
16 Spatial Behavior, Food Storing, and the Modular Mind

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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 the 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 the 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 et al. 1998; Dukas 1998; Hauser 1996; Shettleworth 1998). This essay briefly reviews aspects of one research program taking this approach—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). 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 important 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 re-

membering 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 possess to some degree. 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 precisely in 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.

Accurate spatial orientation can be accomplished by any of a variety of distinct mecha-

nisms (Gallistel 1990; Shettleworth 1998). When intact animals find their way in the real world, more than one of these mechanisms may be at work, and the way in which such modules interact is an important topic of current research. An animal active during daylight can see the global visual panorama as well as landmarks like rocks and bushes near its nest, potential mates, or profitable food sources. Smells, sights, and sounds emanating directly from such places may serve as beacons, drawing the animal directly to them. The global geometry of visible space may be perceived and used independently of the features that make it up (Cheng 1986). Internal cues generated by an animal's own movement potentially allow it to keep track of where it is relative to a known starting point (dead reckoning or path integration; Biegler 2000). In well-traveled parts of its territory, stereotyped motor routines may carry it from place to place (Stamps 1995).

These different kinds of cues demand different implicit mental computations. For example, approaching a goal identified by a beacon is a simple hill-climbing process, whereas locating a place identified by one or more distal landmarks depends on a process like vector addition (Cheng 1989) or visual template matching (Cartwright and Collett 1987). Triggering and executing a stored motor routine is another thing again. Thus the various kinds of spatial information might be processed in dedicated mental modules, or memory systems (Gallistel 1990; Shettleworth 1998). Cognitive mapping (O'Keefe and Nadel 1978; Tolman 1948) refers to a unified allocentric (or earth-centered) representation of space that goes beyond, or perhaps integrates, the capacities of such separable orientation mechanisms to permit novel shortcuts between known locations. However, the term is often used more loosely to indicate, for instance, the use of configurations of distal cues as opposed to beacons (Pearce et al. 1998) or specific responses (Tolman 1948; see also Gallistel 1990). Moreover, once the subtle and sophisticated orientation possible with well-

specified spatial modules is taken into account, little, if any, evidence remains for cognitive mapping in the strict sense in any nonhuman species (Bennett 1996; Shettleworth 1998; but see Gould, chapter 6 in this volume).

Modularity in spatial cognition is delineated by testing animals in artificial environments that offer limited kinds of information. A comparison of species is another approach to defining cognitive modules. Just as there are species-characteristic adaptations of beaks, eyes, or feet, we might expect species-characteristic adaptations of specific aspects of behavior, brain, and cognition. The way in which studying such adaptations can help to illuminate the modular organization and evolution of cognitive processes is well illustrated by studies of natural history, brain, and memory in birds that store food. Here I emphasize work in my laboratory in which black-capped chickadees (*Poecile atricapillus*), birds that store food, were compared with nonstoring dark-eyed juncos (*Junco hyemalis*). Similar research on corvids is discussed by Balda and Kamil (chapter 17 in this volume). This research has been thoroughly reviewed elsewhere (Sherry and Duff 1996; Shettleworth 1995; Shettleworth and Hampton 1998); the focus here is on a series of experiments on memory for locations and colors and its connection with ideas about cognitive modularity.

As I write, the ground outside is deep in snow and the temperature has not risen above freezing for several weeks. The nights, when small passerine birds cannot forage, are 14 hours long. Yet black-capped chickadees spend the winter here in southern Ontario and throughout the higher latitudes of North America. The selective pressure is intense on a 10-g animal with high metabolism. A single day in which a bird does not accumulate enough energy to survive the frigid night is all it takes to eliminate all future breeding opportunities. However, the abundance of chickadees testifies to the fact that many of them do survive, and they do it with the aid of

adaptively specialized behavior, memory, and brain.

Black-capped chickadees, like most other chickadees and tits (Paridae), nuthatches (Sittidae), and many corvids (Balda and Kamil, chapter 17 in this volume), store food in scattered locations and later retrieve and consume it. Most early naturalists who saw birds storing food in the wild (e.g., Haftorn 1956) assumed that animals with such tiny brains could not remember the locations of all the individual items they stored. Rather, storing of food must function for the good of the group by moving seeds from locations that become inaccessible under snow to places like the undersides of branches, where any conspecific would encounter them during normal foraging. However, food storing can evolve under individual selection provided that the animals that invest time and energy in hoarding are more likely to retrieve their stores than lazy conspecifics that do not hoard but only pilfer the hoards of others (Andersson and Krebs 1978).

Nonmemory mechanisms such as idiosyncratic foraging site preferences could, and probably do, promote a bird's successful retrieval of its own stores. Nevertheless, the memory of individual hoarding sites clearly plays a role (Brodin 1994). This raises the question of whether, along with the specialized behaviors of storing and retrieving food, food-storing species have some sort of specialization of memory, say in accuracy, capacity, or durability. This is inherently a comparative question, ideally answered by comparing a number of food-storing species with species that store little or not at all, but are otherwise as similar as possible to the food storers in phylogeny and in perceptual or motivational factors that could affect their performance in tests of memory. Methodological nightmares await anyone seeking a clear answer to such a question (Kamil 1988; Shettleworth 1998; Shettleworth and Hampton 1998). It is clearly not enough to compare only two species, one that stores food and one that does not.

Nevertheless, that is the approach we have taken in my laboratory, but the comparative base has then been broadened by other researchers testing other species similarly.

If food-storing species have better memory in any sense than species that do not store, it is most likely spatial memory as opposed to memory for other features of the world, such as patterns and colors of objects. This is especially true of the Clark's nutcrackers and other very long-term storers described by Balda and Kamil (chapter 17 in this volume), but in a snowy climate, local appearances can change drastically in even a few hours. In a series of experiments begun by David Brodbeck (Brodbeck 1994; Brodbeck and Shettleworth 1995), we asked whether chickadees are more likely to remember or use spatial than nonspatial information on the location of food. So we could also test non-storing species, we devised a task that captures important features of food storing without requiring the birds to store food. Chickadees and juncos were allowed to return after a few minutes or hours to food that they had encountered briefly once before. The food was a peanut hidden in a brightly decorated block of wood on the wall of a large aviary. Four new feeders in four new locations were used on every trial. When the birds returned directly to the baited feeder on a high proportion of trials, they were tested to see what they remembered by swapping the formerly baited feeder with another one of the feeders on occasional unrewarded tests, thus dissociating location from pattern and color cues. Chickadees nearly always went first to the former location of the baited feeder, even though it was now occupied by a feeder that looked entirely different. In contrast, juncos chose about 50:50 between that feeder and the formerly baited feeder in its new location (Brodbeck 1994). Because there were four feeders to choose from and none of them had food in the tests, the birds continued to search after their first choice. Birds of both species were very likely to visit the

spatially correct feeder second if they had not visited it first, and vice versa.

Thus both chickadees and juncos seem to remember both location and color, but they differ in their relative weightings of these features. We obtained this same species difference in an operant delayed matching-to-sample task, in which the birds pecked at colored shapes on a computer touch screen (Brodbeck and Shettleworth 1995). Chickadees also remember location better than color when the features are presented separately, whereas juncos do not (Shettleworth and Westwood 2002). In an important test of the generality of these findings, Clayton and Krebs (1994) obtained similar results in parallel experiments with European species of tits, which are closely related to our black-capped chickadees, as well as two corvid species (but see Healy 1995). Similarly, although Clark's nutcrackers excel at operant spatial nonmatching-to-sample, they are no better than other corvids in operant tests of color memory (Olson et al. 1995; but see Gould-Beierle 2000).

Just as in mammals, in birds the hippocampus is important for spatial memory. Chickadees with hippocampal lesions still store food, but cannot remember where they put it (Sherry and Vaccarino 1989). Hippocampal lesions degrade the performance of both chickadees and juncos on spatial delayed matching-to-sample, but leave the same individuals' color matching unaffected (Hampton and Shettleworth 1996). Consistent with the idea that food storing involves the evolution of a modular cognitive capacity, in food-storing species of birds, the hippocampus is larger relative to body size and telencephalon volume (most of the rest of the brain) than in nonstoring species (Krebs et al. 1989; Sherry et al. 1989). These findings have stimulated studies of how the volume as well as the detailed structure of the hippocampus changes as food storing changes both seasonally (Smulders et al. 2000) and developmentally (Clayton 1995b). The hippocampal enlargement that occurs as chickadees

store more food during the autumn is accompanied by increased neurogenesis (see Smulders et al. 2000). Experience storing food and/or using spatial memory contributes to the development of the relatively enlarged hippocampus of food storers, but the effects of experience do not explain all of the species differences (Clayton 1995a). In terms of this essay's theme of modularity and cognitive evolution, these findings mean that the specialized behavior of storing food rather than eating it immediately, a species-specific behavioral module that appears prefunctionally, helps to shape the specialization of a part of the brain which, in turn, presumably plays a role in helping that behavior function adaptively by facilitating memory for the food's location. These discoveries in food-storing birds suggest that any animals with lifestyles that make extraordinary demands on spatial cognition should also have specializations of the hippocampus and spatial cognition (Sherry et al. 1992). This hypothesis has inspired studies of rodents and of several other species of birds, and most have produced results consistent with it. Included are studies in which males and females of the same species differ, perhaps only seasonally, in space use and concomitantly in hippocampal volume (see Sherry and Duff 1996).

The development of food storing deserves special attention in the context of some themes in this book. Food storing has been cited (Griffin 1984) as a behavior suggesting that animals have conscious foresight. In storing food that will be used later, chickadees certainly look as if they are behaving in a consciously planful manner. However, the way in which storing behavior develops and later can be modified, in parids at least, indicates that storing is better described as a hardwired behavior that the birds perform relatively independently of current need and anticipation of future consequences. Fledglings begin storing avidly at around 40 days of age, even when they have ample food and efforts are made to deprive them of storable items and suitable

substrates (see Clayton 1995b). The items chosen and the expertise with which they are inserted into suitable sites change with experience, as does the selection of sites by adults (Hampton and Sherry 1994). However, parids store food even under circumstances where they seem unlikely to be anticipating retrieving it. For instance, in our laboratory some birds persist indefinitely in storing peanuts in places where they drop out of reach. These observations do not necessarily rule out conscious planning. However, they do make it clear that the cognitive and brain mechanisms underlying a fascinating natural behavior like storing and retrieving can be studied while remaining at best agnostic about the nature of the animals' possible awareness. The study of food storing and indeed the broader study of animal spatial cognition is but one example of how studying the mechanisms by which animals behave adaptively in their worlds illuminates general questions about the evolution of mind.

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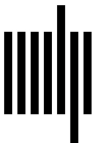
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