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Adaptive Memory: Controversies and Future Directions

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Human memory is adaptive. Our capacity to remember and forget helps us solve problems, everything from remembering where the car is parked to recognizing the person who owes us money. Remembering is the product of an evolutionary process as well. At some point in our ancestral past, memory systems developed because their presence helped us solve problems related to survival and reproduction. An organism with the capacity to remember where the food is located, or categories of potential predators, is more likely to survive than an organism lacking this capacity. There is currently little or no debate on this point.

More controversial, however, is the notion that nature's criterion—the enhancement of inclusive fitness—has relevance to modern memory functioning. The visual system evolved, as did the organs of the body, but it is not necessary to consider evolutionary pressures to gain insight into the structural and functional properties of these systems. Evolutionary theory does not demand that evolved systems maximize current fitness, or even work most efficiently when asked to solve the problems that led to their development (Symons, 1992). Yet those systems might well bear the imprint of those selection pressures. In the case of the visual system, for example, the specific tunings of cone photopigments appear to dovetail nicely with the adaptive problem of identifying ripe fruit in natural environments (e.g., Nathans, 1999).

Research on adaptive memory originated from the claim that our memory systems are functionally specialized to solve adaptive, or fitness-based, problems. Included are problems such as remembering sources of nourishment, threats to survival, activities of kin, potential mating partners, cheaters and free-riders, and so on (Nairne & Pandeirada, 2008). Most of the things we remember are unrelated to fitness, such as where I left my pencil or the movie I saw last night, but the fact that people are capable of general remembering does not mean that our memory systems were *designed* (by nature) to remember generally. On the contrary, from an evolutionary perspective content and specificity are likely to matter (Klein, Cosmides, Tooby, & Chance, 2002).

This brief chapter is divided into three sections. First, I comment on the nature of evolutionary arguments, particularly the distinction between ultimate and proximate explanations of cognitive traits. This distinction can be a confusing one (Scott-Phillips, Dickens, & West, 2011) and has led to some misunderstandings in the literature on the evolutionary determinants of remembering. Second, I discuss two important ancillary issues—domain-specificity and the role of ancestral priorities in empirical accounts of remembering. Third, and finally, I offer suggestions on future directions for adaptive memory research and evolutionary functional analysis.

ULTIMATE VERSUS PROXIMATE: ON THE NATURE OF EVOLUTIONARY ARGUMENTS

Functional accounts of memory do not require an evolutionary stance. One can approach the study of remembering by investigating the problems that memory systems solve—such as remembering the face of a cheater—without worrying about when and why those systems evolved. As I have discussed elsewhere, there are significant advantages to adopting a functional perspective, including the fact that it gives one concrete criteria against which to measure progress (see Nairne, 2005). However, if one chooses an evolutionary stance, which is a special form of functionalism, it is useful to consider the nature of evolutionary arguments—especially the distinction between ultimate and proximate questions about evolved traits (Mayr, 1963).

Ultimate explanations are statements about the functions of a trait and "why" it would have been selected by nature during an evolutionary process. Natural selection is governed by a criterion, the enhancement of inclusive fitness, so ultimate explanations appeal to (and are judged by) this criterion. *Proximate explanations* focus on the mechanisms that produce the trait—that is, they are statements about "how" the trait works and the conditions under which the trait is likely to be expressed. To cite a common example, crying is a behavior that increases an infant's chances of gaining the care and comfort needed for survival; an ultimate explanation of crying focuses on its fitness effects and why such a trait likely gained traction in the population over generations. Alternatively, and perhaps concurrently, one can choose to study the biological mechanisms that induce and control crying, such how glands secrete lachrymal fluid, along with the external triggering conditions that produce the behavior (e.g., separation from the caretaker). The latter would constitute an investigation of the proximate mechanisms that underlie the behavior.

Evolutionary theorists generally agree that both kinds of explanations are necessary for a full accounting of an evolved trait, but it is important not to confuse the two. Proximate mechanisms do not generally provide answers to ultimate questions, which deal with how traits affect inclusive fitness. In the case of adaptive memory, our lab originally proposed an ultimate hypothesis: If nature "tuned" our memory systems to process and remember fitness-relevant information, then our ancestors likely possessed an improved ability to survive and propagate their genetic record (Nairne, Thompson, & Pandeirada, 2007, p. 263). This is an evolutionary argument, one that generated an *a priori* empirical prediction: People should be particularly good at remembering information that is processed in a fitness context. The survival processing effect, among other phenomena, supports this prediction (see Erdfelder & Kroneisen, Chapter 10 in this volume; Nairne, 2010).

Notice that our hypothesis focuses on "why" our memory systems might show tunings and not on "how" those characteristics are actually implemented. Enhanced fitness is the engine driving natural selection, so it seemed sensible to propose that memory evolved because it solved specific problems related to fitness (e.g., remembering information processed in a fitness context). But we were careful not to specify the proximate mechanisms that drive the retention advantages. We speculated that survival processing might tap a special cognitive adaptation—a kind of evolved fitness-based memory module—but questioned the viability of such a mechanism (e.g., "survival" is too broad a construct). We suggested as well that survival processing advantages might be explained by other processes such as rehearsal, elaboration, distinctive processing, or self-referent processing (Nairne et al., 2007, p. 270). Fitness-based tunings seemed certain to produce fitness advantages, we argued, but nature could have achieved those tunings in a variety of ways.

One possibility is that our retention systems are simply reactive to novel or unusual events in the environment (e.g., Sokolov, 1963). It is well known that organisms orient to novel events, such as the sudden appearance of a predator. Orienting responses, in turn, could activate elaborative machinery that promotes good long-term recall of the attended item. From an evolutionary perspective the adaptive problem is solved—we are likely to show excellent retention of predators in our environment. Framed in this way, however, novelty and elaboration are proximate mechanisms that produce a stable mnemonic trait: enhanced retention of new and potentially dangerous things. The question of "why" such a memory tuning developed—the ultimate question—is answered by considering its effects on inclusive fitness. One would need to make the case that novelty tunings increase inclusive fitness; that is, organisms with retention systems tuned uniquely to novelty are associated with greater reproductive success. For reasons discussed below, I believe the case for novelty-based mnemonic tunings, although valid as an ultimate hypothesis, is not compelling.

The ultimate/proximate distinction is important here because proximate analyses are sometimes used to argue against Nairne et al.'s (2007) evolutionary account. Howe and Otgaar (2013) used evidence from scenario-based manipulations of elaboration to conclude that "the mnemonic value 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" (p. 19; see also Howe & Derbish, 2010, and Chapter 5 in this volume); Similar arguments have been made by others: "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 & Erdfelder, 2011, p. 1554). Such statements confuse the ultimate hypothesis—nature evolved memory systems sensitive to fitness—with hypotheses about possible proximate mechanisms (e.g., novelty-induced elaboration). The fact that survival situations might naturally invite elaborate, distinctive forms of encoding is consistent with the Nairne et al. (2007) hypothesis, not evidence against it.

To determine what proximate mechanisms actually evolved, of course, the supreme court of appeal is inclusive fitness. Following Howe and Otgaar (2013), one could propose evolved memory systems that show no special sensitivity to fitness-relevant information or contexts (see also Bell & Buchner, Chapter 3 in this volume). As noted above, our memory systems might simply be "tuned" to novelty or to information that has been processed meaningfully (Craik & Lockhart, 1972); one could also subscribe to the conventional notion that we retrieve information that is matched by cues in the retrieval environment (Tulving & Thomson, 1973). However, in these cases, as ultimate hypotheses, one would need to establish that such designs were likely to have become the targets of natural selection. As I have argued elsewhere (Nairne, 2010), viewed through the lens of nature's criterion—the enhancement of inclusive fitness—memory mechanisms that fail to differentiate among the adaptive consequences of an event seem unlikely to have evolved. Our memory systems need "crib sheets," or ways to differentiate between important and unimportant events (e.g., Ermer, Cosmides, & Tooby, 2007). Remembering everything that has been processed meaningfully, or every novel event, leads to combinatorial explosion of storage; similarly, a system that is merely driven by an encoding–retrieval match remembers continuously. Selection advantages will "accrue to memory systems that remember appropriately—that is, to systems that remember information pertinent to improving survival and reproduction" (Nairne, 2010, p. 14).

For this reason, our laboratory has maintained that we evolved domain-specific memory mechanisms that are inherently sensitive to content—specifically, information that is processed for its fitness consequences (either naturally or through experimental manipulations). Such "tunings" are likely to have evolved, as opposed to domain-general systems, because, again, the engine driving natural selection is the enhancement of inclusive fitness. Such reasoning does not rule out a role for elaboration—in fact, elaboration or "richness of encoding" may be the natural consequence of fitness-relevant processing, as argued in the original Nairne et al. (2007) report. But to claim that a domain-general process such as elaboration was the main target of evolution, rather than fitness-relevant processing *per se*, conflicts with what we know about the nature of physical and cognitive adaptations.

DOMAIN-SPECIFICITY AND ANCESTRAL PRIORITIES

The study of proximate mechanisms can be relevant to ultimate hypotheses. Evolved traits, for example, need to arise from proximate mechanisms that are heritable. Others have suggested that adaptations show evidence of special design (e.g., Williams, 1966)—that is, they are engineered to solve specific problems, such as pumping blood (the heart), filtering impurities (kidneys), or transducing environmental messages into the electrochemical language of the brain (the retina). A related characteristic, just mentioned, is domain-specificity, which means that evolved mechanisms are engaged selectively for some kinds of input and not others.

As defined by Barrett and Kurzban (2006), domain-specificity "refers to the idea that a given system accepts or is specialized to operate on only specific classes of information ('domains') for processing" (p. 631). For example, one could propose a face-recognition system that operates or is engaged only by faces, or at least by stimuli that share the formal statistical properties of faces (Kanwisher, 2000). Other possibilities include systems that are designed to handle living things, such as animals, and particular sorts of manmade objects, such as tools (Boyer & Barrett, 2005). Neuropsychological evidence, such as a selective impairment in the ability to process faces or animals, and neuroimaging data have helped build the case for such domain-specific systems (e.g., Caramazza & Shelton, 1998).

Within evolutionary cognitive psychology, Tooby and Cosmides (1992, 2005) have suggested that humans evolved systems specialized to detect cheaters or, more specifically, neurocognitive adaptations designed for social exchange. People show an enhanced ability to reason about violations of social contracts, especially in general reasoning tasks that often produce poor overall reasoning performance. These neurocognitive systems are assumed to be domain-specific, meaning that they are triggered by the processing of social contracts (much like a face-recognition system is initiated only by face-like stimuli). But, importantly, it is the general structure of a social contract rather than any particular kind of social contract that engages the system. Cosmides and Tooby (2005) have shown that people can reason exceptionally well about "wildly unfamiliar" situations as long as the situation fits the form of a social contract. Similarly, our retinae are domain-specific, in that they only process electromagnetic input, but they are capable of handling countless different patterns of electromagnetic information.

Returning to adaptive memory, the hypothesis that our memory systems are "tuned" to the processing of fitness-relevant information certainly implies domain-specificity. We suggested that "special" mnemonic advantages accrue whenever fitness-relevant processing is engaged, presumably because we evolved proximate mechanisms designed specifically to solve fitness-relevant problems. We placed the emphasis on processing, rather than on inherent content, because fitness relevance is often context-specific. As we noted, "food is survival relevant, but more so at the beginning of a meal than at its completion; a fur coat has high [survival]-value at the North Pole, but low at the Equator" (Nairne & Pandeirada, 2008, p. 240). What engages the memory system(s) is fitness-relevant processing, broadly conceived, rather than any particular environmental event.

This emphasis on processing, rather than specific content, helps to explain a puzzling finding in the survival processing literature. In the typical procedure, people are given lists of unrelated words and are asked to rate the relevance of each word to a survival scenario. Retention performance can then be examined as a function of relevance rating, and memory often increases accordingly. Items deemed highly relevant to the survival scene are often (but not always) remembered better than items given lower ratings (Butler, Kang, & Roediger, 2009; Nairne & Pandeirada, 2011). But strong survival effects are still typically found for items given the lowest ratings—that is, people remember words rated as irrelevant to survival better than words rated comparably in control conditions. This result is puzzling because it is not immediately apparent why we would have evolved memory mechanisms that show enhanced retention of information that lacks survival relevance. The reason, though, is straightforward: The survival processing paradigm *forces* participants to consider the fitness-relevant properties of all presented words, regardless of whether those stimuli are considered relevant or not. In natural settings, only fitness-relevant events are likely to engage fitness-relevant processing and show the enhanced retention.

Once again, what is important is fitness-relevant processing, not the particular event or setting that happens to induce the processing. Artificial laboratory tasks can engage survival processing, as can events in natural settings—both presumably lead to enhanced retention of the processed material. Recently, much has been made of the fact that scenarios using settings discrepant from the environment of evolutionary adaptedness (EEA) can produce retention advantages comparable to (or even exceeding) those found using the traditional Nairne et al. (2007) grasslands scenario. Kostic, McFarlan, and Cleary (2012) found strong survival advantages using a scenario in which people imagined themselves "stranded in a spaceship in space." Even more impressive, Soderstrom and McCabe (2011) discovered that "zombie processing"—rating the relevance of words to a possible attack from zombies—produced better retention than the Nairne et al. (2007) grassland-based survival scenario. At face value, these data seem surprising: there were no zombies in the EEA. But again, it is fitness-relevant processing that drives the retention advantage. Zombies are clearly predators and could activate other self-preservation systems as well (e.g., contamination), so it is not surprising that zombie processing leads to retention advantages. Similar arguments apply to "stranded spaceship" scenarios—again, basic self-preservation systems are likely to be activated, which in turn engender fitness-relevant processing.

More pertinent to the present discussion, though, is the issue of domain-specificity. In describing the zombie and spaceship results, Soderstrom and Cleary (Chapter 6 in this volume) conclude the following: "Taken together, these data suggest that survival processing advantages in memory are domain-general insofar as they are not optimally suited for any one environment or situation in particular, but rather operate effectively in a wide range of scenarios" (p. XXX). Although this conclusion is partly true, it confuses the concept of domain-specificity with another issue, *ancestral priorities*, which I discuss below. Our claim is that we evolved mnemonic mechanisms that are specialized to handle fitness-relevant events, particularly ones related to survival or self-preservation. If there is special mnemonic machinery to handle such events, then the input "domain" would be events that activate self-preservation systems regardless of the particular setting or event that happened to initiate the processing. Just as face-recognition systems respond to any face and "cheater modules" respond generally to violations of social contracts, we evolved memory mechanisms that respond generally to survival threats, or fitness processing in general.

In fact, we have known for some time that it is not the "setting" *per se* that produces survival processing advantages. Survival processing advantages have repeatedly been found when both the fitness-relevant and the control scenarios are set in the same natural (even grasslands) environment. For example, Nairne, Pandeirada, and Thompson (2008) compared the standard survival scenario to one in which people were vacationing at a fancy resort—a strong survival effect was obtained. Nairne, Pandeirada, Gregory, and Van Arsdall (2009) compared survival-based "hunting" and "gathering" scenarios to control scenarios that involved exactly the same activities (hunting for food in a natural environment to win a hunting contest, or searching for food in the grasslands as part of a scavenger hunt)—again, a strong survival effect was obtained. It is now clear that survival advantages can be obtained in virtually any environment, even outer space, as long as the scenarios activate basic predator-avoidance and/or self-preservation systems. This does not mean that the evolved memory "tunings" are domain-general; they are domain-specific, in the sense that they are activated by situations that are survival- or fitness-relevant.

Accepting that we may have evolved domain-specific memory tunings—for example, for events that induce fitness-relevant processing (predators, edible foods, potential mating partners, cheaters, etc.)—does not imply that all domain-specific input will activate those tunings to the same degree. Domain-specific systems, such as the auditory and visual systems, characteristically respond best to certain kinds of input. For example, the auditory system responds well to frequencies of sound that match what is produced by spoken language. From an evolutionary perspective, we might expect cognitive systems to respond most efficiently when faced with the problems (and corresponding input stimuli) that were critical to their development. Given that unique aspects of the human brain were sculpted primarily during the Pleistocene, the EEA favored by evolutionary theorists, optimal cognitive performance might well emerge when the task at hand mimics the foraging problems faced by our hunter-gatherer ancestors.

Note, though, that this is merely a hypothesis, not a strong prediction of evolutionary theory. Evolved systems do not necessarily maximize fitness, even when dealing with the selection pressures that led to their development. It is an interesting empirical question, however, and a number of laboratories have produced data consistent with ancestral priorities. For example, our visual and attentional systems may be tuned to the detection of threatening stimuli (LoBue & DeLoache, 2008) or animates (New, Cosmides, & Tooby, 2007). There is evidence as well for enhanced learning and conditioning for aversive stimuli that were likely to be relevant during the EEA (e.g., snakes; Öhman & Mineka, 2001). Some of these data are controversial, however, because of item-selection concerns (Nairne, 2010; Quinlan, in press).

With respect to adaptive memory, both Nairne and Pandeirada (2010) and Weinstein, Bugg, and Roediger (2008) found evidence for ancestral priorities in the survival processing paradigm. People were asked to rate the relevance of words to either ancestral or modern scenarios. Both scenarios described survival-relevant situations, but one described escaping from a predator in the grasslands (ancestral) whereas the other involved escaping from an attacker in a city (modern). People using the ancestral scenario subsequently remembered the rated words better than those using the modern scenario. This ancestral advantage was replicated using several different wordings of the scenarios—for example, when searching for medicinal plants versus antibiotics to cure an infection (Nairne & Pandeirada, 2010, Experiment 2) or when gathering edible plants in the grasslands versus searching for and buying food in a city (Experiment 3).

Again, it is not the setting *per se* that is important—grasslands versus the city—but the processing systems that are activated by those settings. As Nairne and Pandeirada (2010) argued, dealing with an infection or an attacker in a city is clearly survival-relevant and should activate self-preservation systems, but cities contain support systems, such as police and hospitals, that are absent in the grasslands. Faced with an attacker in the city, or a raging infection, one probably thinks about calling the police or visiting the local pharmacy to get some antibiotics. You also have lots of social support systems in the city that are absent when you are stranded in the grasslands. At the same time, we argued, asking people to search for edible plants in the grasslands presumably activates processing scenarios that are closer to those employed in the EEA, compared to those activated when one attempts to buy food in a modern market, and the "fit" between the problem and the evolved system might contribute to the obtained retention differences.

The important point here is that the demonstration of ancestral priorities is only tangentially related to the question of domain-specificity. Both the ancestral and modern scenarios used by Nairne and Pandeirada (2010) were designed to induce fitness-relevant processing, thus engaging any special mnemonic systems that may have evolved to handle such situations. Indeed, Nairne and Pandeirada (2010), and several other researchers as well (e.g., Klein, 2013), have found strong survival processing effects using scenarios that do not directly reference the conditions of the EEA. Variations in the efficiency of processing, within the selected domain, are important to theory too but do not speak directly to the issue of domain specificity.

FUTURE DIRECTIONS

The functionalist agenda proposes that cognitive systems are functionally designed. As a product of natural selection, our capacity to remember and forget evolved because it helped us solve adaptive problems consistent with nature's criterion—the enhancement of inclusive fitness. As noted throughout, this conclusion does not guarantee that memory's operating characteristics will maximize current fitness or even lead to adaptive behavior in all situations. At the same time, given its origins, it seems unwise to ignore the selection pressures that presumably led to memory's development. Imagine attempting to understand the machinery in a factory without worrying about the product the machinery is designed to produce.

In evolutionary functional analysis, one attempts to generate empirically testable hypotheses about cognitive systems based on an analysis of the recurrent adaptive problems faced by our ancestors. Although we can never be certain about the specific selection pressures that drove the evolution of a memory system, such as episodic memory, we can make reasonable guesses: It would be important to remember the characteristics of predators or prey, the location of potable water or edible plants, the actions of those who violate social contracts, prospective mates, authority figures, and so on. Organisms with memory systems biased to retain such information likely held adaptive advantages over those who did not. Still, these are merely coarse-grained hypotheses rather than airtight predictions of evolutionary theory. One needs to conduct the relevant empirical tests to confirm (or disconfirm) hypotheses about the adaptive nature of a cognitive system. Much of the work described in this volume is directed toward this end.

It is also worth emphasizing that evolutionary functional analysis, as described here, is specifically designed to avoid *post hoc* reasoning—that is, fanciful adaptive explanations of existing phenomena. Evolutionary accounts are frequently criticized for relying on "just-so" stories (e.g., Gould & Lewontin, 1979), but this kind of criticism does not apply to most research on adaptive memory. The mnemonic advantages found for survival processing were predicted *a priori*, based on a hypothesis about possible fitness advantages that might accrue for remembering fitness-relevant information (Nairne et al., 2007). Much of the work described elsewhere in this volume flows from a similar foundation. For instance, work on memory for cheaters, or their personal attributes, follows naturally from social contract theory and various assumptions about the role of reciprocal altruism in human actions (see Bell &

Buchner, Chapter 3 in this volume, for a review). One of the exciting consequences of thinking functionally, especially in evolutionary terms, is the discovery of new empirical phenomena.

With this in mind, researchers should be wary about identifying the concept of adaptive memory exclusively with survival processing. "Survival" is a very broad concept—too general, in fact, to have been the likely target of selection. In our original work, we suggested that survival processing might tap into multiple modules or adaptations working in concert, each one activated to one degree or another by the survival processing task (see Nairne et al., 2007, p. 270). Although effective retention mechanisms might be activated strongly by any form of fitness-relevant processing, echoing the idea of novelty-based encoding, we almost certainly evolved unique mechanisms to deal with different adaptive problems. Retaining critical information about predators, food sources, possible violations of social contracts, potential mating partners, and so forth is unlikely to be handled successfully by a single mnemonic mechanism (e.g., elaboration). Nature usually evolves problem-specific structures because the "solution" to one problem can conflict with the requirements of another (Sherry & Schacter, 1987).

Our laboratory has recently turned its attention to more specific adaptive dimensions. For example, we have conducted experiments exploring the mnemonic effects of animacy, or the distinction between living and nonliving things (Nairne, VanArsdall, Pandeirada, Cogdill, & LeBreton, in press; VanArsdall, Nairne, Pandeirada, & Blunt, in press). Animacy is a foundational dimension, appearing early in development, and people seem to prioritize the visual processing of animate objects (e.g., New et al., 2007). From an evolutionary perspective, it is reasonable to propose that our memory systems are selectively tuned to process and remember animate things. Predators are animate beings, as are potential mating partners. Methodological issues loom, however, because animate and inanimate stimuli presumably differ along a number of relevant dimensions (e.g., imageability, frequency, meaningfulness, and so on). In our work, we have attempted to equate or control for these potentially confounding dimensions and have found strong animacy advantages in both free recall and paired-associate learning. This research suggests that animacy may turn out to be one of the most important item dimensions ultimately controlling retention (see Nairne et al., in press).

We have also conducted experiments showing that animacy *processing* produces mnemonic advantages (see VanArsdall et al., in press). Here, instead of using existing words or pictures of real objects, we asked participants to process novel events—pronounceable nonwords (e.g., FRAV)—as either living or nonliving things. The nonwords were paired during presentation with properties characteristic of either living ("dreams at night") or nonliving ("assembled with screws") stimuli. People were then asked to decide whether each nonword likely represented a living thing or an object prior to a final surprise recall or recognition test. We found that memory was significantly enhanced when the nonwords were associated with animate properties. Methodologically, these experiments are important because across conditions everyone was asked to process and remember exactly the same nonwords, thus effectively eliminating item-selection concerns. Again, this research suggests that our cognitive systems may be prepared or tuned to detect and remember animate things, a conclusion that follows nicely from a functional/evolutionary perspective.

We have also been investigating the mnemonic effects of contamination. There is certainly adaptive value in remembering objects in the environment that have been potentially contaminated by disease. There is a large literature on the social-cognitive effects of contamination and disgust (e.g., Tybur, Lieberman, Kurzban, & DeScioli, 2013), but the mnemonic effects of contamination remain unexplored. Specifically, we asked the following empirical question: Will people remember objects that have been touched by a sick person better than ones touched by a healthy person? To address the question, people were shown pictures of everyday objects and were told that each object had been recently touched by a sick or a healthy individual. Accompanying each picture was a short description that helped to categorize who had touched the object. For example, a picture of a "ball" appeared with the descriptor "person with a constant cough" or the descriptor "person with a straight nose." After every third item, the three preceding items appeared again and the task was to decide whether that object had been touched by a sick or a healthy person. Following a series of these trials, everyone received a surprise free recall test for the pictured objects. The free recall results revealed a strong advantage for the "contaminated" items—proportion correct recall for the items touched by a sick person averaged 0.42 whereas the "healthy" items averaged only 0.34, a statistically significant effect. We think this is another important and novel finding because it demonstrates the functional value of remembering and suggests, once again, that our memory systems may be biased to remember information that is fitness-relevant.

Still, as discussed previously about survival processing, the simple demonstration of memory-based contamination or animacy effects does not tell us much about the proximate mechanisms involved. From an ultimate perspective, one can make a compelling argument for *why* animacy and contamination tunings might have evolved—they enhance inclusive fitness—but the *how* remains unknown. As chapters in the current volume show, the study of proximate mechanisms can be revealing, both in establishing the generality of phenomena (Klein, Chapter 2 in this volume; Altarriba & Kazanas, Chapter 7 in this volume) and in establishing boundary conditions (Otgaar, Howe, Smeets, Raymaekers, & van Beers, Chapter 11 in this volume; Schwartz & Brothers, Chapter 9 in this volume). The study of boundary conditions may be particularly important because boundary conditions encourage one to consider the function of a mnemonic mechanism. As discussed above, it is unlikely that we evolved a single mnemonic mechanism to cover all memory-based adaptive problems. The functional requirements associated with mating, for instance, may differ fundamentally from those connected with finding food or avoiding predators (see Klein, 2013). Thus, memory adaptations that work well in one context might not work well in another. The fact that survival processing produces robust effects across a wide variety of materials and designs, but apparently does not transfer well to implicit tests (Tse & Altarriba, 2010) or paired-associate learning (Schwartz & Brothers, Chapter 9 in this volume), undoubtedly will tell us something important about the functional design of the memory mechanisms involved.

Recent work on the development of adaptive memory provides insight into the functional properties of memory mechanisms as well. As Sellers and Bjorklund (Chapter 15 in this volume) perceptively note, cognitive development undoubtedly reflects the age-specific problems faced by the developing organism. A particular mechanism (or adaptation) appropriate for solving the adaptive problems of a

2-year-old might not be adaptive for an adolescent or an adult. We should also expect to find development differences in the appearance of certain mnemonic traits—for example, survival-relevant traits might appear early and remain relatively constant across the lifespan (see also Howe & Otgaar, 2013), whereas adaptations relevant to mating could appear later. Focusing on development is important for another reason as well: Experience almost certainly plays a critical role in shaping the operating characteristics of many evolved systems. The fact that people might have evolved "tunings" for certain recurrent problems does not mean that experience is unimportant in shaping the final characteristics of those traits.

Memory is adaptive—few, if any, researchers would disagree with this conclusion. Yet the bulk of memory research since Ebbinghaus has focused primarily on structure rather than function. Researchers have defined their mission as one of understanding the contents of the mind, much like a chemist deconstructs a chemical compound into its more elemental components. Although a structural stance can produce significant advances in our understanding of cognitive systems, functionless tinkering often leads to directionless research, or to theoretical frameworks designed to explain tasks rather than psychological processes (Klein et al., 200; Nairne, 2005). As William James once said, it is difficult to understand a house by focusing on its bricks and mortar—one needs to know what the house is for, what the house is designed to do, and it is only in this functional context that bricks and mortar make sense. Identifying the adaptive problems that our memory systems evolved to solve provides just such a functional context in which structural investigations of remembering potentially make sense.

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