Classification of Learning in tethered flying *Drosophila*

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With tethered flies in stationary flight at the torque meter many different kinds of experiments can be performed that reveal some sort of learning and memory in the yaw torque and orientation traces. The question is adressed whether any of these are different *types* of learning or whether only the behavioral context differs by which a uniform learning process is revealed. In the original procedure in the flight simulator ('standard experiment') the fly is conditioned by heat to prefer certain flight orientations with respect to the patterned drum surrounding it. This experiment has been performed with many different pairs of patterns (e.g. an upright and an inverted T, vertical and horizontal bars, etc.). Variation of the patterns is generally assumed not to affect the *type* of learning. Two observations, however, question this assumption. Surprizingly, certain pairs of patterns that are spontaneously discriminated by the flies do not support conditioned pattern discrimination. Also, flies adjust their strategies of learning to the special situation. With isolated figures (e.g. T's) they remember the positively and negatively reinforced pattern orientations whereas with random-dot textures filling the whole arena (Dill et al., 1995) they remember only certain positively reinforced orientations.

Recently, instead of heat, benzaldehyde odour has successfully been used as a reinforcer (Guo and Götz, 1997). Moreover, pattern learning occurs at the torque meter even without any explicit reinforcement (novelty choice; Dill and Heisenberg, 1995). Whether these three variants which differ in the training (heat, aversive odour, novelty choice) but use the same memory test reveal the same underlying learning process, remains to be investigated. A further variation of the training is a classical conditioning procedure. In this case, pattern motion and heat/no-heat are controlled by the experimenter rather than the fly. Distinctly more reinforcement is required under these (open-loop) conditions compared to the standard experiment. In other words, learning is 'facilitated' if the reinforcement is under the command of the fly.

If the range of spontaneous yaw torque (without any visual feedback) is split into two domains (right turns/left turns) and these are coupled to a switch between heat and no-heat, the fly quickly learns to keep its torque in the no-heat range and sticks to this motor bias even after heat is permanently switched off (motor memory). Here, a different type of learning is involved since the fly's yaw torque range reflects speed and direction of angular motion, whereas in the standard experiment the fly needs to control angular orientation. In an extension of this experiment the two domains of the torque range can be coupled to two stationary orientations of the panorama during the training. In this situation the fly will display its motor memory during the test only if the same very artificial visual "context" is provided.

A further classification of learning types may be achieved using genetic or drug intervention. So far, however, only few data are available. Comparing some of the above experiments to olfactory discrimination learning (Tully and Quinn, 1985) we have found that two genes, *dunce* and *rutabaga* which control cAMP signaling are involved in both olfactory and visual memory (standard experiment; Eyding, 1993). In contrast, in flies with genetic (Heisenberg et al., 1985) or ontogenetic (deBelle and Heisenberg, 1994) lesions of the mushroom bodies odour discrimination memory but neither visual nor motor memory at the torque meter are impaired. Recently, Xia et al. (1997) have shown that similar to olfactory memory (deZazzo and Tully, 1995), visual memory can be dissected into several components: an anesthesia sensitive short term memory, KCl sensitive middle term memory and a protein synthesis dependent long term memory.

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