The Survival Advantage: Underlying Mechanisms and Extant Limitations

Stephanie A. Kazanas, Department of Psychology, University at Albany, SUNY, Albany, NY, USA. Email: skazanas@albany.edu (Corresponding author).

Jeanette Altarriba, Department of Psychology, University at Albany, SUNY, Albany, NY, USA.

Abstract: Recently, researchers have begun to investigate the function of memory in our evolutionary history. According to Nairne and colleagues (e.g., Nairne, Pandeirada, and Thompson, 2008; Nairne, Thompson, and Pandeirada, 2007), the best mnemonic strategy for learning lists of unrelated words may be one that addresses the same problems that our Pleistocene ancestors faced: fitness-relevant problems including securing food and water, as well as protecting themselves from predators. Survival processing has been shown to promote better recall and recognition memory than many well-known mnemonic strategies (e.g., pleasantness ratings, imagery, generation, etc.). However, the survival advantage does not extend to all types of stimuli and tasks. The current review presents research that has replicated Nairne et al.’s (2007) original findings, in addition to the research designs that fail to replicate the survival advantage. In other words, there are specific manipulations in which survival processing does not appear to benefit memory any more than other strategies. Potential mechanisms for the survival advantage are described, with an emphasis on those that are the most plausible. These proximate mechanisms outline the memory processes that may contribute to the advantage, although the ultimate mechanism may be the congruity between the survival scenario and Pleistocene problem-solving.

Keywords: survival processing, incidental learning, mnemonic strategy, elaboration, fitness

Introduction

Within the past decade, memory researchers have begun to consider the function of memory from an evolutionary perspective. Did the human memory system evolve as our other systems and bodily organs evolved—to enhance fitness and promote survival (Tooby and Cosmides, 2005)? Might memory be then “tuned” or specialized to remember information that is survival-relevant or presented in a survival context? Certainly, a highly
evolved memory system would prioritize certain types of information over others, such as information that helped us remember the location of a water source, secure a mate, and protect our kin. Can we use the scientific method to assess whether these evolutionary principles affect memory performance (Otgaar, Howe, Schwartz, and Toglia, 2014)? These empirical questions were originally explored by Nairne and colleagues (e.g., Nairne, Pandeirada, and Thompson, 2008; Nairne, Thompson, and Pandeirada, 2007), who reported higher recall for words processed according to their survival-relevance, as compared to other types of processing (e.g., pleasantness ratings, imagery, etc.) known to promote retention (Packman and Battig, 1978). These findings have encouraged a wide array of interesting research, from standard replications to far-reaching extensions of the original findings. The current review presents findings in support of this “survival advantage,” as well as findings that limit the generalization of the effect. Although some of these findings have been described elsewhere (e.g., Nairne, 2010; Nairne and Pandeirada, 2008b, 2010b), to our knowledge, no single paper has presented a large-scale review of this kind, with accompanying critiques and evaluations of each finding. Thus, this article is necessary to this growing area of research.

The Survival Advantage

The survival advantage—a mnemonic benefit from processing material for its survival-relevance—was first described by Nairne et al. (2007). In their paper, they presented findings from four unique but related experiments. In these experiments, they compared the effects of survival processing to very well-known and lauded methods of deep processing. Deep processing is believed to enhance retention relative to shallow forms of processing (see e.g., Craik and Tulving, 1975) and serves as a fair control condition for these kinds of comparisons. In the typical survival paradigm, participants are presented with a scenario, such as the following:

In this task, we would like you to imagine that you are stranded in the grasslands of a foreign land, without any basic survival materials. Over the next few months, you’ll need to find steady supplies of food and water and protect yourself from predators. We are going to show you a list of words, and we would like you to rate how relevant each of these words would be for you in this survival situation. Some of the words may be relevant and others may not—it’s up to you to decide. (Nairne et al., 2007, p. 264)

The words are presented one at a time, and participants typically have no difficulty rating each word, from 1 (totally irrelevant) to 5 (extremely relevant). In Experiment 1, Nairne et al. (2007) instructed another group of participants to rate the pleasantness of each word, a well-known deep processing control condition. These participants rated words from 1 (totally unpleasant) to 5 (extremely pleasant). A third group of participants was given a scenario describing moving to a new location:

In this task, we would like you to imagine that you are planning to move to a new home in a foreign land. Over the next few months, you’ll need to locate and purchase a new home and transport your belongings. We are going to show you a
The survival advantage

list of words, and we would like you to rate how relevant each of these words would be for you in accomplishing this task. Some of the words may be relevant and others may not—it’s up to you to decide. (p. 264)

Using a moving scenario as an additional control condition was important because it relies on schematic processing similar to the survival scenario.

Each of the three groups rated the same set of unrelated words. That is, the words were unrelated to each other, as well as unrelated to survival or moving. Then, they completed a brief distractor task and were given a surprise free recall task to measure incidental learning. Nairne et al. (2007) found a survival advantage: Recall was highest for the group of participants who had rated words for their survival-relevance (moving and pleasantness ratings did not differ significantly). Average ratings and response times (RTs, the length of time a word was presented before it was rated by the participant) were also similar in the survival and moving conditions. Thus, these factors could not account for the significant difference in recall. These findings were replicated in both Experiments 2 and 3, which directly compared survival and moving processing using a within-subjects design (i.e., alternating blocks of survival- and moving-relevance ratings). Across this area of research, within-subjects designs have included both blocked and randomized scenario presentations. In a blocked scenario presentation, eight words are rated according to their survival-relevance, followed by eight words rated according to their moving-relevance, and so forth. In a randomized scenario presentation, participants receive rating instructions for each trial in a randomized order of survival-relevance and moving-relevance. There are no noticeable differences in effect sizes between results from blocked and randomized within-subjects designs. Experiment 3 was unique in its measure of retention, as it used a recognition test (recognizing old versus new words). Again, survival processing led to better memory than moving processing.

Experiment 4 compared survival processing to self-reference processing. In this new condition, participants rated “how easily the word [brought] to mind an important personal experience” (p. 269). Nairne et al. (2007) considered whether the survival advantage could be a function of self-referential processing, although they did not test this directly. Using recall, Nairne et al. (2007) reported better memory for words rated for their survival-relevance than for their self-reference, though Klein (2012a, 2014) has astutely noted that self-referential processing plays a significant role in survival processing itself.

Taken together, these four experiments provided some early support for a memory system evolved to remember survival-relevant material. In addition, they suggest that survival processing is a widely effective encoding strategy—perhaps, one of the most effective—for promoting both recall and recognition performance. Again, the words themselves were not survival-relevant until they were processed that way, as they themselves are primarily neutral, concrete words. As the rating × recall interaction is not typically significant in this paradigm, congruity effects are not a likely explanation for these findings. What kinds of explanations are likely? According to Nairne et al. (2007), these findings can provide insight into what our memory system evolved to do: solve fitness-related problems, such as the need to create sophisticated tools from neutral objects and use those tools to supply ourselves and our kin with nourishment, shelter, and safety from animal predators. If memory performance for modern humans appears optimized to remember items processed for their survival-relevance, we can hypothesize that this
particular ability had some adaptive function for our ancestors. This hypothesis has been described as the evolutionary account for the survival advantage, as it aims to examine the function of memory via the conditions in which memory performance exceeds other mnemonic strategies.

Nairne et al. (2007) also acknowledged that the effect could be a function of other proximate mechanisms, as well. They suggested four possibilities that could account for the effect: (1) a memory module specialized for survival-relevant materials (or, several modules for food, predators, etc.); (2) a memory mechanism unrelated to survival (e.g., rehearsal, elaboration, or distinctiveness); (3) media exposure to survival programs or films (e.g., Survivor, Lost); or (4) arousal or emotionality. One additional explanation for the effect could be a combination of the evolutionary account and several of these proximate mechanisms, as it is certainly plausible that considering our survival hinges on elaboration and arousal, for example. Many of these explanations have since been explored, as well as several additional theory-driven mechanisms.

Using the Google Scholar search engine, the Nairne et al. (2007) article has been independently cited 223 times (and counting!). Moreover, a recently published volume edited by Schwartz, Howe, Toglia, and Otgaar (2014) has increased the visibility of this area of research. As this review is not designed to be exhaustive, we have selected only those sources within the central area of survival processing research. These sources are organized in the following way. First, standard replications of Nairne et al.’s (2007) findings are presented. Next, we discuss experimental manipulations: individual differences, different types of stimuli, and several others. We then present and critique potential mechanisms for the effect, both unlikely and likely. Limitations for the effect are discussed next, as we present the conditions when the effect does not occur, including some potentially problematic findings from the false memory literature. Finally, we conclude with recommendations for several viable research questions for future endeavors.

Standard Replications of the Survival Advantage

A number of the articles included here are also well-cited (e.g., Nairne et al., 2008; Weinstein, Bugg, and Roediger, 2008), primarily because they greatly extended the efforts of Nairne et al. (2007). Others are more recent (e.g., Fellner, Bäuml, and Hanslmayr, 2013), displaying the utility of modern innovations in cognitive neuroscience.

Nairne et al. (2008) extended the findings described previously by testing additional mnemonic strategies known to promote retention. Experiment 1 was a very straightforward between-subjects manipulation, with participants assigned to either the standard survival scenario or one of several control conditions: pleasantness, imagery, self-reference, generation, or intentional learning. We should mention that, with intentional learning, we do not know the precise strategies that these participants used, as they were simply instructed to “try to remember [the] words for a future memory test” (p. 177). Testing their recall performance, Nairne et al. (2008) determined that memory was best following survival processing. There was no difference in recall performance across the control conditions.

In Experiment 2, Nairne et al. (2008) tested the possibility that the survival advantage could be due, at least in part, to the survival scenario encouraging more schematic processing. This experiment was an extension of Nairne et al.’s (2007) original
findings, as they had compared survival processing to moving processing, another type of schema, or stored routine of an experience. This experiment utilized a within-subjects design, comparing survival processing to vacation processing—a scenario describing a fancy, all-inclusive resort, in which participants have to find their own entertainment. Perhaps unknowingly, Experiment 2 seems to have also manipulated valence. The survival scenario is quite negative, while the vacation scenario is highly positive. In a way, we cannot know if this valence manipulation affected recall performance (though negative stimuli have been shown to direct attention; e.g., Öhman and Mineka, 2001). Regardless of this additional manipulation, words rated for their survival-relevance were remembered better than words rated for vacation-relevance. Thus, findings from these two experiments have supported those described by Nairne et al. (2007), in that survival processing promoted better retention than several deep processing mnemonic strategies. Moreover, this mnemonic advantage does not appear to be the result of the survival scenario encouraging more schematic processing.

Weinstein et al. (2008, Experiment 2) continued to investigate the role of schematic processing in explaining the survival advantage. They challenged the roles of self-referential processing and ancestral priorities in producing the survival advantage. For the latter point, they questioned whether the scenario needed to take place in the grasslands in order to enhance retention. Is a grasslands context necessary to activate the survival mode responsible for the advantage? An ancestral versus modern manipulation created two opposing predictions: (1) Participants could remember more words rated for modern survival-relevance (i.e., in a city) because they can use their own experiences to elaborate on the list of words; or (2) Participants could remember more words rated for ancestral survival-relevance (i.e., in the grasslands) because the evolutionary account suggests that our ancestors’ fears and needs shaped our attitude toward survival. Participants rated words according to either ancestral survival relevance or modern survival relevance, in addition to moving-relevance. The survival scenarios were written in either a first-person or third-person perspective, to further test the role of self-referential processing in the survival advantage.

Overall, Weinstein et al. (2008) failed to find any differences between processing for personal survival and a friend’s survival. Thus, the survival advantage is not merely a function of self-referential processing (supporting previous findings by Nairne et al., 2007, 2008). Moreover, ancestral survival processing led to better recall than modern ancestral processing. Thus, general schematic processing cannot account for the survival advantage, as the two survival scenarios did not promote similar memory performance (though both scenarios led to better recall than the moving scenario). This effect was also present in the participants who reported that they did not watch survival-relevant television programs.

Nairne and Pandeirada (2010a, Experiment 1) replicated this effect, with better memory following ancestral survival processing than modern survival processing. They attributed the survival advantage to ancestral priorities—the Pleistocene pressures that drove our hunter-gatherer ancestors’ evolution, or the “environment of evolutionary adaptedness” (Tooby and Cosmides, 2005). This line of research follows from the evolutionary account of the survival advantage. We should be especially good at remembering fitness-relevant information if our memory system truly evolved to enhance fitness (Nairne, 2010; but see Soderstrom and Cleary, 2014 for a review that challenges this assumption). There is some evidence from other cognitive domains to support this idea. For
The survival advantage

example, in a change-detection paradigm, New, Cosmides, and Tooby (2007) found faster and more accurate detection of animate objects (e.g., animals) than inanimate objects (e.g., vehicles) (for similar results related to location memory, see Wilson, Darling, and Sykes, 2011). Within the learning literature, Öhman and Mineka (2001) have described the ease with which ancestrally-relevant stimuli (e.g., snakes) can be associated with aversive stimuli (for a review, see Nairne, Vasconcelos, and Pandeirada, 2012). Perhaps ancestral priorities also included detection of animate things.

Testing an additional ancestral priority, Nairne and Pandeirada (2010a) manipulated foraging for medicine to combat an infection: finding medicinal plants (the ancestral scenario) versus searching for and finding antibiotics (the modern scenario). Participants were assigned to one of these conditions, in addition to pleasantness ratings. As we might expect, survival-relevance ratings led to better recall than pleasantness ratings, with the ancestral scenario promoting the best retention. These findings support the evolutionary account as an explanation for the survival advantage, as both scenarios were survival-based, but only the ancestral scenario described ancestral priorities. Thus, the advantage might be a function of ancestral priorities, in particular.

Nairne and Pandeirada (2010a) continued to explore the foraging aspect of survival in Experiment 3. They tested a need for nourishment: finding edible plants (the ancestral scenario) versus searching for and buying food (the modern scenario). Again, participants were assigned to one of these conditions, in addition to pleasantness ratings. It is important to critique that these conditions are not necessarily equated on realism or imageability. Participants may have had difficulty imagining or reconciling that they could be facing starvation, but have the financial resources to purchase food once they found it. Potential mechanisms underlying the differences between these conditions were explored with a new set of scenario ratings. After the surprise free recall task, all participants rated their survival scenario (ancestral or modern) on interest, imageability, emotionality, and familiarity. Effects of recall replicated those of Experiment 2, with ancestral and modern survival scenarios matched across all four rating dimensions. This finding limits the possibility that their findings from this particular experiment can be a function of one processing condition being more interesting, imageable, emotionally arousing, or familiar.

Experiment 4 provided additional support for ancestral priorities underlying the advantage, with a direct comparison of the ancestral and modern survival scenarios. Participants rated words according to both of these scenarios (in blocks), without any control condition. Again, the ancestral survival scenario led to better memory than the modern survival scenario. However, unlike Experiment 3, the scenario ratings differed on two important dimensions. Participants rated the modern version as more familiar, and the ancestral version as more unusual. However, this difference in familiarity ratings is difficult to explain. According to Nairne and Pandeirada (2010a), familiarity should not decrease memory performance, as it should lead to increased elaboration. For example, when presented with a familiar scenario, a participant may be able to draw on related experiences or knowledge. The difference in unusualness ratings between the two scenarios may provide some additional insight. The novelty of the ancestral version, depicted by a lower familiarity rating and a higher unusualness rating, may explain some of the survival advantage. In other words, a novel scenario may capture attention and enhance memorability for that scenario, because it is particularly distinctive to participants.
However, 16 of the participants from Experiment 4 (approximately 1/3 of their sample) rated the ancestral and modern survival scenarios as equally unusual, but still recalled more words rated for their ancestral survival-relevance. This is an important finding, as participants in this experiment rated words according to both ancestral and modern survival-relevance. This direct comparison of the two survival scenarios reduces some of the likelihood that the unusual dimension can account for the survival advantage. Fitness-relevance, as described by Nairne, Pandeyrada, Gregory, and VanArsdall (2009), is also an unlikely possibility (with these data, in particular) as both ancestral and modern survival scenarios described fitness-relevant problems. Thus, matching scenarios on these dimensions is especially important when researchers are attempting to uncover any potential mechanisms underlying the survival advantage. Without careful matching, it is also difficult to make any definitive statements about recall comparisons.

A recent replication of the survival advantage involved cognitive neuroscience methodology, which extends the behavioral findings discussed previously. In their study, Fellner et al. (2013) used the subsequent memory effect (SME) paradigm: a comparison of neural activity during encoding (the rating task) for items that were remembered versus those that were not. Neural activity is measured by analyzing electroencephalogram (EEG) recordings. If activity from the electrodes is synchronized, then perhaps those cortical areas are in communication, as would be the case during memory formation. Fellner et al. (2013) used a within-subjects design comparing survival processing to animacy processing: rating whether the words are animated or related to something animated. The authors reported the standard survival advantage, in addition to EEG findings. For example, they found widespread simultaneous cortical activity during survival processing (significantly more so than for animacy processing). This suggests extensive communication across several cortical networks. What might these networks represent? The authors suggest that survival processing might involve processing along several dimensions, an indicator of semantic richness. Perhaps rating words according to their survival-relevance makes the individual words become more salient as their utility is considered. Can I eat or drink this item? Can I use this item to defend myself from predators? While their findings cannot directly answer these questions, they do suggest that processing in a survival context is neurologically complex and does not reflect a simple survival module. Instead, global synchronization of EEG activity hints at multiple mechanisms contributing to the effect, though their research design cannot provide specific insights regarding those mechanisms.

These results, when combined with those discussed previously, largely support the survival advantage. Moreover, they have been replicated in both between- and within-subjects designs (as well as with recall and recognition memory tasks). However, they ultimately do not provide any specific mechanism (or mechanisms) that can fully account for such a robust effect. This is largely due to the general purpose of these studies, as they were primarily designed to extend original findings with additional control conditions, rather than definitively answer any larger “why” or “how” questions. Ancestral priorities—the functional hypothesis first described by Nairne et al. (2007)—was reported to be the driving force behind an evolved human memory system. In later sections, additional mechanisms will be considered.
Other Manipulations

When studying the generalizability of the effect itself, the majority of studies have focused on components of the task itself, such as its control conditions or design (between-subjects versus within-subjects, with some mixed designs as well). The studies that follow have extended the findings described by Nairne et al. (2007) in other ways, by testing the impact of individual differences across participants, using different types of stimuli for their tasks, and increasing the complexity of the research design with additional variables of interest.

Individual differences

Few cognitive psychologists consider how everyday individual differences in their participants affect how they perform in the laboratory. Those that do are considered non-traditional, but have much to contribute to their respective areas of research. Thus, several of the following studies are especially important because they provide some insight into memory performance for participants other than the typical college-age student (the vast majority of participants, as depicted in the Supplemental Material: Table 1).

One particularly interesting debate in this area is that of ancestral priorities. How much of the survival advantage is due to a match between ancestral priorities and processing scenarios? Nairne et al. (2009) assessed one aspect of these ancestral priorities: sex roles (i.e., hunting responsibilities designated to males and gathering responsibilities designated to females). Some previous research conducted by Silverman and Eals (1992) had suggested that evidence for these hunter-gatherer sex roles lies in sex-specific cognitive specializations (e.g., heightened navigation and orientation abilities in males). Across two experiments, Nairne et al. (2009) found a survival advantage for hunting and gathering scenarios, relative to scavenger hunt and hunting contest control conditions. However, there were no significant interactions with sex, indicating that male and female participants had similar memory performance for hunting and gathering processing. Thus, their findings do not support the hypothesis that Pleistocene sex roles would affect memory performance in today’s populations. However, research in other domains has consistently supported sex differences as a function of ancestral priorities (see e.g., Platek, Burch, Panyavin, Wasserman, and Gallup, 2002 for an experiment investigating parental investment as a function of resemblance). Meanwhile, others argue against evolutionary explanations for sex differences (e.g., Eagley and Wood, 1999; Hyde, 2014). Therefore, it is important to continue investigating the role of sex differences in accounting for the survival advantage.

Another area of interest that has received attention compares the survival advantage across the lifespan. For example, Aslan and Bäuml (2012) and Otgaar and Smeets (2010) have both tested the generalization of the effect to young children. Otgaar and Smeets (2010) found better memory for survival processing than moving processing, using 8- and 11-year-old children. Aslan and Bäuml (2012) continued this line of research with younger children: 4–6 year olds, 7–8 year olds, and 9–10 year olds. The evolutionary account would predict that children who remembered survival-relevant material were more likely to survive childhood and reach reproductive age. In their two experiments, words were presented auditorily and memory was tested with a surprise recognition task. Experiment 1 compared recognition performance between a survival scenario, pleasantness control condition, and word length rating (a shallow processing task). This experiment was unique...
in that the authors used a shallow processing control task: a task that does not encourage deep processing of each of the to-be-rated words (e.g., considering a word’s length does not involve activating its synonyms, utility in various scenarios, etc.). Of these, survival processing promoted the highest retention, and the survival advantage did not vary according to age. Experiment 2 replicated the survival advantage with more age-appropriate control conditions: a sleepover party and being forgotten at school. These effects, when combined with those of Otgaar and Smeets (2010) indicate that the survival advantage is also present in very young children, even those believed to be too young to use mnemonic strategies.

An additional two studies also compared the survival advantage across the lifespan, but these studies used healthy, older adults (see Pandearada, Pinho, and Faria, 2014 for a study with cognitively-impaired older adults). These studies are particularly interesting, as survival processing entails a great deal of imagining specific skills that require strength and virility, which are more common among young adults than older adults. As a result, if we are to believe that the standard survival scenario reflects the environmental conditions of our ancestors, it is possible that an elderly population would have needed additional resources or protection from the environment. Moreover, allotting resources for the elderly—at the expense of those who are more reproductively-fit—can be considered maladaptive (Gallup and Weedon, 2013). On the other hand, it is also possible that our ancestors would have wanted to support an elderly population, given their wisdom and experiences to share with their kin, beyond their reproductive years.

To compare the survival advantage between young adults and older adults, Nouchi (2012) used a within-subjects design and compared recall performance between survival processing and a self-reference control condition. Some previous research has indicated a relationship between aging and incidental learning, in that deeper, semantic processing of words can lead to better memory across the lifespan (akin to a levels-of-processing effect: Eysenck, 1974). Nouchi (2012) replicated the typical survival advantage and found better overall performance in the young adult group. Moreover, the survival advantage was significantly larger for the young adults (+30% versus +16%). Thus, older adults’ memories do not appear to benefit as much from survival processing. One possible explanation for their findings is related to their modified methodology. Nouchi (2012) gave participants 5 minutes to recall the list of words, whereas 10 minutes is the more commonly used length of time. Although this may have affected recall performance, Nairne and Pandearada (2008a, Experiment 1) had used cumulative recall curves (counting the number of words recalled per minute) and identified a survival advantage 5 minutes into their recall task. Moreover, as ratings and RTs did not differ between younger and older adults, we should not expect that the older adults had greater difficulty with the task and would have needed additional time for recall.

Stillman, Coane, Profaci, Howard, and Howard (2014) predicted similar effects—that age would attenuate the size of the survival processing advantage—citing research showing poor memory performance in older adults (e.g., Balota, Dolan, and Duchek, 2000). Stillman et al. (2014) also compared young and older adults. In addition, they included a divided-attention young adult group, designed to measure retention with limited attention on survival-relevance rating (using a tone-detection task). If focused attention contributes to the effect, this group should show a smaller survival advantage relative to the full-attention young adults. When analyzing recall performance, the divided-attention
young adults had the lowest overall recall. However, both young adult groups showed approximately the same survival advantage. Results for the older adults were quite surprising. Older adults had numerically higher recall in the moving control condition than the survival scenario (though this difference was not significant). Experiments 2 and 3 replicated this finding with new samples of older adults. These results are important: The divided-attention group showed lower overall recall, but still had a robust survival advantage. Thus, the tone-detection task did not impair survival processing to a large degree. Perhaps focused attention cannot be the proximate mechanism explaining this effect. RT data from many studies would support this conjecture, as it does not appear that better memory performance comes at a cost from increased time spent processing words during the rating task. However, how can the evolutionary account explain findings with older adults from both Nouchi (2012) and Stillman et al. (2014)? Is it possible that the ancestral priorities described thus far—those contributing to fitness—are more salient to younger participants in experimental settings?

Nouchi (2011; Nouchi and Kawashima, 2012) considered additional individual differences factors with a “combination hypothesis.” The functional hypothesis (Nairne et al., 2007) can explain the survival advantage by the connection between ancestral priorities and the survival-relevant problems described in the scenario. However, the magnitude of the advantage may be a function of several additional, or combinatory, factors, including elaboration (considering the meaning of each word, previous experiences with the object, and imagining potential future uses). Thus, elaboration ability could be dependent on personal experiences and abilities. For example, Nouchi (2011) tested the effect of visual imagery on the survival advantage and found that participants with high imagery ability also had the largest survival advantage. Whereas participants with low imagery ability also showed the survival advantage, these results indicated that imagery certainly facilitates the advantage. Paivio’s (1971, 1986) work ties in nicely here, as the imagery component of concrete words largely distinguishes them from other types of words in the mental lexicon.

In a similar design to that of Nouchi (2011), Nouchi and Kawashima (2012) tested the impact of negative mood (using the Beck Depression Inventory; Beck, Steer, and Brown, 1996) on the survival advantage. The authors found that negative mood attenuated the survival advantage. However, a major limitation of these findings resides in their methodology. As was the case with Nouchi (2011), the authors dichotomized continuous variables (imagery ability into low and high ability; negative mood into nondepressed and subclinically depressed). Treating complex variables in this manner does a disservice to individual differences research, but it is encouraging for future research. Importantly, these findings do support the role of individual differences in the combination hypothesis. Depression has been demonstrated to lower memory performance, even when using deep processing encoding techniques (e.g., Derry and Kuiper, 1981). Perhaps aging, imagery ability, and negative mood are factors affecting the magnitude of the survival advantage.

Changes in stimuli

Other researchers have extended this area of work by manipulating the type of stimuli used in the rating task. For example, Otgaar, Smeets, and van Bergen (2010) tested whether the survival advantage would replicate in a study using pictures, as it does for words. In their first experiment, they manipulated the valence (positive versus negative) and arousal (low versus high) of their pictures. Participants were assigned to a survival,
The survival advantage

moving, or pleasantness condition and were instructed to both label the pictures they remembered (the recall task) and draw them in detail (scored for both accuracy and number of distortions). Although recall was highest in the survival condition (recall for moving and pleasantness did not differ significantly), participants’ images also had the most distortions in the survival condition. Nairne et al. (2007) had noted a similar finding in their experiments with words, as if words and pictures behave in similar ways in the survival paradigm. The authors propose that general schematic processing led to these distortions, as the survival and moving groups had approximately the same number of distortions. However, greater recall—at the expense of memory for details—is quite a tradeoff. This tradeoff can be likened to other tradeoffs with cognitive tasks (e.g., speed-accuracy), which complicate how we interpret the data. Additionally, comparing data from different types of stimuli can be difficult across experiments. Experiment 2 directly compared the survival advantage for pictures and words. Otgaar et al. (2010) found better memory for pictures than words, a “picture superiority effect” (as described by Rajaram, 1996). Recall for pictures was highest in the survival condition, a new variety of the survival advantage.

In another paradigm investigating the impact of new stimuli, Nairne and Pandeirada (2008a) were the first to assess the effects of item-specific and relational processing in the survival advantage. Item-specific processing involves encoding specific characteristics about the words, as they are rated. They wondered whether a seemingly unrelated list of words become related as they are rated along the same dimension (i.e., relational processing). However, if the words are already related (e.g., they belong to a small number of categories: fruits, vegetables, four-legged animals, human dwellings), will survival processing provide some additive effect? Or, would relational processing during the rating task be redundant with the already-related category members? Experiment 1 used a between-subjects design, comparing survival processing to pleasantness ratings. The authors found a survival advantage after five minutes of cumulative recall, but more intrusions in the survival condition. More importantly, participants in both conditions recalled category items together, an indication of similar levels of relational processing. Experiment 2 replicated the survival advantage with a within-subjects design. However, the results from these two experiments alone could not eliminate the possibility that schema-based processing—not survival processing—enhanced category item retention. In other words, processing a schema, such as the highly complex survival scenario, may afford certain mnemonic benefits that the pleasantness rating task may lack. Thus, Experiment 3 compared a vacation scenario (used previously, by Nairne et al., 2008) to a pleasantness control condition. The authors found better recall for the pleasantness condition, indicating that (1) pleasantness remains an effective deep processing technique, and (2) survival processing (not simply schematic processing) can enhance memory for items in categorized lists.

Burns and colleagues (Burns, Burns, and Hwang, 2011; Burns, Hart, Griffith, and Burns, 2013) have greatly extended this area of research by using words from ad hoc categories (e.g., things women wear) that require item-specific processing to group together. The authors describe the control conditions used in this area of research as one of two types: scenarios (e.g., a vacation, where participants rate each word’s relevance to the scenario) and non-scenarios (e.g., pleasantness ratings, where participants rate a word on a specific dimension). The former type, like the survival scenario, encourages a great deal of both item-specific and relational processing, whereas the latter requires primarily item-
specific processing. In a series of experiments, Burns et al. (2011) found a survival advantage only when the control condition utilized item-specific (e.g., pleasantness ratings) or relational processing (e.g., category sorting), but not both (for a recent replication of these findings, see Luo and Geng, 2013). Thus, the survival advantage may be a function of both item-specific and relational processing during encoding, particularly when control conditions utilize only one type of processing. These findings are important for several reasons. First, they provide a valuable insight into the generalizability of the effect. Moreover, they reveal a critical flaw in this research area. A large number of these studies have not used matched control conditions, which we now know should match the survival scenario on the need for both item-specific and relational processing.

Burns et al. (2013) extended these findings by analyzing both cumulative recall and recognition for survival processing and moving processing. Cumulative recall was assessed by comparing the rate of recall per minute. For the recognition test, the authors included lures from the same ad hoc categories. These specific analyses allowed the authors to assess differences in item-specific processing, because (1) item-specific processing results in a gradual cumulative recall curve; and (2) effective recognition relies on item-specific processing. They found that survival processing encourages more item-specific processing than moving processing. These findings were consistent across both between-subjects (Experiment 1) and within-subjects (Experiment 2) designs. From these studies, we may conclude that survival processing increases retention better than control conditions because of improved relational (Burns et al., 2011) and item-specific (Burns et al., 2013) processing.

Researchers have also investigated the relationship between item-scenario congruity and recall performance. For example, Butler, Kang, and Roediger (2009) found no evidence of a survival advantage when words were preselected to match the scenarios. When participants rated a list of survival words (e.g., fire, rescue, shelter) for survival-relevance, or a list of robbery words (e.g., alarm, mask, deposit) for bank robbery-relevance, recall performance did not differ significantly. Nairne and Pandeirada (2011) found quite different results. In Experiments 1A and 1B, they provided a unique set of words for each participant, to reduce the likelihood that any one list could be more congruent with the survival scenario, in particular. Compared with both pleasantness and moving control conditions (assessed in 1A and 1B, respectively), survival processing led to better recall performance. Experiments 2 and 3 manipulated the congruity between their words and scenarios (survival and a bank robbery control condition assigned between-subjects). Experiment 2 used only incongruent words and Experiment 3 used only congruent words. Both experiments produced standard survival advantages, which is compelling because Butler et al. (2009) failed to find an advantage with their word lists. However, Butler et al. (2009) had intermixed congruent and incongruent words, whereas Nairne and Pandeirada (2011) had tested congruent and incongruent words in separate experiments.

When intermixing their words, Nairne and Pandeirada (2011, Experiment 4) replicated some of Butler et al.’s (2009) findings. For example, there was no evidence of a survival advantage for congruent (i.e., related to survival) words, as recall in the bank robbery condition (presented with a list of robbery-related words) matched recall in the survival condition (presented with a list of survival-related words). However, the incongruent words (i.e., unrelated to survival) produced a survival advantage. Thus, the
critical component of the survival advantage is not the materials, per se, but how the materials are processed for their survival-relevance. For example, a *screwdriver* is a tool ordinarily used in the home, but could have many uses in survival settings (e.g., draining water from a vine, fashioning a weapon, etc.). This result replicates findings from Experiment 2, as well as dozens of additional studies that have used lists of unrelated words—presumably incongruent with the assigned scenario. Both of these sets of findings are important, as they caution future researchers to take care when selecting their stimuli. Congruity between words and scenarios has a reliable effect on recall performance.

### Additional variables of interest

The following three studies have introduced additional variables to this paradigm to test their impact on the survival advantage. The first two introduced a delay between the word rating task and the memory task (Abel and Bäuml, 2013; Raymaekers, Otgaar, and Smeets, 2014). In the third study, Smeets, Otgaar, Raymaekers, Peters, and Merckelbach (2012) investigated the impact of stress on the survival advantage.

In the first of these studies, Raymaekers, Otgaar, and Smeets (2014) used a mixed design: Scenario was manipulated within subjects (survival processing versus moving processing) and delay was manipulated between subjects (immediate versus 24 hours versus 48 hours). The immediate condition resembled the majority of studies in this paradigm, as participants rated the words, engaged in a very brief distractor task, and were then asked to remember the words (approximately three minutes of actual delay). Using recall and recognition tasks, the authors found better memory for survival-rated words at all levels of delay. However, the size of the survival advantage decreased with the length of the delay. These findings are troubling. Why would memory for survival-relevant materials decrease with time? Memory appeared to stabilize at 24 hours (with no significant decrease in retention from 24 to 48 hours), but we might expect that our ancestors would have benefited from more long-term retention of information crucial to their survival. We should expect that memory for survival-relevant materials would be quite robust over time, particularly with regards to the evolutionary account for the survival advantage. Is it also possible that their findings indicate that this effect with words is limited to relatively brief lengths of time? Perhaps these findings are limited to their research design; future research should investigate the relationship between survival-relevance ratings and long-term memory for words. A truly adaptive memory mechanism would ensure that objects successfully contributing to survival would be remembered for future use.

Abel and Bäuml (2013) also manipulated their scenarios within subjects (survival processing versus pleasantness ratings), so we cannot fully disentangle the effects of delay on a single scenario. As very little is known about how a delay between encoding and test affects memory in an incidental learning paradigm, the authors extended Raymaekers, Otgaar, and Smeets’s (2014) findings with an additional between-subjects manipulation: a sleep versus wake delay. The delay conditions included immediate (approximately 6 minutes), 12 hours awake, and 12 hours asleep. The 12-hour delay conditions were further manipulated with 9am and 9pm recall times (to test the effect of circadian rhythm), but the authors found no effect of the time of the memory task. Using recall (Experiment 1) and recognition (Experiment 2) tasks, the authors found the largest survival advantage at the immediate delay, followed by the 12-hour sleep delay. These results support those of Raymaekers, Otgaar, and Smeets (2014) and indicate that significant forgetting begins 12
The survival advantage

hours after encoding (perhaps earlier!), even in the very robust survival paradigm. Clearly, further research is necessary to support these claims, particularly with a between-subjects design and several shorter delays between the rating task and the memory task. The length of time between the rating task and memory task appears to create a significant limitation to this effect.

Smeets et al. (2012) tested the impact of a different variable on the survival advantage: stress. There is some evidence suggesting that stress at the time of encoding can affect memory (e.g., Smeets, Otgaar, Candel, and Wolf, 2008). Stress was manipulated between subjects. All participants gave a brief speech on any topic and performed some simple math. The stress group was also required to describe their personality to an audience in English (not their native language), while being videotaped. Stress level was assessed with cortisol levels, and participants had similar cortisol levels before the stress manipulation. Scenario was manipulated between subjects, with participants rating words according to either survival- or moving-relevance. The authors found that the scenario and stress manipulations independently affected memory. Participants in the survival condition had better recall than those in the moving group, and added stress also improved memory. However, the interaction was not significant. This is quite surprising, as the survival scenario appears to induce stress, particularly when compared with many of the control conditions. Perhaps more surprising, cortisol levels were elevated only with the added stress manipulation, as survival processing alone did not have an effect on cortisol levels. Although these findings are surprising, they do mimic some arousal rating data. For example, Nairne and Pandeira da (2010a) reported that participants rated an ancestral and modern version of the survival scenario as equally arousing, though the ancestral version led to better memory. Although quite preliminary, these findings reduce the likelihood that some level of emotional arousal or stress can explain the survival advantage.

Problem-solving performance

Finally, in a recent application of the survival advantage, Garner and Howe (2013) assessed the impact of survival processing on a different task, with compound remote associate test (CRAT) performance. In this type of task, participants are presented with words that are seemingly unrelated: apple, family, and house. Participants are instructed to respond with a single word that is associated with each of the three words: tree. Previous research had noted that associatively-related lists can prime better CRAT performance (Howe, Garner, Dewhurst, and Ball, 2010). Memory researchers refer to these stimuli as Deese/Roediger-McDermott (DRM) lists (Deese, 1959; Roediger and McDermott, 1995). Each list includes a series of related words (e.g., climber, peak, hike) that are all semantically related to a single critical item (mountain) not presented in the list. Thus, Garner and Howe (2013) used DRM lists, with participants rating each word according to survival- or moving-relevance. Then, they completed the CRATs, with half of the problems primed by the previous rating task (e.g., rating the survival- or moving-relevance of climber, peak, and hike, followed by completing a CRAT with mountain). Participants completed more primed CRATs than they did unprimed CRATs. In addition, Garner and Howe (2013) replicated the survival advantage, with better CRAT performance after rating words for survival-relevance than for moving-relevance. These findings are unique in that they are the first to demonstrate the benefit of survival processing on problem-solving performance, as well as the first depiction of the effect in another cognitive domain. Far-
reaching extensions of Nairne et al.’s (2007) work—such as those described by Garner and Howe (2013)—are especially important, as this area of research grows over time. For the effect to be truly meaningful, it should be generalizable, as was the case here.

Unlikely Mechanisms for the Survival Advantage

Several of the studies discussed previously have inadvertently ruled out potential mechanisms. For example, Nairne and Pandeirada (2010a) noted how participants rated their scenarios as equally imageable, interesting, etc. The studies in this section used a different approach, by directly testing the plausibility of different mechanisms underlying the survival advantage. These studies tested the following mechanisms: media exposure, stereotype activation, scenario location, perceived social isolation, negativity/mortality salience, and perceived threat. It is important to note that conclusions drawn from these studies are tentative, as several are based on a small set of findings and cannot definitively rule out these mechanisms. As such, they are primarily listed as unlikely contributors to the effect.

In the first of these, Kang, McDermott, and Cohen (2008) tested one of the potential mechanisms outlined by Nairne et al. (2007): media exposure. In their two experiments, the authors compared survival processing to a bank robbery scenario. These scenarios are better matched on excitement and novelty than some of the previous designs comparing survival processing to mnemonic strategies (e.g., pleasantness ratings) or less arousing scenarios (e.g., moving). Using both recall (Experiment 1) and recognition (Experiment 2), Kang et al. (2008) replicated the survival advantage. Importantly, these sets of experiments provide a more direct comparison of memory performance from two comparable scenarios. In both experiments, survival processing led to better memory than robbery processing. Moreover, in Experiment 1, memory following robbery processing did not differ significantly from pleasantness rating (Experiment 2 did not use a pleasantness control condition). This finding is especially important. Despite being both exciting and novel, the robbery scenario led to the same level of retention as pleasantness ratings. Thus, their findings reduce the likelihood that the survival advantage is due to survival processing being a more exciting or novel task.

Next, Otgaar et al. (2011) tested whether the survival advantage is an effect of stereotype activation. From some related studies, we know that activating a “professor” stereotype can increase performance on trivia questions (Dijksterhuis and van Knippenberg, 1998), but activating an “elderly person” stereotype can decrease walking speed (Bargh, Chen, and Burrows, 1996, Experiment 2). In a pilot study, the authors asked participants to describe “the type of person they were thinking of when reading the [survival] scenario” (Otgaar et al., 2011, p. 1035). Responses included: having a good memory, healthy, intelligent, physically strong, and energetic. Otgaar et al. (2011, Experiment 2) used this description to test whether the activation of these specific traits would be as effective as the survival scenario itself. The authors used a between-subjects design, testing the survival scenario, survival “stereotype,” and moving. They replicated the survival advantage, but only with the survival scenario; memory following processing a survival stereotype was similar to moving processing. This effect is surprising, as the stereotype described a person with an excellent memory, which should have alerted participants that they were participating in a memory experiment. However, we should
mention that stereotype activation, as an area of research, has recently been scrutinized for its lack of replication in experimental settings (e.g., Shanks et al., 2013). Nevertheless, these results indicate that the survival advantage may be due to more than the mere activation of or imagining how a healthy and intelligent person would behave in a survival situation.

Kostic, McFarlan, and Cleary (2012) conducted four experiments to test two additional potential mechanisms: the scenario location and perceived social isolation. In Experiments 1A and 1B, they tested survival processing with additional wilderness settings, some of which did not imply an ancestral context. This challenges some of the claims made by Weinstein et al. (2008) and Nairne and Pandeirada (2010a) pertaining to the role of ancestral priorities in the survival advantage. In these two experiments, the authors used grasslands, desert, jungle, space, and sea locations in their survival scenarios. When compared with pleasantness and self-reference control conditions, the authors found that all versions of the survival scenario promoted better retention than the control conditions. In addition, the following comparisons indicated that the survival scenarios were equally effective: grasslands and desert (Experiment 1A), space and jungle (Experiment 1B), and grasslands and sea (Experiment 1B). These findings have been replicated in several studies: Soderstrom and McCabe (2011) with grasslands and city scenarios, Klein (2013) with grasslands and geography-free survival scenarios, and Howe and Derbish (2014) with grasslands, desert island, foreign planet, and sea scenarios. Thus, these findings challenge the need for an ancestral context to produce the survival advantage; survival in general drove the effect in this set of experiments. That is, the advantage does not necessarily need to be confined to ancestral contexts, as survival itself may be the primary motivator for better encoding and retrieval.

In their second set of experiments, Kostic et al. (2012) tested another potential mechanism underlying the survival advantage: perceived social isolation. One element common to the many tested versions of the survival scenario is an implied sense of social isolation by being stranded in some location. This is an interesting observation, as there are both benefits and costs with group interactions. For example, a group can offer protection and a large mating pool, but can also increase competition, disease transfer, and aggression (Buss, 1995). Group living can also foster social interaction, which has been shown to greatly enhance memory (Mickes et al., 2013). In Experiments 2A and 2B, Kostic et al. (2012) compared two sets of survival scenarios. In Experiment 2A, being lost at sea (alone) was compared with being lost at sea (with a group of people). In Experiment 2B, surviving in a ghost town was compared with surviving in a city filled with strangers. The authors used a pleasantness rating control condition in their experiments. Across both of these experiments, the authors found comparable levels of recall in the “alone” and “group” survival scenarios. Thus, the social isolation hypothesis cannot explain the survival advantage, as memory did not differ for these scenarios. Moreover, the size of the advantage—the benefit of processing words according to their survival-relevance, relative to rating their pleasantness—was similar across these scenarios.

Testing another implied aspect of the survival scenario, Bell, Röer, and Buchner (2013) investigated the role of negativity in the survival advantage. Pilot testing found that participants rated the survival scenario as more “negative” than a moving control condition. A scenario describing suicide was perceived as more negative than the survival scenario. In Experiment 1, Bell et al. (2013) tested the mnemonic benefit of these three scenarios, in
addition to a pleasantness rating control condition. Overall, survival processing led to the best retention, followed by suicide processing. Memory for the two control conditions did not differ significantly. Findings from Experiment 3 are also of interest, as the authors simplified their manipulation. In this experiment, participants rated words according to survival-relevance and death-relevance (presented as mere concepts, instead of described within scenarios). They also manipulated concreteness within their word list, testing memory for concrete and abstract words. It is important to note two preliminary observations here: (1) Some of their concrete words included living things (e.g., rabbit, chicken), which is potentially problematic given the processing advantage for animacy described earlier (New et al., 2007; see also, VanArsdall, Nairne, Pandeirada, and Blunt, 2013); (2) Previous research has found recall differences between concrete and abstract words (e.g., Altarriba and Bauer, 2004). Overall, survival processing led to better memory than death processing, particularly for the concrete words.

Given the two observations that we have described, these findings are what we might expect. However, it is quite important that the mere concept of survival can lead to better memory. Perhaps we should consider what survival truly means: a call to action to avoid death. It is then possible that death processing may discourage additional cognitive processing. Klein (2012b) has made a similar case for differences between survival processing and death processing (i.e., that participants imagine they are about to die), arguing, “In the case of survival the individual is motivated to seek out solutions to perpetuate his or her continuance, whereas in the case of mortality salience the individual considers an unavoidable outcome and thus will be less motivated to take steps to actively avoid the eventuality” (p. 74). Thus, survival processing does not appear to be a superior mnemonic device because of any similarity to death processing.

In the last of these studies, Olds, Lanska, and Westerman (2014) questioned the role of perceived threat in the survival advantage. In other words, if survival is threatened, does the level of threat significantly affect memory? The authors manipulated threat by creating two versions of the survival scenario. The “low threat” condition included the following sentence: “Importantly, we would like you to imagine that food and water are easy to obtain and that predators are easy to detect and avoid” (p. 29). The high threat condition replaced instances of “easy” with “difficult.” Olds et al. (2014) also manipulated the survival context (ancestral versus modern), but found similar results in both contexts. This finding, similar to that of Kostic et al. (2012), challenges the proposal that an ancestral context contributes to the survival advantage, or that an ancestral environment is needed for the effect itself. The authors found a survival advantage across all levels of threat (when compared with the pleasantness rating control condition), though the recall advantage did increase with level of threat (a 9% versus 13% versus 15% improvement over pleasantness ratings). Thus, level of threat can affect memory, though it cannot account for the effect alone. One possibility is that the high threat scenario may increase the level of elaboration while processing the words for survival-relevance. However, this conjecture cannot fully explain how a low level of threat (i.e., when survival appears “easy”) could activate the same survival mechanism that improves memory performance. Is considering one’s very survival enough to activate the mechanism?
Potential Mechanisms for the Advantage

Unlike the studies presented in the previous section, the next set of studies present more likely mechanisms for the survival advantage: elaboration, self-referential processing, and planning. Although several of these studies have been discussed elsewhere (see Burns and Hart, 2014; Erdfelder and Kroneisen, 2014; Howe and Otgaar, 2013; Otgaar et al., 2011), they are typically presented as evidence against the evolutionary account for the advantage. A recent review by Nairne (2014) took a different approach, suggesting that the scenario itself may activate these mechanisms (e.g., increased elaborative processing). Thus, there is some debate in the literature as to whether the survival advantage is the result of one or more of these proximate mechanisms, rather than the result of some ultimate mechanism that we cannot directly test. Nairne and his colleagues (e.g., Nairne et al., 2007, 2008; Nairne and Pandeirada, 2010a) have maintained that the survival advantage persists in memory research because of a match between ancestral priorities and the survival problems presented in the scenario. Thus, they are interested in answering a “why” question: Why does the advantage exist? Other researchers (including Burns et al., 2011, described earlier) have investigated a “how” question: How does the advantage occur (i.e., the mechanisms)? We should note that this review is not designed to promote any one mechanism in particular. Instead, we present a series of the potential mechanisms currently being studied.

Elaboration

One of the more explored mechanisms is elaboration, as previously described in research investigating the role of individual differences in the survival advantage (e.g., Nouchi, 2011; Nouchi and Kawashima, 2012). According to Kroneisen and Erdfelder’s (2011) richness of encoding hypothesis, elaborative encoding can predict the survival advantage. This hypothesis is not necessarily at-odds with the evolutionary account for the survival advantage, because it is certainly possible that processing a survival scenario encourages deep, meaningful processing, as is the case with elaboration. Across a series of experiments, Kroneisen and Erdfelder (2011) compared survival processing to moving processing. Their unique contribution to this area of research was a new version of the survival scenario that was much simpler than the version originally used by Nairne et al. (2007). This simpler version included a single survival problem: a need for water. The authors considered whether a highly complex survival scenario encouraged greater elaboration than less complex control conditions. Across both within-subjects (Experiment 1) and between-subjects (Experiment 2) designs, the authors found the typical survival advantage only when comparing the original survival scenario to moving processing. The shorter version of the survival scenario did not promote better recall than the moving scenario. These findings indicate that, when the scenarios are matched on the number of problems that they describe, there is no benefit to processing the words according to either scenario. This may be because the more complex survival scenario provides additional connections and retrieval cues to the words from the rating task.

According to Röer, Bell, and Buchner (2013), survival processing may also activate additional ideas for how the to-be-rated words might be used (but see Kroneisen, Erdfelder, and Buchner, 2013 for findings indicating that the advantage is due to more than simply imagining these ideas). Perhaps when scenarios are better equated on the number of
problems or ideas that they contain, the advantage is reduced. This conjecture is similar to what Burns et al. (2011) had hypothesized, when they noted how the survival scenario promotes both relational and item-specific processing (wherein control conditions like pleasantness promote item-specific processing only).

Additional research has assessed the elaboration hypothesis from a different perspective, by increasing the cognitive demands of the task and limiting elaboration. Will the survival advantage persist under dual-task conditions? Across several experiments, Kroneisen, Rummel, and Erdfelder (2013) and Nouchi (2013) failed to find the survival advantage when a high cognitive load was implemented (replicating findings presented previously by Stillman et al., 2014). Kroneisen, Rummel et al. (2013) used a tone-detection task, whereas Nouchi (2013) used a digit memory task. These findings suggest that survival processing is effortful, which could not be detected by previous research with simple RT data. The dual-task condition limited the cognitive resources available for processing these scenarios, particularly the highly complex survival scenario.

**Self-referential processing**

The role of self-referential processing in the survival advantage has been studied extensively. Some early research dismissed the importance of self-referential processing in the advantage, which we now know was in haste. For example, Nairne et al. (2008, Experiment 1) compared recall memory from survival processing to a self-reference control condition. Processing words according to their survival-relevance was a better mnemonic strategy when compared to self-reference and other control conditions. Thus, survival processing appeared to be a better strategy than self-referential processing. Moreover, Kang et al. (2008, Experiment 3) replicated the survival advantage when both the survival scenario and the bank robbery control condition were written about a character from a film clip. In other words, the advantage did not necessarily rely on self-referential processing if it persisted in situations that did not require participants to consider how they will survive (or commit a bank robbery, for that matter).

However, the vast majority of research conducted in this area utilizes the standard version of the survival scenario (Nairne et al., 2007), which instructs participants to imagine that they are the character described in the scenario. Thus, the best assessment for the role of self-referential processing in the survival advantage will include the standard survival scenario as a baseline measure. Two experiments have used this procedure. The first, conducted by Weinstein et al. (2008, Experiment 2) included both first- and third-person scenarios. The third-person scenarios were written about “a friend,” and the magnitude of the advantage over the moving scenario did not differ for first- or third-person survival. The authors decided that these results were not in favor of self-referential processing playing a role in the survival advantage.

However, some more recent findings suggest a different interpretation for these results. Cunningham, Brady-Van den Bos, Gill, and Turk (2013) tested an additional third-person survival scenario. Their “third person” was Prime Minister David Cameron. Cunningham et al. (2013) found better memory after first-person survival processing, relative to third-person survival processing. Thus, there is a difference (when comparing their results to those described by Weinstein et al., 2008, Experiment 2) between considering a friend’s survival and a well-known stranger’s survival. In other words, processing a friend’s survival resulted in a memory benefit comparable to that of
processing personal survival. This finding relates to the importance of kin and caring for those closest to us, and is certainly adaptive. It is somewhat amusing that processing David Cameron’s survival was not equally memorable, as Cunningham et al. (2013) sampled from a population of British undergraduate students!

Despite these interesting results, Klein (2012a, 2014) has argued that these self-reference manipulations are not truly assessing self-referential processing. In two experiments with more explicit instructions to activate an autobiographical memory for each of the words (adapted from Klein, Loftus, and Burton, 1989), Klein (2012a) compared survival and self-reference scenarios that were better equated on effort needed to process each word. Across both experiments, Klein (2012a) found similar levels of recall for the standard survival scenario (Nairne et al., 2007) and the self-reference scenario first used by Klein et al. (1989). Both of these scenarios promoted better memory than the self-reference scenarios used by other researchers (for a recent replication of these findings, see Klein, 2014). Thus, there is evidence that self-referential processing can certainly benefit memory—and perhaps just as much as the survival scenario. This may be because both scenarios are relying on some element of self-referential processing, which may also rely on the elaborative mechanism previously described. As we are more likely to elaborate on personal experiences, there is reason to believe that these mechanisms may be interrelated.

**Planning**

Other researchers have assessed the role of planning in the survival advantage (see Sellers and Bjorklund, 2014 for a review of mental time travel). At its very essence, the purpose of a memory system is to store information in the event that it will assist us in the future. In other words, planning has great adaptive value, in ways similar to those described within this paradigm. According to Klein and his colleagues (Klein, 2014; Klein, Robertson, and Delton, 2010, 2011), storing information for the future is our mind’s way of planning for some future event that will utilize this stored information. Klein et al. (2010, 2011) have noted that the standard survival scenario (Nairne et al., 2007) does invoke some sense of future planning (e.g., locating food and water), which may account for some amount of the effect.

To first assess how survival processing compares with planning processing, Klein et al. (2010) created four scenarios. Each of these scenarios took place in a woodland setting. Participants rated words according to one of the four scenarios: (1) survival in the woods; (2) prior planning (i.e., whether they were used in a prior camping trip); (3) future planning (i.e., whether they would be relevant to planning a camping trip); or (4) an imagined camping trip (i.e., whether they came to mind when imagining a camping trip). Participants in the future planning condition recalled the most words, followed by those in the survival condition. Participants in the imagined camping trip and prior planning condition recalled the fewest words, indicating that memory benefits most from future-associated processing, or planning (for similar findings with children, see Raymaekers, Otgaar, Peters, and Smeets, 2014). Klein et al. (2010) suggest this to be an evolved mechanism, as planning for the future likely helped our ancestors “remain active long enough to reproduce and care for [their] offspring” (p. 18).

Klein et al. (2011) continued this line of research by directly assessing the role of planning in the survival advantage. They first pilot tested their word list to limit any congruity between scenarios and words. Participants rated words according to one of three
scenarios: (1) survival with planning (i.e., whether they would bring the item to help them survive); (2) survival without planning (i.e., whether they would eat the item, if they came across it); or (3) planning without survival (i.e., whether they would purchase the item for an upcoming dinner party). Across two experiments, participants remembered more items in the survival with planning condition than in the survival without planning condition. More importantly, in their first experiment, recall between the two planning conditions (survival with planning and planning without survival) did not differ significantly. These findings emphasize the function of planning in memory. Moreover, as planning can certainly improve the likelihood of survival, it is possible that a survival scenario that includes some element of planning is activating or tapping into two of the adaptive functions of memory. These findings can also explain previous comparisons between survival and moving processing, which both require planning, but only one scenario benefits from the survival mechanism.

Again, it is important to note that each of these mechanisms may explain some portion of the advantage, though it is unlikely that any one mechanism can fully explain the advantage. From these findings, we might assume that some of the advantage of survival processing relative to control conditions (e.g., pleasantness ratings) can be explained by relational processing (Burns et al., 2011), elaboration (Kroneisen and Erdfelder, 2011), self-referential processing (Klein, 2012a), and planning (Klein et al., 2011). However, they cannot eliminate the possibility that survival processing itself drives additional processing during encoding. If the human memory system evolved to solve specific, adaptive problems, then memory mechanisms that aid in problem-solving—elaboration, self-referential processing, and planning—will also be activated. However, this hypothesis cannot explain situations in which the survival scenario and control conditions appear to be well-matched on these dimensions, yet the survival scenario promotes better memory (e.g., moving, planning a bank robbery, taking a vacation). Thus, the survival advantage is perhaps a combination of these mechanisms, in addition to something that has yet to be accounted for in the literature.

Failures to Replicate the Survival Advantage

Several lines of research have failed to replicate the survival advantage. These findings are highly informative in that they tell us the specific parameters with which the effect does and does not result. Some have been described previously, such as the null effect in older adults reported by Stillman et al. (2014). Others have led to great scrutiny concerning the congruity between word lists and processing scenarios (Butler et al., 2009; Nairne and Pandeirada, 2011). The findings discussed in this section include other paradigms using implicit memory tests (McBride, Thomas, and Zimmerman, 2013; Tse and Altarriba, 2010), paired-associate learning (Schwartz and Brothers, 2014), attention tasks (Altarriba and Kazanas, 2014), and several other tasks. Collectively, their findings imply a need to further specify the mechanism(s) underlying the survival advantage, as it does not appear to be a broad “memory” effect. In addition, they limit the generalizability of the effect to other domains of cognitive processing.
Implicit processing tasks

Each of the studies previously discussed utilized an explicit memory task to examine survival processing (with the exception of CRAT performance, as described by Garner and Howe, 2013). What happens to the survival advantage when an implicit memory task is used instead? Across a series of experiments with several different implicit tasks, both Tse and Altarriba (2010) and McBride et al. (2013) failed to replicate the survival advantage. In Experiment 1, Tse and Altarriba (2010) used a stem-completion task to compare survival processing to moving and pleasantness control conditions. Participants were instructed to either complete the stem with one of the studied words (the explicit condition) or to complete the stem with the first word that came to mind (the implicit condition). In the explicit task, they replicated some elements of a survival advantage, with faster completions in the survival condition (relative to the moving and pleasantness rating conditions). However, in the implicit task, the authors found no difference in memory across their conditions. Experiment 2 used a different task for the implicit condition, with participants identifying words as either concrete or abstract words. Tse and Altarriba (2010) replicated the survival advantage, with better recognition in the survival condition. In the implicit condition, accuracy (concrete/abstract identification) and RTs did not differ significantly across their conditions. Across their two implicit tasks, the authors failed to replicate the survival advantage. This may seem surprising, given the robustness of the effect. However, we might expect that engaging in deep processing tasks in the laboratory may share some similarities with the deep processing that would occur in real-life survival situations. Considering the problems described in the survival scenario, each of them would require consciously considering how best to find food, water, and shelter. Implicit processing tasks may not provide enough of a match with the manner in which the words were encoded (a type of encoding-specificity effect).

Tse and Altarriba’s (2010) findings were later supported by McBride et al. (2013). These authors used additional implicit tasks, along with concrete words only (the stimuli used by Tse and Altarriba, 2010 were a bit unique in that they used concrete and abstract words). In Experiment 1, McBride et al. (2013) used the same conditions and replicated the null effect. Next, in Experiment 2, they used categories of words, as well as unrelated words, in their stimuli. For their implicit and explicit tasks (manipulated between-subjects), participants were presented with a category. In the explicit condition, they were instructed to generate exemplars from what had been presented earlier. In the implicit task, they were instructed to simply generate exemplars as quickly as possible. In this case, McBride et al. (2013) failed to replicate the survival advantage with either an explicit or implicit task. Thus, it appears (though this has not been thoroughly explored) that these cued explicit and implicit tasks are not conducive to generating the survival advantage. Again, this may be a case of an incompatibility between processing during the rating task and processing during the cued tasks—particularly the implicit tasks that tap into more automatic processing. Perhaps additional research can clarify the relationship between survival processing and differences between explicit and implicit memory effects.

Learning tasks

The majority of research conducted in this area has followed a simple design, by testing the mnemonic potential of one encoding scenario over another. As we’ve described, this design assesses memory for lists of words. Schwartz and Brothers (2014) measured
memory in a different way, with paired-associate learning. Swahili-English word pairs were used in Experiments 1 and 2; Lithuanian-English word pairs (suggested to be easier to learn) were used in Experiments 3 and 4. Across these four experiments, the authors compared survival processing to pleasantness ratings. Recall performance was assessed by presenting the Swahili/Lithuanian word from each pair as a cue. Participants were instructed to recall the English word presented from the pair. In each of these experiments, participants were able to recall more of the English words following pleasantness ratings. Thus, their findings did not replicate the typical survival advantage. In addition, this failure to replicate was consistent across both intentional (Experiment 1) and incidental (Experiment 2) learning situations. Perhaps pleasantness ratings encourage associative processing between a word and its translation, which would be beneficial in their research design. According to Burns et al. (2011), survival processing may encourage participants to process the relations among words, instead. Thus, presenting a Swahili/Lithuanian word and instructing participants to recall its translation may not benefit from relational processing. Moreover, metamemory judgments could not account for their findings. Both feeling-of-forgetting (Experiment 3) and feeling-of-knowing (Experiment 4) judgments were similar across pleasantness and survival scenario conditions. Participants’ judgments of their own learning did not differ according to the type of processing during encoding. Importantly, these results indicate that survival processing does not necessarily motivate memory for words across all types of experimental manipulations and tasks.

Judgments of learning (JOLs) have also been assessed with the more typical research design for this area. Palmore, Garcia, Bacon, Johnson, and Kelemen (2012, Experiment 1B) found some surprising results. For example, with JOLs, participants predicted that they would remember more words after survival processing. However, in their study, memory did not differ between survival processing and a bank robbery control condition (Kang et al., 2008). Thus, there is much to discover in this area of research. Why do metamemory judgments fail to reflect actual learning in the survival processing paradigm? Can these judgments also impact memory performance?

Memory for faces

While researchers have replicated the survival advantage with stimuli other than words (e.g., pictures, from Otgaar et al., 2010), the advantage has not been replicated with faces (for a recent review of research related to recognizing others, see Maguinness and Newell, 2014). Across five experiments, Savine, Scullin, and Roediger (2011) assessed recognition for old faces versus new faces. These faces included computer-generated faces (Experiment 1), as well as real faces (Experiments 2-5). The authors collected several ratings for these faces, including how helpful each face looked, as well as whether the face looked afraid, angry, attractive, or trustworthy. Scores on these rating dimensions were not related to memory performance. More importantly, Savine et al. (2011) failed to replicate the survival advantage in any of these experiments, including one experiment that presented survival-relevant information with each face. In Experiment 5, participants saw faces and learned about a person’s particular skill: survival, social, kin, navigation, reproduction, or neutral. While some of these pieces of information were memorable, memory for the actual faces was not affected by the processing scenario (survival versus moving). Thus, the survival advantage for word memory does not appear to generalize to face memory. However, there may be both evolutionary and nonevolutionary explanations
The survival advantage

for this surprising set of findings. For example, as humans evolved, they lived in small (potentially isolated) groups and may not have benefited from recognizing a large number of faces. On the other hand, there may have been some benefit to recognizing a stranger as someone new, so that they would not be confused with someone from the group, and in the event of future encounters with that stranger. Processing concrete objects for their survival-relevance may have occurred more frequently and been a more adaptive mechanism. In addition, if the survival advantage can be at least partially accounted for by cognitive components of the scenario (e.g., elaboration, planning, etc.), recognizing faces would not benefit from these components.

Additional fitness-relevant scenarios

One very recent set of experiments is potentially problematic for the evolutionary account of the survival advantage (e.g., Nairne and Pandeirada, 2010a; Weinstein et al., 2008). Sandry, Trafimow, Marks, and Rice (2013) tested the advantage with additional fitness-relevant processing scenarios. These scenarios included fear/phobia, mate-selection, incest-avoidance, cheater-detection, jealousy, and social status. These scenarios were compared with two control conditions: pleasantness and imagery ratings. The authors also collected scenario ratings to determine if these scenarios differed on interesting, imageable, emotional, familiar, or unusual dimensions (Nairne and Pandeirada, 2010a). However, only the standard survival scenario promoted better memory than the two control conditions. In other words, their data indicate that these survival-relevant scenarios may not activate the same memory mechanism as the standard survival scenario. In addition, these findings were not the result of differences in participant-rated interest, imagery, emotionality, familiarity, or unusualness dimensions. These results were replicated with an additional control condition (ratings for moving-relevance, in Experiment 3) and better matched scenarios equated on the number of problems described in each one (e.g., Kroneisen and Erdfelder, 2011). Their findings are quite surprising, given previous research with other fitness-relevant scenarios. For example, Nairne et al. (2009) replicated the survival advantage with hunting and gathering scenarios, and Nairne and Pandeirada (2010a) replicated the survival advantage with a scenario describing foraging for medicinal plants to heal an infection. Thus, there is some evidence to suggest that other fitness-relevant scenarios can be effective mnemonic strategies.

However, in one of their follow-up experiments, Sandry et al. (2013, Experiment 2) noted that participants recalled more words in the fear/phobia condition than the pleasantness control condition. Recall was consistently greatest with the standard survival scenario. If the standard survival scenario is the best mnemonic strategy because of a fitness-relevant mechanism (as the evolutionary account purports), we might expect that these new fitness-relevant scenarios would enhance memory relative to the control conditions. Thus it is, at the very least, somewhat surprising that Sandry et al. (2013) did not find a memory advantage for scenarios based on psychological constructs that rely on memory, such as cheater-detection and jealousy. However, we cannot expect that this effect is broadly applicable, as it has not been observed in paired-associate learning or implicit memory paradigms. The fear/phobia scenario enhanced memory relative to the pleasantness control condition, though to a lesser degree than the standard survival scenario. Moreover, emotional arousal ratings for the fear/phobia scenario ($M = 3.15$) were greater than those for the pleasantness scenario ($M = 2.20$). Thus, some amount of
emotional arousal can play a role in these findings. This indicates that memory may be specialized for fear-relevant stimuli (e.g., dangerous situations, predators, etc.). In fact, a portion of the survival advantage may be accounted for with this fear/phobia mechanism: a fear of starvation, a fear of predation, and so forth.

**Story memory**

The survival advantage is primarily a memory advantage for words. These words are often selected from unrelated categories to limit any congruity between scenarios and stimuli. Seamon et al. (2012) designed a very different kind of study. In a series of experiments, they also tested memory for words, but these words were presented within stories. At certain points during the story, words would be repeated and participants would rate them either according to their relevance to understanding the story or to their relevance to survival within the story. The topics of the stories ranged from exploring to flying, with survival and neutral versions to assess memory for the stories themselves. Their experiments varied greatly, as they manipulated incidental versus intentional learning, and used both cued-recall and free recall tests to assess memory. In only one of their experiments did they find some evidence of a survival advantage. Recall following survival-exploring processing was greater than survival-flying and neutral-exploring processing (though it did not differ from neutral-flying processing). In their other experiments, Seamon et al. (2012) largely failed to find a survival advantage for story memory. This null effect included details from these stories, as well as the rated words within them.

**Attention and memory for location**

Testing the impact of survival processing on another cognitive ability, Altarriba and Kazanas (2014) used an n-back task to measure online processing. In the n-back task, participants must continuously update the contents of their working memory such that they retain n items and respond to each trial. In their experiment, participants first read either a survival or moving scenario (akin to a priming passage). Then, they performed either a verbal or spatial two-back task. In the verbal condition, participants indicated whether a letter presented on the screen was either the same or different from the letter presented two trials earlier. In the spatial condition, participants indicated whether the location of that letter was the same as or different from the location of the letter presented two trials earlier. Overall, RTs (in this case, the length of time before a participant responded same or different on a keyboard) for the survival condition were equal to the moving condition, indicating that the prime did not have an overall effect on n-back performance. Participants performed the spatial two-back task faster than the verbal two-back task. The significant interaction revealed several interesting findings. For example, participants in the moving-spatial condition were both faster and more accurate than those in the other conditions. This finding is surprising, as we might expect that survival processing and spatial memory (or memory for location) would be positively related, as the scenario describes specific situations where searching will be needed. Although Nairne, VanArsdall, Pandeirada, and Blunt (2012) have demonstrated location memory for survival-relevant items, other researchers (e.g., Bröder, Krüger, and Schütte, 2011) have been unable to replicate a location memory advantage for pictures of common objects following survival processing (including experiments where the number of locations was reduced to two). Thus, research
investigating the relationship between survival processing and location information has been mixed, with several studies failing to replicate the typical survival advantage. This particular area of research is important, as it intends to test the effect with new tasks and has found some divergent results. Location memory appears to be a viable area of research for additional studies.

Specific types of predators

Soderstrom and McCabe (2011) investigated the impact of scenario location (as related to the advantage of ancestral survival processing, relative to modern survival processing; see Weinstein et al., 2008), as well as specific types of predators in the survival scenario. Soderstrom and McCabe (2011) included five conditions in their study: the standard survival scenario (Nairne et al., 2007), a survival scenario with a zombie predator, a modern (city) survival scenario with attackers, a modern (city) survival scenario with zombies, and a pleasantness rating control condition. In what was initially described as a controversial finding, recall with the zombie predator scenarios was greater than recall with the predator and attacker scenarios, regardless of whether the scenario was described as ancestral or modern (for a replication of this finding with a demon predator, see Kazanas and Altarriba, 2013). These findings challenged the role of ancestral priorities underlying the survival advantage, as supernatural predators were not a likely foe for our Pleistocene ancestors. In addition, previous manipulations of context (ancestral versus modern) had found a larger survival advantage with ancestral survival scenarios (e.g., Nairne and Pandeirada, 2010a; Weinstein et al., 2008).

However, it is important to further investigate these findings. For example, Soderstrom and McCabe (2011) used a between-subjects design; both Weinstein et al. (2008) and Nairne and Pandeirada (2010a) used a within-subjects design. Perhaps the design is crucial when comparing the effects of setting (ancestral versus modern) on the survival advantage. Researchers have found an ancestral survival advantage with a within-subjects design, and a modern survival advantage with a between-subjects design. This conclusion is tentative, and would require replication to be more definitive. With regards to the zombie advantage, the controversy may instead be further evidence of the evolutionary account for the survival advantage. Zombies could, in fact, represent a “super predator” that increases the magnitude of the effect (Nairne, 2014). Consider the way in which we characterize zombies in films and television shows. They represent the undead, with an insatiable appetite for human brains. Thus, presenting a survival scenario that describes a super predator is perhaps an even more effective mnemonic technique.

False memory effects

The current review has presented findings involving accurate memory: the proportion of correct recall or recognition. However, some overlooked findings from Nairne et al. (2007, Experiment 1) and Nairne and Pandeirada (2008a, Experiment 1) have led to another area of inquiry: the relationship between survival processing and false memories. In each of these experiments, the authors reported a large number of intrusions in the survival condition. How can this be? Why would survival processing increase both accurate and false memory, relative to control conditions? Unfortunately, very few studies report their intrusions, and those that do include only the total number and omit the actual words. Thus, we cannot make any explicit comparisons between conditions. However, the
following section explores the research that has been specifically designed to address this question.

Howe and Derbish (2010) were the first to explore this false memory effect, and they used associatively-related DRM lists. In Experiment 1, the authors used neutral (e.g., mountain, school), negative (e.g., sad, cry), and survival (e.g., fight, sick) lists. The words in the lists were intermixed and participants rated them according to either survival-relevance or pleasantness (a between-subjects manipulation). The authors found that participants in the survival condition recognized more of the words from the lists (e.g., climber, peak, hike) and the critical items (e.g., mountain) that were not presented: a measure of "false memory." Howe and Derbish (2010) replicated this finding in Experiments 2A and 2B, which included a moving control condition. However, it is important to resist forming a negative interpretation of these findings. The finding that survival processing encourages accurate and false memory for semantically-related materials may be beneficial, as it is quite useful to activate a concept and its associates. As such, this finding is consistent with theories of spreading activation (Roediger, Balota, and Watson, 2001) that explain how the activation of one concept spreads to its semantic associates (e.g., robin activates bird, egg, etc.). Thus, these results are a reflection of memory performance in naturalistic settings.

Thus, research in this area has continued. For example, Luo and Geng (2013, Experiment 1) replicated the findings described by Howe and Derbish (2010) using a within-subjects design. In addition, Otgaar and Smeets (2010) and Otgaar, Howe, Smeets, and Garner (2014) found similar results with recall tasks, demonstrating that these false memory effects generalize to additional research designs and memory tasks.

Of particular interest are Otgaar and Smeets’ (2010) and Otgaar, Howe, Smeets, and Garner’s (2014) findings with children, as several of their experiments with false memory included child samples. In Experiment 2, Otgaar and Smeets (2010) included a group of 8-year old children and a group of 11-year old children. The authors found the typical survival advantage (replicating other findings with child samples by Aslan and Bäuml, 2012; Otgaar and Smeets, 2010). More importantly, both age groups demonstrated this false memory effect (i.e., recalling the semantically-related critical item not presented). However, the older children were more susceptible to the effect. Extending this developmental trend, Otgaar, Howe, Smeets, and Garner (2014, Experiment 1) reported that adults recalled more critical items than 11-year-olds. Thus, these results indicate—as we might expect—that these false memory effects are a function of experience with these words and how they are related to each other. Naturally, these experiences come with age, so very young children are less likely to activate additional semantically-related words than adults (but see Otgaar, Howe, Smeets, Raymaekers, and van Beers, 2014 for larger false memory effects in children, using an intentional learning paradigm). These authors appear to be in agreement that survival processing may increase memory for gist (and, likely elaboration). As we consider a possible explanation for these findings, misremembering related information could have adaptive value (e.g., recalling a location similar in appearance to where they last found food or water). This false memory could then lead to an additional food or water source, based on a likelihood. On the other hand, frequent mistakes would be costly, which could explain why intrusions are not often reported in these experiments. Thus, theories of spreading activation and semantic memory may have adaptive value that has not yet received consideration.
Summary and Future Directions

The current review presented research investigating the survival advantage, as well as several related areas of research. The original findings described by Nairne et al. (2007) suggested that processing a word for its survival-relevance may be one of the best encoding strategies for later retrieval. Nairne and colleagues (Nairne, 2010; Nairne and Pandeirada, 2010a; Nairne et al., 2009) have argued that the advantage reflects a match between the problems presented in the survival scenario—a need for food, water, and protection from predators—and the problems that our memory system evolved to solve. In other words, our ancestors faced a number of problems that threatened their survival; evolving specific mechanisms to solve these problems enhanced their reproductive value and fitness. Processing the survival scenario may enhance memory because it utilizes these specific mechanisms.

Several researchers have investigated this hypothesis and supported this evolutionary account for the survival advantage (e.g., Nairne and Pandeirada, 2010a; Weinstein et al., 2008). Moreover, the advantage is present in both between- and within-subjects designs (Nairne and Pandeirada, 2008b), as well as with recall and recognition memory tasks (Kang et al., 2008). Finally, the advantage is not necessarily limited to memory for words, as Otgaar et al. (2010) have replicated the advantage with picture stimuli.

However, there are specific circumstances that limit the generalizability of the advantage. Both McBride et al. (2013) and Tse and Altarriba (2010) have noted that survival processing does not benefit memory (relative to control conditions) in implicit tasks. In addition, the survival advantage has not been replicated with face stimuli (Savine et al., 2011), in a paired-associate learning paradigm (Schwartz and Brothers, 2014), or in dual-task conditions (Kroneisen, Rummel, et al., 2013). These findings indicate that one of the primary limiting factors of the advantage is the task itself, which should motivate researchers to continue exploring additional tasks within this paradigm. Researchers have also noted that the survival advantage is present only when control conditions require item-specific or relational processing, but not both (Burns et al., 2011, Luo and Geng, 2013). There is also evidence to suggest that survival processing is a powerful mnemonic strategy because it encourages greater elaboration than control conditions. When the survival scenario and control conditions are matched on the number of problems that they describe, there is no benefit to processing words for their survival-relevance (Kroneisen and Erdfelder, 2011). Thus, selecting appropriate control conditions can have a large impact on whether a difference in memory performance will materialize.

These findings have encouraged researchers to seek out the mechanism(s) underlying the effect. Nairne (2014) has suggested an evolutionary account, in which memory is specifically tuned to retain information perceived to be fitness-relevant. Other researchers have proposed that elaboration (Kroneisen and Erdfelder, 2011), self-referential processing (Klein, 2012a, 2014), or planning (Klein, 2014a; Klein et al., 2010, 2011) may account for the advantage. Future research investigating these potential mechanisms will lead to a greater understanding of the advantage itself. The ultimate mechanism may be one based in ancestral priorities or cognitive abilities. Perhaps a combination of these mechanisms will ultimately account for the largest proportion of variance in the data. Nevertheless, the empirical foundation of this area of research is beneficial for studying the
relationship between what the human memory system evolved for and how it is used now. With better-matched scenarios, we can continue to generate interesting predictions along these lines, driven by theory and previous empirical work.

It is readily apparent that Nairne et al.’s (2007) original findings have inspired memory researchers to ask new research questions. What are the mechanisms underlying the survival advantage? What are the circumstances that limit the generalizability of the effect? Having presented dozens of experiments that have contributed to this area of research, we have some preliminary ideas, though many are based on a small number of experiments. The following is a brief selection of additional research questions.

First, several experiments have tested the role of individual differences in the survival advantage. For example, aging, imagery ability, and negative mood may affect the magnitude of the effect (Nouchi, 2011, 2012; Nouchi and Kawashima, 2012). One might also ask how a bilingual sample would perform on these kinds of tasks. The “bilingual advantage” is well-documented (e.g., Cook, 1997) and suggests that bilinguals are afforded cognitive processing benefits, relative to their monolingual peers. If the survival advantage is a function of one or more of the mechanisms outlined in this review (e.g., elaboration, planning, etc.), would bilinguals and monolinguals perform differently? As bilingualism has been shown to enhance cognitive processing, might it also enhance the magnitude of the survival advantage? In a similar vein, what is the impact of culture in this paradigm? Might we expect differences in the survival advantage between individualistic and collectivist cultures, if survival is described as either in isolation or in a group (e.g., Kostic et al., 2012)?

Sandry et al. (2013) presented some controversial findings. Despite replicating the survival advantage, additional fitness-relevant scenarios (e.g., mate-selection, cheater-detection) did not promote better memory than standard control conditions (e.g., pleasantness ratings). How can this be? Researchers should continue to investigate the mnemonic potential of fitness-relevant scenarios, with new scenarios that also relate to fitness: reproduction, protecting kin, fear of the dark, additional threats to survival, etc. As the standard survival scenario (Nairne et al., 2007) lists such a small number of fitness-relevant problems, relative to those that may have existed in our ancestral past, these are opportunities for future research. Sandry et al.’s (2013) null effects do not support the evolutionary account for the survival advantage, though we should not forgo future efforts to investigate these additional survival scenarios. Moreover, their findings may be specific to their research design or procedures. These particular types of investigations are fruitful in that they denote the limitations of the survival advantage, while casting some doubt on the evolutionary account and the role of fitness-relevance in the effect. We encourage researchers to take this particular approach in their research, with theory-driven manipulations in their research design.

A seemingly necessary manipulation to the standard survival scenario would be to create more age-appropriate versions (akin to creating age-appropriate scenarios for children, such as being forgotten at school, as described by Aslan and Bäuml, 2012). For example, future research could compare the mnemonic benefit of processing a scenario embedded in ancestral priorities (e.g., mating for reproductive purposes) to one embedded in modern, college priorities (e.g., mating for “hooking up” purposes). Several previous experiments comparing ancestral and modern survival scenarios had found greater memory following ancestral survival processing, however, they had not used scenarios that reflected
the typical habits or culture of their participants (e.g., Weinstein et al., 2008). Perhaps these more habitual behaviors—while still related to fitness—would promote better memory.

One particularly interesting finding described in the current review could generate an extensive line of additional research. When Kroneisen and Erdfelder (2011) tested an elaboration hypothesis for the survival advantage, they compared moving processing to a “short version” of the standard survival scenario that included a single survival problem: the need for water. When the scenarios were matched on the number of problems that they described, memory did not differ significantly. Thus, the authors suggested that the survival advantage may be due to the standard survival scenario encouraging greater elaboration than control conditions or scenarios. However, only one of the survival problems was tested and their results could be interpreted differently. Is it possible that Kroneisen and Erdfelder’s (2011) null effect could be the result of selecting a survival problem that does not contribute to the advantage? What if the threats of starvation or predation were more salient during encoding? What if just one of these survival problems is responsible for the effect? In addition, would manipulating the severity or threat (e.g., Olds et al., 2014) of the survival problem affect the magnitude of the advantage (e.g., a desperate need for water versus a mild need for water)? Results from these future studies could challenge some of the assumptions of the elaboration hypothesis.

One additional suggestion for future research involves a more explicit processing task. The majority of research conducted in this area instructs participants to rate the relevance of each word to a specific scenario (or, to rate the pleasantness of each word). Perhaps a better encoding strategy would be to instruct participants to process each word according to how it is used or manipulated (an embodied approach to survival processing). In a way, each word could then be considered a viable tool. Participants would then rate the ease with which a possible use came to mind.

Finally, one particular aspect of evolutionary theory has been largely ignored within this area of research. With the exception of a small number of studies (Sandry et al., 2013; Savine et al., 2011), the mnemonic value of processing stimuli for their reproduction-relevance has not been assessed. Two sets of experiments incorporated aspects of reproduction within their research designs. Sandry et al. (2013) included mate-selection, cheater-detection, and jealousy scenarios, while Savine et al. (2011) paired faces with fitness-relevant information (including statements about a particular person’s reproductive ability). Both sets of experiments failed to replicate the survival advantage with these stimuli. As these results are quite preliminary, we urge researchers to shift their focus from mere survival to the perpetuation of genes (G. G. Gallup Jr., personal communication, June 9, 2014). While securing survival materials is certainly important—and has demonstrated great potential for an effective mnemonic technique—evolutionary theory is primarily based in differential reproduction. The most effective mnemonic technique may then be one that emphasizes reproduction, instead.

Acknowledgements: Special thanks to Gordon G. Gallup and Frank R. Vellutino for their support and guidance regarding an earlier version of this manuscript. We also thank three anonymous reviewers for their expert insights and recommendations.

Received 10 July 2014; Revision submitted 29 January 2015; Accepted 25 February 2015
The survival advantage

References

Abel, M., and Bäuml, K.-H. T. (2013). Adaptive memory: The influence of sleep and wake delay on the survival-processing effect. *Journal of Cognitive Psychology, 25*, 917-924.

Altarriba, J., and Bauer, L. M (2004). The distinctiveness of emotion concepts: A comparison between emotion, abstract, and concrete words. *American Journal of Psychology, 117*, 389-410.

Altarriba, J., and Kazanas, S. A. (2014). Survival processing and attentional processing. In B. Schwartz, M. Howe, M. Toglia, and H. Otgaar (Eds.), *What is adaptive about adaptive memory?* (pp. 123-138). New York: Oxford University Press.

Aslan, A., and Bäuml, K.-H. T. (2012). Adaptive memory: Young children show enhanced retention of fitness-related information. *Cognition, 122*, 118-122.

Balota, D. A., Dolan, P. A., and Duchek, J. M. (2000). Memory changes in healthy young and older adults. In E. Tulving and F. I. M. Craik (Eds.), *Handbook of memory* (pp. 395-410). Oxford, UK: Oxford University Press.

Bargh, J. A., Chen, M., and Burrows, L. (1996). The automaticity of social behavior: Direct effects on trait concepts and stereotype activation. *Journal of Personality and Social Psychology, 71*, 230-244.

Beck, A. T., Steer, R. A., and Brown, G. K. (1996). *Manual for the Beck Depression Inventory-II*. San Antonio, TX: Psychological Corporation.

Bell, R., Röer, J. P., and Buchner, A. (2013). Adaptive memory: The survival-processing memory advantage is not due to negativity or mortality salience. *Memory and Cognition, 41*, 490-502.

Bröder, A., Krüger, N., and Schütte, S. (2011). The survival processing memory effect should generalize to source memory, but it doesn’t. *Psychology, 2*, 896-901.

Burns, D. J., Burns, S. A., and Hwang, A. J. (2011). Adaptive memory: Determining the proximate mechanisms responsible for the memorial advantages of survival processing. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 37*, 206-218.

Burns, D. J., and Hart, J. (2014). Lying, dying, and remembering: The encoding processes involved in survival processing. In B. Schwartz, M. Howe, M. Toglia, and H. Otgaar (Eds.), *What is adaptive about adaptive memory?* (pp. 53-73). New York: Oxford University Press.

Burns, D. J., Hart, J., Griffith, S. E., and Burns, A. D. (2013). Adaptive memory: The survival scenario enhances item-specific processing relative to a moving scenario. *Memory, 21*, 695-706.

Buss, D. M. (1995). Evolutionary psychology: A new paradigm for psychological science. *Psychological Inquiry, 6*, 1-30.

Butler, A. C., Kang, S. H. K., and Roediger, H. L., III. (2009). Congruity effects between materials and processing tasks in the survival processing paradigm. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 35*, 1477-1486.

Cook, V. (1997). The consequences of bilingualism for cognitive processing. In A. M. B. de Groot and J. F. Kroll (Eds.), *Tutorials in bilingualism: Psycholinguistic perspectives* (pp. 279-299). Mahwah, NJ: Erlbaum.
The survival advantage

Craik, F. I. M., and Tulving, E. (1975). Depth of processing and the retention of words in episodic memory. *Journal of Experimental Psychology: General, 104*, 268-294.

Cunningham, S. J., Brady-Van den Bos, M., Gill, L., and Turk, D. J. (2013). Survival of the selfish: Contrasting self-referential and survival-based encoding. *Consciousness and Cognition, 22*, 237-244.

Deese, J. (1959). On the prediction of occurrence of particular verbal intrusions on immediate recall. *Journal of Experimental Psychology, 58*, 17-22.

Derry, P. A., and Kuiper, N. A. (1981). Schematic processing and self-reference in clinical depression. *Journal of Abnormal Psychology, 90*, 286-297.

Dijksterhuis, A., and van Knippenberg, A. (1998). The relation between perception and behavior or how to win a game of Trivial Pursuit. *Journal of Personality and Social Psychology, 74*, 865-877.

Eagly, A. H., and Wood, W. (1999). The origins of sex differences in human behavior: Evolved dispositions versus social roles. *American Psychologist, 54*, 408-423.

Erdfelder, E., and Kroneisen, M. (2014). Proximate cognitive mechanisms underlying the survival processing effect. In B. Schwartz, M. Howe, M. Toglia, and H. Otgaar (Eds.), *What is adaptive about adaptive memory?* (pp. 172-198). New York: Oxford University Press.

Eysenck, M. W. (1974). Age differences in incidental learning. *Developmental Psychology, 10*, 936-941.

Fellner, M.-C., Bäuml, K.-H. T., and Hanslmayr, S. (2013). Brain oscillatory subsequent memory effects differ in power and long-range synchronization between semantic and survival processing. *NeuroImage, 79*, 361-370.

Gallup, G. G., Jr., and Weedon, S. L. (2013). Suicide bombers: Does an evolutionary perspective make a difference? A review and extension of A. Lankford, “The myth of martyrdom: What really drives suicide bombers, rampage shooters, and other self-destructive killers.” *Evolutionary Psychology, 11*, 791-794.

Garner, S. R., and Howe, M. L. (2013). False memories from survival processing make better primes for problem-solving. *Memory, 22*, 9-18.

Howe, M. L., and Derbish, M. H. (2010). On the susceptibility of adaptive memory to false memory illusions. *Cognition, 115*, 252-267.

Howe, M. L., and Derbish, M. H. (2014). Adaptive memory: Survival processing, ancestral relevance, and the role of elaboration. In B. Schwartz, M. Howe, M. Toglia, and H. Otgaar (Eds.), *What is adaptive about adaptive memory?* (pp. 77-109). New York: Oxford University Press.

Howe, M. L., Garner, S. R., Dewhurst, S. A., and Ball, L. J. (2010). Can false memories prime problem solutions? *Cognition, 117*, 176-181.

Howe, M. L., and Otgaar, H. (2013). Proximate mechanisms and the development of adaptive memory. *Current Directions in Psychological Science, 22*, 16-22.

Hyde, J. S. (2014). Gender similarities and differences. *Annual Review of Psychology, 65*, 373-398.

Kang, S. H. K., McDermott, K. B., and Cohen, S. M. (2008). The mnemonic advantage of processing fitness-relevant information. *Memory and Cognition, 36*, 1151-1156.

Kazanas, S. A., and Altarriba, J. (2013, November). *Predators v. demons v. clowns: When fear of the supernatural improves recall in a survival scenario*. Poster presented at the 54th annual meeting of the Psychonomic Society, Toronto, ON.
Klein, S. B. (2012a). A role for self-referential processing in tasks requiring participants to imagine survival on the savannah. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 38*, 1234-1242.

Klein, S. B. (2012b). The effects of thoughts of survival and thoughts of death on recall in the adaptive memory paradigm. *Memory, 22*, 65-75.

Klein, S. B. (2013). Does optimal recall performance in the adaptive memory paradigm require the encoding context to encourage thoughts about the environment of evolutionary adaptation? *Memory and Cognition, 41*, 49-59.

Klein, S. B. (2014). Evolution, memory, and the role of self-referent recall in planning for the future. In B. Schwartz, M. Howe, M. Toglia, and H. Otgaar (Eds.), *What is adaptive about adaptive memory?* (pp. 11-34). New York: Oxford University Press.

Klein, S. B., Loftus, J., and Burton, H. A. (1989). Two self-referent effects: The importance of distinguishing between self-descriptiveness judgments and autobiographical retrieval in self-referent encoding. *Journal of Personality and Social Psychology, 56*, 853-865.

Klein, S. B., Robertson, T. E., and Delton, A. W. (2010). Facing the future: Memory as an evolved system for planning future acts. *Memory and Cognition, 38*, 13-22.

Klein, S. B., Robertson, T. E., and Delton, A. W. (2011). The future-orientation of memory: Planning as a key component mediating the high levels of recall found with survival processing. *Memory, 19*, 121-139.

Kostic, B., McFarlan, C. C., and Cleary, A. M. (2012). Extensions of the survival advantage in memory: Examining the role of ancestral context and implied social isolation. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 38*, 1091-1098.

Kroneisen, M., and Erdfelder, E. (2011). On the plasticity of the survival processing effect. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 37*, 1553-1562.

Kroneisen, M., Erdfelder, E., and Buchner, A. (2013). The proximate memory mechanism underlying the survival-processing effect: Richness of encoding or interactive imagery? *Memory, 21*, 494-502.

Kroneisen, M., Rummel, J., and Erdfelder, E. (2013). Working memory load eliminates the survival processing effect. *Memory, 22*, 92-102.

Luo, M., and Geng, H. Y. (2013). How can survival processing improve memory encoding? *Science China, 56*, 1028-1037.

Maguinness, C., and Newell, F. N. (2014). Recognizing others: Adaptive changes to person recognition throughout the lifespan. In B. Schwartz, M. Howe, M. Toglia, and H. Otgaar (Eds.), *What is adaptive about adaptive memory?* (pp. 231-257). New York: Oxford University Press.

McBride, D. M., Thomas, B. J., and Zimmerman, C. (2013). A test of the survival processing advantage in implicit and explicit memory tests. *Memory and Cognition, 41*, 862-871.

Mickes, L., Darby, R. S., Hwe, V., Bajic, D., Warker, J. A., Harris, C. R., and Christenfeld, N. J. S. (2013). Major memory for microblogs. *Memory and Cognition, 41*, 481-489.

Nairne, J. S. (2010). Adaptive memory: Evolutionary constraints on remembering. *Psychology of Learning and Motivation, 53*, 1-32.
The survival advantage

Nairne, J. S. (2014). Adaptive memory: Controversies and future directions. In B. Schwartz, M. Howe, M. Toglia, and H. Otgaar (Eds.), *What is adaptive about adaptive memory?* (pp. 308-321). New York: Oxford University Press.

Nairne, J. S., and Pandeirada, J. N. S. (2008a). Adaptive memory: Is survival processing special? *Journal of Memory and Language, 59*, 377-385.

Nairne, J. S., and Pandeirada, J. N. S. (2008b). Adaptive memory: Remembering with a stone-age brain. *Current Directions in Psychological Science, 17*, 239-243.

Nairne, J. S., and Pandeirada, J. N. S. (2010a). Adaptive memory: Ancestral priorities and the mnemonic value of survival processing. *Cognitive Psychology, 61*, 1-22.

Nairne, J. S., and Pandeirada, J. N. S. (2010b). Adaptive memory: Nature's criterion and the functionalist agenda. *American Journal of Psychology, 123*, 381-390.

Nairne, J. S., and Pandeirada, J. N. S. (2011). Congruity effects in the survival processing paradigm. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 37*, 539-549.

Nairne, J. S., Pandeirada, J. N. S., Gregory, K. J., and VanArsdall, J. E. (2009). Adaptive memory: Fitness relevance and the hunter-gatherer mind. *Psychological Science, 20*, 740-746.

Nairne, J. S., Pandeirada, J. N. S., and Thompson, S. R. (2008). Adaptive memory: The comparative value of survival processing. *Psychological Science, 19*, 176-180.

Nairne, J. S., Thompson, S. R., and Pandeirada, J. N. S. (2007). Adaptive memory: Survival processing enhances retention. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 33*, 263-273.

Nairne, J. S., VanArsdall, J. E., Pandeirada, J. N. S., and Blunt, J. R. (2012). Adaptive memory: Enhanced location memory after survival processing. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 38*, 495-501.

Nairne, J. S., Vasconcelos, M., and Pandeirada, J. N. S. (2012). Adaptive memory and learning. *Encyclopedia of the Sciences of Learning*, 118-121.

New, J., Cosmides, L., and Tooby, J. (2007). Category-specific attention for animals reflects ancestral priorities, not expertise. *Proceedings of the National Academy of Sciences, 104*, 16598-16603.

Nouchi, R. (2011). Individual differences of visual imagery ability in the benefit of a survival judgment task. *Japanese Psychological Research, 53*, 319-326.

Nouchi, R. (2012). The effect of aging on the memory enhancement of the survival judgment task. *Japanese Psychological Research, 54*, 210-217.

Nouchi, R. (2013). Can the memory enhancement of the survival judgment task be explained by the elaboration hypothesis? Evidence from a memory load paradigm. *Japanese Psychological Research, 55*, 58-71.

Nouchi, R., and Kawashima, R. (2012). Effect of the survival judgment task on memory performance in subclinically depressed people. *Frontiers in Psychology, 3*, 1-11.

Öhman, A., and Mineka, S. (2001). Fears, phobia, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review, 108*, 483-522.

Olds, J. M., Lanska, M., and Westerman, D. L. (2014). The role of perceived threat in the survival processing memory advantage. *Memory, 22*, 26-35.

Otgaar, H., Howe, M. L., Schwartz, B. L., and Toglia, M. P. (2014) What is adaptive memory? In B. Schwartz, M. Howe, M. Toglia, and H. Otgaar (Eds.), *What is adaptive about adaptive memory?* (pp. 1-7). New York: Oxford University Press.
Otgaar, H., Howe, M. L., Smeets, T., and Garner, S. R. (2014). Developmental trends in adaptive memory. *Memory, 22*, 103-117.

Otgaar, H., Howe, M. L., Smeets, T., Raymaekers, L., and van Beers, J. (2014). Memory errors in adaptive recollections. In B. Schwartz, M. Howe, M. Toglia, and H. Otgaar (Eds.), *What is adaptive about adaptive memory?* (pp. 201-214). New York: Oxford University Press.

Otgaar, H., and Smeets, T. (2010). Adaptive memory: Survival processing increases both true and false memory in adults and children. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 36*, 1010-1016.

Otgaar, H., Smeets, T., Merckelbach, H., Jelicic, M., Verschuere, B., Galliot, A.-M., and van Riel, L. (2011). Adaptive memory: Stereotype activation is not enough. *Memory and Cognition, 39*, 1033-1041.

Otgaar, H., Smeets, T., and van Bergen, S. (2010). Picturing survival memories: Enhanced memory after fitness-relevant processing occurs for verbal and visual stimuli. *Memory and Cognition, 38*, 23-28.

Packman, J. L., and Battig, W. F. (1978). Effects of different kinds of semantic processing on memory for words. *Memory and Cognition, 6*, 502-508.

Paivio, A. U. (1971). *Imagery and verbal processes*. New York: Holt, Rinehart, and Winston.

Paivio, A. U. (1986). *Mental representations: A dual coding approach*. New York: Oxford University Press.

Palmore, C. C., Garcia, A. D., Bacon, L. P., Johnson, C. A., and Kelemen, W. L. (2012). Congruity influences memory and judgments of learning during survival processing. *Psychonomic Bulletin and Review, 19*, 119-125.

Pandeirada, J. N. S., Pinho, M. S., and Faria, A. L. (2014). The mark of adaptive memory in healthy and cognitively impaired older adults and elderly. *Japanese Psychological Research, 56*, 168-179.

Platek, S. M., Burch, R. L., Panyavin, I. S., Wasserman, B. H., and Gallup, G. G., Jr. (2002). Reactions to children’s faces: Resemblance affects males more than females. *Evolution and Human Behavior, 23*, 159-166.

Rajaram, S. (1996). Perceptual effects on remembering: Recollective processes in picture recognition memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 22*, 365-377.

Raymaekers, L. H. C., Otgaar, A., Peters, M. J. V., and Smeets, T. (2014). The adaptive value of survival processing in childhood trauma victims. In B. Schwartz, M. Howe, M. Toglia, and H. Otgaar (Eds.), *What is adaptive about adaptive memory?* (pp. 215-230). New York: Oxford University Press.

Raymaekers, L. H. C., Otgaar, H., and Smeets, T. (2014). The longevity of adaptive memory: Evidence for mnemonic advantages of survival processing 24 and 48 hours later. *Memory, 22*, 19-25.

Roediger, H. L., III., Balota, D. A., and Watson, J. M. (2001). Spreading activation and arousal of false memories. In H. L. Roediger, III, J. S. Nairne, I. Neath, and A. M. Suprenant (Eds.), *The nature of remembering: Essays in honor of Robert G. Crowder* (pp. 95-115). Washington, DC: American Psychological Association.
Roediger, H. L., III., and McDermott, K. B. (1995). Creating false memories: Remembering words not presented in lists. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 21*, 803-814.

Röer, J. P., Bell, R., and Buchner, A. (2013). Is the survival-processing memory advantage due to richness of encoding? *Journal of Experimental Psychology: Learning, Memory, and Cognition, 39*, 1294-1302.

Sandry, J., Trafimow, D., Marks, M. J., and Rice, S. (2013). Adaptive memory: Evaluating alternative forms of fitness-relevant processing in the survival processing paradigm. *PLOS ONE, 8*, e60868.

Savine, A. C., Scullin, M. K., and Roediger H. L., III. (2011). Survival processing of faces. *Memory and Cognition, 39*, 1359-1373.

Schwartz, B. L., and Brothers, B. R. (2014). Survival processing does not improve paired-associate learning. In B. L. Schwartz, M. L. Howe, M. P. Toglia, and H. Otgaar (Eds.), *What is adaptive about adaptive memory?* (pp. 159-181). New York: Oxford University Press.

Schwartz, B. L., Howe, M. L., Toglia, M. P., and Otgaar, H. (2014). *What is adaptive about adaptive memory?* New York: Oxford University Press.

Seamon, J. G., Bohn, J. M., Coddington, I. E., Ebling, M. C., Grund, E. M., Haring, C. T., … Siddique, A. H. (2012). Can survival processing enhance story memory? Testing the generalizability of the adaptive memory framework. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 38*, 1045-1056.

Sellers II, P. D., and Bjorklund, D. F. (2014). The development of adaptive memory. In B. L. Schwartz, M. L. Howe, M. P. Toglia, and H. Otgaar (Eds.), *What is adaptive about adaptive memory?* (pp. 284-307). New York: Oxford University Press.

Shanks, D. R., Newell, B. R., Lee, E. H., Balakrishnan, D., Ekelund, L., Cenac, Z, … Moore, C. (2013). Priming intelligence behavior: An elusive phenomenon. *PLOS ONE, 8*, e56515.

Silverman, I., and Eals, M. (1992). Sex differences in spatial abilities: Evolutionary theory and data. In J. H. Barkow, L. Cosmides, and J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 533-549). New York: Oxford University Press.

Smeets, T., Otgaar, H., Candel, I., and Wolf, O. T. (2008). True or false? Memory is differentially affected by stress-induced cortisol elevations and sympathetic activity at consolidation and retrieval. *Psychoneuroendocrinology, 33*, 1378-1386.

Smeets, T., Otgaar, H., Raymaekers, L., Peters, M. J. V., and Merckelbach, H. (2012). Survival processing in times of stress. *Psychonomic Bulletin and Review, 19*, 113-118.

Soderstrom, N. C., and Cleary, A. M. (2014). On the domain-specificity of survival processing advantages in memory. In B. Schwartz, M. Howe, M. Toglia, and H. Otgaar (Eds.), *What is adaptive about adaptive memory?* (pp. 110-122). New York: Oxford University Press.

Soderstrom, N. C., and McCabe, D. P. (2011). Are survival processing memory advantages based on ancestral priorities? *Psychonomic Bulletin and Review, 18*, 564-569.

Stillman, C. M., Coane, J. H., Profaci, C. P., Howard, J. H., and Howard, D. V. (2014). The effects of healthy aging on the mnemonic benefit of survival processing. *Memory and Cognition, 42*, 175-185.
Tooby, J., and Cosmides, L. (2005). Conceptual foundations of evolutionary psychology. In D. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 5-67). Hoboken, NJ: Wiley.

Tse, C.-S., and Altarriba, J. (2010). Does survival processing enhance implicit memory? *Memory and Cognition, 38*, 1110-1121.

VanArsdall, J. E., Nairne, J. S., Pandeirada, J. N. S., and Blunt, J. R. (2013). Adaptive memory: Animacy processing produces mnemonic advantages. *Experimental Psychology, 60*, 172-178.

Weinstein, Y., Bugg, J. M., and Roediger, H. L. III. (2008). Can the survival recall advantage be explained by basic memory processes? *Memory and Cognition, 36*, 913-919.

Wilson, S., Darling, S., and Sykes, J. (2011). Adaptive memory: Fitness-relevant stimuli show a memory advantage in a game of pelmanism. *Psychonomic Bulletin and Review, 18*, 781-786.