

Nairne, J. S., & Pandeirada, J. N. S. (in press). Adaptive Memory: The Evolutionary Significance of Survival Processing. *Perspectives on Psychological Science*.

Adaptive Memory: The Evolutionary Significance of Survival Processing

JAMES S. NAIRNE¹ AND JOSEFA N. S. PANDEIRADA^{1,2}

¹*Purdue University, USA and* ²*CINTESIS, University of Aveiro, Portugal*

A few seconds of survival processing, during which people assess the relevance of information to a survival situation, produces particularly good retention. One interpretation of this benefit is that our memory systems are optimized to process and retain fitness-relevant information. Such a “tuning” may exist, in part, because our memory systems were shaped by natural selection using a fitness-based criterion. However, recent research suggests that traditional mnemonic processes, such as elaborative processing, may play an important role in producing the empirical benefit. Boundary conditions have been demonstrated as well, leading some to dismiss evolutionary interpretations of the phenomenon. In this article, we discuss the current state of the evolutionary account and provide a general framework for evaluating evolutionary and purportedly non-evolutionary interpretations of mnemonic phenomena. We suggest that survival processing effects are best viewed within the context of a general survival optimization system, designed by nature to help organisms deal with survival challenges. An important component of survival optimization is the ability to simulate activities that help to prevent or escape from future threats which, in turn, depends importantly on accurate retrospective remembering of survival-relevant information.

Human memory is an evolved trait, fine-tuned over generations by the process of natural selection. Memory could be the byproduct of some other evolved process, perhaps perceptual processing, but it is likely to be an evolved adaptation (or a set of adaptations) given its complexity and functionality. Adaptations are ultimately “selected” by nature because they enhance fitness: Traits that increase the likelihood of successful reproduction, either through promoting survival or successful mating strategies, persist and gain traction in an evolving population. To an evolutionist, then, the function of remembering (and forgetting) is to generate adaptive behavior that ultimately enhances fitness (Klein, Cosmides, Tooby, & Chance, 2002; Paivio, 2007; Sherry & Schacter, 1987).

For the last decade, our laboratory has been investigating whether the footprints of nature’s criterion—the enhancement of fitness—persist in modern memory functioning (Nairne, 2005; Nairne, Thompson, & Pandeirada, 2007).

Given that our memory systems were “built” using a fitness-based criterion, we reasoned, mnemonic processes might operate more efficiently when dealing with fitness-relevant problems. Indeed, we have shown that a few seconds of survival processing, during which people assess the relevance of information to a survival situation, produces particularly good retention—better, in fact, than most known encoding techniques (Nairne, Pandeirada, & Thompson, 2008). Similar mnemonic “tunings” may exist for animate items (Nairne, VanArsdall, Pandeirada, Cogdill, & LeBreton, 2013), objects that have been potentially contaminated (Nairne, 2015a), items processed in a “planning” mode (Klein, Robertson, & Delton, 2010), natural predators such as snakes and spiders (Öhman, & Mineka, 2001), and for certain sex-specific characteristics related to foraging and mate choice (Silverman & Eals, 1992; Smith, Jones, Feinberg, & Allan, 2012).

Empirically, the mnemonic benefits of survival processing are well-established (see Kazanas & Altarriba, 2015, for a recent review), but the evolutionary interpretation remains controversial. To explain the benefit, critics have appealed instead to more traditional mnemonics such as elaborative, self-referential, or distinctive processing (Erdfelder & Kroneisen, 2014; Howe & Otgaar, 2013). Although it is important to separate proximate mechanisms from evolved function (Scott-Phillips, Dickens, & West, 2011), a distinction we return to later in this article, it is not immediately obvious how one chooses between purportedly evolutionary and non-evolutionary accounts of remembering. For example, does the involvement of a “basic” process (e.g., elaboration or relational processing) really undercut an evolutionary interpretation? Do boundary conditions—e.g., cases in which survival processing advantages fail to appear or even reverse—rule out an evolutionary locus as well? What is the proper way to frame an evolutionary hypothesis about memory and, importantly, in what sense is it meaningful to propose a “non-evolutionary” account?

This theoretical note is designed to address some of these questions and to outline a particular evolutionary hypothesis in more detail. Memory researchers rarely appeal to evolutionary influences, and are sometimes even hostile to the approach, so misunderstandings are commonplace. Our goal here is to clear up some of these misunderstandings, at least as they pertain to evolutionary accounts of mnemonic phenomena. At the outset, however, it is useful to keep two important points in mind. First, the proposal that survival processing taps an evolutionary adaptation does not differ in any fundamental way from other hypotheses in science. The goal is to accumulate converging evidence for the position and rarely, if ever, will a single piece of data prove conclusive. Some have argued that evolutionary accounts of cognitive phenomena are fundamentally flawed because they rely on assumptions about ancestral variability that can never be verified (e.g., Richardson, 2007), but evolutionary biologists

often face similar verification problems and seem to carry on. Second, any mnemonic phenomenon, survival processing effects included, must ultimately be grounded in some kind of heritable adaptation. Our capacity to remember evolved and, consequently, expressions of remembering will always reflect evolved mnemonics. In this sense, evolutionary accounts of cognitive phenomena cannot be avoided and are, in fact, implicitly assumed by everyone. Because this last point might not be immediately obvious, we expand on it briefly in the next section.

We Are All Evolutionary Psychologists

Even the most ardent advocates of experience-based accounts—i.e., proponents of the proverbial “blank slate”—believe that we are born with chalk and a means to record the messages delivered by the environment. Nature supplied us with basic sensory and perceptual systems along with the capacity to learn, remember, and draw inferences. Stimuli that co-occur in time and space are likely to become associated, and the learning process follows well-defined rules (e.g., Rescorla & Wagner, 1972). Few would claim that the principles of contiguity, or informativeness (Kamin, 1969; Ward, Gallistel, & Balsam, 2013), come from experience. Instead, we agree that natural selection crafted a cognitive toolkit that enables us to learn about the important signaling properties of events (Rescorla, 1988).

Nature also supplied “crib sheets” specifying the kinds of stimuli that are important to learn about (Cosmides & Tooby, 2013). It is easier to associate neutral stimuli with fitness-relevant events—bells are easily conditioned to food or shock, but not to bricks or books. The term *unconditioned stimulus*, by definition, refers to an event that automatically elicits a response in the absence of any learning or conditioning. Neither dogs nor humans need to be taught to drool to food, or to withdraw from shock. We also acknowledge cue-to-consequence effects: For example, tastes are more easily associated with gastric distress than with other events such as foot

shock (Garcia & Koelling, 1966). These biases or “tunings” are assumed to be part of our inherited learning equipment. Substantial evidence supports this claim—for example, selective associations in aversion learning have been found in 1-day-old rat pups (Gemberling & Domjan, 1982; see also Domjan, 2005). Similar tunings almost certainly exist in other cognitive systems as well, such as the tendency for babies to orient more readily to faces than to wall hangings (Kanwisher, 2010), or for our attentional systems to be captured by animate motion, novelty, or threat (see Scholl & Gao, 2013).

Thus, we are all evolutionary psychologists, at least in accepting that nature sculpted our basic cognitive equipment. What is controversial is the amount of specialization: How much adaptive tuning is there, and to what extent can any given specialization be attributed, at least in part, to the influence of natural selection? The default position of most scholars, we assume, is that natural specializations are few in number and “domain-general,” applicable to a wide range of events (e.g., Bolhuis, Brown, Richardson, & Laland, 2011). For example, effective remembering might depend primarily on *elaboration*, or the number of connections that one draws between a processed item and other information in memory (e.g., Craik & Tulving, 1975). To explain adaptive memory effects, then, one would simply appeal to the extent of elaboration, the same mechanism used to explain a variety of other mnemonic effects (e.g., see Howe & Derbish, 2010). But importantly, as we discuss next, the fact that a domain-general process like elaboration might be involved in survival processing is largely irrelevant to the question of whether or not survival processing represents an evolved adaptive bias or tuning.

Adaptations versus Exaptations

Evolutionary arguments can be framed more precisely by distinguishing between adaptations and exaptations. *Adaptations* are inherited specializations that were “built” by natural selection because they improved survival en route

to successful reproduction (Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998). Adaptations can also develop to further the chances of reproduction itself, sometimes at the expense of survival, but sexual selection is not of main concern here. Survival-based adaptations in the physical body include things such as the heart, lungs, kidneys, and the immune system. Each developed over generations because it helped solve an adaptive problem, such as filtering impurities from the blood or maintaining a sufficient amount of oxygen in the body. In the cognitive domain, adaptations include elements of sensory processing, such as a system to detect color or depth in vision, and basic learning and memory processes. Most memory researchers would probably agree that characteristic features of remembering, such as negatively-accelerated forgetting or the reconstructive nature of memory, are part of an inherited mnemonic architecture as well (Anderson & Schooler, 1991; Nairne & Pandeirada, 2008a).

Exaptations are traits that may enhance fitness, but they were not built by natural selection for that specific purpose; instead, they result from other evolved processes (or byproducts) that have been co-opted for their current role (Gould & Vrba, 1982). Driving a car or riding a bicycle are examples of exaptations. Each is a highly specialized skill, with adaptive consequences, but neither is an evolved skill. Reading and writing are cognitive exaptations, as are mnemonic techniques such as the method of loci. Reading and writing are complex and highly adaptive specializations, but they are late developments in the evolutionary history of our species. Each likely reflects a co-opting of basic object recognition systems along with elements tied to language processing (e.g., Dehaene, Cohen, Sigman, & Vinckier, 2005). The method of loci is a learned skill as well, piggybacking on basic associative mechanisms among other core processes (e.g., imagery; see Paivio, 2007).

What we want to know, then, is whether a given mnemonic effect, such as the survival processing benefit, is best described as an adaptation or an exaptation. Is episodic memory

naturally “tuned” to fitness-relevant processing, much like our natural bias to associate taste and illness, or does survival processing merely reflect the co-opting of other evolved processes that are important to remembering? Survival processing is sometimes characterized as just another form of “deep processing,” which suggests that its advantages accrue from the co-opting of other more basic processes. But importantly, the presence of co-opting, by itself, does not allow us to differentiate between an adaptation and an exaptation. Adaptations arise from pre-existing structures and almost always involve some degree of co-opting (Buller, 2005; Burke, 2014). The immune system is an adaptation, but it co-opted the circulatory system to function. Basic reflexes are adaptations, but they rely on communication links among neurons. Flying is an adaptation in birds, but it relies on feathers that likely evolved for thermo-regulation or sexual display (Chatterjee, 2015). Co-opting, by itself, is simply not diagnostic—nor is the involvement of any particular co-opted process (e.g., elaborative processing). We would never describe the immune system as “just another example of the circulatory system” nor would we say that flying is “just feathers.” Adaptations regularly recruit basic processes, in systematic and controlled ways, as part of their normal response repertoire. To differentiate between an adaptation and an exaptation, then, we need to know something about *why* the co-opting is occurring.

Consider the fight-or-flight response, an evolved adaptation that prepares the organism to respond effectively when danger is present. The reaction depends on a host of co-opted systems—the release of hormones, changes in blood pressure and blood sugar, suppression of the immune system, and so on. Fight-or-flight is part of a more general survival system that coordinates the body’s reaction to threat (e.g., Mobbs, Hagan, Dagleish, Silston, & Prevost, 2015). The fact that a basic process is involved, such as the regulation of blood pressure, in no way threatens its status as an adaptation. No one believes that the response is learned, or an artifact of some other system or process. Rather, we

accept that fight-or-flight qualifies as a “front-end” adaptation, one that coordinates and controls other processes to enhance the fitness status of the organism.

Fight-or-flight is notable for its generality as well. Its underlying processes are triggered by the attribution of perceived danger or threat, but threat is often context specific (Adolphs, 2013). Natural triggers could exist in the environment, such as a snake or a looming object, but the response system is flexible enough to be triggered by a variety of situations, some learned. Its flexibility is relevant here because some critics have suggested that a mnemonic adaptation based on survival processing is unlikely to have evolved because the concept of “survival” is too general (e.g., Klein, 2012; Klein et al., 2010). But the fight-or-flight response shows us that adaptations can be broadly tuned to environmental events, yet still produce quite specific fitness-relevant reactions.

It is worth contrasting this view of an adaptation, as a functionally-driven system that co-opts other processes, with more narrowly-defined concepts of modularity. Evolutionary accounts are often identified with a particular conception of modularity, one proposing that adaptations or “modules” are reflex-like, automatic, and encapsulated (Fodor, 1983; Grossi, 2014). So-called Fodorian modules are thought to act independently of other systems, via their own processing pipelines, and to be impervious to higher-order influences. Some cognitive adaptations may meet these requirements, perhaps in the realm of sensory or perceptual processing, but few evolutionary psychologists currently subscribe to a Fodorian checklist—at least as necessary defining characteristics of cognitive adaptations (Barrett & Kurzban, 2006; Confer et al., 2010). It is better to think of cognitive adaptations as functionally specialized traits or “programs” (Cosmides & Tooby, 2013) that often rely on other evolved processes to function and whose primary role may be to modulate and coordinate otherwise domain-general mechanisms. As we shall see, survival processing may represent a similar kind

of process—a flexible front-end adaptation that, once triggered, relies on other evolved mnemonics to achieve an adaptive end.

Survival Processing: Adaptation or Exaptation?

The survival processing paradigm is modeled after the classic incidental learning experiments of Hyde and Jenkins (1973) and Craik and Tulving (1975). People are presented with random sets of words which they are required to rate via one of several orienting tasks. In the critical condition, people are asked to imagine themselves stranded in the grasslands of a foreign land, where they need to find steady supplies of food and water and avoid predators. The task is to rate the relevance of words, or more appropriately the concepts referenced by the words, to this survival scenario—e.g., how relevant is “corn” or “book?” For control comparisons, we have typically included a standard deep processing task (rating words for pleasantness) along with an equally-complex scenario that is fitness-irrelevant (moving to a foreign land) (see Table 1). Later surprise retention tests (free recall and recognition) have consistently produced strong retention advantages for items processed with respect to the survival scenario (Nairne et al., 2007).

Notice that our paradigm is not designed to explain an existing mnemonic effect, but rather to

generate new data about the adaptive consequences of remembering. Evolutionary psychologists are often criticized for concocting post-hoc adaptive explanations of behavior—so-called “just-so stories”—in which observed behaviors are interpreted in terms of their possible adaptive consequences. There are few constraints in this type of reasoning, meaning that one can develop convincing adaptive stories for just about any empirical effect (Gould & Lewontin, 1979). Our research relies instead on a kind of forward engineering in which functional questions take the driving role (see Nairne, 2015a). Rather than looking backward at an existing empirical effect, we focus on the recurrent adaptive problems that our memory systems presumably need to solve, such as remembering the location of food, and then generate *a priori* predictions about mnemonic behavior. In this case, we predicted that processing information in a survival context would lead to excellent retention.

One might wonder whether laboratory-based simulations of survival situations, using scenarios of the type shown in Table 1, are reasonable approximations of actual survival situations. Is it justifiable to assume that the processes evoked by an imagined scenario resemble those activated by the real thing? Obviously it is not possible to put people in real survival situations, but considerable research suggests that there is a close tie between real and imagined events (e.g., Finke, 1980).

Table 1: Scenarios used in Nairne, Thompson and Pandeirada (2007)

Survival: In this task we would like you to imagine that you are stranded in the grasslands of a foreign land, without any basic survival materials. Over the next few months, you’ll need to find steady supplies of food and water and protect yourself from predators. We are going to show you a list of words, and we would like you to rate how relevant each of these words would be for you in this survival situation.
Moving: In this task we would like you to imagine that you are planning to move to a new home in a foreign land. Over the next few months, you’ll need to locate and purchase a new home and transport your belongings. We are going to show you a list of words, and we would like you to rate how relevant each of these words would be for you in accomplishing this task.
Pleasantness: In this task, we are going to show you a list of words, and we would like you to rate the pleasantness of each word.

For example, Robinson and Clore (2001) asked participants to imagine scenes described by a short vignette and compared the participants' emotional reactions to others who viewed pictures of the actual events. A close correspondence was found between the emotional reactions engendered by the imagined and real events. Others have found considerable overlap in the physiological and neural substrates of imagined and perceived events, including emotional threats (e.g., Lang, Greenwald, Bradley, & Hamm, 1993; Suess & Rahman, 2015). As we discuss later, the ability to simulate future events, in a realistic fashion, is likely to be an important component of a more general survival optimization system (Mobbs et al., 2015; Szpunar, 2010).

The mnemonic advantage of survival processing has now been replicated widely, against a variety of control conditions—including against superior encoding techniques such as forming a visual image or relating information to the self (Nairne et al., 2008). The survival advantage has been demonstrated in small children (Aslan & Bäuml, 2012), in elderly populations (Nouchi, 2012), and in populations suffering from cognitive impairment (Pandeirada, Pinho, & Faria, 2014). The effect remains robust in both within- and between-subject designs, in intentional and incidental learning environments, for both pictures and words (Otgaar, Smeets, & van Bergen, 2010), and when alternative versions of the original survival scenario are used (Nairne & Pandeirada, 2010; Soderstrom & Cleary, 2014). The advantage does not generally depend on the particular relevance rating given to an item (Nairne et al., 2007) and holds when each participant receives a different sample of to-be-rated words (Nairne & Pandeirada, 2011). The basic effect has been replicated as well as part of the Open Science Project (Müller & Renkewitz, 2015).

But does the empirical benefit of survival processing reflect an inherent mnemonic tuning? Recent research suggests that exapted processes, particularly elaborative processing, may play a key role in the memory advantage. For example,

Butler, Kang, and Roediger (2009) found that when word lists were highly congruent or incongruent with the processing scenario, survival advantages disappeared (although see Nairne & Pandeirada, 2011). Kroneisen and Erdfelder (2011) showed that when the survival scenario is narrowed to a single activity—finding potable water—the survival advantage is eliminated as well, at least when compared to the standard “moving” control (but see Ceo, 2008). Other boundary conditions include a failure to find significant survival advantages for abstract words (Bell, Röer, & Buchner, 2013), faces (Savine, Scullin, & Roediger, 2011), stories (Seamon, Bohn, Coddington, et al., 2012), and possibly for certain retrieval situations such as cued recall (McBride, Thomas, & Zimmerman, 2013; Tse & Altarriba, 2010). What is significant about these findings is the failure to find retention benefits even though the processing itself remains fitness-relevant.

Erdfelder and Kroneisen (2014) suggested that these boundary conditions are broadly consistent with a “richness of encoding” or encoding variability interpretation of survival processing effects (see also Röer, Bell & Buchner, 2013). The proposal is that survival processing leads to multiple, rich encodings that enable privileged access during retrieval, possibly through the establishment of multiple retrieval pathways. Boundary conditions are expected whenever the stimulus or the rating task prevents, or constrains, the elaboration process. Consider, for example, the finding that narrowing the traditional grasslands scenario to a single activity—finding potable water—eliminates the survival advantage (Kroneisen & Erdfelder, 2011). Here, finding potable water is an impoverished activity, at least compared to the standard grasslands scenario, which limits the potential “richness” of any encoding. A similar analysis applies to the null effect of survival processing on faces—how many different ways can the characteristics of a face be relevant to survival?—and to well-specified stories, abstract words, and situations in which the match between the encoding task and the rated item is high. If the

relevance of the to-be-rated word to the survival scenario is immediately obvious, which is likely when one uses highly relevant or irrelevant words, then there is little need to engage in much fitness-relevant processing. The “richness” account also explains why the survival advantage is sometimes reduced under a secondary memory load, where people lack the capacity to produce variable encodings (Kroneisen, Rummel, & Erdfelder, 2014; Nouchi, 2013). Furthermore, if people are given a specific cue at test, one that biases them toward a particular retrieval route, then the advantage of multiple retrieval routes is rendered moot (McBride et al., 2013; Tse & Altarriba, 2010).

Additional evidence for the “richness of encoding” account comes from studies that have directly measured the amount of elaborative processing that occurs during survival processing. Röer et al. (2013) simply recorded the number of ideas that people generate during survival processing and various controls. Across several experiments, they found that people generated more ideas or “uses” when rating items for survival than they did for control scenarios, and the number of ideas generated tracked how well the rated items were later recalled. Intrusions in recall often occur after survival processing as well, a finding that is also consistent with an elaborative or encoding variability account (Howe & Derbish, 2010). At face value, then, survival processing seems like a good candidate for an exaptation, wherein a domain-general process—elaboration—is simply exapted or co-opted to produce a mnemonic advantage.

However, as discussed earlier, co-opting, while a necessary condition for an exaptation, is fully consistent with an adaptive “tuning” as well. Adaptations often co-opt other basic processes—e.g., the fight-or-flight response “works” via activation of the sympathetic nervous system. The more diagnostic question asks: Why does survival processing produce more elaboration, or variable encodings, than rating an item for, say, pleasantness, forming a visual image, or intentional learning? There are three possibilities. First, a mnemonic adaptation is responsible—

that is, an inherited mnemonic “tuning” that was built by natural selection because it improved survival en route to successful reproduction. Elaboration, or encoding variability, is simply the proximate mechanism that produces the fitness-relevant tuning. Once a survival situation is detected, or a threat directly encountered, elaborative machinery kicks into gear and items at the focus of processing gain a mnemonic edge. As discussed earlier, this kind of “front-end” adaptation, one that successfully recruits other cognitive processes, is likely common in the human processing architecture.

Second, consistent with an exaptation, the co-opting might result from experience. People may have learned to encode fitness-relevant information in a rich and variable way as a byproduct of prior experience. Reading and writing are almost certainly exaptations rather than adaptations—we have learned to exapt other evolved processes to achieve these ends. However, it is unlikely that experience is responsible for the survival processing benefit because few people have actually been stranded in the grasslands of a foreign land, or in any serious survival situation. The environment has simply failed to deliver the appropriate context for learning about how to best allocate resources when survival is at stake. Moreover, a few seconds of survival processing produces significantly better retention than intentional learning, where people are told explicitly to remember the presented material (Nairne et al., 2008). If people simply try to remember fitness-relevant events, because they suspect that fitness-relevant events are important, then performance under survival processing should resemble performance found under intentional learning, but it does not. Robust survival processing effects have also been found for small children who, again, have had limited experiences with survival situations or media programs based on survival situations (Aslan & Bäuml, 2012).

The third possibility is that the co-opting is an *artifact* of the methodology. In other words, there is something about the survival scenario or the rating task, rather than fitness-relevancy *per*

se, that affords richer processing. Nairne et al. (2007) might have simply chosen a scenario that is unusually complex, novel, arousing, or difficult. As noted above, few participants are familiar with grassland scenarios, so survival processing might require especially deep thought, at least compared to rating an item for pleasantness or moving to a foreign land. However, survival scenarios have now been compared to numerous control scenarios, some specifically designed to equate for possible confounds. Kang, McDermott and Cohen (2008) controlled for the novelty and excitement of the grasslands scenario by comparing it to a robbery control in which people rated the relevance of words to planning a bank robbery. Röer et al. (2013) equated for distinctiveness by using an “afterlife” control in which people imagined that they had died and were searching for new companions and interesting things to do in the afterlife. Bell et al. (2013) controlled for negative affect by comparing survival processing to a “suicide” control scenario; Yang, Lau, and Truong (2014) used a “winning the lottery” scenario to control for positive affect. Strong survival processing advantages were obtained in each of these cases, effectively ruling out accounts that appeal to the uniqueness or emotionality of the survival scenario.

The best evidence against “artifact” accounts, however, comes from studies using matched control scenarios. In these cases, people are asked to rate the relevance of items to *exactly the same activities*, but in a context that is either fitness-relevant or not. Nairne, Pandeirada, Gregory, and VanArsdall (2009) asked people to rate the relevance of words to a hunting scenario, one in which they were required to hunt big game, trap small animals, and fish, but either to survive or to win a hunting contest. Both scenarios required tracking and hunting for food, in exactly the same way, but only the survival-based version was expected to induce fitness-relevant processing. Significantly better recall performance was found in the survival-based hunting condition. In another experiment, people were asked to search for and gather edible food, either to survive or to

win a scavenger hunt; again, the same activities were used in each scenario, but framing the scenario around survival produced a stronger mnemonic effect. Ceo (2008) asked people to search for and find apples to eat, either to survive or for a picnic while vacationing at a fancy resort. Again, exactly the same activities were involved in both the survival and the control scenario, but the survival framing produced the best recall. Each of these matched scenarios is shown in Table 2; the corresponding recall results are presented in Figure 1.

These data suggest that the survival processing effect is not an artifact of a particular scenario or rating task. Instead, the evidence is consistent with a “front-end” adaptation that is activated selectively by survival situations. When confronted with a survival situation, people naturally engage in a rich and elaborative form of processing, one that aids long-term retention. People naturally generate more ideas, or consider more potential uses for objects, when they are assessing the consequences of a survival situation. Note that attributing the advantage to elaboration, or to some other basic memory process, is consistent with a general evolutionary account (see also, Nairne, 2014). As discussed throughout, adaptations often “co-opt” basic processes to achieve their intended function. Elaboration may simply be the proximate mechanism that is co-opted by the front-end adaptation to achieve the desired “tuning.”

Similar reasoning explains the occurrence of boundary conditions. The fact that survival processing may tap an evolved adaptation does not guarantee that it will produce a mnemonic benefit. Indeed, as discussed earlier, if the processing at encoding is constrained in such a way that it prevents elaboration, or renders variable encodings ineffective during the retrieval process, then the benefits of survival processing should be reduced or eliminated. For example, when elaboration is blocked by a demanding secondary task, survival processing advantages are eliminated (Kroneisen et al., 2014). The occurrence of boundary conditions should not be surprising—most, if not all, adaptations or

inherited “tunings” show boundary conditions. Block the circulatory system and the immune system will cease to function; if you deplete neurotransmitters, reflexes will be impaired; if you cover a bird’s feathers with oil, it will not be able to fly. No one would claim that these “failures” rule out evolutionary interpretations of

the immune system or flying. Similarly, if the proximate mechanisms that help produce survival processing benefits are blocked or rendered ineffective then survival processing advantages will disappear even though survival processing may ultimately reflect a mnemonic tuning.

Table 2: Hunting and Scavenging scenarios used in Nairne, Pandeirada, and Thompson (2008) and Finding Apples scenarios used by Ceo (2008).

Hunting	
<i>Survival framing</i>	In this task, please imagine that you are living long ago in the grasslands of a foreign land. As a part of a small group, you are in charge of contributing meat to feed your tribe. You will need to hunt big game, trap small animals, or even fish in a nearby lake or river. Hunters often have to travel great distances, pursue animals through unfamiliar terrain, and successfully return home. Whatever the conditions, you must hunt successfully to feed your tribe. We are going to show you a list of words, and we would like you to rate how relevant each of these words would be in your attempt to hunt successfully for food.
<i>Contest</i>	In this task, please imagine that you have been invited to participate in a hunting contest. As a part of a team, you are in charge of contributing captured game to the team effort. You will need to hunt big game, trap small animals, or even fish in a nearby lake or river. Members of the team often have to travel great distances, pursue animals through unfamiliar terrain, and successfully return to the contest center. Whatever the conditions, you must hunt successfully to help your team win the contest. We are going to show you a list of words, and we would like you to rate how relevant each of these words would be in your attempt to hunt successfully.
Scavenging	
<i>Survival framing</i>	In this task we would like you to imagine that you are living long ago in the grasslands of a foreign land. As a part of a small group, you are in charge of gathering food for your tribe. You need to scavenge for edible fruits, nuts, vegetables, etc. Gatherers often have to have knowledge about the locations and seasonal availability of edible foods, but no matter what the conditions (extreme heat, flooding, drought), you must gather edible food successfully for your tribe to eat. 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 your attempt to gather edible food successfully and bring it back to your tribe.
<i>Contest</i>	In this task we would like you to imagine that you have been invited to participate in a scavenger hunt. As a part of a team you are in charge of locating food items from the search list for your team (e.g., fruits, meats, etc.). You need to look for clues that might indicate the location of an item, search in various locations, and transport found items to the game center. Members of the team might need to travel great distances to find the items and interpret clues that indicate locations, but no matter what the conditions you must scavenge successfully for your team. We are going to show you a list of words, and we would like you to rate how relevant each of these words would be in your attempt to scavenge successfully for the food items and bring them back to the game center.
Finding Apples	
<i>Survival framing</i>	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 apples to eat to survive and maintain your health. 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 to finding apples to eat.
<i>Picnic</i>	In this task, we would like you to imagine that you are enjoying an extended vacation at a fancy resort with all your basic needs taken care of. One fun thing you think of doing is to gather local apples to use as part of a picnic. 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 to finding apples to eat.

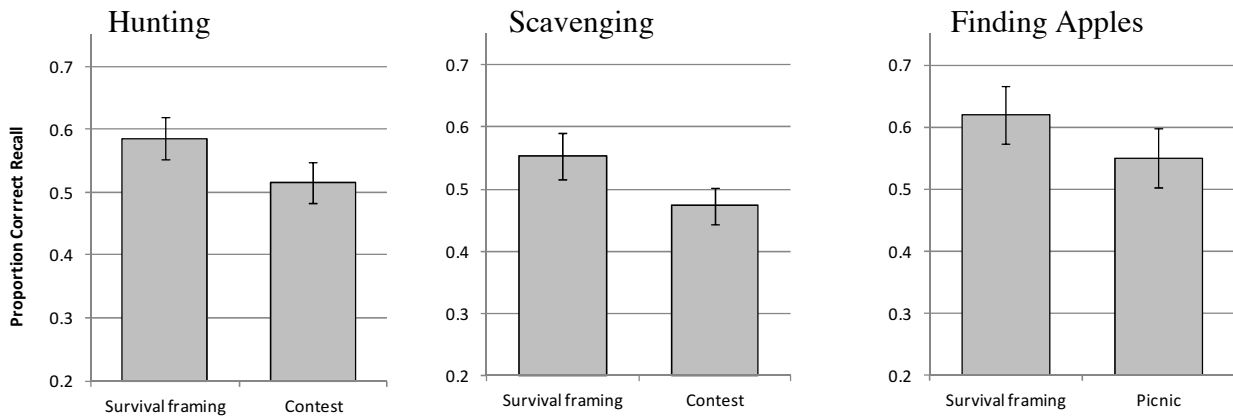


Figure 1: Proportion of correct recall obtained for the Hunting and Scavenging scenarios used in Nairne, Pandeirada, and Thompson (2008) and Finding Apples scenarios used by Ceo (2008). Error bars represent 95% confidence intervals.

At the same time, we recognize that building a definitive case for an adaptation, especially a cognitive one, is notoriously difficult. We have no “fossilized” memory traces, and we have only limited knowledge about the ancestral environments in which our memory systems actually evolved (Buller, 2005). To establish that a given cognitive mechanism, such as a mnemonic tuning, reflects an adaptation—that is, a mechanism arising directly as a consequence of evolution through natural selection—requires satisfying multiple criteria (e.g., Richardson, 2007). Among other things, we would need to establish that the trait can be inherited, or promoted across generations through differential reproduction. It would also be helpful to show that at some point in our ancestral past there were individual differences among people along the trait dimension, and that certain *forms* (such as a special memory tuning for fitness-relevant information) were *selected* because they promoted differential survival and reproduction relative to other forms. Obtaining this kind of evidence is difficult for the cognitive adaptations of interest to evolutionary psychologists, although one can use modeling to simulate the viability and likelihood of evolutionary outcomes (see Dawkins, 2006). The evolution of simple learning preferences has been studied successfully across

generations in fruit flies (Dunlap & Stephens, 2014), but similar experiments are out of reach for survival processing. One could assess the heritability of survival processing, however, using monozygotic and dizygotic twins—similar methods have been used to establish the heritability of fear conditioning (Hettema, Annas, Neale, Kendler, & Fredrikson, 2003).

Of course, cognitive adaptations of the sort we have been discussing almost certainly do exist. No one disputes that basic learning and memory processes are adaptations, even though “definitive” data, such as heritability or ancestral variation, is lacking. We can be certain, though, that if domain-general mechanisms evolved, such as elaboration or “deep processing,” they need some kind of front-end control—a set of rules or guidelines for how and when they are applied. Such control can be learned, induced by the task demands of a procedure, but also through natural “tunings” that increase the chances of fitness-relevant behavior. The brunt of the evidence, at this point, suggests that survival processing may activate such a front-end mechanism. In the next section, we consider the benefits of such a mechanism in a bit more detail.

Survival Processing: What Is It For?

If we assume that survival processing taps an inherent mnemonic “tuning” for fitness-relevant events, then what adaptive advantage does it hold for the organism? For any adaptation to evolve there must be a clear fitness advantage, one that increases the net likelihood of survival and/or reproduction directly. In the case of general learning mechanisms, such as Pavlovian conditioning and habituation, researchers have been reasonably successful at documenting fitness advantages (see Krause, 2015, for a review). For example, we now know that male fish who learn that certain environmental events signal access to prospective mates show greater reproductive success than control fish who lack the relevant learning (see Hollis, Pharr, Dumas, Britton, & Field, 1997). There is also considerable comparative and anatomical evidence to support evolution’s role in shaping spatial memory in certain species (see Pravosudov & Roth, 2013). But evidence of this kind is certainly lacking for survival processing.

The mnemonic effects of survival processing are best viewed within the context of a more general survival optimization system, crafted by natural selection because it helped organisms prepare for and react to recurring and novel threats (e.g., Ledoux, 2012; Mobbs et al., 2015). Most animals come equipped with a kind of survival intelligence that includes a repertoire of survival circuits that are specialized to activate or inhibit motivational systems and shift processing priorities to relevant internal and environmental stimuli. Learning is an important component of the overall system, as the phenomena of Pavlovian conditioning clearly demonstrate. Our survival circuits are optimized to detect signals for threat and to learn about the fitness consequences of behavior in general. For example, animals who learn about signals for food under different deprivation levels generally prefer the cues that were present during the highest deprivation levels—that is, they prefer the cues that signaled events with the highest fitness

value (see McNamara, Trimmer, & Houston, 2012; Pompilio & Kacelnik, 2005).

One important part of our survival optimization system is the ability to envisage, predict, and simulate future scenarios. Actively generating possible outcomes, in the form of episodic future thought, enables us, and possibly other animals as well, to modify our behavior proactively to deal with potential threats or food sources (Hassabis & Maguire, 2007; Raby & Clayton, 2012; Schacter & Addis, 2007). Memory plays a central role in this process because accurate simulations depend on accessing relevant past experiences. Remembering how predators move, or successful escape routes from the past, promotes effective strategies in the present. Moreover, our ability to simulate future events seems to depend directly on our ability to remember the past. Studies of patients with medial temporal lobe amnesia show parallel deficits in episodic remembering and episodic future thought (Klein, Loftus, & Kihlstrom, 2002; Tulving, 1985). Brain imaging studies show as well that remembering the past and imagining the future activate the same “default mode network” in the brain (Addis, Wong, & Schacter, 2007; Buckner & Carroll, 2007; Szpunar, Watson, & McDermott, 2007). Thus, we can draw a relatively straightforward connection between systems that might be “tuned” to remember fitness-relevant events and the adaptive ability to simulate possible scenarios in fitness-relevant contexts.

Fitness-relevant simulations need to be flexible and creative as well. If we can generate a range of possible predator behaviors or food sources, we increase our arsenal of strategic responses. It would not be surprising, then, if survival situations naturally induced one to consider multiple “uses” or interpretations of objects. As mentioned earlier, Røer et al. (2013) directly measured the number of ideas that people generate when simulating survival scenarios and found that significantly more ideas or “uses” were generated for survival scenarios than for control scenarios. The ideas that were generated tended to be more creative as well, in that people

generated both common and novel uses for objects when considering their relevance to a survival situation (Bell, Röer, & Buchner, 2015). Variable encoding of this kind acts as an aid to future explicit remembering, but also enhances our ability to create sophisticated simulations of future situations.

This last point provides an impetus for future empirical work. For example, can people simulate *future* events more effectively after survival processing or, more generally, when those events are relevant to fitness than when they are not? Are the qualitative characteristics of episodic future thought richer or more vivid when the focus is on fitness-relevant situations (see McDermott & Gilmore, 2015)? Does experience in a survival context increase one's ability to solve survival problems in future contexts? At this point, the mark of nature's criterion on episodic future thought or general problem solving ability has yet to be investigated (although see Nairne, 2010, for an earlier discussion). If survival processing advantages are simply an artifact of a unique scenario or rating task, then we would not expect to see the same advantages or sensitivities in new empirical domains.

Placing survival processing within the context of a more general survival system, one that relies on and co-opts multiple other systems, allays the concern that "survival" is too broad a construct to drive an adaptive specialization. Given stereotypical views of cognitive modules, one might expect cognitive adaptations to be independent and narrowly constructed as well as specialized to solve a very particular kind of adaptive problem, such as detecting snakes or spiders. Although specializations of this form may exist, adaptations can evolve that process domain-specific information in a quite general way. As noted previously, the fight-or-flight response is initiated by "threat" but "threat" is a broad domain that can be quite context-specific. Evolving an attribution system that enables organisms to interpret the environment, sample from a variety of threat-based cues, and initiate defensive reactions when appropriate has clear

fitness benefits. Similarly, once a survival situation is detected, or survival processing is induced, appropriate mnemonic mechanisms are likely to be engaged because enhanced retention of relevant material forms an important part of the survival optimization system, including the ability to simulate future encounters effectively.

We recognize, though, that our characterization of survival situations remains vague. What exactly qualifies as a survival context? Most evolutionary psychologists believe there are recurrent triggers in the environment—e.g., ancestral predators such as snakes or spiders—and that we evolved mechanisms for sensing and reacting to those triggers, or at least to environmental features that are predictive of those triggers (e.g., Barrett, 2005). In the case of survival processing, there is some evidence that processing items with respect to ancestral scenarios yields larger mnemonic benefits than modern scenarios. For example, searching for edible plants to survive in the grasslands produces stronger mnemonic effects than searching for food to survive in a city (Nairne & Pandeirada, 2010; Weinstein, Bugg, & Roediger, 2008). Ancestral priorities have been found in other domains as well (Öhman & Mineka, 2001) and suggest that our cognitive systems evolved to solve problems that were particularly relevant in the environment of evolutionary adaptation (e.g., Symons, 1992).

Yet, the fact that some cognitive processes might operate more efficiently in an ancestral context does not mean those processes will be inefficient when dealing with modern problems, or that they cannot be used to solve novel tasks (Buss et al., 1998). As discussed earlier, core evolved processes are commonly co-opted to perform novel tasks (e.g., reading, writing, and riding a bicycle). Survival processing effects have been obtained in many simulated settings, including modern cities and even outer space (Kostic, McFarlan, & Cleary, 2012). In one simulated scenario people were asked to rate the relevance of items to fending off an attack from zombies, entities that were clearly not present during the environment of evolutionary adaptation; strong survival advantages were

found (Soderstrom & McCabe, 2011). However, zombies are clearly processed as predators, and may activate death and disgust systems as well, so they are likely to activate survival triggers that share properties with ancestral predators. Again, the recruitment of elaboration, or other memory-enhancing processes, is assumed to be part of a more general survival system that helps us react to threat in all of its varied forms.

Summary and Conclusions

At this point, there can be little doubt that processing the relevance of an item to a survival context can be a potent way of improving its long-term retention. The mnemonic advantages of survival processing are well-established, and our previous claim that survival processing may be “one of the best encoding techniques yet discovered in the memory field” (Nairne et al., 2008, p. 176) remains largely intact. However, a variety of laboratories have now documented boundary conditions, situations in which survival processing produces no significant advantage over other deep processing controls, as well as the involvement of certain core processes, such as elaboration or self-referential processing (see Erdfelder & Kroneisen, 2014; Kazanas & Altarriba, 2015, for recent reviews). Our main concern here was to consider the implications of these recent findings for evolutionarily-based interpretations of the survival processing effect.

The idea that memory might be naturally “tuned” to the processing of fitness-relevant events is consistent with what we already know about adaptive specializations in learning and perception. Even basic associative learning, which is often held up as the prototype of a domain-general process (Bolhuis et al., 2011), is tuned to biologically-significant stimuli (shock, food, sex, etc.) and to relationships between particular cues and consequences (Domjan, 2005; Hollis, 1997). After all, the engine that drives natural selection is the enhancement of inclusive fitness (Hamilton, 1964) so it is not surprising that systems built using nature’s criterion continue to bear its footprint (Nairne &

Pandeirada, 2008b). Everywhere one looks in the physical body, there are goal-directed systems— hearts, lungs, kidneys, etc.—that solve problems related to survival and/or reproduction.

Of course, accepting that our learning and memory systems may contain adaptive specializations does not mean that survival processing is an adaptation, or a key part of a more general survival optimization system. The fact that retention is excellent after survival processing could be attributed to other core processes that evolved for different reasons. For example, as Kroneisen and Erdfelder (2011) have argued, it may not be the evolutionary significance of survival processing that explains the benefit. Rather, they suggest, it may be “the degree to which survival processing invites elaborative, distinctive forms of encoding” that explains the mnemonic benefit of survival processing (p. 1554). In other words, the survival processing advantage may be better classified as an *exaptation*, one involving the co-opting of other more basic processes (for a similar position, see Howe & Otgaar, 2013).

However, as we have argued throughout, the involvement of core processes, such as elaboration or distinctive processing, does not mean that survival processing is an exaptation. One also needs to determine *why* the co-opting occurs. Adaptations regularly interact with and recruit other core processes to achieve an adaptive end, so identifying the relevant core process, while important, is not particularly diagnostic. In the case of survival processing, one possible candidate is the relevance rating task itself. Perhaps there is something unique about the task, or the survival scenario, that recruits elaborative processing. At this point, though, the data do not support this kind of interpretation. First, care has been taken to equate the survival and control scenarios along a number of mnemonically-relevant dimensions, such as emotionality and distinctiveness, and the survival advantage has remained intact. Second, the use of matched scenarios (Table 2), in which people make ratings about exactly the same activities in either a fitness-relevant or fitness-irrelevant

context, shows that the mnemonic benefit is not an artifact of either the rating task or any unusual features of the scenario. Rather, invoking a survival context, rather than the task itself, induces a rich and variable form of processing that improves long-term retention of processed information. This is what we mean by an evolved mnemonic “tuning”—namely, that core mnemonic processes operate more efficiently, or are recruited more effectively, when encodings occur in a survival context.

It is worth noting as well that Nairne et al.’s (2007) original evolutionary hypothesis about survival processing could easily have been falsified. We generated an *a priori* prediction, based on evolutionary reasoning, that processing information for its survival value would be a potent way to improve long-term retention. The fact that survival processing consistently produces better long-term recall and recognition than standard deep processing tasks supports our hypothesis, but the data could have turned out differently; in fact, there is some evidence that other forms of fitness-relevant processing, such as rating scenarios that focus on reproduction, may not yield the same retention benefits (Sandry, Trafimow, Marks, & Rice, 2013). Moreover, as just discussed, the mnemonic benefits of survival processing might have been attributable to some unknown artifact or confounding, perhaps related to a specific survival scenario or rating task. But again, the empirical record does not support this kind of alternative account at the present time.

If survival situations naturally recruit elaborative processing, as part of a general survival optimization system (Mobbs et al., 2015), then we should not be surprised to find that survival processing fails to enhance retention under some conditions. All traits show boundary conditions, regardless of whether they arise from exaptations or adaptations. For example, neurotransmitters play a key role in many nervous system adaptations, including basic reflexes. But if the relevant neurotransmitter is blocked or depleted, through an external agent or repetition, then the reflex disappears. Yet, no one would use such an observation to claim that basic reflexes

are not adaptations. In the case of survival processing, conditions that limit the potential for elaboration, such as restricting the survival scenario to a narrow activity, should reduce the mnemonic benefit even though survival processing remains as a natural mnemonic tuning. Boundary conditions become an issue only when they challenge the ultimate functional value of the trait. The fact that survival processing benefits occur primarily for concrete objects, rather than abstract words or faces, and are reduced under dual task conditions does not seem to be particularly damaging to the functional account.

These arguments are meant to be general and do not depend on accepting any particular proximate mechanism (e.g., elaboration). Evolutionary theorists traditionally distinguish between *ultimate* explanations of traits, which focus on evolved function (why the trait evolved), and *proximate* explanations, which focus on how trait mechanisms actually work (Mayr, 1961; Tinbergen, 1963). These two types of explanation are meant to be complementary and one should not generally be used to undercut the other (Scott-Phillips et al., 2011). To understand crying, one can focus on its adaptive function and attempt to explain why such a behavior might have gained traction in the population over generations (the ultimate explanation). Concurrently, one can seek to understand the biological mechanisms that control crying (the proximate explanation) without directly referencing the evolutionary arguments. More importantly, it would make little sense to diminish the study of crying as an evolved trait by claiming that it is just the production of tears by the lacrimal gland. Similarly, one has not “explained” the survival processing effect by identifying elaboration as a potential proximate mechanism, at least as an evolutionist views it. Elaboration, by itself, has no fitness consequences; it is the role that elaboration potentially plays in solving an adaptive problem that is of concern to the evolutionary analyst.

Still, the search for proximate mechanisms is important and will likely motivate future work on survival processing. Ultimate and proximate

explanations are complementary, but one can inform or constrain the other. For example, elaboration is a proximate mechanism—that is, a process through which a richly encoded memory trace is established—but what were the specific selection pressures that led to its development? Why would nature craft a memory system that benefits from drawing connections between a current event and previous events? Why would nature favor memory traces that by virtue of elaboration are robust, or accessible to a broad range of retrieval cues (Lockhart, 2002)? Adaptations are often characterized by a tight fit between structure and function, so understanding how elaboration works is likely to provide clues about why such a process ultimately developed. Note that elaboration, if it is a core memory process, is subject to the same evidentiary standards as any other evolved process. Thus, one would need to make the case, as we have tried to do for survival processing, that elaboration is likely to have evolved as a mnemonic process because it solves problems related to the inclusive fitness of the organism.

Regardless of the proximate mechanism that ultimately drives the survival processing effect—e.g., elaboration, relational, or self-referential processing—some kind of front-end control is necessary for cognitive systems to operate efficiently. From a functional perspective, the problem with domain-general systems is that they come with too many degrees of freedom—*inherent constraints* are needed to avoid combinatorial explosion (Cosmides & Tooby, 2013). We cannot associate all events that occur contiguously, or attend to every novel event, because contiguous and novel events occur continuously in our environments. We need crib sheets to help us determine what kinds of events are important to learn about. As learning theorists have shown, these crib sheets are often tied directly to the adaptive problems that organisms face in their regular environments, such as learning to avoid predators and learning about the types of stimuli that signal a mating opportunity (Domjan, 2005; Hollis, 1997).

Memory researchers tend to focus primarily on proximate mechanisms and rarely consider ultimate or functional explanations of remembering. There are some exceptions (e.g., Anderson & Schooler, 1991; Pillemer, 2003), but for the most part memory scholars are satisfied with providing proximate analyses of empirical phenomena (Nairne, 2005; 2014). Memory textbooks are replete with empirical phenomena—e.g., the spacing effect, the forgetting curve, retrieval practice effects—but little consideration is given to why our memory systems actually work this way. Discussions of memory principles tend to be devoid of a functional context as well. Consider the well-established claim that retrieval cues are successful to the extent that they match the conditions of encoding (Tulving & Thomson, 1973). Although generally true (but see Nairne, 2002), discussions of the encoding–retrieval match rarely consider the functional context in which the principle holds. Throughout the day, each of us regularly encounters events that “match” prior episodes in our lives—think about the “matches” engendered by a daily encounter with a colleague or even your coffee cup—but few of these events yield instances of conscious recollection (Nairne, 2015b) or induce what Tulving has called a “retrieval mode” (e.g., Tulving, 1985). To understand how people remember and forget, it will be necessary to develop effective theories about how retrieval cues are generated and used in the world (see Berntsen, 2009).

There is an additional advantage to thinking functionally about psychological processes—it can lead to the generation of new research questions and to the discovery of new phenomena (Buss et al., 1998; Nairne, 2005). Our work on survival processing was motivated entirely from a functional/evolutionary perspective. We were concerned with the question of why memory evolved and the extent to which its functioning is colored by the criterion nature used to shape its development. Even if the benefits of survival processing on remembering are not grounded in an evolved adaptation, and much work remains to

be done to determine its ultimate roots, survival processing will continue to be an effective way to promote long-term retention. Other findings in our laboratory, such as the effect of animacy on retention (Nairne et al., 2013), were motivated by functional thinking as well. As stated initially, few memory researchers question the assertion that memory evolved, in response to particular selection pressures in our ancestral past, so it would not be surprising if the key to understanding how memory works lies at least partly in its evolutionary lineage.

References

- Addis, D. R., Wong, A. T., & Schacter, D. L. (2007). Remembering the past and imagining the future: Common and distinct neural substrates during event construction and elaboration. *Neuropsychologia*, *45*, 1363-1377. doi:10.1016/j.neuropsychologia.2006.10.016
- Adolphs, R. (2013). The biology of fear. *Current Biology*, *23*, R79-R93. doi:10.1016/j.cub.2012.11.055
- Anderson, J. R., & Schooler, L. J. (1991). Reflections of the environment in memory. *Psychological Science*, *2*, 396-408. doi:10.1111/j.1467-9280.1991.tb00174.x
- Aslan, A., & Bäuml, K.-H. T. (2012). Adaptive memory: Young children show enhanced retention of fitness-related information. *Cognition*, *122*, 118-122. doi:10.1016/j.cognition.2011.10.001
- Barrett, H. C. (2005). Adaptations to predators and prey. In D. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 200-223). New Jersey: John Wiley & Sons, Inc.
- Barrett, H. C., & Kurzban, R. (2006). Modularity in cognition: Framing the debate. *Psychological Review*, *113*, 628-647. doi:10.1037/0033-295X.113.3.628
- Bell, R., Röer, J. P., & Buchner, A. (2013). Adaptive memory: The survival-processing memory advantage is not due to negativity or mortality salience. *Memory & Cognition*, *41*, 490-502. doi:10.3758/s13421-012-0290-5
- Bell, R., Röer, J. P., & Buchner, A. (2015). Adaptive memory: Thinking about function. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *41*, 1038-1048. doi: 10.1037/xlm0000066
- Berntsen, D. (2009). *Involuntary autobiographical memories: An introduction to the unbidden past*. Cambridge: Cambridge University Press.
- Bolhuis, J. J., Brown, G. R., Richardson, R. C., & Laland, K. N. (2011). Darwin in mind: New opportunities for evolutionary psychology. *PLOS Biology*, *9*, 1-8. doi: 10.1371/journal.pbio.1001109
- Buckner, R. L., & Carroll, D. C. (2007). Self-projection and the brain. *Trends in Cognitive Sciences*, *11*, 49-57. doi:10.1016/j.tics.2006.11.004
- Buller, D. J. (2005). *Adapting minds: Evolutionary psychology and the persistent quest for human nature*. Cambridge, Mass: The MIT Press.
- Burke, D. (2014). Why isn't everyone an evolutionary psychologist? *Frontiers in psychology*, *5*, 1-8. doi: 0.3389/fpsyg.2014.00910
- Buss, D. M., Haselton, M. G., Shackelford, T. K., Bleske, A. L., & Wakefield, J. C. (1998). Adaptations, exaptations, and spandrels. *American Psychologist*, *53*, 533-548. doi: 10.1037/0003-066X.53.5.533
- Butler, A. C., Kang, S. H. K., & 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. doi: 10.1037/a0017024
- Ceo, D. (2008). *Memory for survival processing of hierarchical categories*. PhD Thesis, Purdue University.
- Chatterjee, S. (2015). *The rise of birds* (Second Edition). Baltimore, MD: Johns Hopkins University Press.
- Confer, J. C., Easton, J. A., Fleischmann, D. S., Goetz, C. D., Lewis, D. M. G., Perilloux, C., & Buss, D. M. (2010). Evolutionary psychology:

- Controversies, questions, prospects, and limitations. *American Psychologist*, 65, 110-126. doi: 10.1037/a0018413
- Cosmides, L., & Tooby, J. (2013). Evolutionary psychology: New perspectives on cognition and motivation. *Annual Review of Psychology*, 64, 201-229. doi: 10.1146/annurev.psych.121208.131628
- Craik, F. I. M., & Tulving, E., (1975). Depth of processing and the retention of words in episodic memory. *Journal of Experimental Psychology: General*, 104, 268-294. doi: 10.1037/0096-3445.104.3.268
- Dawkins, R. (2006). *The selfish gene* (30th anniversary edition. Oxford: Oxford University Press.
- Dehaene, S., Cohen, L., Sigman, M., & Vinckier, F. (2005). The neural code for written words: A proposal. *Trends in Cognitive Sciences*, 9, 335-341. doi:10.1016/j.tics.2005.05.004
- Domjan, M. (2005). Pavlovian conditioning: A functional perspective. *Annual Review of Psychology*, 56, 179-206. doi: 10.1146/annurev.psych.55.090902.141409
- Dunlap, A. S., & Stephens, D. W. (2014). Experimental evolution of prepared learning. *Proceedings of the National Academy of Sciences*, 111, 11750-11755. doi: 10.1073/pnas.1404176111
- Erdfelder, E., & Kroneisen, M. (2014). Proximate cognitive mechanisms underlying the survival processing effect. In B. Schwartz, M. Howe, M. Togliani, and H. Otgaar (Eds.), *What is adaptive about adaptive memory?* (pp. 172-198). New York: Oxford University Press.
- Finke, R. A. (1980). Levels of equivalence in imagery and perception. *Psychological Review*, 87, 113-132. doi: 10.1037/0033-295X.87.2.113
- Fodor, J. A. (1983). *The modularity of mind*. Cambridge, MA: MIT Press.
- Garcia, J., & Koelling, R. A. (1966). Relation of cue to consequence in avoidance learning. *Psychonomic Science*, 4, 123-124. Doi: 10.3758/BF03342209
- Gemberling, G. A., & Domjan, M. (1982). Selective associations in one-day-old rats: Taste-toxicosis and texture-shock associative learning. *Journal of Comparative and Physiological Psychology*, 96, 105-113. doi: 10.1037/h0077855
- Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society of London, Series B*, 205, 581-598. doi: 10.1098/rspb.1979.0086
- Gould, S. J., & Vrba, E. S. (1982). Exaptation: A missing term in the science of form. *Paleobiology*, 8, 4-15.
- Grossi, G. (2014). A module is a module is a module: evolution of modularity in evolutionary Psychology. *Dialectical Anthropology*, 38, 333-351. doi: 10.1007/s10624-014-9355-0
- Hamilton, W. D. (1964). The genetical evolution of social behavior: 1. *Journal of Theoretical Biology*, 7, 1-16. doi: 10.1016/0022-5193(64)90038-4
- Hassabis, D., & Maguire, E. A. (2007). Deconstructing episodic memory with constructions. *Trends in Cognitive Sciences*, 11, 299-306. doi:10.1016/j.tics.2007.05.001
- Hettema, J. M., Annas, P., Neale, M. C., Kendler, K. S., & Fredrickson, M. (2003). A twin study of the genetics of fear conditioning. *Archives of General Psychiatry*, 60, 702-708. doi: 10.1001/archpsyc.60.7.702
- Hollis, K. L. (1997). Contemporary research on Pavlovian conditioning: A "new" functional analysis. *American Psychologist*, 52, 956-965. doi: 10.1037/0003-066X.52.9.956
- Hollis K. L., Pharr V. L., Dumas M. J., Britton G. B., Field J. (1997). Classical conditioning provides paternity advantage for territorial male blue gouramis (Trichogaster trichopterus). *Journal of Comparative Psychology*, 111, 219-225. doi: 10.1037/0735-7036.111.3.219
- Howe, M. L., & Derbish, M. H. (2010). On the susceptibility of adaptive memory to false memory illusions. *Cognition*, 115, 252-267. doi:10.1016/j.cognition.2009.12.016

- Howe, M. L., & Otgaar, H. (2013). Proximate mechanisms and the development of adaptive memory. *Current Directions in Psychological Science*, *22*, 16-22. doi: 10.1177/0963721412469397
- Hyde, T. S., & Jenkins, J. J. (1973). Recall for words as a function of semantic, graphic, and syntactic orienting tasks. *Journal of Verbal Learning and Verbal Behavior*, *12*, 471-480. doi:10.1016/S0022-5371(73)80027-1
- Kamin, L. J. (1969). Predictability, surprise, attention, and conditioning. In B. A. Campbell & R. M. Church (Eds.), *Punishment and aversive behavior*. New York: Appelton-Century-Crofts.
- Kang, S., McDermott, K. B., & Cohen, S. (2008). The mnemonic advantage of processing fitness-relevant information. *Memory & Cognition*, *36*, 1151-1156. doi: 10.3758/MC.36.6.1151
- Kanwisher, N. (2010). Functional specificity in the human brain: A window into the functional architecture of the mind. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 11163-11170. doi: 10.1073/pnas.1005062107
- Kazanas, S. A., & Altarriba, J. (2015). The survival advantage: Underlying mechanisms and extant limitations. *Evolutionary Psychology*, *13*, 1-54.
- Klein, S. B. (2012). 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. doi: 10.1037/a0027636
- Klein, S. B., Cosmides, L., Tooby, J., & Chance, S. (2002). Decisions and the evolution of memory: Multiple systems, multiple functions. *Psychological Review*, *109*, 306-329. doi: 10.1037/0033-295X.109.2.306
- Klein, S. B., Loftus, J., & Kihlstrom, J. F. (2002). Memory and temporal experience: the effects of episodic memory loss on an amnesic patient's ability to remember the past and imagine the future. *Social Cognition*, *20*, 353-379. doi: 10.1521/soco.20.5.353.21125
- Klein, S. B., Robertson, T. E., & Delton, A. W. (2010). Facing the future: Memory as an evolved system for planning future acts. *Memory & Cognition*, *38*, 13-22. doi: 10.3758/MC.38.1.13
- Kostic, B., McFarlan, C. C., & 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. doi: 10.1037/a0026974
- Krause, M. A. (2015). Evolutionary perspectives on learning: Conceptual and methodological issues in the study of adaptive specializations. *Animal Cognition*, *18*, 807-820. doi: 10.1007/s10071-015-0854-4
- Kroneisen, M., & Erdfelder, E. (2011). On the plasticity of the survival processing effect. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *37*, 1553-1562. doi: 10.1037/a0024493.
- Kroneisen, M., Rummel, J., & Erdfelder, E. (2014). Working memory load eliminates the survival processing effect. *Memory*, *22*, 92-102. doi: 10.1080/09658211.2013.815217
- Lang, P. J., Greenwald, M. K., Bradley, M. M., & Hamm, A. O. (1993). Looking at pictures: Affective, visceral, and behavioral reactions. *Psychophysiology*, *20*, 261-173. doi: 10.1111/j.1469-8986.1993.tb03352.x
- LeDoux, J. (2012). Rethinking the emotional brain. *Neuron*, *73*, 653-676. doi: 10.1016/j.neuron.2012.02.004
- Lockhart, R. S. (2002). Levels of processing, transfer-appropriate processing, and the concept of robust encoding. *Memory*, *10*, 397-403. doi: 10.1080/09658210244000225
- Mayr, E. (1961). Cause and effect in biology. *Science*, *131*, 1501-1506. doi: 10.1126/science.134.3489.1501
- McBride, D. M., Thomas, B. J., & Zimmerman, C. (2013). A test of the survival processing advantage in implicit and explicit memory tests. *Memory and Cognition*, *41*, 862-871. doi: 10.3758/s13421-013-0304-y

- McDermott, K. B., & Gilmore, A. W. (2015). The role of context in understanding similarities and differences in remembering and episodic future thought. In B. H. Ross (Ed.), *The psychology of learning and motivation* (Vol. 63, pp 45-76): Academic Press.
- McNamara, J. M., Trimmer, P. C., & Houston, A. I. (2012). The ecological rationality of state-dependent valuation. *Psychological Review*, *119*, 114-119. doi: 10.1037/a0025958
- Mobbs, D., Hagan, C. C., Dalgleish, T., Silston, B., & Prevost, C. (2015). The ecology of human fear: Survival optimization and the nervous system. *Frontiers in Neuroscience*, *9*, 1-22. doi: 10.3389/fnins.2015.00055
- Müller, S., & Renkewitz, F. (2015). Replication of Study 2 by Nairne, J. S., Pandeirada, J. N. S., & Thompson, S. (Psychological Science, 2008). *Open Science Framework: Reproducibility Project*.
- Nairne, J. S. (2002). The myth of the encoding-retrieval match. *Memory*, *10*, 389-395. doi: 10.1080/09658210244000216
- Nairne, J. S. (2010). Adaptive memory: Evolutionary constraints on remembering. In B. H. Ross (Ed.), *The psychology of learning and motivation* (Vol. 53, pp. 1-32): Academic Press. doi:10.1016/S0079-7421(10)53001-9
- Nairne, J. S. (2005). The functionalist agenda in memory research. In A. F. Healy (Ed.), *Experimental cognitive psychology and its applications: Festschrift in honor of Lyle Bourne, Walter Kintsch, and Thomas Landauer*. Washington, DC: American Psychological Association.
- Nairne, J. S. (2014). Adaptive memory: Controversies and future directions. In B. Schwartz, M. Howe, M. Togliola, and H. Otgaar (Eds.), *What is adaptive about adaptive memory?* (pp. 308-321). New York: Oxford University Press.
- Nairne, J. S. (2015a). Adaptive memory: Novel findings acquired through forward engineering. In D. S. Lindsay, C. M. Kelley, A. P. Yonelinas, & Roediger, H. L. III (Eds.), *Remembering: Attributions, processes, and control in human memory: Papers in honor of Larry L. Jacoby* (pp. 3-14). New York: Psychology Press.
- Nairne, J. S. (2015b). Encoding and retrieval: Beyond Tulving and Thomson's (1973) encoding specificity. In M. W. Eysenck & D. Groome (Eds.) *Cognitive psychology: Revisiting the classic studies*. Thousand Oaks, CA: Sage.
- Nairne, J. S., & Pandeirada, J. N. S. (2008a). Forgetting. In H. L. Roediger, III. (Ed.), *Cognitive psychology of memory. Vol. 2* of J. Byrne (Ed.), *Learning and memory: A comprehensive reference* (pp. 179-194). Oxford, England: Elsevier.
- Nairne, J. S., & Pandeirada, J. N. S. (2008b). Adaptive memory: Remembering with a stone-age brain. *Current Directions in Psychological Science*, *17*, 239-243. doi: 10.1111/j.1467-8721.2008.00582.x
- Nairne, J. S., & Pandeirada, J. N. S. (2010). Adaptive memory: Ancestral priorities and the mnemonic value of survival processing. *Cognitive Psychology*, *61*, 1-22. doi: 10.1016/j.cogpsych.2010.01.005
- Nairne, J. S., & 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., & VanArsdall, J. E. (2009). Adaptive memory: Fitness-relevance and the hunter-gatherer mind. *Psychological Science*, *20*, 740-746. doi: 10.1111/j.1467-9280.2009.02356.x
- Nairne, J. S., Pandeirada, J. N. S., & Thompson, S. R. (2008). Adaptive memory: The comparative value of survival processing. *Psychological Science*, *19*, 176-180. doi: 10.1111/j.1467-9280.2008.02064.x
- Nairne, J. S., Thompson, S. R., & Pandeirada, J. N. S. (2007). Adaptive memory: Survival processing enhances retention. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *33*, 263-273. doi: 10.1037/0278-7393.33.2.263
- Nairne, J. S., VanArsdall, J. E., Pandeirada, J. N. S., Cogdill, M., & LeBreton, J. M. (2013).

- Adaptive memory: The mnemonic value of animacy. *Psychological Science*, *24*, 2099-2105. doi: 10.1177/0956797613480803
- Nouchi, R. (2012). The effect of aging on the memory enhancement of the survival judgment task. *Japanese Psychological Research*, *54*, 210-217. doi: 10.1111/j.1468-5884.2011.00483.x
- 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. doi: 10.1111/j.1468-5884.2012.00531.x
- Öhman A. & Mineka S. (2001) Fears, phobias, and preparedness: toward an evolved module of fear and fear learning. *Psychological Review*, *108*, 483-522. doi: 10.1037/0033-295X.108.3.483
- Otgaar, H., Smeets, T., & 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. doi: 10.3758/MC.38.1.23
- Paivio, A. (2007). *Mind and its evolution: A dual coding theoretical approach*. Mahwah, NJ: Erlbaum.
- Pandeirada, J. N. S., Pinho, M. S., & Faria, A. L. (2014). The mark of adaptive memory in healthy and cognitively impaired older adults and elderly. *Japanese Psychological Research*, *56*, 168-179. doi: 10.1111/jpr.12040
- Pillemer, D. (2003). Directive functions of autobiographical memory: The guiding power of the specific episode. *Memory*, *11*, 193-202. doi: 10.1080/741938208
- Pompilio, L., & Kacelnik, A. (2005). State-dependent learning and suboptimal choice: when starlings prefer long over short delays to food. *Animal Behaviour*, *70*, 571-578. doi: 10.1016/j.anbehav.2004.12.009
- Pravosudov, V. V., & Roth, T. C. II. (2013). Cognitive ecology of food hoarding: The evolution of spatial memory and the hippocampus. *Annual Review of Ecology, Evolution, and Systematics*, *44*, 173-193. doi: 10.1146/ammurev-ecolsys-110512-135904
- Raby, C. R., & Clayton, N. S. (2012). Episodic memory and planning. In T. Schackelford & J. Vonk (Eds.), *The Oxford handbook of comparative evolutionary psychology* (pp. 217-235). Oxford, UK: Oxford University Press.
- Rescorla, R. A. (1988). Pavlovian conditioning: It's not what you think it is. *American Psychologist*, *43*, 151-160. doi: 10.1037/0003-066X.43.3.151
- Rescorla, R. A., & Wagner, A. R. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In A. H. Black & W. F. Prokasy (Eds.), *Classical conditioning II*. New York: Appleton-Century-Crofts.
- Richardson, R. C. (2007). *Evolutionary psychology as maladapted psychology*. Cambridge, Mass: The MIT Press.
- Robinson, M. D., & Clore, G. L. (2001). Simulation, scenarios, and emotional appraisal: Testing the convergence between real and imagined reactions in emotional stimuli. *Personality and Social Psychology Bulletin*, *27*, 1520-1532. doi: 10.1177/01461672012711012
- Röer, J. P., Bell, R., & Buchner, A. (2013). Is the survival-processing advantage due to richness of encoding? *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *39*, 1294-1302. doi: 10.1037/a0031214
- Sandry, J., Trafimow, D., Marks, M. J., & Rice, S. (2013). Adaptive memory: Evaluating alternative forms of fitness-relevant processing in the survival processing paradigm. *PLoS ONE* *8*(4): e60868. doi:10.1371/journal.pone.0060868
- Savine, A. C., Scullin, M. K., & Roediger H. L., III. (2011). Survival processing of faces. *Memory & Cognition*, *39*, 1359-1373. doi: 10.3758/s13421-011-0121-0
- Schacter, D. L., & Addis, D. R. (2007). The cognitive neuroscience of constructive

- memory: remembering the past and imagining the future. *Philosophical Transactions of the Royal Society (B)*, 362, 773e786. doi: 10.1098/rstb.2007.2087
- Scholl, B. J., & Gao, T. (2013). Perceiving animacy and intentionality: Visual processing or higher-level judgment? In M. D. Rutherford & V. A. Kuhlmeier (Eds.), *Social perception: Detection and interpretation of animacy, agency, and intention* (pp. 197-230). Cambridge, MA: MIT Press.
- Scott-Phillips, T. C., Dickens, T. E., & West, S. A. (2011). Evolutionary theory and the ultimate-proximate distinction in the human behavioral sciences. *Perspectives on Psychological Science*, 6, 38-47. doi: 10.1177/1745691610393528
- 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. doi: 10.1037/a0027090
- Sherry, D. F., & Schacter, D. L. (1987). The evolution of multiple memory systems. *Psychological Review*, 94, 439-454. doi: 10.1037//0033-295X.94.4.439
- Silverman, I., & Eals, M. (1992). Sex differences in spatial abilities: Evolutionary theory and data. In J. H. Barkow, L. Cosmides & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 533-549). New York, NY: Oxford University Press.
- Smith, D. S., Jones, B. C., Feinberg, D. R., & Allan, K. (2012). A modulatory effect of male voice pitch on long-term memory in women: Evidence of adaptation for mate choice. *Memory & Cognition*, 40, 135-144. doi: 10.3758/s13421-011-0136-6
- Soderstrom, N. C., & Cleary, A. M. (2014). On the domain-specificity of survival processing advantages in memory. In B. Schwartz, M. Howe, M. Toglia, & H. Otgaar (Eds.), *What is adaptive about adaptive memory?* (pp. 110-122). New York: Oxford University Press.
- Soderstrom, N. C., & McCabe, D. P. (2011). Are survival processing memory advantages based on ancestral priorities? *Psychonomic Bulletin & Review*, 18, 564-569. doi: 10.3758/s13423-011-0060-6
- Suess, F., & Rahman, R. A. (2015). Mental imagery of emotions: Electrophysiological evidence. *NeuroImage*. doi: 10.1016/j.neuroimage.2015.03.063
- Symons, D. (1992). On the use and misuse of Darwinism in the study of human behavior. In J. H. Barkow, L. Cosmides & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 137-159). New York: Oxford University Press.
- Szpunar, K. K. (2010). Episodic future thought: An emerging concept. *Perspectives in Psychological Science*, 5, 142-162. doi: 10.1177/1745691610362350
- Szpunar, K. K., Watson, J. M., & McDermott, K. B. (2007). Neural substrates of envisioning the future. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 642-647. doi: 10.1073/pnas.0610082104
- Tinbergen, N. (1963). On the aims and methods of ethology. *Zeitschrift für Tierpsychologie*, 20, 410-433.
- Tse, C-S., & Altarriba, J. (2010). Does survival processing enhance implicit memory? *Memory and Cognition*, 38, 1110-1121. doi: 10.3758/mc.38.8.1110
- Tulving, E. (1985). Memory and consciousness. *Canadian Psychologist*, 26, 1-12. doi: 10.1037/h0080017
- Tulving, E., & Thomson, D. M. (1973). Encoding specificity and retrieval processes in episodic memory. *Psychological Review*, 80, 352-373. doi: 10.1037/h0020071
- Ward, R. D., Gallistel, C. R., & Balsam, P. D. (2013). It's the information! *Behavioural Processes*, 95, 3-7. doi: 10.1016/j.beproc.2013.01.005
- Weinstein, Y., Bugg, J. M., & Roediger, H. L. (2008). Can the survival recall advantage be

explained by basic memory processes? *Memory & Cognition*, 36, 913-919. doi: 10.3758/MC.36.5.913.

Yang, L., Lau, K. P. L., & Truong, L. (2014). The survival effect in memory: Does it hold into old age and non-ancestral scenarios? *PLOS One*, 9, e95792. doi: 10.1371/journal.pone.0095792

Author Notes

Preparation of this article was supported, in part, by a grant from the National Science Foundation (BCS-1532345). Josefa N. S. Pandeirada was supported by the Portuguese Foundation for Science and Technology [grant numbers FCOMP-01-0124-FEDER-029610 - PTDC/MHC-PCN/5274/2012 and IF/00058/2012].

Corresponding Author

Nairne@psych.purdue.edu