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Adaptive Memory in Humans from a Comparative Perspective

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Testing hypotheses about evolved psychological adaptations is the purview of human evolutionary psychology (HEP). A basic tenet of HEP is that the brain is comprised of specialized modules that evolved in response to selection pressures present in ancestral environments, and these modules support domain specific behavioral and cognitive processes that promoted survival and reproductive fitness during human evolutionary history. One set of cognitive domains involves learning and memory, and HEP has attempted to account for how evolutionary processes have shaped the design features supporting how humans acquire, store and retrieve information. Similarly, comparative psychology recognizes that cognitive traits of humans and animals are specialized to meet specific environmental challenges. However, these specializations are not regarded as species-specific, but rather reflect either adaptive modifications of general memory processes (e.g., episodic), or are processes that support a specific type of learning (e.g., taste aversions, imprinting, song learning). These alternatives to HEP emphasize the presence of quantitative rather than qualitative differences in learning and memory abilities. The goal of this paper is to examine these contrasting approaches of HEP and comparative psychology, and, using the survival processing effect (Nairne, Thompson, & Pandeirada, 2007, 2008) as an example, evaluate the plausibility of domain-specific adaptive hypotheses of human memory.

Adaptive Memory in Humans from a Comparative Perspective

Comparative and experimental psychologists have described numerous ways in which evolution has likely influenced cognitive processes in a diversity of species (Shettleworth, 2009). Decades of research has revealed that animal learning and memory can evolve in specialized ways, though there does not appear to be a distinct type of learning or memory process that is unique to a particular nonhuman species. Rather, adaptive variation in learning and memory abilities among species arises through selection pressures encountered in different ecological circumstances. For example, complex episodic-like and spatial memory abilities are found in many scatter hoarding species (Feeney & Roberts, 2012), and primates that have a history of geographic overlap with venomous snakes show enhanced perceptual sensitivity and fear acquisition toward this particular stimulus more readily than do species with less historical overlap with snakes (Isbell, 2006; Ohman & Mineka, 2001; Van Le et al.,

2013). In addition to adaptive variation among species, convergence among distantly related species, or parallel evolution among closely related ones further accounts for the role of evolution in adaptive variation in learning, memory, and other complex cognitive abilities (Emery & Clayton, 2004; Marino 2002).

Similar to comparative psychologists, human evolutionary psychologists hypothesize that learning and memory processes reflect adaptive specializations. However, the two disciplines have differing perspectives on how to test hypotheses about behavioral adaptations. In HEP hypotheses are often based on evolutionary scenarios placed within a time period post-dating the lineage split between hominids (humans and extinct relatives) and pongids (great apes). This approach restricts the focus to explaining possibly unique derived psychological adaptations to a relatively narrow temporal and environmental space. Also, HEP espouses the functionalist hypothesis that the human brain is comprised of adaptations that evolved via natural selection to solve problems encountered by our ancestors. These cognitive adaptations consist of domain-specific modules of the brain that support processes such as perception, reasoning, decision making, mating, and learning and memory. Domain-specific adaptive modules possess design features that are (1) universal to our species, (2) structurally and functionally complex, (3) efficient, (4) solve a specific problem related to survival and reproduction, and (5) are visible to the effects of natural selection (Schmitt & Pilcher 2004). For extensive discussion on applying adaptationist thinking to human behavior see Andrews, Gangestad, and Matthews (2002), Buss, Haselton, Shakelford, Bleske, and Wakefield (1998), Confer et al. (2010), Cosmides and Tooby (2013), and Schmitt and Pilcher (2004). An illustrative example of an adaptationist approach to human memory can be found in literature dealing with a specific aspect of episodic memory.

The Survival Processing Effect

Numerous investigators have reported a mnemonic advantage for processing information that is relevant to survival and fitness (Nairne et al., 2007; Schwartz, Howe, Toggia, & Otgaar, 2014). In these experiments, a key experimental condition requires participants to read a passage depicting a harsh, grassland environment representative of conditions present during the Pleistocene epoch (1.8 million to 10,000 years ago) and a significant phase of human evolution (see Table 1). After reading the passage, words are rated for their relevance to surviving in this setting, and following a delay during which a distraction task is completed, the participants are given a surprise memory test for the previously rated words. The survival processing effect (SPE) is the term given to describe superior memory performance in the survival scenario relative to control conditions, which include scenarios of challenging modern tasks (e.g., moving to a foreign city) and word pleasantness ratings (Nairne et al., 2007; Schwartz et al., 2014).

Table 1
Sample Scenarios from Adaptive Memory Experiments

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

Moving scenario: 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. Some of the words may be relevant and others may not—it's up to you to decide.

Pleasantness ratings: 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. Some of the words may be pleasant and others may not—it's up to you to decide.

Note. After reading a scenario, subjects first rate the relevance of different words (e.g., blood, weapon, rose) presented on a screen, then complete a distractor task, and are finally given a surprise memory test that includes the previously rated words. The scenarios in this table are identical to those in Nairne et al., 2007.

The ultimate-level explanation of the SPE is that historical selective pressures favored those who were better able to remember survival relevant information. Many investigators have replicated and conducted follow-up studies of Nairne and colleagues' work to better understand the proximate factors that might

Table 2

Potential Proximate Mechanisms Mediating the Survival Processing Effect (SPE, based on Erdfelder & Kroneiser, 2014)

Proximate Mechanism	Description and Prediction	Mediates SPE?	Citations
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survival module	a specialized cognitive process giving mnemonic advantage to information relevant to survival in ancestral conditions	Mixed	Nairne et al., 2007; Soderstrom & McCabe, 2011; Otgaar & Smeets, 2010
media exposure	previous experience with survival scenario	No	Kang, McDermott, & Cohen, 2008
arousal/valence	self-rated arousal and valence in response to	Mixed	Soderstrom & McCabe, 2011; Otgaar & Smeets, 2010
physiological stress	induced stress and/or cortisol release enhances	No	Smeets, Otgaar, Raymaekers, & Smeets, 2010
planning	future tense perspective improves memory for all words (regardless of scenario)	Mixed	Klein, Robertson, & Delton 2010, 2011; Kang et al., 2008
schema related encoding	distinctiveness of script associated with survival scenario, relative to other scenarios presented, enhances retention	Mixed	Weinstein, Bugg, & Roediger, 2008; Howe & Derbish, 2010
word congruity	relationships among words in survival scenario are more consistent/compatible than in other scenarios	Mixed	Butler, Kang, & Roediger, 2009; Nairne & Pandeirada, 2011
self-referential processing	the survival scenario requires one to process information in reference to the self, which enhances retention	Mixed	Klein, 2012
richness of encoding	The elaborative and distinctive encoding that occurs in the survival scenario enhances retention	Yes	Kroneisen & Erdfelder, 2011; Kroneisen, Erdfelder, & Buchner, 2013
single-item and relational processing	survival scenario is superior because words are processed as both single items, as well as in terms of their interrelatedness. control tasks only involve single-item processing	Mixed	Nairne & Pandeirada, 2008a; Burns et al., 2011
interactive imagery	imagining how items in survival scenario are related and interact improves retention (e.g., stones)	No	Kroneisen et al., 2013
gist processing	words for survival scenario are better remembered because they comprise a common theme and are thus easy to link together	Mixed	Howe & Derbish, 2010; Erdfelder & Kroneisen, 2014; Nairne et al., 2007

Note. Yes = results testing this mechanism show superior memory for survival relevant words compared with control conditions/scenarios. No = results testing this mechanism show no differences. Mixed = some studies confirm and others do not confirm, either directly or indirectly, the hypothesized mechanism for the SPE.

determine why memory for the survival scenario is superior to comparison and control conditions (see Schwartz et al., 2014). For example, perhaps the survival scenario elicits greater physiological arousal than do contemporary scenarios, and therefore facilitates memory consolidation processes. Or, the ancestral survival scenario cues subjects to think about how stimuli are interrelated to each other, which could also explain why they are better remembered than are items from comparison scenarios and control conditions. Erdfelder and Kroneisen (2014) review whether these and several other possible mechanisms, including affective (stress, arousal), structural (modular) and process (encoding richness, congruity) explanations account for the SPE. Table 2 summarizes these purported mechanisms, what they predict about the SPE, and provides a general summary about relevant study results and key citations. This is not intended to be an exhaustive list of work in this area, but rather to illustrate the diversity of ways in which the SPE is conceived, the large number of purported

mechanisms accounting for it, and whether they mediate the SPE (See Erdfelder & Kroneiser, 2014 for elaboration and discussion)

Based on the information presented in Table 2 there are at least eight candidate mechanisms contributing to this small but significant memory advantage. One possible conclusion is that an adaptive interpretation of the SPE is unnecessary because normal phenomena that generally explain variance in declarative memory performance account for why more words in the survival condition are remembered. For example, if the survival scenario is simply encoded at a richer level than are others scenarios, or the planning mindset that the scenario prompts leads to greater memory performance, then the adaptive specialization hypothesis does not necessarily add anything to what could be accounted for by general processes of declarative memory.

Another issue that is germane to this debate but sparsely addressed in the literature summarized in Table 2 concerns the ecological validity of the SPE, specifically how natural selection could account for such a narrow aspect of memory performance, and whether it is just one of many facets of an evolved episodic memory system.

Although many have replicated the SPE, whether it can be traced to actual (and not speculated) survival advantages in ancestral humans would need further exploration. Also, whether the SPE is a cognitive holdover from a stone-age brain depends on how people with stone-aged brains actually behaved in ancestral environments. Either possibility presents a rather challenging, if not intractable, problem common to evolutionary hypotheses – particularly ones about behavioral traits. Because it is not feasible to correlate variance in the SPE with reproductive success, and observing human memory in a hypothesized ancestral environment is not possible, a comparative approach could serve to help advance our understanding of the evolution of the episodic memory system of which the SPE is a component.

Comparative Approaches to Adaptive Episodic Memory

A distinctive property of episodic memories is that they, at very least, bind structural, temporal and spatial dimensions of events (the “what”, “when” and “where”). Comparative studies reveal evidence for these memory components in scrub jays (Clayton & Dickinson, 1998; Raby, Alexis, Dickinson, & Clayton, 2007), rats (Crystal, 2012; Eichenbaum, Fortin, & Ergorul, , 2005), primates (Schwartz & Evans, 2001), black-capped chickadees (Feeney, Roberts, & Sherry, 2009), magpies (Zinkivskay, Nazir, & Mulders, 2009), dogs (Kaminksi, Fischer, & Call, 2008), and many other species (see Clayton, Bussey, & Dickinson, 2003; Roberts, 2012; Templer & Hampton, 2013; Zentall, 2013 for reviews). A more complex and perhaps speculative conceptualization of episodic memory is that it invokes conscious self-awareness and a subjective sense of how personal memories are relevant to the past, present and future (autonoetic consciousness, Tulving, 1985). Furthermore, episodic memory is linked with the capacity for mental time travel: The ability to retrieve and re-experience a past event and also to plan for potential future ones. This richer conceptualization is thought by some investigators to transcend the what/where/when properties of episodic memory and represents a qualitative difference between human and animal episodic memory (Suddendorf & Corballis, 1997, 2007). The Bischof-Kohler hypothesis asserts that animals orient to the future only insofar as doing so satisfies an immediate biological drive, and thus they do anticipate future motivational states. Debate over this

hypothesis continues in comparative psychology and is beyond the scope of the present paper. Regardless of how it is resolved, there is much empirical support that animals possess the what/when/where dimensions of episodic memory. Also, mental time travel, which would allow for planning to occur, is a capacity that is expressed in at least some form by several animal species that have been tested (Feeney & Roberts, 2012).

Although methodology and tasks differ vastly, work on episodic memory and mental time travel in animals can be integrated with work done on the SPE. Experiments by Klein and colleagues suggest that the SPE can be explained by the planning that it elicits (Klein, Robertson, & Delton, 2010, 2011; see Table 2). Klein et al. (2011) found that participants remembered about the same number of words when asked to rate their relevance to planning a dinner party as they did planning for survival needs in a savannah. In fact, memory for words associated with dinner party planning was superior to a savannah survival scenario in which subjects were not explicitly prompted to plan for the future, but rather simply rated the degree to which words were relevant to the scenario. The findings by Klein and colleagues do not preclude an evolutionary explanation for episodic memory, or even the SPE specifically. Indeed, Klein et al. (2002) hypothesize that planning for future contingencies is one of the key adaptive properties of episodic memory. There is a substantial literature supporting the hypothesis that memory for items or events that are relevant to future situations is superior to memory for past ones (Klein et al., 2010). Thus, human episodic memory may be adaptively specialized, but not in the highly domain-specific manner suggested by the SPE. Rather, episodic memory may be specialized for using past events of personal significance to predict important upcoming ones. For example, remembering details about the location and nature of a food source is evolutionarily relevant if that memory serves to bring future food resources. The planning (also referred to as mental time travel) as adaptive specialization hypothesis of episodic memory allows for integration of comparative findings because it does not commit to verbal tasks.

A growing body of research indicates that various nonhuman species can use current conditions to anticipate future ones - which can be interpreted as a form of planning. The anticipatory contrast paradigm was developed to test whether animals can learn to adjust their foraging decisions based on feeding experiences with foods of varying quality (Flaherty & Checke, 1982). The procedure tests whether animals can suppress feeding on a lower valued food at one time if they anticipate a more valued food source is forthcoming. Rats that received a high value 32% sucrose solution five minutes after receiving a less valued 0.15% saccharin solution subsequently avoided filling up on the saccharin and waited for the 32% sucrose, whereas control animals that did not receive the 32% sucrose in this arrangement consumed the 0.15% saccharin (Flaherty & Checke, 1982; Lucas, Gawley, & Timberlake, 1988). Work on rats using a transitive inference paradigm offers both behavioral and hippocampal evidence of episodic memory and anticipation of future reward (Eichenbaum & Fortin, 2009). Furthermore, comparative work suggests common evolutionary adaptive functions for declarative memory processes that are supported by homologous regions of the hippocampus and parahippocampal regions (Allen & Fortin, 2013).

The anticipatory contrast procedure has also been used in studies of episodic memory and mental time travel in birds. Birds are initially given a chance to forage on a food item such as sunflower seeds. Following this, half of the birds are given the chance to eat a higher value food item such as mealworms. If birds are able to predict

or anticipate when the preferred food item will be available they should, over repeated trials, learn to eat less of the non-preferred sunflower seeds and wait for mealworms. Black-capped chickadees learned to suppress eating sunflower seeds if mealworms were made available up to 30 minutes later in both laboratory cage environments as well as a naturalistic aviary that included foraging patches (Fenney, Roberts, & Sherry, 2011). Clayton and Dickinson (1998) report that scrub jays are sensitive to the relative perishability of different food items, and thus alter their foraging behavior to either maximize intake of preferred items that perish (wax worms) relative to less perishable food (peanuts), or to avoid wax worms and search for peanuts instead if too much time elapsed between caching and foraging. This and subsequent experiments demonstrate episodic-like memory abilities in scrub jays (Clayton et al, 2003). Another challenge to the Bischof-Kohler hypothesis are data showing that anticipation of food cache recovery in scrub jays is not driven by current motivational state and needs (Correia, Dickinson, & Clayton, 2007).

Primates show similar episodic memory and planning abilities reported in birds. Squirrel monkeys, *Saimiri sciureus* (but not rats) learned that choosing a smaller portion over a larger portion of food that induces thirst (dates) resulted in quicker return of a water source that had been previously removed. Furthermore, they reversed their preference when the contingency was altered such that choosing the larger portion of dates was rewarded with faster reintroduction of water (Naqshbandi & Roberts, 2006). Martin-Ordas, Haun, Colmenares, and Call (2010) used a similar procedure to Clayton and Dickinson (1998) to test for episodic memory in chimpanzees, bonobos, and orangutans. Subjects were offered a preferred but quickly perishable food (frozen juice) and grapes, which are less preferred but relatively less perishable. Food items were then hidden for either five minutes or one hour. If food became available after only five minutes some, but not all, apes chose the frozen juice, but if one hour elapsed they chose the grapes instead. A follow up experiment in which different food items were placed in two locations but at different times revealed that some animals remember when and where aspects of the events they observed. A different paradigm that also tests planning involves giving primates an opportunity to choose a tool that they can later use to access food. In these experiments only one of the possible tools to choose from will actually work to retrieve food (Mulcahy & Call, 2006). Relatedly, Osvath and Osvath (2008) report that chimpanzees and orangutans forego an immediate reward in exchange for a tool that can later be used to access a favored reward (see also Osvath & Persson, 2013). It should be noted that although associative accounts of these results have been addressed (Osvath, 2010), debate continues over whether these behavioral examples satisfy the richer, subjective properties thought to comprise the capacity for mental time travel (Suddendorf, Corballis, & Collier-Baker, 2009).

Domain-specificity and Phenotypic Variation in Episodic Memory

Comparative work suggests that episodic memory and mental time travel capacities are not domain-specific designs of human memory. However, the presence of these capacities in both humans and many nonhuman species does not alone warrant concluding that episodic memory is a general, all-purpose system for encoding and storing personally relevant events for later retrieval. Whether episodic memory is expressed and in what ways may reflect species-specific adaptations to different

ecological circumstances. So what selective pressures and ecological circumstances seem most critical for the evolution of this memory system?

Different mechanisms account for how episodic memory and mental time travel abilities are expressed. Distance-based cues involve an estimation of the elapsed time passed between event encoding and retrieval. In contrast, location-based cues involve estimating the age of individual memories using temporal cues that were present at the time of encoding (Friedman, 1993). Humans use both cues. Whether nonhuman species use either or both cues has been the subject of recent study. Rats default to using distance-based mechanisms in foraging decisions, whereas black-capped chickadees use both distance-based and location-based cues (see Feeney & Roberts, 2012 for discussion). Thus, species variation in phenotypic expression of mental time travel capacities may depend on ecological circumstances as well as species-specific biological constraints.

Experiments on tool-use and food choice in chimpanzees show some evidence of planning (Mulcahy & Call, 2006). Also, complex episodic memory abilities may be important to highly social primates. Remembering specific social interactions, the actors, and the outcome may be an important capacity for navigating life in a large social group. The critical binding feature of “when” important social interactions occurred may be less well-established, namely due to a lack of experimental control over their occurrence. However, in addition to tool-use and foraging situations, episodic memory processes may have become adaptively modified to navigate complex social dynamics among primates (Schwartz & Evans, 2001). Having a large brain and complex social structure is not even required for episodic memory-like capacities. Honeybees integrated where, what, and when information in a laboratory foraging task, in which circadian information was thought to be the key timing mechanism (Pahl, Zhu, Pix, Tautz, & Zhang, 2007).

The preponderance of comparative literature examining mental time travel capacities focuses on foraging, which leads to the hypothesis that episodic memory evolved so that animals could effectively store and retrieve food. Species-specific variation in strategies for food-caching are related to seasonal climate variation and the degree to which natural dietary items degrade. Thus, variation in episodic memory abilities among species may reflect unique foraging demands. However, animals that do store and retrieve their food show evidence of episodic memory and planning. Feeney and Roberts (2012) propose an adaptive niche hypothesis that does not commit to a specific behavioral system, such as foraging, to make predictions about adaptive variation in episodic memory and mental time travel. According to the adaptive niche hypothesis mental time-travel capacities could evolve where there are selective pressures affecting foraging decisions, brood parasitism, social behavior (e.g., complexity, size), and any other potential circumstances in which anticipating future outcomes could possibly be affected by natural selection.

The widespread phylogenetic distribution of episodic and episodic-like memory abilities in animals raises interesting questions about their evolutionary origins, and changes that have occurred over time and speciation events. One possibility is that the capacities that support episodic memory evolved once and have been adaptively modified (or are not expressed) depending on species-specific ecological circumstances. Alternatively, given the diversity of species showing episodic memory (or rudiments of

it) it is also quite possible that it evolved in parallel and convergent pathways in different lineages. Either scenario warrants further testing – hopefully using established phylogenetic comparative methods.

Conclusions

Evolution by natural selection is the most plausible mechanism accounting for the complexity of brain organization and function, and natural selection has resulted in both species similarities as well as diversification of behavioral and cognitive traits. Human evolutionary psychologists and comparative psychologists are likely in universal agreement over these statements. However, within HEP the focus on domain-specific adaptive specializations sometimes precludes attention given to relevant behaviors found in nonhuman species. The purpose of the present paper was to emphasize that comparative data place an upper limit upon the plausibility of highly domain-specific interpretations of a phenomenon like the SPE. Indeed, survival is of obvious evolutionary importance, and, therefore, any animal that has memory should show survival processing effects of some form. If a capacity such as planning is evident in episodic memory among both humans and nonhumans, and planning is an important proximate explanation of the SPE, then concluding that there is a highly specialized brain module uniquely evolved to support enhanced memory for survival relevant words may be unwarranted.

As shown in Table 2 there are proximate mechanisms in addition to planning that could account for the SPE. Further work is needed to sort out which of these best fit the data. It is possible that a combination of these mechanisms supports a uniquely human quality of episodic memory – one that requires a linguistic, verbal memory capacity not found in nonhuman species. Nairne and Pandeirada (2010) have carefully considered functionalist and general process interpretations of the SPE, but with a specific focus on what the effect tells us about the evolution of human memory. Parsimony suggests that the episodic memory and mental time travel capacities present in various species, expressed behaviorally rather than linguistically, accomplish the same goals inherent to the survival scenario from Table 1. A chimpanzee successfully choosing a tool it will later need to obtain food, and an undergraduate research participant remembering that the word *tool* appeared on a list previously encountered while planning to survive in a hypothetical ancestral environment, may both be expressing the same fundamental capacity. Formally testing whether this is the case would require (1) a task that both human and nonhuman primates could possibly complete, (2) manipulations that make the task relevant to survival processing and testing against a non-survival control condition(s), and (3) a scenario in which subjects would have to plan for a future contingency. Relatedly, Perdue, Beran, Williamson, Gonsiorowski, and Evans (2014) developed a common, non-linguistic procedure for testing prospective memory in children and chimpanzees, both of which successfully completed the task.

The SPE is thought to reflect an evolutionary “footprint” of a stone-age brain, revealing historical influences of natural selection on human memory (Nairne & Pandeirada, 2008b; Nairne, VanArsdall, Pandeirada, & Blunt, 2012). The common evolutionary psychological view that modern day human behavior reflects adaptive responses to ancestral environments experienced by the hominin lineage serves as a valuable guiding heuristic for hypothesis testing and for interpreting much of the data

collected in this area. However, this same view can lead to the omission of important comparative data that could be used to strengthen arguments for evolutionary cognitive adaptations. This is one of many examples revealing the value of integrating comparative and evolutionary psychology, and their continued cross-fertilization will likely yield rigor in the evolutionary analysis of both human and animal behavior (Vonk & Shakelford, 2012). The evolutionary footprints we see in the modern day expression of a stone-age brain may not belong to hominins, but rather reflect more phylogenetically ancient adaptations.

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