Proximate Mechanisms and the Development of Adaptive Memory

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Abstract

The scientific study into the functional properties of memory has recently undergone a rapid increase. These studies reveal that processing stimuli for its survival value results in superior memory performance in children and adults. In the current article, we critically evaluate this claim and conclude that survival-processing advantages in childhood and adulthood are not an indication that fitness-relevant information has adaptive priority. Instead, we argue that general memory principles (e.g., item-specific and relational processing, self-reference, elaboration and distinctiveness) are more probative explanations of the functional engineering of memory. We stress the importance of these memory processes because these are the processes that comprise our memory adaptation, are present early in life, and are developmentally invariant.

Keywords: Adaptive memory, Survival processing, elaboration, distinctiveness, item-specific processing, relational processing

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Information processed for its importance to survival is remembered better than that same information processed in other contexts (Nairne, 2010; Otgaar, Smeets, & van Bergen, 2010). Not only does *survival processing* accrue mnemonic benefits, but *survival information* itself enjoys similar advantages (Howe & Derbish, 2010; see Table 1). These benefits are thought to arise because human (and perhaps some nonhuman animal) memory systems have evolved to prioritize survival-related information over other information due to its greater adaptive significance.

Although survival-related effects are well documented in adults, questions remain about the importance of the discovery that survival-processing effects appear early in ontogeny (Aslan & Bauml, 2012; Otgaar, Howe, Smeets, & Garner, 2012; Otgaar & Smeets, 2010; see Table 2). This question is important to theories of adaptive memory[1] because many of the adaptive behaviors we see in adults, ones that have arisen through ancestral selection pressures, can and should be found in children (Bjorklund & Pelligrini, 2000; Volk & Atkinson, 2008). Indeed, for some, a particularly critical test of the adaptive nature of a specific behavior can be found in whether it is present in younger members of the species[2].

However appealing this idea may seem, we argue that the answer to ontological questions concerning the beginnings of fitness-relevant mnemonic advantages are not important to theories of adaptive memory per se. To be specific, we are only referring to the fitness-relevant functions of memory although similar arguments might apply to non-fitness-relevant aspects of children's memory that may also be adaptive (e.g., context dependent memory, infantile and childhood amnesia, suggestibility). Although questions concerning age-related changes in adaptive memory are important in the context of understanding memory development more generally, they are perhaps of limited value when determining the origins of adaptive memory. Indeed, that our memory system has been shaped by evolutionary pressure is not in question. Neither should there be a question about the adaptive functions associated with memory from very early in life (Howe, 2011). Thus, the questions answered by developmental investigations of adaptive memory are important to a complete theory of memory development but they do not settle issues concerning the priority of fitness-relevant information early in ontogeny.

Developmental Assumptions

Consider the assumption that biases that have evolved to retain survival-related information should already be present early in life. Although this may be true, it is equally plausible that adaptive behaviors do not emerge until later in development. Indeed, particular developmental events may have to occur prior to the appearance of an adaptive behavior (i.e., the expression of an adaptation may be *experience expectant* or *experience dependent*; Howe, 2011). Specifically, the expression of a fitness-relevant memory system may not occur until there has been sufficient experience with and knowledge of survival-relevant situations. Because developmental events may differ across individuals within as well as across cultures, fitness-relevant memory may not emerge at the same time in all children. Although we may all eventually exhibit an advantage for storing and retrieving fitness-relevant information, the ontogenetic course of the emergence of this adaptive memory effect may vary considerably.

Of course, to qualify as an adaptation, a characteristic must emerge at some point during an organism's life. However, this does not mean that adaptations need to be present early in life, as many emerge long after birth (Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998; Confer et al., 2010). Examples include bipedal locomotion (approximately one year after birth), language (during the second year of life), and secondary sex characteristics (during puberty). Indeed, it is frequently not until this latter development occurs that thoughts about sex emerge, something that is clearly relevant to adaptation, particularly reproductive behavior. Simply because thoughts about sex and the biological mechanisms necessary for reproduction do not emerge until puberty would not lead one to argue that these behaviors and thoughts are not adaptive.

To return to the memory issues at hand, what these examples illustrate is that the emergence of a behavior or characteristic, if it is adaptive, is guaranteed during the life of an organism. However, the timing of its emergence is not a defining feature of whether a particular behavior or characteristic is or is not adaptive. In terms of adaptive memory, and, more specifically survival processing, it is reasonable to assume that thoughts about, experiences with, or knowledge of survival only emerge later in life when adult hunter-gatherer ancestors would actually have needed to act on these survival-related cognitions. These cognitions might emerge even later in some of today's (Western) cultures given the rather extended periods of infancy and childhood that many people experience these days. From this perspective, the timing of the emergence of survival-processing effects in memory does not necessarily provide critical information about the adaptive nature or evolutionary origins of this form of mnemonic benefit[3].

Proximate Mechanisms and Developmental Invariance in Adaptive Memory

If these developmental survival-processing effects are not the result of the early emergence of fitness-relevant memory system, then what are they indicative of? Although we agree that our memory system is the result of evolutionary pressures, we argue that survival-processing effects can be explained within the context of an adaptive memory system whose proximate mechanisms are reasonably well documented (see Table 3). When examined in the context of proximate mechanisms, many of the important features turn out to be developmentally invariant. For example, distinctiveness effects (e.g., features that discriminate among stimuli) play an important role in memory from infancy (Rovee-Collier & Cuevas, 2009) onward (Howe, 2011, 2006a). Item (e.g., stimulus-specific features), relational (e.g., common features among stimuli), and self-referential processing (e.g., processing information relevant for the self; Ross et al., 2011) also appears to have an early emergence (Rovee-Collier & Cuevas, 2009; Symons & Johnson, 1997) in memory and have developmentally invariant characteristics across childhood (Howe, 2011, 2006a). Importantly, distinctiveness, item- and relational-processing, and self-referential processing are factors that underlie the survival-processing advantage and that contribute to the elaborate structure of traces that are best preserved in memory. Perhaps these are the adaptive tools of memory that were carved out throughout evolution that account for adaptive memory effects and not the storage of fitness-relevant information per se. Although much of survival- or fitness-relevant information is distinctive and well elaborated in memory, the mnemonic advantage of such information may simply be a byproduct of these more general memory principles. In what follows, we suggest that it is these types of processing, individually or combined, that can contribute to adaptive memory effects more generally, as well as those observed in children.

To explain, survival-processing tasks require participants to engage in both item-specific (e.g., encoding information about a specific predator such as it has large eyes and attacks at night) and relational (e.g., encoding information about how it is like other predators such it attacks from the sky and has large talons) processing. In contrast, the usual control processing tasks only require participants to engage in either one or the other type of processing but not both. Although each type of processing enhances retention, their combination has especially powerful effects on retention. Whereas relational processing enhances retention by providing an integrated structure to organize items within the memory trace, item-specific processing enhances the discriminability (distinctiveness) of items within the trace (Burns, 2006). These effects in tandem enhance the storage and retrieval of information, resulting in better memory performance in adults (Burns, 2006) and children (Howe 2006b). Indeed, survival tasks induce high levels of self-referential processing and this processing enhances memory performance.

The role of self-reference in the survival-processing effect has been addressed in previous research (Nairne & Pandeirada, 2010; Nairne, Pandeirada, Gregory, & van Arsdall, 2009; Nairne, Pandeirada, & Thompson, 2008). Some of this research showed that the survival processing advantage remained when directly compared to a self-reference condition. However, these tasks simply required participants to rate how easily a word brought to mind an important personal experience, an instruction that often fails to find a self-reference effect (Klein, in press; Klein, Loftus, & Burton, 1989). When participants are first asked to *retrieve* an episodic memory and then rate how easily the words bring to mind a personal experience, the survival processing effect is eliminated. Therefore, self-referential processing is an important contributor to the survival processing effect.

The idea that item-specific and relational processing might also underlie the survival processing advantage was examined in a series of experiments (Burns, Hwang, & Burns, 2011). When control tasks involved only a single processing type (item specific vs. relational), survival processing produced better memory performance. However, when the control task involved both types of processing, the survival memory task did not evince a mnemonic advantage. What this finding suggests is that both item-specific and relational processing might underlie the survival processing advantage.

Elaboration and distinctiveness effects have been found to account for survival processing effects in other experiments as well. If greater unusualness of the survival instruction equates to greater elaborative processing, then more relational processing should occur which should to superior memory performance. Indeed, many of the control scenarios (e.g., moving homes, going on a holiday) used in adaptive memory experiments tend to be more ordinary and familiar to participants than survival scenarios and there is a growing body of evidence that greater elaboration might contribute to the survival-processing effect. For example, when the richness (elaborateness) of encoding and item distinctiveness are comparable, performance differences between survival processing and control tasks disappear (Kroneisen & Erdfelder, 2011; Kroneisen, Erdfelder, & Buchner, in press). Similarly, when the degree of elaboration is equated across rating scenarios (regardless of whether these were high or low levels of elaboration), there is no performance advantage associated with survival processing (Howe & Derbish, in press). Specifically, when the survival scenario was compared with control scenarios that were unusual and ancestrally irrelevant (i.e., traveling to a foreign planet, exploring an underwater city), the typical memory superiority effect disappeared (Howe & Derbish, in press; Kostic, McFarlan, & Cleary, 2012). Indeed, memory performance in the standard survival scenario can be worse when compared to extremely unusual scenarios (i.e., being attacked by zombies in the city and grasslands; Soderstrom & McCabe, 2011). Overall, these studies show that at least part of the survival memory effect can be attributed to elaborate processing, independent of the ancestral relevance of the survival scenario. Indeed, the common feature among the ever increasing number of studies that have not found such a survival processing advantage is that they have all provided direct tests of well known, general memory factors that may have arisen because of evolutionary pressures on retention, ones that are correlated with the mnemonic demands imposed by requests to engage in survival processing (Seamon et al., 2012).

Together, these studies show that survival processing enhances memory over some other tasks because it recruits a powerful set of memory processes. These processes (item-specific and relational processing, self-referential processing, elaboration and distinctiveness) account for a whole host of memory phenomena including the advantages associated with processing fitness-relevant information. Indeed, "it is not the evolutionary significance of survival per se that explains the survival processing effect. Rather, the degree to which survival processing invites elaborative, distinctive forms of encoding would predict the mnemonic benefit of survival processing" [Kroneisen & Erdfleder, 2011, p. 1554]. Importantly, just because these effects are developmentally invariant (Howe, 2011, 2006a, 2006b), does not allow one to conclude that survival-processing advantages in childhood are an indication that fitness-relevant information has adaptive priority. Rather, what this shows is that the proximate mechanisms (item-specific and relational processing, self-referential, elaboration and distinctiveness) sculpted through evolution that comprise our memory adaptation are present early in life and are indeed, developmentally invariant.

The synopsis that we have presented so far has mainly centered on the concept of adaptive memory using the survival-processing paradigm. Of course, the evolutionary crafting of memory has also received scientific attention using other processes, paradigms, and perspectives (see Table 4). For example, faces that are experienced as untrustworthy are better remembered than faces perceived as trustworthy (Rule, Slepian, & Ambady, 2012), a finding that is related to the possibility of an evolved "cheater detection module" (Cosmides, 1989). Also, myriad studies show that face recognition is a highly unique ability that offers humans an obvious advantage in survival (Maguinnes & Newell, in press ; but see Savine, Scullin, & Roediger, 2011). Research has also shown that the increased rates of false memories that can occur in survival-processing tasks and with survival-related materials can have positive and adaptive consequences. Indeed, Howe, Garner, Charlesworth, and Knott (2011) showed that memory illusions were able to prime solutions on complex problem solving tasks in both children as adults. Overall, our stance is that adopting an evolutionary view of such findings has significant value, yet will benefit even more when considering that certain well studied memory principles are likely to underpin these effects.

Conclusion

We have critically evaluated claims that developmental studies of memory for fitness-relevant information provide a touchstone for evolutionary models of adaptive memory. Specifically, we have argued that the assumption that there exists a preference to store and process survival-related information early in life is not necessarily the whole story. In fact, there are many developmental outcomes that could be consistent with the assumption that our memory system has been shaped by evolutionary pressures and that no one outcome is diagnostic of this fact. Indeed, many adaptations emerge long after birth (e.g., language, secondary sex characteristics) and it is equally plausible that the mnemonic advantages associated with survival processing could occur later in life when individuals have had more experience with and knowledge of fitness-relevant behaviors and situations. We have argued that many of the mnemonic processes (item-specific and relational processing, self-referential, elaboration and distinctiveness) that have been found to account for performance in survival-processing tasks also provide a compelling explanation for the developmentally invariant advantages observed for fitness-relevant information in children's memory.

Finally, we have argued that the mnemonic advantage associated with survival processing may not lie in the adaptive significance of such processing, but in the fact that such processing recruits other well-known memory processes that enhance retention. Many of these processes occur relatively automatically and can be observed in numerous mnemonic situations regardless of age. It is undoubtedly true that our memory system is the outcome of evolutionary pressures, ones that have sculpted today's adaptive mnemonic processes. However, that a survival-processing advantage is a specific component of an adaptive memory system, one that is developmentally invariant, is not necessarily demanded by an evolutionary hypothesis. Indeed, developmental outcomes are agnostic on this issue. Perhaps a profitable focus of future scientific study into the functional properties of memory would be to identify the possible proximate mechanisms that play a role in adaptive memory generally, and survival-processing specifically. Although we have mentioned some of these variables, the identification of additional mechanisms operating throughout development will help us understand how our adaptive memory systems changes from childhood to adulthood.

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Recommended Reading

Howe, M. L. (2011). (See References). This book outlines an adaptive theory of memory and its development.

Klein, S. B. (in press). (See References). This chapter provides an excellent exegesis of the role of the self in planning and episodic future thought.

McCormack, T., & Atance, C. M. (2011). (See References). This article provides an excellent overview of the development of the planning aspects of adaptive memory.

Nairne, J. S. (2010). (See References). This article provides an excellent review of the theory and research on survival-processing effects and adaptive memory.

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Notes

[1]We use the term *adaptive memory* to refer to the general collection of tasks used to study fitness-relevant functions of memory. That is, this term is used to refer not just to survival-processing tasks (the primary focus of this article) or survival-relevant information, but also to other processes [e.g., self-referential processing (see Klein, in press; Ross, Anderson, & Campbell, 2011)] and tasks [e.g., episodic future thinking (see Atance & O'Neill, 2005)].

[2] As an example, the finding that priming rates in memory appear to be relatively constant across age in childhood has been used as evidence that implicit memory is an evolutionarily earlier, more primitive memory system than explicit memory (see Reber, 1989).

[3]Some would claim that the emergence of a survival-processing advantage in childhood is evidence that this is an adaptive memory advantage for fitness-relevant information. However, we argue that these findings simply show that the proximate mechanisms, ones that may be more likely to be engaged in survival-processing tasks or with survival-relevant information, are what emerge in childhood. Although these mechanisms may have some implicit fitness relevance (e.g., remembering a caregiver's face or voice may promote survival), the explicit fitness-relevant benefits may not be present until children have had more experience with, or knowledge about, survival-relevant situations.

Table 1. Survival Processing and Survival Information Effects

1. Survival processing effect: Participants are provided with a scenario, such as being stranded in the grasslands of a foreign land, and given the following instructions:

> "We would like you to imagine that you have been stranded in the grasslands of a foreign land. You are completely alone and have no supplies or basic survival materials, so over the next couple of weeks you will 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 them for how relevant each word would be for your survival in this scenario."

Participants are then presented with a list of concepts (e.g., items from categories such as fruit, vegetable, four-footed animals) and asked to rate each of them for their relevance to the survival scenario using a Likert Scale (where 1 = least relevant to 7 = most relevant).

A typical control condition might involve asking participants to rate these same words for pleasantness given the following instructions:

> "We are going to show you a list of words and we would like you to rate each word for how pleasant you find that word."

Where the pleasantness scale ranged from 1 (least pleasant) to 7 (most pleasant).

Alternatively, participants may be asked to rate these same items for their relevance to some other activity such as moving:

> "We want you to imagine you are in the process of moving house, but there is no one around to help you so you must arrange the move by yourself. While imagining this scenario, your job will be to rate the following words on a scale from 1-7 for how relevant the meaning of that word would be for you successfully moving house on your own."

After participants have rated the words, they receive a surprise recall or recognition test. Typically, memory for concepts is better when participants rate their relevance in a survival scenario (e.g., stranded in the grasslands of a foreign country) than when they rate them for pleasantness or engage in other forms of deep processing (e.g., moving to a new house).

2. Survival information effect: In addition to survival processing effects, survival-related concepts (e.g., *injury*, *death*, *struggled*, *virus*, *battle*) are also better remembered than more neutral concepts (e.g., *mountain*, *school*, *piano*, *tennis*, *quiet*) or even similarly valenced (negative) and arousing concepts (e.g., *sad*, *bad*, *fat*, *cry*, *anger*) (Howe & Derbish, 2010; Otgaar, Howe, Smeets, & Garner , 2012). That is, independent of whether these concepts are rated with respect to pleasantness, being stranded in the grasslands, or moving to a new house, survival-linked concepts are better remembered than negatively-valenced or neutral concepts.

Table 2. Experiments on Survival Memory Advantages in Childhood

1. Otgaar and Smeets (2010) were the first to address the question concerning the emergence of adaptive memory effects in childhood. Here, 8- and 11-year-olds were asked to rate concepts in a manner similar to that used with adults for their relevance to survival, moving, or pleasantness. Children evinced a similar survival recall advantage when rating words for their utility in a survival scenario as opposed to rating those same words in a moving scenario or for pleasantness. Further, a recent study by Otgaar, Howe, Smeets, and Garner (2012) even found that survival processing effects in children could be generalized to different stimuli (i.e., words and pictures) as well as different memory paradigms (i.e., intentional and incidental paradigms).
2. Aslan and Bauml (2012) used a modified survival-processing paradigm to contrast children's incidental recognition memory performance given either an earlier survival-processing task or an alternative, non-adaptive processing task.
   Experiment 1: Three age groups were tested, 4- to 6-year-olds, 7- to 8-year-olds, and 9- to 10-year-olds. The results showed the usual memory improvements with age, with older children outperforming younger children. More importantly, the findings indicated that regardless of age, items rated for survival were better recognized than items rated for pleasantness or word length.
   Experiment 2: Using the same three age groups, children rated items either for their relevance to survival or to two other scenarios that were designed to control for the use of schematic and self-referential processing. One of these scenarios had to do with staying overnight at a friend's house and the other, one that also controlled for valence, had to do with being forgotten at school/kindergarten. Like the first experiment, these results showed that older children remembered more than younger children and that regardless of age, children's incidental recognition performance was superior for items rated for survival.

Summary: Together, these experiments paint a consistent picture of children's incidental memory for items that have undergone survival-related processing. Indeed, these results would appear to provide ample support for the idea that the usual mnemonic advantages of processing information for its survival value appear very early (4 to 6 years of age) in children's recollection repertoire and remains important throughout memory development (9 to 10 years of age). Thus, it may not be unreasonable to conclude that adaptive memory is functional early in life and that our memory systems have been shaped by our ancestral past to be particularly sensitive or "tuned" to remember fitness-relevant information, even very early in childhood before we have had much experience with or knowledge of survival-related situations.

Table 3. Ultimate versus Proximate Explanations of Survival Processing

To properly understand behavior (e.g., survival processing advantage) in evolutionary terms, one should obtain both ultimate and proximate explanations (Scott-Phillips, Dickens, & West, 2011). Importantly, such explanations are said not to stand in opposition to each other. Rather, both levels of explanation can complement each other, providing a more complete understanding of the evolution of certain trait or behavior. Furthermore, in the present article, we propose that the ultimate explanation of adaptive memory (see below) can only be relevant for the scientific study in memory if one takes into account which proximate mechanisms mediate the survival processing effect.

Ultimate Explanations

Ultimate explanations are involved in *why* a certain trait or behavior evolved and which fitness consequences such a trait or behavior possesses. With respect to the survival processing advantage, Nairne et al. (2007) were the first to address the ultimate functional value of memory by asking why memory should show sensitivity to survival-relevant information. So the ultimate explanation concerning the evolutionary "necessity" of memory is that it is "prepared" to give priority to fitness-relevant information.

Proximate Explanations

Proximate explanations refer to understanding *how* a certain trait or behavior evolved and which mechanisms underpin that trait or behavior. In our article, we argue that the following proximate mechanisms might underlie the survival processing advantage: Elaboration (i.e., using related information, imagination, inflation to execute a certain task), relational processing (i.e., encoding of relationships among concepts or objects), item-specific processing (i.e., encoding of individual details about specific concepts and objects), and self-reference (i.e., encoding information relevant for the self). So, the proximate explanation relies on processes that have emerged to accomplish the evolutionary function of memory.

Table 4. Related Adaptive Memory Processes and Paradigms

1. Processes: Experiments on Stress
   Survival situations, such as being attacked by a vicious animal, are often accompanied by an increase in stress hormones. Therefore, it might seem that there is an obvious connection between survival processing and the experience of stress. Indeed, it might be the case that stress is also a proximate variable underlying the adaptive memory phenomenon. A recent examination of stress and survival processing found that each of these variables independently enhanced memory performance (Smeets, Otgaar, Raynaekers, Peters, & Merckelbach, 2012). It would seem that stress, at least as these experimenters operationalized it, does not serve as a proximate mechanism for the adaptive memory phenomenon.
2. Paradigms: Episodic Future Thought
   One of memory's adaptive functions is to help organisms navigate their future. That is, to plan for contingencies that may come about that could threaten survival. Such planning might include storage of food supplies, creating strategies for securing mates for reproduction, or trying out hypothetical alternative courses of action to solve problems. Interestingly, research on episodic future thought has found that many of the requirements for engaging in this behavior (e.g., projecting one's self into the future) are also available to young children (see McCormack & Atance, 2011).