RUNNING HEAD: Evolution and Adaptive Memory

What Kind of Memory has Evolution Wrought?

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Introductory Article for the Special Issue of *Memory*:
Adaptive Memory: The Emergence and Nature of Proximate Mechanisms
Edited by Mark L. Howe and Henry Otgaar

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Abstract
It is without question that our memory system evolved through a process of natural selection. However, basic research into the evolutionary foundations of memory has commenced with earnest only recently. This is quite peculiar as the majority, perhaps even all, of memory research relates to whether memory is adaptive or not. In this Special Issue, we have assembled a variety of papers that represent the cutting edge in research on the evolution of memory. These papers are centered on issues about the ultimate and proximate explanations of memory, the development of the adaptive functions of memory, as well as the positive consequences that arise from the current evolutionary form that our memory has taken. In this article we briefly outline these different areas and indicate why they are vital for a more complete theory of memory. Further, we argue that by adopting a more applied stance in the area of the evolution of memory, one of the many future directions in this field could be a new branch of psychology that addresses question in evolutionary legal psychology.

Keywords: Adaptive memory, Evolution, Proximate mechanisms, Ultimate mechanisms,

Memory and the law, Applications of memory

What Kind of Memory has Evolution Wrought?

That our memory system evolved through a process of natural selection is not in question. Indeed, all of the articles in this Special Issue of *Memory* take this as a given, a kind of starting point for each of their inquiries into the nature of the mechanisms that evolutionary pressures selected to produce what is today our memory. Rather, what the articles amassed in this Special Issue of *Memory* all attempt to address is the question posed in the title of this article and each of them does this in a very unique way. Before we provide a synopsis of these contributions, we outline the origins of this question and then provide a 21st century context for how memory researchers have examined this problem. Although the final word on what evolutionary pressures begat memory has yet to be written, we hope that this special issue brings us somewhat closer to understanding the proximate (and ultimate) mechanisms involved in a fitness-relevant memory system.

We begin with current speculation concerning the origins of today's memory system, a system that is said to have its beginnings some 500 million years ago during what is known as the Cambrian explosion (see Ginsburg & Jablonka, 2007a, 2007b, 2010b; Paivio, 2007). Before this, a more rudimentary form of memory existed, one that controlled short- and long-term sensitization and habituation (see Ginsburg & Jablonka, 2007a). However, during the Cambrian explosion, a memory system emerged, one that preserved newly learned associations (associative memory) in stable, long-term memory traces. A number of neurobiological evolutionary changes, including cephalization, contributed to this advance, ones that afforded the composition of better integrated and more durable memory traces (Eccles, 1989; Ginsburg & Jablonka, 2007b, 2010a). The evolution of associative memory, a system that binds together otherwise disparate pieces of information into unified and enduring traces, provided organisms that possessed it with at least three survival-related advantages that the earlier form of memory did not provide:

> First, the binding of stimuli, which at the previous stage of evolution (before associative learning had evolved) merely accompanied experiencing, becomes advantageous because it makes it possible to distinguish between complex (combined) stimuli. Second, learning-dependent experiencing allows recognition and discrimination on the basis of *partial cues*: for the hungry animal contingent associations (e.g., vibrations) may be recognized and elicit an adaptive response, food-seeking. Third, since for the food-deprived but already experienced [animal], food had become embodied, it gives the animal clues as to *what to do*, since some of the activated traces are associated with successful navigation towards the attractor-related stimuli (food, shelter and their contexts). The animal can now make an *educated guess*, based on past experience. (Ginsburg & Jablonka, 2010a, p. 114; emphases in original).

Thus, this newly evolved associative memory system provided animals with a memory system that could be utilized to store its past experiences, interpret current cues to satisfy its needs in the present, and to anticipate its future. In addition, some have argued that the emergence of associative memory, because it permits the mapping of past experiences onto future needs, may have been in part responsible for the emergence of self-consciousness (see Edelman, 1989, 2003). Although an in-depth discussion of this possibility is beyond the scope of this article, it does auger well for many of the proposed links between our memory system and other cognitive processes,

including anticipating the future and problem solving, issues raised in the various articles in this Special Issue.

Of course one of the problems with discussing the adaptive nature of memory today is that we do not have any physical (e.g., fossil) records of associative memory from the past. This ties our hands in terms of being able to trace its evolutionary history or examine the evolutionary pressures that led to its creation and change throughout time. What this means is that speculation concerning the adaptive nature of memory can lead us into a "just so" or "Panglossian" tautology. As Gould and Lewontin (1979) suggested, despite the existence of adaptations, it is difficult to know whether what you are studying is an adaptation unless you can trace its evolutionary heritage. That is, it is not clear which aspects of memory are the adaptations and which are "spin-offs" of those elements that are adaptations.

Although such weighty issues will not be resolved in this article or in the articles contained in this Special Issue, the articles presented in this issue will reveal fresh perspectives on how such weighty issues could be resolved some day. All of the papers show that our memory system does facilitate fitness-relevant behaviors, ones that can enhance our survival and reproductive fitness. One way to partially avoid the pitfalls of just-so stories is to make a distinction between ultimate and proximate explanations of a behavior (e.g., memory). Ultimate explanations answer the question of *why* a behavior evolved; in this case, why did memory evolve and what are its fitness consequences? Proximate explanations answer the question of *how* a behavior evolved; in this case, how the processes of memory accomplish the evolutionary function of memory? By asking these more pointed questions, we can attempt to address the more general questions about the adaptive nature of memory.

This is exactly what the articles contained in this special issue do. We can roughly divide these contributions into three types that are not independent and contain overlapping areas: (1) proximate and ultimate precursors of adaptive memory, (2) evolutionary developmental psychology, and (3) salutary consequences of memory. We will briefly deal with the contributions contained each of these areas.

Proximate and Ultimate Precursors of Adaptive Memory

The view that our memory is functionally designed has been adopted by many researchers (e.g., Anderson & Milson, 1989; Klein, Cosmides, Tooby, & Chance, 2002). However, only recently has the examination of the evolutionary "layers" of memory seen what appears to be an almost exponential increase in activity. This increase is probably due in large part to the novel research program introduced by Nairne and his colleagues (e.g., Nairne, Thompson, & Pandeirada, 2007). Their intention was to assess these evolutionary layers in an a priori manner by assuming that memory should be especially engineered to process information relevant for its fitness value.

In their first scientific undertaking, they had participants imagine being stranded on the grasslands of a foreign country, lacking any food and water and in potential danger from predators. Other participants were allocated to control conditions (e.g., imagining moving to another country, pleasantness ratings). Participants in all conditions were presented with a set of unrelated words that had to be rated for the relevance of the imagined scenario. When subsequently given a surprise memory test, participants who processed information in a survival-related situation evidenced enhanced memory performance above that seen in the other processing conditions. This effect, also known as the survival processing advantage, has been confirmed in a plethora of subsequent studies (for reviews see Howe & Otgaar, 2013; Nairne & Pandeirada, 2008).

Although boundary conditions have been demonstrated as well in the survival-processing paradigm (e.g., Howe & Derbish, 2010; Otgaar & Smeets, 2010; Savine, Skullin, & Roediger, 2010), a shift in this paradigm has recently been advocated, one that allows the detection of the proximate mechanisms behind this survival-processing advantage. This shift was needed because studies began to show that the survival processing advantage was eliminated under certain conditions (see Howe & Otgaar, 2013). As outlined above, the discovery of proximate mechanisms was imperative because they have the potential to show that survival processing *per se* is perhaps not so special after all and that many of these effects may have been mediated by a set of already well-known memory principles. Thus, although addressing ultimate explanations for the adaptive course of memory is vital, a new line of research has commenced, one that shows that the survival processing advantage might be better specified by relying on already well-documented proximate memory mechanisms.

In this Special Issue, we have followed this important line of research and hence, several papers are included that concentrate on the proximate explanations of adaptive memory. Although these explanations are not exhaustive, they do provide critical and novel perspectives on how we should view the evolutionary constraints of memory. The question that these papers do attempt to address is whether our memory is primarily tuned for the encoding, storage, and retrieval of survival-relevant material, narrowly defined, or whether part of the survival processing advantage also might be triggered by susceptibility to threat (paper by Olds and colleagues) or the anticipation of death (papers by Klein and by Burns and colleagues). As well, other papers in this section address questions concerning the longevity of the survival-processing advantage over testing delays (paper by Raymaekers and colleagues) and whether there exist working memory constraints on adaptive memory (paper by Kroneisen and colleagues). Together, these papers provide fresh insights into the proximate mechanisms associated with adaptive memory.

Evolutionary Developmental Psychology

As well as focusing on the underlying proximate mechanisms of adaptive memory, there is increasing interest in an examination of the developmental trajectories of fitness-relevant memory when explicating evolutionary-related behavior (Bjorklund & Pellegrini, 2000). Why this is an important issue becomes obvious when taking a look at the amount of evolutionary research in children and adults. Indeed, the majority of evolutionary theorizing and research is concentrated on reproductive success and social functioning in *adults* (e.g., Buss, 1995). This is partly due to the fact that the *sine qua non* of Darwinian theory is centered on the reproduction of adults. This absolute focus on evolutionary-related behavior in adults creates some disparities in the literature as, of course, individuals must learn to survive through infancy and childhood in order to get to the adult, reproductive stage. Therefore, one might expect that natural selection exerts significant pressure during childhood as it does throughout adulthood and that the consequences of this early pressure should be apparent when researchers take the time to examine them in infancy and childhood. Thus, it is not surprising that researchers have advocated a closer examination of this pressure early in life within the area of evolutionary developmental psychology (Bjorklund & Pellegrini, 2000).

According to Bjorklund and Pellegrini (2000, p. 1687), "[e]volutionary developmental psychology involves the expression of evolved, epigenetic programs in interaction with an individual's physical and social environment over the course of ontogeny." It is clear from this definition that this new brand of evolutionary psychology embraces both the emergence of new systems through development, also called epigenesis, together with the influence of the external

environment (Gottlieb, 1991). With respect to the adaptive nature of memory, this implies that one should be wary about solely focusing on adults, and that a complete picture will not emerge until scientists include the developmental context in which adaptive memory emerges in the individual.

In line with the evolutionary developmental psychological account, memory researchers have recently examined whether mnemonic superiority for fitness-relevant processing appears in childhood as well (Aslan & Bauml, 2012; Otgaar & Smeets, 2011). To put it simply, younger (4- to 8-year-olds) and older (9- to 11-year-olds) children also displayed a memory preference for fitness-relevant processing. The observation of these findings was crucial as one could suggest that the survival processing advantage is only adaptive if it showcases in childhood too. As we will explain below, the timing of this advantage does not say anything about its functional role. This idea is reflected in the concept of *ontogenetic adaptations*: neurobehavioral characteristics that exert specific adaptive effects in developing species (Oppenheim, 1981). Concretely, what this means is that certain adaptations can have a specific function for survival during infancy, but then vanish later in childhood.

Take, for example, the finding that the young of many species display certain special survival behaviors (e.g., sucking reflex) that disappear when no longer needed. Regarding the developmental course of adaptive memory, we have recently argued that the timing and emergence of the survival processing advantage in childhood does not indicate that our memory is adaptive (Howe & Otgaar, 2013). On the contrary, many adaptations emerge long after birth (Confer et al., 2010), including bipedal locomotion (approximately one year after birth) or language (during the second year of life). We have argued that well-known memory principles such as distinctiveness or elaboration effects are proximate mechanisms that are the cornerstone of the survival processing advantage. However, that they appear early in development and have developmentally invariant characteristics is merely coincidental and is not necessarily diagnostic of their adaptive value (Howe & Otgaar, 2013).

In this Special Issue, we follow the suggestion of Bjorklund and Pellegrini (2000) and have included several papers dealing with the development of adaptive memory in both non-human and human species (paper by Martin-Ordas and colleagues), children (papers by Atance and colleagues as well as Otgaar and colleagues), and younger and older adults (paper by Gerlach and colleagues). As will be shown, adaptive memory effects are evident across species and are evident in children as well as younger and older humans. These are the findings that will stimulate further research in the domain of evolutionary developmental psychology and will provide fundamental knowledge about the developmental paths of adaptive memory.

Salutary Consequences of Memory

It is without doubt that our memory has many positive consequences for adaptation. Without our memory, we would not, for example, be able to remember our partner, to drive, or to complete an exam. However, because memory is a reconstructive (as opposed to reproductive) system, some of our recollections can be illusory. These false memories or memories for events and details that were not experienced are especially hazardous when they appear in the legal arena (e.g., Otgaar, Howe, Peters, Sauerland, & Raymaekers, in press; Loftus, 2005). However, there are also a number of salutary or positive consequences to memory illusions (Howe, 2011; Schacter, Guerin, & St. Jacques, 2011). The question that is important here is whether these errors are by any chance advantageous or are they simply by-products of a flexible and reconstructive memory system?

One of the first indications that false memories are adaptive was delivered by research

showing that survival processing increased the formation of not just true memories but also the creation of false memories (Howe & Derbish, 2010). Furthermore, it was not just adults whose true and false memories increased, but so too did children's memories (Otgaar & Smeets, 2010). These findings eventually stimulated research into the positive consequences of false memories. For example, Howe and his colleagues (Howe, Garner, Charlesworth, & Knott, 2011; Howe, Garner, Dewhurst, & Ball, 2010) showed that false memories serve as effective primes when children and adults attempt to solve insight-based problems. That is, participants who were presented with lists of associatively-related words and remembered associatively-related but not-presented words were better at solving insight-based problems than child and adult participants who did not develop a false memory. These effects have recently been extended to more complex problem-solving tasks such as proportional analogical reasoning (Howe, Threadgold, Norbury, Garner, & Ball, in press). This Special Issue encompasses contributions that speak to this more positive side of memory errors (papers by Garner and Howe and by Gerlach and colleagues).

In addition to examining the positive side of false memories, there is research on how adaptive memory, more generally, has positive consequences that may not have been considered outside of this evolutionary context. For example, as mentioned, memory is used not just to remember the past, but also to interpret the present and anticipate the future. Indeed, this latter area, episodic future thought, has been an emerging area of interest for the past few years and this line of research is well represented in this Special Issue as well (paper by Atance and colleagues). Curiously, simulations of future events can also have negative consequences on memories for the past, distortions that Gerlach and colleagues term *adaptive constructive processes*.

The intent of these papers is to show that many facets of memory have beneficial and positive reconstructive consequences – that is, our survival and reproductive success may not necessarily be related to the *accuracy* of memory, but rather, on how well our memories (true or false) help us navigate the world we live in. Of course, it is not just the memories that are critical, but it is also how we view what we remember that is important. Indeed, humans rely to some extent on how confident they are in their memories, with higher confidence leading to perhaps more reliance on these memories. Of course, the link between confidence and reliance on memories may be a trickier one than first thought, and the adaptive consequences of this relationship is explored in the paper by Roediger and DeSoto. Together, all of these papers shed more light on the adaptive nature of our memory by exploiting the larger sphere of influence in which memory operates, including its effects on cognitive and metacognitive processes.

Concluding Remarks

A logical next step is to speculate on how the study of the evolution of memory could change. This is not easy because each new development herein should be critically evaluated because "just-so" explanations are constantly lurking in this area. One plausible direction would be to see which area of investigation would potentially benefit from findings regarding the evolutionary course of memory. This should be an area that could profit from both an ultimate and proximate explanation of memory.

Here, we suggest that one area for further exploration is in a more applied domain, specifically, in memory and the law. Much (or sometimes all) of the evidence brought into court relies on eyewitness evidence and thus focuses on memory performance. In court, it is not uncommon for legal professionals to ask questions pertaining to the ultimate (e.g., "Why do we have memory illusions?"; "Why do psychopaths lie?") or proximate (e.g., "How do such memory illusions develop?"; "How do people lie?") explanations of memory performance. What we should keep in mind in this exercise is that asking ultimate and proximate questions in court

indirectly points to an *assumption of existence.* To give a clear example, if a judge asks why (i.e., an ultimate question) people become amnesic when they experience a traumatic event (Peters, van Oorsouw, Jelicic, & Merckelbach, in press), one assumes that amnesia for a traumatic experience is a common phenomenon. So, asking a why-question indirectly assumes that a certain phenomenon exists.

Evolutionary legal psychology could aid in such circumstances and could provide a more complete overview of why (e.g., research on the survival processing advantage) and how (e.g., research on which mechanisms influence memory performance) certain psychological phenomena occur and how these explanations are best situated within a courtroom context. That is, this new branch of psychology would refer to the manifestation of evolved psychological phenomena that could be relevant in legal situations. Of course, this branch would not be restricted to only evolutionary research on memory, it would include all those areas of psychological research that often manifest themselves in the legal field (e.g., lying, malingering, dissociation, amnesia, false memory, facial processing, eyewitness identification).

What is important to take into account in this discussion is that many memory experts are called upon as expert witnesses in court. Situations in which memory serves as the only evidence, for example in cases involving claims about historic child sexual abuse, answers to questions about the why and how of memory functioning necessarily take center stage (Howe, in press). These cases are often about an alleged victim who, when very young (e.g., 2 to 5 years of age), was allegedly abused and now, many years later (frequently some 20 or more years later), can ostensibly remember quite vividly being abused these many years ago. In such cases, it is not unusual that a diverse set of so-called "well-established" memory phenomena is at the foreground. Ideas like repression and dissociation are frequently used by legal professionals to argue that memories can be hidden from consciousness for considerable periods of time and that such traumatic events, especially those from early in life (i.e., before the sixth year) can be vividly recollected many years later. We argue that to offer these legal professionals with a better grasp of the intricacies of these phenomena, one could adopt an evolutionary legal psychological approach. That is, besides focusing on which (proximate) mechanisms are involved in these phenomena, it would significantly add to provide an ultimate account of these phenomena.

Take for example the idea of repression. Although repression is well appreciated by many clinicians, scientific evidence does not instill strong confidence in the idea that repression actually exists (McNally, 2005). Indeed, the concept of repression does not really seem plausible from an evolutionary point of view. That is, why (i.e., ultimate question) should we have a memory system that evolved to repress memories that are experienced as traumatic? One could argue that a more fitness-relevant memory system would be one that better remembered such negative events so that the person could make more effective future plans to avoid or deal more effectively with similar events. This view is corroborated by research showing that negative events are indeed better recollected than more mundane events (McNally, 2005).

An evolutionary psychological argument could help immensely in such cases, one that included both why- and how-explanations. Such an approach has two advantages. On the one hand, legal professionals (e.g., judges, jurors) would be more informed about the precise details of certain phenomena and hence, could make better decisions. On the other hand, expert witnesses are forced by this evolutionary legal psychological account to focus not only on the proximate mechanisms of certain phenomena, but to examine whether an ultimate explanation can also be addressed. Indeed, legal scholars are already increasingly embracing knowledge from evolutionary psychology to understand behavior in a legal context (see Confer et al., 2010). One

specific example is the formation of the Society for Evolutionary Analysis in Law (SEAL: see www.sealsite.org) in which interdisciplinary issues between law, biology, and evolutionary psychology are combined into a more coherent view about law and behavior. Such work could, for example, lead to better insight in decision-making processes among legal professionals (Jones & Goldsmith, 2005). It is important to contrast this new area of psychology with evolutionary forensic psychology (Duntley & Shackelford, 2008) that stresses the more clinical and evolutionary aspects of psychology (e.g., question related to the why and how of rape, violence). Evolutionary legal psychology has the potential to stimulate research in novel directions and certain new research avenues could already be placed under this flag (e.g., Howe, 2011).

It is clear that the papers included in this Special Issue have the potential to push the field of adaptive memory a step further. We think it is imperative that scholars become acquainted with research on the evolution of memory, as it will likely apply to their domain of research as well. If true, then we would expect to see many future papers handling these more fundamental and evolutionary aspects of memory, ones that will eventually lead to a better understanding of the proximate and ultimate questions about why and how our memory evolved. Importantly, such an understanding does not necessarily need to remain within the confines of psychological science, but as we have argued in this section, may have some very important pragmatic consequences as well.

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