Adaptive memory: Nature's criterion and the functionalist agenda

JAMES S. NAIRNE
Purdue University

JOSEFA N. S. PANDEIRADA
University of Aveiro

Memory researchers traditionally ignore function in favor of largely structural analyses. For example, it is well known that forming a visual image improves retention, and various proximate mechanisms have been proposed to account for the advantage (e.g., elaboration of the memory trace), but next to nothing is known about why memory evolved such sensitivities. Why did nature craft a memory system that is sensitive to imagery or the processing of meaning? Functional analyses are critical to progress in memory research for two main reasons: First, as in applied research, functional analyses provide the necessary criteria for measuring progress; second, there are good reasons to believe that modern cognitive processes continue to bear the imprint of ancestral selection pressures (i.e., cognitive systems are functionally designed). We review empirical evidence supporting the idea that memory evolved to enhance reproductive fitness; as a consequence, to maximize retention in basic and applied settings it is useful to develop encoding techniques that are congruent with the natural design of memory systems.

What role should function play in our understanding of human memory? Outside a few select domains, function occupies a secondary role in most modern theories of remembering. Researchers focus intently on the "how" of remembering—the principles and parameters of retention—but largely ignore the "why." For example, it is well established that forming a visual image improves long-term retention, as do repetition, self-generation, and practicing retrieval, but few researchers can explain why retention is sensitive to these particular variables (although see Paivio, 2007). Why should forming a visual image engender an accessible and elaborate memory trace? Why did nature engineer a memory system with special sensitivity to repetition or meaning, as opposed to other methods of encoding?

In ignoring function, researchers treat memory instead as a capacity to be understood, to be picked apart and studied as one might break down a chemical compound into its more basic elements. Taxonomies are developed, systems identified and cataloged, and parametric properties investigated (for a summary, see Tulving & Craik, 2000). The net result is a collection of facts but few formal or principled criteria that enable one to mark progress or distinguish important from unimportant phenomena. Memory is defined operationally as well through its assessment techniques (e.g., recall, recognition,

word fragment completion). Consequently, theories of tasks (e.g., recognition) often masquerade as theories of memory with little or no grounding of the theory components in the problems that memory presumably evolved to solve.

This article is divided into three sections. First, we briefly comment on the nature of modern memory theory, which champions the relativity of remembering (e.g., Roediger, 2008). Our focus is on episodic memory, which taps the ability to remember specific episodes from our past—events that occurred in a particular temporal–spatial context (Tulving, 1983). Here, remembering is seen largely as a byproduct of an encoding–retrieval match that, in turn, obviates any serious consideration of function. Second, we consider why it is useful to treat episodic memory from a functional perspective, as a system that evolved to accomplish specific purposeful ends. Finally, we review recent research suggesting that episodic memory may have evolved, in part, to solve adaptive problems relevant to fitness (i.e., to enhancing survival or reproduction). To understand the capacity to remember and forget, and to maximize retention in basic and applied settings, it is useful to develop encoding techniques that are congruent with the natural design of memory systems.

On the primacy of domain-general remembering

With some important exceptions, the theoretical zeitgeist among active memory researchers is nonfunctional, marked by two major assumptions: equipotentiality, wherein memory traces are assumed to be largely equivalent in their ultimate value, and relativity, in which the control of remembering is delegated primarily to the match, or overlap, between the conditions present at encoding and retrieval (e.g., Tulving & Thomson, 1973). Equipotentiality and relativity comprise the main components of what can be seen as a domain-general view of episodic memory: Memory traces reflect the conditions of encoding and are recoverable, or not, based simply on the constellation of retrieval cues present at the point of remembering.

Consider the levels of processing framework, proposed originally by Craik and Lockhart (1972; Craik & Tulving, 1975; see also Craik, 2007). Here, the memory trace is conceptualized as a byproduct of perceptual encoding processes. Prevailing conditions at the point of encoding determine the content

of memory trace: If one is thinking about the meaning of an event during processing, then the resulting memory trace is likely to be a rich one, linked to lots of existing knowledge in memory. If encoding focuses on more peripheral properties, such as an item's sound or appearance, then only peripheral (or "shallow") features are retained. The memory trace is conceived as a faithful record—or lasting remnant—of an active encoding process.

The levels framework assumes that retention depends on the depth of initial processing, where *depth* is defined as the extent of meaningful or conceptual processing. Deep processing is effective because, again, the analysis of meaning leads to richer, more elaborate memory traces; as one thinks about the meaning of an item, one draws connections between the item and existing knowledge structures, and those connections are reflected faithfully in the memory trace. Craik recently used a library metaphor:

> If a new acquisition is "encoded deeply" it will be shelved precisely in terms of its topic, author, date, etc., and the structure of the library catalog will later enable precise location of the book. If the new book was simply categorized in terms of its surface features ("blue cover, $8'' \times 10''$, weighs about a pound") it would be stored with many similar items and be difficult or impossible to retrieve later. The ability to process deeply is thus a function of a person's expertise in some domain—it could be mathematics, French poetry, rock music, wine tasting, tennis, or a multitude of other types of knowledge. (2007, p. 131)

Deeply processed items tend to be remembered well because their processing records are congruent with established knowledge structures, ones that can be accessed easily at a later time. However, importantly, nothing special is assumed about the content of the memory trace per se; again, it is simply a faithful record of initial processing, and its role in retention is ultimately subservient to the conditions present at retrieval. In fact, as noted by many, it is easy to arrange retrieval environments in which deeply processed items will be difficult to recover. For example, Morris, Bransford, and Franks (1977) had participants encode words phonemically or semantically. Performance on a standard memory test (recognition) revealed a ro-

bust advantage for the words processed semantically; however, the advantage reversed when a novel rhyme recognition test was used: "Does this word rhyme with a word seen during encoding?" In this last situation, the relevant cues in the retrieval environment better matched the mnemonic byproducts of the shallow encoding task, thus affording better performance (for other examples, see Surprenant & Neath, 2009; Tulving, 1983).

Reduced to its core, then, standard episodic memory theory embraces the assumption of equipotentiality, wherein faithful records of mnemonic processing are recoverable or not based simply on the nature of the retrieval environment. Although certain kinds of retrieval environments may be more likely than others and certain retrieval structures more accessible (e.g., areas of expertise), the ultimate arbiter of retention is the encoding–retrieval match (Tulving, 1983; Nairne, 2002). As Craik notes, one need "postulate no special 'store' or 'faculty' of memory—or even special memory processes" to explain retention (2007, p. 132). To account for when and why we remember, one needs merely to determine the nature of initial processing and the kind of processing, and therefore the functional retrieval cues, that occurs during retrieval process.

The case for the functionalist agenda

Although one can easily demonstrate the "relativity" of remembering, based on manipulations of the encoding–retrieval match, this empirical and theoretical insight alone does little to advance our understanding of remembering. Notably lacking is any attempt to specify a goal for memory's operation (i.e., what is memory for?) or the environmental conditions that determine initial processing or the operative retrieval environment (for a similar argument, see Glenberg, 1997). Instead, most researchers seem satisfied with using the standard framework to "explain" empirical phenomena once they are discovered. For example, visual imagery is deemed effective because it leads to a rich memory trace that is likely to be matched in many retrieval contexts; mnemonic devices are effective because they force people to encode information into fixed retrieval structures that are easily accessed when needed. Therefore, it is not surprising that researchers rarely explore memory's functional roots—memory is not

"for" anything other than to respond appropriately to the encoding–retrieval match.

Yet, one can reasonably ask, would nature craft a memory system that fails to differentiate between types of information or one that relies on the whims of changing retrieval environments to determine what is remembered? There are simply too many critical problems for the developing human to solve—avoiding predators, locating nourishment, selecting an appropriate mate—to rely on such general, content-free principles. Contrast the domain-general characterization of memory just described with the active properties of sensory and perceptual systems. The visual system aggressively processes and interprets the visual signal, beginning in the retina and continuing throughout the visual pathways, to accomplish very specific ends. The visual system has well-defined problems to solve (e.g., extracting color, detecting edges, maintaining constancies in size and shape). This is true for the organs and structures of the body as well. The heart is uniquely designed to pump blood, the kidneys are specially designed to help filter impurities, and the lungs are adapted to control respiration. Nature builds physical structures that solve specific problems, not general systems that remain insensitive to content (Ermer, Cosmides, & Tooby, 2007; Symons, 1992).

As we have argued extensively elsewhere (e.g., Nairne, 2010; Nairne & Pandeirada, 2008b), our capacity to remember, like the visual system, did not develop in a vacuum. Memory evolved through the process of natural selection; consequently, memory's form and function were subject to the constraints of nature's criteria. The engine that drives natural selection, and the development of physical and cognitive structures, is fitness enhancement. Structural features exist, and work the way they do, because at some point in our ancestral past they increased the chances for survival or the likelihood of securing an appropriate mate. Memory evolved because it directly or indirectly improved fitness—again, by increasing the chances of successful reproduction. Consequently, we can anticipate that our memory systems are geared or "tuned" to solving adaptive problems related to fitness.

With nature's criterion in mind, is it reasonable to assume that a system based on equipotentiality is well suited for solving the wide range of mnemonic

problems that humans faced throughout their evolutionary history—everything from food locations, predator routes, potential mate choices, cheaters on social contracts, and so on? One might argue that knowledge structures germane to survival and reproduction are simply better described than non–fitness-relevant events—that is, more organized, differentiated, or easily accessed in a variety of retrieval environments. Yet these characteristics, if present, are unlikely to have developed simply through experience or expertise, as most memory theorists assume (e.g., Craik, 2007). Remembering information related to fitness is too important to rely on the chance effects of environments that may or may not deliver the experiences necessary to build appropriate retrieval structures. Instead, our memory systems must come equipped with crib sheets, natural ones that specifically increase our ability to handle fitness-relevant challenges (see Tooby & Cosmides, 1992).

Nonfunctional (or structuralist) reasoning raises practical concerns as well, concerns that have long been recognized by those working in applied settings. Failing to adopt a problem-oriented perspective makes it difficult to gauge the importance of the phenomena or structures being studied—to distinguish the useful from the useless. Klein, Cosmides, Tooby, and Chance (2002) used the analogy of a three-hole punch (see also Nairne, 2005). One could attempt to understand such a device in a structural way, by measuring the tension of the spring-controlled hand-press or the spacing of the sharpened cutting pegs. But without some understanding of what the device is for—cutting holes in paper so it fits in a binder—we lack ground rules for gauging the importance of features in the operation of the device as a whole. For example, one might notice that confetti falls out when the device is shaken and promptly label it as a confetti-maker or develop sophisticated theories of how and when confetti is generated. Of course, confetti is an unimportant byproduct of the device, and not worthy of intensive study, but this insight is readily apparent only in a functional context. Might this be true for memory phenomena as well? Our memory textbooks are filled with empirical phenomena (e.g., false recall, the generation effect, the testing effect), but without a firm understanding of memory's function how are we to decide which are mnemonic confetti and which are not?

The mnemonic value of fitness processing

Although a compelling case can be made that our memory systems are functionally designed, specifically with respect to fitness-relevant problems, the arguments are better served empirically. Unfortunately, as noted, memory researchers have historically veered away from a problem-centered approach, so the amount of relevant data is limited.

We do know that fitness-relevant events can produce salient long-term retention. One powerful example would be flashbulb memories, which track the retention of significant life events (Brown & Kulik, 1977; for a recent review, see Luminet & Curci, 2009). Highly emotional events, particularly life-threatening situations, produce vivid and long-lasting mnemonic experiences as well (Buss, 2005; Winograd & Neisser, 1992). There is also compelling evidence that people find it easier to associate fitness-relevant stimuli, such as snakes and spiders, with certain aversive outcomes (e.g., shock; see Öhman & Mineka, 2001). People are also particularly good at attributing statements about the violation of social contracts (e.g., "This person has a background as a cheater") to faces (Buchner, Bell, Mehl, & Musch, 2009). Finally, perhaps not surprisingly, people tend to remember attractive faces better than average-looking faces, although the effect is somewhat larger for female than male faces (see Kenrick, Delton, Robertson, Becker, & Neuberg, 2007).

Sex-based differences in spatial retention also provide potentially relevant evidence. Women tend to remember the locations of fixed objects in an array better than men, whereas men show advantages in tasks requiring navigation and orientation skills (for a review see Voyer, Postma, Brake, & Imperato-McGinley, 2007). Female advantages in object location memory have been demonstrated routinely both in the laboratory and in real-world settings. For example, New, Krasnow, Truxaw, and Gaulin (2007) recently found that women were more accurate than men in pointing to recently visited food locations in an outdoor market. Although somewhat controversial, these data have been used to support the imprint of ancestral selection pressures on modern cognitive functioning. Silverman and Eals (1992) suggested that current sex-based differences in spatial memory can be traced, at least in part, to the division of labor that existed throughout our ancestral past as hunter–

gatherers. Women primarily did the gathering, which required superior object location memory, whereas men engaged in navigationally based hunting.

THE SURVIVAL PROCESSING PARADIGM.

Overall, these studies are consistent with the hypothesis that our memory systems may be tuned to solve problems related to fitness. However, the fact that fitness-relevant events are remembered well, or that women show superior object location memory, is open to a variety of interpretations. For example, much of the existing evidence requires one to compare retention across different events (e.g., emotional vs. nonemotional stimuli), which could differ along dimensions other than fitness relevance. Our laboratory has taken a somewhat different approach. Rather than comparing retention across item type (fitness relevant or not), participants in our studies are asked to remember the same information (usually unrelated words). What differs across conditions is how those items are processed before a subsequent memory test (i.e., either in terms of fitness relevance or not).

In the paradigmatic case, people are asked to imagine themselves stranded in the grasslands of a foreign land without any survival materials. Over the next few months, the instructions explain, they will need to find steady supplies of food and water and protect themselves from predators. Words are presented on a laboratory-based computer screen, and everyone is then asked to rate the relevance of each word to the imagined survival scenario (i.e., how relevant might this item be in the described survival situation?). After the rating task, there is a short retention interval, and then participants are given a surprise recall or recognition test for the just-rated words. The main empirical question examines whether processing information in terms of its survival value increases later retention relative to a variety of control conditions. Indeed, across a number of experiments survival processing has been shown to produce exceptionally good retention—better, in fact, than most known encoding procedures (Nairne, Thompson, & Pandeirada, 2007; Nairne & Pandeirada, 2008a).

For example, Nairne, Pandeirada, and Thompson (2008) showed that a few seconds of survival processing can produce better long-term recall than a veritable "who's who" of classic encoding manipulations. Using a between-group design, survival processing (based on the grasslands scenario described earlier) was pitted against groups instructed to use visual imagery, self-reference (relate the items to a personal experience), generate the items from anagrams, rate the items for pleasantness, and use intentional learning. Each of these comparison conditions is widely recognized to increase retention—in fact, these are the encoding manipulations widely championed in human memory textbooks—yet survival processing produced the best recall. Again, everyone was asked to remember exactly the same information, so the locus of the mnemonic advantage must lie in the nature of the processing rather than in the characteristics of the individual items.

Survival processing advantages have now been demonstrated in a number of laboratories and with a variety of experimental designs and materials (e.g., Kang, McDermott, & Cohen, 2008; Otgaar, Smeets, & van Bergen, 2010; Weinstein, Bugg, & Roediger, 2008). The effect is robust in both within- and between-subject designs, using pictures or words, in both recognition and free recall, and using either categorized and uncategorized lists (Nairne & Pandeirada, 2008a). The fact that survival processing advantages are seen in within- and between-subject designs is important because a number of classic mnemonic effects, such as the advantages normally seen for bizarre imagery or emotionality, depend importantly on design (Schmidt & Saari, 2007). For example, the generation effect is highly robust in a within-subject design but less so when the presence or absence of generation is manipulated across participants (for a general review, see McDaniel & Bugg, 2008).

WHAT IS THE PROXIMATE MECHANISM?

We developed the survival processing paradigm to test an evolutionary hypothesis—namely, that our memory systems are specially tuned to remember information that is processed for fitness. Because nature's criterion demands that evolving structures confer fitness advantages, we anticipated that our capacity to remember might show sensitivity to survival-based processing. Note that the retention advantages described earlier represent an a priori prediction of an evolutionary analysis; therefore, work in this domain is not subject to the common complaint that evolutionary analyses are simply post hoc "just-so stories" (e.g., Gould & Lewontin, 1979).

At the same time, the evolutionary analysis remains silent about the proximate mechanisms that actually produce the advantage. It is certainly possible that existing explanatory mechanisms will ultimately account for the effect.

For example, one might argue that survival processing simply enables one to integrate rated information into a rich thematic context. Asking people to rate the relevance of unrelated words to a common theme may induce a form of relational processing that is known to benefit retention, especially compared with encoding tasks that focus on the characteristics of the individual items (such as pleasantness ratings; see Hunt & McDaniel, 1993). In an effort to control for thematic processing, we originally compared survival processing with another thematic control, a scenario in which people were required to rate the relevance of words to the task of moving to a foreign land (e.g., transporting belongings, purchasing a home). The survival and moving scenarios were matched as closely as possible, and the intrusion data in free recall suggested that both produced equivalent amounts of thematic processing, but survival processing still produced the best retention (Nairne et al., 2007). Subsequently, we have used control scenarios in which people were asked to imagine themselves vacationing at a fancy resort with all their needs taken care of, eating dinner at a restaurant, or planning a charity event with animals at the local zoo (Nairne & Pandeirada, 2007; Nairne et al., 2007, 2008). Moreover, in an effort to better match the survival scenario in terms of novelty and excitement, Kang et al. (2008) compared survival processing to a thematic scenario involving the planning and execution of a bank heist. In each case, retention performance was best after survival processing.

As noted earlier, one also finds survival processing advantages when to-be-rated words are drawn from salient semantic categories (Nairne & Pandeirada, 2008a). This finding is important because the effectiveness of encoding tasks that encourage relational or thematic processing is reduced when list items are inherently related (Hunt & Einstein, 1981). When list items are unrelated, as in the typical survival processing experiment, survival processing may induce people to encode unrelated words into an ad hoc category representing things that occur in a survival situation. Such a category, in turn, provides an efficient retrieval structure (recall items from the category) that is lacking when items are encoded using tasks that focus on the individual item (e.g., rating items for pleasantness). However, individual-item tasks, which can help one discriminate between the list items, produce the best recall when the lists are categorized because the category structure is salient and obvious. In fact, rating items for pleasantness in categorized lists is widely considered to be the gold standard task for enhancing free recall (Hunt & McDaniel, 1993; Hunt & Einstein, 1981). Nairne and Pandeirada (2008a) found that survival processing led to better free recall than pleasantness processing in categorized lists.

Finally, perhaps the best evidence against a thematic or relational processing account comes from recent work using more focused survival scenarios (Nairne, Pandeirada, Gregory, & Van Arsdall, 2009). Evolutionary psychologists have traditionally argued that people continue to house a "stone-age mind," one filled with adaptations uniquely designed to handle problems relevant to early hunter–gatherer environments (e.g., Tooby & Cosmides, 1992). With this in mind, Nairne et al. (2009) designed scenarios to tap prototypical hunting and gathering activities. In the hunter scenario, people were asked to imagine themselves living in the grasslands as part of a small group; their task was to contribute necessary meat to the tribe by hunting big game, trapping small animals, or fishing in a nearby lake. In the gathering condition, the task was to gather food for the tribe by scavenging for edible fruits, nuts, or vegetables. Following our earlier work, participants were asked to rate the relevance of random words to these activities before taking a surprise memory test.

Because the hunting and gathering scenarios described very specific and focused activities, it was possible to create matched control scenarios—that is, scenarios that described virtually the same activities but in a context that was not fitness relevant. The control scenario for hunting instructed participants to imagine hunting for food but as part of a hunting contest rather than for survival; in the gathering control, participants were instructed to search for and collect food items but in an attempt to win a game—a scavenger hunt. This constitutes a methodological advance over previous work in which the control scenarios often described activities that differed greatly from the

ones used in the fitness-relevant scenarios (e.g., moving to a foreign land, planning a bank heist). Again, processing information in a fitness-relevant context improved final free recall of the rated materials. Because both the experimental and control scenarios described essentially the same activities—scavenging or hunting for food—it is difficult to imagine how differential thematic processing could possibly explain the advantage found for fitness-relevant processing.

ESTABLISHING AN EVOLUTIONARY LOCUS.

Although the preceding experiments make a compelling case for the mnemonic power of fitness-relevant processing and argue against some standard explanatory accounts of the advantage (e.g., thematic processing), they still do not establish an evolutionary locus. Unfortunately, it is difficult to gather definitive evidence for an evolutionary locus—that is, a specific adaptation designed to improve memory for fitness-based processing—for a variety of reasons (see Nairne, 2010, for a comprehensive review). For instance, there are no "fossilized" memory traces, there is little evidence for the heritability of cognitive phenomena, and our knowledge about the ancestral environments in which our memory systems actually evolved is limited (Buller, 2005). Moreover, adaptive behavior can arise indirectly, by piggybacking on adaptations that evolved for different reasons (exaptations), or as a result of natural constraints in the environments (e.g., the physical laws of nature or genetic constraints).

However, empirical data can be used to bolster evolutionary accounts. For example, one striking piece of evidence demonstrates ancestral priorities (i.e., experiments showing that our cognitive systems operate most effectively when dealing with ancestral problems or events, particularly those associated with our foraging past). Evidence of this sort is compelling for an evolutionary account because it is difficult to see how experience, or general learning mechanisms, can possibly account for an ancestral priority. For example, New, Cosmides, and Tooby (2007) found that people were faster and more accurate at detecting animate than inanimate objects in a change detection paradigm, even when the inanimate objects were more salient and familiar (e.g., familiar vehicles versus unfamiliar animal species). Evolutionarily significant stimuli (e.g., snakes or spiders) are also easier to asso-

ciate with aversive stimuli than modern fear-relevant stimuli (e.g., guns or electric outlets) (see Öhman & Mineka, 2001, for a review).

Evidence consistent with ancestral priorities has been found using the survival processing paradigm. Weinstein et al. (2008) had people process the relevance of words to a survival situation but varied whether the scenario was set in an ancestral or a modern context. In one condition, people were asked to imagine themselves stranded in the grasslands of a foreign land without basic survival materials. Following Nairne et al. (2007), people were told they would need to find steady supplies of food and water and protect themselves from predators. In a second condition, exactly the same scenario was used but two critical words were changed: *city* was substituted for *grasslands,* and *predators* was replaced by *attackers*. The authors reasoned that escaping from predators in the grasslands closely mimics the problems faced in the environments of evolutionary adaptation; consequently, the ancestral scenario should induce more efficient mnemonic processing than the modern scenario, even though the latter is more familiar and presumably taps a more coherent and stable knowledge base. In support of their hypothesis, better memory for the rated words was found for the group processing the ancestral scenario.

We recently replicated this work and extended it to domains requiring gathering activities rather than escaping from a potential predator (Nairne & Pandeirada, 2010). In the first case, the survival scenario was once again set either in the grasslands or in a city, and participants were asked to imagine they had been hurt and a dangerous infection might be developing. People were told to rate the relevance of words to the task of finding "relevant medicinal plants" to cure the infection (ancestral) or finding "relevant antibiotics" (modern). In a second experiment, again using either a grassland or a city scenario, people were asked to imagine they had not eaten for several days and needed to "search for and gather edible plants" (ancestral) or "search for and buy food" (modern). In all other respects the scenarios were matched exactly. The rating task was followed by a surprise recall test for the rated words. Even though the scenarios differed in only a few words, processing with the ancestral scenario led to better retention than the modern survival context. These data suggest that

the ancestral scenarios may have induced a unique form of survival processing, one congruent with the selection pressures that originally drove the processes of natural selection (see Nairne & Pandeirada, 2010, for an extended discussion).

Conclusions

Once again, it is difficult to make a definitive case for an evolutionary adaptation, especially a cognitive one, although cognitive adaptations must certainly exist. At best, one can develop a convincing and multipronged case, based on a wide foundation of logical and empirical arguments. Memory certainly evolved, which means that the designs of memory systems and their operating characteristics were subject originally to nature's criterion: the enhancement of fitness. Whether the mark of nature's criterion continues to shape and control memory's operation is an empirical question, one that receives support from experiments of the type described earlier.

More generally, though, we have argued for a realignment of theoretical focus in the memory field—away from a solely structural focus (the "how" of remembering) toward a functional one (the "why" of remembering). It is reasonable to assume that our memory systems are functionally designed, regardless of their origins, and any complete understanding of remembering will entail recognition of this fact. Episodic memory did not develop in a vacuum, to react to chance variations in encoding and retrieval environments, but rather to solve particular problems, probably adaptive ones that relate specifically to fitness. As in the rest of the body, we can anticipate a tight fit between memory's form and function; selection pressures, or adaptive problems, constrain how and why structures develop and the final forms they take (Nairne & Pandeirada, 2008b).

As noted earlier, the majority of memory researchers continue to provide primarily structural analyses of memory phenomena, although functional perspectives do exist. For example, there is a growing consensus that our memory systems may be fundamentally prospective, that is, oriented toward the future rather than the past (Schacter & Addis, 2007; Szpunar & McDermott, 2008). The past can never occur again, at least in exactly the same form, so memory systems gain their adaptive edge by improving future responding (Suddendorf

& Corballis, 1997). Other researchers have argued that episodic memory evolved in part to reflect the statistical regularities of events in the environment. There is a processing cost to remembering, so it is adaptive to consider the probabilities that specific memories will be relevant, and therefore needed, in a given environment (Anderson & Schooler, 2000; Shiffrin & Steyvers, 1997). Memory researchers also generally recognize that certain mnemonic processes are adaptive, at least in helping one process information in the present. For instance, the ability to forget is highly adaptive because it helps to eliminate useless clutter; we need to remember where we parked our car today, not yesterday or the week before (Bjork & Bjork, 1988; Nairne & Pandeirada, 2008c).

In a functional analysis, recognition of the goal—the specific problem that the system is attempting to solve—is given priority. Problem-oriented analyses give the investigator a means for measuring progress and a way to separate important from unimportant features in a design. Of course, this is standard operating procedure in applied fields, where the viability of a design is judged by a strict criterion: Does the system solve the design problem that led to its development? To facilitate our understanding of remembering, we are well advised to adopt a similar criterion. To maximize retention in basic and applied settings we should seek to develop encoding techniques that are congruent with the natural design of memory systems. Semantic-based processing and self-referential processing have been used for years in clinical settings to improve retention (Bird, 2001; De Vreese, Neri, Fioravanti, Belloi, & Zanetti, 2001; Mimura et al., 2005), yet a few seconds of survival-based processing produces better free recall than either of these encoding tasks. Thus, understanding the functional problems that drive remembering, and the particular role that fitness-relevant processing plays in long-term retention, should help improve retention in a variety of populations and practical settings.

University, 703 Third Street, West Lafayette, IN 47907-2081
(e-mail: nairne@psych.purdue.edu).

REFERENCES

Anderson, J. R., & Schooler, L. J. (2000). The adaptive nature of memory. In E. Tulving & F. I. M. Craik (Eds.), *The Oxford handbook of memory* (pp. 557–570). New York, NY: Oxford University Press.

Bird, M. (2001). Behavioural difficulties and cued recall of adaptive behaviour in dementia: Experimental and clinical evidence. *Cognitive Rehabilitation in Dementia, 3,* 357–375.

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

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

Buchner, A., Bell, R., Mehl, B., & Musch, J. (2009). No enhanced recognition memory, but better source memory for faces of cheaters. *Evolution and Human Behavior, 30,* 212–224.

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

Buss, D. M. (2005). *The murderer next door: Why the mind is designed to kill.* New York, NY: Penguin.

Craik, F. I. M. (2007). Encoding: A cognitive perspective. In H. L. Roediger III, Y. Dudai, & S. M. Fitzpatrick (Eds.), *Science of memory: Concepts* (pp. 129–135). New York, NY: Oxford University Press.

Craik, F. I. M., & Lockhart, R. S. (1972). Levels of processing: A framework for memory research. *Journal of Verbal Learning and Verbal Behavior, 11,* 671–684.

Craik, F. I. M., & Tulving, E. (1975). Depth of processing and the retention of words in episodic memory. *Journal of Experimental Psychology: General, 104,* 268–294.

De Vreese, L. P., Neri, M., Fioravanti, M., Belloi, L., & Zanetti, O. (2001). Memory rehabilitation in Alzheimer's disease: A review of progress. *International Journal of Geriatric Psychiatry, 16,* 794–809.

Ermer, E., Cosmides, L., & Tooby, J. (2007). Functional specialization and the adaptationist program. In S. W. Gangestad & J. A. Simpson (Eds.), *The evolution of mind: Fundamental questions and controversies* (pp. 86–94). New York, NY: Guilford.

Glenberg, A. M. (1997). What is memory for? *Behavioral and Brain Sciences, 20,* 1–55.

Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society of London: B, 205,* 581–598.

Hunt, R. R., & Einstein, G. O. (1981). Relational and item-specific information in memory. *Journal of Verbal Learning and Verbal Behavior, 20,* 497–514.

Hunt, R. R., & McDaniel, M. A. (1993). The enigma of organization and distinctiveness. *Journal of Memory and Language, 32,* 421–445.

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

Kenrick, D. T., Delton, A. W., Robertson, T., Becker, D. V., & Neuberg, S. L. (2007). How the mind warps: A social evolutionary perspective on cognitive processing disjunctions. In J. P. Forgas, M. G. Haselton, & W. von Hippel (Eds.), *Evolution and the social mind: Evolutionary psychology and the social mind.* New York, NY: Psychology Press.

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

Luminet, O., & Curci, A. (Eds.). (2009). *Flashbulb memories: New issues and new perspectives.* New York, NY: Psychology Press.

McDaniel, M. A., & Bugg, J. M. (2008). Instability in memory phenomena: A common puzzle and a unifying explanation. *Psychonomic Bulletin & Review, 15,* 237–255.

Mimura, M., Komatsu, S. I., Kato, M., Yoshimasu, H., Moriyama, Y., & Kashima, H. (2005). Further evidence for a comparable memory advantage of self-performed tasks in Korsakoff's syndrome and nonamnesic control subjects. *Journal of the International Neuropsychological Society, 11,* 545–553.

Morris, C. D., Bransford, J. D., & Franks, J. J. (1977). Levels of processing versus transfer-appropriate processing. *Journal of Verbal Learning and Verbal Behavior, 16,* 519–533.

Nairne, J. S. (2002). The myth of the encoding–retrieval match. *Memory, 10,* 389–395.

Nairne, J. S. (2005). The functionalist agenda in memory research. In A. F. Healy (Ed.), *Experimental psychology and its applications* (pp. 115–126). Washington, DC: American Psychological Association.

Nairne, J. S. (2010). Adaptive memory: Evolutionary constraints on remembering. In B. H. Ross (Ed.), *The psychology of learning and motivation* (Vol. 53, pp. 1–32). London, England: Academic Press.

Nairne, J. S., & Pandeirada, J. N. S. (2007). *Adaptive memory: Is survival processing special?* Paper presented at the 48th Annual Meeting of the Psychonomic Society.

Nairne, J. S., & Pandeirada, J. N. S. (2008a). Adaptive memory: Is survival processing special? *Journal of Memory and Language, 59,* 377–385.

Nairne, J. S., & Pandeirada, J. N. S. (2008b). Adaptive memory: Remembering with a stone-age brain. *Current Directions in Psychological Science, 17,* 239–243.

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Nairne, J. S., & Pandeirada, J. N. S. (2008c). Forgetting. In H. L. Roediger III (Ed.), *Cognitive psychology of memory*. Vol. 2 of J. Byrne (Ed.), *Learning and memory: A comprehensive reference,* 4 vols. (pp. 179–194). Oxford, England: Elsevier.

Nairne, J. S., & Pandeirada, J. N. S. (2010). Adaptive memory: Ancestral priorities and the mnemonic value of survival processing. *Cognitive Psychology, 61,* 1–22.

Nairne, J. S., Pandeirada, J. N. S., Gregory, K. J., & Van Arsdall, J. E. (2009). Adaptive memory: Fitness-relevance and the hunter–gatherer mind. *Psychological Science, 20,* 740–746.

Nairne, J. S., Pandeirada, J. N. S., & Thompson, S. R. (2008). Adaptive memory: The comparative value of survival processing. *Psychological Science, 19,* 176–180.

Nairne, J. S., Thompson, S. R., & Pandeirada, J. N. S. (2007). Adaptive memory: Survival processing enhances retention. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 33,* 263–273.

New, J., Cosmides, L., & Tooby, J. (2007). Category-specific attention for animals reflects ancestral priorities, not expertise. *Proceedings of the National Academy of Sciences, 104,* 16598–16603.

New, J., Krasnow, M. M., Truxaw, D., & Gaulin, S. J. C. (2007). Spatial adaptations for plant foraging: Women excel and calories count. *Proceedings of the Royal Society of London: B, 274,* 2679–2684.

Öhman, A., & Mineka, S. (2001). Fears, phobia, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review, 108,* 483–522.

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

Paivio, A. (2007). *Mind and its evolution: A dual coding theoretical approach*. Mahwah, NJ: Erlbaum.

Roediger, H. L., III. (2008). Relativity of remembering: Why the laws of memory vanished. *Annual Review of Psychology, 59,* 225–254.

Schacter, D. L., & Addis, D. R. (2007). The cognitive neuroscience of constructive memory: Remembering the past and imagining the future. *Philosophical Transactions of the Royal Society of London: B, 362,* 773–786.

Schmidt, S. R., & Saari, B. (2007). The emotional memory effect: Differential processing or item distinctiveness? *Memory & Cognition, 35,* 1905–1916.

Shiffrin, R. M., & Steyvers, M. (1997). A model for recognition memory: REM: Retrieving effectively from memory. *Psychonomic Bulletin & Review, 4,* 145–166.

Silverman, I., & Eals, M. (1992). Sex differences in spatial abilities: Evolutionary theory and data. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary theory and the generation of culture* (pp. 531–549). New York, NY: Oxford University Press.

Suddendorf, T., & Corballis, M. C. (1997). Mental time travel and the evolution of the human mind. *General, Social, and General Psychology Monographs, 123,* 133–167.

Surprenant, A. M., & Neath, I. (2009). *Principles of memory*. New York, NY: Psychology Press.

Symons, D. (1992). On the use and misuse of Darwinism in the study of human behavior. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 137–159). New York, NY: Oxford University Press.

Szpunar, K. K., & McDermott, K. B. (2008). Episodic memory: An evolving concept. In D. Sweat, R. Menzel, H. Eichenbaum, & H. L. Roediger III (Eds.), *Learning and memory: A comprehensive reference* (pp. 491–510). Oxford, England: Elsevier.

Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary theory and the generation of culture* (pp. 19–136). New York, NY: Oxford University Press.

Tulving, E. (1983). *Elements of episodic memory*. New York, NY: Oxford University Press.

Tulving, E., & Craik, F. I. M. (Eds.). (2000). *The Oxford handbook of memory*. Oxford, England: Oxford University Press.

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

Voyer, D., Postma, A., Brake, B., & Imperato-McGinley, J. (2007). Gender differences in object location memory: A meta-analysis. *Psychonomic Bulletin & Review, 14,* 23–38.

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

Winograd, E., & Neisser, U. (1992). *Affect and accuracy in recall: Studies of "flashbulb memories."* New York, NY: Cambridge University Press.