



# **Invertebrate Learning and Memory: Chapter 29. In Search of the Engram in the Honeybee Brain (Handbook of Behavioral Neuroscience)**

*Randolf Menzel*

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What is the engram, the memory trace that stores the content of memory? Here, I argue that the engram is more than just the sum of all learning-related neural changes. Rather, it is an integrated part of the whole nervous system, from sensory integration to interneuron processing and motor control. Emphasis is given to those neural processing components that do not express themselves in the behavior of the animal. To date, the search for the olfactory engram in the bee brain has focused on network properties in the antennal lobe (AL), the input and output regions of the mushroom body region (calyx), the mushroom body extrinsic neurons, and the reward pathway. I conclude that the olfactory memory trace in the AL relates predominantly to attention-generating properties. The memory trace in the calyx is characterized by the high-order combinatorial integration of multiple sensory inputs. Mushroom body extrinsic neurons are tentatively related to multiple processing categories that represent the acquired values (e.g., favorable conditions and to be avoided condition) and provide neural commands for goal-directed behavior and decision making. The system of VUM neurons stores appetitive memory related to appetitive internal states and controls nonassociative and associative memories. A model is presented that aims to capture the multifaceted and distributed nature of the engram and may help to guide our future search of the engram at a systems level.

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