retrieval of associative memories [2]. The wealth of anatomical, physiological and behavioral data makes the mushroom body a powerful system for theoretical studies that use mathematical models highly constrained by data. With these models, learning can be replicated and features critical for its function can be identified. In a recent paper in *Current Biology*, Peng and Chittka [3] use a computer model of the mushroom body to examine its capacity to learn and reveal how that capacity depends on circuit features.

The mushroom body integrates input from multiple sensory systems, but its

connections to the olfactory system have been extensively characterized in different insects including honeybees and *Drosophila melanogaster* [2]. Insects detect odors through sensory neurons covering their antennae. As demonstrated in *Drosophila melanogaster*, most of these neurons express a single type of olfactory receptor [4]. Neurons expressing the same receptor converge in the antennal lobe, an olfactory relay center analogous to the vertebrate olfactory bulb, where they innervate a single glomerulus. Because most odorant molecules bind to multiple receptors, each odor is represented in the antennal lobe of both honeybees and *Drosophila* by a combination of active glomeruli. Olfactory information is transferred from the antennal lobe to higher brain centers, including the mushroom body, through projection neurons, each of which carries information from a single glomerulus. In *Drosophila*, it has been shown that individual mushroom body neurons, the Kenyon cells, receive on average seven inputs from an apparently random set of projection neurons [5]. Such randomization of sensory input is an important feature of the mushroom body, allowing it to construct an informative representation of olfactory stimuli useful for extracting associations.

The Kenyon cells connect to a small number of output neurons that are thought to mediate different learned behaviors, such as attraction and aversion [6]. Studies in locusts and *Drosophila* show that, when learning to associate a particular odor with reward or punishment, the connections between the Kenyon cells activated by that odor and the output neurons mediating an appropriate behavioral response are modified [7–9]. This experience-dependent modification requires the action of dopaminergic neurons that innervate the compartments where connections between the Kenyon cells and output neurons are made [6]. Anatomical and functional evidence suggests that there might be additional sites where learning takes place, at least in the honeybee mushroom body: the VUMmx1 neuron, an octopaminergic neuron activated by sugar that could mediate plasticity, innervates the input region of the mushroom body where projection neuron to Kenyon cell synapses are located [10]. In their study, Peng and Chittka [3] examine the effect of this additional site of plasticity on the learning performance of the mushroom body.

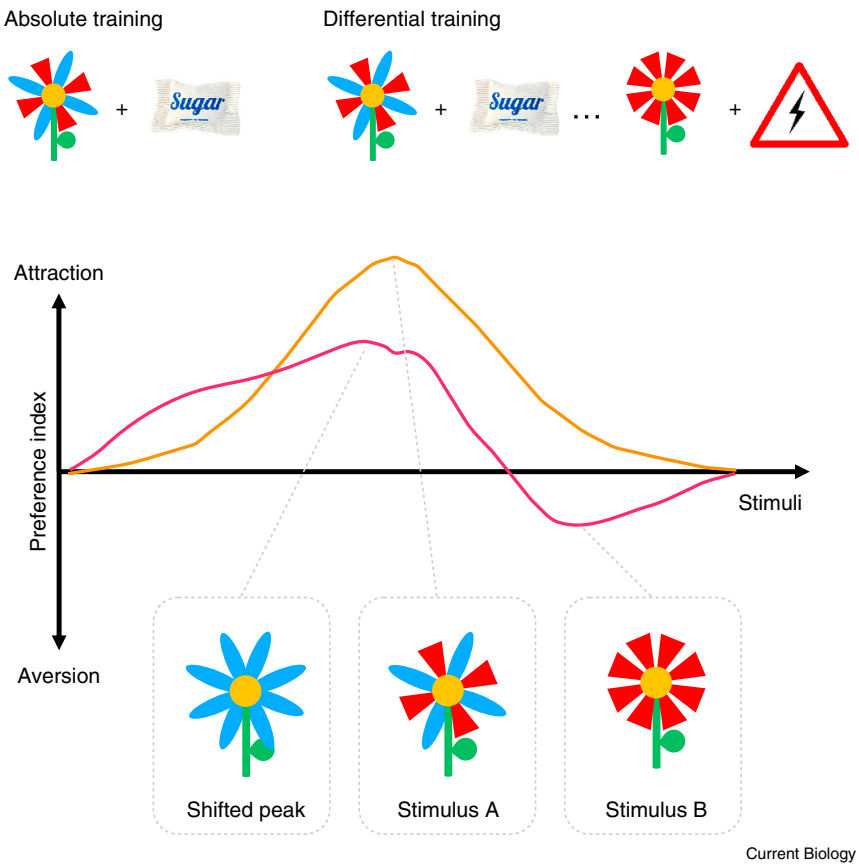

Figure 1. Peak-shift in the honeybee mushroom body.
The model of the honeybee mushroom body devised by Peng and Chittka [3] was trained with different learning paradigms. During an absolute learning task, the model learns to associate stimulus A (depicted as a red and blue flower) with a sugar reward. After training, the attraction of the modeled mushroom body peaks for the stimulus it was trained with (in this case, the red and blue flower). During a differential learning task, the model learns the same association as well as to associate stimulus B (depicted as a red flower) with a punishment. After training, the attraction of the modeled mushroom body peaks for a stimulus it was trained with (a blue flower). This phenomenon is called 'peak-shift' and is a form of learning that enables the brain to form inferences based on different past experiences.

The model of the mushroom body developed by Peng and Chittka [3] contains 100 projection neurons that connect to 4000 Kenyon cells — numbers smaller than those for the real honeybee mushroom body but large enough to duplicate some of its functions. The model's Kenyon cells connect to two output neurons, one mediating attraction and the other aversion, again a simplification compared to the multiple attractive and aversive outputs in the actual mushroom body. In the model, each odor activates 50% of the projection neurons and 5% of the Kenyon cells. The sparser activity in the mushroom body is the result of both low convergence of input (each Kenyon cell receives, on average, ten inputs from a random set of projection neurons) and global feedback inhibition. The behavior generated by the model in response to a panel of odors was determined by the preference index, a measure proportional to the difference in the activities of the appetitive and aversive output neurons.

Prior to training, odors activate the two output neurons approximately equally. Thus, the preference index is near zero, and odors trigger neither attraction nor aversion. Associations between a particular odor and a reward are learned through modification of the synapses between the Kenyon cells activated by that odor and the appetitive output neuron. Conversely, if the odor is associated with punishment, synapses

to the output neuron mediating aversion are modified. This feature of the model is based on several recent studies that provide evidence for synaptic plasticity between Kenyon cells and output neurons [7–9]. This form of plasticity allows the model to exhibit simple associative learning, but Peng and Chittka [3] were interested in more complex relationships between stimulus and reward or punishment.

One task that Peng and Chittka [3] considered, which they call 'patterning', is similar to the exclusive-or problem famous in machine learning. Two odors, A and B, are associated with one valence (either attraction or aversion), while the mixture A–B is associated with the opposite valence. The variety of inputs that the different Kenyon cells receive through their random inputs produce a representation that is well suited to support such a task. Indeed, the model can perform this task solely on the basis of plasticity at Kenyon cell to output neuron synapses.

In another task, odor A is associated with reward and odor B with punishment. When a range of different odors is then tested, the most appetitive odor is A, meaning that the aversion to B does not affect the behavioral appetitive responses to odors similar to A. This result, which is due to the relatively narrow tuning of the trained aversive output neuron, disagrees with results observed in honeybees. Honeybees show a phenomenon called 'peak shift' in which the most appetitive odor is not A but an odor similar to A that is more different from B (Figure 1) [11–14]. In other words, the aversion to B affects the attraction to A in the honeybee but not in the model.

To fix this discrepancy, Peng and Chittka [3] extended plasticity in the model to the synapses between the input projection neurons and the Kenyon cells. In this version of the model, reward strengthens the connections between active projection neurons and Kenyon cells, whereas punishment weakens them. This plasticity broadens the tuning of the output neurons so that the aversion to B now modifies the preference index in response to A, producing a peak shift. This improvement in the model comes with a cost, however. Performance on the patterning task is worse in the model with extended plasticity than in the original model, suggesting a decrease in discrimination that appears to disagree with the extremely good discrimination ability of bees [15].

The honeybee mushroom body contains two types of Kenyon cell: class I, also called 'spiny Kenyon cells', that have wide-field dendritic arbors, and class II or clawed Kenyon cells that have more localized arbors [16]. On the basis of results from the locust [17], Peng and Chittka [3] assumed that class I Kenyon cells receive input from a large number of projection neurons, in contrast to class II, the only Kenyon cells in the original model, which receive few inputs (ten on average). The expanded model indicates that class II Kenyon cells perform better in the patterning task, whereas class I Kenyon cells show a stronger peak-shift and thus show broader 'generalization'. If type I Kenyon cells are, indeed, extensively connected to projection neurons, this observation provides insight into why two types of neuron are found in the honeybee mushroom body: to strike a balance between generalization (the peak shift) and discrimination (the patterning task). Together, these results imply that plasticity should be present at synapses from projection neuron to class I, but not class II, Kenyon cells [18]. Interestingly, the *Drosophila* mushroom body contains only sparsely connected Kenyon cells. This suggests that fruit flies may be more limited in their ability to generalize across appetitive and aversive odors.

Over the years, the mushroom body field has generated a large body of experimental data, but the function and significance of certain mushroom-body features have remained unclear. For example, spiny and clawed Kenyon cells were described more than two decades ago [16], but their role in learning is not immediately obvious from their morphology. The study by Peng and Chittka [3] suggests that these two types of neuron carry out different functions: spiny Kenyon cells appear better at generalizing, whereas clawed Kenyon cells may be better at discrimination. Although it remains unclear why not all mushroom bodies contain two types of Kenyon cell with different extremes of connectivity, this may be related to whether or not modulator-regulated plasticity developed at the projection neuron to Kenyon cell synapse.

Two-stage learning with extensive input connectivity in type I Kenyon cells may significantly enhance the ability of the mushroom body in bees to support complex inference.

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Protist Evolution: Stealing Genes to Gut It Out

David Moreira* **and Purificación López-García**
Ecologie Systématique Evolution, CNRS, Université Paris-Sud, AgroParisTech, Université Paris-Saclay, 91400, Orsay, France
*Correspondence: david.moreira@u-psud.fr
http://dx.doi.org/10.1016/j.cub.2017.02.010

The amount and evolutionary impact of horizontal gene transfer in eukaryotes remain contentious issues. A new phylogenomic study suggests that gene transfer from prokaryotes has contributed significantly to the adaptation and metabolic evolution of *Blastocystis*, the most widespread human gut eukaryotic parasite.

Eukaryotic cells usually possess complex structures, including sophisticated cytoskeleton and endomembrane systems, which allow many species to feed by phagocytosis upon other cells or particles. Phagocytosis is instrumental for the facility, observed across eukaryotic phyla, to acquire endosymbionts. The best-known examples are mitochondria and chloroplasts, ancient endosymbiotic bacteria evolved into cell organelles, but many other endosymbioses — involving members of the three domains of life — have been described in a vast spectrum of eukaryotic hosts. They provide a variety of new functions, ranging from detoxification to cell defense and, in most cases, endosymbionts are recruited because their metabolic abilities are useful for their hosts [1]. By contrast, prokaryotic cells are structurally simpler and unable to carry out phagocytosis, so that endosymbiosis is much rarer. Nonetheless, prokaryotes can easily gain new, notably metabolic, functions by acquiring genes from more or less distant organisms via horizontal gene transfer (HGT). Although the importance of HGT in prokaryotic evolutionary history is widely recognized [2–4], the frequency and evolutionary role of HGT in eukaryotic evolution remain controversial. Some authors claim that, except for the numerous genes transferred long ago from mitochondria and chloroplast ancestors to the host genome, recent gene acquisitions from prokaryotes are too rare to have broad evolutionary significance in eukaryotes [5]. In this issue of *Current Biology*, Eme *et al.* [6] present a counterpoint to this view by showing that several strains of the human parasite *Blastocystis* sp. appear to have acquired up to 2.5% of their genes by HGT from different donors, mostly bacteria.

Blastocystis is a genus of unicellular parasites belonging to the Stramenopiles, a large eukaryotic group exhibiting wide phenotypic diversity. Its very simplified cellular structure has long hindered the recognition of the diversity existing within this genus, but 18S rRNA gene sequence analysis has revealed considerable cryptic diversity. *Blastocystis* species appear to have low host specificity and infect a variety of animal taxa, both vertebrates and invertebrates. Although its implication in disease remains uncertain, *Blastocystis* is highly prevalent in humans and up to 9 different lineages — called subtypes ST1 to ST9 — can be distinguished in the human gut based on their 18S rRNA sequences [7]. Complete genome sequences were available for subtypes ST4 and ST7 and Eme *et al.* have now determined the genome sequence of the highly prevalent ST1 subtype [6]. Living in the intestinal tract, *Blastocystis* coexists with the extremely diverse gut microbiome, being exposed to multifarious sources of exogenous DNA [8]. Thus, *Blastocystis* genome sequences represent an excellent material to evaluate the impact of HGT on eukaryotic genomes.

Accurate HGT detection is challenging since many confounding factors can blur phylogenetic signal and lead to false positive and negative results. It is well known that different HGT detection methods very often produce incongruent results, and some of them — notably sequence similarity-based methods — are prone to HGT overestimation [9]. In addition, contamination in the samples used for genome sequencing can lead to spurious assemblages containing genes from mixed origins and producing a high number of false HGTs. This problem is especially important for predatory eukaryotes as the DNA samples usually contain DNA from both the targeted species and their prey. The recent controversy on HGT levels in tardigrades, a group of minute animals, exemplifies this problem. Analysis of the first tardigrade genome sequence (*Hypsibius dujardini*) suggested that more than 17% of its genes derived from HGT from various sources, mostly bacteria but also plants, fungi, archaea, and viruses [10]. However,