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Adaptive Memory

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Abstract

Adaptive memory researchers study evolutionary influences on remembering. Our memory systems are the product of an evolutionary process, guided by natural selection, so one might reasonably assume that the footprints of nature's criterion (fitness) remain in memory's operating characteristics. In this chapter we review relevant evidence across several domains, both for stimuli that are naturally fitness-relevant (e.g., a snake) and for neutral information that is processed in a fitness-relevant manner. Our review provides support for the view that ancestral selection pressures continue to influence how we remember and forget.

2.28.1. Introduction

The study of *adaptive memory* focuses on the evolutionary determinants of remembering (Nairne, 2010; Schwartz, Howe, Toglia, & Otgaar, 2014). Memory is assumed to be functional, meaning that the systems that control remembering (and forgetting) are goal-directed and purposive. Memory is "for" something and its operating characteristics likely reflect the problems that it evolved to solve (Klein, Cosmides, Tooby, & Chance, 2002). As a product of natural selection, memory is apt to bear the imprint of nature's criterion as well—the enhancement of fitness (e.g., survival en route to differential reproduction). Our retention systems were "built" using a fitness-based criterion, so mnemonic processes likely operate more efficiently when dealing with fitness-relevant problems (Nairne, Thompson, & Pandeirada, 2007).

The adaptive memory framework is distinctive because human memory researchers have traditionally assumed that retention systems operate similarly across materials and domains. Researchers generally acknowledge that memory is adaptive (e.g., Bjork & Bjork, 1988), but most believe that successful retention is determined primarily by domain-general processes, such as the functional "match" between the conditions present at encoding and those existing at the point of retrieval (see Roediger, this volume). A memory record is established at encoding that, in turn, determines what retrieval cues can effectively access that record in the future (Tulving & Thomson, 1973). Encoding tasks that promote the generation of multiple retrieval cues through elaboration, or focus on processing that is "appropriate" for a given retrieval environment, increase the chances that an effective (matching) retrieval cue will be present. However, the process itself is assumed to be domain-general. Retention is controlled by the presence of a diagnostic retrieval cue and it is the characteristics of the retrieval environment, rather than the content of the information, that largely determine when (or if) an effective cue will be present. Inherent memory "tunings" are absent from the vocabulary of the researcher who, in turn, assumes only taxonomies relating encoding and retrieval contexts.

From the perspective of natural selection, of course, not all events are created equal. Remembering the location of food, the appearance of a predator, or the activities of a prospective mate are more important than remembering events and activities that are irrelevant to fitness. Selection would have favored modifications that led to enhanced retention of fitness-relevant information or strategies that improved the likelihood of survival or reproduction. Our ability to simulate future events depends on episodic retention as well. Actively generating possible outcomes, known as episodic future thought, enables us to modify our behavior proactively to deal with potential threats or food sources (Hassabis & Maguire, 2007; Raby & Clayton, 2012; Schacter & Addis, 2007). Remembering how predators move, or successful escape routes from the past, promotes effective strategies in the present. For these reasons, natural selection likely favored fitness-relevant mnemonic tunings or "crib sheets" in memory's design.

Whether our retention systems show sensitivity to fitness-relevant dimensions, as predicted by the adaptive memory framework, is ultimately an empirical question. A well-designed memory system shows sensitivity to the likelihood that a past event will be needed, or appropriate, to a future situation (see Anderson & Schooler, this volume), but whether fitness-relevance plays a key role remains an open question. In this chapter we review relevant evidence across several domains, both for stimuli that are naturally fitness-relevant (such as a spider or a snake) and for neutral information that is processed in a fitness-relevant manner. We focus mainly on human memory, although the search for evolutionary influences on learning and memory has a long history in comparative psychology (e.g., Domjan, 2005; Krause, 2015b; Shettleworth, 2010). To begin, however, we briefly discuss some characteristics of evolutionary arguments, particularly as they pertain to the investigation of remembering, because evolutionary arguments remain controversial in cognitive research.

2.28.2. On the Nature of Evolutionary Arguments

Memory researchers rarely consider the functional roots of mnemonic phenomena, evolutionary or otherwise. Much is known about how memory “works”—e.g., serial position curves, negatively-accelerated forgetting, and so on—but less is known about *why* our memory systems actually show these sensitivities. Nairne (2015) suggested that the use of reverse engineering is partly responsible for the neglect. Ever since Ebbinghaus (1885/1964), researchers have queried the retention system, by asking people to process and remember information, primarily to detect empirical regularities. For example, what happens if presentations are spaced prior to retention (see Carpenter, this volume), or if we present material in a visual rather than verbal form (see Worthen & Hunt, this volume)? Explanations for the observed patterns therefore become essentially post-hoc—the empirical pattern comes first followed by explanation—which is troubling to many researchers.

In fact, this is one of the most common criticisms of evolutionary hypotheses, namely, that evolutionary accounts are “just-so” stories, created post-hoc with too many degrees of freedom (Gould & Lewontin, 1979). An empirical regularity is detected, such as men preferring to date younger women, and an adaptive explanation is manufactured to explain the data (improved fertility). Given that neither behavior nor cognitive processes can be “fossilized,” the evolutionary lineage of psychological phenomena cannot be easily traced, thereby rendering the adaptive account untestable. But of course, post-hoc accounts are not inherently untestable—for either cognitive or evolutionary hypotheses. An account can be used to generate empirical predictions that have not yet been tested; for example, one might look for age preferences cross-culturally or speculate about how they might depend on the age of the male (see Buss, 2012). As noted, most cognitive theories are post-hoc explanations of empirical regularities. Theories are proposed to explain empirical patterns and success or failure hinges on the ability to generate new predictions that are verified or falsified in follow-up research.

More importantly, characterizing evolutionary accounts as “just-so” stories ignores the basic methodology of evolutionary functional analysis. Rather than reverse engineering, evolutionary psychologists often engage in a form of forward engineering in which empirical predictions are generated *a priori* based on a consideration of historical selection pressures. Our ancestors faced recurrent adaptive problems, ones related to survival and reproduction, and these problems shaped how our cognitive processes developed. Virtually all work on adaptive memory has been motivated from this perspective. From a fitness standpoint, for example, it makes sense for us to notice and remember living things; among other things, predators are animate beings as are prospective mating partners. Consequently, we might expect memory to be biased or “tuned” to the animate characteristics of stimuli. As we discuss later, animacy turns out to be one of the best predictors of whether or not an item will be recalled—a finding of both theoretical and methodological importance because animacy is almost never controlled as an item characteristic in cognitive research. There is nothing “post-hoc” about this discovery, and the proposal of an animacy “tuning” is not a just-so story; rather, it is a textbook case of the application of evolutionary functional analysis (see Nairne, 2015).

At the same time, evolutionary hypotheses do raise special concerns. For example, evolutionary accounts are historical in nature and our knowledge about the ancestral environments in which any given process might have evolved is limited (e.g., Buller, 2005). We can be confident that the capacity to retain prior experiences gained traction over generations because remembering helped solve recurrent problems related to fitness—i.e., survival and reproduction—but we can only make educated guesses about the relative importance of selection pressures (albeit guesses that can be subject to empirical test). Moreover, to establish that a cognitive trait is an *adaptation*—that is, a mechanism arising directly as a consequence of evolution through natural selection—requires evidence that the trait can be inherited, or promoted across generations through differential reproduction. At some point in our ancestral past there must have been individual differences among people along the trait dimension, and certain *forms* were *selected* because they promoted differential survival and reproduction relative to other forms (Nairne & Pandeirada, 2010b; Richardson, 2007). It is not easy to obtain evidence of this kind, especially for the cognitive adaptations of interest to evolutionary psychologists. But notably, evolutionary biologists often face similar limitations and yet successfully formulate and test a variety of hypotheses about evolved adaptations.

An additional interpretive concern is that traits that evolved for one purpose can be used to solve other kinds of problems. Reading and writing are highly adaptive cognitive traits, but they are not evolved traits. They were acquired too recently in our species history to be the outcome of an extended process of evolution. Instead, reading and writing are the byproduct of other evolved traits, perhaps related to perception and language, that have been co-opted to achieve an adaptive outcome. Thus, for any given adaptive memory effect, such as enhanced retention for animate entities, the finding could reflect nothing more than a co-opting of other more general mnemonic processes. This kind of argument is still evolutionary, in that the phenomenon is attributable to a core set of evolved mechanisms, but the effect itself may not reflect any kind of core mnemonic “tuning.” We will return to this issue at length in our discussion of survival processing.

Finally, it is also worth noting that evolved adaptations almost always involve some co-opting of other processes. The fight-or-flight response, which prepares the organism to respond effectively when danger is present, is a case in point. 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 general survival system that coordinates the body’s reaction to threat (e.g., Mobbs, Hagan, Dalgleish, Silston, & Prévost, 2015). The fact that a basic process is involved, such as the regulation of blood pressure, does little to diminish its status as an adaptation. Rather, we accept that fight-or-flight qualifies as a “front-end” adaptation, one that coordinates other processes to enhance the fitness status of the organism. As we shall see, many adaptive memory effects may represent similar kinds of front-end adaptations—special “tunings” that rely on other core mnemonic processes to operate efficiently.

2.28.3. The Mnemonic Value of Survival-relevant Events

Content matters—for memory and other cognitive processes. For remembering, as previously noted, some events are inherently more important than others (e.g., remembering the appearance of a predator versus remembering where you left your keys). We could have evolved a general learning system, one that simply linked contiguous events together or established memory traces for novel events, but an organism with such a content-free system would not have survived very long. Nature just does not deliver the necessary precursor experiences—e.g., that babies should attend to faces and not wall hangings—and general learning systems suffer from problems of combinatorial explosion. We cannot associate all contiguous events.

Stimuli are constantly occurring together and the number of stored associations would quickly become unwieldy. There needs to be top-down control, some way to distinguish between contiguous events that need to be associated and those that do not. One way to achieve this kind of control is to build tuning or biases into the learning process.

Psychologists often appeal to general learning processes (Bolhuis, Brown, Richardson, & Laland, 2011), but the learning process is not truly general. In fact, there is considerable empirical support for learning-based “crib sheets,” especially along dimensions that are fitness-relevant. Consider Pavlovian conditioning, the prototype of a general learning preparation. Pavlovian conditioning taps the learning of inter-event relations, namely that one event signals another, but it is clearly easier to condition a signaling stimulus with food or shock (unconditioned stimuli) than with a neutral stimulus such as a brick or a book. Unconditioned stimuli are stimuli that automatically produce responses, irrespective of experience, and are ingrained parts of the biological architecture. The ability to learn about the signaling properties of events presumably evolved to enhance an organism’s ability to solve survival- or mating-relevant problems; indeed, there is now considerable evidence to support a connection between basic learning processes and the subsequent enhancement of fitness (Krause, 2015b; Shettleworth, 2010)

There is also evidence for prepared learning, again for stimuli and events that are fitness-relevant. Cue-to-consequence effects have been demonstrated repeatedly across species, such as the well-known finding that tastes are more easily associated with gastric distress than with foot shock (Garcia & Koelling, 1966). Selective associations in aversion conditioning have been found in 1-day-old rat pups (Domjan, 2005), suggesting that such tendencies are likely to be part of an inherited learning equipment. Conditioning advantages have also been found in people for evolutionarily-relevant stimuli such as snakes and spiders. Öhman and Mineka (2003) found that it was easier for people to learn that the appearance of a snake signaled the occurrence of an aversive event than when a neutral stimulus (e.g., flowers) signaled the same event. There is even some evidence that ancestrally-relevant stimuli (snakes) yield faster conditioning than matched fitness-relevant stimuli that are modern in origin (e.g., guns; see Cook, Hodes, & Lang, 1986).

Events that are generally threatening to survival produce processing advantages across a number of domains. In vision, for example, threatening objects tend to persist longer in iconic memory and are often easier to identify in visual arrays (e.g., Feldmann-Wüstefeld, Schmidt-Daffy, & Schubö, 2011; Fox, Griggs, & Mouchlianitis, 2007). Stimuli that are related to survival and reproduction (e.g., sexual images or predators) capture more attention and induce more automatic processing than social stimuli that have been matched for valence and arousal (e.g., smiling people or pictures of neo-Nazis). People also preferentially remember the locations of threatening stimuli when they are presented in a visual array (e.g., Wilson, Darling, & Sykes, 2011). Threatening stimuli show greater representational momentum effects as well—that is, when viewing dynamic scenes, people often remember the final position of an object as further along its path of motion than what actually occurred. This forward displacement effect is exaggerated for threatening stimuli (see Greenstein, Franklin, Martins, Sewack, & Meier, 2016). But it is not just threatening objects that yield selective mnemonic effects. People's memory for the spatial locations of food in markets depends partly the nutritional quality of the food (New, Cosmides, & Tooby, 2007).

Examples of enhanced retention of survival-relevant stimuli abound. Emotionally-laden events are remembered well (e.g., Buchanan, 2007; see Talmi & Ramdeen, this volume) and biological (evolutionary) relevance appears to be an important component of the emotional memory advantage (Sakaki, Niki, & Mather, 2012). Flashbulb memories (Brown & Kulik, 1977), which are typically survival relevant, are characteristic of episodic retention as well. Flashbulb memories are highly vivid and confident memories surrounding emotional events, such as the terrorist attacks in the United States on September 11, 2001. Flashbulb memories consist primarily of "where and when" information, rather than details about the event itself—in other words, where was I and what was I doing when I first heard about the terrorist attacks. Studies have tracked these memories over years (e.g., Hirst, Phelps, Meksin et al., 2015) and, although recall is often inaccurate and inconsistent over time, people continue to report elaborate recollections and especially high confidence in their memories after a decade or more.

Finally, there is a survival-related bias in the transmission of urban legends and oral narratives such as epic ballads (Rubin, 1995). Urban legends often revolve around survival-relevant information, especially food contamination (e.g., razor blades in Halloween candy; Eriksson & Coultas, 2014). Using a version of the classic "telephone" game (also known as "Chinese Whispers"), Stubbersfield, Tehrani, and Flynn (2015) asked people to read and recall urban legends that had been rated previously as high in survival-relevant information or control material that was survival-neutral. They used a linear transmission chain design, in which each participant in the chain was presented with material that had been recalled by a previous participant; only the participants at the beginning of the chain read the original legends. Across the different recall generations, the survival-relevant legends were recalled more accurately, meaning that the original legend material was maintained in the recall output, compared to the control materials.

These data indicate that there may be a mnemonic bias or "tuning" for survival-related information. But the concept of survival-relevance remains hard to pin down because "relevance" is apt to be context-dependent. Think about a pencil. Normally, we would not consider a pencil to be survival-relevant, and we would not expect it to receive any special mnemonic boost, but pencils can become survival relevant under some circumstances. If suddenly attacked while holding a pencil, it becomes survival-relevant as a potential weapon. As Nairne and Pandeirada (2008b) put it: "food is survival relevant, but more so at the beginning of a meal that at its completion; a fur coat has high s-value at the North Pole, but low at the Equator" (p. 240). Consequently, we probably did not evolve brains filled with too much content-specific "survival" information; instead, what likely evolved was a sensitivity or tuning to survival *processing*. Once an attribution is made about a survival situation, perhaps engendered by the sudden appearance of a predator, evolved mnemonic machinery kicks into gear and relevant material is remembered well. As we discuss shortly, there is now considerable empirical evidence to support this view.

2.28.4. The Survival Processing Paradigm

In 2007, Nairne et al., introduced a procedure to test the effect of survival-based processing on long-term episodic retention. In the key experimental condition, people were asked to read a short passage depicting a survival situation, one modeled after conditions that might have been present in an ancestral setting (see Table 1). The task was to rate the relevance of unrelated target words to this survival scenario. So, for example, how relevant might the words "corn" or "rock" be to surviving in the grasslands using a scale from 1 (totally irrelevant) to 5 (extremely relevant)? No mention was made of a later memory test, but everyone received a surprise test of free recall (or recognition) at the end of the rating task. Superior memory was found for those receiving the survival processing task, relative to several control conditions. The control conditions included two traditional “deep processing” tasks (Craik & Tulving, 1975)—rating the items for pleasantness or for self-relevance—along with an additional condition that involved rating the words with respect to a non-fitness relevant scenario (moving to a foreign land).

An important feature of this procedure is that everyone is asked to remember exactly the same information on the final memory test; what differentiates the conditions is the context in which the item is processed (survival-relevant or not). This focus on processing helps to eliminate item-selection concerns that potentially plague experiments of the type described in the previous section. For example, one can compare retention of fitness-relevant stimuli (e.g., snakes or spiders) to fitness-irrelevant materials (e.g., books or flowers), but these two classes of stimuli might differ in ways other than their fitness relevance. Attempts can be made to equate the stimuli along dimensions that are known to be of interest (e.g., imagery, frequency, meaningfulness), but unknown and uncontrolled dimensions might still be present. For example, as discussed in the next section, whether an item represents a living or a nonliving thing can dramatically influence retention, even though the importance of this animacy dimension has only recently been discovered (Nairne, VanArsdall, Pandeirada, Cogdill, & LeBreton, 2013).

The retention levels found after survival processing typically exceed those found for traditional encoding techniques, which is a noteworthy feature of the procedure. In fact, Nairne, Pandeirada, and Thompson (2008) claimed that a few seconds of survival processing represents “one of the best—if not the best—encoding procedures yet identified in human memory research, at least when free recall is used as the retention measure” (p. 180). Their claim originated from work in which they directly compared survival processing to a sampling of the “best of the best” encoding procedures, including such things as forming a visual image, self-generation, self-reference, and intentional learning. A few seconds of survival processing, with no expectation of a later memory test, produced better long-term retention than any of these well-established encoding procedures. Survival processing can even produce retention levels comparable to those obtained with traditional mnemonic techniques, such as the method of loci (Kroneisen & Makerud, 2016).

The survival processing advantage has been replicated many times using a variety of target stimuli, control conditions, and subject populations. For example, significant survival processing advantages are found in young children (Aslan & Bäuml, 2012; Otgaar & Smeets, 2010) as well as in both healthy and cognitively-impaired older adults (Nouchi, 2012; Pandeirada, Pinho, & Faria, 2014). The survival advantage occurs in within- and between-subject designs, in categorized and uncategorized lists (Nairne & Pandeirada, 2008a), and for both words and pictures (Otgaar, Smeets, & van Bergen, 2010). Survival processing advantages are found across a variety of retention intervals (Clark & Bruno, 2016; Raymaekers, Otgaar, & Smeets, 2014), when recognition or recall is used as the retention measure, for item memory as well as for location memory (Clark & Bruno, 2016; Nairne, VanArsdall, Pandeirada, & Blunt, 2012), when every participant receives a unique sample of target words (Nairne & Pandeirada, 2011), and the effect remains under different levels of arousal or stress (Smeets, Otgaar, Raymaekers, Peters, & Merckelbach, 2012). There is even evidence that survival processing may improve problem-solving performance using the compound remote associate test (Garner & Howe, 2014). The basic effect has been replicated as well as part of the Open Science Project (2015).

Moreover, survival processing advantages are found when a range of different survival and control scenarios are used. It is not necessary to imagine oneself stranded in the grasslands, for example—strong retention advantages have been found for survival contexts embedded in a city (Weinstein, Bugg, & Roediger, 2008), in the desert (Kostic, McFarlan, & Cleary, 2012), on a desert island (Howe & Derbish, 2014), in the mountains (Yang, Lau, & Truong, 2014), when lost at sea (Kostic et al., 2012), on a foreign planet (Howe & Derbish, 2014), or even in the absence of context when one is merely asked to rate words with respect to survival (Klein, Robertson, & Delton, 2011). The effect remains significant across various types of survival problems (finding food, avoiding predators or attackers, treating an infection) as well as across various levels of survival threat (Olds, Lanska, & Westerman, 2014). There is some evidence that survival effects are larger in ancestral contexts (Nairne & Pandeirada, 2010a; Weinstein et al., 2008), although this is not always the case (see Soderstrom & McCabe, 2011). Control scenarios have included the standard “moving” scenario, as well as other scenarios designed to equate for potential confounds such as emotionality, familiarity, or level of arousal. For example, 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, Bell, and Buchner (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, Röer, and Buchner (2013) controlled for negative affect by comparing survival processing to a “suicide” control scenario. In each case, survival processing produced superior memory.

Of course, the fact that survival processing is an excellent encoding procedure, one that may have significant applications in education contexts (Nairne, 2016), does not mean that it reflects some kind of evolved mnemonic "tuning." Traditional mnemonic processes, such as elaboration or emotional or distinctive processing, might ultimately explain the effect (Howe & Otgaar, 2013; Kroneisen & Erdfelder, 2011; Nairne et al., 2007). In fact, Krause (2015a) recently identified twelve different proximate mechanisms that can potentially account for survival processing effects, only one of which represented a specialized "tuning" designed by natural selection. Over the past decade, dozens of papers have appeared seeking evidence for one or more of these proposed mechanisms. In one recent case, Fiacconi, Peter, Owais, and Köhler (2016) used a variety of physiological markers to provide support for the involvement of neurobiological fear responses; other investigators have directly assessed the "richness" of survival processing lending support for elaboration-based accounts of the effect (e.g., Wilson, 2016).

However, as Nairne and Pandeirada (2016) recently argued, it is misguided to pit "traditional" versus "evolutionary" interpretations of the survival processing advantage. For one thing, "traditional" mnemonic processes, such as elaboration, are ultimately rooted in evolutionary processes. If, in fact, nature evolved domain-general processes such as elaboration to guide retention, then such a process must have evolved because it satisfied nature's criterion—the enhancement of fitness. Elaboration, by itself, has no fitness consequences; it is the role that elaboration plays in solving an adaptive problem that would have driven its evolution as a trait. Consequently, anyone proposing that elaboration is responsible for the survival processing effect is implicitly proposing his or her own "evolutionary" account.

More importantly, however, evolved adaptations or "tunings" often rely on other evolved traits to function. As we discussed earlier, the fight or flight response activates the sympathetic nervous system which, in turn, produces changes in blood pressure, respiration, blood flow to the muscles, digestion, and so on. The involvement of these "basic" processes, which may have evolved for other reasons, does not disqualify fight or flight as an evolved adaptation. Similarly, the immune system is an adaptation, but it co-opted the circulatory system to function. We would never describe the immune system as "just another example of the circulatory system"—we recognize that it is an adaptation that co-opted another process to function. Adaptations regularly recruit basic processes, in systematic and controlled ways, as part of their normal response repertoire. Consequently, the fact that survival processing may recruit one or more "basic" mnemonic processes tells us nothing about whether or not it reflects an evolved mnemonic adaptation.

To make the case for (or against) a mnemonic tuning, we need to know something about *why* the co-opting is occurring. In the case of survival processing, there is support for the involvement of several well-known mnemonic processes, particularly elaboration. Some of the relevant evidence has come from studies documenting boundary conditions on the survival processing effect. For example, Kroneisen and Erdfelder (2011) found that when the survival scenario is narrowed to a single activity—finding potable water—the survival advantage is eliminated, at least when compared to the standard "moving" control (but see Ceo, 2008). Others have failed to find significant survival advantages for abstract words (Bell et al., 2013), faces (Savine, Scullin, & Roediger, 2011), certain stories (Seamon, Bohn, Coddington et al., 2012), and when survival processing occurs with a concurrent memory load (see Kroneisen, Rummel, & Erdfelder, 2016). In each of these cases the potential for elaboration is reduced, constraining the main mechanism that is responsible for the retention advantage.

More direct evidence for elaboration, or “richness of encoding” (Kroneisen & Erdfelder, 2011), has come from studies measuring 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. 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 those rated items were later recalled. Wilson (2016) asked people to think of as many possible functions or alternative uses of an object either in a survival context or in various control scenarios. The survival context led to the greatest number of generated functions or uses. Wilson concluded that survival situations may lead people to think more creatively about objects or generate more unusual or divergent uses (also see Bell, Röer, & Buchner, 2015).

However, again, the critical question focuses on *why* the survival situation or survival processing produces enhanced elaboration or creativity. Proponents of the adaptive memory framework believe that the enhancements are likely due to an engrained mnemonic tuning, an evolved adaptation that gained traction in the population because of its adaptive significance. Elaboration is simply the proximate mechanism that is recruited to produce the tuning. Core mnemonic processes operate more efficiently, or are recruited more effectively, when encodings occur in a survival context. Nairne and Pandeirada (2016) referred to this kind of adaptation as “front-end,” meaning that its primary role is to recruit and coordinate other, perhaps general, mechanisms. As noted previously, many evolved traits work this way—e.g., the fight or flight response activates and coordinates a number of survival-relevant processes to produce an adaptive response to threat.

Alternatively, it is possible that the co-opting of elaboration (or some other general process) is an *artifact* of the methodology. In other words, there could be something about the rating task, or the grasslands scenario, rather than fitness-relevancy *per se*, that affords richer processing. Rating items with respect to an unfamiliar grasslands scenario might be unusually complex, novel, arousing, or difficult. Few participants are familiar with grassland scenarios, so survival processing might require especially deep processing, at least compared to rating an item for pleasantness or moving to a foreign land. According to this view, the survival processing effect is essentially a methodological artifact, rather than a product of an evolved bias or tuning related to fitness-relevant processing.

Nairne and Pandeirada (2016) recently contrasted these two interpretations of survival processing—tuning versus artifact—and found little evidence to support the artifact-based account. As noted earlier, survival processing advantages occur when using a variety of survival scenarios and many control scenarios have been employed to rule out confounding factors (e.g., emotionality, familiarity and distinctiveness). The Röer et al. (2013) "afterlife" scenario is certainly unusual and there is no obvious reason to think that rating the relevance of words to being dead and living in the afterlife is easier or less novel that rating words in the grasslands scenario. More importantly, survival processing advantages are found using *matched scenarios* in which people rate items with respect to the same activities, but in a context that is either fitness-relevant or not. For example, 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; in another experiment, people were asked to search for and gather edible food, either to survive or to win a scavenger hunt. Both scenarios required people to rate the relevance of activities involving tracking and hunting for food, in a similar way, but only the survival-based version produced a mnemonic advantage (for replications see Clark & Bruno, 2016; Nairne et al., 2012).

These data suggest that there is something about the survival framing that produces the mnemonic advantage. People naturally generate more ideas, or consider more novel and potential uses for objects, when they are assessing the consequences of a survival situation. These elaborations, in turn, produce effective mnemonic encodings, perhaps because they induce encoding variability that increases the number of potentially matching retrieval environments (see Roediger, this volume). Note that appealing to elaboration as the proximate mechanism behind the memory advantage is fully consistent with an evolutionary account. As discussed throughout, adaptations often “co-opt” basic processes to achieve their intended function. During survival processing, effective mnemonic processes are recruited and coordinated to produce lasting memories. Whether or not survival processing is sufficient to recruit elaborative processing in all cases remains a legitimate topic for future research, but the fact that such processes are involved certainly does not rule out an evolutionary interpretation of the phenomenon.

At face value, it is sensible to assume that the mnemonic effects of survival processing are adaptive. However, as Nairne and Pandeirada (2016) pointed out, survival processing advantages are best viewed within the context of a more general survival optimization system (Mobbs et al., 2015; Woody & Szechtman, 2011). People are born with a kind of survival intelligence that helps them activate or inhibit motivational systems and shift processing priorities to relevant internal and external events. An important feature of survival intelligence is the capacity to simulate future scenarios—to actively generate possible outcomes and adjust behavior proactively.

Remembering how a predator might have moved, a successful escape route from the past, or an accessible food patch can be used to promote strategic behavior in the present. Moreover, as noted previously, the ability to simulate future events depends intimately on our ability to remember the past. Medial temporal lobe amnesia patients show parallel deficits in episodic remembering and episodic future thought (Klein, Loftus, & Kihlstrom, 2002; Tulving, 1985). Brain imaging studies have shown 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, our ability to remember fitness-relevant events successfully, along with the adaptive ability to simulate possible scenarios in fitness-relevant contexts, enables us to modify our behavior proactively and deal effectively with potential threats or food sources (Hassabis & Maguire, 2007; Schacter & Addis, 2007).

2.28.5. The Mnemonic Value of Animacy

As noted throughout, the adaptive memory framework assumes that content matters. In general, things that are inherently fitness-relevant should receive processing priority and be remembered better. Living things represent a case in point—among other things, animate beings can be predators, food, competitors for resources, and prospective mating partners. Consequently, we might expect an adaptive memory system to be biased or "tuned" to the animate characteristics of stimuli (that is, whether an object is living or not) because living things are more apt to be fitness-relevant. In fact, there is already evidence suggesting that animacy plays a central role in many cognitive processes including language (Silverstein, 1976), cognitive development (Opfer & Gelman, 2011), the organization of semantic knowledge (Caramazza &

Shelton, 1998), and visual perception and attention (Pratt, Radulescu, Guo, & Abrams, 2010).

Perceptually, there is a “tripwire” for animacy, or at least to cues that are usually associated with animacy. A branch cracking in the woods leads to a physiological state of readiness in most of us, along with the attribution that something alive is lurking nearby. People readily impart animacy to inanimate objects that move in animate ways (Heider & Simmel, 1944) and attribute animacy to inanimate objects moving randomly if other cues evoke animacy (e.g., the wolfpack effect; Gao, McCarthy, & Scholl, 2010). New et al. (2007) proposed that the human attention system evolved to monitor and detect animates. Indeed, people can more quickly and accurately detect changes to visual scenes when the feature that changes is the presence or absence of an animate (people and animals; although see Hagen & Laeng, 2016).

Among memory researchers, though, animacy has received scant attention. Whether something is alive or not is a salient feature of an entity, so it is somewhat surprising that animacy has not been investigated in detail. One reason for the neglect may be that item characteristics are often correlated, which makes it difficult to disentangle the relative influence of any given dimension. For example, animate things are likely to be concrete and familiar. Any mnemonic advantage could then be attributed to the ease of forming a visual image of the object or its “spread” in an associative network. There are two ways to handle item selection concerns—one can carefully match to-be-remembered target words along various dimensions known to be important to memory, or one can induce animacy processing (or not) for a common target word. We have recently pursued both of these strategies in our laboratory.

Taking the second case first, people were given novel stimuli (nonwords) paired with properties characteristic of either animate (e.g., believes in God) or inanimate objects (e.g., has a round shape). Everyone was asked to decide whether each object, which the participants were told were things they had never seen before and had unusual names, likely represented a living thing or an object, using the paired property to decide. People made their judgments on a six-point scale ranging from 1 (‘‘very likely to be an object’’) to 6 (‘very likely to be a living thing’). After the initial rating task, everyone received either a recognition or recall test for the rated words. Across two experiments. memory was better when nonword ‘‘names’’ were associated with animate properties (VanArsdall, Nairne, Pandeirada, & Blunt, 2013). As with survival processing experiments, the key element of the design is that everyone is asked to remember exactly the same information; what matters is whether the item is processed as an animate or not. Aslan and John (2016) recently replicated this advantage, using the same general design, but with young children as participants. A robust animacy processing advantage was found in both kindergartners and elementary school children (ages 4 to 11).

These animacy processing experiments effectively eliminate the item selection concerns that arise when animate and inanimate stimuli are directly compared. However, it is possible to match stimuli along relevant dimensions, or to use statistical techniques that isolate the relative contributions of different item characteristics. For example, Nairne et al. (2013) used regression techniques to determine the extent to which animacy is a significant predictor of recall relative to a host of other variables. Animacy correlated strongly with recall (r = 0.42) and its incremental importance (the unique contribution of the variable to R^2) was nearly twice that of its nearest competitor (imagery). VanArsdall (2016) recently replicated these results, with a much larger word pool, and found that the animacy advantages were independent of list composition (the proportion of animate words in a list) and age of the participant. Consequently, animacy seems to be an extremely important determinant of whether or not an item is recalled.

Most of the recent work on animacy and memory has used matched stimuli. Nairne et al. (2013) created two pools of words—one animate and the other inanimate—and matched them on ten different dimensions including age of acquisition, category size, category typicality, concreteness, familiarity, imagery, frequency, meaningfulness, word length, and semantic relatedness. Animate and inanimate words were mixed together in study lists which participants were then asked to study for a retention test. A later free recall test revealed strong animacy advantages across three study-test trials. Similar animacy advantages have now been reported in other labs, using different word pools, and the advantage is found for pictures of animate entities, on recognition and some cued-recall tests, in between-list designs, and when an additional memory load is required during encoding (e.g., Bonin, Gelin, & Bugaiska, 2014; Bonin, Gelin, Laroche, Méot, & Bugaiska, 2015; Popp & Serra, 2016).

Moreover, if the categorical nature of the stimuli (animate versus inanimate) is masked during presentation by embedding a small sample of matched animate and inanimate words in a much larger list of unrelated words, the animacy advantage remains robust (VanArsdall, Nairne, Pandeirada, & Cogdill, 2015). The advantage holds as well when the animate words are drawn from tightly-constrained categories (*four-footed animals* versus *furniture*). These data help rule out the possibility that animate stimuli simply come from stronger or more accessible categories than inanimate stimuli—e.g., the category “living things” might be smaller or more diagnostic than the category “inanimate objects.” In addition, Nairne et al. (2013) found no evidence for categorical clustering during recall output; in other words, people tended not to recall animate items together during output, nor did they recall them especially early.

VanArsdall et al. (2015) were interested in whether animacy advantages might have educational applications, particularly to foreign language vocabulary learning. People were shown unfamiliar Swahili words that were assigned various English “translations.” The task was to produce the appropriate English translation when given the Swahili word as a cue. Rather than pairing the Swahili words with their actual translations, translation targets were chosen that were either animate or inanimate but otherwise matched (e.g., *rembo*-duck versus *sahani*-stove). People were told to learn the pairs such that they could produce the translation (duck) when provided the cue (*rembo*). Across three study-test trials, a strong translation advantage was found for the animate pairs. Popp and Serra (2016) reported similar results, but found that animate stimuli did not enhance associative learning in all cases. For example, an advantage existed for acquiring English “definitions” for Swahili words, but it did not for English-Swahili pairs, or other types of cued recall in English-English word pairs.

Li, Jia, Li, and Li (2016) recently investigated whether animacy advantages extend to higher cognitive processes such as metamemory. People were given matched animate and inanimate words to learn but were also asked to produce judgments of learning (JOLs) during study. Responses were made on a scale ranging from 0% (definitely will not remember the word) to 100% (definitely will remember the word). Participants gave higher JOL estimates for the animate words than they did for the inanimate words and recall was substantially better for the animate words as well. The authors also found that when perceptual fluency was manipulated, by varying study time or font size, the JOL advantage for animate words was unaffected. This led Li et al. to conclude that people may hold prior beliefs about the influence of animacy on memory—that is, people may naturally believe that remembering is tuned to the animacy dimension.

The fact that animate stimuli are better remembered than inanimate stimuli is important for theoretical and methodological reasons. Methodologically, animacy is rarely controlled in cognitive research, despite the consistent finding that it plays an important role. Theoretically, of course, the empirical advantage confirms an important prediction of the adaptive memory framework, namely, that our retention systems should be tuned to the retention of information that is relevant to fitness. However, as in the case of survival processing, the relevant proximate mechanisms need to be identified. One possibility is that animate items naturally recruit more attention which simply maps onto a more accessible memory trace. Another possibility is that animate items, on average, possess richer attributes or features (see Cree & McRae, 2003), which makes their corresponding encodings more diagnostic during retrieval. Bonin et al. (2014) provided a measure of sensorial "richness" for matched animate and inanimate words and found no difference between the word types, but further investigation is needed. A related view is that animate words tend to have more overlapping semantic features; some support for this view was obtained recently using objective rating data and some global measures of neural activation during the processing of animate and inanimate words (Xiao, Dong, Chen, & Xue, 2016). Again, though, the animacy effect in retention is a relatively new discovery, so the investigation of proximate mechanisms remains in an early stage.

2.28.6. The Mnemonic Value of Contamination

Pathogenic microorganisms have posed a recurring threat to survival and reproduction over human evolutionary history (Fumagalli, Sironi, Pozzoli et al., 2011; Tooby, 1982; Tybur, Lieberman, & Griskevicius, 2009). To face these threats, natural selection designed a sophisticated set of physiological mechanisms to detect and destroy pathogens that enter the body - the *Biological Immune (BIO) System* (Parham, 2014).

An additional suite of mechanisms also evolved to avoid sources of potential infection that could arise from physical contact - the *Behavioral Immune (BEH) System* (Schaller, 2006; Schaller & Duncan, 2007). Evolved behavioral disease-avoidance strategies have been observed in human beings as well as in a wide range of animal species. For example, just as herbivores avoid grazing in patches contaminated by feces (e.g., Brambilla, von Hardenberg, Kristo, Bassano, & Bogliani, 2013), people avoid intake of potentially contaminated foods (e.g., Rozin, Millman, & Nemeroff, 1986).

The BEH-system is adaptively tuned to perceive potential contamination threats in the immediate environment (Neuberg, Kenrick, & Schaller, 2011).The perception of such cues triggers affective (e.g., disgust), cognitive (e.g., allocation of attention), and behavioral (e.g., avoidance) responses that work in concert to promote an organism's survival (Schaller & Duncan, 2007; Schaller & Park, 2011). For example, people are disgusted by, are particularly attentive to, and inhibit social contact from those with disease-connoting cues (Ackerman, Becker, Mortensen et al., 2009; Oaten, Stevenson, & Case, 2009; Schaller & Park, 2011). Simply put, we tend to avoid people who look and act sick.

Disgust is a basic emotion universally expressed and accurately recognized across cultures (Curtis & Biran, 2001; Curtis, de Barra, & Aunger, 2011). Whereas other emotional experiences, such as fear, anger, and sadness, have a well-established research background, disgust has received relatively less empirical attention. Disgust is believed to have evolutionary roots in distaste, an initial form of response towards contaminated foods (Rozin, Haidt, & McCauley, 2008). However, its adaptive value is not exclusively confined to preventing the ingestion of harmful substances; it extends to a broader disease-avoidance function, constituting a key component of the BEH-system (Curtis et al., 2011; Oaten et al., 2009; Tybur, Lieberman, Kurzban, &

DiScioli, 2013). In fact, there seems to be a straightforward relationship between disgust elicitors and disease sources: Things most likely to hold infectious agents are usually considered disgusting, including rotting foods, dead bodies, potentially contaminating animals, bodily products such as feces, vomit, phlegm, and blood, among others (Oaten et al., 2009; Rozin et al., 2008).

From a fitness perspective, it is beneficial to attend to and remember disgusting and disease-relevant stimuli in order to prevent potential contamination. Accordingly, a heightened allocation of attentional resources for disgusting, compared to neutral or fear-evoking stimuli, has been found (Ackerman et al., 2009; van Hooff, Devue, Vieweg, & Theeuwes, 2013). This effect is even stronger when participants are primed with disease concerns (Ackerman et al., 2009). Charash and McKay (2002) found better memory for disgusting over frightening and neutral words. More recently, Croucher, Calder, Ramponi, Barnard, and Murphy (2011) found higher recognition memory for disgusting relative to frightening images taken from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 1999). In the Croucher et al. study, the images were carefully matched for pleasantness, approach-avoidance tendency, distinctiveness, visual complexity, anger and sadness in an effort to control for other potentially relevant memory variables. Additionally, the disgust advantage was apparently not mediated by arousal because the disgusting images were considered as significantly less arousing than the frightening ones. Chapman, Johannes, Poppenk, Moscovitch, and Anderson (2013) also replicated the mnemonic advantage for disgusting stimuli while controlling for arousal, valence, distinctiveness, visual salience or complexity of the stimuli, and attention at encoding. In their study, participants were given an incidental encoding task in which they performed a line location discrimination task while disgusting, fearful, and neutral images (also from the IAPS) were presented. After a short (10 min) or long delay (45 min and 1 week) participants were given a surprise free recall task for the images. They found a slight mnemonic advantage for the disgusting images after the short delay which became highly significant when memory was tested at the longer delays. Importantly, additional analyses revealed that disgust accounted for this memory advantage over and above other variables (e.g., arousal or valence).

In a different type of study, Bell and Buchner (2010) asked participants to rate the likability of faces paired with descriptions of behaviors that were either disgusting, pleasant or neutral. Disgusting information included references to lack of hygiene, intake of spoiled food, body secretions, animals, and injuries; an example would be: "K.S. is a laborer. To save money, he cooks dog food in a big pot to eat it all by himself." (p. 32) Examples of pleasant and neutral descriptions used in this study included, respectively: "O.H. is a miller. When he has friends over, the smell of freshly baked cakes and cookies fills his apartment.", and "J.L. is a gardener. He often orders lunch at work from a local Italian restaurant, because he cannot cook very well." (p. 34). After the encoding phase, participants performed an old/new recognition task for the faces and a source memory task for the type of behavior previously associated to the face. Although no recognition advantage was found for the faces, source memory performance was better for faces of people associated with the disgusting behaviors. According to the authors, this enhanced source memory could not be explained by negativity or arousal, "rather, the information has to be threatening (i.e., associated with negative consequences for other people) to be especially well remembered" (Bell & Buchner, 2012, p. 406).

These mnemonic advantages may well be tied to the fact that disgusting objects reliably hold harmful infectious disease-causing agents, and therefore carry a high potential for contamination. Interestingly, innocuous objects that have been in close contact with disgusting objects are also treated in a special way because people believe there is a transference of the disgusting or contaminating properties through contact (Rozin & Fallon, 1987). This ‘magical’ spread of contamination is referred to as the “law of contagion”, one of the laws of sympathetic magic (Frazer, 1890/ 1992/ 1959; Mauss, 1902/ 1972; Tylor, 1871/ 1974), which holds that “once in contact, always in contact” (Frazer, 1922, p. 12, as cited in Coughtrey, Shafran, & Rachman, 2014). Empirical support for this idea comes from studies demonstrating that people evaluate more negatively and are unlikely or unwilling to interact with objects that have been in contact with disgusting stimuli (e.g., Morales & Fitzsimons, 2007; Rozin et al., 1986). For example, people are reluctant to drink a juice that has briefly contacted a sterilized dead cockroach (Rozin et al., 1986) or eat foods that have been handled or bitten by unsavory or disliked persons (Rozin, Nemeroff, Wane, & Sherrod, 1989). In work by Rozin et al. (1989), participants were instructed to imagine interacting with a variety of objects (e.g., wearing a sweater or brushing their hair with a hairbrush) that once belonged to and were used by different people (e.g., a friend, a lover, a disliked, or an unsavory person). Objects that previously belonged to a disliked or unsavory person were rated as significantly more unpleasant. Likewise, knowing that a piece of clothing had been touched and tried on by strangers, negatively impacts both a consumer’s evaluation and intention to purchase (Argo, Dahl, & Morales, 2006).

Employing a scenario in which participants were shown a set of products in a grocery cart, Morales and Fitzsimons (2007) found that the mere physical contact between a tightly sealed package of a disgusting product and another non-disgusting product, such as placing feminine napkins next to cookies, substantially decreased participants’ willingness to try the latter product along with judgments of its quality.

Another study recently explored the impact of superficial packaging damage on consumers' product evaluations and purchase intentions (White, Lin, Dahl, & Ritchie, 2016). People showed negative reactions and avoidance of these products, which seemed to be driven by perceptions of contamination and subsequent concerns with health and safety risks. Such behaviors are congruent with an evolutionary perspective, given that the successful avoidance of potentially contaminated items increases the chances of surviving and reproducing.

Inspired by the law of contagion, we have recently begun investigating mnemonic tunings for contamination by asking if people remember objects that have been touched by sick people better than objects touched by healthy people (Fernandes, Pandeirada, Nairne, & Soares, 2016; Nairne, 2015). In one experiment, participants saw pictures of everyday objects presented with a short descriptor conveying information about the health status of a person who had recently touched the object. For example, a picture of a cup might be presented along with the statement "person with a runny nose" (sick condition) or the statement "person with brown hair" (healthy condition). After every third item, an immediate memory test followed in which the three preceding objects were shown again and participants were asked to identify whether each had been touched by a sick or a healthy person. Performance on this task allowed us to ensure that participants were relating the descriptor to the object and to confirm that the sentences were being correctly interpreted as descriptive of a sick or a healthy person. After a series of these trials, and a short distractor period, participants were surprised with a free recall test for the objects. Participants performed close to perfect in the immediate memory task with no differences between the sick and healthy conditions. However, on the final test they recalled significantly more of the objects paired with descriptions of sick people than those paired with descriptions of healthy people—in other words, they retained more of the potentially contaminated objects. These results have been obtained in two independent studies conducted in two different countries (USA and Portugal; Fernandes, Pandeirada, Soares, & Nairne, submitted).

Relying on the idea that some disease signals can be observed directly on a person's face, we designed an experiment using photographs of faces displaying disease-connoting cues, such as perioral dermatitis, conjunctivitis, eczema, herpes, and sweet syndrome. We followed the procedure just described but rather than presenting the objects with descriptions, we presented them along with faces containing cues indicative of contagious diseases (sick faces) or containing no such cues (healthy faces). The same memory pattern emerged: Participants recalled more of the objects associated with the sick than with the healthy faces. We also asked participants to indicate who had "touched" each of the recalled items. People were better at identifying that the object had been touched by a sick person than by a healthy person. In a follow-up experiment, we found that it is not the cues themselves that produce the memory advantage, but the attribution of potential disease. If exactly the same faces and disease-related cues are associated with the objects, but the participant is told that the "sick" faces belong to actresses with makeup preparing to portray sick people in a television show, the mnemonic advantage disappears.

It is worth noting that the set of experiments just described differs in important ways from the previous memory literature on disgust. Most studies have investigated memory performance for stimuli that directly trigger the emotion of disgust compared to items that elicit fear or a neutral reaction. Here, everyone is asked to recall or recognize exactly the same "neutral" items. What matters is the context in which the items are presented - a context of potential contamination or not (also see Bell & Buchner, 2010). This kind of design eliminates item-selection concerns that have plagued earlier research. More generally, as a part of the cognitive toolkit of the BEH-system, the memory advantage for contamination observed in our experiments is undoubtedly adaptive because it maximizes our chances of survival by helping us avoid coming into contact with potential sources of infection.

2.28.7. The Mnemonic Value of Mating-Relevant Events

Reproduction is the mechanism through which organisms ultimately pass along adaptive traits to future generations. Without reproduction, evolution simply would not be possible. The selection of a mate who will ensure successful reproduction and high-quality offspring is a challenge faced by all organisms. One key question about this process is how are mates selected? And, more importantly for our purposes, does memory play a role in this process?

G. Miller (2001) has argued that the human mind—including such traits as creativity, intelligence and language—evolved in the service of sexual selection (see also G. F. Miller & Todd, 1998). Comparable to how a peacock's tail is used to display mating value (e.g., Petrie & Halliday, 1994), behavior that showcases superior mental traits is indicative of higher mate value (G. Miller, 2001). Prokosch, Coss, Scheib, and Blozis (2009) reported that females considered males with higher intelligence and creativity, as measured by objective tests, to be more appealing potential mates. All of these faculties recruit, to some extent, core processes, memory included. In fact, G. Miller (2001) suggested that one specific type of memory, autobiographical memory, evolved in response to mate selection pressures and that memory functioning in general is an effective signal for fitness. Individuals with superior autobiographical memories are more capable of integrating and framing previous personal experiences in a way that reflects high fitness value to potential mates.

Memory performance is closely related to age—a strong indicator of fitness—which walks hand-in-hand with fertility, particularly in women: Both reach their maximum around the twenties, start to decline in the third decade of life, and deteriorate more significantly thereafter. Thus, in the absence of direct information about chronological age during human evolution, memory loss could have been used as a cue for age (G. Miller, 2001; see also Conroy-Beam, Buss, Pham, & Shackelford, 2015).

Some models of mate choice have assigned a very active role to memory. Bateson and Healy (2005), for example, argued that choosing a mate involves a comparative evaluation process in which one chooses among previously-encountered mating candidates in order to select the one that carries the highest fitness value. In their model, memory is crucial as the comparative process is only possible if one is able to retain information about each of the alternatives. Additionally, one needs to retrieve relevant information to feed the comparison process when the moment to reach a decision arrives. Ideally, one should selectively remember elements of the episodes that involved more desirable potential mates in order to increase the chances of selecting a suitable option and of rejecting an unsuitable one (Allan, Jones, DeBruine, & Smith, 2012).

Some studies have adopted the survival processing paradigm to investigate whether memory is tuned to reproduction. Here, memory for information (typically random words) considered in a mating-related context is compared to various fitness-irrelevant controls. Sandry, Trafimow, Marks, and Rice (2013) used a mate selection scenario in which participants were asked to rate the relevance of words to searching for a partner who would satisfy them sexually. In three other reproduction-related scenarios, words were rated for their relevance to identifying potential relatives in order to avoid committing incest (incest avoidance scenario), to identifying potential mating rivals (jealousy scenario), and to confirming their spouse’s infidelity (infidelity scenario). All of these conditions failed to produce better recall performance than control conditions in which people simply rated words for pleasantness or a task in which participants had to imagine themselves performing tasks and then evaluate how possible those tasks were (e.g., balancing an object in head). In another experiment the authors reformulated the mating scenario to include problems more directly related to sexual selection, such as finding a partner with whom to reproduce and mate and who would also help raise children. Again, this scenario did not produce better memory performance than rating the relevance of words to a control moving scenario. Klein (2013) also tested a “mate choice” scenario in which participants rated the relevance of words to selecting a mate. No memory advantage was found in this condition compared to a pleasantness-rating control. In sum, the investigation of a mnemonic tuning to mating-related aspects using the survival processing paradigm has failed to produce evidence consistent with such tuning.

However, other studies have focused more directly on memory for properties relevant to the selection of a good mate. As noted before, it would be advantageous to have particularly good memory for individuals, or aspects related to them, who display fitness indicators—that is, traits that signal that an individual possesses a high probability of surviving and reproducing successfully. For example, facial attractiveness and symmetry have been associated with better immune functioning as well as other characteristics indicative of higher mating value (Rantala, Coetzee, Moore et al., 2013; Rantala, Moore, Skrinda et al., 2012; Thornhill & Gangestad, 1999). A number of studies have examined the effect of attractiveness on memory and have generally found that attractive faces are remembered better, particularly when female faces are used as target stimuli (e.g., Marzi & Viggiano, 2010; Shepherd & Ellis, 1973; Tsukiura & Cabeza, 2011).

Male face masculinity can be another indicator of mate value because it relates to health status (for a review see Tybur & Gangestad, 2011). Allan et al. (2012) presented faces of males and females along with random object pictures. Half of the faces were previously manipulated to be more masculinized and the other half to be more feminized. Memory for the objects was then tested using a two-alternative forced-choice task in which participants had to indicate which of the two-presented objects had been previously presented. Finally, participants indicated their preferences for each type of face (i.e., the masculinized and the feminized) by indicating which they considered most attractive. The results revealed: 1) females preferred the masculinized faces more than the most feminized ones; 2) female participants showed enhanced memory for the objects when they were presented with their preferred male faces but not when they were presented with their preferred female faces; and, 3) no significant effects were obtained for the male participants.

Another fitness indicator is a man’s voice, with lower pitched voices suggesting greater reproductive success (e.g., Apicella, Feinberg, & Marlowe, 2007). In work by Smith, Jones, Feinberg, and Allan (2011) object pictures were presented to female participants and were concurrently named aloud by either a male or a female voice. Importantly, these voices were manipulated to be more or less masculinized. Later on, in a surprise recognition task, participants had to choose which of the two presented objects had been previously presented. Memory was better for the objects presented by a masculinized male voice than for those presented by a feminized male voice; no differences were found for the objects spoken with the manipulated female voices.

In women, a waist-to-hip ratio (WHR) of around .70 has been suggested to be a physical attribute that signals fitness, such as reproductive age, the ability to bear offspring, and health status (Singh, 2002; see also Lassek & Gaulin, 2016). Men seem to favor females with a WHR around .70: They are rated as more attractive (Streeter & McBurney, 2003), men prioritize looking at their waist region at first glance (Dixson, Grimshaw, Linklater, & Dixson, 2011), and they are looked at for longer periods of time (Garza, Heredia, & Cieslicka, 2016). Fitzgerald, Horgan, and Himes (2016) tested whether information about a potential female mate would be best remembered if she exhibited a WHR close to the ideal of.70. In two experiments, a female's photograph was presented along with a paragraph describing personal information. Using a cover story unrelated to mating intentions, participants were initially instructed to remember as many details as they could about that person. Participants then rated the attractiveness of the female and responded to a set of open questions about physical aspects of the image and biographical details described in the text (Exp. 1), or to a set of multiple-choice recognition questions regarding the same content (Exp. 2). As expected, the female figures displaying the ideal WHR (Exp. 1) or close to ideal WHR (Exp. 2) were evaluated as significantly more attractive than the remaining figures. Participants also recalled more information, related both to the physical and the personal aspects, when the female displayed a WHR closer to .70. These data suggest that memory may be biased to retain information associated to cues indicative of higher mate value.

Work in our laboratory has compared women's memory for male faces when those faces are considered in the context of a long-term relationship or in the context of a long-term working partner (Pandeirada, Fernandes, Nairne, Marinho, & Vasconcelos, 2015, 2016). In these experiments, male faces were presented along with a descriptor and female participants were asked to rate how desirable that person (represented by the face and the descriptor) would be (1) when looking for someone with whom to create a family and spend the rest of their life (mating condition), or (2) when looking for someone with whom to create a team and develop a number of important projects for the company (worker condition). The descriptors presented with the faces were equally desirable (e.g., “is responsible”), irrelevant (e.g., “has a white t-shirt”), or undesirable (e.g., “lies frequently”) across the two conditions. After a short distractor task, participants performed a recognition task for the faces. A memory advantage was obtained when faces were considered in the mating condition as compared to the worker condition. These results suggest that when the information relates directly to the mate value of the potential mates, memory is indeed enhanced.

Evidence for a memory involvement in mate choice also comes from studies that have examined how different aspects are valued in a potential mating partner depending on the type of relationship one is seeking (e.g., Buss & Schmitt, 1993; Gangestad & Simpson, 2000). For example, females tend to value physical aspects when looking for a short-term encounter, as these are more indicative of good genetic quality. On the other hand, they tend to value aspects more related to being a good provider (i.e., status and resources) when thinking about a long-term context (e.g., Buss, 2006). In experiments reported by Horgan, Broadbent, McKibbin, and Duehring (2016) female participants were encouraged to think about a male they watched in a video as a potential short or long-term mate. The authors predicted that physical aspects (e.g., information about their eyes, shoulders, facial hair) should be better remembered in the short-term condition, whereas verbal information (e.g., workout habits, scholarship, feelings about competition) should be better remembered in the long-term condition. Participants then responded to a surprise multiple-choice memory test for the male’s physical aspects and also for the information transmitted verbally. Even though the participants' memory in the two conditions did not differ overall, participants in the short-term condition remembered the physical characteristics better than those in the long-term condition, whereas the opposite occurred for the verbally-transmitted information.

This same reasoning was applied by Smith, Jones, and Allan (2013) who predicted that the masculinity of the face should be a relevant cue for females interested in pursuing a short-term relationship, but not for those more prone to engage in long-term relationships. In a couple of experiments, the authors examined whether memory for the context in which a male face was encountered (e.g., was the face surrounded by a green or a yellow frame) was influenced by the level of sexual dimorphism of the presented face and also by the socio-sexuality of the participant—that is her preference to engage in short (less restrictive socio-sexual orientation) or long-term relationships (more restrictive socio-sexual orientation). During encoding, females were shown faces manipulated to present more masculinized or more feminized characteristics surrounded by a yellow or green frame. During the source memory test, the faces were shown again and participants were asked to indicate the color of the frame that previously accompanied each face. The authors found that females with less restrictive socio-sexual orientation, had better memory for the context of faces with exaggerated masculine features, whereas the context associated with less masculine facial features was better remembered by the more restrictive females.

Overall, these studies reveal that when information directly related to the assessment of potential mate partners is present, be it through the presence of physical cues indicative of higher fitness or through descriptions of prior behavioral history, memory for that individual is improved. Memory for elements that are part of the episode tend to be better retained as well. Furthermore, consistent with evolutionary reasoning, these memory enhancements seem to be mediated by an individual's mating goals or intentions.

2.28.8. Conclusions

Adaptive memory researchers are interested in understanding evolutionary influences on remembering. Our memory systems are the product of an evolutionary process, guided by natural selection, so one might reasonably assume that the footprints of nature's criterion remain in memory's operating characteristics. Natural selection is guided by a specific criterion—the enhancement of fitness—so functional questions about what memory is "for" best center on how our retention systems solve adaptive problems related to fitness. The adaptive memory framework makes *a priori* predictions about mnemonic tunings or "crib sheets" based on this assumption. However, as noted initially, whether remembering actually shows sensitivity to fitness-relevant information and processing remains an empirical question.

The research reviewed in this chapter provides initial support for the assumptions of the adaptive memory framework. The idea that our learning and memory systems are tuned to fitness is not a new idea—e.g., cue to consequence effects in Pavlovian conditioning—but it has historically received little attention in the human memory literature. Even today textbooks on human memory rarely consider evolutionary influences or even include the term "evolution" in their indices. Memory researchers are generally satisfied with a proximate analysis of existing empirical effects, ones that were initially discovered by the simple reverse engineering of retention. Reverse engineering can be a successful strategy for advancing knowledge about memory, particularly about how memory processes work, but it typically leaves functional questions about memory unanswered. In effect, *why* do our retention systems show the properties described in the literature or by existing models of remembering?

One of the unique contributions of the adaptive memory framework, and forward engineering in general, is that it enables the researcher to generate novel predictions about mnemonic sensitivities. Evolutionary psychologists generate empirical predictions *a priori* based on a consideration of historical selection pressures. Our ancestors faced recurrent adaptive problems, ones related to survival and reproduction, and these problems presumably shaped how cognitive processes developed and operate. A number of the phenomena reviewed in the chapter—e.g., the survival processing effect and animacy advantages—represent newly-discovered empirical phenomena that were acquired through forward engineering. Each potentially can be exploited for memory improvement regardless of whether or not its ultimate roots reflect an evolved adaptive tuning.

Although much of the reviewed data is consistent with the adaptive memory framework, evolutionary hypotheses face special hurdles that can make them difficult to test. There are no “fossilized” memory traces, and our knowledge about the ancestral environments in which our memory systems evolved is clearly limited. Adaptive solutions to recurrent problems can also arise indirectly, by piggybacking on processes that evolved for different reasons, or as a result of natural constraints in the environments (e.g., the physical laws of nature). Our cognitive systems were also not built from scratch—natural selection “tinkers,” which means that changes typically develop out of existing structures. The design of these preexisting structures, in turn, introduces constraints that limit how evolution can ultimately solve critical adaptive problems. Each of these factors can make it difficult to identify the true nature of an adaption or to falsify the possibility that the behavioral trait in question is simply a byproduct of some other existing process.

However, as Nairne and Pandeirada (2016) emphasized, evolutionary biologists face similar verification problems yet continue to thrive. In practice, one seeks to accumulate converging evidence for a cognitive or behavioral "tuning," recognizing that any single piece of evidence will rarely prove conclusive. The research reviewed in this chapter represents a step in this direction. Our capacity to remember clearly evolved and is ultimately grounded in some kind of heritable adaptation. Therefore, the issue is not whether evolutionary accounts of remembering are valid—they must be. Any expression of remembering will always reflect evolved mnemonics. Adaptive memory researchers are convinced that the key to understanding how and why memory works, therefore, lies at least partly in understanding its evolutionary lineage.

2.28.9. References

Ackerman, J. M., Becker, D. V., Mortensen, C. R., Sasaki, T., Neuberg, S. L. and Kenrick, D. T. (2009). A pox on the mind: Disjunction of attention and memory in the processing of physical disfigurement. *Journal of Experimental Social Psychology* **45**, 478-485.

Addis, D. R., Wong, A. T. and 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.

Allan, K., Jones, B. C., DeBruine, L. M. and Smith, D. S. (2012). Evidence of adaptation for mate choice within women's memory. *Evolution and Human Behavior* **33**, 193-199.

Apicella, C. L., Feinberg, D. R. and Marlowe, F. W. (2007). Voice pitch predicts reproductive success in male hunter-gatherers. *Biology Letters* **3**, 682-684.

Argo, J. J., Dahl, D. W. and Morales, A. C. (2006). Consumer contamination: How consumers react to products touched by others. *Journal of Marketing* **70**, 81-94.

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

Aslan, A. and John, T. (2016). The development of adaptive memory: Young children show enhanced retention of animacy-related information. *Journal of Experimental Child Psychology* **152**, 343-350.

Bateson, M. and Healy, S. D. (2005). Comparative evaluation and its implications for mate choice. *Trends in Ecology & Evolution* **20**, 659-664.

Bell, R. and Buchner, A. (2010). Valence modulates source memory for faces. *Memory & Cognition* **38**, 29-41.

Bell, R. and Buchner, A. (2012). How adaptive is memory for cheaters? *Current Directions in Psychological Science* **21**, 403-408.

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 & Cognition* **41**, 490-502.

Bell, R., Röer, J. P. and Buchner, A. (2015). Adaptive memory: Thinking about function. *Journal of Experimental Psychology: Learning, Memory, and Cognition* **41**, 1038-1048.

Bjork, E. L. and Bjork, R. A. (1988). On the adaptive aspects of retrieval failure in autobiographical memory. In M. M. Gruneberg, P. E. Morris & R. N. Sykes (Eds.), *Practical aspects of memory: Current research and issues, Vol. 1: Memory in everyday life*. pp. 283-288. Oxford, England: John Wiley & Sons.

Bolhuis, J. J., Brown, G. R., Richardson, R. C. and Laland, K. N. (2011). Darwin in mind: New opportunities for evolutionary psychology. *PLoS Biology* **9**, e1001109.

Bonin, P., Gelin, M. and Bugaiska, A. (2014). Animates are better remembered than inanimates: Further evidence from word and picture stimuli. *Memory & Cognition* **42**, 370-382.

Bonin, P., Gelin, M., Laroche, B., Méot, A. and Bugaiska, A. (2015). The "how" of animacy effects in episodic memory. *Experimental psychology* **62**, 371-384.

Brambilla, A., von Hardenberg, A., Kristo, O., Bassano, B. and Bogliani, G. (2013). Don't spit in the soup: Faecal avoidance in foraging wild Alpine ibex, Capra ibex. *Animal Behaviour* **86**, 153-158.

Brown, R. and Kulik, J. (1977). Flashbulb memories. *Cognition* **5**, 73-99.

Buchanan, T. W. (2007). Retrieval of emotional memories. *Psychological Bulletin* **133**, 761-779.

Buckner, R. L. and Carroll, D. C. (2007). Self-projection and the brain. *Trends in cognitive sciences* **11**, 49-57.

Buller, D. J. (2005). *Adapting minds: Evolutionary psychology and the persistent quest for human nature*. Cambridge, MA: MIT Press.

Buss, D. M. (2006). Strategies of Human mating. *Psychological Topics* **15**, 239-260.

Buss, D. M. (2012). *Evolutionary psychology: The new science of the mind* (4th edn.). New York, NY: Psychology Press.

Buss, D. M. and Schmitt, D. P. (1993). Sexual strategies theory: An evolutionary perspective on human mating. *Psychological Review* **100**, 204-232.

Caramazza, A. and Shelton, J. R. (1998). Domain-specific knowledge systems in the brain: The animate-inanimate distinction. *Journal of Cognitive Neuroscience* **10**, 1-34.

Ceo, D. (2008). *Memory for survival processing of hierarchical categories.* (PhD thesis), Purdue University.

Chapman, H. A., Johannes, K., Poppenk, J. L., Moscovitch, M. and Anderson, A. K. (2013). Evidence for the differential salience of disgust and fear in episodic memory. *Journal of Experimental Psychology: General* **142**, 1100-1112.

Charash, M. and McKay, D. (2002). Attention bias for disgust. *Journal of Anxiety Disorders* **16**, 529-541.

Clark, D. P. A. and Bruno, D. (2016). Fit to last: Exploring the longevity of the survival processing effect. *The Quarterly Journal of Experimental Psychology* **69**, 1164-1178.

Conroy-Beam, D., Buss, D. M., Pham, M. N. and Shackelford, T. K. (2015). How sexually dimorphic are human mate preferences? *Personality and Social Psychology Bulletin* **41**, 1082-1093.

Cook, E. W., Hodes, R. L. and Lang, P. J. (1986). Preparedness and phobia: Effects of stimulus content on human visceral conditioning. *Journal of Abnormal Psychology* **95**, 195-207.

Coughtrey, A. E., Shafran, R. and Rachman, S. (2014). The spread of mental contamination. *Journal of Behavior Therapy and Experimental Psychiatry* **45**, 33-38.

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.

Cree, G. S. and McRae, K. (2003). Analyzing the factors underlying the structure and computation of the meaning of chipmunk, cherry, chisel, cheese, and cello (and many other such concrete nouns). *Journal of Experimental Psychology: General* **132**, 163-201.

Croucher, C. J., Calder, A. J., Ramponi, C., Barnard, P. J. and Murphy, F. C. (2011). Disgust enhances the recollection of negative emotional images. *PLoS ONE* **6**, e26571.

Curtis, V. and Biran, A. (2001). Dirt, disgust, and disease: Is hygiene in our genes? *Perspectives in Biology and Medicine* **44**, 17-31.

Curtis, V., de Barra, M. and Aunger, R. (2011). Disgust as an adaptive system for disease avoidance behaviour. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **366**, 389-401.

Dixson, B. J., Grimshaw, G. M., Linklater, W. L. and Dixson, A. F. (2011). Eye-tracking of men’s preferences for waist-to-hip ratio and breast size of women. *Archives of Sexual Behavior* **40**, 43-50.

Domjan, M. (2005). Pavlovian conditioning: A functional perspective. *Annual Review of Psychology* **56**, 179-206.

Ebbinghaus, H. (1885/1964). *Memory: A Contribution to experimental psychology.* Oxford: Dover.

Eriksson, K. and Coultas, J. C. (2014). Corpses, maggots, poodles and rats: Emotional selection operating in three phases of cultural transmission of urban legends. *Journal of Cognition and Culture* **14**, 1-26.

Feldmann-Wüstefeld, T., Schmidt-Daffy, M. and Schubö, A. (2011). Neural evidence for the threat detection advantage: Differential attention allocation to angry and happy faces. *Psychophysiology* **48**, 697-707.

Fernandes, N. L., Pandeirada, J., Nairne, J. and Soares, S. C. (2016). *Adaptive memory: The mnemonic value of contamination*. Paper presented at the 57th Annual meeting of the Psychonomic Society, Boston, MS, USA.

Fernandes, N. L., Pandeirada, J. N. S., Soares, S. C. and Nairne, J. S. (submitted). Adaptive memory: The mnemonic value of contamination.

Fiacconi, C. M., Peter, E. L., Owais, S. and Köhler, S. (2016). Knowing by heart: Visceral feedback shapes recognition memory judgments. *Journal of Experimental Psychology: General* **145**, 559-572.

Fitzgerald, C. J., Horgan, T. G. and Himes, S. M. (2016). Shaping men's memory: The effects of a female's waist-to-hip ratio on men's memory for her appearance and biographical information. *Evolution and Human Behavior*.

Fox, E., Griggs, L. and Mouchlianitis, E. (2007). The detection of fear-relevant stimuli: Are guns noticed as quickly as snakes? *Emotion* **7**, 691-696.

Frazer, J. G. (1890/ 1992/ 1959). *The new golden bough: A study in magic and religion*. New York, NY: Macmillan.

Fumagalli, M., Sironi, M., Pozzoli, U., Ferrer-Admettla, A., Pattini, L. and Nielsen, R. (2011). Signatures of environmental genetic adaptation pinpoint pathogens as the main selective pressure through human evolution. *PLoS Genetics* **7**, e1002355.

Gangestad, S. W. and Simpson, J. A. (2000). The evolution of human mating: Trade-offs and strategic pluralism. *Behavioral and Brain Sciences* **23**, 573-587.

Gao, T., McCarthy, G. and Scholl, B. J. (2010). The Wolfpack effect: Perception of animacy irresistibly influences interactive behavior. *Psychological Science* **21**, 1845-1853.

Garcia, J. and Koelling, R. A. (1966). Relation of cue to consequence in avoidance learning. *Psychonomic Science* **4**, 123-124.

Garner, S. R. and Howe, M. L. (2014). False memories from survival processing make better primes for problem-solving. *Memory* **22**, 9-18.

Garza, R., Heredia, R. R. and Cieslicka, A. B. (2016). Male and female perception of physical attractiveness: An eye movement study. *Evolutionary Psychology* **14**.

Gould, S. J. and 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.

Greenstein, M., Franklin, N., Martins, M., Sewack, C. and Meier, M. A. (2016). When anticipation beats accuracy: Threat alters memory for dynamic scenes. *Memory & Cognition* **44**, 633-649.

Hagen, T. and Laeng, B. (2016). The change detection advantage for animals: An effect of ancestral priorities or progeny of experimental design? *i-Perception* **7**.

Hassabis, D. and Maguire, E. A. (2007). Deconstructing episodic memory with construction. *Trends in cognitive sciences* **11**, 299-306.

Heider, F. and Simmel, M. (1944). An experimental study of apparent behavior. *The American Journal of Psychology* **57**, 243-259.

Hirst, W., Phelps, E. A., Meksin, R., Vaidya, C. J., Johnson, M. K., Mitchell, K. J., . . . Olsson, A. (2015). A ten-year follow-up of a study of memory for the attack of September 11, 2001: Flashbulb memories and memories for flashbulb events. *Journal of Experimental Psychology: General* **144**, 604-623.

Horgan, T. G., Broadbent, J., McKibbin, W. F. and Duehring, A. J. (2016). Show versus tell? The effects of mating context on women's memory for a man's physical features and verbal statements. *Journal of Social and Personal Relationships* **33**, 733-750.

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

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

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

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 & Cognition* **41**, 49-59.

Klein, S. B., Cosmides, L., Tooby, J. and Chance, S. (2002). Decisions and the evolution of memory: Multiple systems, multiple functions. *Psychological Review* **109**, 306-329.

Klein, S. B., Loftus, J. and 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.

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.

Krause, M. A. (2015a). Adaptive memory in humans from a comparative perspective. *International Journal of Comparative Psychology* **28**.

Krause, M. A. (2015b). Evolutionary perspectives on learning: Conceptual and methodological issues in the study of adaptive specializations. *Animal Cognition* **18**, 807-820.

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. and Makerud, S. E. (2016). The effects of item material on encoding strategies: Survival processing compared to the method of loci. *The Quarterly Journal of Experimental Psychology*, 1-13.

Kroneisen, M., Rummel, J. and Erdfelder, E. (2016). What kind of processing is survival processing? *Memory & Cognition*, 1-16.

Lang, P. J., Bradley, M. M. and Cuthbert, B. N. (1999). International affective picture system (IAPS): Technical manual and affective ratings. *Gainesville, FL: The Center for Research in Psychophysiology, University of Florida*.

Lassek, W. D. and Gaulin, S. J. C. (2016). What makes Jessica Rabbit sexy? Contrasting roles of waist and hip size. *Evolutionary Psychology* **14**.

Li, P., Jia, X., Li, X. and Li, W. (2016). The effect of animacy on metamemory. *Memory & Cognition* **44**, 696-705.

Marzi, T. and Viggiano, M. P. (2010). When memory meets beauty: Insights from event-related potentials. *Biological Psychology* **84**, 192-205.

Mauss, M. (1902/ 1972). *A general theory of magic*. New York, NY: Norton.

Miller, G. (2001). The mating mind: How sexual choice shaped the evolution of human nature. New York, NY: Anchor Books.

Miller, G. F. and Todd, P. M. (1998). Mate choice turns cognitive. *Trends in cognitive sciences* **2**, 190-198.

Mobbs, D., Hagan, C. C., Dalgleish, T., Silston, B. and Prévost, C. (2015). The ecology of human fear: Survival optimization and the nervous system. *Frontiers in neuroscience* **9**, 55.

Morales, A. C. and Fitzsimons, G. J. (2007). Product contagion: Changing consumer evaluations through physical contact with “disgusting” products. *Journal of Marketing Research* **44**, 272-283.

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.

Nairne, J. S. (2015). Adaptive memory: Novel findings acquired through forward engineering. In D. S. Lindsay, C. M. Kelley, A. P. Yonelinas & H. L. Roediger (Eds.), *Remembering: Attributions, processes, and control in human memory: Papers in honor of Larry L. Jacoby*. pp. 3-14. New York, NY: Psychology Press.

Nairne, J. S. (2016). Adaptive memory: Fitness-relevant “tunings” help drive learning and remembering. In D. C. Geary & D. B. Berch (Eds.), *Evolutionary Perspectives on Child Development and Education*. pp. 251-269: Springer International Publishing.

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. *The 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. and Pandeirada, J. N. S. (2016). Adaptive memory: The evolutionary significance of survival processing. *Perspectives on Psychological Science* **11**, 496-511.

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., VanArsdall, J. E., Pandeirada, J. N. S., Cogdill, M. and LeBreton, J. M. (2013). Adaptive Memory: The mnemonic value of animacy. *Psychological Science* **24**, 2099-2105.

Neuberg, S. L., Kenrick, D. T. and Schaller, M. (2011). Human threat management systems: Self-protection and disease avoidance. *Neuroscience & Biobehavioral Reviews* **35**, 1042-1051.

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

Oaten, M., Stevenson, R. J. and Case, T. I. (2009). Disgust as a disease-avoidance mechanism. *Psychological Bulletin* **135**, 303-321.

Öhman, A. and Mineka, S. (2003). The malicious serpent: Snakes as a prototypical stimulus for an evolved module of fear. *Current Directions in Psychological Science* **12**, 5-9.

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.

Open Science Collaboration (2015). Estimating the reproducibility of psychological science. *Science* **349**, 943.

Opfer, J. E. and Gelman, S. A. (2011). Development of the animate-inanimate distinction. In U. Goswami (Ed.), *The Wiley-Blackwell handbook of childhood cognitive development.*2 ed., pp. 213-238. Oxford: Wiley-Blackwell.

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

Pandeirada, J. N. S., Fernandes, N. L., Nairne, J. S., Marinho, P. I. and Vasconcelos, M. (2015). *Better recognition memory for faces when looking for a long-term partner.* Paper presented at the 56th Annual Meeting of the Psychonomic Society, Chicago, USA.

Pandeirada, J. N. S., Fernandes, N. L., Nairne, J. S., Marinho, P. I. and Vasconcelos, M. (2016). *Enhnaced recognition memory for faces of potential mates.* Paper presented at the Annual Meeting of the Portuguese Association of Experimental Psychology, Lisbon, Portugal.

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.

Parham, P. (2014). *The immune system* (4th edn.). New York, NY: Garland Science.

Petrie, M. and Halliday, T. (1994). Experimental and natural changes in the peacock's (Pavo cristatus) train can affect mating success. *Behavioral Ecology and Sociobiology* **35**, 213-217.

Popp, E. Y. and Serra, M. J. (2016). Adaptive memory: Animacy enhances free recall but impairs cued recall. *Journal of Experimental Psychology: Learning, Memory, and Cognition* **42**, 186-201.

Pratt, J., Radulescu, P. V., Guo, R. M. and Abrams, R. A. (2010). It's Alive! Animate motion captures visual attention. *Psychological Science* **21**, 1724-1730.

Prokosch, M. D., Coss, R. G., Scheib, J. E. and Blozis, S. A. (2009). Intelligence and mate choice: Intelligent men are always appealing. *Evolution and Human Behavior* **30**, 11-20.

Raby, C. R. and Clayton, N. S. (2012). Episodic memory and planning. In J. Vonk & T. K. Shackelford (Eds.), *The Oxford handbook of comparative evolutionary psychology*. New York, NY: Oxford University Press.

Rantala, M. J., Coetzee, V., Moore, F. R., Skrinda, I., Kecko, S., Krama, T., . . . Krams, I. (2013). Facial attractiveness is related to women's cortisol and body fat, but not with immune responsiveness. *Biology Letters* **9**, 20130255.

Rantala, M. J., Moore, F. R., Skrinda, I., Krama, T., Kivleniece, I., Kecko, S. and Krams, I. (2012). Evidence for the stress-linked immunocompetence handicap hypothesis in humans. *Nature Communications* **3**, 694.

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.

Richardson, R. C. (2007). *Evolutionary psychology as maladapted psychology*. Cambridge, MA: MIT press.

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.

Rozin, P. and Fallon, A. E. (1987). A perspective on disgust. *Psychological Review* **94**, 23-41.

Rozin, P., Haidt, J. and McCauley, C. (2008). Disgust. In M. Lewis, J. M. Haviland-Jones & L. F. Barrett (Eds.), *Handbook of emotions*.3 ed., pp. 757-776. New York, NY: Guilford Press.

Rozin, P., Millman, L. and Nemeroff, C. (1986). Operation of the laws of sympathetic magic in disgust and other domains. *Journal of Personality and Social Psychology* **50**, 703-712.

Rozin, P., Nemeroff, C., Wane, M. and Sherrod, A. (1989). Operation of the sympathetic magical law of contagion in interpersonal attitudes among Americans. *Bulletin of the Psychonomic Society* **27**, 367-370.

Rubin, D. C. (1995). *Memory in oral traditions: The cognitive psychology of epic, ballads, and counting-out rhymes*. New York, NY: Oxford University Press.

Sakaki, M., Niki, K. and Mather, M. (2012). Beyond arousal and valence: The importance of the biological versus social relevance of emotional stimuli. *Cognitive, Affective, & Behavioral Neuroscience* **12**, 115-139.

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. (2011). Survival processing of faces. *Memory & Cognition* **39**, 1359-1373.

Schacter, D. L. and 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**, 773-786.

Schaller, M. (2006). Parasites, behavioral defenses, and the social psychological mechanisms through which cultures are evoked. *Psychological Inquiry* **17**, 96-137.

Schaller, M. and Duncan, L. A. (2007). The behavioral immune system: Its evolution and social psychological implications. In J. P. Forgas, M. G. Haselton & W. von Hippel (Eds.), *Evolution and the social mind: Evolutionary psychology and social cognition*. pp. 293-307. New York, NY: Psychology Press.

Schaller, M. and Park, J. H. (2011). The behavioral immune system (and why it matters). *Current Directions in Psychological Science* **20**, 99-103.

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

Shepherd, J. W. and Ellis, H. D. (1973). The effect of attractiveness on recognition memory for faces. *The American Journal of Psychology* **86**, 627-633.

Shettleworth, S. J. (2010). *Cognition, evolution, and behavior*. New York, NY: Oxford University Press.

Silverstein, M. (1976). Hierarchy of features and ergativity. In R. Dixon (Ed.), *Grammatical categories in Australian languages.*, pp. 163-232: Australian Institute of Aboriginal Studies.

Singh, D. (2002). Female mate value at a glance: Relationship of waist-to-hip ratio to health, fecundity and attractiveness. *Neuro endocrinology letters* **23, Suppl 4**, 81-91.

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

Smith, D. S., Jones, B. C. and Allan, K. (2013). Socio-sexuality and episodic memory function in women: Further evidence of an adaptive "mating mode". *Memory & Cognition* **41**, 850-861.

Smith, D. S., Jones, B. C., Feinberg, D. R. and Allan, K. (2011). A modulatory effect of male voice pitch on long-term memory in women: Evidence of adaptation for mate choice? *Memory and Cognition* **40**, 135-144.

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

Streeter, S. A. and McBurney, D. H. (2003). Waist–hip ratio and attractiveness: New evidence and a critique of "a critical test". *Evolution and Human Behavior* **24**, 88-98.

Stubbersfield, J. M., Tehrani, J. J. and Flynn, E. G. (2015). Serial killers, spiders and cybersex: Social and survival information bias in the transmission of urban legends. *British Journal of Psychology* **106**, 288-307.

Szpunar, K. K., Watson, J. M. and McDermott, K. B. (2007). Neural substrates of envisioning the future. *PNAS Proceedings of the National Academy of Sciences of the United States of America* **104**, 642-647.

Thornhill, R. and Gangestad, S. W. (1999). Facial attractiveness. *Trends in cognitive sciences* **3**, 452-460.

Tooby, J. (1982). Pathogens, polymorphism, and the evolution of sex. *Journal of Theoretical Biology* **97**, 557-576.

Tsukiura, T. and Cabeza, R. (2011). Remembering beauty: Roles of orbitofrontal and hippocampal regions in successful memory encoding of attractive faces. *Neuroimage* **54**, 653-660.

Tulving, E. (1985). Memory and Consciousness? *Canadian Psychologist* **26**, 1-12.

Tulving, E. and Thomson, D. M. (1973). Encoding specificity and retrieval processes in episodic memory. *Psychological Review* **80**, 352-373.

Tybur, J. M. and Gangestad, S. W. (2011). Mate preferences and infectious disease: Theoretical considerations and evidence in humans. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366**, 3375-3388.

Tybur, J. M., Lieberman, D. and Griskevicius, V. (2009). Microbes, mating, and morality: Individual differences in three functional domains of disgust. *Journal of Personality and Social Psychology* **97**, 103-122.

Tybur, J. M., Lieberman, D., Kurzban, R. and DiScioli, P. (2013). Disgust: Evolved function and structure. *Psychological Review* **120**, 65– 84.

Tylor, E. B. (1871/ 1974). *Primitive culture: Researches into the development of mythology, philosophy, religion, art, and custom*. New York, NY: Gordan Press.

van Hooff, J. C., Devue, C., Vieweg, P. E. and Theeuwes, J. (2013). Disgust-and not fear-evoking images hold our attention. *Acta Psychologica* **143**, 1-6.

VanArsdall, J. E. (2016). *Exploring animacy as a mnemonic dimension.* (PhD Thesis), Purdue University.

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.

VanArsdall, J. E., Nairne, J. S., Pandeirada, J. N. S. and Cogdill, M. (2015). Adaptive memory: Animacy effects persist in paired-associate learning. *Memory* **23**, 657-663.

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

White, K., Lin, L., Dahl, D. W. and Ritchie, R. J. B. (2016). When do consumers avoid imperfections? Superficial packaging damage as a contamination cue. *Journal of Marketing Research* **53**, 110-123.

Wilson, S. (2016). Divergent thinking in the grasslands: Thinking about object function in the context of a grassland survival scenario elicits more alternate uses than control scenarios. *Journal of Cognitive Psychology* **28**, 618-630.

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

Woody, E. Z. and Szechtman, H. (2011). Adaptation to potential threat: The evolution, neurobiology, and psychopathology of the security motivation system. *Neuroscience & Biobehavioral Reviews* **35**, 1019-1033.

Xiao, X., Dong, Q., Chen, C. and Xue, G. (2016). Neural pattern similarity underlies the mnemonic advantages for living words. *Cortex* **79**, 99-111.

Yang, L., Lau, K. P. L. and Truong, L. (2014). The survival effect in memory: does it hold into old age and non-ancestral scenarios? *PLoS ONE* **9**, e95792.

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.