Adaptive Education: Learning and Remembering with a Stone-Age Brain

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Abstract

Educators generally accept that basic learning and memory processes are a product of evolution, guided by natural selection. Less well accepted is the idea that ancestral selection pressures continue to shape modern memory functioning. In this article, I review evidence suggesting that attention to nature's criterion—the enhancement of fitness—is needed to explain fully how and why people remember. Thinking functionally about memory, and adopting an evolutionary perspective in the laboratory, has led to recent discoveries with clear implications for learning in the classroom. For example, our memory systems appear to be tuned to animacy (the distinction between living and nonliving things) which, in turn, can play a role in enhancing foreign language acquisition. Effective learning management systems need to align with students' prior knowledge, skill, and interest levels, but also with the inherent content biases or "tunings" that are representative of all people.

Keywords Adaptive memory · Evolution · Survival processing · Animacy · Adaptive education

As every instructor knows, students arrive in the classroom with preexisting skills, interests, and proclivities. If study materials can be aligned with these "priors," learning benefits. This is the signature assumption of *adaptive education*, in which learning management systems are tailored to the unique profile of the learner (e.g., Martin et al., 2020). The evidence for individual learning "styles" (e.g., visual learners) is questionable (see Pashler et al., 2008), but people do differ, and teaching pedagogies must be flexible enough to adapt to students' prior knowledge, skill, and interest levels, as well as their moment-to-moment performance in the classroom. Compatibility between learning strategies, materials, and the student is a key ingredient of success in the classroom.

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At the same time, not all forms of compatibility will reflect the idiosyncratic life history of the student. Our learning management systems should also align with any natural "tunings" or innate content biases that are representative of all human learners (Geary, 2002; Geary & Berch, 2016). The capacity to learn and remember is a product of evolution, guided by the criterion of fitness. Heritable traits that increase the chances of reproduction, either directly or indirectly by enhancing survival, gain traction in the architecture of the species across generations. Importantly, this means that the footprints of nature's criterion—the enhancement of fitness—are likely present in the operating characteristics of basic biological and psychological systems.

For example, in vision the spectral sensitivities of primate cone receptors reflect a visual system that evolved partly to detect ripe fruit or edible leaves (Regan et al., 2001), meaningful variations in primate face color (Hiramatsu et al., 2017), or possibly the detection of snakes in the grass (Isbell, 2006). The frequency range of spoken language coincides with the region of heightened auditory sensitivity in humans (Quam et al., 2012). Our reasoning skills appear tuned to problems of social exchange, such as the ability to detect cheaters and violations of social contracts (Cosmides et al., 2005). In simple learning contexts, such as Pavlovian conditioning, the relation of cue-to-consequence is important—in rats, for example, taste predicts gastric distress better than a flashing light, presumably because animals are prepared by evolution to learn about tastes that signal gastric problems (Garcia & Koelling, 1966; Krause, 2015). Evolution, guided by natural selection, has shaped the fundamentals of mind, including its limitations (e.g., Sweller, 2016), to enhance the chances of survival and reproduction.

Evolutionary educational psychology seeks to align instructional design with our evolved cognitive architecture to improve educational outcomes. Obviously, most of the material that is taught in the classroom is secondary knowledge (i.e., non-evolved academic activities such as learning to read; see Geary, 2002) which may not match up well with inherent cognitive biases, problems directly related to survival or reproduction, or general student interest. However, we can manipulate the learning context (examples, materials, and processing), along with the style of instruction (e.g., explicit instruction versus discovery learning), to bring material more in line with those natural tunings. It is possible, for example, that framing secondary knowledge in fitness-based terms or contexts may reduce the cognitive load needed for effective processing and retention (see Sweller, 2020, for a discussion of cognitive load theory). Indeed, recent evidence suggests that the rules of formal logic may be easier to learn, or students might be more motivated to learn, if the example content is fitness-relevant (e.g., food, animal characteristics; see Lespiau & Tricot, 2019).

In the present article, my focus is on human memory, and I will identify some specific content biases or mnemonic tunings that have relevance for educational practice. Like other cognitive systems, our capacity to remember did not arise in a vacuum nor is remembering quite as general as researchers typically assume. An infant must remember its mother's face, more so than a wall hanging in the nursery; our ancestors needed to remember the location of food rich in calories, more so than foodstuffs that were low in nutritious value. From an evolutionary standpoint, events are not created equal—content matters. As I will show, this conclusion is bolstered

by recent research on the memorability of fitness-relevant information. I review this research and then consider how such natural "tunings" might be exploited in the classroom. To begin, however, I consider the advantages and pitfalls of adopting an evolutionary perspective on remembering. Evolutionary accounts remain controversial, for a variety of reasons, and it is worthwhile considering the arguments, pro and con. Evolutionary perspectives can have great value in research and application and, as I argue, they need not conform to the stereotypical characterizations that are often reported in the psychological literature.

Adopting an Evolutionary Perspective

The idea that our learning and memory systems are tuned to specific content, or serve as solutions to adaptive problems, remains novel to most cognitive psychologists. This is partly because students of memory have rarely shown much interest in the origins of the empirical regularities that arise in their data. Why do our memory systems work the way they do? Imagine you were designing a memory system from scratch—would you make it sensitive to the spacing of material and show a negatively accelerated retention function or a retention bias for things that occur near the beginning or end of a sequence? Cognitive researchers generally ignore these questions (for an exception, see Anderson & Schooler, 1991); instead, they are satisfied with documenting regularities, developing models to fit the data, and applying those regularities to real-world problems. The goal is to build a model of cognition that fits empirical data. The modern memory researcher tries to formulate assumptions that produce negatively accelerated forgetting, such as a constantly changing context, rather than attempting to discover why we have memory systems that work this way.

But understanding the origins of memory processes—the source of their limits and tunings—is instructive for many reasons. Perhaps most important, if our cognitive systems evolved in the service of nature's criterion of fitness, then their operating characteristics will likely reflect the adaptive problems they were designed by nature to solve. In vision, as noted earlier, spectral sensitivities arose as a response to selection pressures present during ancestral environments; the same should be true for our memory systems. The limited capacity of working memory, a system critical to executive functioning and the basis for retention over the short term (e.g., Baddeley, 2012), is a case in point. Psychologists first documented capacity limits decades ago—i.e., the magic number 7 plus or minus 2 (Cowan, 2005; Miller, 1956)—but have traditionally offered no reason for why these limitations exist. Given the enormous capacity of long-term memory—we can remember thousands of images presented for a few seconds each (see Brady et al., 2008)—why constrain our short-term system in such a significant way? The answer lies partly in a critical adaptive problem that our working memory system needs to solve—predicting future perceptions and actions accurately. As Trapp et al. (2021) explain, to avoid exponential explosion of possible outcomes, it is essential to constrain the number of active environmental representations in mind. Form follows function in this case—capacity limits are a critical feature of a system designed to generate predictions about

the future, not simply to maintain information in the present. Without a functional analysis—one that considers the adaptive problems that shaped the evolution of a system—we are unlikely to understand how the system works or how to maximize its functioning.

Still, the field remains skeptical about functional or evolutionary reasoning. In fact, evolutionary analyses are anathema in modern cognitive psychology, as evidenced by a failure to find evolution mentioned in most textbooks or in talks at the major conventions. This might seem shocking given psychology's close ties to biology, where everything is seen through the lens of evolution, but one can raise legitimate concerns about the viability of evolutionary approaches to human cognition. For example, to qualify as an evolutionary adaptation—an inherited specialization that was built by natural selection—one typically needs evidence that the trait is heritable or promoted across generations through differential reproduction. In addition, at some point in our ancestral past, there must have been individual differences among people along the trait dimension and evidence that certain *forms* were *selected* because they promoted differential survival and reproduction relative to other forms. This kind of historical evidence is unavailable for cognitive traits, which cannot be fossilized, although it is possible to do comparative analyses across species to some extent (see Krause, 2015).

There is considerable evidence that basic learning processes, such as Pavlovian conditioning, can promote differential survival and reproduction, but the data are largely confined to nonhuman species (e.g., Hollis, 1997). Cues that signal the appearance of a sexually receptive mate trigger more efficient mating behavior, along with physiological changes that promote reproduction (such as increased sperm production; for a recent review, see Krause & Domjan, 2022). Moreover, using fruit flies, Dunlap and Stevens (2014) were able to show that a form of prepared learning—color or odor cues that predicted an aversive chemical—could be selected for across generations. Data such as these demonstrate that content biases or "tunings" could certainly have evolved, but any direct genetic evidence in humans remains unavailable.

Evolutionary analyses raise other concerns. For example, it is often argued that we lack the necessary historical information about cognitive processing—e.g., its antecedent forms—and we can only speculate about the selection pressures that may have been present in ancestral environments (Buller, 2005). Another concern is the potential for post hoc reasoning about the causes of behavioral patterns—what are often described as "just-so" stories (Gould & Lewontin, 1979). For example, it is well-known that practicing retrieval or testing enhances recall for educational materials (Roediger & Karpicke, 2006). One might argue that retrieval is such an effective learning procedure because for most of our evolutionary history, retrieving previously presented information was the only route to re-exposure—put simply, there were no paper or writing tools in the Pleistocene. But this is a "just-so" story, emblematic of the reasoning that is rightly criticized by most cognitive psychologists. Cognitive psychologists accept that cognitive processes evolved through natural selection but are unwilling to speculate about evolutionary roots when the necessary information to validate the claims is likely unavailable.

However, it is possible to take a different approach. Rather than attempting to reverse engineer existing empirical regularities, by speculating about possible evolved features that might explain the patterns, we can rely on a technique called *forward engineering* (see Nairne, 2015). Empirical predictions are generated a priori by focusing on the recurrent adaptive problems that are known to drive natural selection—e.g., finding food, avoiding predators and disease, and finding a suitable mate. Given nature's criterion of fitness, it is reasonable to assume that such problems shaped how our cognitive processes developed. For instance, from a fitness standpoint it makes sense for us to preferentially notice and remember living things; predators are animate beings as are prospective mating partners. Consequently, we might expect memory to be biased or "tuned" to the animate characteristics of stimuli. Notice this proposal about a potential memory bias is not a just-so story—it is an empirical prediction that can be verified or falsified in the laboratory.

The Adaptive Memory Project

Over the past 15 years, the strategy of forward engineering has led to the discovery of novel empirical phenomena, including the fact that animate items are indeed remembered better than inanimate items (Nairne et al., 2013). In each case, the research has been guided by the prediction that our memory systems will perform especially well when dealing with fitness-based events—more specifically, we will preferentially remember things associated with survival and/or reproduction. At first glance, this prediction may seem obvious or even trivial. Whenever a fitness-related event occurs in our life—e.g., something survival-related—we repeat it endlessly to friends and neighbors (e.g., encountering a dangerous animal while camping; barely avoiding a swerving car in the snow; developing COVID-19). These are typically some of our strongest memories. But there is a difference between relying on personal anecdotes and demonstrating a true content bias in the laboratory.

To begin, there are important methodological obstacles that need to be overcome. It is easy to compare the retention of fitness-relevant and irrelevant events in the laboratory. For example, one could compile a list of disgusting and non-disgusting items, ask people to learn the list, and then look for a retention advantage for the disgusting items, which are presumably fitness-relevant (see Tybur et al., 2013). However, disgusting and non-disgusting events differ in many ways besides fitness-relevance (e.g., emotionality, frequency of occurrence, interest), so it can be difficult to isolate the responsible property. More importantly, the term "fitness-relevance" is slippery and hard to define. Invoking the image of a tiger or a snake might seem fitness-relevant but only if encountered in the wild; seeing a tiger in the zoo does not engender the same kind of survival reaction. Even innocuous items such as a book or a pencil, nominally irrelevant to fitness, can become relevant under attack (a book can be thrown or a pencil can be used to stab or write a message for help). Put simply, fitness-relevance is context-bound. As Nairne and Pandeirada (2008) said: "food is survival relevant, but more so at the beginning of a meal that at its completion; a fur coat has high value at the North Pole, but low at the Equator" (p. 240).

Consequently, it is unlikely that evolution filled our brains with survival "templates" representing particular survival-relevant events. Certain events may be naturally fear-inducing—e.g., looming objects or possibly spiders (Gerdes et al., 2009)—but we are more likely to rely on an attribution process, one that uses multiple cues, including the situation at hand, to arrive at a decision about survival relevance. The "fight or flight" response works this way. A car hurtling toward us as we cross the street is not part of an inherited toolkit of natural events, but it is sufficient to trigger a fight-or-flight response; we use learned experiences as well as natural biases to arrive at a split-second "decision" about danger. Once the attribution process is complete, and a survival context is identified, the sympathetic nervous system kicks into gear and our bodies respond appropriately. Fight-or-flight is part of a general survival system that coordinates the body's reaction to threat (e.g., Mobbs et al., 2015). Adaptive memory theory assumes that one component of the threat reaction is enhanced retention of threatening material and its associated context. After the situation is classified as fitness-relevant, survival-based processing of the event occurs and retention for its contents improves. The procedure described below is designed to simulate such a process in the laboratory.

The Survival Processing Paradigm

The idea that memory is a product of how an item is interpreted or processed, rather than inherent characteristics of the item itself, is consistent with mainstream thinking in cognitive psychology. Craik and Lockhart (1972) tied retention to perceptual processing, arguing that the strength of the memory trace is determined by the level or depth of perceptual processing obtained. "Depth" in this case was defined in terms of a perceptual hierarchy ranging from shallow types of analysis (orthographic or phonological) to more complex forms of semantic processing (meaning or gist). Empirical studies, using incidental learning in which final retention tests are not anticipated, have provided considerable support for the "levels" view (e.g., Craik & Tulving, 1975). Given the same material (usually lists of unrelated words), very large differences in retention can be obtained by directing a person to focus on deep (how pleasant is this word?) versus shallow (does the word contain any capital letters?) forms of processing. What matters to memory, according to the consensus, is how the material is processed, not the material itself.

Notice, though, that there is nothing in the levels of processing framework that relates to survival or evolutionary fitness. In fact, there is nothing about depth or semantic processing that guarantees enhanced survival or reproduction. Given the criterion driving natural selection, memory likely evolved because of the advantages it produced in fitness-relevant situations—e.g., remembering a food source, predator location, or the movements of a prospective mating partner. From this perspective, the processing of meaning or gist, the bedrock driver of retention in levels of processing, is likely derivative of forms of fitness-based processing (see Nairne, 2010). It was the processing and retention of fitness-relevant events that promoted the evolution of memory, not semantic processing per se. This is not meant to be a just-so story; instead, it is the basis for an empirical prediction. Because our memory

systems evolved using a criterion of fitness, fitness-based processing should provide a better fit to the operating characteristics of remembering and, therefore, produce better long-term retention than other forms of semantic processing.

To test this idea, Nairne et al. (2007) developed a procedure that mimicked the traditional levels of processing experiment (Craik & Tulving, 1975): Participants were given lists of unrelated nouns and asked to process each item in a predefined way prior to an unexpected retention test. In the critical condition, people were asked to think about the relevance of each item to a survival situation. People were asked to imagine that they were stranded in the grasslands of a foreign land; over the next few months, they would need to find food and water and protect themselves from predators. People were then required to rate the relevance of individual words to the survival context. For example, how relevant might the words "book" or "rock" be to surviving in the grasslands using a scale from 1 (totally irrelevant) to 5 (extremely relevant)? After the rating task, everyone was given a surprise free recall test (i.e., "recall all the words you just rated in any order"). In the original series of experiments (Nairne et al., 2007), the comparison conditions included two traditional "deep processing" tasks (Craik & Tulving, 1975)—rating the items for pleasantness or for self-relevance—along with an additional condition that involved rating words with respect to a non-fitness relevant scenario (moving to a foreign land).

In each case, strong recall advantages were found for the survival processing condition. For example, survival processing led to a roughly 16% recall advantage over a self-reference condition, which is known to be an extremely effective encoding procedure (see Challis et al., 1996). In a follow-up study, survival processing was compared to a sampling of the "best of the best" encoding procedures, including such things as forming a visual image, self-generation, self-reference, and intentional learning. The survival condition produced the best retention in each case—e.g., a few seconds of survival processing, with no anticipation of a final memory test, produced better retention than purposeful memorizing of the words. These data, among others, led Nairne et al. (2008) to conclude that survival processing is "one of the best—if not the best—encoding procedures yet identified in human memory research, at least when free recall is used as the retention measure" (p. 180). In the decade and a half since the survival advantage was first reported, it has been replicated in laboratories across the world (for a recent meta-analysis, see Scofield et al., 2017), including as part of the now famous Open Science Collaboration project (2015). The advantage is found in retention tests other than free recall, including recognition, source memory, and spatial memory tests, and is robust in young children (Aslan & Bäuml, 2012; Otgaar et al., 2010) as well as in both healthy and cognitively impaired older adults (Nouchi, 2012; Pandeirada et al., 2014).

The empirical power of survival processing is well-established, but its interpretation remains controversial. Many memory researchers have been reluctant to accept the evolutionary account, choosing instead to explain the advantage using standard mnemonic tools (see Erdfelder & Kroneisen, 2014). For example, survival processing could be considered as a "deeper" form of semantic analysis, inducing greater amounts of elaborative processing than control conditions. The details of this debate are beyond the scope of the present article and can be found elsewhere (e.g., Nairne & Pandeirada, 2016). Some interpretive concerns

have been methodological, focusing on use of a proper control condition. Even though everyone is asked to remember the same material, asking people to think about survival may encourage other forms of processing—e.g., unusual, distinctive, emotional—or the survival task itself may be inherently more interesting than rating an item for pleasantness or thinking about moving to a foreign land. These concerns have been largely addressed in subsequent work (Nairne & Pandeirada, 2016). In one case, Nairne et al. (2009) used a matched-scenario design in which people rated the relevance of items to *exactly the same activities* but in a context that was either fitness-relevant or not. People rated the relevance of words to a hunting scenario, in which they were required to hunt big game, trap small animals, and fish, but either to survive or to win a hunting contest. Both scenarios required tracking and hunting for food, in the same way, but only the survival-based version was designed to induce fitness-relevant processing. Significantly better retention was found in the survival-based hunting group.

Moreover, it is not necessary to use a specific scenario to obtain the effect. Klein (2013) found a significant survival processing advantage when participants were simply asked to "imagine that you are trying to stay alive" (p. 52). In more recent work, participants were asked to generate their own survival situations rather than react to an experimenter-provided scenario (Nairne et al., 2019). The generation process was not constrained in any way other than it needed to be survival-related and refer to a target stimulus. For example, when given the word LAMP, a participant might respond "I threw the LAMP at an intruder as he barged through the door." The control conditions also required generation but in contexts that were not fitness-relevant (e.g., "Generate an instance from your personal life in which the target item was relevant."). Robust retention advantages were again found for the survival condition. One advantage of this generation procedure is that it decouples survival processing from any particular ancestral scenario (e.g., the grasslands), thus providing more flexibility in the use of control tasks (see Nairne et al., 2019, for details).

Inducing people to think about the relevance of material to a survival situation clearly leads to enhanced retention compared to standard encoding procedures. This result was predicted a priori from an evolutionary analysis, but it does not mean that we evolved some kind of special "survival module" that is activated only in survival situations. The encoding process itself might be quite general—that is, the same neural processes might underlie all forms of episodic retention—but simply activated more strongly when confronted with a fitness-relevant context. Because of nature's criterion, selection pressures would have favored mechanisms that promote the retention of fitness-relevant information, regardless of how those mechanisms are implemented. As noted earlier, our sensory systems show sensitivities that reflect the selection pressures that led to their development—we are most sensitive to wavelengths of light, for example, that are associated with ripe fruit or possibly edible leaves. But we use the same retina to process visual scenes that are not directly fitness-relevant.

The Mnemonic Effect of Animacy

Work on survival processing indicates that our retention systems may be tuned to survival contexts, but objects and events can be fitness-relevant in situations that are not immediately survival-relevant. We might expect social stimuli to be remembered better than nonsocial stimuli, for example, because of their potential relevance to fitness. In fact, posts from Facebook, which naturally elicit social thinking, are remembered far better than matched sentences from books or even faces (Mickes et al., 2013); similarly, people show better long-term recognition of Twitter posts than matched headlines from news sources (Bourne et al., 2020). More generally, as suggested earlier, animate (living) things, such as people and animals, should be remembered better than inanimate (nonliving) objects. Predators, prey, potential mating and social partners, and kin are all animates. Again, if designing a retention system from scratch, it would be reasonable to install a content tuning or bias for animate things—it is more important for a newborn to remember a mother's face than a wall hanging behind the crib.

The retention advantage for animate over inanimate stimuli is another a priori prediction derived from the application of forward engineering. Prior to the initial investigations of animacy effects and memory, no data existed on the question except for some interesting neurological deficits tied to animacy. Some patients lose the ability to name living things, such as animals, but not nonliving entities (Caramazza & Shelton, 1998). However, there was ample evidence from other research domains that animacy is an important variable in cognitive processing. The animate-inanimate distinction is a central component of cognitive development, for example, organizing children's experiences from an early age (Opfer & Gelman, 2011). Newborns are sensitive to the motion cues that drive the perception of animacy—for example, 2-day-old babies prefer to look at biological motion compared to non-biological motion; (Simion et al., 2008). Infants' early understanding of causality has been linked to the development of animate agency. By 10 months, infants use animacy cues (e.g., the presence or absence of eyes) to classify objects (Kominsky et al., 2022) and by early childhood use such cues to draw inferences about item properties (such as whether an object has "insides"). Most children show an affinity for animate things, and children's movies often assign animate properties to inanimate objects.

Perceptually, people seem to have a "tripwire" for animacy. We famously impart animacy to inanimate objects that move in animate ways (Heider & Simmel, 1944); people also attribute animacy to inanimate objects moving randomly if other cues evoke animacy (e.g., the wolfpack effect; Gao et al., 2010). Animate objects are also more likely to capture visual attention. For example, people are more likely to detect change in the change-detection paradigm if the change involves an animate being (Altman et al., 2016; New et al., 2007). Similarly, people respond more quickly in a detection task when the target objects show animate movement (Pratt et al., 2010). Animacy advantages have been detected in other classic attention paradigms as well, such as the Stroop task (Bugaiska et al., 2019) and the attentional blink task (Guerrero & Calvillo, 2016).

To assess whether the animacy advantage extends to memory, Nairne et al. (2013) adopted two strategies. First, using existing free recall norms (Rubin & Friendly, 1986), regression techniques were applied to assess how well animacy predicted recall outcomes. When the study began, there were no animacy norms, so independent raters were asked to make judgments about the words on a 5-point scale: Words that clearly represented a nonliving thing were coded as 1 and words clearly representing a living thing as 5. It is worth noting that animacy is not an unambiguous dimension—there are words, such as virus, blood, devil, or society, that are not easily categorized as animate or not. Once collected, these ratings, along with existing normative values for other dimensions relevant to recall, were subjected to a series of regression analyses. The results revealed that animacy is one of the strongest predictors of recall, at least as strong as imagery, word frequency, or familiarity. Since this initial work, a more complete data set of 1200 concrete nouns have been normed for animacy along with 15 other known word dimensions (see VanArsdall & Blunt, 2022). Principal component analyses established that the animacy scales were conceptually different from other existing word variables. Madan (2020) used these norms, also published in VanArsdall (2016), to predict free recall data from the Penn Electrophysiology of Encoding and Retrieval Study (PEERS; available at http://memory.psych.upenn.edu/Penn_ Electrophysiology_of_Encoding_and_Retrieval_Study) and replicated the strong relationship between recall and animacy ratings (Nairne et al., 2013). Interestingly, Madan (2020) also found that two fitness-related properties (danger and survival-usefulness) were robust predictors of recall.

Nairne et al.'s (2013) second empirical strategy was to compare the recall of matched animate and inanimate words in the same experiment. Two pools of words were created—one animate and the other inanimate—which were then matched on ten different dimensions including age of acquisition, category size, category typicality, concreteness, familiarity, frequency, imagery, meaningfulness, semantic relatedness, and word length. The animate and inanimate words were then intermixed in lists that participants were asked to study for a retention test. Strong recall advantages were found for the animate words. Considerable follow-up work has been conducted since the original demonstration and, like the survival processing advantage, the animacy advantage replicate across a variety of retention tests, word pools, subject characteristics, and encoding manipulations. For example, large animacy advantages are found in children and the elderly, in recognition memory, source memory, spatial memory, and paired-associate learning, and the effect remains under divided attention and deep and shallow forms of encoding (see Nairne et al., 2017a, Nairne et al., 2017b, for reviews).

Animacy advantages also extend to forms of animacy processing. To counter concerns about item selection confounds—again, it is difficult to control for all possible differences between item types—VanArsdall et al. (2013) gave people novel nonwords and paired them with properties characteristic of either animate (e.g., believes in God) or inanimate objects (e.g., has a round shape). People were asked to decide whether each item, which they were told were things they had never seen before and had unusual names, likely represented a living thing or an object, using the paired property to decide. Judgments were made on a 6-point scale ranging from 1 ("very likely to be an object") to 6 ("very likely to be a living thing"). After the

rating task, everyone received either a surprise recognition or recall test for the rated words. Across two experiments, memory was better when nonword "names" were associated with animate properties. Analogous to survival processing, memory for the same item varies depending on whether it is processed in a manner that is fitness-relevant (animate) or not (inanimate).

There is now a rich literature on animacy and memory. As with survival processing, much of the work has focused on determining the proximal "cause" of the animacy advantage. Some have argued, for example, that animate items might have richer semantic representations (Rawlinson & Kelley, 2021), lead to a richer form of elaborate encoding (Meinhardt et al., 2020), or recruit greater amounts of attention or emotional arousal (Leding, 2020; Popp & Serra, 2018). None of these explanations seem to account for the advantage completely (see Van Arsdall & Blunt, 2022), but research is ongoing.

Other Fitness-Relevant Dimensions

Work on adaptive memory has been concerned primarily with survival processing and animacy, but other fitness-relevant mnemonic "tunings" have been explored in the laboratory. For example, it is well-known that disgusting items tend to be remembered better than non-disgusting items, even when the items have been equated along potentially confounding dimensions such as arousal or emotion (e.g., Chapman et al., 2013). The emotion of disgust has clear adaptive value in helping organisms avoid ingesting potentially harmful foods or to avoid sickness and disease (e.g., Rozin et al., 2008; Tybur et al., 2013). Behavioral reactions to potentially contaminating items form part of the *Behavioral Immune System* (Schaller & Duncan, 2007) of which memory can be assumed to play an important role.

In the laboratory, Fernandes et al. (2017) investigated the mnemonic effects of contamination. As Rozin and Fallon (1987) have shown, people commonly believe that contact between objects can lead to a transference of the disgusting or contaminating properties. This spread of contamination is referred to as the "law of contagion," which holds that "once in contact, always in contact" (Frazer, 1959, p. 12, as cited in Coughtrey et al., 2014). People are reluctant to touch or wear clothing, for example, that has recently been worn by an undesirable person. Given that some infectious diseases can be transmitted directly through touch (fomite transmission), evolving systems that are sensitive to contact have clear adaptive value. Fernandes et al. (2017) were interested in whether people were more apt to remember an object if it had been recently touched by someone with a disease. Notice that this is another example of a novel empirical prediction generated by the strategy of forward engineering.

In these experiments (Fernandes et al., 2017), people were shown pictures of everyday objects along with short descriptors conveying information about the health status of a person who had recently touched the object. For example, a picture of a ball was shown along with the statement "person with a constant cough" or the statement "person with a straight nose." After every third item, the three preceding items were presented again and people were instructed to classify whether each had

been touched by a sick or a healthy person. This immediate test was included simply to ensure that people paid attention to the descriptor. After a series of these presentations, everyone was given a surprise free recall test for the presented objects. People performed close to perfect in the immediate memory task with no differences between the sick and healthy conditions. However, on the final test significantly more of the objects paired with descriptions of sick people were recalled than those paired with descriptions of healthy people—in other words, more of the potentially contaminated objects were remembered.

This result, enhanced retention of potentially contaminated objects, has now been replicated multiple times (e.g., Bonin et al., 2019; Gretz & Huff, 2019). In one replication Fernandes et al. (2021) used pictures of real objects held by hands that were either dirty or clean; participants were told that the dirty hands were covered with a substance signaling disease (e.g., vomit). In another case, objects were paired with faces containing disease-connoting cues, such as perioral dermatitis, conjunctivitis, or eczema. Again, the potentially contaminated items were remembered best (Fernandez et al., 2017). The effect even replicates when participants are simply told that the objects are being held by a person who has recently contracted the coronavirus that produces COVID-19 (Thiebaut et al., 2022). These data are consistent with the main assumption of adaptive memory theory—namely, that our retention systems show sensitivity to the kinds of fitness-relevant problems that likely led to their development.

There is also a growing literature on memory for eating and how those memories are affected by the fitness-relevance of the food consumed. There is a long history of research on taste aversions, primarily in nonhuman animals, but less work has been conducted historically on the episodic retention of food and the act of consumption (Seitz et al., 2021a). Some researchers believe that selection pressures related to eating and the search for high-value food content were particularly important to the evolution of memory, especially with respect to the success of foraging (e.g., Sherry et al., 1992). For example, there is evidence for a sex-difference in object location memory, favoring adolescent girls and women, perhaps because historically females were required to remember the fixed locations of food sources (Silverman & Eals, 1992; Voyer et al., 2007). Moreover, memory for how much you consumed in your last meal affects how much you will consume in the next one (Higgs, 2002), so we can reasonably anticipate that our memory systems are tuned, in part, to food consumption. Indeed, recent research suggests that memory for eating is enhanced relative to comparable actions in people and that the caloric density of the food consumed improves its later retention (Seitz et al., 2021b).

Finally, the fitness-relevant dimensions that we have considered so far relate primarily to survival, directly or indirectly, but it is reasonable to assume that similar biases exist for activities related to reproduction. Indeed, there is an extensive literature on the evolutionary psychology of sex and mating (see Buss, 2019) but, surprisingly, the memory work has revealed mixed results. Some studies support a sex- or mating-based content bias. For example, people remember more physical information about women when their physical characteristics, such as waist-to-hip ratio, signal health, and fitness (Fitzgerald et al., 2016). Women also remember more about the physical and personal characteristics of men when they are first told to

consider the man as a potential short-term mate (Horgan et al., 2016). Pandeirada et al. (2017) found that women retained the faces of men better when asked to consider how desirable the men would be as a long-term mating partner compared to a long-term work partner. However, when processing scenarios of the type used in the survival processing paradigm—for example, rate the relevance of words to a potential mating situation—little, if any, memory benefit is found (see Derringer et al., 2017; Sandry et al., 2013). As Nairne and Coverdale (2022) recently argued, it is almost certainly adaptive to remember information that helps to secure an effective mating partner, but at this point the existing evidence on the relationship between mating and memory remains somewhat equivocal.

Implications for Student Learning

Given the strong evidence for fitness-based content biases or tunings, how might they be applied to educational settings? This is potentially a very rich area for future investigation. Obviously, we cannot put our students in survival situations, present the lesson of the day, and then assess the outcomes. But there are educational materials and contexts that are relevant to fitness, and it is worth considering how well learning proceeds under these situations.

Barrett and Broesch (2012) investigated how using the label "dangerous" affects children's abilities to learn things about unfamiliar animals. Children aged 4 to 8 were shown flashcards of novel animals and told the animal's name, whether it ate other animals or plants, and whether it was dangerous or not. A week later, the flashcards were shown again, and the children were asked to recall the properties. Whereas recall of the names was poor after a week, hovering near chance, the children were quite good at remembering whether the animal was dangerous or not compared to the matched binary decision about eating habits. In a follow-up study, Barret et al. (Barrett et al., 2016) extended the procedure to include food and artifacts (e.g., unfamiliar tools and utensils) and obtained similar results. Children were most likely to remember whether an animal was dangerous ("could it hurt you?"), food was dangerous ("could it make you sick?"), or the artifact was dangerous ("could it hurt you if handled?"). The effect was found across two cultures (US children and the *Shuar* of Amazonian Ecuador), and, with respect to animacy, animals were remembered significantly better than the other two categories.

Prokop and Fančovičová (2017) found similar results in fifth and sixth grade students with the added twist that the memory target was the same animal presented across participants in either a neutral or aggressive posture. In this case pictures of familiar animals were shown (e.g., hyena, snow leopard, baboon), but the picture showed the animal in either an aggressive posture (e.g., with bared teeth) or not. Basic information including the name of the animal, where it lived, its food habits, and whether it was dangerous to humans was presented below the animal on each slide. Students were also asked to rate the animal for dangerousness and whether they felt the species should be protected by laws. In a later memory test, students remembered information about the animal better if it had been presented in an aggressive posture. This result is important, the authors argued, because animals

are among the most common subjects of photographs in science textbooks. Consequently, learning can be enhanced, the authors suggested, by altering the appearance of the animal when presented. Whether such a strategy would be useful on a wide scale, though, is unknown. Students susceptible to anxiety or rumination may not benefit and constant use of aggressive formats throughout a text might lessen their distinctiveness. But it could be an important technique for information deemed particularly important in a text.

Fančovičová et al. (2020) explored how well secondary school students could learn information about mushrooms, particularly their toxicity. People often have trouble discriminating between edible and poisonous mushrooms from appearance, so toxicity information is clearly adaptive to learn about. The students were shown color pictures of different mushrooms (half were toxic and half were not) accompanied by the name, where it occurs in nature (e.g., forest versus meadow) or whether it was toxic. After presentation, the pictures were presented again, and the students were tested for the name, occurrence information, or toxicity. Similar to Barrett and Broesch (2012), the students retained information about danger (toxicity) the best. In addition, Prokop and Fančovičová (2014) found that students in a high school class were able to retain more information about red and black fruits, colors that can signal ripeness, compared to green (i.e., unripe) fruits. In each case, the results were interpreted from an evolutionary perspective, namely, that survival-relevant information is retained better than survival-irrelevant information. It was further suggested that science educators could improve overall learning in biology classes by introducing toxicity as a salient dimension, when appropriate, during the lesson.

Several studies have established that animacy can enhance learning of novel words, which is a vital component of foreign language vocabulary acquisition. VanArsdall et al. (2015) asked people to learn unfamiliar Swahili words that were assigned various English "translations." The task required them to produce the appropriate English translation when given the Swahili word as a cue. Participants were unfamiliar with the Swahili words, so the translation targets were chosen to be either animate or inanimate but otherwise matched (e.g., *rembo*-duck versus *sahani*-stove). Everyone was required to learn the pairs such that they could produce the translation (duck) when provided the cue (*rembo*). Across repeated testing trials, a strong translation advantage was found for the animate pairs.

Laurino and Kaczer (2019) extended this finding to the recovery of a novel word's meaning. Once again, people were shown novel stimuli (nonwords) which were paired with a picture of an artificial object (taken from existing norms) and a definition (which was either an animal, furniture, or tool). People were later required to produce the name in response to the picture or the definition in response to the name. Significant memory advantages were found in both cases—people were better able to name the nonword and its definition if the nonword's referent had been animate. This animacy advantage was found after a 30-min retention interval as well as 48 h later. A test of lexical processing was also included, and the animate novel words were processed faster than the inanimate items, although this advantage was found only when the test occurred at the 30-min interval.

Animacy has also been shown to improve performance when using traditional mnemonic techniques, which are often applied in the classroom (e.g., Qureshi

et al., 2014). For example, the method of loci is an ancient technique in which a person forms a visual image of a place or location and systematically imagines adding to-be-remembered information to that location (e.g., in the different rooms of an imagined house). This is an extremely powerful encoding technique, one that is commonly employed by memory "athletes" in competition (Foer, 2011). Blunt and VanArsdall (2021) presented a list of matched animate and inanimate words and asked people to remember them using the method of loci or a traditional deep processing task (rating words for pleasantness); prior to word presentation, the participants were given thorough instructions on how to use the method of loci technique. Memory performance in the method of loci condition was far superior to the deep processing control, and, importantly, animacy significantly improved performance in each task.

In a follow-up experiment, the authors showed that the recall of inanimate words could also be improved if those words were associated with animate imagery (e.g., a kite attempting to escape). The idea that the processing of inanimate things can be improved by assigning the item animate properties is a familiar one. As discussed earlier, children are tuned to the presence of animate cues (e.g., eyes) and use those cues throughout cognitive development (Opfer & Gelman, 2011). It is not an accident that children's books, Hollywood movies, and Disney cartoons often bring to life inanimate things (e.g., cars, trees, houses). It attracts children's attention, increases likeability, and makes the actions more comprehensible and memorable. As the studies just discussed make clear, the same is true for adults. There is a rich literature on the effectiveness of pedagogical agents in virtual learning environments (e.g., Mayer & DaPra, 2012), and these benefits likely extend to inanimate "agents" as well. Animacy is a powerful and universal construct in human cognition and its role as a pedagogical tool in the classroom can certainly be exploited.

It is also possible that survival- or fitness-based content can be used to improve comprehension and retention of classroom materials. As mentioned briefly earlier, there is evidence that a fitness-based framing can affect the learning of formal rules of logic. Lespiau and Tricot (2019) had high-school students practice solving logic problems (syllogisms) with content that was fitness-relevant (food, animal characteristics) or not (grammar rules, mathematics). In the test phase, the syllogisms used neutral terms (ABC). Although no advantage was found for the fitness-relevant content on the final test, during training better performance was found for the problems with the fitness-based content; the students were also more motivated and experienced less cognitive load when solving the fitness-based problems. It remains to be seen how well manipulations of this kind—comparing fitness-relevant and fitness-irrelevant content—can be exploited in the classroom, but it is a promising avenue for future research.

It should also be possible to manipulate how students process educational content while it is being studied. There is an extensive literature on how the principles of cognitive psychology can be applied during study in the classroom (e.g., spaced practice, self-testing, blocking versus interleaving; see Dunlosky & Rawson, 2015, for a review), but very few at this point have focused on the application of adaptive memory. It would be easy to give students exercises requiring them to think about course content in a fitness-relevant manner. They could be asked to consider

the relevance of the material to a survival situation or to generate examples of how the material could be used in a fitness-relevant context. Such a strategy represents a form of elaborative interrogation, a technique that has been studied for decades in the educational literature, but with the added focus on fitness-relevance. Elaborative interrogation has been successful in helping students recall course content and, in some cases, improve comprehension (see Dunlosky et al., 2013). Directly comparing fitness-relevant and irrelevant interrogations would be an interesting extension of the interrogation technique.

Summary and Conclusions

To maximize performance in the classroom, it is important to recognize that our capacity to learn and remember did not arise from chance but rather evolved over generations in accordance with nature's criterion of enhanced fitness. Memory, along with other cognitive processes, is purposive; it was designed by nature because it improved the chances of successful survival en route to reproduction. As a consequence, the footprints of nature's criterion are likely present in the encoding and retrieval processes that underlie remembering. Just as we would expect the operating characteristics of an engineered product (e.g., an *iPhone*) to reflect its intended purpose—the problem that it was designed to solve—remembering should be sensitive as well to the adaptive problems that led to its development (see Nairne, 2005).

Over the past decade and a half, the adaptive memory project has produced strong evidence in support of this assumption. Fitness-based processing (e.g., in the form of survival processing) as well as fitness-relevant events (e.g., animate as opposed to inanimate things) shows robust retention advantages when compared to a variety of fitness-neutral control tasks or events. It is worth emphasizing that these control conditions have included some of the best-known encoding strategies in the memory field, including standard deep (semantic) processing, visual image formation, and intentional learning (see Nairne et al., 2008). Regardless of one's ultimate interpretation of these findings—evolutionary adaptations versus byproducts (see Nairne & Pandeirada, 2016)—the empirical advantages are well established and potentially useful across a range of applied domains.

In the present case, I have reviewed some applications of adaptive memory theory to educational domains, although this research remains in an early stage. Given the strength of adaptive memory effects in the laboratory, it seems likely that course content, or the methods of instruction, can be tweaked to align with the content biases demonstrated here. This is already the case in foreign language learning where it has been shown that animate translations are easier to learn than inanimate ones. Much of foreign language learning involves inanimate things, but it could be beneficial to introduce the animate translations first or to ask the students to use animate imagery throughout. As noted earlier, one of the main goals of evolutionary educational psychology is to align instructional design with our evolved cognitive architecture to improve educational outcomes. To obtain an adaptive educational design, it is necessary to consider the student's idiosyncratic proclivities but also the content biases and tunings that reflect the human species as a whole.

The adaptive memory project also demonstrates the value of thinking functionally about the learning process. Traditionally, researchers have investigated learning from a neutral perspective, one that seeks to document the empirical characteristics of learning first followed by reverse engineering of the obtained patterns. This strategy has led to successful models of the learning process, and applications in the classroom, but has remained silent on the origins and purpose of our knowledge acquisition systems. As the work reviewed here demonstrates, adopting a forward engineering strategy, one that focuses on the adaptive problems that our learning and memory systems evolved to solve, can lead to the discovery of novel empirical phenomena. These discoveries have added to our understanding of learning and memory in the laboratory, and it seems clear that they represent a rich source for future applications in the classroom.

Declarations

Conflict of Interest The author declares no competing interests.

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