

## 2 The Role of Social Selection in the Evolution of Hippocampal Specialization

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### How Do Memory Specializations Evolve?

An important question facing both evolutionary biology and cognitive neuroscience is how the evolution of behavior might be constrained or, possibly, accelerated by innovations or limits to a species' memory capacity. Understanding how this memory capacity evolves may lead to a better understanding of how memory is (or is not) organized into specialized, dissociable memory systems (Sherry and Schacter 1987; Moscovitch et al. 2006). In the case of episodic memory, both its characteristics in humans and its scope and distribution in nonhumans remain a source of controversy (Hampton and Schwartz 2004). This remains the case even several decades after the term was first introduced by Tulving (1984) to characterize what appeared to be a unique ability of humans to recall an event from their personal past. Yet recalling events from the past is an attribute found widely in animals, both invertebrate and vertebrate. Even recalling information that is linked to a specific time and place has been described in insects, mammals, and birds (Gallistel 1990; Shettleworth 1998; Collett and Collett 2002). The knowledge of an event in the past also appears to be a common ability found in animals that store food. In species such as the common raven (*Corvus corax*) or the western scrub jay (*Aphelocoma californica*), individuals remember the association of a social event with a certain individual, such as being observed while caching (Bugnyar and Heinrich, 2006; Clayton et al. 2007). Individual scrub jays also use the time elapsed since caching to make economic decisions about cache retrieval, such as the decision to forgo a favorite but perishable food after long delays. The birds' ability to recall the location of each food type was a strong argument for the existence of an episodic-like memory in nonhumans (Clayton et al. 2001). Recent studies have demonstrated that nonhuman species peer not only into the past but also into the future. Two species of great ape, bonobos (*Pan paniscus*) and orangutans (*Pongo pygmaeus*), presciently took tools to bed that they needed not in the present but would need on the next day (Mulcahy and Call 2006). Western scrub jays, learning that their morning will be spent in a room without food, cache food in that room the day before (Raby et al. 2007).

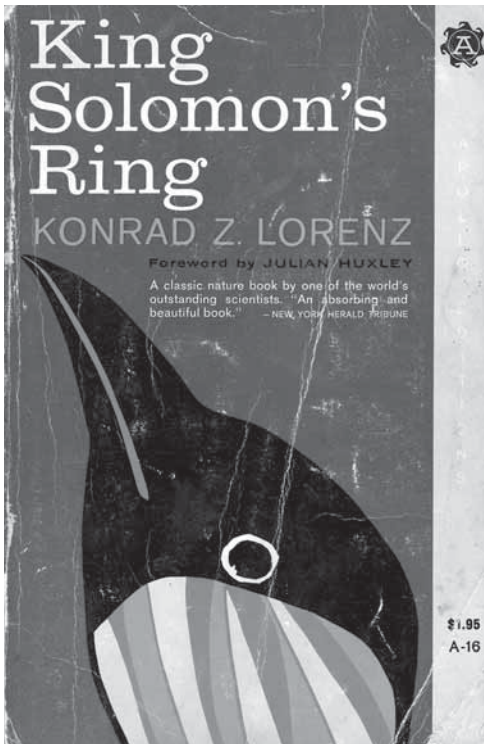
None of the above examples supply proof of autoevidence, however, in light of Tulving's requirement that episodic memory also is a recollection of the self having had the experience. Self-awareness in nonhuman (and nonverbal) individuals has always been problematic (Griffin 1981), despite demonstrations of behaviors such as mirror-guided self-exploration (De Haan and van den Bos 1999) and, more recently, a demonstrated awareness of knowing (metacognition), both in the laboratory rhesus monkey (*Macaca mulatta*; see Hampton 2001) and the laboratory rat (*Rattus norvegicus*; see Foote and Crystal 2007). These results challenge our understanding of what self-awareness might look like in another species.

In the meantime, however, among us humans self-awareness is not only obvious but necessary for the whole concept of episodic memory. I give the following as an example of a typical episodic memory in humans, where the memory not only yields images of linked scenes located in time and space but also becomes incorporated into a sense of self as a "story with a moral," a causal explanation for an individual's later behavior (Campbell 1994).

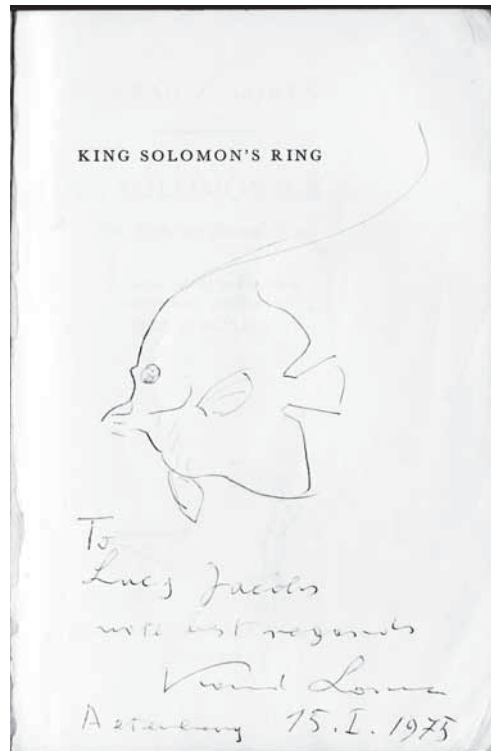
### Meeting Konrad Lorenz

On the afternoon of January 15, 1975, I stood in a room in an elegant villa in the village of Altenberg, Austria, not far from Vienna. Three decades later, in this very villa, we would hold the workshop that eventually resulted in the present book. In 1975 it was still Konrad Lorenz's study and I was a college freshman, home for Christmas. I had just returned from my first semester at Cornell, battered by the twin onslaughts of attending college in a foreign country and taking premed biology, after spending four years as a student at a tiny international school in Vienna. Perhaps this is why I had finally found the nerve to contact Lorenz, a Nobel laureate, as some kind of confirmation that I was on the right path—a path that his classic work, *King Solomon's Ring* (Lorenz 1952), had set me on when I was fourteen. I clutched my family's battered paperback copy of this book, which he had written to support his research after his return from a Soviet prisoner-of-war camp in 1948 (Lorenz 1996). I had telephoned the home of Professor Lorenz and his wife answered. I must have asked in German whether I could visit. She asked me whether a particular Thursday would be convenient for me. For a college freshman who had yet to meet a full professor at her own university, to be asked by the wife of a god if a Thursday was convenient made it already a memorable occasion. Even more remarkable was the atmosphere of collegiality and respect with which I was greeted upon my arrival at the Lorenz home—I was treated as a serious, if somewhat less experienced, colleague. I remember being taken to the greenhouse. Now the home for studies of cognition in captive marmosets at the Konrad Lorenz Institute for Evolution and Cognition Research, at that time it housed numerous aquaria filled with tropical fish. I remember feeling like a sparrow meeting a famous cobra, as I attempted to formulate intelligent sentences about animal behavior. I remember his fierceness, his enthusiasm, his dramatic white beard. I remember

a)



b)

**Figure 2.1**

(a) Cover of *King Solomon's Ring* (Lorenz 1952) (b) Lorenz's autograph on the title page.

his speaking wistfully of the aquaria he had yet to build. Finally, I asked whether he would autograph the all-important beat-up paperback I had brought with me; he not only signed and dated it but added a brilliant illustration of an angelfish (see figures 2.1a and 2.1b). Later, I remember worrying that he had mistaken me for the daughter of a rich American who might be able to help his research, and not simply the humble fanatic that I was.

The next time I stood in his office, it was on the morning of June 16, 2006, and I was presenting my thoughts on the evolution of spatial and episodic memory.

### The Birth of Ethology

How do we translate rich experiences, many of which may be tied up with human language, to the mind of another species? One answer, from Lorenz among others, was to understand, first, how minds evolve (Lorenz 1952). In the summer of 1937, at the Altenberg property, Konrad Lorenz and Niko Tinbergen dug ponds to study the development of behavior in the greylag goose (*Anser anser*). The two scientists had met a year earlier

at a conference where they found themselves in enthusiastic agreement that behavior is constructed not just from malleable mortar—nurture—but also from the hard bricks of innate programs that they eventually would call releasers, fixed-action patterns, and innate releasing mechanisms. These species-specific bricks could be recognized, embedded in their mortar, not unlike fossilized bones embedded in geological layers. In the process Lorenz and Tinbergen also established the discipline of ethology, which they defined as the biological study of behavior (Lorenz and Tinbergen 1938). To dissect behavior they focused on behaviors with many such bricks: egg management by a brooding goose, conflict signals in the herring gull, courtship signals in the duck family Anatidae—all of these could be deconstructed into their sign stimuli and fixed-action patterns. The two pond-digging theorists also studied the mortar that held the bricks of such actions together—all the data that had to be learned for a greylag's survival, such as the recognition of nest or chick. Thus, Lorenz's studies of imprinting in the greylag geese that inhabited the ponds along with Tinbergen's study of spatial memory and orientation in the wasp known as the bee wolf (*Philanthus triangulum*; see Tinbergen 1972) together laid a foundation for the study of the ecology of animal cognition. This frame remained empty, however, not only for the duration of the war that engulfed and separated them but for many decades thereafter. Moreover, it was a mental outlook incompatible with radical behaviorism. Fortunately, scientific paradigms wax and wane, and the insights on animal cognition voiced by Lorenz, Tinbergen, von Frisch, Tolman, and others finally began to reemerge and gain traction in the late twentieth century (Zentall 1984; Wasserman 1997).

### **Cognitive Psychology—or Cognitive Biology?**

Consequently it felt appropriate that the workshop where we struggled to come up with a new term for what we were discussing took place in the historic Lorenz villa. I call what I do “cognitive biology.” The term subtly rearranges our assumptions as psychologists, effecting a quasi-Copernican reformulation. If cognitive biology is the goal, then the fundamental organizing principle is not cognition of the human species (as psychology is generally assumed to be) but cognition itself, regardless of species. The objects of study are not cognitive processes in humans but cognitive processes generally in the animal kingdom (the question of possible cognition in nonanimal kingdoms is one that perhaps can be raised in future conferences; see Trewavas 2005).

Let us return to episodic memory as an example of a phenomenon of cognition. It appears to be such an efficient way to organize recall that it would be puzzling if it were to be limited to our own species. Perhaps variants—without auto-noesis, for example—are found in other species. An important structure in the mediation of episodic memory is the hippocampus (Burgess et al. 2002; see also chapter 4, this volume). Because this physiological structure has homologues in all vertebrates and is highly developed in birds and nonhuman mammals, it would be particularly intriguing to discover whether episodic-like

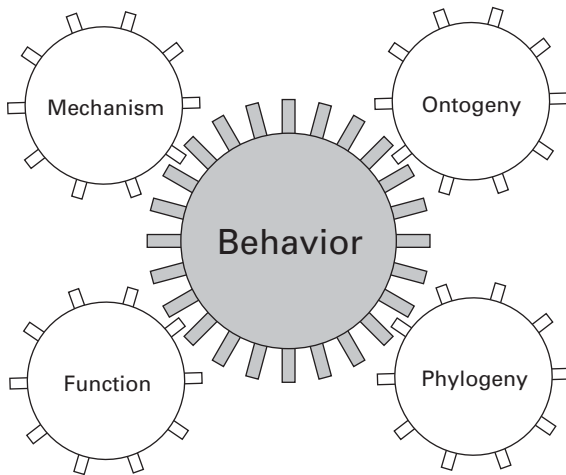
memory occurs in such groups. At least one ancestral function of this structure, mapping allocentric space, appears to be highly conserved in vertebrates (Rodriguez et al. 2002; Jacobs and Schenk 2003).

So it is valid to ask how these two cognitive traits, spatial navigation and autothetic memory for a location in space and time, are related. As with any biological trait, the evolution of a cognitive ability must proceed through stages that are each adapted to the current environment. It is reasonable to assume that vertebrates first learned to represent the world around them and only later used the hippocampus to compute abstract relations among objects. In this case the concrete functions of the hippocampus, such as allocentric navigation, preceded the evolution of abstract functions, such as episodic encoding. This is simply the more parsimonious explanation based on principles of brain evolution (Butler and Hodos 1996; Striedter 2005), although some argue that hippocampal abstract functions are ancestral to spatial functions (Eichenbaum et al. 2007). This question will no doubt be answered with future research, especially given the rapid pace of research in the field of comparative cognition (Bugnyar and Heinrich 2005; Csanyi 2005; Clayton et al. 2007; Tomasello and Carpenter 2007).

How shall we best study whether our nonhuman, nonverbal subjects manipulate representations of past and future time, such as in a recall of episodic memories? We could do worse than start with Tinbergen's exhortation to ethology. Building on the three fundamental levels of analysis proposed by Eric von Holst—phylogeny, function, and mechanism—Tinbergen demanded of himself and his fellow ethologists that they also understand the development of a behavior (Tinbergen 1963), a framework that has been described as the four “legs” of ethology.

In fact, though, a better metaphor might be the interacting gears of a clockwork mechanism, in which levels of analysis are geared together with feedback mechanisms (see figure 2.2). For example, phylogenetic constraints dictate the range of a physiological mechanism, the actions of other species dictate the size of a species's ecological niche, etc. In reality, therefore, any movement of one gear impedes or accelerates the movement of its neighbors—such is the dynamic interdependence of development, physiological mechanism, ecological function, and evolutionary history.

Take the question of human episodic memory as an example. If unique to humans, the answer could lie in phylogeny—there was a unique event—a novel mutation—in the hominin clade. This argument could be supported, as there is increasing evidence for novel alleles in our recent history (Pollard et al. 2006). Or the larger force could come from ontogeny: our peculiar, extended development and verbal language is necessary to support the development of this mental representation. There is also evidence for this point of view: the acceleration of episodic memory with language acquisition (de Haan et al. 2006). Or the best answer could be that it is simply the function, or adaptive value, in our species' cognitive niche that sustains and allows it. Other species have the potential for its development but they face less attractive cost/benefit ratios (being shorter-lived or working in less



**Figure 2.2**  
Schematic representation of Niko Tinbergen's four questions (Tinbergen 1963).

cooperative groups) for the use of such memory. Finally, the question might lie in mechanism: the computations require a certain circuitry of brain structures found only in the most recent hominin apes, i.e., our own species.

As the metaphor of interacting gears implies, the answer must always be all of the above. A hypothetical example would be the following: hominins, with their efficient cooperative hunting of high-protein food sources, were able to support the extended development required by this mental representation and subsequently required this mental representation to survive as an individual in our intensely competitive species. Thus, one gear, the ecological function of cooperative hunting, could have pushed another, brain size, which then pushed the length of development, allowing new ecological niches to be opened and exploited.

Another value of the geared-mechanism metaphor is that it identifies not only the all-important interdependence of levels but also sets up the important question: What first causes a certain gear to start to rotate more quickly than its fellows? The answer to this must ultimately come from understanding the interaction of development and evolution—how development is limited by evolutionary constraints and how developmental plasticity can be the engine for evolutionary acceleration (West-Eberhard 2003). The goal for the rest of this chapter is to answer the following question: Can we identify a gear whose acceleration could have led to episodic memory? And if so, can this help us analyze and predict its existence in other species? Because of the landmark work of Milner and colleagues (1998) and O'Keefe and Nadel (1978), we have a very good idea that the hippocampus plays a large role in spatial and episodic memory in humans (Burgess et al. 2002; see also chapter 4, this volume). What common function of the hippocampus can

be found across vertebrates and what selective pressures might have led to the evolution of autozoetic memory for locations in space and time in our own species?

### The Ecology of the Hippocampus

The phylogeny of the hippocampus, an ancient, conserved structure in vertebrates, is one of the best-documented cases of brain evolution (Striedter 2005). We can therefore proceed immediately to the current literature on functional patterns of spatial learning and its relation to the hippocampus or other medial pallium homologues. This literature now includes striking patterns of sex, season, species and/or population differences in birds, mammals, reptiles, and fish (see table 2.1), as well as strain differences within domesticated birds and mammals. Add to this the voluminous literature on the physiology of spatial cognition in laboratory-domesticated pigeons, rats, and mice, and we cognitive biologists should be grateful to have such a rich literature to ponder.

Instead of this pleasure, however, what we often feel is confusion. The studies and the field—whether you call it cognitive biology, neuroecology (Hampton et al. 2002), or evolutionary neuroscience (Striedter 2005)—is relatively new. Its adaptationist approach, with theory perhaps a nose ahead of the data, recently provoked fairly bitter attacks by skeptics (Macphail and Bolhuis 2001), engendering quick replies from those attacked (Hampton et al. 2002). This has had the healthy result of clarifying many issues, even the swapping of raw data for new analyses that have confirmed the original proposition that hippocampal size is related to spatial behavior (Lucas et al. 2004). For example, the greater variation of food-storing behaviors in Eurasian parids and corvids may be one reason for the stronger correlations between scatter hoarding and hippocampal size on that continent, compared to that of the more closely related birds studied so far in North America; however, there are also effects that cannot yet be explained by food hoarding (Garamszegi and Lucas 2005).

The patterns that have been documented are based on the assumption that the hippocampus “does” spatial learning. The results from studies summarized in table 2.1 imply that there are two ways to make your hippocampus bigger and better: storing food in scattered locations or searching for mates (Sherry et al. 1992). We cognitive biologists have long argued that the nature of selection on hippocampal size and function has therefore been one of two types: natural selection leading to differences among species or sexual selection leading to differences between the sexes within a species (Jacobs 1995, 1996a, 1996b, 2000). This is not inconsistent with what we know of brain evolution, for example, the models of concerted evolution of Finlay and Darlington (Finlay and Darlington 1995). In concerted evolution, developmental constraints strictly limit the degree to which an individual brain structure can be shaped by selection independent of other brain structures, as most changes in brain structures appear to occur in concert. In contrast, mosaic selection is the process by which an individual brain structure is independently selected for increased

**Table 2.1**

Studies of spatial cognition and correlations with hippocampus and medial pallium homologue structures among vertebrates

Taxonomic group	Spatial memory	Activity that brain structure is related to		
		Mating system	Foraging mode	Habitat use, including seasonal changes
<b>Fish</b>				
Cichlid: multiple-species study		Pollen et al. 2007		Pollen et al. 2007
Goldfish: single-species study	Rodriguez et al. 2002 <sup>b</sup>			
<b>Reptiles</b>				
Lizards: multiple-species study	Day et al. 2001 <sup>b</sup>		Day et al. 2001 <sup>b</sup>	
Snake: single-species study	Holtzman et al. 1999			
Turtle: single-species study	Rodriguez et al. 2002 <sup>b</sup>			
<b>Mammals</b>				
Microchiropteran bats: multiple-species study			Safi and Dechmann 2005; Ratcliffe et al. 2006	Yaskin 1984 <sup>a</sup> Safi and Dechmann 2005; Ratcliffe et al. 2006
Bats: single-species study	Winter and Stich 2005	Ulanovsky and Moss 2007		
Voles and mice: multiple-species study	Gaulin and FitzGerald 1986; Galea et al. 1996	Jacobs et al. 1990 <sup>a</sup>		Pleskacheva et al. 2000 <sup>a</sup>
Voles and mice: single-species study	Galea et al. 1994 <sup>a</sup>			Galea and McEwen 1999; Ormerod and Galea 2001
Sciuridae: multiple species			Barker et al. 2005 <sup>a</sup>	
Sciuridae: single-species study	Jacobs and Liman 1991; Vander Wall 1991; Macdonald 1997; Jacobs and Shiflett 1999; Devenport et al. 2000; Vlasak 2006a, 2006b; Gibbs et al. 2007 <sup>a</sup>			Lavenex et al. 2000a, 2000b <sup>a</sup>
Heteromyidae (kangaroo rats and pocket mice): multiple-species study	Daly et al. 1992; Leaver and Daly 2001; Preston and Jacobs 2005; Barkley and Jacobs 2007 <sup>a</sup>	Jacobs and Spencer 1994 <sup>a</sup>	Jacobs and Spencer 1994 <sup>a</sup>	



Table 2.1 (continued)

Taxonomic group	Spatial memory	Activity that brain structure is related to		
		Mating system	Foraging mode	Habitat use, including seasonal changes
Kangaroo rats: single-species study	Jacobs 1992b; Langley 1994; Barkley and Jacobs 1998; Preston and Jacobs 2001			
<b>Birds</b>			Healy and Hurly 2004	
Nonpasserines: single-species study	Bingman et al. 2003 <sup>b</sup>			Volman et al. 1999; Abbott et al. 1999 <sup>a</sup>
Passerines: multiple-species study	Brodbeck 1994		Hampton and Shettleworth 1996 <sup>b</sup> ; Lucas et al. 2004 <sup>a</sup>	Lucas et al. 2004 <sup>a</sup>
Cowbirds: single- and multiple-species studies		Sherry et al. 1993; Reboreda et al. 1996 <sup>a</sup>		Clayton et al. 1997 <sup>a</sup>
Corvids: multiple-species studies	Clayton and Krebs 1994; Balda and Kamil 1989			
Corvids: single-species studies	Bugnyar and Heinrich 2006; Clayton et al. 2007		de Kort and Clayton 2006	
Paridae: multiple-species studies	Biegler et al. 2001	Healy and Hurly 2004		
Paridae: single-species studies	Sherry et al. 1981; Sherry 1984; Herz et al. 1994	Petersen and Sherry 1996	Sherry et al. 1989; Smulders et al. 1995; Shiflett et al. 2002 <sup>a</sup>	Pravosudov and Clayton 2002 <sup>a</sup>

<sup>a</sup>Free-ranging subjects<sup>b</sup>Lesion study

size or function (Striedter 2005). However, as Striedter has discussed, the scale of species differences in hippocampal size falls well under the ratios that concerted processes must be operating, namely, less than a factor of 2 or 3 (Striedter 2005, p. 149). Therefore, if we can assume that the patterns summarized in table 2.1 characterize typical species differences in vertebrates, then such medial pallium homologues could have arisen through mosaic selection, or at least through mosaic selection that is no doubt still influenced by concerted selection processes and could thus properly be called partial mosaic selection (Striedter 2005).

The next question is how this form of selection is driven by natural and sexual selection. I would like to introduce a third candidate into this discussion, one that has not been previously considered. This is social selection, an evolutionary process that is neither natural nor sexual selection but one that encompasses sexual selection and is distinct from natural selection (West-Eberhard 2003). In the next section I shall describe how adding social selection to the discussion of hippocampal evolution might help us understand its role not only in nonhuman cognition but also in human episodic memory.

### **Social Selection as an Evolutionary Force**

In 1983, Mary Jane West-Eberhard formulated an important theory of evolutionary change: the concept of selection through social competition, or social selection (West-Eberhard 1983). Although Darwin had articulated the effects of social competition in the development of sexual selection, West-Eberhard expanded this to include all social competition, not just the intraspecific competition for reproductive partners, but all aspects of morphology and behavior driven by competition within a species. This landmark hypothesis continues to gain support as a model of the selective pressures unique to social interactions and has recently been reformulated in a book-length treatment (West-Eberhard 2003). West-Eberhard's theory should not be confused with Roughgarden's recent theory of social interaction, also called social selection (Roughgarden et al. 2006); the present discussion is in reference to the West-Eberhard concept.

Social selection is selection arising from competition within a species. An important implication of this definition is that sexual selection is part of social selection, and both are differentiated from natural selection. As West-Eberhard (1983) explains, "Seen in this broader perspective, sexual selection refers to the subset of social competition in which the resource at stake is mates. And social selection is differential reproductive success (ultimately, differential gene replication) due to differential success in social competition, whatever the resource at stake" (p. 158).

West-Eberhard identifies three critical characteristics of social selection: first, that social selection pressures differ from natural selection by having virtually no stasis. Competition within a species becomes a continual arms race, where the opponent can move competition into a new arena or to new levels, by introducing a new behavior or structure. The exaggeration of characters used in such competition is finally brought to a stop only by the cost of their production or use.

By contrast, change in ordinary or ecological characters—those responding to unchanging aspects of the physical environment, or organic aspects either not evolving or evolving very slowly in response to the adaptations in question—can approach a ceiling of perfection (optimum). Divergence in such characters in closely related species is therefore expected to be more limited than divergence in social traits (West-Eberhard 1983).

Second, social selection is constant. Because the trait exists in a species where there are always conspecifics attempting to solve the same problem in the same way, the pressure to improve in competition is unceasing. A response to a change in predation tactics or food distribution can be constructed and then an advantage can be enjoyed. But within a population, with genetic and cultural transmission, there is no such lag between competitors. As stated by West-Eberhard (1983), “Under intraspecific social competition every reproducing individual of every generation is involved in the same increasingly specialized unending contest” (p. 159). The implication of this is that greater evolutionary change is expected in species with greater social selection.

Third, there is the “accelerating effect of novelty” (West-Eberhard 1983). Successful competition within a species, to best one’s conspecifics by means of overt or covert actions of song, deed, or wit often depends on the novelty of the production. For example, a new fighting maneuver, a new shortcut, or a new song—all of these behaviors depend on cognitive processes that will affect the outcome of social competition.

### **Social Selection and Social Intelligence**

Despite the importance of these ideas for evolutionary biology, the connection has yet to be made between West-Eberhard’s social selection and the rapidly emerging data sets and models for the evolution of social intelligence. Recent data and quantitative methods to test these ideas rigorously has led to an explosion of new results. Brain size has long been known to correlate with social factors, such as group size in primates (Harvey and Krebs 1990). More recently it has been shown that larger-brained bird species are more likely to use novel foraging techniques (Sol et al. 2005b), live longer (Sol et al. 2007), and be more successful at surviving in the new habitats that they occupy as invasive species (Sol et al. 2005a). Primate species with larger brains are more likely to show greater innovation, tool use, and, interestingly, social learning (Reader and Laland 2002). The dominant interpretation of these patterns has typically been that of Machiavellian intelligence, namely, it is necessary to have greater processing capacity (a larger brain) to keep track of and manipulate a quickly shifting social scene (Byrne and Whiten 1988). In their analysis, however, Reader and Laland offer an alternative view to the impact of social intelligence, asserting that the data suggest asocial innovation and social interaction cannot be distinguished as engines for change in brain size.

### **Social Selection and Hippocampal Evolution**

In her original postulation, West-Eberhard used the example of signal evolution to illustrate the concept of social selection. Yet if we think of the hippocampus or spatial learning simply as a biological trait that has evolved, perhaps into quasi-independent modules

(Jacobs and Schenk 2003), then we can ask what the utility of this theory is to its evolution. In her 2003 book on development, plasticity, and evolution, West-Eberhard extends this further, to the question of all interactions of plasticity and how these are shaped by all evolutionary forces, including social selection, natural selection and even genetic drift. She also addresses the question of learning, but as a biologist, not a cognitive biologist; for example, she limited the 1983 discussion to “animals that can learn,” even if it now seems clear that all animals indeed can learn (Shettleworth 1998). In the 2003 book, learning is still discussed in circumscribed terms; there is no mention of spatial learning in this (otherwise masterful!) book of 800-plus pages.

Yet there is an obvious relationship between sexually selected signals, such as birdsong, and spatial learning in the context of mate competition. Both modes of competition can be used to build predictive theories of sexual dimorphism in mammalian and other vertebrate brains (Jacobs 1996b).

What this leaves us with is a powerful theory of evolutionary change—social selection—that explicitly addresses the evolution of plastic behaviors (e.g., learning), yet is currently unsophisticated about evolutionary neuroscience (Striedter 2005) or cognitive biology. Yet the theory of social selection may be the key to the question of hippocampal function and its evolution. Currently, there are at least three different patterns emerging from the comparative literature on the hippocampus and its homologues (table 2.1). These are: differences between females and males within a species; seasonal shifts in such sex differences, and, finally, species differences, as a result of either the mating system, the foraging mode, or habitat use. In the following sections, I shall discuss how these might relate to West-Eberhard’s framework of social selection.

### **Mating Systems and Social Competition**

Social selection encompasses sexual selection as competition arising within a sex for access to sexual partners and successful reproductive encounters with sexual partners. Steve Gaulin first linked a century of documented sexual dimorphisms in spatial learning in the lab rat with the mechanism and function of sexual selection and mate competition (Gaulin and FitzGerald 1986). His work on voles was the first to predict the link between mating system and spatial cognition, present in scramble polygynous species (where roaming males physically contest each other for access to a female) and absent in monogamous species, where the sexes defend a joint territory. We later made the link between mating system and the relative volume of the hippocampus in voles (Jacobs et al. 1990); this was inspired by David Sherry’s discoveries of hippocampal size differences in birds, with variations connected to both food-storing habits (Krebs et al. 1989; Sherry et al. 1989) and to sex differences in eastern cowbirds (*Molothrus ater*; Sherry et al. 1993). In both examples, the direction of the dimorphism could be predicted by sex-specific behavior—the relatively larger hippocampus was found in the sex where successful competition required superior spatial orientation. In the polygamous meadow vole, it was the

males who had to relocate receptive females, while in the nest-parasitic cowbird, it was the females who had to relocate available host nests.

Even more convincing evidence of this functional link between hippocampal structure and social competition was the striking seasonal patterns of sex differences in both birds and mammals (Jacobs 1996b). Hippocampal and forebrain structures change with season in the eastern cowbird (Clayton et al. 1997), the meadow vole (*Microtus pennsylvanicus*) (Galea and McEwen 1999), the eastern gray squirrel (*Sciurus carolinensis*) (Lavenex et al. 2000a, 2000b), and many species of small mammals, such as shrews and voles (Yaskin 1984). Seasonal sex differences in spatial learning have also been demonstrated in deer mice and voles (Galea et al. 1996; Galea and McEwen 1999). Thus the social competition for mating opportunities, either the nests of a host bird species or a receptive female, can be seen to correlate directly with spatial ability and hippocampal structure.

Finally, some new results that are still being understood are interesting correlations between brain structures and mating systems in East African cichlid fish. The explosive speciation of these fish has been described as a natural laboratory of evolution (Pollen et al. 2007). The connection of changes in brain size to changes in mating systems in this highly complex and interesting group is clearly an area for future work.

The wealth of such patterns, however, could be the result of a sex-by-species predisposition for greater function or it could be the outcome of a life-long exercise of sex-specific spatial behaviors, in other words, the result and not the cause. Such sexual dimorphisms, however, have been documented in domesticated laboratory animals, with much less scope for sex-specific behaviors, long before these patterns were found in free-ranging animals. Second, if it were true that the hippocampus is monomorphic in females and males and it is only experience that induces sex differences, then it is still significant and important that social competition is capable of molding intraspecific variation. In this case, the capacity for such molding—the plasticity of the structure—is as much a trait under selection as the behavioral output. Indeed, the question of selection for “evolvability” has been an important new issue in the field of evolutionary developmental biology (West-Eberhard 2003). It could be the capacity for such molding and not what is learned that is under selection. The evolution of such plasticity has as much or more implications for cognitive evolution as a preprogrammed response to steroid hormones. Given the seasonal plasticity and the long evolutionary history of sex differences in vertebrates, it will probably turn out to be a combination of both. Referring once again to figure 2.2, the developmental and functional gears may be larger than those of the mechanism for plasticity or the phylogenetic constraints.

### **Scatter Hoarding as Social Competition**

Of course the same argument applies equally to patterns of hippocampus development that vary with foraging mode, particularly with food storing. The idea that the hippocampus could vary in nature according to spatial behavior was first suggested in comparisons of

scatter-hoarding bird species, described above. Here, too, the link between structure and function is one of interacting gears. Marsh tits (*Parus palustris*), a small scatter-hoarding passerine bird, have a relatively larger hippocampus than blue tits (*Parus caeruleus*), which scatter-hoard less. However, this is seen only when marsh tits are given access to the right combination of photoperiod and caching experience (Healy et al. 1994; Clayton 1995).

Sex differences clearly arise from social selection within a species. But food storing can also be seen as a competitive game (Andersson and Krebs 1978) and the social competition that arises with scatter hoarding could also be driving specializations in tracking items in space and time.

Any species that extracts food from a limited resource must negotiate with its fellows—a flock of sparrows jostling for crumbs is everyday evidence of this. Yet within food-storing strategies, scatter hoarding is an innately social competition. This relation of food storing to social competition may seem counterintuitive because at first glance, most scatter hoarders are either solitary or they store food in isolation. Yet no squirrel is an island: early experiments on the use of spatial memory in cache retrieval in mammals were specifically designed to simulate social competition. Mammalian scatter hoarders have a keen sense of smell and flexibly use odor or memory to retrieve caches, depending on environmental conditions (Vander Wall 2000).

In a typical experiment on scatter-hoarding mammals, gray squirrels cached nuts in a common arena. After a delay of several days the squirrel was faced with a social-competitive test: its ten caches were surrounded by ten other caches, nuts placed in sites chosen by seven competitors in the preceding week. A hungry squirrel responded by retrieving and eating more nuts from sites it had created than from the caches of its competitor (Jacobs and Liman 1991).

A study of Merriam's kangaroo rats (*Dipodomys*; Jacobs 1992b) also used social competition as an assay for the adaptive value of memory in cache retrieval. The cache distributions from a single individual were placed in the arena for solitary naïve competitors. Despite the small size of the arena (1 × 2 m) and plenty of time for the hungry pilferers to find the caches, their success rate was on average 30 percent less than that of the original owner (Jacobs 1992b).

Unlike birds, mammalian scatter hoarders can also identify the pilferer by the unique odor that the individual leaves behind in the form of scent marks, urine, and feces. Merriam's kangaroo rats, however, did not change their caching strategy or their behavior in the presence of this evidence that a conspecific had been present. But when these signs were accompanied by the sudden loss or redistribution of caches, kangaroo rats showed an increase in anxiety behaviors and a significant shift in foraging strategy (Preston and Jacobs 2001). A similar pattern was seen when the competitor was a heterospecific kangaroo rat species that co-occurs with the Merriam's, the Great Basin kangaroo rat (*Dipodomys microps*; see Preston and Jacobs 2005). These results nicely confirm Stephen Jenkin's

prior work demonstrating population differences in cache distribution by kangaroo rats in the lab, with individuals from high-competition areas showing more distributed caches (Jenkins and Breck 1998). Such population differences in behavior have been found to predict patterns of caching behavior, memory, and hippocampal size in the black-capped chickadee (*Poecile atricapilla*) (Pravosudov and Clayton 2002).

It is important to try to disentangle the roles of natural and social selection in such guilds of competitive species, such as those of desert heteromyid rodents or passerine food-storing birds, where pilferage occurs both between and within species (Daly et al. 1992). The occurrence of pilferage and how caching can be maintained in the face of such pilferage is still not completely understood. Vander Wall and Jenkins have recently proposed a new model of scatter hoarding based on the idea of reciprocal pilfering (Vander Wall and Jenkins 2003). But social competition is present in all aspects of scatter-hoarding decisions, not simply cache maintenance but cache creation as well. After all, the goal of scatter hoarding is to compete with others over food items from a source that cannot be monopolized or defended (Jacobs 1995). All else being equal, it takes less time to hoard a large food item than to eat it. So when time—as at a rich but undefendable food source—is short, a scatter hoarder is able to “seclude” many more food items per unit time than it can consume, putting them in locations that it alone can relocate economically (Jacobs 1992a).

Scatter hoarding, then, is not simply about space—what was put where—but also reflects the difference between a foraging strategy that is socially mediated and one that is solitary. This could be the link between scatter hoarding and episodic memory. The ability of common ravens or western scrub jays to recall who was watching as they cached will not help them remember their cache locations—neither of these species encodes large numbers of caches. Obviously the importance of who was watching is a question of social competition: how to avoid the group member’s later making off with the cache. Thus, among corvids, species that live in permanent competitive groups, such as piñon and Mexican jays (*Gymnorhinus cyanocephalus* and *Aphelocoma ultramarina*), can observe and remember where a conspecific is caching, but the solitary Clark’s nutcracker apparently does not (Bednekoff and Balda 1996). Social competition in this case is not correlated with hippocampal size, since the Clark’s nutcracker has a larger relative hippocampal size than the others (Basil et al. 1996). However, the question of phylogeny was not raised in these earlier studies; recent studies show a more complicated picture, indicating two lines of convergently evolving hippocampal specialization in corvids (de Kort and Clayton 2006).

In fact, the Clark’s nutcracker is more closely related to Eurasian nutcrackers, all of whom have a group-specific larger hippocampus (Lucas et al. 2004). What this suggests is that hippocampus and brain structure in corvids might also show convergent evolution, with social selection for spatial memory to avoid cache pilferage in social jays, and natural selection for spatial memory to create and retrieve food distributions in nutcrackers. This

social–natural selection hypothesis would lead to novel predictions not only for behavior but also for hippocampal function in these taxonomic groups.

### **Specialized Forms of Navigation: Migration and Echolocation**

The example of convergent evolution in hippocampal size among corvids reminds us that such patterns must always be a product of more than one “gear” turning (see figure 2.2). If the hippocampus’s role in spatial orientation evolved through natural selection, then specializations in navigational abilities that have no direct connections to social competition no doubt also arise via the same process. Two obvious examples are migratory patterns in songbirds and habitat-use patterns in microchiropteran bats (see table 2.1). Both of these behaviors—the continent-crossing migrations of songbirds and the ability of bats to navigate and forage using ultrasonic echolocation—are clearly remarkable feats of spatial orientation.

Nonetheless, it is worth considering whether the evolution of such specializations has been also affected by social selection. Migration is an old solution that decreases energy costs during the winter months and also reduces competition for food. But it is only one way to solve the problem of winter. There are two strategies, in terms of cognition, to survive this season: to stop thinking or to think harder (Jacobs 1996a). Nonstoring mammals use the first strategy—reduce activity by torpor or hibernation, often leading to a concomitant decrease in brain size. Scatter hoarders utilize the second strategy—though at a cost: the scatter-hoarding gray squirrel’s brain is largest in October, when it is making thousands of scattered caches, but is significantly smaller in January and June (Lavenex et al. 2000a, 2000b).

Flying animals such as birds and insects instead use migration when temperatures drop and food is scarce. Although the act of migration itself is a remarkable act of spatial orientation, what the birds find on their arrival is an environment with warm temperatures and abundant food (the tropics in the winter for nonbreeding behavior; the Arctic in the summer for breeding behavior; Alerstam 1990). Exactly what one would expect from a specialized spatial orientation to a land of plenty has now been demonstrated: migrant species have smaller brains than resident species (Sol et al. 2005b), but those small brains have relative larger hippocampi (Healy et al. 1996). Given that we are comparing species, it is not clear whether the larger hippocampus is the result of a tradeoff, involving a loss of volume in another forebrain structure in birds. But it is clearly more parsimonious to conclude that such increases in hippocampal size are related to the actual migration, not to an increased difficulty of tracking food or social resources.

The pattern of structure and volume of the hippocampus in microchiropteran bats is another example that appears largely driven by natural selection. These patterns have been better documented in bats than in any other vertebrate group (Baron et al. 1996). In addition, there is now sophisticated research appearing on the spatial cognitive strategies of flower bats (Winter and Stich 2005; Toelch and Winter 2007). Yet attempts to correlate



these patterns with behavior are still somewhat controversial. A first study reported that bat hippocampal size is related to habitat complexity and foraging style, specifically, a larger hippocampus is found in species that forage in cluttered environments than in open fields (Safi and Dechmann 2005). Yet a more recent study has reported no correlations of hippocampus size with foraging strategy but instead found an increase in isocortical volume in species that use both gleaning (picking prey from surfaces) and hawking (picking prey from midair) when compared to species that use only one of these strategies (Ratcliffe et al. 2006).

It is not clear what is driving the expression of this behavioral flexibility. It is possible that high levels of competition for prey force bats to search in many different habitats, which supports the notion of the role of social competition as a driver of hippocampal structure. Alternately, because the physiology of echolocation differs according to foraging substrate, with surface gleaners and aerial hawkers using different ultrasound frequencies, it may be that more complex input affects how the hippocampus computes locations. But recent work continues to underline similarities and differences between hippocampal function in terrestrial mammals and bats. As in laboratory rats and mice, single-unit recording from bat hippocampus confirmed the interplay between echolocation—whose function is to create a mental representation of space—and hippocampal activity (Ulanovsky and Moss 2007). In contrast to laboratory rodents, little to no adult neurogenesis was found in the hippocampus of nine species of microchiropteran bats (Amrein et al. 2007), however. Such results suggest that hippocampal function in flying mammals may be significantly different in form and function from that of rodents and primates. Understanding the bat hippocampus may thus allow us to understand the similarities and differences between bird and mammal hippocampus and to establish whether these are the results of homology or of convergent evolution, as Striedter (2005) has argued.

## Conclusion

Let us return to the original question: How do memory specializations evolve? To answer this we must answer all of Tinbergen's questions. We need to understand not only memory's physiological mechanism but also its development, its adaptive value in light of the problems of living faced by a species, and, equally important, its evolutionary past. This means not only understanding the homologies in structure but also identifying the evolutionary processes that are at work. Although human episodic memory is clearly mediated by many brain structures, among them the hippocampus plays a major role. And because of hippocampal development in species, such as the western scrub jay, that appear to use episodic-like memory, asking what forces lead to this ability in nonhumans is a good place to start. West-Eberhard's theory of social selection has not been previously discussed as a force in hippocampal evolution. Viewing scatter hoarding, in particular, as a specialized foraging behavior that evolved in the forge of social competition from hoarding strategies

that demand less cognitive capacity, such as larder hoarding, gives us a new perspective on hippocampal specialization. If the larger hippocampus seen in scatter-hoarding birds and mammals is related to tracking conspecific activity, then it is not significantly different in function from the larger hippocampus seen in polygynous male rodents or female nest-parasitic cowbirds (table 2.1). If these groups show a common ecological function, then understanding the selective forces underlying the evolution of the specialization in each group may lead to a better understanding of the physiological and anatomical homologies of the hippocampus in vertebrates.

These patterns of hippocampal increases in size and complexity suggest that episodic memory in humans may be derived from similar evolutionary forces as in the relevant animal species. Perhaps it was the need for social intelligence that led to the evolution of human episodic memory—the need for self-awareness and causal narrative to solve the great problems of within-species competition. Seen in this light, episodic memory, with or without its attendant specializations of autoecology, might simply be one product of hippocampal evolution by social selection and one that we might already share with other species.

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