CHAPTER ONE

Adaptive Memory: Evolutionary Constraints on Remembering

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Contents

Abstract

Human memory evolved subject to the constraints of nature's criterion—differential survival and reproduction. Consequently, our capacity to remember and forget is likely tuned to solving fitness-based problems, particularly those prominent in the ancestral environments in which memory evolved. Do the operating characteristics of memory continue to bear the footprint of nature's criterion? This is ultimately an empirical question, and I review evidence consistent with this claim. In addition, I briefly consider several explanatory assumptions of modern memory theory from the perspective of nature's criterion. How well-equipped is the toolkit of modern memory theory to deal with a cognitive system shaped by nature's criterion? Finally, I discuss the inherent difficulties that surround evolutionary accounts of cognition. Given there are no fossilized memory traces, and only incomplete knowledge about ancestral environments, is it possible to develop an adequate evolutionary account of remembering?

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1. Introduction: Nature's Criterion

Imagine you were given the task of designing a human memory system from scratch. What features would you include and why? As memory's architect, you would need a criterion, a metric against which you could judge the acceptability of design features. Modern memory theorists use a task-based criterion: People are asked to remember information for a test, such as recall or recognition, and proffered features must help predict or explain performance on the test. Although rarely justified, the choice of criterial task is obviously important. It constrains theory development and colors the theory's final form. For example, theories of free recall lean heavily on a construct called ''temporal context'' because free recall requires people to remember information in the absence of explicit cues (e.g., Howard & Kahana, 2002; Raaijmakers & Shiffrin, 1981).

Yet, the capacity to remember and forget did not emerge from the mind of a memory theorist—it evolved through a tinkering process called natural selection (Darwin, 1859; Jacob, 1977). Design through natural selection has its own stringent criterion: Structural features, once they arise, are maintained if they enhance fitness—that is, survival en route to differential reproduction. If the capacity to remember failed to confer a fitness advantage, modern brains would likely lack a tendency to reference the past. Memory systems need to be adaptive or, at least, they needed to have *been* adaptive at some point in our evolutionary past (e.g., Symons, 1992). In building a memory system from scratch, then, the lesson of evolutionary biology is clear—pay heed to nature's criterion.

In this chapter, I consider how nature's criterion potentially shaped the human capacity to remember and forget. In Section 2, I review recent empirical evidence indicating that our memory systems may be specially tuned to remember information that is processed for fitness. Memory evolved because it helped us survive and reproduce and, not surprisingly, it shows sensitivity to fitness-relevant processing in these domains. In Section 3, I scan the landscape of modern memory theory through the lens of nature's criterion. How well-equipped are the postulates, principles, and perspectives of modern memory theory to deal with a cognitive system shaped by nature's criterion? Finally, I discuss strategies for developing an evolutionary account of remembering. There are no fossilized memory traces, our knowledge about the heritability of ancestral memory ''traits'' is limited, nor can we pinpoint the exact environments in which selection took place. Can we ever hope to develop a truly evolutionary account of remembering?

2. The Mnemonic Value of Fitness-Relevant Processing

If memory evolved, crafted by the forces of natural selection, then its operating characteristics likely bear some imprint of ancestral selection pressures (Klein, Cosmides, Tooby, & Chance, 2002; Nairne & Pandeirada, 2008a). This is true throughout the physical body, where the footprints of nature's criterion are easily observed. Each of the body's major organs plays a crucial role in helping us survive and reproduce and, typically, the fit between form and function is tight. Remnants of the original adaptive problem, or selection pressure, are readily gleaned from the organ's architecture. The function of the heart is to pump blood and its physical structure reflects that end; the eye's function is to transduce electromagnetic energy, and retinal cells are uniquely tuned to this task. The body also divides its labor into component parts, each designed to accomplish a particular goal (pumping and filtering blood, collecting and processing oxygen, and so on). Only adaptive problems can engage the design tools of natural selection—problems directly applicable to survival or reproductive fitness—so specificity abounds.

The central thesis of evolutionary psychology is that the architecture of the mind—our cognitive processes—shows similar specificity (Tooby & Cosmides, 1992). Particular selection pressures, or adaptive problems, fueled the development of human memory systems; consequently, the proximate mechanisms that enable us to remember and forget are likely tuned to solving such problems, particularly as prominent in the ancestral environments in which memory evolved. Although we can never fully know ancestral environments, it is reasonable to suppose that our ancestors faced recurrent adaptive problems, ones that remained relatively constant across situations. Table 1 lists some potential candidates that apply specifically to remembering (from Nairne & Pandeirada, 2008a). Note that each entry potentially relates to fitness, either through affecting the likelihood of survival, protecting kin, or increasing the chances of successful reproduction.

Human memory researchers rarely investigate the specific functional problems listed in Table 1, but relevant data do exist. For example, we have long known that fitness-relevant events can produce salient long-term retention. One compelling example is flashbulb memories, which track the retention of significant life events (Brown & Kulik, 1977; for a recent review, see Luminet & Curci, 2009). Both children and adults report strong and vivid memories for highly emotional events, such as situations in which their lives were in danger, although such memories tend to be reconstructive (e.g., Buss, 2005; Winograd & Neisser, 1992). Additional evidence comes from the study of cultural transmission: What kinds of information are most likely transferred from person to person and across generations?

Table 1 Potential Candidates for Domain-Specific Mnemonic Processes.

Type of fitness-relevant selection pressure	Examples of potential mnemonic targets relevant to each type of selection pressure
Survival-related events	Food (edible vs. inedible), water, shelter, medicinal plants, predators, prey
Navigation	Landmarks, constellations, weather patterns
Reproduction	Physical and/or social characteristics of potential mating partners and/or rivals
Social exchange	Altruistic acts, reciprocation, violation of social contracts, social status or hierarchy
Kin	Physical features and social actions of kin versus nonkin

Note: For each category, our memory systems might be tuned to remember the examples on the right; for example, remembering the locations of edible food, medicinal plants, the meaning of weather patterns, family members, and altruistic acts.

Not surprising, fitness-relevant information, such as information about social interactions or heroic exploits, tends to transmit easily and effectively (Mesoudi & Whiten, 2008; Rubin, 1995).

In the laboratory, studies have consistently found that people can easily associate fitness-relevant stimuli, such as snakes and spiders, with aversive events (Öhman & Mineka, 2001). So-called "taboo" words, which are often sexual in nature, are also remembered particularly well and may induce prioritized "binding processes" between items and their context (Guillet & Arndt, 2009; Schmidt & Saari, 2007). In the word recognition literature, people are faster at recognizing words that rate highly along a "usefulness to survival" dimension relative to matched controls (e.g., Wurm, 2007). There is also evidence for a kin-related bias in autobiographical memory: Unpleasant events resulting from social interactions with kin are remembered as having occurred farther back in time than similar interactions with nonkin (Lu & Chang, 2009). People are also particularly good at attributing statements about the violation of social contracts to faces in a source attribution paradigm (Buchner, Bell, Mehl, & Musch, 2009). Not surprisingly, people also tend to remember attractive faces better than average-looking faces, although the effect is larger for female than male faces (see Kenrick, Delton, Robertson, Becker, & Neuberg, 2007).

2.1. The Survival Processing Paradigm

As the studies just described illustrate, one can attempt to identify fitness-relevant events or situations and assess their mnemonic power. Collectively, the evidence suggests that our memory systems effectively retain information pertinent to situations such as those listed in Table 1. However, studies of this sort suffer from an inherent methodological problem because comparisons are typically made across different items—for example, taboo words and nontaboo words. One can attempt to equate the stimuli on other relevant dimensions, but item-selection effects are always a lingering concern. One can never be completely certain that the stimuli differ only along the particular dimension of interest.

Our laboratory has taken a different approach. Rather than comparing retention across item-type (fitness-relevant or not), participants in our experiments are asked to remember the same information (usually unrelated words). What differs across conditions is how those items are *processed* prior to a subsequent memory test—that is, either in terms of fitness-relevance or not. Table 2 lists the typical survival processing scenario we have used along with two relevant control conditions (Nairne, Thompson, & Pandeirada, 2007). Words are presented individually and people respond by producing a rating—for example, would this item be relevant if stranded in the grasslands of a foreign land without any survival materials? Surprise recall or recognition performance for the survival rating condition is then compared to performance in the ''control'' conditions, which also require meaningful, or ''deep,'' processing (Craik & Tulving, 1975).

Table 2 Scenarios Used in Nairne et al. (2007).

Survival	In this task we would like you to imagine that you are stranded in the grasslands of a foreign land, without any basic survival materials. Over the next few months, you will need to find steady supplies of food and water and protect yourself from predators. We are going to show you a list of words, and we would like you to rate how relevant each of these words would be for you in this survival situation. Some of the words may be relevant and others may not—it is up to you to decide.
Moving	In this task we would like you to imagine that you are planning to move to a new home in a foreign land. Over the next few months, you will need to locate and purchase a new home and transport your belongings. We are going to show you a list of words, and we would like you to rate how relevant each of these words would be for you in accomplishing this task. Some of the words may be relevant and others may not—it is up to you to decide.
Pleasantness	In this task, we are going to show you a list of words, and we would like you to rate the pleasantness of each word. Some of the words may be pleasant and others may not—it is up to you to decide.

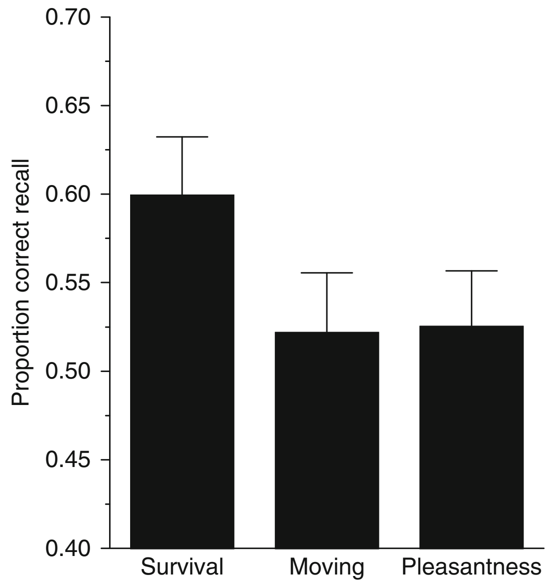

Figure 1 Proportion correct recall for words rated for their relevance to a survival scenario, a scenario involving moving, or for pleasantness (data adapted from Nairne et al., 2007).

Figure 1 shows the standard finding: Survival processing enhances retention relative to other forms of meaningful processing. In this particular example, survival processing produces better retention than processing for pleasantness, a condition known to be a highly effective form of deep processing (Packman & Battig, 1978). The "moving" condition is included as schematic or thematic control. One might argue that survival processing is effective simply because it forces people to encode information into a rich and coherent schema, one that is particularly salient and accessible at retrieval. In fact, both survival processing and the moving control do tend to produce more nonlist intrusions in recall compared to pleasantness processing, suggesting that some kind of schematic processing may be involved, but survival processing still produces the best retention. (Nairne et al., 2007).

The survival processing effect has been replicated a number of times in our laboratory and in other laboratories as well (Kang, McDermott, & Cohen, 2008; Weinstein, Bugg, & Roediger, 2008). The effect occurs in both within- and between-subject designs, when either recall or recognition is used as the retention measure, and when pictures instead of words are used as the to-be-remembered stimuli (Otgaar, Smeets, & Van Bergen, 2010). Perhaps most impressively, a few seconds of survival processing produces better long-term recall than a veritable "who's who" of classic encoding manipulations. Nairne, Pandeirada, and Thompson (2008) used a between-group design to compare the effects of survival processing against

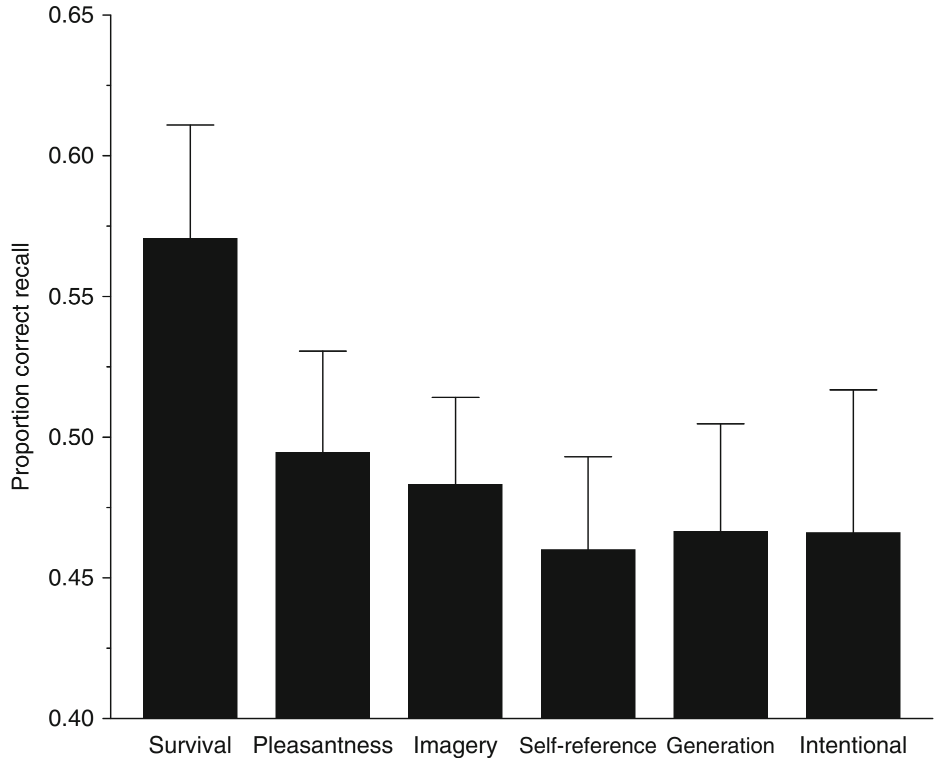

Figure 2 Proportion correct recall for words rated for their relevance to a survival scenario along with recall proportions for a host of other recognized encoding techniques (data adapted from Nairne et al., 2008).

forming visual images, self-reference (relating the item to a personal experience), generating an item from an anagram, and intentional learning. Each of these comparison conditions is widely recognized to enhance retention—in fact, these are the encoding manipulations typically championed in human memory textbooks—yet survival processing produced the best retention. The relevant data are shown in Figure 2.

Once again, everyone in these experiments is asked to remember exactly the same stimuli, so survival advantages cannot be attributed to the inherent qualities of the to-be-remembered items. Rather, it is the nature of the processing that produces the enhancement. Inducing participants to process information in a survival "mode" leads to effective long-term retention, regardless of whether information is rated as relevant to survival or not (see Nairne et al., 2007). This last result may seem surprising—one might have expected that only survival-relevant stimuli would be remembered well. In fact, participants usually are more likely to remember items given a high survival relevance rating (see Butler, Kang, & Roediger, 2009; Nairne et al., 2007), but such comparisons suffer from the item-selection concerns noted earlier. In addition, the fit, or congruence, between to-be-remembered material and the encoding context is an important determinant of retention as well (Craik & Tulving, 1975; Schulman, 1974). Items deemed highly relevant to survival could be remembered better simply because they are more congruent with the survival-based encoding scenario. This makes comparisons between survival relevant and irrelevant stimuli difficult in the survival processing paradigm.

The fact that survival processing enhances retention even for items that are seemingly unrelated to fitness provides another indication of its mnemonic power. Any stimulus bathed in the spotlight of survival processing seems to receive some kind of mnemonic boost. Of course, in natural settings it will be the fitness-relevant stimuli that typically receive the spotlight of processing attention—irrelevant events, unlike in the laboratory, will either be ignored or processed with less vigor. At the same time, importantly, fitness-relevance is not an inherent property of most stimuli; instead, fitness-relevance is context-dependent. As Nairne and Pandeirada (2008a) put it: ''food is survival relevant, but more so at the beginning of a meal than at its completion; a fur coat has high s-value at the North Pole, but low at the Equator'' (p. 240). Even mundane stimuli, such as a pencil, can become quite fitness-relevant under the right circumstances (e.g., a pencil can be used as a weapon in an attack). For this reason we have suggested that survival *processing* may be the key to long-term enhancement, although stimuli that are naturally fitness-relevant (at least most of the time) might show better retention as well. As noted earlier, words rated as useful to survival are recognized faster and more accurately in a lexical decision task than are matched control words (e.g., Wurm, 2007).

2.2. Explaining the Survival Processing Advantage

Still, the fact that survival processing yields particularly good retention does not tell us much about the proximate mechanisms that produce the advantage. The survival advantage is an *a priori* prediction of an evolutionary analysis, but standard memory principles might explain it. For example, survival processing could simply lead to greater emotional arousal than control conditions, boosting later recall of information encoded in such a context (see Nairne et al., 2007; Weinstein et al., 2008). Such an account would be consistent with an evolutionary locus—that is, nature solved the adaptive problem of remembering fitness-relevant information indirectly by linking memory to emotional arousal (e.g., McGaugh, 2003, 2006).

2.2.1. Emotional Processing

However, there does not appear to be any simple link between memory and emotional processing; the relevant literature is filled with complex and conflicting findings. Increased arousal does not always lead to enhanced retention and may, in fact, reduce retention in some circumstances (Kensinger, Garoff-Eaton, & Schacter, 2007; LaBar & Cabeza, 2006). In addition, if emotional arousal mediates the survival advantage, the size of the effect should depend on the emotional rating or valence of the processed stimuli. Otgaar et al. (2010) obtained separate measures of arousal and valence for pictures and assessed recall after people rated the pictures for survival relevance, moving to a foreign land, or pleasantness. Both arousal and valence affected recall performance overall, but failed to interact with the size of the survival recall advantage. Nairne et al. (2007) performed a similar analysis with word stimuli and also failed to find any relationship between emotionality rating and the size of the survival processing advantage.

Research on memory for emotional words often shows design effects as well—that is, retention advantages for emotional words are confined to mixed designs in which both emotional and neutral words are contained in the same list (e.g., Schmidt & Saari, 2007). Such a pattern suggests that emotional words tend to be remembered well only when they ''stand out'' or are distinctive relative to neutral words presented in the same context. As noted earlier, the survival processing effect remains highly robust in both within- and between-subject designs. In fact, we have directly compared survival processing in within- and between-subject designs—for example, survival and pleasantness processing occurred either randomly intermixed in the same list or in different lists—and the size of the survival advantage in recall remains essentially the same in both designs.

This last finding—that survival processing advantages do not show design effects—also helps distinguish the effect of survival processing from many other standard findings in the memory literature. For example, the generation effect (generated items are remembered better than read items), the effect of bizarre imagery (forming a bizarre image of an item produces better memory than a common image), the enactment effect (subject-performed actions are remembered better than experimenter-performed actions), and the perceptual interference effect (perceptually masked words are remembered better than unmasked words) all show strong design effects, at least when free recall is used as the retention measure. Each effect is typically stronger in a within-subject design and may even fail to materialize in a between-subject design (for other examples, see McDaniel & Bugg, 2008). Again, survival processing shows no such sensitivity.

2.2.2. Thematic Processing

One could also argue that survival processing is effective simply because the rated information is processed in a rich thematic context. Thematic processing affords a number of mnemonic benefits, including enhanced relational processing, that are absent or minimized in item-based processing tasks of the type compared in Figure 2. In our original work we attempted to counter this interpretation by comparing survival to another thematic scenario—*moving* to a foreign land. Although we matched the moving and survival scenarios as closely as possible, one could still argue that thinking about survival is inherently more arousing, interesting, or novel than moving. Since our original report (Nairne et al., 2007), we have replicated the survival benefit using a number of alternative thematic scenarios. For example, we have compared survival to scenarios in which (a) people are asked to imagine themselves vacationing at a fancy resort with all of their needs taken care of, (b) eating dinner at a restaurant, and (c) planning a charity event with animals at the local zoo (Nairne & Pandeirada, 2007; Nairne et al., 2007, 2008)—in each case, a survival processing advantage was found. Our survival scenario also produces better memory than one involving the planning and execution of a bank heist (Kang et al., 2008). In this case, the bank heist scenario was chosen because Kang et al. felt our original moving condition was somewhat mundane, lacking the novelty and excitement of the survival scenario.

Nairne and Pandeirada (2008b) also found robust survival processing advantages when people rated words in categorized lists. We reasoned that survival processing might induce people to encode unrelated words into an "ad hoc" category representing "things that occur in a survival situation." Once primed by the rating task, the ad hoc category could then provide an efficient retrieval structure relative to item-based tasks such as pleasantness processing. However, such an account predicts that if the to-be-rated words are inherently related (i.e., the list is categorized), then any relational processing induced by the survival rating task should be less beneficial to retention. Many studies have shown that relational processing of items in a related list, such as sorting items from an obviously categorized list into categories, yields few mnemonic advantages compared to identical processing of words in an unrelated list (e.g., Hunt & Einstein, 1981). In fact, encoding procedures that focus on the item itself, such as rating the item for pleasantness, produce the best recall when a list is categorized. Nairne and Pandeirada (2008b) found that survival processing continued to produce better recall than pleasantness processing, even when the lists were categorized and the items were drawn from survival-relevant categories.

Perhaps the most convincing evidence against a thematic or relational processing account, though, comes from a recent study using more focused survival scenarios (Nairne, Pandeirada, Gregory, & Van Arsdall, 2009). Evolutionary psychologists often argue that extant cognitive processes evolved primarily during the Pleistocene when our species survived largely as foragers or hunter-gatherers. We continue to house a "stone-age mind," one filled with adaptations uniquely designed to handle problems relevant to early hunter-gatherer environments (e.g., Tooby & Cosmides, 2005). With this in mind, we developed scenarios to tap prototypical "hunting" and "gathering" activities. In the hunter scenario, people were asked to imagine themselves living in the grasslands as part of a small group; their task was to contribute needed meat to the tribe by hunting big game, trapping small animals, or fishing in a nearby lake. In the gathering condition, the task was to gather food for the tribe by scavenging for edible fruits, nuts, or vegetables. In line with our earlier work, participants were asked to rate the relevance of random words to these activities prior to a surprise memory test.

Of main interest are the two control conditions. In the gathering control condition, participants were asked to rate the relevance of words to a task involving searching for and locating food items, but under the guise of a nonfitness-based *scavenger hunt*. The hunter scenario was compared to a matched control in which participants rated the relevance of words to participating in a *hunting contest*. Importantly, both control scenarios required people to imagine tracking and hunting for food—the same activities required in the survival scenarios—but only in the survival versions were the activities fitness-relevant (necessary for continued survival). As shown in Figure 3, significantly better recall performance was found when the scenarios induced people to process information in a survival mode (Nairne et al., 2009).

2.2.3. Special Adaptation?

Does processing information in a survival "mode" engage special mnemonic machinery—perhaps some kind of targeted adaptation uniquely sculpted by the processes of natural selection? I address this possibility in more detail later in the chapter, but some clear conclusions are possible at this point. First, at a

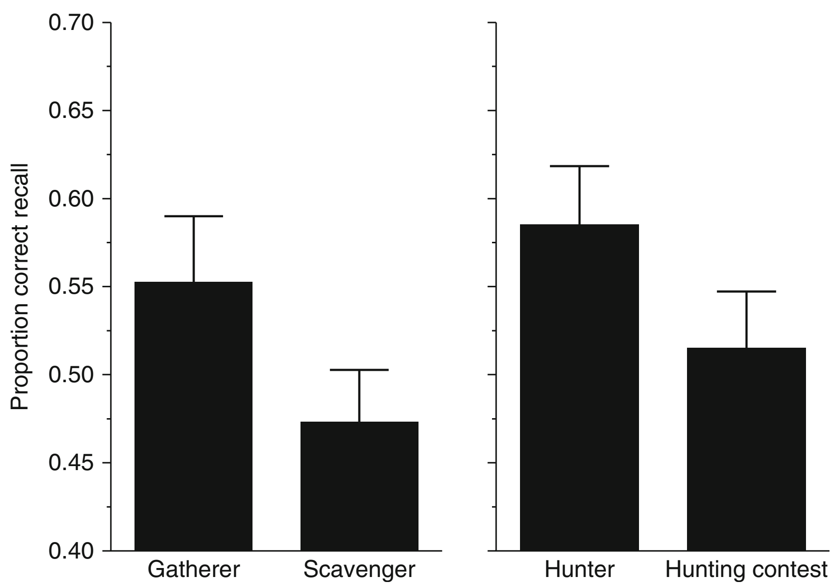

Figure 3 The left-hand side shows proportion correct recall for words rated with respect to a "gathering" scenario, which was fitness-relevant, and a matched "scavenger hunt" scenario, which was not. The right-hand side shows data for the "hunting" and matched "hunting contest" scenario (data adapted from Nairne et al., 2009).

purely empirical level, survival processing produces excellent retention—better, in fact, than virtually all known encoding techniques. For example, as just noted, survival processing produces better retention than pleasantness processing in a categorized list—the latter is generally considered to be the "gold standard" against which effective encoding techniques are compared (see Hunt & McDaniel, 1993). From the perspective of nature's criterion, this is the anticipated result—memory needs to be adaptive, particularly with respect to the maintenance and use of information related to fitness.

Second, as the experiments discussed in this section illustrate, it is unlikely that domain-general factors, such as interest, novelty, emotional or thematic processing, will easily account for the retention advantages found after survival processing. "Standard" memory processes may yet explain the advantage, but the proximate mechanisms involved remain unknown. In the next section, I consider some of the standard explanatory mechanisms used by memory theorists in more detail, but viewed from the unique perspective of nature's criterion. To preview, most memory theorists rely on general purpose processes to explain retention, ones that fail to consider either nature's criterion or any specific purposeful end. It is widely accepted that our sensory systems evolved to solve a set of highly specified problems—for example, detecting edges, extracting wavelength information, maintaining shape constancy—but little is known about the comparable problems that drive our capacity to remember. Instead, researchers focus on explaining retention performance in a few well-specified tasks, such as free recall or recognition, rather than isolating the adaptive problems that memory presumably evolved to solve.

Regardless of the proximate mechanisms that actually underlie the advantage, however, survival processing remains an extremely effective encoding technique. To maximize retention in both normal and impaired populations, it is critical to develop encoding techniques that are congruent with the natural design of memory systems. Semantic-based processing and self-referential processing have been used for years in clinical settings to improve retention (e.g., Bird, 2001; De Vreese, Neri, Fioravanti, Belloi, & Zanetti, 2001; Mimura et al., 2005), yet a few seconds of survival-based processing produces better free recall than either of these encoding tasks. Thus, understanding the functional problems that drive remembering, and the particular role that fitness-relevant processing contributes to long-term retention, should help to improve retention in a variety of populations and retrieval settings.

3. Memory Theory and Nature's Criterion

As noted earlier, very few of the topics listed in Table 1 have received much attention in the human memory literature. This is partly due to the emphasis that cognitive psychologists place on understanding tasks, but there is the propensity to rely on domain-general learning and memory processes as well. Most memory theorists accept that memory evolved, but fail to factor nature's criterion into their task analyses. The possibility that there are a host of domain-specific memory processes, each uniquely crafted to solve particular fitness-relevant problems, is either ignored or rejected by the community of modern memory researchers (for some exceptions, see Klein, Cosmides, et al., 2002; Paivio, 2007; Sherry & Schacter, 1987). Instead, theorists appeal to a few general constructs or principles to explain how retention varies across situations. I discuss two of the most popular constructs below—encoding specificity and levels of processing—and then consider some recent functionally themed approaches that fit more snugly with nature's criterion.

3.1. The Encoding–Retrieval Match

One of the most widely used theoretical constructs in memory theory is encoding specificity or, more generally, the principle of the encoding–retrieval match (see Tulving, 1983; Tulving & Thomson, 1973). This principle can be summarized as follows: Conditions present at encoding establish memory records that, in turn, are differentially accessible depending on the retrieval environment. What ultimately determines retention, at least with respect to a particular target event, is the relative match between the encoded record and the retrieval cue(s) in effect. The better the match, or more precisely the extent to which the retrieval cue matches the target better than other possible retrieval candidates, the more likely the target memory will be retrieved (see Jacoby & Craik, 1979; Nairne, 2002). Things remembered best are those with memory records that match or resemble the cues likely to be present in the testing or retrieval environment.

The key element in this principle is equipotentiality: Neither events, processes, nor retrieval cues are assumed to have any special mnemonic properties (see Surprenant & Neath, 2009; Tulving, 1983). What matters is simply the functional match between the encoding and retrieval environments. Consider the picture-superiority effect: One generally finds that pictures are easier to remember than words, but the advantage is dependent on the nature of the retrieval environment (usually recall or recognition). Retrieval environments can be arranged in which words are remembered better than pictures—one merely needs to employ retrieval cues at test that are more diagnostic of previously encoded words than they are of pictures (e.g., using word fragments as cues at retrieval; see Weldon & Roediger, 1987). It is the relationship between the encoding and retrieval conditions that reigns supreme, not the content of information or the manner in which it is processed.

As a result, survival processing must be beneficial because it produces diagnostic memory records—that is, those that are likely to be matched in later retrieval environments. By itself, of course, this reasoning is circular; additional assumptions are needed to explain why one type of encoding produces more ‘‘matchable’’ retrieval records than another. Historically, memory researchers have appealed to ‘‘elaboration’’ or ‘‘spread of encoding’’ to help solve this problem (e.g., Craik & Tulving, 1975). Effective encoding procedures are those that promote the generation of multiple retrieval cues through the linking of the target item to other information in memory. As the number of linkages—or ‘‘spread’’ of the encoding—increases, the chances that an effective retrieval cue will be encountered later increase as well. But the process itself is domain-general. Retention is controlled by the presence of a diagnostic retrieval cue; environmental factors, rather than information content alone, determine when (or if) an effective retrieval cue will be present. There are no inherent memory ‘‘tunings,’’ only taxonomies relating encoding and retrieval contexts.

Viewed through the lens of nature’s criterion, of course, equipotentiality seems unworkable. How could such a system evolve—that is, one that does not discriminate among the adaptive consequences of the processed event? There are simply too many critical problems for the developing human to solve—avoiding predators, locating nourishment, selecting an appropriate mate—to rely on such a general, content-free principle. Again, the engine that drives natural selection and structural change is fitness enhancement. Any evolved system, as a result, likely guarantees that fitness-relevant events receive some processing priority, at least relative to events that are largely fitness-irrelevant. Nature builds physical structures that solve specific problems—livers, hearts, visual systems—not general systems that remain insensitive to content.

Moreover, a system that relies merely on the match between encoded records and retrieval environments remembers continuously. On-line experiences always yield cues that will match some elements of previous experience, so restrictions are essential for the memory system to function. Decisions need to be made about how to restrict the retrieval cues that are processed, as well as the range of allowable memory records that can be matched. Selection advantages will accrue to memory systems that remember appropriately—that is, to systems that remember information pertinent to improving survival and reproduction. The match between encoding and retrieval environments may be important, perhaps even critical to successful retention, but its role in remembering must ultimately be understood in terms of some larger functional agenda.

3.2. Levels of Processing

A similar argument applies to the popular encoding theory known as the levels of processing framework (Craik & Lockhart, 1972; Craik & Tulving, 1975). According to this view, successful retention depends on the depth of processing that an item receives, in which "depth" is defined as the extent of meaningful or conceptual processing. Empirically, it is well established that thinking about the meaning of an item produces excellent long-term retention compared to more superficial forms of processing, such as attending to the shape or sound of a verbal item (e.g., Hyde & Jenkins, 1973). However, as with the picture-superiority effect, the advantage of meaningful processing depends on the characteristics of the retrieval environment. One can arrange retrieval environments in which nonmeaningful (shallow) forms of processing lead to comparatively better retention (Stein, 1978; also see Roediger, Gallo, & Geraci, 2002). But for traditional retrieval environments (e.g., free recall or recognition) processing for meaning remains an excellent vehicle for long-term retention.

At first glance, the levels of processing framework seems like a domain-specific theory—our memory systems are "tuned" to the processing of meaning. Yet, the theory ultimately subscribes to a kind of equipotentiality as well—meaningful processing "works" only because it promotes the encoding of information into highly organized and differentiated retrieval structures. Craik (2007) has used the analogy of a library:

> If a new acquisition is 'encoded deeply' it will be shelved precisely in terms of its topic, author, date, etc., and the structure of the library catalog will later enable precise location of the book. If the new book was simply categorized in terms of its surface features ('blue cover, 8" × 10", weighs about a pound') it would be stored with many similar items and be difficult or impossible to retrieve later. The ability to process deeply is thus a function of a person's expertise in some domain—it could be mathematics, French poetry, rock music, wine tasting, tennis, or a multitude of other types of knowledge. (p. 131)

From the standpoint of theory, then, memory is conceptualized in a completely domain-general way. Successful retention depends on fitting to-be-remembered material into rich, established knowledge structures that are easy to access when retrieval is needed. Moreover, it is experience, or expertise, that is the ultimate arbiter of effectiveness. Although recurrent aspects of the environment may lead to common knowledge structures across people, an individual's unique interests and life experiences build those domains of expertise that afford the best opportunity for excellent long-term retention. As Craik (2007) notes, the levels of processing framework "postulates no special 'store' or 'faculty' of memory—or even special memory processes" (p. 132).

Again, is it reasonable to assume that such a domain-general process is well suited for solving the wide range of mnemonic problems that humans faced throughout their evolutionary history, everything from remembering food locations, predator routes, potential mate choices, cheaters on social contracts, and so on? One might argue that fitness-relevant knowledge structures, those germane to survival and reproduction, are simply better described than nonfitness-relevant events—that is, more organized and differentiated. However, it is unlikely that these characteristics, if present, developed with experience or expertise. Most people have limited experience with survival situations, particularly those involving predators in the grasslands of a foreign land. More importantly, remembering fitness-relevant information is too important to rely on the whims of environments that may or may not deliver the experiences necessary to build appropriate retrieval structures.

Empirically, as reviewed earlier, a few seconds of survival processing leads to enhanced retention relative to traditional "deep" processing tasks, including ones that should activate highly organized and differentiated retrieval structures. For example, Nairne et al. (2008) compared survival processing to a self-reference task. People were asked to make survival relevance ratings about words or to rate the ease with which the word brought an important personal experience to mind. So-called "self schemas" are highly organized and differentiated, and well practiced, yet survival processing produced better retention. Moving and spending time at a restaurant are also well practiced compared to surviving in the grasslands, and should activate highly organized knowledge structures, yet it is survival processing that produces the better memory. Finally, as Nairne et al. (2009) have shown, one can use rating scenarios that trigger *exactly the same activities* (e.g., hunting or searching for food) but retention depends importantly on whether the activities are deemed fitness-relevant or not.

There is little question that depth of processing and the encoding–retrieval match are important to retention; it would be folly to suggest otherwise. Decades of research have established that retention is retrieval-cue dependent and improved by encoding techniques that maximize the chances that effective cues will be present when needed (see Tulving & Craik, 2000). However, to suggest that these two principles are sufficient to capture the essential properties of memory's evolved architecture is nonsense. The idea that our memory systems are insensitive to content—that neither events, processes, nor retrieval cues are "special"—ignores the specificity and defining characteristics of nature's criterion.

3.3. Episodic Future Thought

Although the majority of memory researchers remain focused on understanding specific retrieval environments, invoking general constructs such as encoding specificity or levels of processing to explain retention, more functionally oriented perspectives do exist. One relatively recent idea is that our memory systems are fundamentally prospective—that is, oriented toward the future rather than the past (Schacter & Addis, 2007; Szpunar & McDermott, 2008). Of course, from the perspective of nature's criterion such a conclusion must be true. It is the ability to use the past, in combination with the present, that produces adaptive behavior (Nairne & Pandeirada, 2008a; Suddendorf & Corballis, 2007).

The core idea behind the emerging concept of episodic future thought is adaptive simulation (Atance & O'Neill, 2001). People possess the unique ability to imagine, or pre-experience, events that may happen in the future, thereby enabling them to cope more effectively with future events. To consider an obvious case, the nervous teenager anticipating his first date actively envisions scenarios—what his partner might do or say and he can practice witty retorts. One can also re-create scenarios from the personal past—for example, a botched job interview—and cast alternative versions of events in the hope of performing more effectively in the future. The adaptive value of mental simulation is widely practiced across domains. Golfers, for example, often mentally picture the trajectory of a shot before addressing the ball.

It has been suggested that one of the primary functions of episodic memory, one reason why the system might have evolved, is to provide the key elements or building blocks from which future thoughts can be constructed (Schacter & Addis, 2007). Indeed, evidence from a variety of sources—neuropsychological, neuroimaging, and behavioral data—indicates a close relationship between episodic retrieval and future thought simulation. For example, individuals who have lost the capacity to remember personal episodes from the past have trouble imagining personal events in the future (Klein, Loftus, & Kihlstrom, 2002; Tulving, 2002). Neuroimaging studies suggest that a common core brain network may be engaged during both episodic remembering and episodic future thought (Buckner & Carroll, 2007; Szpunar, Watson, & McDermott, 2007). Behaviorally, the ability of normal people to imagine vivid and detailed future scenarios depends on the availability of relevant past episodes (Szpunar & McDermott, 2008).

If our memory systems truly evolved to anticipate and plan for the future, then processing information in a future-oriented ''planning mode'' might produce particularly good retention. Evidence consistent with this idea has been reported recently by Klein, Robertson, and Delton (2010). People were asked to make ratings about objects in the context of a camping trip in the woods. In one condition, focused on the *past*, people were asked to rate the likelihood that particular objects had been taken on a past camping trip; in a second *atemporal* condition, people were asked simply to imagine a camping site and to rate the chances that objects were contained in the image; in the future-oriented *planning* condition, people were asked to rate the likelihood that they would plan to take a particular object with them on a future trip. A surprise recall test revealed that future-oriented planning produced the best retention—even better, in fact, than yet another condition in which people were asked to rate the survival value of each of the objects.

Again, to satisfy nature's criterion, cognitive systems must be adaptive—that is, they need to produce behavior that directly or indirectly increases survivability and reproduction. A system designed merely to remember the past could not have easily evolved. The past can never occur again, at least in exactly the same form, so memory systems gain their adaptive edge by improving future responding (Suddendorf & Corballis, 1997). At the same time, a memory system that is designed simply to simulate the future falls short of nature's criterion as well—the concept is too general. If the ability to construct future scenarios is an evolved characteristic, it arose because it ultimately enhanced fitness. Consequently, as with survival processing, we might expect the imprint of nature's criterion to be observable in the operating characteristics of episodic future thought. For example, we might anticipate that people will simulate future events more effectively when those events are relevant to fitness than when they are not. At this point, though, the mark of nature's criterion on episodic future thought remains to be investigated.

Interestingly, the survival processing paradigm can be conceived as one that induces episodic future thought. People are asked to imagine a grasslands scenario and then to rate the relevance of events to surviving in such a context. It is easy to imagine that people in these experiments are actively simulating the scenario and anticipating how the presented events apply (or not). Memory is enhanced relative to conditions in which events receive only item-based processing, such as rating for pleasantness or forming a visual image—but also to simulated scenarios that involve activities that are not fitness-relevant (such as moving to a foreign land or participating in a hunting contest). However, one difference between a simulated survival scenario and "planning" a specific future event, such as a camping trip, is that the survival scenario is more likely to rely on generic knowledge than on personally relevant episodes. Few, if any, college-age participants have a background in grasslands-based survival situations, so it is unlikely that a survival simulation is constructed from personally relevant episodes (Klein, Loftus, et al., 2002; Szpunar, 2010). Unraveling the connections between the building blocks of episodic future thought and their evolutionary roots should prove to be a productive avenue for future research.

3.4. Rational Analysis of Memory

Another functional perspective on retention proposes that our memory systems evolved, in part, to reflect the statistical regularities of events in the environment. These "rational" models of memory adopt a Bayesian framework, assuming that one important function of memory is to calculate the conditional probabilities associated with event occurrence. There is presumably a cost to remembering, so it is adaptive to consider the probabilities that particular memories will be relevant, and therefore needed, in a particular environment (Anderson & Milson, 1989; Shiffrin & Steyvers, 1997).

In fact, our retention functions do seem to track the way events actually occur and recur in the environment. Forgetting functions are negatively accelerated, meaning that most of the retention loss occurs early in the function and slows thereafter. It turns out that the statistical properties of event occurrence follow essentially the same form. For example, Anderson and Schooler (1991) assessed the probability that a particular word would appear in the headlines of the New York Times as a function of the number of days that passed from an initial occurrence. So, if the phrase ''Cap and Trade'' appears in the headlines today, there is a relatively good chance that the same phrase will appear tomorrow. But the odds fall off with each successive day in a form that mimics the classic forgetting function. Anderson and Schooler's (1991) results suggest that ''forgetting'' is simply an optimal reflection of the way events actually occur and recur in the environment. We are less likely to remember a specific occurrence with time, but that is because the event is less likely to occur again and be needed (for other supporting applications, see Anderson & Schooler, 2000).

The rational approach successfully captures the idea that our cognitive systems are inherently constrained by nature—we think and remember in particular ways in order to optimize expected utilities (gains vs. costs) in a given situation. Unlike most approaches to human memory, the rational viewpoint is also functional; it assumes that memory systems are purposeful and crafted to solve specific problems in the environment. However, from the perspective of nature's criterion, two caveats deserve mention. First, evolutionary psychologists generally believe that our brains developed to solve adaptive problems prevalent during the so-called environment of evolutionary adaptedness (e.g., Symons, 1992; Tooby & Cosmides, 1992). Thus, although our cognitive systems may be optimally designed, they evolved to solve problems in ancestral environments, particularly those associated with foraging lifestyles. This means that our memory systems may not be optimal in modern environments, and it may be a mistake to assume that they are designed merely to detect statistical regularities in such environments (for a discussion of optimality modeling and evolution, see Gangestad & Simpson, 2007).

The second caveat emerges from a recurrent theme of this chapter—the engine that drives structural change through natural selection is the enhancement of fitness. Consequently, it is unlikely that our memory systems evolved simply to reflect the statistical properties of events—in either modern or ancestral environments; instead, the content (or, more specifically, the fitness-relevance) of the information needs to be taken into the account. Our memory systems should be optimally designed to reflect the occurrence and recurrence of fitness-relevant information, rather than information in general. In fact, Anderson and Schooler (2000) suggest that it might be less costly to process or retrieve certain kinds of memories, based on the content or ''importance'' of the events involved, although they have not pursued the issue empirically.

4. Remembering with a Stone-Age Brain

Throughout the chapter, I have developed logical arguments for specially tuned memory systems, those sculpted by the processes of natural selection. For example, memory's tunings are unlikely to have emerged entirely from experientially based learning mechanisms—on-line experiences often do not deliver the information necessary to respond appropriately. In addition, memory systems could not have evolved to record and remember everything—problems of combinatorial explosion arise quickly so selectivity in storage is required (see Ermer, Cosmides, & Tooby, 2007). Instead, given the severity of nature's criterion, cognitive systems likely come equipped with ''crib sheets'' or built-in biases about how to respond rapidly and efficiently to fitness-relevant input (Tooby & Cosmides, 1992).

At the same time, there is a difference between recognizing that our memory systems are functionally designed—that is, ''tuned'' to solve particular kinds of problems—and discovering the ultimate origins of those tunings. Identifying an adaptation, especially a cognitive one, is notoriously difficult. There are no ''fossilized'' memory traces, and we have only limited knowledge about the ancestral environments in which our memory systems actually evolved (Buller, 2005). Adaptive solutions to recurrent problems can arise indirectly, by piggybacking on adaptations that evolved for different reasons (*exaptations*), or as a result of natural constraints in the environment (e.g., the physical laws of nature or genetic constraints). The proximate mechanisms that enable us to read and write, for example, could not have evolved directly for those ends even though reading and writing are very adaptive abilities.

To establish that a given cognitive mechanism, such as a mnemonic tuning, reflects an adaptation—that is, a mechanism arising directly as a consequence of evolution through natural selection—requires satisfying multiple criteria (e.g., Brandon, 1990; Williams, 1966). In principle, one would need to establish that the trait can be inherited, or passed along across generations through differential reproduction. One would also want to show that at some point in our ancestral past there were individual differences among people along the trait dimension, and that certain *forms* (such as a special memory tuning for fitness-relevant information) were *selected* because they promoted differential survival and reproduction relative to other forms. Obtaining this kind of evidence is difficult, if not functionally impossible, for most of the cognitive adaptations of interest to evolutionary psychologists (e.g., see Richardson, 2007).

It is also important to recognize that our cognitive systems were not built from scratch—natural selection ''tinkers,'' which means that changes emerge from preexisting structures. The design of these structures, in turn, introduces constraints that color how the adaptive problems that drive evolution are ultimately solved. Thus, even if we could correctly identify the ancestral selection pressures that drove the development of our memory systems, it would still be difficult to predict how nature solved the relevant adaptive problems. As noted above, the task becomes even more difficult with the recognition that adaptations can be co-opted to solve problems that are ostensibly unrelated to their functional design (Gould & Vrba, 1982). Even worse, some mnemonic phenomena may even be artifacts—so-called ''spandrels'' or incidental byproducts of other design features. For example, sensory persistence (e.g., iconic memory) may occur simply as a byproduct of the fact that neural responses are extended in time (Haber, 1983; Loftus & Irwin, 1998).

4.1. Building the Case for Cognitive Adaptations

Despite these inherent problems, one can still build compelling arguments in favor of evolutionary loci (see Andrews, Gangestad, & Matthews, 2002). Evolutionary biologists, ethologists, and comparative psychologists have been proposing adaptationist hypotheses for generations, without satisfying the stringent criteria mentioned above (see Bolles & Beecher, 1988; Shettleworth, 1998). Most scholars agree that cognitive adaptations exist in humans—for example, sensory and perceptual systems—although the evolutionary lineage is unavailable or difficult to track even in the most obvious cases. Moreover, the absence of relevant evidence is not sufficient to falsify adaptationist arguments, nor does it mean that nonadaptationist hypotheses are correct (e.g., all memory ''tunings'' emerge from experience). Both adaptationist and nonadaptationist hypotheses need to be constructed (and judged) on an empirical base. One can infer the existence of an adaptation, generate and test empirical predictions, and systematically rule out alternative explanations (Williams, 1966).

As the research reviewed in this chapter illustrates, it is possible to adopt a functional/evolutionary perspective and generate empirically-testable hypotheses. One common complaint against evolutionary psychology is the proliferation of ''just-so'' stories—that is, post-hoc explanations for phenomena that seem apt from an evolutionary perspective but lack relevant empirical grounding (e.g., giraffes have long necks because they could reach more easily for food; Gould & Lewontin, 1979). By themselves, these kinds of accounts have explanatory value, but mainly to the extent that they can be used to generate empirically-testable predictions. Recognizing that our memory systems evolved, and were subject to the constraints of nature's criterion, led to the prediction that processing information for fitness would lead to especially good retention. Because of how labor was divided during early environments of adaptation, Silverman and Eals (1992) generated the clear prediction that women may be better equipped than men to remember the locations of objects set in fixed locales (see also New, Krasnow, Truxaw, & Gaulin, 2007). Similarly, recognizing that males and females differ in their relative amounts of parental investment generates predictions about sex-based mating strategies and parental behavior that, in turn, can be confirmed or disconfirmed empirically (Buss, 2006).

It is also possible to attempt comparative analyses, across cultures and species, either to establish the universality of the trait or to demonstrate that it occurs only in environments affording the relevant selection pressures. Given an evolutionary locus, one would presumably expect to find fitness-based retention advantages across species and peoples. This may seem like a trivial prediction but, in fact, an early criticism of our work was that survival processing advantages might have arisen from exposure to culture-specific media, such as the television program *Survivor*—they do not (see Nairne et al., 2007; Weinstein et al., 2008). At the same time, comparative analyses, by themselves, do not provide unequivocal support for the presence of an adaptation. Universality can arise for many reasons—for example, common experiences or natural constraints across environments—and the presence of a trait across species does necessarily mean that common adaptations are involved. Comparative analyses can be effective in helping to eliminate alternative hypotheses and may serve as one piece in a larger argument in favor of an adaptationist account.

One can also look for tunings or specificity in development. For example, many scholars believe that language learning in children is biologically prepared—the capacity for language develops easily and reliably and follows rules that cannot be readily gleaned from everyday experiences (e.g., Pinker, 1994). Moreover, the human ear and vocal tract seem perfectly tailored to meet the needs of speech, and there are specific regions in the brain that control the production and comprehension of spoken language. Many developmental psychologists argue as well that babies are born knowing all kinds of things about the world, everything from an intuitive sense of motion and the physical world to differences between animate and inanimate objects (Bloom, 2005; Gelman, 2003). Babies may also be born with a bias to recognize and remember faces, gender-specific voices, and fear natural predators such as snakes (DeLoache & LoBue, 2009). Again, none of these data, by themselves, can decisively confirm an adaptationist locus—for example, these abilities could be exaptations, co-opted from other adaptations—but they help to bolster an adaptationist case. It would be interesting to know, for example, whether fitness-based retention effects arise easily in children or fitness-relevant processing activates regions in the brain that overlap (or not) with other forms of mnemonic processing.

Another criterion that is sometimes used to defend an evolutionary locus is optimality. Proximate mechanisms resulting from evolved adaptations should show a special ability to maximize adaptive behavior. So, one can investigate the operating parameters of remembering and forgetting and establish (usually through some form of quantitative model) that the system rationally maximizes benefits and minimizes costs (e.g., Anderson & Milson, 1989). However, as noted earlier, adaptations, by definition, are rooted in the past; consequently, we should not necessarily expect to detect optimal behavior from an evolved system operating in a modern environment. Instead, at least in principle, we should expect to find ancestral priorities—that is, we should find that the system is tuned to operate most effectively in past environments, particularly environments associated with our foraging past. Evidence of this sort is particularly compelling for adaptationist accounts because it is difficult to see how general learning mechanisms could possibly account for an ancestral priority.

In fact, evidence consistent with ancestral priorities exists in several cognitive domains. For example, New, Cosmides, and Tooby (2007) found that people are faster and more accurate at detecting animals, both human and nonhuman, than inanimate objects using the change-detection paradigm, a procedure in which people are asked to detect changes in rapidly alternating images. People were slower at detecting changes in familiar vehicles across images than they were at detecting changes in rarely experienced animal species. In the learning domain, some studies have found that ancestrally relevant fear stimuli, such as snakes and spiders, are easier to associate with aversive stimuli than modern fear-relevant stimuli such as guns and electrical outlets (see Öhman & Mineka, 2001). In addition, specific phobias are more apt to develop to ancestral stimuli (e.g., spiders) than to aversive stimuli experienced exclusively in modern environments (e.g., weapons; De Silva, Rachman, & Seligman, 1977). Although not definitive, these data are consistent with the notion that some aspects of cognitive processing may be better tuned to ancestral than to modern priorities.

4.2. Ancestral Priorities in Survival Processing

There is evidence indicating that ancestral priorities may help drive retention performance in the survival processing paradigm as well (Nairne & Pandeirada, 2010; Weinstein et al., 2008). Weinstein et al. asked people to process the relevance of words to a survival situation, but varied whether the scenario described an ancestral or a modern setting. In one condition, using the typical survival scenario (see Table 2), people were asked to imagine themselves stranded in the grasslands of a foreign land without basic survival materials. Over the next few months, they would need to find steady supplies of food and water and protect themselves from predators. In a second condition, exactly the same scenario was used but two critical words were changed: *city* was substituted for *grasslands* and *predators* was replaced by *attackers*. Escaping from predators in the grasslands, the authors reasoned, is a closer fit to the problems faced in the environment of evolutionary adaptation; as a result, it should produce better memory than processing in a modern context, even though the latter is arguably more familiar and likely to lead to greater amounts of elaboration. Consistent with their hypothesis, better retention for the rated words was found for the group processing the ancestral scenario.

Our laboratory has recently replicated this work and extended it to two new domains—attempting to cure an infection and finding necessary nourishment. In the first case, the survival scenario was once again set either in the grasslands or in a city, and participants were asked to imagine they had been hurt and a dangerous infection might be developing. Participants were instructed to rate the relevance of words to the task of finding ''relevant medicinal plants'' to cure the infection (*ancestral*) or finding ''relevant antibiotics'' (*modern*). In a second experiment, again employing either a grasslands or a city scenario, people were asked to imagine they had not eaten for several days and needed to ''search for and gather edible plants'' (*ancestral*) or ''search for and buy food'' (*modern*). In all other respects the scenarios were matched exactly. The rating task was followed by a surprise recall test for the rated words.

The main results of interest are shown in Figure 4. In both experiments, people who imagined themselves in an ancestral context remembered more of the rated words than those who imagined themselves in a city. Importantly, both of the scenarios depicted survival situations and the adaptive problems involved (curing an infection and finding nourishment) were essentially the same. Moreover, typical for the survival processing paradigm, everyone in both experiments was asked to remember exactly the same stimuli. Despite the fact that the scenarios were very closely matched—differing in only a few words—processing an item in an ancestral survival context led to better retention than processing the same item in a modern survival context. It is tempting to conclude from these data that the ancestral scenarios induced a unique form of survival processing, one congruent with the selection pressures that originally fed the processes of natural selection.

4.3. What Is the Adaptation?

Assuming that mnemonic adaptations exist, and account partly for the fitness-based ''tunings'' seen in the survival processing paradigm, what form would these adaptations be likely to take? Do we have minds filled

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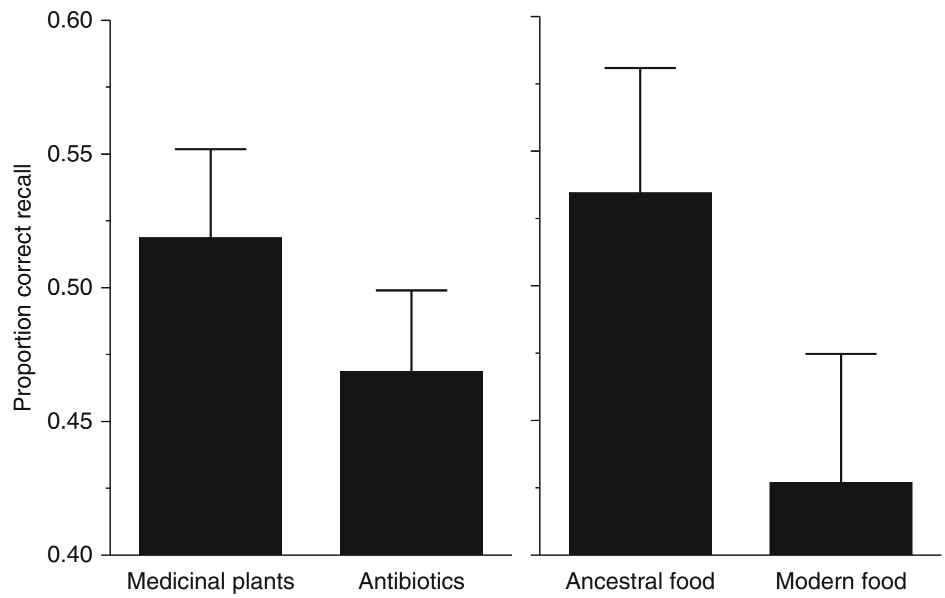

Figure 4 **Proportion correct recall for the ''ancestral'' conditions (searching for medicinal or edible plants) and the matched ''modern'' conditions (searching for antibiotics or shopping for food). Data are from Nairne and Pandeirada (2010).**

with highly specialized memory adaptations, each crafted to solve a particular kind of memory problem (e.g., remembering faces, edible plants, or predator types)? Or, did we evolve a few general systems defined more by flexibility than by domain-specificity? Memory researchers sometimes propose multiple memory systems (e.g., Schacter & Tulving, 1994), but those systems are typically defined by the source of information rather than by its content (see Tooby & Cosmides, 2005). For instance, we may have evolved systems for dealing with personal autobiographical events, general knowledge, or perceptual representations, but not for specific situations related to fitness (e.g., predators, food sources, or potential mates). Some neuroscientists have argued for domain-specific knowledge systems in the brain (e.g., Caramazza & Shelton, 1998), but such proposals are rarely considered by mainstream cognitive psychologists.

As argued throughout, adaptations develop to solve adaptive problems, those defined by nature's criterion. Evolutionary psychologists tend to reject content-free architectures because it is difficult to see how such structures could evolve. Structural features evolve because they enhance fitness—so, in the case of memory, our capacity to remember and forget likely developed because our memory systems helped us solve fitness problems of the sort listed in Table 1. Adaptive problems can be solved by general systems, but general systems are rarely engineered by natural selection. For example, consider a retention system based merely on meaning—information that is processed for meaning is remembered better than information processed along more ‘‘shallow’’ perceptual dimensions (Craik & Lockhart, 1972). One could argue that processing in a survival ‘‘mode’’ induces meaningful processing, and concomitant ‘‘elaborations,’’ and therefore fitness-relevant information would typically be remembered well. However, as noted earlier, failing to differentiate between important and unimportant material (i.e., the assumption of equipotentiality) leads to a host of potential problems (e.g., combinatorial explosion of information). It is more likely that a system evolved to detect and remember fitness-relevant information, a system that could then be co-opted to remember generally.

At the same time, we probably did not evolve any simple kind of ‘‘survival module.’’ The concept of survival is too general as well. As Nairne et al. (2007) argued, the retention advantages that accrue from survival processing could easily result from ‘‘multiple modules working in concert—each activated to one degree or another by the survival processing task’’ (p. 270). From an evolutionary perspective, specific processing systems may have developed for dealing with particular foods, predators, potential mating partners, and the like (e.g., see Barrett, 2005). It is probably necessary to differentiate among retention environments as well. For example, most of the work conducted to date on survival processing has used free recall as the retention measure. Free recall requires a search engine, or retrieval process, that accesses stored information using a criterion of recent occurrence. It is an episodic task, one that requires people to recall information that occurred at a specific time, in a specific location, as defined by the experiment. For some kinds of fitness-relevant problems—perhaps remembering the location of a predator or a food source—enhanced episodic retrieval might be especially beneficial. However, for other fitness-relevant problems, such as remembering whether someone is a cheater or a potential mate, remembering temporal and spatial information may be less useful.

At this point, it is not possible to characterize mnemonic adaptations in any satisfactory fashion. We can use the lessons of evolutionary biology to speculate—for example, adaptations tend to be domain-specific and functionally designed—but logic alone is not a substitute for building a strong empirical case. Again, as the data reviewed in this chapter clearly show, it is possible to generate *a priori* empirical predictions about the possible functions and evolutionary roots of our memory systems. Future research will need to compare and contrast alternative accounts and ‘‘visions’’ of memory’s evolved architecture. However, regardless of the proximate mechanisms that are ultimately uncovered, it will be important to recognize initially that cognitive systems are functionally designed. Our memory systems are purposeful—they evolved to solve adaptive problems—and memory’s architecture is likely to reflect those functional ends.

5. Conclusions

Theories naturally evolve, based on the criterion of successfully predicting and describing performance on a criterial task. In the case of memory theory, psychologists have relied on an ever-expanding toolkit of memory measures—for example, recall, recognition, fMRI scans—but rarely explain or justify why one task should be preferred over another. Adopting such a ''structuralist'' mindset means, of course, that our theories tend to be task-based and rarely connected to actual problems (see Nairne, 2005). Which is likely to provide the clearest window into what it means to remember—free recall, recognition, or some other task?

Most notably absent from current memory debates, however, is the recognition that nature designed our memory systems with her own criterial task—reproductive fitness. For a memory system to evolve, it must satisfy the constraints of nature's criterion; it must easily solve the kinds of adaptive problems that engineer change through natural selection (e.g., situations of the type listed in Table 1). Accordingly, one might hypothesize, the imprints—or footprints—of those criterial problems should remain visible in the operating characteristics of memory systems. This is ultimately an empirical question, but recent research suggests that our memory systems may indeed be ''tuned'' to remember information and events that are relevant to fitness. In fact, as discussed earlier, a few seconds of survival processing produces better free recall performance than a veritable ''who's who'' of established memory encoding techniques (Nairne et al., 2008).

Recognizing a role for nature's criterion in the design and function of memory systems has implications for our theoretical conceptions of memory as well. The crux of the functionalist agenda is the recognition that memory is functionally designed (Klein, Cosmides, et al., 2002; Nairne, 2005; Sherry & Schacter, 1987). Our memory systems are not engineered to remember everything; decisions need to be made about storage and retrieval and content matters. It is much more important to have memory systems that track the locations of predators and food, or the statements of potential mating partners, than other random events in the environment—regardless of the ultimate origins of those biases or tunings. Yet, many modern memory theorists continue to champion equipotentiality, expressed in the form of domain-general constructs such as encoding specificity or levels of processing. Again, the ultimate arbiter of whether our memory systems are indeed domain-specific, and whether it is appropriate to propose multiple highly specialized memory systems, is empirical. Adopting a truly functional perspective, recognizing that our memory systems are designed to solve adaptive problems, should help to establish productive empirical pathways in the future.

Finally, despite the compelling logic of an evolutionary perspective, it is important to acknowledge the difficulties that surround the search for adaptations, cognitive or otherwise. As noted, there are no fossilized memory records, the heritability of cognitive processes remains largely unknown, and we can only speculate about the selection pressures that operated in ancestral environments. There is also the troubling temptation to concoct adaptationist accounts based on plausibility rather than empirical fact (i.e., ''just-so'' stories; Gould & Lewontin, 1979). At the same time, relevant evidence can be collected about our foraging past (Tooby & Cosmides, 2005); and, as illustrated throughout, it is certainly possible to generate empirically-testable predictions about how recurrent adaptive problems impact modern memory functioning. Few scholars question the assertion that cognitive adaptations must exist, but to build a convincing empirical case for their existence requires much more. Recent research on the evolutionary determinants of memory is seeking to provide an empirical foundation on which just such a case can be made.

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