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Adaptive memory: Ancestral priorities and the mnemonic value of survival processing

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ABSTRACT

Evolutionary psychologists often propose that humans carry around "stone-age" brains, along with a toolkit of cognitive adaptations designed originally to solve hunter–gatherer problems. This perspective predicts that optimal cognitive performance might sometimes be induced by ancestrally-based problems, those present in ancestral environments, rather than by adaptive problems faced more commonly in modern environments. This prediction was examined in four experiments using the survival processing paradigm, in which retention is tested after participants process information in terms of its relevance to fitness-based scenarios. In each of the experiments, participants remembered information better after processing its relevance in an ancestral environment (the grasslands), compared to a modern urban environment (a city), despite the fact that all scenarios described similar fitness-relevant problems. These data suggest that our memory systems may be tuned to ancestral priorities.

1. Introduction

The capacity to remember evolved, having been shaped and sculpted by the processes of natural selection. Specific selection pressures, related to survival and reproduction, conferred selection advantages to organisms capable of using the past in the service of the present. No scholar seriously questions these claims, although the functional properties of memory are rarely considered explicitly by modern memory theorists (Nairne, 2005; Klein, Cosmides, Tooby, & Chance, 2002). Instead, the main

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empirical and theoretical effort over the past century has been directed at understanding the proximate mechanisms that control performance on specific tasks—i.e., the "how" rather than the "why" of remembering (see also, Bruce, 1985; Sherry & Schacter, 1987).

Yet, from an evolutionary perspective, it is reasonable to ask whether vestiges of the selection pressures that led to memory's development remain apparent in its operating characteristics. If memory systems evolved to enhance fitness (survival and reproduction), then are organisms especially good at encoding and retaining material from fitness-relevant situations? This is ultimately an empirical question, one that need not suffer from the criticisms usually directed at investigations in evolutionary psychology (e.g., "just-so" and "Panglossian" reasoning; see Gould & Lewontin, 1979). Indeed, there is now substantial empirical evidence showing that memory is enhanced when people process information in terms of its fitness value (Kang, McDermott, & Cohen, 2008; Nairne, Thompson, & Pandeirada, 2007; Weinstein, Bugg, & Roediger, 2008). For example, Nairne, Pandeirada, and Thompson (2008) found that a few seconds of survival processing, during which participants were asked to rate the relevance of random words to a survival scenario, produced better long-term retention than a host of traditionally strong encoding procedures (e.g., forming a visual image or engaging in semantic processing; see also Nairne & Pandeirada, 2008a).

Still, establishing an empirical advantage for fitness-relevant processing tells us little about the cognitive mechanisms that produce those advantages, or about their ultimate origins. One could argue that organisms evolved domain-general mechanisms for retaining information, ones that are material- and situation-independent. In fact, memory researchers virtually always employ general mechanisms to explain superior mnemonic performance, mechanisms such as elaboration (connecting information to other things in memory), distinctive processing (creating unusual representations), or processing that is transfer-appropriate (encoding representations that are likely to be matched in a targeted retrieval environment). Certain types of material, or situations, may naturally afford elaborate, distinctive, or appropriate encodings, but the mechanisms themselves are assumed to operate similarly across domains (see Surprenant & Neath, 2009).

Evolutionary psychologists tend to eschew domain-general mechanisms for a variety of compelling reasons. Nature usually "selects" one physical design over another when it effectively solves a specific adaptive problem related to fitness—thus, we have hearts uniquely designed to pump blood, kidneys to filter impurities, and so forth. From a social and cognitive perspective, there are too many critical problems to be solved, such as avoiding predators, locating nourishment, or selecting an appropriate mate, to rely on the whims of general learning mechanisms that are simply designed to extract information from individual experiences (e.g., Cosmides & Tooby, 2005). Relevant experiences may occur naturally with too low a probability, and problems of combinatorial explosion arise quickly with a cognitive system that is designed to store everything. Selective storage, based on inherent cognitive "biases" or "tunings," would appear to be necessary for species to survive and reproduce effectively. Of course, these are not airtight arguments (see Buller, 2005), but they can serve as the impetus and foundation for empirical investigation.

1.1. Ancestral priorities

To the extent that our brains were sculpted primarily during the Pleistocene, the period usually considered as the environment of evolutionary adaptation (e.g., Symons, 1992), natural selection would have been driven by Pleistocene pressures—that is, the unique set of adaptive problems faced by our hunter–gatherer ancestors. Evolutionary psychologists commonly argue that we continue to carry around these "stone-age" brains, along with a toolkit of cognitive adaptations that were designed originally to solve hunter–gatherer problems (Tooby & Cosmides, 1992). One might predict, therefore, that optimal cognitive performance should be induced by ancestrally-based problems, particularly those present in ancestral foraging environments, rather than by problems faced in modern environments. If, in fact, our cognitive systems evolved to solve particular adaptive problems then the fit between problem and process should account, at least in part, for processing efficiency. This is not a strong prediction of evolutionary theory, because adaptations can be effectively exapted to perform roles that are unrelated to the original selection environment (see Andrews, Gangestad, & Matthews, 2002), but it represents an interesting empirical test.

There is some support for the notion of ancestral priorities in cognitive processing. For example, it is widely accepted that organisms, including humans, have an inborn attentional bias for threatening stimuli—particularly stimuli that were relevant in ancestral environments (see Öhman & Mineka, 2001, for a review). Both adults and very young children detect evolutionarily-relevant stimuli, such as snakes and spiders, more quickly than non-threatening stimuli (LoBue & DeLoache, 2008). Even 7- to 9-month-old infants, who presumably have limited experience with snakes, show an attentional bias to snakes compared to other unfamiliar animals (DeLoache & LoBue, 2009). In addition, New, Cosmides, and Tooby (2007) found faster and more accurate detection for animals, both human and non-human, than for inanimate objects using the change-detection paradigm, a procedure in which people are asked to detect differences between two rapidly-alternating images. Change detection for nonhuman animals was faster than for vehicles, even though the latter are commonplace in everyday experience and can be survival-related. A variety of alternative explanations for the data were discounted, including the interest value and low-level visual characteristics of the stimuli, leading the authors to conclude that people possess an animate monitoring system that is "better tuned to ancestral than to modern priorities" (New et al., 2007, p. 16603).

In the learning domain, evolutionarily-significant stimuli can be easier to associate with aversive stimuli (e.g., shock or loud noise) than comparable modern controls (Öhman & Mineka, 2003). For example, some studies have found that snakes and/or spiders are easier to associate with aversive stimuli, or show more resistance to subsequent extinction, than ontogenetic fear-relevant stimuli such as guns or electrical outlets (see Öhman & Mineka, 2001, for a review). People are also more likely to perceive illusory correlations between pictures of snakes and shock than between pictures of damaged electrical equipment and shock (Tomarken, Sutton, & Mineka, 1995). In addition, specific phobias are more likely to develop to ancestral stimuli (e.g., predators) than to aversive stimuli exclusively encountered in modern environments (e.g., weapons; see De Silva, Rachman, & Seligman, 1977). Collectively, these data suggest a certain amount of "preparedness" for associating ancestrally-relevant stimuli with particular outcomes.

Demonstrating that our cognitive systems show ancestral priorities in processing is an important step in furthering evolutionary accounts. As noted by many (e.g., Buller, 2005; Richardson, 2007), evolutionary accounts can be difficult to defend, largely because critical data are either missing or impossible to obtain (e.g., cognitive processes cannot be fossilized). To establish an evolutionary locus—that is, the presence of an adaptation sculpted by natural selection—requires building a multipronged case based partly on the systematic ruling out of alternative accounts (see Andrews, Gangestad, & Matthews, 2002; Nairne, in press). Establishing ancestral priorities is relevant partly because it is difficult to see how general learning mechanisms, those essentially tuned by experiences throughout development, could yield superior performance for situations and stimuli that are rooted in the distant past rather than in the present. At the same time, each of the studies conducted to date suffers from an inherent confound—ancestral versus modern comparisons require one to compare across different stimuli (e.g., snakes versus guns) and such stimuli can differ in many uncontrolled ways (Blanchette, 2006; Fox, Griggs, & Mouchlianitis, 2007).

1.2. The current research

The present experiments were designed to investigate ancestral priorities in the survival processing paradigm (Nairne et al., 2007). As noted earlier, processing information in terms of its relevance to fitness can improve retention dramatically, at least compared to traditional encoding procedures (Nairne et al., 2008). This paradigm presents some methodological advantages over the work just-reviewed, mainly because all participants are asked to remember exactly the same material. What matters to retention is how people process the information—i.e., in terms of survival or some other relevant control. This means that fitness-based retention differences cannot easily be attributed to the characteristics of the stimuli, or to assumptions about what those stimuli naturally afford (e.g., natural fear versus learned fear).

Research based on the survival processing paradigm has firmly established the mnemonic power of fitness-relevant processing, but the locus of the processing advantage remains controversial. There is some evidence that survival processing may be special, at least compared to other forms of encoding, and not easily interpreted via standard theoretical frameworks (see Nairne, in press; Nairne & Pandeirada, 2008a). However, the fact that fitness-relevant processing may be powerful or "special" does not mean that its mnemonic advantages accrue from a specific evolutionary tuning—more and varied evidence is needed to make such a case. As noted earlier, establishing an evolutionary locus for any cognitive phenomenon is difficult and no single empirical attack is likely to be definitive. Demonstrating that survival processing is sensitive to ancestral priorities would expand the existing database on survival processing considerably and strongly bolster the evolutionary account.

A recent experiment reported by Weinstein et al. (2008; Experiment 2) provides initial support for the contention that survival processing may be sensitive to ancestral priorities. Those authors compared retention after people processed the relevance of words to a survival situation, but varied whether the scenario invoked an ancestral or a modern context. In one situation, following Nairne et al. (2007), people were asked to imagine themselves stranded in the grasslands of a foreign land without basic survival materials. Over the next few months, the instructions explained, they would need to find steady supplies of food and water and protect themselves from predators. The experimental task was to rate the relevance of words to this survival situation. 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 obtained in the group processing the ancestral scenario.

The experiments reported here had three main goals: first, given their potential importance to the evolutionary hypothesis, we sought initially to replicate the findings of Weinstein et al. (2008). Will rating the relevance of words to an ancestral scenario lead to better retention than processing those same words in a matched modern context? Second, to help establish the generality of the phenomenon we explored the role of ancestral priorities in two new domains, healing a dangerous infection and collecting food to eat. Both described recurrent adaptive problems that were likely to be present in the environment of evolutionary adaptation, but the new domains were designed to activate "gathering" strategies rather than predator avoidance strategies such as those used in the Weinstein et al. experiment. Once again, all participants were asked to process the relevance of words to a survival scenario. What differed across conditions was the ancestral nature of the scenario: participants were presented with the same general survival problem but in either an ancestral (grasslands) or a modern context (city). To the extent that our memory systems are "prepared" to process information in ancestral environments (foraging as hunter–gatherers in the grasslands), we anticipated better retention after processing with the ancestral scenario. Finally, in an effort to provide greater insight into the proximate mechanisms that might underlie ancestral advantages, and to gain additional support for the evolutionary account, in the last two experiments we also asked participants to evaluate the ancestral and modern scenarios along a number of mnemonically-relevant dimensions (e.g., interest, familiarity, etc.).

2. Experiment 1

In the survival processing paradigm, participants are asked to rate the relevance of words to a survival scenario. The rating task is then followed by a surprise retention test, usually free recall, and performance is compared to a non-fitness-based control. Following Nairne et al. (2007), Weinstein et al. (2008) used a schematic control, moving to a foreign land, as their comparison. The "moving" control is closely matched to the survival scenario, but is not fitness-relevant (that is, it does not require dealing with issues directly related to survival or reproduction). Better recall for the words rated with the survival scenario, compared to the moving condition, defines the basic survival processing advantage.

Following the Weinstein et al. (2008) study (Experiment 2) we compared two versions of the survival scenario in Experiment 1—one rooted in an ancestral environment (avoiding predators in the grasslands) and one in a modern context (avoiding attackers in a city). The critical question asked whether the size of the survival processing advantage would vary across these two survival scenarios.

Weinstein et al. found that the survival processing advantage was larger when people rated the relevance of words to the ancestral (grasslands) scenario, consistent with an evolutionary account.

2.1. Method

2.1.1. Participants and apparatus

Eighty Purdue undergraduates participated for credit in an introductory psychology course. Stimuli were presented and controlled by personal computers in sessions lasting approximately 30 min. Sessions were conducted in groups of up to four participants.

2.1.2. Materials and design

Thirty-two unrelated concrete nouns, drawn largely from the updated Battig and Montague norms (Van Overschelde, Rawson, & Dunlosky, 2004) or from the extended Paivio norms (Clark & Paivio, 2004), were used as target words in the experiment (six additional concrete nouns were used in a practice phase). The stimuli are presented in the Appendix A. Everyone rated and recalled exactly the same 32 words, presented in the same order. Within a session participants rated the relevance of 16 target words to the survival (S) scenario and 16 to the moving (M) control. Rating condition was blocked in trials of eight words in the form SMSM or MSMS; half of the participants received each version, ensuring that each word was rated equally often under both scenarios. The content of the survival scenario was manipulated between-subjects: one group of participants was given the ancestral (grasslands) scenario ($N = 40$); the other group received the modern (city) scenario ($N = 40$). Both groups received the same "moving" instructions. Immediately following the last block of ratings, everyone completed a short digit-distractor task followed by a surprise free recall test.

2.1.3. Procedure

On arrival in the laboratory, participants were assigned randomly to either the ancestral or the modern group. The instructions for the two survival scenarios are presented below, along with the instructions for the moving control.

2.1.3.1. Ancestral. In this task, please imagine that you are stranded in the grasslands of a foreign land, without any basic survival materials. You have recently received word that a dangerous predator has been seen in the area. You will need to avoid and/or escape from the predator to ensure your survival. 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 in your attempt to avoid the predator.

2.1.3.2. Modern. In this task, please imagine that you are stranded in the city of a foreign land, without any basic survival materials. You have recently received word that a dangerous attacker has been seen in your area. You will need to avoid and/or escape from the attacker to ensure your survival. 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 in your attempt to avoid the attacker.

2.1.3.3. Moving. In this task, please 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.

The to-be-rated words were presented individually, centered on the screen, for 5 s apiece. People were asked to rate the words on a 5-point scale, with 1 indicating totally irrelevant to the scenario and 5 signifying extremely relevant. The rating scale was shown just below each word and people responded by clicking on their value of choice. They were cautioned to respond quickly, within the 5-s presentation window, and the later retention test was not mentioned. A short practice session preceded each of the first two blocks (one S and one M).

After the last word was rated, instructions appeared for the digit recall task. For this task, seven digits, ranging between zero and nine, were presented sequentially for 1 s apiece and participants were required to recall the digits in order by typing responses into a text box. The digit recall task lasted for approximately 2 min. Recall instructions then appeared. Participants were asked to write down the earlier-rated words, in any order, on a response sheet. The final recall phase lasted for 10 min and participants were asked to draw a line on the recall sheet, under the last recalled word, after each min of recall. A clock was displayed on the computer monitor and a "beep" sounded every min signaling the participants to draw the line. Using this procedure allows one to construct cumulative recall curves, but they are not reported here.

2.2. Results and discussion

The level of statistical significance, unless otherwise noted, was set at $p < .05$ for all comparisons. Participants had little difficulty producing the relevance ratings within the allotted time, and no significant differences in completion rates were found across groups or conditions.

The data of main interest are shown in Fig. 1. These data show proportion correct recall for the rated target words for each of the main comparisons. The left-hand side of the figure shows recall for those participants receiving the ancestral scenario; the modern data are shown to the right. An overall analysis of variance (ANOVA) on these data, with group (ancestral versus modern) as a between-subject variable, and rating condition (survival versus moving) as a within-subject variable, revealed only a significant interaction between group and rating condition, [$F(1, 78) = 6.27$, MSe = .016, $\eta_p^2 = .074$]. Planned *t*-tests revealed a significant survival advantage in the ancestral group (ancestral versus moving; $t(39) = 2.91$, $p < .01$); the comparable comparison in the modern group (modern versus moving) failed to approach significance [$t(39) < 1.0$]. Turning to the direct planned comparison between the ancestral and modern scenarios, participants recalled more words after rating with the ancestral scenario but the difference was only marginally reliable [$t(78) = 1.65$, $p = .052$]. Additional analyses using items as the analytic unit, rather than participants, revealed the same patterns of significance—however, the recall difference between the ancestral and the modern scenarios did reach conventional levels of statistical significance in the item analysis [$t(31) = 1.93$, $p = .031$].

These results confirm the main predictions of the evolutionary account. There was a significant interaction between group and rating condition, indicating a larger survival effect for the ancestrally-based grasslands scenario. In fact, although there was a robust fitness effect for the ancestral scenario, there was no indication that survival-based processing produced any mnemonic advantages in the modern scenario. Interestingly, Weinstein et al. (2008) found essentially the same pattern, although the interaction of group and rating condition is not reported in their article. They report only the overall means for the ancestral (.38), modern (.31), and moving conditions (.28), but the pattern is clearly similar to the one reported here. It is somewhat surprising that the city scenario failed to produce a retention advantage over the moving control. Surviving in a city and escaping from attackers

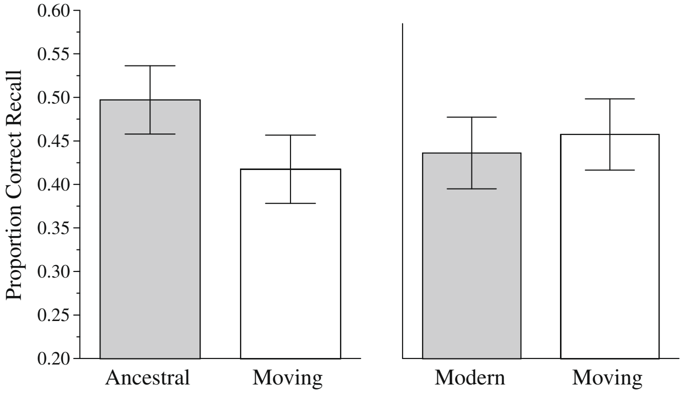

Fig. 1. Proportion correct recall performance for each of the conditions in Experiment 1. The data on the left are from the group receiving the ancestral (predator) scenario; data from the group receiving the modern (attacker) scenario are shown on the right. Error bars represent within-subject 95% confidence intervals (as per Masson and Loftus (2003)).

Table 1
Rating and response time (ms) averages for the various conditions in Experiment 1.

	Ancestral		Modern	
	Predator	Moving	Attacker	Moving
Rating	3.30	2.63	3.07	2.74
Response time	2341	2486	2362	2322

are clearly fitness-relevant, yet there was no memory enhancement for survival processing in this context. We return to this issue in Experiments 2 and 3.

It is also of interest to examine the average ratings and response times for each of the conditions; these data are shown in Table 1. Turning first to the rating data, an overall ANOVA revealed a main effect of rating condition [$F(1, 78) = 95.77$, MSe = .104, $\eta_p^2 = .551$]; the target words were rated as more relevant to the survival scenarios than to the moving scenario. There was also a reliable interaction between group and rating condition [$F(1, 78) = 11.22$, MSe = .104, $\eta_p^2 = .126$], reflecting a larger difference in rating between the survival scenario and moving for the ancestral group. Individual post-hoc comparisons determined that the differences between the survival and moving conditions were reliable for both the ancestral and the modern groups (both t-test values were greater than 4.5) and there was a significant rating advantage for the ancestral scenario over the modern scenario [$t(78) = 2.29$, $p < .03$]. This pattern is a little troubling because it mirrors the pattern found in recall, suggesting that the recall differences may have been determined by the rating differences. However, there are several reasons to discount this possibility. First, prior research in the survival processing paradigm has consistently shown that rating differences cannot account for observed differences in recall (Nairne & Pandeirada, 2008a; Nairne et al., 2007). Second, supporting this conclusion, the current data show a highly reliable rating advantage for the modern scenario over the moving control, yet there is no evidence for a comparable difference in recall. Finally, the recall results of Experiment 1 essentially replicate those of Weinstein et al. (2008), who found no significant rating differences across conditions.

Analysis of the response time data showed no main effects of condition or group, but did show a reliable group $\times$ condition interaction [$F(1, 78) = 7.27$, MSe = 46782.17, $\eta_p^2 = .085$]. Post-hoc tests revealed that participants in the ancestral group took significantly longer to make relevance ratings to the moving scenario than they did to the survival scenario [$t(39) = -2.97$, $p < .01$]; there were no similar significant differences for the participants in the modern group. As a result, differences in response times cannot easily be used to explain the recall differences that were obtained.

The results of Experiment 1 replicate the general patterns found previously by Weinstein et al. (2008). The recall difference between the ancestral and modern scenarios was smaller than reported by Weinstein et al. (2008), and statistically significant only in the item analysis, but the important interaction of group by condition was demonstrated unequivocally. The survival processing advantage, defined as the advantage of survival processing over a non-fitness-based moving control, was larger in the ancestral than in the modern group. This data pattern is broadly consistent with the evolutionary account, suggesting that our memory systems are tuned to fitness-relevant processing, but especially in contexts that mirror those likely to have been present in the environment of evolutionary adaptation.

3. Experiment 2

Critics of evolutionary accounts often focus on our lack of knowledge about ancestral environments, which some scholars believe are essentially unknowable (e.g., Buller, 2005; Reeve & Sherman, 2007). Moreover, the idea that there is a single ancestral environment, which uniquely defined the selection pressures that led to the development of human cognition, is debatable. At the same time, our ancestors likely faced recurrent adaptive problems, ones that remained constant across situations. Our ancestors certainly needed to find food, potential mates, track and escape from predators, and find remedies for injuries and disease (see Tooby & Cosmides, 2005). Cognitive adaptations may have developed to deal with these specific problems (see Barrett, 2008) and, more importantly, those adaptations may continue to bear the general imprint of our specific foraging past.

The ancestral scenario used in Experiment 1 was designed to tap one such recurrent problem faced by our foraging ancestors—surviving and escaping from predators in a grasslands environment. Experiment 2 explores another ancestral problem, one designed to activate a "gathering" strategy rather than one dealing exclusively with predator avoidance. Once again, two versions of the survival scenario were developed, one rooted in a grasslands environment (ancestral) and one in the city (modern). In both cases participants were told they had been hurt and a dangerous infection might be developing. In the ancestral scenario, the task was to search and find relevant medicinal plants in an attempt to cure the infection; in the modern scenario, the task was to find relevant antibiotics. Scenario type was manipulated between-subjects and each group received a non-fitness-based control as well. Rather than using moving as our control in Experiment 2, however, participants were asked to make pleasantness ratings about half of the words. Pleasantness ratings have been used frequently as a control in the survival processing paradigm (e.g., Nairne et al., 2008; Weinstein et al., 2008), and are generally considered to be an effective form of deep processing (e.g., Packman & Battig, 1978).

3.1. Method

3.1.1. Participants and apparatus

One hundred and twenty Purdue undergraduates participated for course credit. Sixty people were assigned to each scenario group. Stimuli were presented and controlled by personal computers. Sessions were conducted in groups of up to four participants.

3.1.2. Materials and design

Target words were drawn from the same pool used in Experiment 1. Once again, everyone rated and recalled exactly the same set of words presented in the same order. However, unlike in Experiment 1, the rating task (survival scenario versus pleasantness) was not blocked, but was distributed randomly throughout the session. (Intermixing can help to reduce variability caused by having different conditions blocked at the beginning and end of a session.) Presentation order was constrained as follows: no more than two ratings of a given type could occur in a row and each rating type had to occur equally often in the first and second half of the list. Rating task was also counterbalanced across participants to ensure that each target word was rated for survival and pleasantness an equal number of times. As in Experiment 1, the rating task was followed by a short distractor task and then a surprise free recall test.

3.1.3. Procedure

On arrival in the laboratory, participants were assigned randomly to either the ancestral or the modern group. The instructions for the two survival scenarios are presented below, along with the instructions for the pleasantness control.

3.1.3.1. Ancestral. For the survival situation, please imagine that you are stranded in the grasslands of a foreign land, without any basic survival materials. You have recently been hurt and a dangerous infection might be developing. You will need to search and find relevant medicinal plants to ensure your survival. We would like you to rate how relevant the word would be in your attempt to cure the infection. The scale of relevance ranges from one to five, with one (1) indicating totally irrelevant and five (5) signifying extremely relevant. Some of the words may be relevant and others may not—it's up to you to decide.

3.1.3.2. Modern. For the survival situation, please imagine that you are stranded in the city of a foreign land, without any basic survival materials. You have recently been hurt and a dangerous infection might be developing. You will need to search and find relevant antibiotics to ensure your survival. We would like you to rate how relevant the word would be in your attempt to cure the infection. The scale of relevance ranges from one to five, with one (1) indicating totally irrelevant and five (5) signifying extremely relevant. Some of the words may be relevant and others may not—it's up to you to decide.

3.1.3.3. Pleasantness. For the other dimension, we would like you to rate the pleasantness of the word. The scale of relevance ranges from one to five, with one (1) indicating totally unpleasant and five (5) signifying extremely pleasant. Some of the words may be pleasant and others may not—it's up to you to decide.

As in Experiment 1, the to-be-rated words were presented individually, centered on the screen, for 5 s apiece. The rating scale was shown just below each word and people responded by clicking on their value of choice. Both the survival scenario (ancestral or modern) and the pleasantness task were fully explained to each participant at the beginning of the session. In the session itself, each word was presented along with a question that explained the rating task to be performed (How relevant is this word to the survival situation?; How pleasant is this word?). Participants were cautioned to respond quickly, within the 5-s presentation window, and the later retention test was not mentioned. The procedure for the short distractor period and the recall test matched Experiment 1.

3.2. Results and discussion

As in Experiment 1, participants had no trouble completing the respective rating decisions within the 5-s presentation window. The data of main interest are shown in Fig. 2, which shows proportion correct recall performance for the words rated in the survival and pleasantness tasks. The left-hand side of the figure shows performance for the group receiving the ancestral scenario; the data for the modern group are shown on the right.

A mixed ANOVA with group (ancestral versus modern) as a between-subject variable and condition (survival versus pleasantness) as a within-subject variable revealed a highly reliable main effect of condition [$F(1, 118) = 45.61$, MSe = .010, $\eta_p^2 = .279$] as well as a reliable interaction between group and condition [$F(1, 118) = 5.31$, MSe = .010, $\eta_p^2 = .043$]. Paired *t*-tests confirmed a survival advantage (compared to pleasantness) for both the ancestral [$t(59) = 6.14$, $p < .001$] and the modern groups [$t(59) = 3.30$, $p < .002$]. Most importantly, rating words with respect to the ancestral scenario led to better recall performance than did rating words about the modern scenario [$t(118) = 2.19$, $p = .03$]. Additional item analyses revealed the same patterns, including the significant advantage for the ancestral over the modern scenario [$t(31) = 2.04$, $p < .05$], but the difference between survival processing and pleasantness did not quite reach statistical significance in the modern condition [$t(31) = 1.88$, $p < .07$].

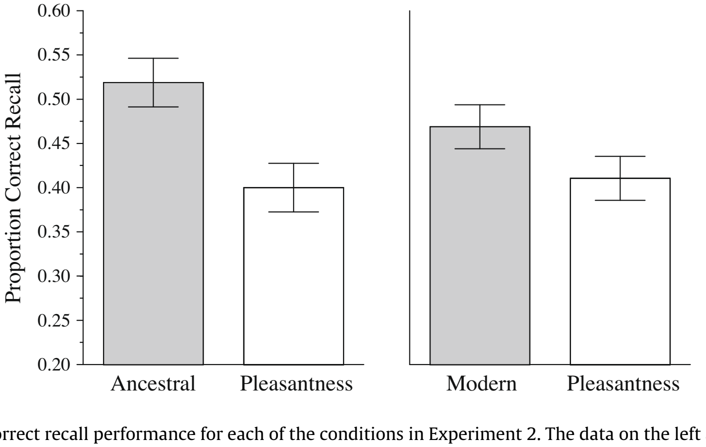

Fig. 2. Proportion correct recall performance for each of the conditions in Experiment 2. The data on the left are from the group receiving the ancestral (medicinal plants) scenario; data from the group receiving the modern (antibiotics) scenario are shown on the right. Error bars represent within-subject 95% confidence intervals (as per Masson and Loftus (2003)).

Table 2
Rating and response time (ms) averages for the various conditions in Experiment 2.

	Ancestral		Modern	
	Medicinal plants	Pleasantness	Antibiotics	Pleasantness
Rating	3.50	2.91	3.38	2.92
Response time	3104	2864	3101	2849

Average rating and response time data are shown in Table 2 for each group and condition. The mixed ANOVA on the rating data showed that the survival ratings were significantly higher than pleasantness ratings [$F(1, 118) = 114.67$, MSe = .145, $\eta_p^2 = .493$]; neither the main effect of scenario nor the group × rating condition interaction was significant in this analysis. The results of a mixed ANOVA on response time revealed only a main effect of rating condition: participants took significantly longer to make survival ratings than pleasantness ratings [$F(1, 118) = 81.15$, MSe = 44685.18, $\eta_p^2 = .407$]. The same patterns of results were obtained in the item-based analysis.

Generally, the results of Experiment 2 replicate the main findings of Experiment 1. Once again, the critical group × condition interaction was significant—there was a larger survival processing effect for the group receiving the ancestral (grasslands) scenario. Moreover, individual planned comparisons confirmed that processing with the ancestral scenario produced higher levels of recall than did the modern scenario—and, importantly, neither the ancestral nor the modern scenarios produced significant differences on either the rating or the response time measures. Consequently, the ancestral advantage reported here provides additional supporting evidence for the evolutionary account: fitness-based processing is particularly effective in contexts that presumably mirror those found in the environments of evolutionary adaptation.

It is interesting to note that survival processing produced enhanced recall for both the ancestral and the modern scenarios in Experiment 2, relative to the pleasantness control (although the modern-pleasantness advantage was only marginally significant in the item analysis). In Experiment 1, there was a robust survival advantage only for the ancestral scenario. The pattern seen here could be due, in part, to our use of the "pleasantness" rather than "moving" control condition. Rating items for pleasantness is a highly effective form of deep processing, but it tends to induce primarily item-specific rather than relational (or across-item) processing. It is well-known that item-specific processing is most effective when to-be-recalled items are related, such as when a list is categorized, because it helps one discriminate between items that did and did not occur (see Hunt & Einstein, 1981; Hunt & McDaniel, 1993). Given that our to-be-rated words were unrelated (see Appendix A), it is possible that both survival scenarios induced greater amounts of relational processing than did the pleasantness task thereby accounting, at least in part, for the survival advantages seen in this experiment. However, Nairne and Pandeirada (2008a) have shown that survival processing produces better recall performance than pleasantness processing even when word lists are categorized, so it is unlikely that enhanced relational processing can completely explain the survival advantages seen here, or in other experiments using the survival processing paradigm. Moreover, importantly, the critical comparison between the ancestral and modern scenarios was reliable in both the subject and the item analyses and does not depend on the use of the pleasantness control (see also Experiment 4).

4. Experiment 3

The ancestral scenarios of Experiments 1 and 2 were designed to evoke recurrent adaptive problems faced by our foraging ancestors—escaping from predators and treating a dangerous infection. Experiment 3 investigates yet another basic requirement—searching for nourishment. Once again, participants were required to rate the relevance of words either to a survival scenario, one rooted in the grasslands and one in a city, or for pleasantness. The survival task asked participants to imagine gaining needed nourishment either by searching for and buying food in a city, or by searching for and gathering edible plants in the grasslands. Consistent with the evolutionary account, and the results of Experiments 1 and 2, we anticipated the best final free recall for words rated with respect to the ancestral scenario.

Experiment 3 included an additional component as well. In each of the previous two experiments we were careful to equate the wording of the two survival scenarios, as did Weinstein et al. (2008). However, the general context and activities clearly differed. Both presumably induced schematic processing, but the scenarios, and the activities involved, undoubtedly differed along many uncontrolled dimensions. In an attempt to assess potential differences, at the end of Experiment 3 we asked each of the participants to rate their survival scenario along four dimensions: interest, imagery, emotionality, and familiarity. Finding significant differences between the ancestral and modern scenarios along these dimensions may help account for any retention differences that are found.

4.1. Method

4.1.1. Participants and apparatus

Seventy-two Purdue undergraduates participated for course credit. Thirty-six people were assigned to each scenario group. Stimuli were presented and controlled by personal computers. Sessions were conducted in groups of up to four participants.

4.1.2. Materials and design

Experiment 3 was an exact replication of Experiment 2, except for the change in the survival scenarios and the final scenario rating task.

4.1.3. Procedure

On arrival in the laboratory, participants were assigned randomly to either the ancestral or the modern group. The instructions for the two survival scenarios are presented below, along with the instructions for the pleasantness control.

4.1.3.1. Ancestral. For the survival situation, please imagine that you are stranded in the grasslands of a foreign land, without any basic survival materials. You have not eaten for several days and it's important for you to gain nourishment. You will need to search for and gather edible plants to ensure your survival. We would like you to rate how relevant the word would be in your attempt to obtain nourishment. The scale of relevance ranges from one to five, with one (1) indicating totally irrelevant and five (5) signifying extremely relevant. Some of the words may be relevant and others may not—it's up to you to decide.

4.1.3.2. Modern. For the survival situation, please imagine that you are stranded in the city of a foreign land, without any basic survival materials. You have not eaten for several days and it's important for you to gain nourishment. You will need to search for and buy food to ensure your survival. We would like you to rate how relevant the word would be in your attempt to obtain nourishment. The scale of relevance ranges from one to five, with one (1) indicating totally irrelevant and five (5) signifying extremely relevant. Some of the words may be relevant and others may not—it's up to you to decide.

4.1.3.3. Pleasantness. For the other dimension, we would like you to rate the pleasantness of the word. The scale of relevance ranges from one to five, with one (1) indicating totally unpleasant and five (5) signifying extremely pleasant. Some of the words may be pleasant and others may not—it's up to you to decide.

All aspects of the rating and recall tasks mimicked those used in Experiment 2. After the recall period, participants were presented with a sheet of paper and were asked to rate their presented survival scenario along the following four dimensions:

1. How interesting was the survival scenario?
   1 – Not interesting at all to 5 – Very interesting.
2. How easy was it for you to create an "image" of the survival scenario in your mind?
   1 – Extremely difficult to 5 – Extremely easy.
3. How emotionally arousing was the survival scenario?
   1 – Not emotionally arousing to 5 – Very emotionally arousing.

4. How familiar are you with the survival situation described?
   1 – No experience at all to 5 – A lot of experience.

Each question was accompanied by a scale of 1–5 and participants marked their answer by circling the number of their choice. This final rating task was self-paced.

4.2. Results and discussion

As in the previous experiments, participants had no trouble completing the rating tasks within the allotted time. The data of main interest are shown in Fig. 3, which shows proportion correct recall performance for the words rated in the survival and pleasantness tasks. The left-hand side of the figure shows performance for the group receiving the ancestral scenario; the data for the modern group are shown on the right.

Overall, the results of Experiment 3 mirror those found in the previous two experiments. A mixed ANOVA with group (ancestral versus modern) as a between-subject variable and condition (survival versus pleasantness) as a within-subject variable revealed a highly reliable main effect of condition [$F(1, 70) = 37.49$, MSe = .015, $\eta_p^2 = .349$] as well as a reliable interaction between group and condition [$F(1, 70) = 11.44$, MSe = .015, $\eta_p^2 = .140$]. Once again, the survival processing effect was larger when participants received the ancestral scenario. Paired *t*-tests confirmed a survival advantage (compared to pleasantness) for the ancestral group [$t(35) = 6.97$, $p < .001$] but the survival effect was only marginally reliable in the modern condition [$t(35) = 1.87$, $p < .07$]. Critically, as in the previous experiments, participants recalled more words correctly after rating with the ancestral scenario than with the modern scenario [$t(70) = 3.18$, $p < .003$]. Exactly the same pattern of results was found in an item-based analysis.

Average rating and response time data are shown in Table 3 for each group and condition. The mixed ANOVA on the rating data showed that survival ratings were significantly higher than pleasantness ratings [$F(1, 70) = 109.12$, MSe = .135, $\eta_p^2 = .609$]; neither the main effect of scenario group nor the group × rating condition interaction was significant in this analysis. The results of a mixed ANOVA on response time revealed only a main effect of rating condition: participants took significantly longer to make survival ratings than pleasantness ratings [$F(1, 70) = 6.0$, MSe = 55395.89, $\eta_p^2 = .079$]. A similar pattern of results was obtained in the item-based analysis, except that response times to the modern scenario were significantly longer than to the ancestral scenario in this analysis [$t(31) = -2.49$, $p < .02$].

A unique feature of Experiment 3 was the final rating task: participants rated their survival scenario along four dimensions—interest, imagery, emotionality, and familiarity. We picked these four dimensions because they seem potentially important to mnemonic processing. For example, it is

Fig. 3. Proportion correct recall performance for each of the conditions in Experiment 3. The data on the left are from the group receiving the ancestral (edible plants) scenario; data from the group receiving the modern (food) scenario are shown on the right. Error bars represent within-subject 95% confidence intervals (as per Masson and Loftus (2003)).

Table 3
Rating and response time (ms) averages for the various conditions in Experiment 3.

	Ancestral		Modern	
	Edible plants	Pleasantness	Food	Pleasantness
Rating	3.49	2.81	3.55	2.95
Response time	2954	2885	3060	2936

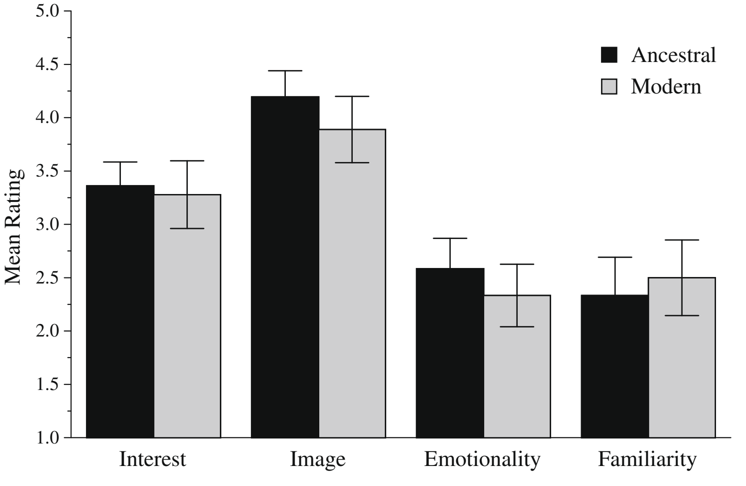

Fig. 4. Average ratings for the survival scenarios processed by the ancestral (edible plants) and modern (food) groups. Error bars represent 95% confidence intervals.

well-known that imaginal processing and emotionality can influence retention (e.g., see Paivio, 2007); interest and familiarity could easily affect retention as well, perhaps by influencing the amount of elaboration that each scenario affords. Average rating responses for each dimension are shown in Fig. 4, separately for the ancestral and modern scenarios. An overall ANOVA on the rating data revealed a highly reliable effect of rating dimension [$F(3, 210) = 73.31$, MSe = .592, $\eta_p^2 = .512$], but neither scenario nor the interaction of scenario × dimension approached significance. Participants were clearly sensitive to the four rated dimensions, but no differences were detected between the ancestral and modern scenarios.

5. Experiment 4

Our final experiment provides yet another replication of the ancestral processing advantage, but in a completely within-subject design. In each of the preceding experiments, separate groups of participants were required to make rating decisions about either an ancestral or a modern scenario, intermixed with additional non-fitness-relevant "control" decisions (moving or pleasantness). In each experiment, ancestrally-rated words were recalled better than modern-rated words, but there was a hint of a "trade-off" in recall of the control words. This was particularly apparent in Experiment 1, in which recall of the control (moving) words suffered in the ancestral condition compared to recall of those same words in the modern condition. Although this kind of trade-off is commonly seen in free recall studies—e.g., the list strength effect (Tulving & Hastie, 1972)—it is important to demonstrate that the ancestral advantage does not depend on the presence of the additional control condition.

In Experiment 4 we eliminated the control decisions—people simply made rating decisions about an ancestral and a modern scenario, presented in separate blocks. Because the trade-off appeared largest in Experiment 1, we used the predator versus attacker scenarios from that experiment. An additional advantage of the current design was that it enabled us to collect further information about the scenarios, along the various rating dimensions used in Experiment 3, but under conditions in which people could use relative information (e.g., how "familiar" was the modern scenario compared to the ancestral scenario).

5.1. Method

5.1.1. Participants and apparatus

Forty-four Purdue undergraduates participated in exchange for partial credit in an introductory psychology course. As in the previous experiments, stimuli were presented and controlled by personal computers. Sessions were conducted in groups of up to four participants.

5.1.2. Materials and design

The 32 words from the previous experiments were used again in this experiment. A simple within-subject design was employed: participants rated 16 words with respect to the ancestral scenario (A) and 16 words with respect to the modern scenario (M). To avoid having people adopt a common rating strategy for both scenarios, because the scenarios were so similar, we returned to a blocked design in Experiment 4. Rating condition was blocked in trials of eight words in the form AMAM or MAMA. Half of the participants received each version of the counterbalancing, ensuring that each word was rated under both scenarios an equal number of times.

5.1.3. Procedure

On arrival in the laboratory, participants were assigned randomly to one of the counterbalancing versions of the experiment. The ancestral and modern scenarios were the same as in Experiment 1.

5.1.3.1. Ancestral. In this task, please imagine that you are stranded in the grasslands of a foreign land, without any basic survival materials. You have recently received word that a dangerous predator has been seen in the area. You will need to avoid and/or escape from the predator to ensure your survival. 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 in your attempt to avoid the predator.

5.1.3.2. Modern. In this task, please imagine that you are stranded in the city of a foreign land, without any basic survival materials. You have recently received word that a dangerous attacker has been seen in your area. You will need to avoid and/or escape from the attacker to ensure your survival. 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 in your attempt to avoid the attacker.

All aspects of the rating, distractor and recall tasks matched those used in Experiment 1, except that at the end of the recall period participants completed an additional scenario evaluation task. As in Experiment 3, participants were asked to rate the two scenarios along a set of dimensions: interest, imagery, emotionality and familiarity; in addition, people were also asked to evaluate how unusual the scenarios seemed. For this final rating task participants were given a sheet in which both scenarios were presented along with the to-be-rated dimensions. The dimensions were presented in the format of a question and the correspondent rating scale was presented along with it as follows:

1. How interesting is the scenario?
   1 – Not interesting at all to 5 – Very interesting.
2. How easy is it for you to create an "image" of the scenario in your mind?
   1 – Extremely difficult to 5 – Extremely easy.
3. How emotionally arousing is the scenario?
   1 – Not emotionally arousing to 5 – Very emotionally arousing.
4. How familiar are you with the activities in the scenario (familiar but not necessarily directly experienced)?
   1 – Not familiar at all to 5 – Very familiar.

5. How unusual do you consider/find the scenario?
   1 – Not unusual at all to 5 – Extremely unusual.

Each question was also accompanied with two scales of 1–5, one to mark the response for the ancestral scenario and the other to mark the response for the modern scenario. Participants registered their evaluation for each scenario by circling or crossing the number of their choice on the appropriate scale. The task was self-paced and the order in which the scenarios were presented and rated was counterbalanced across participants.

5.2. Results and discussion

During the initial presentation phase, participants were able to rate over 99% of the words within the allotted time. The data of main interest are shown in Fig. 5, which shows proportion correct recall for the words as a function of whether the items were rated in the ancestral or the modern scenario. A repeated measures ANOVA with scenario (ancestral versus modern) as a within-subject variable confirmed an ancestral advantage [$F(1, 43) = 12.47$, MSe = .012, $\eta_p^2 = .225$]. The same result was obtained when items were used as the unit in the analyses [$F(1, 31) = 7.97$, MSe = .014, $\eta_p^2 = .205$]. These data replicate the ancestral processing advantage and show that it does not depend on including fitness-irrelevant control conditions, such as moving or pleasantness. As noted, in the previous experiments there was some indication of a trade-off in recall between the fitness condition and the control (especially in Experiment 1). Experiment 4 replicates the main finding of Experiment 1 under conditions in which all items received some form of fitness-relevant processing.

Average rating and response time data are shown in Table 4 for each scenario. An overall ANOVA on the rating data revealed that relevance ratings to the ancestral scenario were somewhat higher than those given to the modern scenario [$F(1, 43) = 7.52$, MSe = .094, $\eta_p^2 = .149$]; this difference was also reliable in the item analyses [$F(1, 31) = 5.14$, MSe = .096, $\eta_p^2 = .142$]. To help rule out rating as a determinant of the ancestral recall advantage, stimuli were divided into three categories based on their

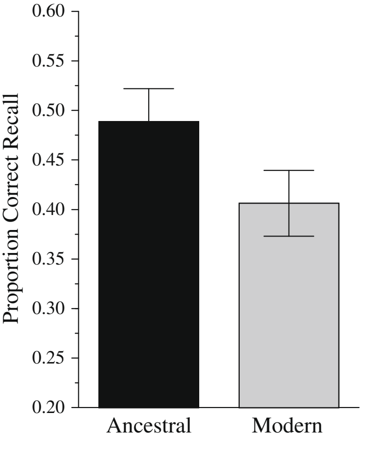

Fig. 5. Proportion correct recall performance for the ancestral (predator) and modern (attacker) scenarios in Experiment 4. Error bars represent within-subject 95% confidence intervals (as per Masson and Loftus (2003)).

Table 4
Rating and response time (ms) averages for the various conditions in Experiment 4.

	Ancestral	Modern
Rating	3.06	2.88
Response time	2407	2345

ancestral ratings: words receiving an average rating of one or two, words with an average rating of three, and words with ratings of four or five. A mixed ANOVA with scenario as a within-subject variable and rating category as a between-item variable revealed a main effect of scenario with a higher proportion of recall for the ancestral scenario [$F(1, 29) = 4.50$, MSe = .014, $\eta_p^2 = .134$]; there was no interaction and no main effect of rating category (both Fs < 1). This analysis confirms that the recall advantage for the ancestral scenario does not depend on the overall rating that an item receives (see the general discussion for further discussion of this issue). For the response time data, no significant differences between the ancestral and modern scenario were found [$F(1, 43) = 3.16$, MSe = 26628.96, $\eta_p^2 = .069$, and $F(1, 31) = 2.30$, MSe = 24627.94, $\eta_p^2 = .069$ for the subject and item analyses, respectively], although the mean response times were somewhat higher for the ancestral scenario.

As in Experiment 3, participants were also asked to provide scenario ratings at the end of the experiment. The present task differed from the one used in Experiment 3 in several respects. First, each participant experienced both scenarios during the initial rating phase and were asked to provide final evaluations about each scenario; this presumably enabled the participant to make relative rating judgments (i.e., is the ancestral scenario more familiar than the modern scenario?). Second, we changed the "familiarity" question slightly—we added the qualifier that the scenario might be familiar but "not necessarily directly experienced". Finally, we added an additional evaluation dimension—how "unusual" do you consider/find the scenario? Scenario rating data were collected for only 38 of the 44 participants (because of an experimenter oversight) and the mean values are shown in Fig. 6. A repeated measures ANOVA with scenario and dimension as within-subject variables revealed no main effect of scenario [$F(1, 37) = 3.25$, MSe = 1.048, $\eta_p^2 = .081$], a main effect of dimension [$F(4,148) = 16.81$, MSe = 1.371, $\eta_p^2 = .312$], and also a reliable interaction between scenario and dimension [$F(4,148) = 4.44$, MSe = .614, $\eta_p^2 = .107$]. Replicating Experiment 3, no significant differences were found between the ancestral and modern scenarios for the dimensions of "interest," "imageability," or "emotionality." However, in the present experiment the modern scenario was rated as significantly more "familiar" than the ancestral scenario [$t(37) = -2.57$, $p < .02$] and the ancestral scenario was also deemed significantly more "unusual" [$t(37) = 3.02$, $p < .01$]. We discuss some implications of these results in the general discussion.

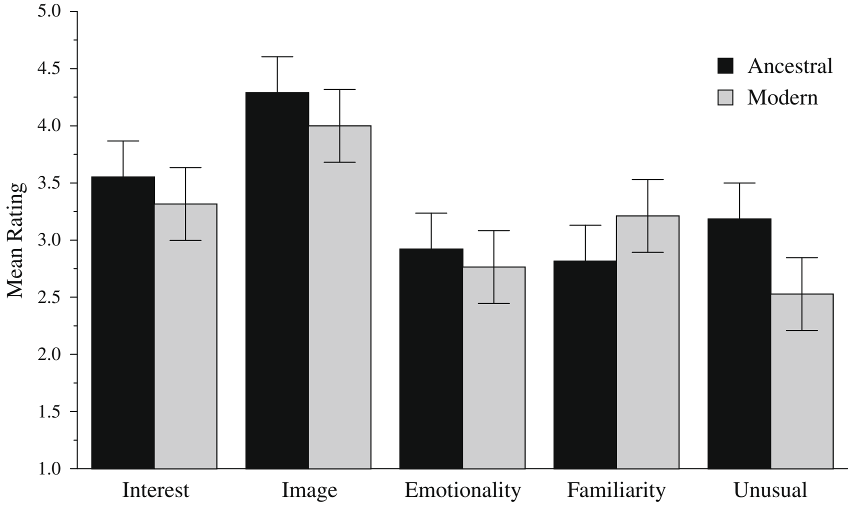

Fig. 6. Average ratings for the ancestral (predator) and the modern (attacker) scenarios. Error bars represent within-subject 95% confidence intervals (as per Masson and Loftus (2003)).

6. General discussion

To the extent that our memory systems evolved, it is reasonable to anticipate a tight fit between processing efficiency and information content. Structure follows function in evolutionary analysis, meaning that nature selects and validates structural change to the extent that fitness is enhanced (i.e., survival and/or reproduction). In the case of memory, it is clearly adaptive to use the past in the service of the present, but particularly so when fitness is involved. After all, remembering the location of food, the path of a predator, or an available mating partner is likely to increase the chances of successful genetic transmission at a later time.

One can also anticipate that the operating characteristics of memory may well bear the imprint of the selection pressures that led to memory's development. As we have argued here and elsewhere (e.g., Nairne & Pandeirada, 2008b; see also Ermer, Cosmides, & Tooby, 2007), there is little adaptive value in a memory system that simply stores information indiscriminately—selectivity is required because some kinds of events are inherently more important than others from a fitness perspective. Evolving a system that is "tuned" to remembering events that are *processed* in terms of potential fitness makes adaptive sense, particularly because it is difficult to know the fitness value of an event or object outside of a particular context (see Nairne et al., 2007). Indeed, as each of the present experiments demonstrates, assessing the relevance of unrelated words to a survival situation enhances their later retention relative to effective deep processing controls (see also Nairne et al., 2008).

More speculative was the notion that ancestral priorities influence retention in the survival processing paradigm. Although evolutionary theorists generally accept that we carry around a stone-age brain—that is, a brain that shares most, if not all, of its features with our foraging ancestors—adaptations can be "exapted" successfully to modern situations and problems. To take a classic case, reading and writing are very adaptive capabilities that could not have evolved as adaptations; rather, given their relatively recent historical development, they must reflect the workings of cognitive adaptations that evolved for other reasons (e.g., Gangestad, 2008). Similarly, our memory systems may have evolved because of their fitness-enhancing properties, yet we are clearly capable of remembering information and events that are largely irrelevant to fitness. Thus, it would not be surprising if survival processing advantages extended broadly across contexts and activities.

Yet, as reviewed earlier, ancestral priorities have been documented in a number of laboratories. It is easy for people to associate evolutionarily-relevant stimuli, such as snakes and spiders, with aversive outcomes—easier, in fact, than it is to associate similar outcomes with ontogenetic fear-relevant stimuli such as guns or electrical outlets (e.g., Öhman & Mineka, 2001). People can also detect ancestrally-relevant stimuli more quickly than matched modern stimuli, even though we may have considerably more experience with the latter (New et al., 2007). Again, people are fully capable of processing and detecting modern stimuli, including those that are not fitness-relevant, but processing efficiencies suggest that ancestral priorities may be active. The fact that people might process ancestral problems more efficiently than modern ones is not a necessary or defining feature of an adaptation, but it can play an important role in supporting an adaptationist case (see Andrews et al., 2002; Gangestad, 2008).

In each of the four experiments reported here, processing information in an ancestral context improved memory relative to a modern context. These findings replicate and extend previous work by Weinstein et al. (2008), and demonstrate that ancestral priorities can be found in contexts other than simple conditioning and attentional paradigms. Importantly, both the ancestral and the modern scenarios outlined similar adaptive problems—escaping from danger (Experiments 1 and 4), attempting to cure a dangerous infection (Experiment 2), and finding needed nourishment (Experiment 3). What differed across the scenarios was the general context, surviving in the grasslands or in a modern city. The grasslands scenario more closely matched the environments in which our cognitive systems evolved, and the activities were designed to reflect recurrent adaptive problems that our ancestors presumably faced (e.g., gathering plants for food). Moving about in a modern city is a familiar occurrence for most of us (e.g., acquiring antibiotics), but processing via a grasslands scenario produced the best retention in our experiments.

In addition, both the ancestral and the modern scenarios were crafted to induce rich schematic processing. The scenarios were very closely-matched—in fact, the ancestral and modern scenarios differed in only a few words—so it is the content of the activities involved rather than the schematic nature of the processing that presumably underlies the ancestral advantage. At the same time, the ancestral–modern comparison does confound the setting (grasslands versus a city) with the activities involved (e.g., collecting plants versus buying food). There is some evidence that interacting with rich natural environments enhances processing, at least attentional capacities (see Berman, Jonides, & Kaplan, 2008). Thus, it may not have been the ancestral nature of the scenario, but the fact that people imagined themselves in a natural grasslands environment that improved mnemonic processing. Although such an account is consistent with an evolutionary perspective, the setting *per se* is unlikely to account for the retention advantages seen in our experiments. In earlier work, our laboratory has compared the typical grasslands survival scenario with control scenarios that were also situated in nature (e.g., an extended vacation at a fancy resort in the grasslands); survival processing advantages were still obtained (see Nairne et al., 2008; Nairne & Pandeirada, 2008a). We have also compared natural scenarios describing exactly the same activities (e.g., hunting and trapping small animals) and we found that memory was enhanced when the activities were labeled fitness-relevant (hunting for food to survive) compared to when they were not (hunting to win a contest) (Nairne, Pandeirada, Gregory, & Van Arsdall, 2009).

It is also worth emphasizing that everyone in these experiments processed and remembered exactly the same stimuli. In most previous work investigating ancestral priorities comparisons have been made across different stimuli (e.g., snakes versus guns) which raises concerns about potential item-selection effects. Although one can attempt to match stimuli on a variety of dimensions, such as their fear-inducing properties, one can never be certain that all relevant dimensions have been considered and controlled. Retention differences in the present experiments must be attributed to processing rather than item differences: processing an item in an ancestral survival context led to better retention than processing the same item in a modern survival context. Moreover, the advantage of ancestral processing was robust and highly consistent across the individual items: each of the 32 words used in these experiments is presented in the Appendix A, along with each word's average rating and recall proportion when processed via an ancestral or a modern scenario (collapsed across all four of the experiments). For the 32 individual words, 29 were recalled better after ancestral processing.

This last result may seem a little surprising and deserves some comment. One might anticipate that the advantages of fitness-relevant processing should depend critically on the characteristics of the individual items—e.g., the advantages of ancestral processing should have been restricted to those items deemed survival relevant. Is it adaptive to possess a memory system that fails to discriminate between events that are relevant to fitness and those that are not? In the survival processing paradigm, however, people are *forced* to consider the survival relevance of every presented item—relevant or not. In natural settings, the situation is likely to be quite different. Fitness-relevant stimuli will receive the spotlight of processing attention in nature whereas irrelevant events are apt to be ignored or processed with less vigor. It is important to recognize as well that fitness-relevance is not an inherent property of most stimuli; instead, fitness-relevance is context-dependent. As Nairne and Pandeirada (2008b) put it: "food is survival relevant, but more so at the beginning of a meal that at its completion; a fur coat has high s-value at the North Pole, but low at the Equator" (p. 240). Even fitness-irrelevant stimuli, such as a pencil, can become extremely 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* is the key to long-term enhancement: any stimulus bathed in the spotlight of survival processing will receive some kind of mnemonic boost. In the laboratory, the tasks demands of the survival processing paradigm focus the spotlight on each presented stimulus; consequently, each item receives the benefits of fitness-relevant processing regardless of its ultimate relevance (for an exception, see Butler, Kang, & Roediger, 2009). In natural settings, both the object and the context will jointly determine the amount of fitness-relevant processing received.

Do ancestral scenarios induce a unique form of survival processing, one congruent with the selection pressures that originally fed the processes of natural selection? Of course, similar arguments have been offered to explain the advantages found for learning about snakes and spiders compared to guns and electrical outlets. Our learning and memory systems were shaped by natural selection, so it is not surprising that those systems remain sensitive to the kinds of situations and stimuli that led to their development. In addition, escaping from a predator in the grasslands, or searching for edible or medicinal plants, raises the stakes for survival relative to a modern setting. One is less likely to die from hunger in a city, or from a raging infection, because modern cities offer a variety of support systems (e.g., the police, food markets, hospitals) that are unavailable in nature. Yet, our cognitive systems must have evolved to handle survival situations engendered in natural environments because those were the situations in play during the environment of evolutionary adaptation.

Note that our argument is a functional one, focusing on the ultimate purpose or adaptive value of memory processing. We cannot make claims about the specific proximate mechanisms that produce the survival processing advantage, or the ancestral advantages seen in the current experiments. There are many possible explanations. For example, one could argue that grasslands survival scenarios more effectively activate the neural systems that underlie emotional processing, leading to increased arousal or more effective consolidation of stored traces (LaBar & Cabeza, 2006; McGaugh, 2006). The scenario rating data of Experiments 3 and 4 suggest that the ancestral and modern scenarios did not differ in emotionality, but those data may not be definitive (see also Nairne et al., 2007). Alternatively, one might simply claim that the ancestral scenario induces more distinctive or novel processing that makes the episodic record easier to retrieve (e.g., Craik, 2002). The scenario evaluation data of Experiment 4 are consistent with this interpretation: people rated the ancestral scenario as more ‘‘unusual” than the modern scenario, which, in turn, could have led to more distinctive processing of the ancestrally-rated words. We think this explanation is unlikely as well, for reasons we have discussed elsewhere (e.g., Nairne et al., 2007; Nairne & Pandeirada, 2008ab).

We also performed additional post-hoc analyses on the data from Experiment 4, looking for evidence of a relationship between the scenario evaluation ratings and the ancestral memory advantage. For example, for each participant we calculated the difference in rating values given to the ancestral and modern scenarios along the ‘‘unusual” dimension. We then correlated the size of this difference with the difference in recall between the ancestral and modern scenarios—the correlation was small and nonsignificant ($r = .067$). We then looked only at participants who gave the same rating values for the ancestral and modern scenarios along the ‘‘unusual” dimension. This resulted in a sample of 16 people who, on average, rated both scenarios with a value of 2.56 on the ‘‘unusual” dimension. Proportion correct recall for just these participants continued to show an ancestral advantage over the modern scenario (ancestral = .48; modern = .39; $t(15) = 1.85$). Post-hoc analyses of this sort are not definitive, but our analyses provide no support for the contention that the ancestral advantage is mediated by the unusual nature of the scenario.

Moreover, one could just as easily make the opposite case: modern scenarios are less distinctive and more familiar (e.g., the rating data of Experiment 4), so it should be easier for participants to elaborate the rated words, connecting them to other information in memory (see Weinstein et al., 2008). Modern scenarios, because they are better developed in memory, should also be easier to access and use during the retrieval process. It is widely accepted that encoding information into well-established knowledge domains enhances retention; presumably this should shift the mnemonic advantage in favor of the modern scenarios because people have richer knowledge domains about cities than grasslands. Retention, particularly free recall, is sensitive to both elaborative and distinctive processing, but it is difficult to predict *a priori* which factor should play the greater role in any specific encoding context.

Likewise, as discussed previously, it is difficult to make a definitive case for an evolved cognitive adaptation as well. Adaptationist arguments often hinge on satisfying a set of criteria, any one of which can be easily countered. For example, one might appeal to universality—the trait is found in all peoples—but regularities could arise from universal constraints in the environment rather than in the genetic record (e.g., Buller, 2005; see also Gangestad & Simpson, 2007). General learning mechanisms, such as those embodied in neural networks (McClelland, 2000), are also capable of producing an extensive array of behaviors, even those that may suggest the existence of specially-designed modules (e.g., Barrett & Kurzban, 2006). At the same time, there is no obvious reason why general learning mechanisms would lead to fitness-relevant ‘‘tunings” of the type demonstrated in the survival processing paradigm, especially given that most people have limited actual experience in processing information for survival. It is extremely unlikely that undergraduates at a Midwestern university are drawing on survival experiences accumulated in a grasslands environment to bolster retention, yet grasslands processing led to the better memory in our experiments.

Yet, it is also unlikely that the processes of natural selection produced any kind of overarching "survival" module—the concept of survival is simply too general. Instead, the products of natural selection tend to be highly specified, tied to solving particular adaptive problems. For example, in the visual system there are presumably evolved adaptations for dealing with highly-specified visual tasks, such as detecting edges, extracting wavelength information, or maintaining constancies in shape and size. As Nairne et al. (2007) suggested, the retention advantages that accrue from survival processing are more likely to 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, 2008). At the moment, unfortunately, we can provide little insight into the evolved mechanisms that might be involved.

Regardless of whether the locus of these survival processing advantages ultimately lies in a highly-specialized adaptation or in a more general mechanism (e.g., learning or emotion-based), the present experiments illustrate the value of thinking functionally. Memory researchers rarely investigate the "why" of remembering; instead the focus is typically on the "how" which, in turn, can lead to a task- or procedure-based emphasis (the best strategy for measuring recognition memory; see Nairne, 2005). The current experiments were motivated entirely from a functional perspective: do our memory systems, which arose from the machinery of natural selection, continue to bear the imprints of ancestral selection pressures? Although both functional and structural analyses can be productive (see Nairne, 2005), functional analyses lead to the generation of novel ideas, and new empirical phenomena, and are sorely underutilized by the modern memory community.

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Appendix A

Average rating and proportion correct recall collapsed across the four experiments.

	Ancestral scenarios		Modern scenarios	
	Rating	Recall	Rating	Recall
Ant	2.09	0.57	1.80	0.41
Arm	3.78	0.58	3.84	0.58
Blood	3.77	0.61	3.71	0.52
Boy	2.58	0.83	2.67	0.80
Building	3.59	0.71	4.05	0.79
Carrot	3.26	0.38	2.78	0.43
Dust	2.16	0.36	2.26	0.30
Eagle	2.52	0.43	2.08	0.21
Emerald	1.57	0.26	1.69	0.25
Fatigue	3.93	0.24	3.94	0.23
Idea	4.33	0.12	4.41	0.12
Light	4.17	0.67	4.27	0.53
Map	4.78	0.71	4.72	0.58
Mosquito	2.72	0.62	2.21	0.46
Moss	3.01	0.46	2.50	0.37
Mountain	3.27	0.68	2.84	0.55
Oak	2.94	0.47	2.59	0.38
Odor	3.30	0.35	2.88	0.28

Appendix A (*continued*)

	Ancestral scenarios		Modern scenarios	
	Rating	Recall	Rating	Recall
Orange	3.04	0.78	2.60	0.74
Oxygen	4.33	0.42	4.50	0.36
Plank	3.11	0.47	2.98	0.40
Pole	3.09	0.51	3.24	0.56
Rain	3.68	0.54	3.38	0.40
Reflex	4.21	0.10	4.15	0.01
River	4.46	0.77	4.14	0.71
Road	4.22	0.69	4.27	0.67
Rose	1.87	0.46	1.67	0.35
Shadow	3.11	0.56	3.16	0.52
Skull	2.52	0.41	2.70	0.33
String	3.74	0.54	3.56	0.47
Sunburn	2.84	0.43	2.77	0.23
Weapon	4.61	0.72	4.76	0.65
Averages	**3.33**	**0.51**	**3.22**	**0.44**

Note: Ancestral advantages in recall are found for the items "Arm" and "Idea" when proportion recall is calculated to three decimal places.

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