Adaptive Memory

Remembering With a Stone-Age Brain

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ABSTRACT—*If memory evolved, sculpted by the processes of natural selection, then its operating characteristics likely bear the "footprints" of ancestral selection pressures. Psychologists rarely consider this possibility and generally ignore functional questions in their attempt to understand how human memory works. We propose that memory evolved to enhance reproductive fitness and, accordingly, its systems are tuned to retain information that is fitness-relevant. We present evidence consistent with this proposal, namely that processing information for its survival relevance leads to superior long-term retention—better, in fact, than most known memory-enhancement techniques. Even if one remains skeptical about evolutionary analyses, adopting a functional perspective can lead to the generation of new research ideas.*

KEYWORDS—*evolution; memory; survival; fitness relevance*

Psychologists know a lot about human memory but very little about its function. It is well established that forming a visual image of an item improves its later retention, as does processing its meaning or generating the item initially from cues. Yet next to nothing is known about why these particular sensitivities developed or about the roles they play in actual functioning. Why did nature craft a memory system that is especially sensitive to imagery and the processing of meaning? Open any memory textbook and you will find little discussion about either the origins or functions of memory processes.

Instead, researchers focus on structural (or proximate) mechanisms. When a memory effect is discovered—for instance, the discovery that forming a visual image benefits later retention of an item—it is "explained" by appealing to a set of general principles or processes—for example, elaboration (creating rich descriptions of the item in memory), contextual encoding (creating multiple representations of the item in memory), or the encoding–retrieval match (forming retrieval cues that are likely to be present in the retention environment). Thus, one might assume that visual imagery aids retention because it promotes elaborative encoding, produces dual mnemonic codes, or leads to especially accessible retrieval cues; self-generation of material from cues might encourage individual-item processing, making the traces of generated items easier to discriminate from nonoccurring items. Researchers seek to identify the general processes at work, much the same way a chemist analyzes a compound by breaking it down into constituent elements.

The trouble with this kind of analysis, though, is that any complete understanding of structure—that is, the proximate mechanisms—is likely to demand some prior consideration of function. If memory evolved, shaped by the process of natural selection, then its structural properties should reflect their functionality (Tooby & Cosmides, 1992). Nature "selects" one physical design over another because that design has fitness value—it helps the organism solve an adaptive problem that, in turn, increases the chances of genetic transmission. The result is usually a tight fit between form and function; the selection pressure, or adaptive problem, constrains how and why the structure develops and the final form it takes. Thus, retinal cells are uniquely designed to process electromagnetic energy, the heart is uniquely designed to pump blood, and the kidneys are specially designed to help filter impurities. Analyzing these physical structures without reference to their function is inconceivable, yet a similar functional analysis is rarely applied to remembering (at least in the human domain—for some relevant animal work, see Domjan, 2005; Shettleworth, 1998).

One could attempt to provide functional explanations for the mnemonic phenomena we mentioned earlier. For example, one might argue that cognition developed in the service of action, so embodied encodings (e.g., generating or forming a visual image) are beneficial to retention because they are congruent with the way our cognitive processes are designed to operate. However, post-hoc accounts—so-called "just-so stories"—often represent the scourge of evolutionary analysis (Gould & Lewontin, 1979). Our laboratory has advocated a different approach, one that essentially starts from scratch. We have attempted to identify the selection pressures that may have shaped the

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evolution of memory, to generate a priori predictions, and then to design appropriate empirical tests. As we will illustrate, thinking in such a functional manner can lead to new and potentially rich avenues of empirical investigation.

WHY DID MEMORY EVOLVE?

The starting point of a functional analysis is to speculate about the adaptive problems that our memory systems evolved to solve. If we can identify those problems, or selection pressures, their "footprints" should be recognizable in the operating characteristics of the system. Identifying ancestral selection pressures—the so-called "environment of evolutionary adaptedness"—can be a hazardous business, but we join others in believing that such an analysis is possible and heuristically useful (Hagen & Symons, 2007). At the very least, we can generate reasonable hypotheses about the likely (or unlikely) characteristics of any evolved memory mechanism. We offer three here.

First, it is unlikely that memory and its associated mechanisms evolved simply to remember the past. There is little adaptive value in designing a system to recover the veridical past, given that the past can never occur again (at least in exactly the same form). Instead, our memory systems must be engineered to use the past in the service of the present, or perhaps to predict the likelihood of events occurring in the future (Suddendorf & Corballis, 1997; Tulving, 2002). The fact that memory is fundamentally constructive rather than reproductive, often laced with relevant but "false" recollections, provides prima facie evidence for this claim (Schacter & Addis, 2007).

Second, evolved memory mechanisms are likely to be domain-specific, or sensitive to content; they should be tuned to remember certain kinds of information. A memory system that treats all environmental events the same would be maladaptive because not all events are equally important from a fitness perspective—for example, it is particularly important to remember the food source, the predator, or the appearance of a potential mate. Such tunings might develop with experience, but environments can be "clueless," failing to deliver the necessary inputs, and selectivity is required in storage (Tooby & Cosmides, 1992). If we simply stored everything we encountered, our minds would fill with clutter. We need a way to discriminate important from unimportant input, as well as mechanisms to clear away mnemonic clutter once it accumulates (M.C. Anderson, 2003).

Third, and related to the second point, memory mechanisms should be geared especially to helping us perform actions that enhance our reproductive fitness. Again, memory did not develop in a vacuum; memory mechanisms evolved as design "solutions" to problems associated with fitness. Remembering the location of food, an activity preferred by a mate, or perhaps individuals who violate social contracts are likely to improve the chances of successful reproduction, which, in turn, sets the stage for structural modification via descent (Darwin, 1859). Table 1 provides a list of potential candidates for domain-specific mnemonic processes. We make no claims about the proximate mechanisms that might underlie such memory "tunings"—such as separate systems or adaptations—but enhanced retention in situations such as those listed in Table 1 would likely confer a selection advantage.

SURVIVAL PROCESSING ENHANCES RETENTION

Despite more than a century of sustained laboratory investigations, researchers have little to say about how human memory operates in functionally relevant situations. J.R. Anderson and Schooler (1991) detected a strong correspondence between how information naturally recurs in the environment and standard forgetting functions, suggesting that retention depends on the likelihood that information will be reencountered and needed. Silverman and Eals (1992) suggested that women may be better equipped than men to remember information in fixed locales, perhaps because of how labor was divided during early environments of adaptation. Overall, however, functionally driven studies of human memory remain relatively rare.

Our laboratory has begun examining several examples of "adaptive memory," but we restrict our discussion here to survival processing. Given that reproductive fitness is contingent on survival, it is reasonable to hypothesize that our memory systems are specially engineered to retain information relevant to survival. As noted above, it should be easier for us to remember fitness-relevant information, things such as the location of food or the appearance of a predator, than fitness-irrelevant information.

Empirically, there are several ways to test this "survival" hypothesis. For example, one could pick stimuli that seem inherently related to fitness and assess their mnemonic value. Is it easier to remember survival-relevant words such as *corn*, *meat*, or *bear* than it is to remember control words matched on other relevant dimensions? Is there an s-value (survival value) associated with a stimulus that predicts its memorability in the same way that imageability (concreteness) or word frequency predict retention? Perhaps, but survival relevance is likely to be context dependent. 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.

For this reason, we have focused primarily on how survival *processing* affects retention, much like one might ask how forming a visual image or assessing meaning affects retention. If an event is processed in terms of its survival value, from the perspective of a survival context, is that event subsequently remembered better? From an evolutionary perspective, domain-specific memory mechanisms are likely to have specific input criteria and to be activated only by specific cues. For instance, an evolved cheater-detection mechanism presumably operates only during the processing of social contracts, predator-avoidance systems in the presence of a predator, and mate-selection mechanisms in an appropriate social context. Certain events

TABLE 1

Potential Candidates for Domain-Specific Mnemonic Processes

Survival-related events	Food (edible vs. inedible), water, shelter, medicinal plants, predators, prey
Navigation	Landmarks, constellations, weather patterns
Reproduction	Physical and social characteristics of potential mating partners and rivals
Social exchange	Altruistic acts, reciprocation, violation of social contracts, social status or hierarchy
Kin	Physical features and social actions of kin versus non-kin

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

such as the appearance of a spider or snake might automatically induce survival-relevant processing (Öhman & Mineka, 2001), but here again it is the way the stimulus is processed that is important rather than its meaning per se.

In our experiments (Nairne, Thompson, & Pandeirada, 2007), participants imagine themselves in a survival situation and then rate the survival relevance of arbitrarily selected words (see Table 2 for the instructions). We use randomly selected words (e.g., *stone*, *meadow*, *chair*) because, again, we are interested in how the qualitative aspects of processing (e.g., whether or not it is survival-based) affect retention generally. After the rating task, everyone is given a surprise memory test for the rated words. Figure 1 shows final free-recall performance after the survival rating task compared to two control conditions—a pleasantness rating task and a task asking about the relevance of words to a scenario about moving to a foreign country. Rating for survival relevance presumably requires "deep" (or meaningful) processing, so it is important to use control conditions that require meaningful analysis as well. Pleasantness is a standard deep-processing control and the moving condition was included to control for schematic processing. One might argue, for example, that the survival task requires highly self-relevant decisions in an imaginally rich and coherent environment (the grasslands of a foreign land); the moving condition was designed to induce similar processing, but in a context that was not survival-relevant.

Figure 1 shows clearly that survival processing enhanced retention compared to the two control conditions, a result consistent with our hypothesis that memory systems are "tuned" to remember fitness-relevant information. We have replicated this survival effect in a number of experiments, using both within- and between-subject designs and recall and recognition as the retention measures. Moreover, importantly, we have also ruled out a number of uninteresting explanations for the advantage, including the possibility that survival processing simply requires more processing effort or is congruent with a wider range of input stimuli. The effect occurs reliably when the unit of analysis is the participant or the item, and is typically found even when stimuli themselves are rated as irrelevant to the survival scenario. We have also found that the survival advantage remains robust when compared against other encoding scenarios that are not fitness-relevant, such as vacationing at a fancy resort in a foreign land (Nairne, Pandeirada, & Thompson, 2008) or planning a charity event with animals at the local zoo (Nairne & Pandeirada, 2007).

To place the comparative value of survival processing in perspective, we initiated a large study pitting survival processing against some traditionally powerful encoding techniques—a veritable "who's who" of known encoding procedures (Nairne et al., 2008). Separate groups of participants were asked to rate unrelated words for their relevance to a survival scenario, their pleasantness, the ease of generating a visual image of them, or the ease of generating an autobiographical memory of them, or they were asked to generate a word from scrambled letters. We also included an intentional learning condition in which participants were asked to remember the words for a later test. Each of these procedures is known to produce excellent long-term retention—in fact, these are among the best encoding techniques available in the arsenal of the memory researcher—yet

TABLE 2

Scenarios Used in Nairne, Thompson, and Pandeirada (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'll 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's 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'll 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's 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's up to you to decide.

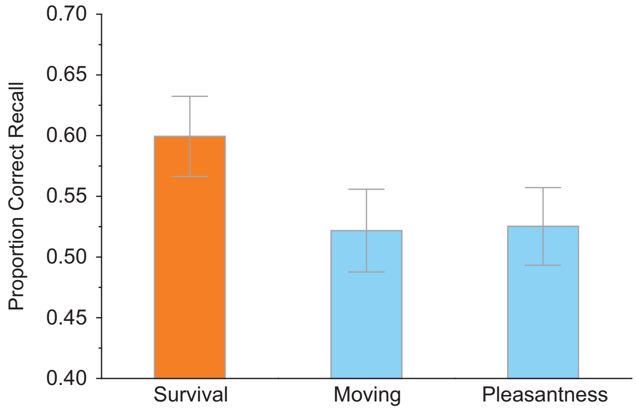

Fig. 1. Average proportion correct on a surprise free-recall test for three groups of participants. The three groups previously rated random words for their pleasantness or for their relevance to a survival scenario or a moving scenario. Data from Experiment 1 in Nairne, Thompson, and Pandeirada (2007). Error bars indicate 95% confidence intervals.

once again, a simple decision about relevance in a survival scenario was sufficient to produce the best recall performance. The data, shown in Figure 2, suggest that survival processing is one of the best encoding procedures yet identified in human memory research.

DOMAIN-SPECIFIC MEMORY MODULES?

If memory is an adaptation engineered to solve problems of reproductive fitness, then it is not surprising that survival processing produces excellent retention. We might also expect that processing information about social contracts, the receipt of altruistic acts, or potential mating partners should improve retention as well. However, at this point the data say very little about the proximate mechanisms that underlie the survival advantage in memory. One could appeal to standard memory processes to explain it. For example, assessing survival relevance might induce people to encode items into a rich, elaborate, and particularly accessible retrieval framework; alternatively, perhaps thinking about survival increases arousal, interest, or emotionality, which, in turn, enhance retention (see Nairne et al., 2007, for further discussion).

Using the physical body as our guide, one is inclined to look for functional specialization or modularity. Just like the organs of the body are specialized to perform particular functions, so too might mnemonic “organs,” or processes, be specialized to recognize and retain information relevant to fitness. Recent advances in cognitive neuroscience are broadly consistent with such a view—for example, evidence for a face recognition system (Farah, 1996)—although debates about the proper defining characteristics of systems and modularity continue. From the standpoint of evolutionary theory, it seems unlikely that nature would have developed a memory-based “survival module” per se. The concept of survival is simply too general; instead, memory adaptations are likely to be more specific—for example, a predator retention system—to reflect the specificity of most selection pressures (see Tooby & Cosmides, 1992). Processing for survival may well activate a number of domain-specific processes, each designed to maximize subsequent retention.

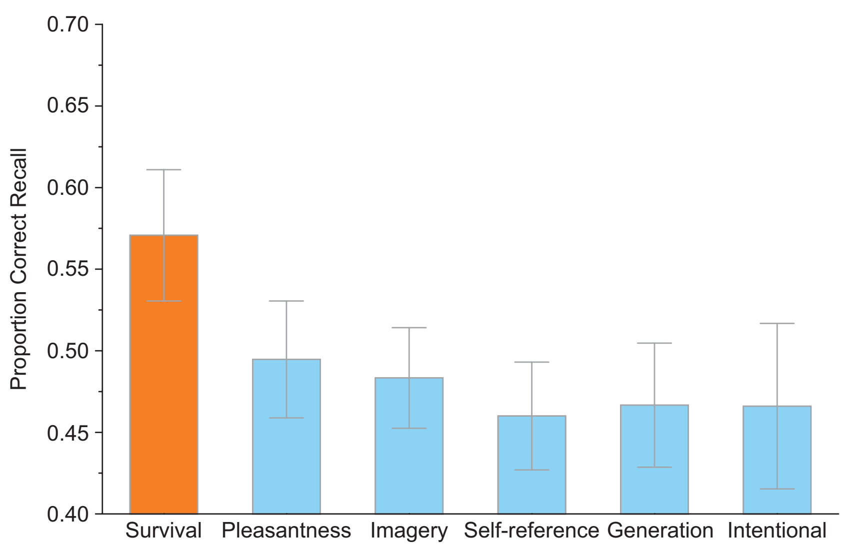

Fig. 2. Average proportion correct free recall for each condition. Separate groups of participants were asked to rate unrelated words for their relevance to a survival scenario, their pleasantness, the ease of generating a visual image of them, or the ease of generating an autobiographical memory of them, or they were asked to generate a word from scrambled letters. An intentional learning condition, in which participants were asked to remember the words for a later test, was also included. Data from Experiment 1 in Nairne, Pandeirada, and Thompson (2008). Error bars indicate 95% confidence intervals.

Regardless of the specific mechanisms involved, our memory systems probably do possess design features that are tuned to particular selection pressures. The capacity to remember would not have evolved without some fitness-enhancing properties; moreover, as noted earlier, storage systems that are insensitive to content, although flexible, lack sufficient constraints to be adaptive. At the same time, despite the logical appeal of domain-specific memory adaptations, we cannot presently offer a strong empirical case for their existence in people. Relevant data do exist for nonhuman animals (see Sherry & Schacter, 1987), but building the case for mnemonic "adaptations" in humans requires considerably more data than currently exist. For example, it will be important to show that the properties of the memory process help to solve a specific adaptive problem in a well-engineered fashion (see Cosmides & Tooby, 2005).

One of the overall advantages of adopting a functional perspective, though, is that it lends itself easily to the generation of new research ideas. As noted earlier, we know little about how memory operates in functionally relevant situations. Thinking functionally—asking questions about the "why" of remembering—should help open new research pathways and, ultimately, provide the necessary empirical and theoretical structure to discover "how" memory operates as well.

Recommended Reading

Gangestad, S.W., & Simpson, J.A. (Eds.), *The evolution of mind: Fundamental questions and controversies*. New York, NY: Guilford Press. A set of concise, focused essays directed at key issues in evolutionary psychology.

Klein, S.B., Cosmides, L., Tooby, J., & Chance, S. (2002). Decisions and the evolution of memory: Multiple systems, multiple functions. *Psychological Review*, *109*, 306–329. An evolutionary analysis of memory function as it pertains to decision making and trait judgment.

Nairne, J.S. (2005). The functionalist agenda in memory research. In A.F. Healy (Ed.), *Experimental cognitive psychology and its applications* (pp. 115–126). Washington, DC: American Psychological Association. A comparison of functional and structural approaches to the study of remembering and the implications of each for memory principles.

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