Adaptive Memory: The Mnemonic Power of Survival-based Generation

Abstract

Four experiments investigated the mnemonic effects of generating survival situations. People were given target words and asked to generate survival situations involving that stimulus (e.g., DOOR: "I'm in a house that's on fire, and I can escape through the door"). No constraints were placed on the generation process, other than it must be survival-related and refer to the target stimulus. Following a series of these generation trials people were given a surprise retention test for the target words. Across four experiments the survival generation task produced significantly better retention than several deep processing controls including: (1) a pleasantness-rating task, (2) an autobiographical retrieval task, and (3) a task that required people to generate unusual uses for the target items. These results demonstrate the power of survival processing in a new way and provide diagnostic information about the proximate mechanisms that may underlie survival processing advantages. They also extend the generality of survival processing beyond the standard relevance-rating procedure that has been used in virtually all prior research.

Key Words: adaptive memory, evolution, recall, survival processing

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The capacity to remember and forget evolved, guided by nature's criterion—the enhancement of inclusive fitness (see Klein, Cosmides, Tooby, & Chance, 2002; Sherry & Schacter, 1987). As a result, we might reasonably expect memory functioning to show sensitivity to the selection pressures that guided its development. Numerous scholars have suggested that sensory and other cognitive systems are likely crafted and tuned to solve the particular adaptive problems presented by a species' environmental niche (for a general review, see Shettleworth, 2010). For example, some have argued that the spectral sensitivities of the visual system emerged from adaptive problems related to the discovery of ripe fruit or edible leaves (Dominy & Lucas, 2001) or to the avoidance of snakes in the grass (Isbell, 2006).

Most psychologists acknowledge the existence of natural learning-based "crib sheets," especially along that fitness-relevant. dimensions are Pavlovian conditioning, the prototype of a general learning system, taps the learning of inter-event relations, namely that one event signals another. Yet it is much easier to condition a signaling stimulus with food or shock (unconditioned stimuli) than with a neutral stimulus such as a brick or a book. Unconditioned stimuli are special stimuli—they automatically produce responses, irrespective experience, and are ingrained parts of the biological architecture. The ability to learn about the signaling properties of such events presumably evolved to enhance an organism's ability to solve survival- or matingrelevant problems; indeed, there is now considerable evidence to support a connection between basic learning processes and the subsequent enhancement of fitness (Hollis, Pharr, Dumas, Britton, & Field, 1997; Krause, 2015; Shettleworth, 2010).

Forms of prepared learning are also well-accepted, again for stimuli and events that are fitness-relevant. Cue-to-consequence effects are persistent across species, such as the well-known finding that tastes are more easily associated with gastric distress than with foot shock (Garcia & Koelling, 1966). Selective associations in aversion conditioning occur in 1-day-old rat pups (Domjan, 2005), suggesting that such tendencies are part of an inherited learning architecture. Conditioning benefits have also been found in people for evolutionarily-relevant stimuli such as snakes and spiders. Öhman and Mineka (2001) reported that it was easier for people to learn that the appearance of a snake

signaled the occurrence of an aversive event than when a neutral stimulus (e.g., flowers) signaled the same event. There is even some evidence that ancestrally-relevant stimuli (snakes) yield faster conditioning than matched fitness-relevant stimuli that are modern in origin (e.g., guns; see Cook, Hodes, & Lang, 1986), although this finding remains somewhat controversial (e.g., Hugdahl & Johnsen, 1989).

In the human memory literature, though, less attention has been paid to natural "tunings" or proclivities to remember that originate from evolutionary selection pressures. There is a literature on value-directed remembering (e.g., Castel, Farb, & Craik, 2007) but value is defined arbitrarily for each target stimulus and little consideration has been given to determining value in natural environments. From an evolutionary perspective, value is defined via nature's criterion, so one might anticipate that stimuli and responses related to fitness will be learned and remembered particularly well (Nairne, 2005). Recent work on "adaptive memory" is confirming this expectation—for example, it is now well-established that animate stimuli, which can be predators, food, mating partners, and competitors for resources, are remembered better than inanimate stimuli that have been equated on numerous dimensions (e.g., Bonin, Gelin, & Bugaiska, 2012; Nairne, VanArsdall, Pandeirada, Cogdill, & LeBreton, 2013). Evidence indicates as well that contaminated stimuli, which are potentially sources for disease, tend to be remembered better than control stimuli (Fernandes, Pandeirada, Soares, & Nairne, 2017) as are potential mating partners under some conditions (Pandeirada, Fernandes, Vasconcelos, & Nairne, 2017).

However, most of the work on adaptive memory has dealt with survival processing, a technique in which people are asked to consider the relevance of to-be-remembered information to an imagined survival situation (see Nairne, Thompson, & Pandeirada, 2007). Survival processing generally produces excellent long-term retention. For example, Nairne, Pandeirada, and Thompson (2008) showed that survival processing can produce recall levels that exceed those of the best-known mnemonic encoding techniques including forming a visual image, relating information to the self, generating information from cue fragments, and intentional learning. Given that biological systems evolve by solving adaptive problems related to survival and reproduction, episodic memory may have been "tuned" by natural selection to

retain fitness-relevant information especially well (Burns, Burns, & Hwang, 2011; Nairne et al, 2007).

The survival processing memory advantage has now been replicated repeatedly (see Kazanas & Altarriba, 2015; Scofield, Buchanan, & Kostic, 2017), including as part of the recent Open Science replication project (Müller & Renkewitz, 2015). However, virtually all work on survival processing has focused on a single rating paradigm. People are shown lists of words or objects and are asked to rate the relevance of each item (typically on a 5-point scale) to an imagined survival scenario, one in which the participant imagines being stranded in the grasslands of a foreign land without food or water and under potential threat from predators. In control conditions, participants produce ratings to the same items, but to a survival-neutral scenario (e.g., moving to a foreign land) or to other deep processing tasks. Superior performance on surprise recall or recognition tests has consistently been found for the survival condition.

Not surprisingly, researchers have been keenly interested in determining the proximate mechanisms that are responsible for the benefit. Common candidates have included traditional domain-general processes, such as elaboration or deep processing, which are assumed to be co-opted successfully in the relevance rating paradigm (see Kroneisen & Erdfelder, 2011; Howe & Derbish, 2010). The presence of co-opting by itself, of course, is not particularly diagnostic. Many adaptations rely on coopting of otherwise general processes to achieve their desired effects. The fight-or-flight response is a case in point. Fight-or-flight relies on a host of co-opted systems—the release of hormones, changes in blood pressure and blood sugar, suppression of the immune system, and so on. The fact that a basic process is involved, such as the regulation of blood pressure, does not diminish its status as an adaptation. In the case of survival processing, our memory systems may be naturally tuned to recruit general processes, such as elaboration, when the processing is survival relevant (see Nairne & Pandeirada, 2016). Explanations can co-exist at several levels, and it is generally considered prudent not to confuse evolutionary (or ultimate) explanations with proximate accounts (Scott-Phillips, Dickens, & West, 2011).

On the other hand, it is possible that co-opting in the survival processing paradigm is simply an artifact of the procedure, particularly the fixed survival scenario that is commonly used in survival processing experiments. Relative to control scenarios, such as imagining locating and purchasing a new home and transporting one's belongings, perhaps the survival scenario is simply richer or more complex producing, on average, relatively more variable encodings across items. Although survival processing benefits have been produced using a variety of survival and control scenarios (see Kazanas & Altarriba, 2015; Nairne & Pandeirada, 2016), including scenarios that are relatively narrow and constrained (see Nairne & Pandeirada, 2010) and even matched (Nairne, Pandeirada, Gregory, & VanArsdall, 2009), in all cases items are compared to a single survival or control scenario that remains constant across all items. In addition, a decade of research has produced apparent boundary conditions—for example, survival advantages are not typically found with faces (Savine, Scullin, & Roediger, 2011), stories (Seamon et al., 2012), perhaps with abstract words (Bell, Röer, & Buchner, 2013), and when the "fit" between the rated word and the scenario is particularly high (Butler, Kang, & Roediger, 2009). Moreover, in some cases forms of processing that are clearly relevant to fitness, such as determining the relevance of target words to successful mating, have not vielded mnemonic advantages (e.g., Seitz, Polack, & Miller, 2018). There is clearly a need to extend the study of survival processing to new experimental procedures. both to establish the generality of the survival benefit and to expand the range of control procedures that can be tested.

The current experiments introduce a novel paradigm for studying survival processing, one that does not rely on any particular imagined scenario. Instead, people are asked to generate their own survival situations within which a target stimulus is potentially relevant. No constraints are placed on the generation process, other than the requirement that it must be survival-based and refer to the target stimulus. Arguably, this new procedure is a more natural way to induce survival processing, more akin to asking a person to freely construct a visual image rather than to glean information about imaginal processing by having a participant focus on a particular printed image. The participant is required to think about survival relevance, but not with respect to a single fixed and unfamiliar context, or to a particular set of activities (as in the normal rating procedure). As we discuss throughout, this procedure enables us to introduce some

new control procedures, ones that directly address existing proximate accounts of the survival advantage.

Four experiments are reported. Experiment 1 introduces the new procedure, comparing survival generation to a traditional deep processing control, rating items for pleasantness. Experiments 2 and 3 introduce a new control procedure, one designed to be self-relevant and accessible: People are asked to generate the last time that they personally saw or interacted with the target stimulus. Not only does this control task induce selfreferential processing, but it also requires people to retrieve particular autobiographical memories of the target; both self-referential processing and retrieval are known to boost episodic recall significantly (e.g., Klein, Loftus, & Burton, 1989; Roediger & Karpicke, 2006). Finally, Experiment 4 compares survival generation to a control task that focuses on generating unusual or distinctive uses for the target stimulus.

Experiment 1

Experiment 1 uses a blocked within-subject design to compare two encoding conditions: *survival generation*, which required participants to construct a survival situation in which a presented word, representing an object, might be involved, and a simple *pleasantness rating* task. Rating for pleasantness is a prototypical "deep processing" task (e.g., Hyde & Jenkins, 1973) known to produce good recall; it has often been used in the survival processing literature as a benchmark control condition (e.g., Nairne et al. 2007). Participants performed two blocks of survival generation trials and two blocks of pleasantness ratings. The encoding trials were followed by a short distractor task and, lastly, a surprise free recall test.

Method

Participants and apparatus. Fifty-two native English speakers were recruited from an undergraduate psychology course at Purdue University. Our choice of sample size was based on experience with the single-item rating procedure. If we use the within-subject effect size recently reported by Scofield et al. (2017) in their meta-analysis of the survival processing effect ($\eta_p^2 = .17$), our sample size of 52 participants would yield a power estimate greater than .99, but it is unclear what the true effect size might be for this new procedure. The sample

size was determined a priori and used as a stopping criterion. Approximately half of the participants were female (52%) and the average age of the sample was 18.77 (SD = 0.94). Subjects were awarded partial course credit for participating in an experimental session lasting fewer than 30 minutes. The procedure was approved by the Purdue University IRB.

Materials and design. Twenty-four object nouns (plus four practice nouns) with familiarity, concreteness, and imageability values above 450 were selected from the MRC psycholinguistic database (Coltheart, 1981; norming data were unavailable for two of the words). The 24 words were organized into four blocks of six words that were equated for average familiarity, concreteness, imageability, and length. This experiment used a within-subject design such that each participant made pleasantness ratings about half the words (12) and generated survival situations about the other half (12).

Procedure. In four alternating blocks of six words, participants were instructed either to rate the pleasantness of each object (P) or to generate a survival situation (S) that involved the object. Condition (S or P) alternated across the blocks and was counterbalanced between participants (SPSP or PSPS). The instructions for the two tasks were as follows:

Survival Generation: "In this task, we are going to show you a series of object names. We would like you to consider how each object might be relevant to your survival—that is, we want you to think of a survival situation in which this object might be involved.

For example:

Door: "I'm in a house that's on fire, and I can escape through the door"

Truck: "I'm walking across the street and a truck is racing towards me"

Umbrella: "I am suffering from hypothermia, I can use the umbrella to create a shelter"

Pillow: "Someone is smothering me with a pillow"

Please try to come up with a different situation for each object. Type a few words or a phrase describing the situation into the text-box. When you have completed typing the situation, click the NEXT button to move on to the next object. You will have as much time as you need to type your response, but please use your time wisely.

Please try to picture yourself in each survival situation and type a few words or a phrase in the text-box provided."

Pleasantness: "In this task, we are going to show you a series of object names, and we would like you to rate the pleasantness of each object. Some of the objects may be pleasant, others may not—it's up to you to decide.

The scale will range from "totally unpleasant" to "extremely pleasant". Make your decision by clicking on the option that you wish to select. Please try to use the whole scale.

Be careful: each object name will appear for only five seconds so you'll need to make your decisions rather quickly."

For the survival generation task, participants saw each object and the prompt "Describe a survival situation in which this object might be involved" along with a text-box into which they could type their response. For the pleasantness rating task, participants saw each object and the prompt "How pleasant is this object?" along with a 5-point rating scale which ranged from "totally unpleasant" to "extremely pleasant". Participants had 5 seconds to make each rating and used the computer mouse to click on the rating that they wished to select. The order of the words within each block was randomized across participants.

Following the encoding trials, participants spent 2 minutes performing an even/odd distractor task in which they saw a series of single digit numbers and had to judge whether each was even or odd. After the distractor task, participants were asked to recall all the objects that had been presented, regardless of the encoding task. Participants were given 8 minutes to type as many words as they could remember in any order into a text-box that was visible on the computer screen for the duration of the recall task.

Results and Discussion

The level of statistical significance, unless otherwise noted, was set at p < .05 for all comparisons. Participants had little trouble with the survival generation task, producing responses on 99.5% of the trials. Generation responses averaged 13.03 words in length (SD = 3.98) and took 27.78 seconds (SD = 8.95), on average, to complete. Response times for the pleasantness rating

task averaged 2.28 (SD = 0.45) seconds and were completed on 98.5% of the trials. Because of the high completion rates, we opted not to conditionalize the recall data on a successful generation or rating.

The results of main interest, from the surprise free recall test, are shown in Figure 1. There was an extremely robust survival processing advantage. Out of the 52 participants, 48 recalled more target words processed for survival than words rated for pleasantness, no one showed the reverse pattern, and there were 4 ties. Not surprisingly, the survival recall advantage was statistically significant at both the subject F(1, 51) = 108.05, MSE = .02, p < .001, $\eta_p^2 = .68$ and the item level, F(1, 23) = 76.77, MSE = .01, p < .001, $\eta_p^2 = .77$.

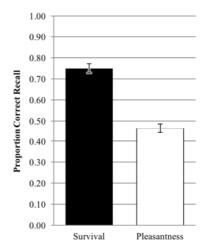


Figure 1. Proportion correct recall per condition for Experiment 1. Error bars represent standard error of the mean.

We acknowledge that a survival advantage under these conditions might not seem surprising given that survival generation is clearly a more effortful task than making a pleasantness rating. However, rating items for pleasantness is a prototypical "deep processing" task, one that requires semantic analysis, and it has repeatedly been shown to yield excellent long-term retention (e.g., Hyde & Jenkins, 1973); perhaps more importantly, it is one of the standard control procedures used in the existing survival processing literature. From this standpoint, the fact that survival generation yielded roughly a 30% recall advantage is certainly noteworthy. But asking people to generate any kind of scenario or situation might yield a more elaborative memory trace than a simple pleasantness rating. To better equate the conditions in Experiments 2-4 we switched to control procedures that also required people to generate responses in written form.

Experiment 2

Experiment 2 attempts to replicate the survival benefit found in Experiment 1 using an alternative control procedure, one that required the participant to generate a written response rather than a single rating score. Because the generation procedure is flexible, we were able to develop a control procedure that addresses at least one prominent account of the survival advantage as well: self-referential processing. A number of researchers have suggested that survival processing may induce, at least in part, a kind of self-referential processing (Burns et al., 2011; Dewhurst, Anderson, Grace, & Boland, 2017; Klein, 2012). Relating information to the self, such as when people are asked to decide if trait adjectives are self-descriptive, is generally agreed to have a powerful effect on long-term retention (for a review, see Symons & Johnson, 1997). Because "few things are more selfrelevant than one's personal survival" (Klein, 2012, p.1235; see also Burns et al., 2011), survival processing may be inherently self-referential, leading to mnemonic benefits (see also, Cunningham, Brady-Van den Bos, Gill, & Turk, 2013).

At the same time, it is important to keep in mind that the benefits of self-referential processing are generally assumed to accrue from one's ability to integrate the to-be-remembered event into a wellestablished and easily accessible self-structure or schema (see Symons & Johnson, 1997). For example, if a participant draws a connection between a "bucket" and an attempt to wash the car last weekend, then he or she has gained an accessible retrieval structure in the form of a specific autobiographical event. It is doubtful that most university undergraduates carry around well-formed and accessible schema about surviving in the grasslands of a foreign land, but it is conceivable that people are able to use some form of autobiographical encoding to secure excellent long-term retention. With this reasoning in mind, we picked a control condition that not only required people to generate their own scenarios, as in the survival generation task, but one that was unambiguously self-relevant. People were asked to think about and write down the last time they had interacted with the target stimulus (e.g., UMBRELLA: "It rained last Thursday and

I used an umbrella"). This is an autobiographical task, one that required the participant to retrieve a specific event from his or her life (see Klein, 2012). Recovery of a known autobiographical episode should set the occasion for elaboration of the target stimulus as well as secure any benefit that results from the retrieval process itself (see Roediger & Karpicke, 2006). Because the benefits of retrieval practice are often greater after a delay, and also to test the longevity of the survival benefit, we decided to test retention either immediately (after a 2-minute distractor task) or after a delay of 48 hours.

Experiment 2 used the same within-subject blocked design employed in Experiment 1. In two of the blocks, participants generated relevant survival situations and in the other two blocks people were asked to generate relevant autobiographical situations. After the encoding trials, everyone was given a surprise free recall test for the target words—either immediately after a short distractor task or after 48 hours; retention interval was manipulated between-subjects.

Method

Participants and apparatus. One hundred and four native English speakers (32% females) from an undergraduate introductory psychology course at Purdue University participated in exchange for partial course credit ($M_{\rm age}=19.30,\ SD=1.37$). Fifty-two participants completed a single experimental session lasting fewer than 30 minutes; the other 52 participants completed two experimental sessions with a 48-hour delay between the first and the second session. Again, our choice of sample size was based on experience, but a power analysis using either the effect size from Scofield et al. (2017) or the effect size obtained in Experiment 1 yields an estimated power greater than .99. The sample size was determined a priori and used as a stopping criterion. The procedure was approved by the Purdue IRB.

Materials and design. The stimuli were identical to those used in Experiment 1. For this experiment, we used a mixed design. Encoding condition (survival versus autobiographical) was manipulated within subjects and recall timing (immediate versus delayed) was manipulated between subjects such that half of the participants were given a surprise free-recall task immediately after the encoding and distractor tasks and the other half were given a surprise free-recall task after a 48-hour delay.

Procedure. The general procedure was the same as described in Experiment 1 except for two changes: (1) for the control task we used an autobiographical recall task instead of a pleasantness rating task and (2) half of the participants performed the free-recall task after a 48-hour delay. As in Experiment 1, participants saw four blocks of six words in alternating conditions (ASAS or SASA). Participants generated survival situations for half of the blocks and described the last time they saw or interacted with the objects (autobiographical recall) for the other half of the blocks. The instructions for the autobiographical recall task were as follows:

Autobiographical: "In this task, we are going to show you a series of object names. We would like you to think about the last time you saw or interacted with each object.

For example:

Door: "I left the house this morning through the front door"

Truck: "I saw someone driving a truck yesterday afternoon"

Umbrella: "It rained last Thursday and I used my umbrella"

Pillow: "Last night I slept with a pillow"

Please try to respond with a specific experience from your life for each object. Type a few words or a phrase describing the event into the text-box. When you have completed typing the event, click the NEXT button to move on to the next object. You will have as much time as you need to type your response, but please use your time wisely.

Please bring to mind your experience and type a few words or a phrase in the text-box provided."

The encoding task was followed by an even/odd distractor task that was identical to the one described in Experiment 1. Following the distractor task participants either performed the surprise free-recall task or were dismissed and given the surprise free-recall task when they returned to the lab after a 48-hour delay. All other aspects of the experiment were as described in Experiment 1.

Results and Discussion

As in Experiment 1, participants had no trouble with the generation tasks, providing responses on over 99% of the trials in both the survival and

autobiographical conditions. For the survival task, participants took 28.52 seconds (SD=11.47), on average, to generate a response and 21.58 seconds (SD=6.73) in the autobiographical condition; this response time difference was significant at both the subject (t(103)=8.37, p<.001, d=0.82) and the item level, (t(23)=5.53, p<.001, d=1.13). There was also a significant difference in the average length of the generated responses: 12.84 (SD=3.44) words in the survival condition and 10.68 (SD=2.54) in the autobiographical condition, $t_{\rm subject}(103)=8.00, p<.001, d=0.78$, and $t_{\rm item}(23)=6.59, p<.001, d=1.35$.

The results of the surprise free recall test are shown in Figure 2, broken down by type of generated response (survival versus autobiographical) and delay (immediate versus delayed). An overall analysis of variance (ANOVA) on the data revealed a main effect of generation condition, F(1,102) = 18.34, MSE = .02, p < .02.001, $\eta_{p}^{2} = .15$, a main effect of delay, F(1,102) =199.97, MSE = .04, p < .001, $\eta_p^2 = .66$, and a significant interaction between condition and delay, F(1,102) =4.93, MSE = .02, p = .03, $\eta_p^2 = .05$. To explore the significant interaction further, we conducted paired *t*-tests performance survival comparing between autobiographical in each delay group. The effect of condition was marginally significant in the immediate recall group and significant in the delay group, t(51) =1.88, p = .065, d = 0.26, and t(51) = 3.89, p < .001, d = 0.060.54, respectively. As in Experiment 1, a significant survival processing benefit was present overall but here it occurred relative to a control condition that also required a form of generation. It is worth noting that survival generation produced smaller effects in this case, compared to pleasantness ratings, suggesting that the effortful nature of the generation task may have played some role in producing the very robust recall advantage seen in Experiment 1. There was considerable forgetting over 48 hours, as expected, but the survival advantage remained intact, and even increased significantly, on the delayed retention test. Again, these data provide strong support for the conclusion that survival processing is a powerful encoding technique, one that generalizes across different experimental procedures.

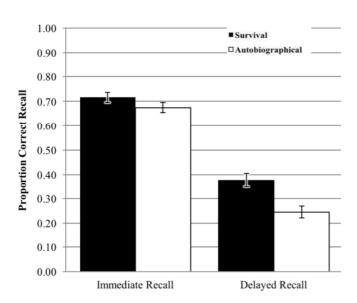


Figure 2. Proportion correct recall per condition for Experiment 2. Error bars correspond to standard error of the mean.

Demonstrating that the survival advantage remains intact when paired against an autobiographical control is important because self-referential processing has frequently been used to account for the survival benefit in the traditional relevance-rating paradigm (e.g., Burns et al., 2011; Cunningham et al., 2013; Dewhurst et al., 2017). In our original report (Nairne et al., 2007), we used a self-relevant control that required people to rate how easily a target word "brings to mind an important personal experience." Survival processing produced significantly better retention than this control condition, but Klein (2012) argued persuasively that participants must actually retrieve the autobiographical experience in order to maximize the beneficial effect of self-relevant processing; simply asking the participant to rate the ease with which something comes to mind may not require retrieval of any specific autobiographical event. With retrieval-based instructions, in which participants were instructed to retrieve then and rate specific autobiographical events, Klein (2012) found no significant survival processing advantage. In the present experiment, of course, people were required to retrieve and write down a specific autobiographical event involving the target stimulus and a significant survival processing advantage occurred. Thus, the results of Experiment 2 demonstrate that self-referential processing cannot provide a complete account of survival processing advantages, although it conceivably plays some role.

It is also worth noting that our autobiographical task required retrieval of a specific prior event, one involving the target stimulus. Practicing retrieval of a target stimulus has been shown to be an extremely effective way of enhancing retention, especially after a delay (see Roediger & Karpicke, 2006). In the present case, we tested retention after 48 hours and detected a strong survival advantage against the retrieval-based autobiographical condition; in fact, the size of the survival advantage actually increased over the delay. At this point we can offer no explanation for the interaction. Previous experiments using the single-item rating procedure have also found strong survival processing benefits after a delay of 48 hours, but the size of the advantage did not change significantly between immediate and delayed testing in those experiments (Raymaekers, Otgaar, & Smeets, 2014; see also Clark & Bruno, 2016).

At the same time, we failed to equate either the timing or the length of the generation response across the survival and autobiographical conditions. However, to analyze the relationship between condition and recall while accounting for response time and length differences, we constructed mixed logit models using the lme4 package (Bates, Mächler, Bolker & Walker, 2015) in R (R Core Team, 2016) and compared the models using parametric bootstrapping with the pbkrtest package (Halekoh & Højsgaard, 2014). We compared a model that included response time, length and delay (immediate recall vs. delayed recall) as fixed effects and random effects of subject and item (Recall ~ Delay + Length + ResponseTime + (1|Subject) + (1|Item)) against a model that included response time, length, delay, and condition as fixed effects and subject and item as random effects (Recall ~ Delay*Condition + Length + ResponseTime + (1|Subject) + (1|Item)). 1 We found that including condition significantly improved the model fit based on a Likelihood Ratio Test ($\chi^2(2) = 17.23$, p = .0002). Specifically, there was a significant effect of condition (z = 3.23, p = .001) and a significant condition by delay interaction (z = 2.64, p = .008) in a model that included RT and length. Thus, condition added additional predictive value above and beyond response time and length.

Experiment 3

Experiment 3 was designed with two goals in mind: First, in an effort to equate the timing and length of the generation response between the autobiographical and survival conditions we tweaked the instructions in the autobiographical condition. In addition to describing an instance from their life in which the target object was involved, participants were also required to specify the particular time and place. This new requirement was intended to increase the length and time required to generate a response and, perhaps, add to the precision of the retrieved memory as well.

Our second goal in Experiment 3 was to replicate the survival advantage using a completely betweensubject design. One of the signature characteristics of the survival processing effect is that it reliably occurs using both within- and between-subject designs (see Nairne et al., 2007). A number of mnemonic phenomena are absent or dramatically reduced in between-subject or betweenlist designs (see McDaniel & Bugg, 2008, for a review). When mnemonic effects are found exclusively in withinsubject designs, distinctive processing might be involved (i.e., Condition A is enhanced because it stands out from control condition B); or, in some cases a manipulation (e.g., generation or word frequency) can have dissociative effects on item and order information that selectively hurt condition performance in a between-subject design (e.g., Nairne, Riegler, & Serra, 1991). If the advantage shown by the survival generation procedure in Experiments 1 and 2 is similar to the survival advantage found in the relevance-rating paradigm, the effect should generalize to a completely between-subject design.

Method

Participants and apparatus. Eighty native English-speaking Purdue University undergraduates (58% females; one participant chose not to report his/her sex) participated in a single experimental session lasting fewer than 30 minutes in exchange for partial course credit. The participant's mean age was of 19 years (SD = 2.08). Using η_p^2 from the main effect of condition obtained in Experiment 2 our sample size yields an estimated power that is greater than .95. The sample size was determined a priori and used as a stopping criterion. The procedure was approved by the Purdue University IRB.

Materials and design. The stimuli were identical to those used in the previous two experiments. Unlike Experiments 1 and 2, condition (survival versus autobiographical) was manipulated between subjects.

Procedure. The general procedure closely followed that of the immediate-memory condition described in Experiment 2 except that participants only performed one type of encoding task, either a survival situation generation task or an autobiographical recall task. The instructions for the autobiographical recall task were changed such that participants were no longer asked to recall the most recent time the object was seen. Instead, participants in the autobiographical condition were asked to describe an instance from their life in which the object was involved and to specify the time and place the instance occurred. The instructions were as follows:

Autobiographical: "In this task, we are going to show you a series of object names. We would like you to think about a specific event in your life when each object was relevant—that is, we want you to think of a specific instance from your life in which each object was involved. Please specify the time, place and relevance in your answer.

For example:

Door: "About a month ago I replaced the handle on the front door of my house"

Truck: "In August of 2016 I used my uncle's truck when I moved to Indiana for college"

Umbrella: "Last Thursday when it rained my umbrella turned inside-out while I was walking from Stewart Hall to the Psychology Building"

Pillow: "When I was five one of the pillows on my bed had an elephant on it"

Please try to respond with a specific experience from your life for each object. Type a few words or a phrase describing the details of the event, including when and where it took place, into the text-box. When you have completed typing the event, click the NEXT button to move on to the next object. You will have as much time as you need to type your response, but please use your time wisely.

Please bring to mind your experience and type a few words or a phrase in the text-box provided."

After the encoding task participants engaged in the distractor task which was immediately followed by the free-recall task. Except for the changes to the instructions and the between subject design, all other aspects of the procedure were the same as those described in the previous experiments.

Results and Discussion

Participants successfully completed the generation tasks on over 99% of the trials in both conditions. In the present case, however, no differences were found in generation times between conditions: Survival generation averaged 27.74 seconds (SD = 13.82) whereas autobiographical generation averaged 30.54 seconds (SD = 16.03); t(78) < 1 for the subject-based analysis and t(23) = -1.88, p = .07, for the item analysis. For length of response, there was an advantage favoring the autobiographical condition with a mean value of 14.35 words (SD = 5.28) versus 12.50 words (SD = 3.73) in the survival condition; this difference was significant at both the subject, t(78) = -2.17, p = .03, d = 0.49, and the item level, t(23) = -6.26, p < .001, d = 1.28.

The results of the final free recall test are shown in Figure 3. Once again, we obtained a survival processing advantage that was significant at both the subject, F(1,78) = 12.11, MSE = 0.019, p < .001, $\eta_p^2 =$ 0.13, and the item level, F(1,23) = 16.26, MSE = 0.01, p < .001, $\eta_p^2 = 0.41$. The fact that a robust survival processing advantage occurs in a between-subject design encourages us to believe that our generation procedure taps the same mnemonic mechanisms that bolster retention in the traditional relevance-rating paradigm. As noted earlier, a number of mnemonic effects are absent or drastically reduced in between-subject designs, but the survival processing effect remains robust regardless of design. The fact that the survival advantage is found in both within- and between-subject designs also lowers the chances that it can be attributed simply to a "distinctiveness" effect, which tends to occur primarily in within-subject designs (see Schmidt, 1991). Survival generation is admittedly an unusual task, one that requires people to think about objects in an atypical way, and it could have led to encodings that simply stood out relative to more typical or familiar autobiographical events. In the present case, all of the events within a list (survival or autobiographical) were processed in the same way, effectively limiting the episodic "background" against which items can be distinctive.

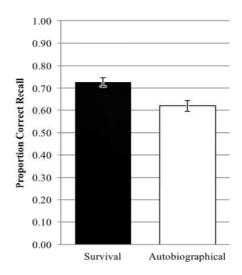


Figure 3. Proportion correct recall per condition for Experiment 3. Error bars represent standard error of the mean.

Experiment 3 is also important because it equated the timing and length of the generation response across conditions—in fact, the autobiographical task actually took longer to produce and averaged more words. Response time and generation length favored the survival condition in Experiments 1 and 2, allowing for an alternative interpretation of the survival benefit. The current experiment effectively rules out this interpretation of the data.

Experiment 4

The between-subject design of Experiment 3 was used again in Experiment 4, but with a new control procedure. As just discussed, asking people to consider how an object might be relevant in a survival situation is an atypical task, one that undoubtedly causes people to think about the target stimulus in an unusual way. Although a traditional distinctiveness account seems untenable given the results of Experiment 3, it is conceivable that the atypical nature of survival generation leads to a more elaborative memory trace, or requires one to engage in a deeper form of processing. In Experiment 4 participants in the control group were asked to think of a situation in which the target stimulus could be used in an unusual way —that is, in a way that is different from its typical use.

This control procedure also requires the participant to generate a functional use for the target object. In the autobiographical control used in Experiments 2 and 3, people simply had to retrieve a situation involving an object which, in turn, may or may not have invoked consideration of the object's function. Bell, Röer, & Buchner (2015) recently suggested that thinking about an item's function may be a crucial component of the survival processing effect. The effect itself, they argued, "may be a byproduct of adaptive mechanisms that constitute the unique human capabilities of making plans, and to flexibly simulate actions with the goal of manipulating the external environment" (p. 1045; see also Klein, Robertson, & Delton, 2010). Although thinking about the function of an object has been a part of control scenarios used previously in the relevance-rating paradigm (such as moving to a foreign land), those control situations have tended to be familiar and, thus, people likely thought about using the object in a typical way. In the present case, people were explicitly instructed to think about how the object can be used in a way that is different from its typical use (e.g., UMBRELLA: "When someone's grocery bad rips, they can turn an umbrella upside down and use it to hold groceries").

Method

Participants and apparatus. Eighty native English-speaking Purdue University undergraduates (61% females, one participant chose not to report his/her sex; $M_{\rm age} = 18.75$, SD = 1.07) participated in exchange for partial course credit. Using $\eta_{\rm p}^2$ from the main effect of condition obtained in Experiment 3 our sample size yields an estimated power that is greater than .93. The sample size was determined a priori and used as a stopping criterion. The procedure was approved by the Purdue IRB.

Materials and design. The stimuli and design were identical to those described in Experiment 3 (except the word "truck" was removed as an example).

Procedure. All aspects of the procedure were identical to those described in Experiment 3 expect that the control condition was changed from an autobiographical recall task to an unusual use generation task. The instructions for the unusual use generation task were as follows:

Unusual Use: "In this task, we are going to show you a series of object names. For each object, we would like you to think of a situation in which

the object would be used in an unusual way — that is, we want you to think of a situation in which this object is used in a way that is different from its typical use.

For example:

Door: "When a table breaks, its legs can be attached to a door for use as a new table"

Umbrella: "When someone's grocery bag rips, they can turn an umbrella upside down and use it to hold the groceries"

Pillow: "To prevent a roommate from stealing, a pillow can be opened to hide money in the stuffing"

Please try to come up with a different situation for each object. Type a few words or a phrase describing the situation into the text-box. When you have completed typing the situation, click the NEXT button to move on to the next object. You will have as much time as you need to type your response, but please use your time wisely.

Please try to picture each situation and type a few words or a phrase in the text-box provided."

As in the previous experiments, the encoding task was followed by a 2-minutes distractor task and 8 minutes of free-recall.

Results and Discussion

Participants had no trouble with the generation tasks, providing responses on over 99% of the trials in both the survival and unusual conditions. For the survival task, participants took 30.87 seconds, on average, to generate a response compared to 33.37 seconds in the unusual condition; this response time difference failed to reach statistical significance in either the subject (t(78)) = -0.83) or the item data, (t(23)) = -1.64, p = .11). There was a significant difference in the average length of the generated responses: 12.59 words in the survival condition and 10.37 in the unusual condition, $t_{\text{subject}}(78)$ = 2.43, p = .02, d = 0.54, and $t_{\text{item}}(23)$ = 9.68, p < .001, d = 1.98

The recall results are shown in Figure 4. Replicating the previous experiments, there was a significant advantage for survival generation at both the subject, F(1, 78) = 9.59, MSE = .02, p < .004, $\eta_p^2 = .11$ and the item level, F(1, 23) = 19.07, MSE = .006, p < .001, $\eta_p^2 = .45$. In this case, of course, the survival benefit

emerged against a condition that required the participant to generate an unusual use for the target object. Presumably constructing a survival situation also induces the participant to think about the object in an atypical way (see the General Discussion). In addition, unlike in the previous experiments, the control task also required people to think about how the object could be *used* which further equates across conditions and helps to rule out another interpretation of the present survival benefits (i.e., thinking about function; Bell et al., 2015).

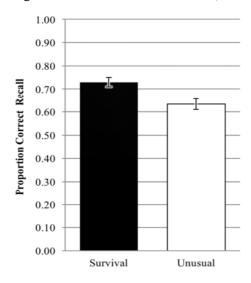


Figure 4. Proportion correct recall per condition for Experiment 4. Error bars represent standard error of the mean.

The only troubling aspect of these data is the failure to equate the length of the generated responses between the survival and control conditions. As in Experiment 2, we analyzed the relationship between condition and recall while accounting for response time and length differences. We compared a model that included response time and length as fixed effects with random effects of subject and item (Recall ~ Length + ResponseTime + (1|Subject) + (1|Item)) against a model that included response time, length, and condition as fixed effects and subject and item as random effects (Recall ~ Condition + Length + ResponseTime + (1|Subject) + (1|Item)). A Likelihood Ratio Test $(\chi^2(1) =$ 11.14, p = .0008 indicated that there was a significant effect of condition above and beyond the effects of response time and length. Thus, although survival generation led to longer responses, length and response time cannot completely account for the survival benefit in recall.

Analysis of the Generated Responses

At this point we collected additional data using Amazon Mechanical Turk to verify that participants were following the generation procedures as instructed. To begin, we were interested in whether the survival generation instructions actually led to generations that were survival-relevant, at least compared to the autobiographical generation condition. A random sample of survival and autobiographical responses, drawn from Experiments 1-4, was given to 100 participants with instructions to decide whether the generated response described how the object might be involved in a survival situation. A given participant received a sample of 30 generations, drawn from a larger sample of 300 generations, half from the survival task and half from the autobiographical task.

On each trial participants were shown a single generated response, along with its associated object, and were asked to click "YES" if the phrase described how the object might be involved in a survival situation or "NO" if they felt the response was unrelated to a survival situation. Example phrases were given: e.g., Fabric: Can provide warmth when freezing (Survival-relevant) and Fabric: The fabric on my shirt is soft (Survival-irrelevant); people were given as much time as needed to complete their response. The results revealed that participants gave a significantly higher proportion of "yes" responses to the sentences generated in the survival condition (M = .81, SD = .17) compared to the autobiographical condition (M = .10, SD = .16), t(99) = 28.43, p < .001, d = 2.84.

Next, to assess the unusualness manipulation of Experiment 4, a second set of 100 participants were given random samples of survival- and unusual-based generations and were asked to respond "YES" or "NO" depending on whether the object was being used in an unusual way—that is, in a way that was different from its typical use. Again, each participant received a random set of 30 generations, half from the survival task and half from the unusual task. Except for the nature of the response, the procedure was identical to the one described above. Examples were given: e.g., Fabric: Can provide warmth when freezing (Usual) and Fabric: Can be attached to sticks to make a sail (Unusual). Participants produced a significantly higher proportion of "yes" responses to generations from the unusual-use task (M = .77, SD = .18) compared to generations from the

survival task (M = .42, SD = .16), t(99) = 17.80, p < .001, d = 1.78.

These additional analyses confirm participants were following instructions and formulating their generations in a task-dependent manner. Over 80% of the survival generations were deemed survival relevant by independent observers compared to 10% of the autobiographical responses. In addition, the independent observers determined that 77% of generated responses in the "unusual" condition showed the target object being used in an atypical way compared to 42% of the survival generations. The relatively large proportion of the survival responses that were deemed "unusual" is interesting and consistent with the speculations of other researchers (e.g., Bell et al., 2015). Survival processing may indeed cause one to think about the function of objects in an unusual or creative way. However, novelty alone clearly cannot explain the survival processing advantage in the present experiments because survival generations led to significantly better retention in Experiment 4 when the control condition was specifically designed to produce atypical uses for the target items.

General Discussion

The experiments reported here provide further evidence that survival processing enhances retention relative to a variety of robust and semantically "deep" control procedures. Given that our memory systems evolved to satisfy nature's criterion—the enhancement of inclusive fitness—this result should not be too surprising. At some point in our ancestral past, the ability to remember evolved because it increased our capacity to survive and/or reproduce. Thus, we can anticipate that the footprints of nature's criterion will continue to color memory functioning.

Reasoning of this sort exemplifies "forward engineering" in evolutionary analysis (see Nairne, 2005, 2015; Richardson, 2007). There are no fossilized memory traces, and it can be difficult to pinpoint the true nature of ancestral environments (Buller, 2005), but we can generate a priori predictions about how evolved systems potentially operate by considering the selection pressures that likely led to their development. In the case of survival processing, as discussed by Nairne and Pandeirada (2016; see also Klein et al., 2002), an important component of survival optimization is the

ability to simulate activities that help to prevent or escape from future threats (Mobbs, Hagan, Dalgleish, Silston, & Prevost, 2015); such simulations, in turn, depend in an important way on retrospective remembering of survival-relevant information. It would be adaptive, as a result, for our memory systems to remember survival-relevant information especially well.

At this point, most researchers accept that rating the relevance of items to an imagined survival scenario is an excellent encoding technique. However, whether this empirical benefit reflects the ancestral "tuning" claimed by Nairne et al. (2007) continues to be somewhat controversial. Some have argued that the benefit arises simply because the standard relevance-rating procedure happens to induce deep or elaborative forms of processing (see Erdfelder & Kroneisen, 2014; Krause, 2015; Howe & Derbish, 2010). But, as discussed earlier, the fact that a well-known or domain-general mnemonic process might be involved, such as elaboration, is not particularly diagnostic with respect to the evolutionary account. Many evolved adaptations work by co-opting otherwise general processing (e.g., the immune system co-opts the circulatory system as part of its operation; see Burke, 2014). Discovering evidence for the circulatory system in immune functioning does not invalidate the latter's status as an evolved adaption; similarly, discovering evidence for elaborative processing in survival processing does not invalidate its status as a mnemonic tuning. Humans might easily have evolved a mnemonic "tuning" that operates by activating domaingeneral processes (Nairne & Pandeirada, 2016).

At issue is whether the activation of these general processes can be attributed to fitness-relevant processing or to some artifactual element of the experimental procedure. For example, it could be that the standard grasslands survival scenario encourages people to think about target stimuli in a way that is more self-referential (Cunningham et al., 2013; Dewhurst et al., 2017) or richer (Kroneisen & Erdfelder, 2011) or more functional (Bell et al., 2015) than common control procedures. One can attempt to equate the survival and control scenarios across such dimensions, and that has motivated much of the research on survival processing (see Kazanas & Altarriba, 2015), but there is no easy way to determine the processing dimensions that are actually activated by any assigned scenario. Nairne et al. (2009) found survival advantages with matched scenarios, in which the same hunting or gathering scenario was framed as survivalrelevant or not (see also Clark & Bruno, 2016), but survival benefits need to be demonstrated under a range of contexts, including ones that do not rely on rating the relevance of information to a fixed scenario. In order to lessen the chances of a methodological artifact, there is a need to untether arguments about survival processing to any particular experimental paradigm.

The current research moves the debate forward by showing that survival processing advantages can be obtained in the absence of any fixed scenario. People generated their own survival situations in the present experiments; no constraints were placed on the type of response that could be generated other than it needed to involve the target stimulus. One nice feature of this procedure is that it forces the participant to think about the survival consequences of the target stimulus on every trial. In the standard rating task, one can never be certain that the participant is actually thinking about the survival element as opposed to the activities or objects referred to in the scenario. For example, one can think about using a bucket to carry water or a rake to gather food without necessarily focusing on the survival elements of the situation (i.e. dehydration and starvation). With the generation task, survival elements are front and center to the response.

Another advantage of the current generation procedure is its flexibility. People can be asked to generate a variety of situations relevant to a target stimulus and this flexibility enabled us to pit survival processing against several theoretically relevant control conditions. For example, survival generation led to better performance than an autobiographical control which required people to retrieve a specific episode from their lives relevant to the target stimulus. This kind of processing is definitely self-referential, and required a form of retrieval practice as well, yet survival generation produced significantly better retention. This survival advantage was replicated at both immediate and delayed testing and when both within- and between-subject designs were used. In Experiment 4, we adopted a control procedure that required people to think about how the target stimulus could be used in an unusual way. In addition to testing the idea that survival benefits are due to the generation of an atypical use (i.e., a type of distinctive processing), this control also required people to think about an object's function in a way that may not

have been induced by pleasantness ratings or by the autobiographical control (e.g., Bell et al., 2015).

In some respects, our results are reminiscent of those obtained earlier by Klein (2013) who also reported a survival processing advantage in the absence of a specific context. In those experiments, participants were simply asked "to imagine that you are trying to stay alive" (p. 52); the task was then to rate the relevance of each target word to accomplishing this end. A significant survival advantage was obtained compared to a pleasantness rating control. Klein's main interest was in assessing whether survival effects depend on eliciting thoughts about the environment of evolutionary adaptation (e.g., a grasslands context). He concluded that survival processing benefits do not depend on activating an ancestral context, a result that we have found in our laboratory as well (Nairne & Pandeirada, 2010). It is unlikely that survival processing benefits require the elicitation of an ancestral context, although it is possible that the activities induced by the standard grasslands scenario provide a better match to evolved traits than activities induced by a modern context (Nairne & Pandeirada, 2010; see also Weinstein, Bugg, & Roediger, 2008). Similar to Klein (2013), in the current experiments we provided no rules or guidelines about the types of survival situations that could be generated—in fact, the examples we provided to the participant were not ancestrally-based—so our data provide additional support for the Klein's (2013) conclusion: It is survival processing, rather than its particular setting or context, that is primarily responsible for the mnemonic benefit.

Our results are also relevant to previous work by Röer, Bell, and Buchner (2013) who asked participants to write down any ideas that came to mind when thinking about the usefulness of target words to a grasslands survival context. Their main interest was in testing whether rating items for survival relevance led to the generation of more ideas (and thus a "richer" encoding) than control scenarios (moving to a foreign land or finding things to do in the afterlife). Indeed, survival processing was associated with more idea generation, along with better recall. In some sense their idea generation task mirrors the survival generation task used in the present experiments, although from our perspective their recall data were confounded by the number of ideas that were generated. In our experiments, participants were asked to generate only a single response and our follow-up analyses (both statistical and experimental) showed that the length of the generated response could not fully account for the effect of condition on recall. Moreover, in our experiments people were asked to generate the survival situation rather than ways in which an item might be relevant to a fixed survival scenario.

provide Although our results diagnostic information about possible proximate mechanisms, much remains to be discovered about the survival benefit. As we have argued throughout, it could be that survival processing triggers a form of elaborative processing that is common to other effective encoding procedures (e.g., visual imagery or semantic analysis). It is also possible that the act of survival generation leads to increased arousal or some other form of emotional processing. It is worth noting, though, that evidence from the standard single-item rating procedure has provided little support for emotion- or arousal-based interpretations of survival benefits (see Bell et al., 2013 for a review). Moreover, emotion and memory experiments typically require people to remember emotional words or events; in the present case, people are asked to remember neutral words that acquire mnemonic salience by virtue of their involvement in a survival situation. From a methodological standpoint this an improvement because it effectively eliminates item-selection concerns—the same item is remembered in both the experimental and control conditions, as opposed to remembering different items (emotional versus neutral). But more research will need to be conducted before we can be certain that the standard interpretations of emotional memory effects even apply in such a context (e.g., see Kensinger, 2009).

Most mnemonic effects are "explained" by selecting from a toolkit of proximate mechanisms, particularly ones that end up improving either the strength or the variability of potential retrieval cues (e.g., Craik & Tulving, 1975). What is often left out of the analysis, though, is any functional consideration—why does the system or process work that way? Why does visual imagery, or attention to meaning, promote rich and elaborative encodings? Is it a byproduct of the task demands, experiential history, or does it reflect a design feature of our memory system? One of the main tenets of the functionalist agenda in memory research (Nairne, 2005) is that memory processes, like other physical systems in the body, are designed to solve adaptive problems. Rather than a general-purpose storage system,

our capacity to remember exists to achieve specific adaptive ends, particularly ends related to survival and reproduction. As a result, memory should function particularly well when encoding tasks tap the adaptive problems that were central to its development.

This kind of reasoning forms the basis for our general research on adaptive memory and for the experiments reported here. Survival processing leads to good retention because it is important for people to remember survival-relevant information, not because it engenders a form of elaboration (or some other form of mnemonic process). Because of nature's criterion, a memory-enhancing process—e.g., elaboration—must have evolved in the service of benefiting survivalrelevant information, not the other way around—that is, selection pressures favored a memory system that selectively retained fitness-relevant information and elaboration likely developed to achieve that end. The fact that we can remember generally must be a byproduct of a system that evolved to meet the needs of survival and reproduction. From this perspective, as reiterated throughout, it is not surprising that memory systems work particularly well when dealing with survival-relevant information.

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Footnote

¹When constructing these models, we initially included random slopes for length and reaction time. However, when we calculated interclass correlations (ICC) for the random effects we found that the proportion of variance accounted for by the all random slopes combined was very small for both Experiment 2 (ICC = .0008) and Experiment 4 (ICC = .002). Therefore, we only included random intercepts for subjects and items in the models that were compared.

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Declaration of Conflicting Interests

The authors declare that there are no conflicting interest.