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Review

Exhumed from thought: Basal ganglia and response learning in the plus-maze

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ABSTRACT

The plus-maze apparatus figured prominently in the historical debate between *cognitive* and stimulus–response *habit* learning theorists concerned with the fundamental question of "what" animals learn. An important feature of this task is that variants of the training procedure can be arranged to allow for an assessment of the relative use of cognitive/place or habit/response learning mechanisms. This brief review describes findings from several neurobiological studies published primarily over the past decade that have re-introduced the plus-maze to investigate the role of the dorsal striatum in learning and memory. Converging evidence from research using brain lesion, pharmacological, and molecular/genetic approaches is described supporting the hypothesis that the dorsolateral striatum plays a selective role in response learning in the plus-maze. Within a multiple systems framework of memory organization, factors that can influence the relative use of place and response learning in the plus-maze are also considered, including the nature of the visual environment, reinforcement/training parameters, and emotional state of the organism. Response learning in the plus-maze may be considered an exemplar task useful for investigating the neurobiological bases of dorsal striatal involvement in habit learning and memory. This mnemonic function of the dorsal striatum generalizes across several sensory modalities and mammalian species, including humans.

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The eminent psychologist Edward C. Tolman used psychological constructs such as knowledge, inference, intention, expectancy, and purpose to explain learned behavior [1]. However, in his assessment of Tolman's "cognitive" theory (1932), the stimulus–response (S–R) learning theorist Edwin R. Guthrie was more than skeptical of such terminology, commenting that "*so far as the theory is concerned the rat is left buried in thought*" [2]. The empirical battle between S–R habit and cognitive learning theorists was fought using several different learning tasks. In particular, a plus-maze apparatus introduced by Tolman and colleagues [3] figured prominently in this debate, and this task provides a straightforward illustration of the differences between S–R and cognitive approaches to understanding "what" animals learn (Fig. 1). The plus-maze is arranged so that a goal box (e.g. east or west), can be approached from one of two start boxes (e.g. north or south). In the standard *dual-solution* version of the task, rats are trained over trials to obtain food from a consistently baited goal box (e.g. west), from the same start box (e.g. south). According to cognitive learning theory, rats trained in this task acquire information concerning the spatial location of the food, and a learned "expectancy" guides an approach response to the baited goal box. In contrast, according to S–R learning theory rats learn to approach the baited goal box by acquiring a response tendency (i.e. a specific body turn at the choice point).

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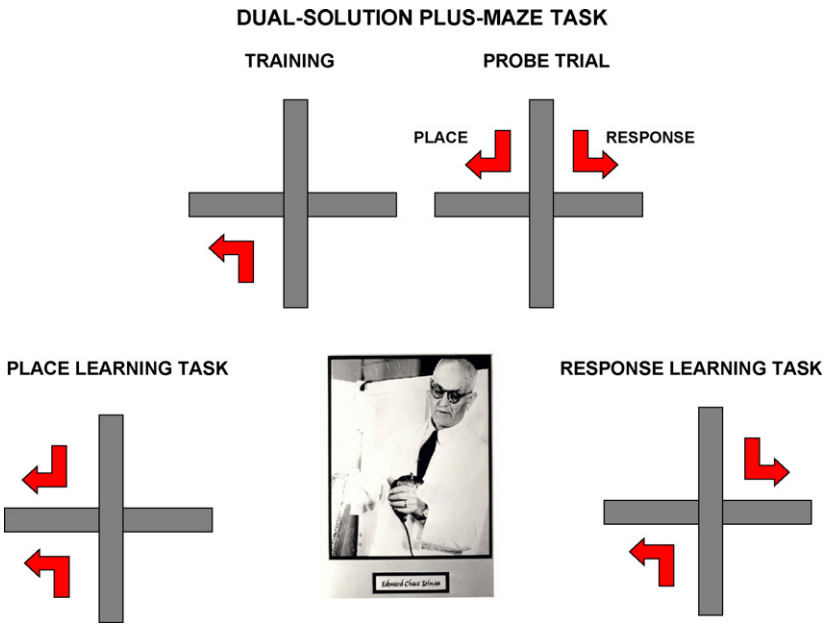

Fig. 1. Three variants of the plus-maze task introduced by Tolman (pictured) and colleagues for examining place and response learning. In the dual-solution task (top), rats are trained from the same start position (e.g. south) to approach the same goal box (e.g. west). Following training, the relative use of place and response learning is examined on a probe trial from the opposite (e.g. north) start point. In a single-solution place task (bottom left), rats are trained from varying start points (e.g. north, south) to approach the same goal box (e.g. west), and body turn responses (left, right) are equally reinforced. In a single solution response task (bottom right), rats are trained from varying start points (e.g. north, south) and reinforced for making the same body turn response (e.g. turn left).

Although cognitive and S–R learning theories can each adequately explain acquisition of this dual-solution plus maze task, a probe trial in which trained rats are started from the opposite start box (e.g. north) can be used to assess the type of learning acquired. Thus, rats with knowledge of the spatial location of the food should continue to approach the baited goal box on the probe trial (i.e. "place" learning), whereas rats that have learned a specific body turn should choose the opposite goal box on the probe trial (i.e. "response" learning). Whereas the dual-solution plus-maze task can be acquired using either place or response learning, *single-solution* versions of the task have also been designed that putatively require the use of only one of these two strategies (Fig. 1). In a single-solution place learning task rats are started from varying start points (e.g. north or south) and trained to approach the same goal location (e.g. west). In contrast, in a single-solution response learning task rats are started form varying start points (e.g. north or south) and same body turn response (e.g. turn left) is consistently reinforced.

The plus-maze task appeared to provide a stringent comparison of the relative merits of S–R habit and cognitive learning theories, and findings indicating that rats can readily employ place learning in the plus-maze were clearly problematic for S–R theory. However, studies conducted across numerous laboratories ultimately demonstrated that depending on experimental conditions and parameters, rats can in fact use place *and/or* response learning in the dual-solution plus-maze task. In an influential review intended to provide a resolution of the plus-maze debate, Restle proposed that the relative use of these two strategies largely reflected an influence of the discriminative properties of multiple maze cues on a single learning system, arguing that the place versus response learning debate was "*specious*" and "*incorrectly drawn*" [4]. However, although he accurately described experimental conditions that could favor the relative use of place or response learning, Restle's oft-cited conclusion that analysis of plus-maze behavior was irrelevant for providing insight into the question of "what" animals learn would be proven erroneous by subsequent brain research. This brief review describes experiments conducted in recent years across several laboratories that have utilized the plus-maze to investigate the role of the basal ganglia (specifically the dorsal striatum or caudate nucleus) in response learning in the plus-maze. Findings from plus-maze studies employing brain lesion, pharmacological, and genetic/molecular methodologies are described, and factors that influence the relative use of place and response learning are considered.

1. Multiple memory systems: the place and response learning debate revisited in the brain

The S–R learning theorist Clark L. Hull wrote that "Nearly all serious students of behavior like to believe that some day the major neurological laws will be known in a form adequate to constitute the foundation principles of a science of behavior" [5] (p. 19). However, S–R and cognitive learning theories were largely derived from observations of overt behavior in brain-intact animals, in the absence of any direct manipulations of the nervous system. Subsequent investigation of the neuroanatomical basis of learning and memory in humans and lower animals gave rise to the hypothesis that the mammalian brain contains multiple memory systems. This hypothesis was originally based on observations of single dissociations in task performance that revealed a pattern of impaired and spared learning abilities in humans and lower animals following damage to the hippocampal system (for historical overviews see refs. [6,7]). Research employing double dissociation methodology provided further support for the existence of multiple memory systems, and indicated that the hippocampal system and components of the basal ganglia (for example the dorsal striatum and substantia nigra) are parts of independent memory systems that mediate cognitive and S–R habit learning, respectively (e.g. refs. [8,9]; for reviews see refs. [10,11]).

In view of the emphasis placed by early learning theorists on the question of "what" animals learn, it is not surprising that when psychological operating principles that distinguish multiple memory systems were proposed, the historic debate between cognitive and S–R learning theorists was extremely influential (e.g. refs.