

Spatial Behavior, Food Storing and the Modular Mind

Sara J. Shettleworth

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Behavior, together with the brain and cognitive processes that underlie it, is an evolved adaptation like eyes, teeth, wings, fins, and feathers. Questions about how behavior functions in the natural environment and how it evolved have long been prominent in ethology, but for much of its history the study of psychological mechanisms underlying behavior, including cognition, has been remarkably abiological (Plotkin 1997). Currently, however, scientists studying all aspects of animal mind and behavior are converging on an integrated approach in which interrelationships among ecology, brain, and behavior across a whole range of species are seen as key to understanding cognition, how it works, what it does for animals in nature, and how it evolved (examples are Balda, Pepperberg, and Kamil 1998; Dukas 1998; Hauser 1996; Shettleworth 1998). This essay briefly reviews aspects of one research program taking this approach, on spatial memory in birds that store food. To introduce this animal-centered, as opposed to anthropocentric (Shettleworth 1998; Staddon 1989), approach to cognition, I begin with a few remarks on the evolution and organization of spatial behavior.

Self-propelled travel is a fundamental feature of animal life. The oldest fossil evidence of behavior is the tracks and burrows of primitive bottom-dwelling organisms (Raff 1996, p. 87). Their movements may have been random and undirected, but eventually animals evolved senses for detecting distant objects and connections between sensation and movement that permitted them to approach or avoid things of importance for survival and reproduction. Even the simplest spatial orientation involves detection and recognition of some correlate of a goal, as when a male moth's antennal receptors detect a species-specific female pheromone and activate searching flight. Orientation toward places of refuge or reliable food sources specific to an individual's own environment may require learning and remembering responses to otherwise neutral cues so the animal can get there from a distance. It is a long way from primitive organisms wriggling and slithering through the mud to cognitive maps, which we come to in a moment. Such creatures and their simple behavior are mentioned to emphasize that as we navigate the gap of computational and neural complexity separating them from rats or human beings, we do not necessarily find a clear divide between the primitive and uninteresting, on the one hand, and the cognitively and computationally demanding, on the other. To develop a general comparative, evolutionary, approach to the mind, it is essential to abandon hard and fast distinctions between cognitive and other mind/brain processes that mediate between sensory input from the environment and behavior.

It is also essential to adopt a modular view of cognition as opposed to assuming some single entity such as learning ability, or intelligence that all species have more of less of. Modularity is a fundamental feature of biological structure (see Raff 1996, Chapter 10), the brain included (Barton and Harvey 2000). Cognitive scientists tend to speak of *modules*, if not always in precisely Fodor's (1983) sense, at least with reference to computationally distinct mechanisms (Coltheart 1999). Similarly, behavioral neuroscientists and neuropsychologists refer to *memory systems*, distinct areas of the brain that do distinct tasks or store distinct kinds of memories (Nadel 1992). And learning theorists speak of *adaptive specializations of learning* (Rozin and Kalat 1971), which have some of the same features as memory systems (Sherry and Schacter 1987) or modules (Gallistel 1999). The divisibility of brain and cognition into analytically distinct and somewhat independent subunits identified by all of these terms is well illustrated by spatial behavior (Shettleworth, in preparation).

Accurate spatial orientation can be accomplished by any of a variety of distinct mechanisms (Gallistel 1990; Shettleworth 1998). When intact animals find their way in the real world, more than one of them may be at work, and how such modules interact is an important topic of current research (Shettleworth, in preparation). An animal active during daylight can see