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Is Memory Enhanced by the Context or Survival Threats? A Quantitative and Qualitative Review on the Survival Processing Paradigm

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Consistent with an evolutionary perspective, memory may be enhanced when people are in precarious situations. Particularly, a survival processing effect (SPE) has been found whereby people have better memory for a list of items when the items are rated for their relevance in a grassland context that contains survival threats including predators, and the lack of food and water. In this article, we systematically review research that investigated the SPE to disentangle the contextual effects (e.g., grassland) from survival effects (e.g., presence of predators) on memory. A total of 56 articles (106 experiments) that reported findings relating to the SPE before January 2016 were identified and reviewed. Ten experiments assessed the contextual effect and 5 experiments assessed survival effects. Meta-analysis showed that both contextual and survival effects made medium contributions to improved memory, with survival effect having a greater overall effect compared to contextual effect. Based on a further qualitative review on the scenarios used in the experiments, we concluded that grassland contexts per se may have a weaker effect relative to the presence of survival threat in generating mnemonic advantage. The remaining articles consist of experiments that did not examine contextual or survival effects specifically. These set of findings support the notion that the improved memory for SPE largely stems from survival threat because of the lack of survival threat in the control conditions.

Keywords: contextual effect, survival processing advantage, stone-age brain, verbal memory, mnemonics

Memory researchers typically investigate cognitive processes, and stimuli involved in memory formation (Cook, Hodes, & Lang, 1986). For instance, retention is enhanced when

words are processed for their meanings compared to their physical characteristics such as the number of syllables (Craik & Tulving, 1975). In recent years, researchers began taking

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an evolutionary perspective, examining human memory as an adaptive system selected to improve inclusive fitness by increasing memory for information relevant to survival (e.g., presence of threats, absence of food). Labeled as the survival processing effect (SPE), memory for a list of items is enhanced when the items are rated for their relevance for survival in a foreign grassland (Nairne, Thompson, & Pandeirada, 2007). This set-up facilitates greater retention compared to not only baseline control conditions but also other well-substantiated memory-enhancing conditions (Eich, 1985), including self-referencing (Cunningham, Brady-Van den Bos, Gill, & Turk, 2013), and mnemonic devices such as deep processing (Nairne, Pandeirada, & Thompson, 2008). Despite the support for survival processing, it remains unclear whether memory is enhanced by the context (i.e., grassland) or by survival threat. Particularly, after controlling for the presence of survival threats across different contexts, some studies demonstrated enhanced memory (e.g., Nairne & Pandeirada, 2010; Weinstein, Bugg, & Roediger, 2008) whereas others did not (e.g., Kostic, McFarlan, & Cleary, 2012; Soderstrom & McCabe, 2011; Yang, Lau, & Truong, 2014). This suggests that context specific effects may enhance or attenuate memory performance observed in the paradigm. To better understand and address this issue, we systematically review the literature to determine the relative contributions between contextual and survival effects in the SPE paradigm. Particularly, we examine the extent to which the presence of a grassland context versus survival threat promotes recall. Distinguishing between the two explanations will allow for a better understanding of two major contextual factors and key pathways that may underlie the evolution of adaptive memory processes.

The SPE

In a typical survival processing paradigm, a survival context is described:

In this task, I would like you to imagine you are stranded on the grasslands in a foreign land, without any basic survival material. Over the next few months, you'll need to find steady supply of food and water and protect yourself from predators. I am going to show you a list of words, and I would like you to rate how relevant each of these words would be for you in this survival situation. Some words may be relevant and

others may not—it is up to you to decide. (Nairne et al., 2007, p. 264).

This scenario, which has been widely used in studies investigating the SPE, consists of two main factors that could account for the memory advantage, and hence, may be confounded. First, there is a threat to survival being conveyed, in the way of obtaining food and water, and avoiding mortal dangers such as predators. The passage requires individuals to process items in conjunction with their survival value. However, there is also the grassland context, which is consistent with the Environment of Evolutionary Adaptation in which our ancestors lived (Nairne & Pandeirada, 2010; Symons, 1995; Tooby & Cosmides, 2005). That is, the primary environmental conditions associated with the emergence of the genus *Homo* (Bobe & Behrensmeier, 2004; Finlayson, 2005), as well as the evolutionary history of *Homo sapiens*, involve grasslands (Mercader, 2002). Given the elongated pairing of hominids and grasslands, people may have developed memory (and other psychological) systems that work most effectively in these conditions. Accordingly, items studied by individuals in analogues to the ancestral environment are postulated to be more amenable to good memory functioning than items studied in a modern, evolutionarily novel environment. Thus, the survival processing necessarily includes both the context of grassland and the presence of survival threats.

The SPE paradigm is typically established by pitting the grassland survival scenario against other control scenarios and types of processing. A common control scenario involves moving to a foreign land (i.e., moving scenario). In addition, another group of participants are told to evaluate the same list of items for their pleasantness. The moving scenario is included because it involves schematic processing like the grassland scenario, but without survival threats. The pleasantness rating is included because it is related to the memory advantage observed in processing the items for their meaning (Craik & Tulving, 1975). From the inception of the SPE paradigm to date (Nairne et al., 2007), various researchers have demonstrated that the SPE is observed across different experimental set-ups such as using nonverbal stimuli (e.g., pictures; Otgaar, Smeets, & Van Bergen, 2010) and verbal materials in other languages (e.g., Japanese;

Nouchi, 2012); that is, it is not a measurement or methodological artifact.

Contextual Effect and Survival Effect

Despite the robustness of the SPE, a small number of studies did not detect it (e.g., Soderstrom & McCabe, 2011). One of the arguments pertinent to the current review is that the effect of context (i.e., grassland) may not be as strong as the influence of survival threat in generating the memory advantage. In contexts where the survival threat is particularly salient, contextual effect may not be observed. This notion is revealed when survival threat is controlled across the scenarios and the scenarios differ only in the context. For instance, one study demonstrates that scenarios that include zombies as survival threat lead to better memory compared to the grassland scenarios, regardless if the zombies are in a grassland or city context (Soderstrom & McCabe, 2011). This suggests that the presence of any survival threat is sufficiently effective in enhancing memory, and the grassland context is superfluous. However, it is also likely that the perceived survival threat associated with zombies—as portrayed in and made salient by several recent movies and TV series—is much greater than that associated with predators and attackers, thereby overriding the contextual effect. When the memory performance for the grassland scenario is compared to a scenario that required the participants to imagine being stranded in a foreign land with dangerous attackers, better memory is observed for the grassland scenario (Nairne & Pandeirada, 2010). The two scenarios are clearly differentiated by their context per se because both include survival threats (i.e., predators and attackers). As such, the greater survival effect observed on the former study may have emerged from the greater threat of zombies compared to attackers in the latter study. In particular, other than being life-threatening, survival threat is accentuated by the risk of deadly infection by the zombies (Nairne, 2014).

Taken together, it remains unclear if the memory advantage associated with survival processing emerges from the context, the presence of the survival threat, or the combined effect of both factors. In the present article, *contextual effect* refers to the memory advantage when items are rated in an ancestral context

(i.e., grassland), relative to other nonancestral context (e.g., city, mountains), independent of the presence (or absence) of survival threats. *Survival effect* refers to the memory advantage when items are rated in terms of survival threats (i.e., lack of food and water, and presence of predators), relative to an absence, higher, or lower threats (e.g., lack of water), independent of the type of environmental context. To date, no paper we know of has comprehensively reviewed and reported findings that dissociate between the effects of context and survival threats—two potentially major evolutionary factors—on memory enhancement. Thus, we conduct a quantitative and qualitative review on the SPE to disentangle the contextual and survival effects.

Method

Search Strategy and Parameters

Computerized databases including PsycINFO[®] (72 articles) and PsycARTICLES[®] (20 articles) were used to locate studies using the search term *survival processing*. To ensure comprehensiveness, we also conducted follow-up searches on Google Scholar[®] for articles that cited Nairne and colleagues (289 articles, 2007), the originators of the SPE. The initial searches were conducted in January of 2016. Hence, only articles published before this date were included. Only published data were included to avoid overlaps with unpublished data such as dissertations and ensure methodological and conceptual rigor.

The present review included both qualitative and quantitative methods because of the heterogeneous nature of the studies; including a qualitative review would provide a more nuanced analysis than could be extracted from a purely quantitative review. Of particular concern, the contexts used in different studies differ qualitatively from each other and the extent to which different contexts exert their effects on memory may not be accurately dissociated from the effects of survival threat. Furthermore, qualitative investigation is less prone to reductionism and can provide a dynamic analysis for complex memory systems (Nelson, 2015).

Study Inclusion/Exclusion Criteria

Abstracts from published works were reviewed and selected for studies that investigated the SPE. To ensure that the studies investigated contextual effects and/or survival threats, the Methods section and the research aims were examined when necessary. The SPE typically involves participants reading scenarios describing the context or setting (e.g., savannah grassland, city, mountain) that may or may not contain direct survival threats (e.g., predators, attackers, zombies). Most studies included several conditions; only conditions that directly compared contextual (e.g., grassland vs. desert) or survival (e.g., grassland low threat vs. grassland high threat) effects were included. Thus, although most studies included pleasantness rating as one of the conditions, we excluded results that compared between the key conditions with pleasantness rating condition. These studies, however, were qualitatively assessed separately in this article. Some studies may investigate other factors such as the proximate mechanisms underlying the SPE without specifically examining contextual factors or survival threats. Nonetheless, these studies may include different scenarios that prime different contexts and survival threats. We did not exclude these studies but analyzed them independent of studies that specifically examined contextual or survival cues. Although these studies did not directly investigate the contextual or survival effect, they nevertheless contain SPE relevant contexts or survival threats. We believe that these studies will also be informative in determining the relative contributions to memory between context and survival threat.

Meta-Analysis

We conducted a meta-analysis to determine the effect sizes and heterogeneity of the studies for the contextual and survival effects. Effect size (i.e., Cohen's d) for significant findings was calculated using online effect size calculators www.lyonsmorrison.com/ma1/ and www.psychometrica.de/effect_size.html. Estimates of effect size were calculated based on the means and standard deviations, t or F statistics for comparisons between the mean recall rate of the experimental condition (i.e., grassland scenario) and the critical control condition/s (e.g.,

city scenario). We expect the effect sizes for the contextual effect to be weaker compared to those for the survival effect because survival threats are more immediately threatening and current evidence appears to suggest that the survival effect is more pertinent than the contextual effect for SPE (Olds, Lanska, & Westerman, 2014; Seamon et al., 2012). In particular, survival threats focus one's attention on the to-be-remembered items leading to greater elaboration, self-referential, item-specific and interitem relational processing (Cunningham et al., 2013; Otgaar, Jelicic, & Smeets, 2015; Yang et al., 2014). In contrast, challenges posed by context per se may not be as immediately dangerous and as such likely does not as strongly induce cognitive processes that would enhance memory for the to-be-remembered items; ancestral environment does not activate fundamental cognitive systems related to survival and reproductive fitness. The Comprehensive Meta-Analysis Version 3 software (Borenstein, Hedges, Higgins, & Rothstein, 2005) was used to analyze the current data. A random-effects approach was used to conduct the meta-analysis because it is suited for data with heterogeneous effect sizes (Field & Gillett, 2010).

Results

Based on the inclusion/exclusion criteria, a final list of 56 peer-reviewed journal articles and book chapters published before January 2016 were located and reviewed. Summaries of these studies, categorized as specifically investigating the contextual effect and the survival effect, are shown in Table 1 and Table 2, respectively; Table 3 summarizes studies that examined the SPE without directly assessing the contextual and survival effects. The types of stimuli and the types of contexts and survival threats are also presented in the tables. Most of the papers included more than one experiment. Of the 56 papers (106 experiments) included in the analysis, eight included at least one experiment that specifically examined contextual effects, 12 included at least one experiment that examined the survival effect, and 37 examined other factors such as the proximate mechanisms and included a variety of contexts and survival threats. Studies consisting of experiments that specifically examined the contextual or survival effect were analyzed separately from the other

Table 1
Summary of Methods and Results for Studies That Examined the Contextual Effect

Study	Stimuli	Context	Survival threat	Significant findings	Cohen's <i>d</i>	<i>n</i>
Weinstein, Bugg, and Roediger (2008) Experiment 2	Words	Grassland (first person) Grassland (third person) City (first person) City (third person) Moving (first person) Moving (third person)	Predators, food and water Predators, food and water Attackers, food and water Attackers, food and water	*Grassland > city	.67	88
Nairne, Pandeirada, Gregory, and Van Artsdall (2009) Experiment 1	Words	Grassland (gatherer) Grassland (hunter) Scavenger-hunt Grassland (hunter) Hunting contest	Extreme heat, flood, drought Extreme heat, flood, drought	*Grassland > scavenger-hunt *Grassland > hunting context	.43	150
Experiment 2	Words		Unfamiliar terrain Unfamiliar terrain		.60	100
Nairne & Pandeirada (2010) Experiment 1	Words	Grassland; Moving City; Moving	Predators; Nil Attackers; Nil	*Grassland > moving	.65	80
Experiment 2	Words	Grassland; Pleasantness City; Pleasantness	Infection; Nil Infection; Nil	*Grassland > city	.40	120
Experiment 3	Words	Grassland; Pleasantness City; Pleasantness	Hunger; Nil Hunger; Nil	*Grassland > city	.75	72
Kostic, McFarlan, & Cleary(2012) Experiment 1a	Words	Grassland Desert Pleasantness	Predators, food and water Predators, food and water	[Grassland = desert]	.15	31
Experiment 1b	Words	Grassland Sea Pleasantness Jungle Space Self-reference	Predators, food and water Predators, food and water Predators, food and water Danger, food and water	[Grassland = sea]	.35	53

(table continues)

Table 1 (continued)

Study	Stimuli	Context	Survival threat	Significant findings	Cohen's <i>d</i>	<i>n</i>
Klein (2013) Main study	Words	Grassland	Predators, food and water Staying alive	Grassland = survival	.01	52
		Survival only				
		Mate selection				
Olds, Lanska, and Westerman (2014)	Words	Pleasantness	Predators, food and water (easy) Predators, food and water Predators, food and water (difficult) Attackers, food and water (easy) Attackers, food and water Attackers, food and water (difficult)	Grassland = city	.20	288
		Grassland (low threat)				
		Grassland (medium threat)				
		Grassland (high threat)				
		City (low threat)				
City (medium threat)						
		City (high threat)				

Note. Comparisons in brackets are within-group design.

* $p < .05$.

experiments. In addition, effect sizes with insufficient statistical information, and where authors were not able provide the necessary information or did not reply to our emails were excluded from the meta-analysis. This resulted in 10 and five effect sizes for contextual and survival effect, respectively. These are reflected in Table 1 and 2.

The present review defines SPE as a statistically significant ($p < .05$) memory advantage for the conventional grassland scenario over other control scenarios within the experiment. In addition, we examined only true recall. Hence, recognition rate, false positive, accuracy, and other types of memory measures were not considered in the current review. In particular, these measures explained criterion shift where performance varies in terms of response biases, instead of differences in memory associated with specific scenarios (Kellen, Klauer, & Singmann, 2012; Miller & Wolford, 1999).

Meta-Analysis

Most of the studies included more than one experiment, and some studies included experiments that independently investigated the contextual, and survival effect. Fifteen experiments were included in the meta-analysis, of which 10 experiments examined the contextual effects and five experiments examined the survival effect in the analyses. Summary information from these experiments is presented in Tables 1 and 2. A total sample size of 1,365 participants were calculated from the studies. The random effects analysis showed that a medium mean overall effect size for contextual effect compared to the relevant control conditions, Cohen's $d = 0.43$ ($SE = 0.07$, 95% confidence interval [CI]: 0.30–0.57; Figure 1), and a medium mean overall effect size for survival effect compared to the relevant control conditions, Cohen's $d = 0.63$ ($SE = 0.12$, 95% CI: 0.39–0.87; Figure 2). Although both contextual effect and survival effect contributed to the memory advantage observed in the studies, survival effect appear to exert a stronger effect compared to contextual effect.

Visual inspection of the funnel plots for the contextual and survival effect displaying the effect sizes with the respective log sample sizes show symmetries, suggesting that publication biases are unlikely (see Figure 3). Further anal-

Table 2
Summary of Methods and Results for Studies That Examined the Survival Effect

Study	Stimuli	Context	Survival threat	Significant findings	Cohen's <i>d</i>	<i>n</i>
Kroneisen & Erdfelder (2011) Experiment 1	Words	Grassland (original); city Grassland (short); city	Predators, food and water; nil Lack of water; nil	*Grassland (original) > city	.58	81
Experiment 2	Words	Grassland (original); city Grassland (short); city	Predators, food and water; nil Lack of water; nil	*Grassland (original) > grassland (short), city	.43	81
Experiment 3	Words	Grassland (4 arguments) City (4 arguments) Grassland (1 argument) City (1 argument)	Predators, food and water Predators, food and water Predators, food and water	*4 arguments > 1 argument	.61	103
Seamon et al. (2012) Experiment 2	Words (in a story)	Island (stranded) Island (exploring) Plane crash	Lack of food and water	*Survival effect	.90	26
Experiment 5	Story content	Plane sightseeing Grassland (survival) Grassland (vacation)	Lack of food, water, shelter	*Grassland (survival) > grassland (vacation)	1.49	40

* $p < .05$.

Table 3
Summary of Methods and Results for Studies That Examined the Survival Processing Effect Without Controlling for Context and Survival Threat

Study	Stimuli	Context	Survival threat	Significant findings
Nairne, Thompson, and Pandeirada (2007) Experiment 1	Words	Grassland Moving Pleasantness Grassland	Predator, food and water	*Grassland
Experiment 2	Words	Moving Grassland	Predator, food and water	*Grassland
Experiment 4	Words	Self-reference	Predator, food and water	*Grassland
Nairne, Pandeirada, and Thompson (2008) Experiment 1	Words	Grassland Pleasantness Mental imagery Self-reference Generation Intentional learning Grassland Vacation	Predator, food and water	*Grassland
Experiment 2	Words		Predator, food and water	*Grassland
Nairne & Pandeirada (2008a) Experiment 1	Words	Grassland Pleasantness Grassland Pleasantness	Predator, food and water	*Grassland
Experiment 2	Words		Predator, food and water	*Grassland
Weinstein et al. (2008) Experiment 1	Words	Grassland Moving Pleasantness	Predator, food and water	*Grassland
Kang, McDermott, and Cohen (2008) Experiment 1	Words	Grassland Bank heist Pleasantness Deserted island Bank heist Pleasantness	Predator, food and water	*Grassland *Deserted island
Experiment 3	Words			
Butler, Kang, and Roediger (2009) Experiment 1	Words	Grassland Pleasantness Grassland Bank Heist Grassland	Predator, food and water	*Grassland
Experiment 2	Words		Predator, food and water	*Grassland = bank heist *Grassland = bank heist
Experiment 3	Words		Predator, food and water	

Table 3 (*continued*)

Study	Stimuli	Context	Survival threat	Significant findings
Nairne & Pandeirada (2010) Experiment 4	Words	Bank Heist	Predators Attackers	*Grassland
	Words	Grassland Moving Pleasantness	Predator, food and water	*Grassland
	Words	Grassland Moving Pleasantness	Predator, food and water	*Grassland
Experiment 2	Words	Grassland Moving Pleasantness	Predator, food and water	*Grassland
	Words	Grassland Moving	Predator, food and water	*Grassland
	Words	Grassland Moving	Predator, food and water	*Grassland
Klein, Robertson, and Delton (2010)	Words	Forest camping (Past) Forest camping (Atemporal) Forest camping (Future) Forest (stranded)		*Forest camping (future)
	Words	Grassland Moving Pleasantness	Predator, food and water	*Grassland
	Words	Grassland Moving Pleasantness	Predator, food and water	*Grassland
Tse & Alharriba (2010) Experiment 1	Words	Grassland Moving Pleasantness	Predator, food and water	<i>n.s.</i>
	Words	Grassland Moving Pleasantness	Predator, food and water	*Grassland = pleasantness
	Words	Grassland Moving Pleasantness	Predator, food and water	*Grassland = pleasantness
Burns, Burns, and Hwang (2011) Experiment 1	Words	Grassland Moving Pleasantness	Predator, food and water	*Grassland = pleasantness
	Words	Grassland Moving Pleasantness	Predator, food and water	*Grassland = pleasantness
	Words	Grassland Moving Pleasantness	Predator, food and water	*Grassland = pleasantness
Experiment 2	Words	Grassland Moving Pleasantness	Predator, food and water	*Grassland = pleasantness
	Words	Grassland Moving Pleasantness	Predator, food and water	*Grassland = pleasantness
	Words	Grassland Moving Pleasantness	Predator, food and water	*Grassland = pleasantness
Experiment 3	Words	Grassland Moving Pleasantness	Predator, food and water	*Grassland = pleasantness
	Words	Grassland Moving Pleasantness	Predator, food and water	*Grassland = pleasantness
	Words	Grassland Moving Pleasantness	Predator, food and water	*Grassland = pleasantness
Experiment 4	Words	Grassland Moving Pleasantness	Predator, food and water	*Grassland = pleasantness
	Words	Grassland Moving Pleasantness	Predator, food and water	*Grassland = pleasantness
	Words	Grassland Moving Pleasantness	Predator, food and water	*Grassland = pleasantness

(table continues)

Table 3 (continued)

Study	Stimuli	Context	Survival threat	Significant findings
Klein, Robertson, and Delton (2011) Experiment 1	Words	Pleasantness Category sorting	Lack of food Lack of food	*Grassland (Planning) = Dinner party (Planning) *Grassland (planning)
	Words	Grassland (Planning) Grassland (No planning) Dinner party (Planning) Grassland (Planning)	Lack of food Lack of food	*Grassland
	Words (Chinese)	Grassland (No planning) Grassland Imagery	Predator, food and water	
	Words	Grassland; Pleasantness Grassland; Moving	Predator, food and water; Nil Predator, food and water; Nil Predator, food and water	*Grassland (both)
Nairne & Pandey (2011) Experiment 1a and 1b	Words	Grassland		*Grassland
	Words	Bank heist		*Grassland
	Words	Grassland		*Grassland
	Words	Bank heist		*Grassland
Orgaer et al. (2011) Experiment 1	Words	Grassland Professor stereotype Elderly with Alzheimer's Moving	Predator, food and water	*Grassland
	Words	Grassland		*Grassland
	Words	Survival stereotype		*Grassland
	Words	Moving Grassland (Predators) Grassland (Zombies) City (Attackers) City (Zombies) Pleasantness	Predators, food and water Zombies, food and water Attackers, food and water Zombies, food and water	*Zombies
Klein (2012) Experiment 1	Words	Grassland Picnic planning Self-reference (Explicit) Self-reference (Not explicit)	Predator, food and water	*Grassland = picnic planning = self-reference (explicit)
	Words	Grassland		*Grassland
	Words	Self-reference (Explicit) Self-reference (Not explicit)	Predator, food and water	
	Words	Grassland Self-reference (Explicit) Self-reference (Not explicit)		
Soderstrom & McCabe (2011)	Words	Grassland (Planning) Grassland (No planning) Dinner party (Planning) Grassland (Planning)	Lack of food Lack of food	*Grassland (Planning) = Dinner party (Planning) *Grassland (planning)
	Words	Grassland (No planning) Grassland Imagery	Lack of food Lack of food Predator, food and water	*Grassland
Experiment 2	Words	Grassland; Pleasantness Grassland; Moving	Predator, food and water; Nil Predator, food and water; Nil Predator, food and water	*Grassland (both)
	Words	Grassland		*Grassland
	Words	Bank heist		*Grassland
	Words	Grassland		*Grassland
Experiment 3	Words	Grassland		*Grassland
	Words	Bank heist		*Grassland
	Words	Grassland		*Grassland
	Words	Bank heist		*Grassland
Experiment 4	Words	Grassland Professor stereotype Elderly with Alzheimer's Moving	Predator, food and water	*Grassland
	Words	Grassland		*Grassland
	Words	Survival stereotype		*Grassland
	Words	Moving Grassland (Predators) Grassland (Zombies) City (Attackers) City (Zombies) Pleasantness	Predators, food and water Zombies, food and water Attackers, food and water Zombies, food and water	*Zombies
Experiment 2	Words	Grassland Picnic planning Self-reference (Explicit) Self-reference (Not explicit)	Predator, food and water	*Grassland = picnic planning = self-reference (explicit)
	Words	Grassland		*Grassland
	Words	Self-reference (Explicit) Self-reference (Not explicit)	Predator, food and water	
	Words	Grassland Self-reference (Explicit) Self-reference (Not explicit)		

Table 3 (continued)

Study	Stimuli	Context	Survival threat	Significant findings
Seamon et al. (2012) Experiment 1	Words	Grassland Intentional learning Island (Stranded) Island (Stranded) Grassland	Predator, food and water Lack of food and water Lack of food and water Predator, food and water	*Grassland <i>n.s.</i> <i>n.s.</i> *Grassland
Experiment 3	Story content	Moving	Predator, food and water	*Grassland
Experiment 4	Story content	Grassland Self-reference	Predator, food and water	*Grassland
Smeets, Ogaar, Raymaekers, Peters, and Merckelbach (2012)	Words	Grassland Autobiographical recall	Predator, food and water	*Grassland
Nouchi (2012)	Words			
Nouchi & Kawashima (2012)	Words (Japanese nouns)			
Palmore, Garcia, Bacon, Johnson, and Kelemen (2012) Experiment 1a	Words	Grassland Bank Heist	Predator, food and water	*Grassland
Experiment 1b	Words	Grassland Bank Heist	Predator, food and water	<i>n.s.</i>
Experiment 2	Words	Grassland Bank Heist	Predator, food and water	<i>n.s.</i>
Sandry et al. (2013) Experiment 1a	Words	Grassland Fear & Phobia Mate selection Incest avoidance Cheater detection Jealousy Infidelity Status Pleasantness Visualization Grassland Fear & Phobia Mate selection Incest avoidance Cheater detection Jealousy Infidelity Status Pleasantness	Predator, food and water	*Grassland
Experiment 1b	Words		Predator, food and water	<i>n.s.</i>

(table continues)

Table 3 (continued)

Study	Stimuli	Context	Survival threat	Significant findings
Experiment 2	Words	Visualization Grassland Fear & Phobia Mate selection Incest avoidance Cheater detection Jealousy Infidelity Status Pleasantness Visualization Grassland Fear & Phobia Mate selection Moving	Predator, food and water	*Grassland
Experiment 3	Words	Grassland Pleasantness	Predator, food and water	*Grassland
Abel & Bäuml (2013) Experiment 1	Words	Grassland Pleasantness	Predator, food and water	*Grassland
Burns, Hart, Griffith, and Burns (2013) Experiment 1	Words	Grassland Moving	Predator, food and water	*Grassland
Experiment 2	Words	Grassland Moving	Predator, food and water	*Grassland
Klein (2013) Experiment 1a	Words	Grassland; Pleasantness Survival only; Pleasantness	Predator, food and water Staying alive; Nil	<i>n.s.</i>
Kroneisen, Erdfelder, and Buchner (2013)	Words	Grassland Moving	Predator, food and water	*Grassland
McBride, Thomas, and Zimmerman (2013) Experiment 1	Words	Grassland Moving Pleasantness Grassland Moving Pleasantness Grassland Autobiographical recall	Predator, food and water	<i>n.s.</i>
Experiment 2	Words	Grassland Moving Pleasantness Grassland Moving Pleasantness Grassland Autobiographical recall	Predator, food and water	<i>n.s.</i>
Nouchi (2013)	Words (Japanese nouns)	Grassland	Predator, food and water	*Grassland
Pandeirada et al. (2014)	Words (Portuguese nouns)	Grassland Moving	Predator, food and water	*Grassland

Table 3 (continued)

Study	Stimuli	Context	Survival threat	Significant findings
Kroneisen, Rummel, and Erdfelder (2014)	Words	Grassland Moving	Predator, food and water	*Grassland
Olds et al. (2014)	Words	Grassland (low threat) Grassland (medium threat) Grassland (high threat) City (low threat) City (medium threat) City (high threat)	Predators, food and water (easy) Predators, food and water (difficult) Attackers, food and water (easy) Attackers, food and water (difficult)	*High threat > medium threat > low threat
Otgaard, Howe, Smeets, and Garner (2014) Experiment 1 Experiment 2	Words Pictures	Grassland Moving	Predator, food and water	*Survival words *Grassland
Experiment 3	Words	Pleasantness Grassland Grassland (Short)	Predators, food and water Lack of water	<i>n.s.</i>
Pandeirada, Pinho, and Faria (2014)	Words	Pleasantness Grassland	Predator, food and water	*Grassland
Raymaekers, Otgaard, and Smeets (2014)	Words	Moving Grassland	Predator, food and water	*Grassland
Savchenko, Borges, and Pandeirada (2014) Experiment 1	Words	Moving	Predator, food and water	<i>n.s.</i>
Experiment 2	Words	Grassland Moving	Predator, food and water	<i>n.s.</i>
Stillman, Coane, Profaci, Howard, and Howard (2014) Experiment 1	Words	Grassland Moving	Predator, food and water	*Grassland
Experiment 2	Words	Grassland Moving	Predator, food and water	<i>n.s.</i>
Experiment 3	Words	Grassland Moving	Predator, food and water	<i>n.s.</i>
Yang, Lau, and Truong (2014) Experiment 1	Words	Grassland Mountain	Food and water Food and water	<i>n.s.</i>

(table continues)

Table 3 (continued)

Study	Stimuli	Context	Survival threat	Significant findings
Bugajska, Mermillod, and Bonin (2015) Experiment 1	Words	Cruise Dying Dental pain		*Dying
Clark & Bruno (2016) Experiment 1	Words	Grassland Pleasantness	Predator	*Grassland
Experiment 2	Pictures	Grassland Scavenger hunt	Lack of food	*Grassland
Nairne, Pandeyrada, VanArsdall, and Blunt (2015) Experiment 1	Words	Grassland Pleasantness	Predator, food and water	*Grassland
Experiment 2	Words	Grassland Pleasantness	Predator, food and water	*Grassland
Experiment 3	Words	Grassland Moving	Predator, food and water	*Grassland
Oggaar, Jelacic, and Smeets (2015)	Words	Grassland (short) Pleasantness	Predator, food and water Lack of water	*Grassland

* $p < .05$.

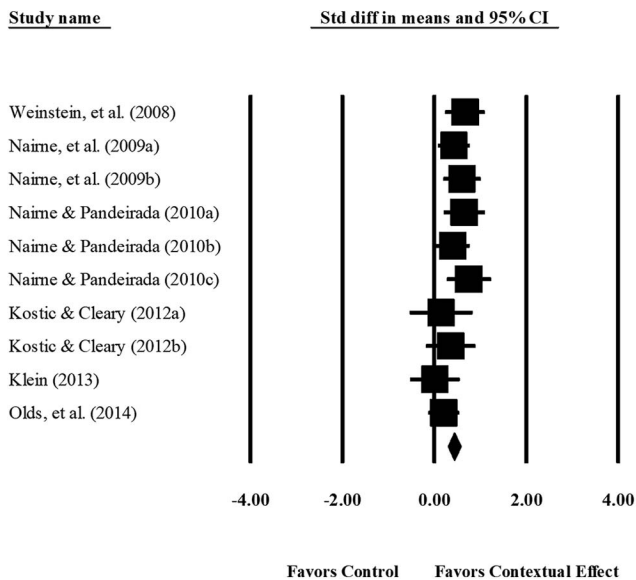


Figure 1. Forest plot of contextual effect vs. control meta-analysis.

ysis using Egger’s regression method (Egger, Smith, Schneider, & Minder, 1997) confirmed that severe publication or selection biases were not likely for contextual effect experiments,

$t(8) = 0.15, p = .88$, and survival effect experiments, $t(3) = 1.79, p = .17$. In addition, to determine whether the effects were confounded by the year of publication, we conducted a

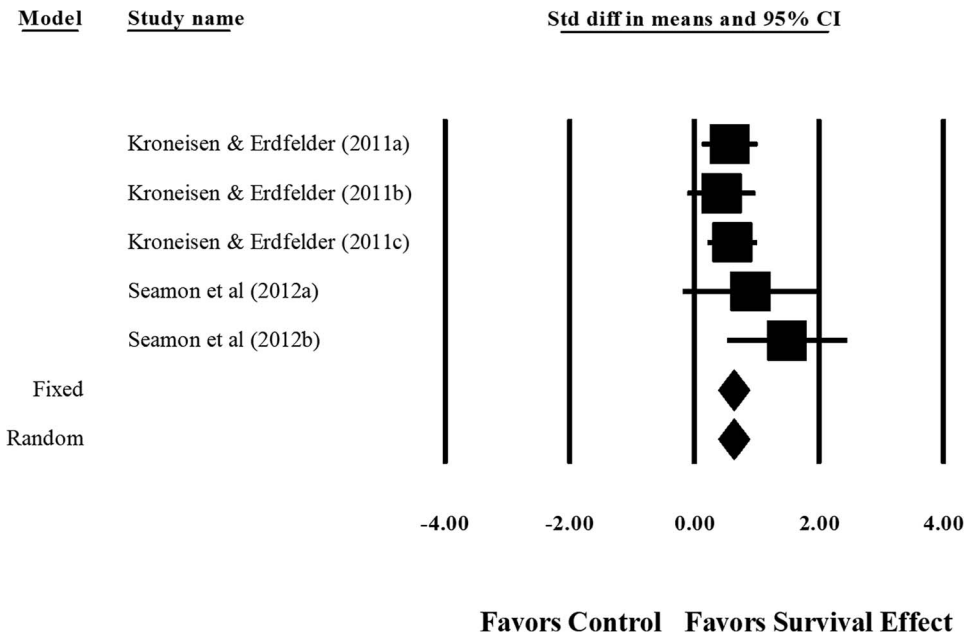
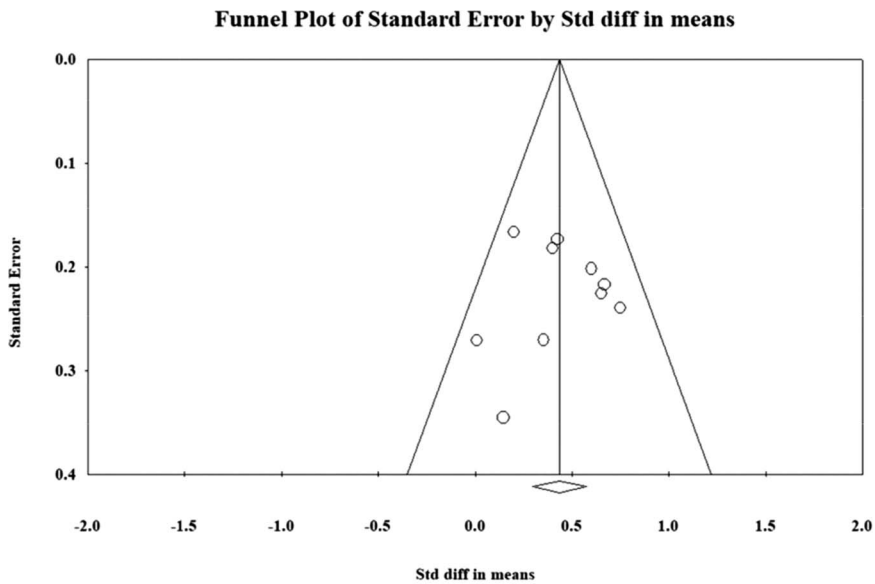
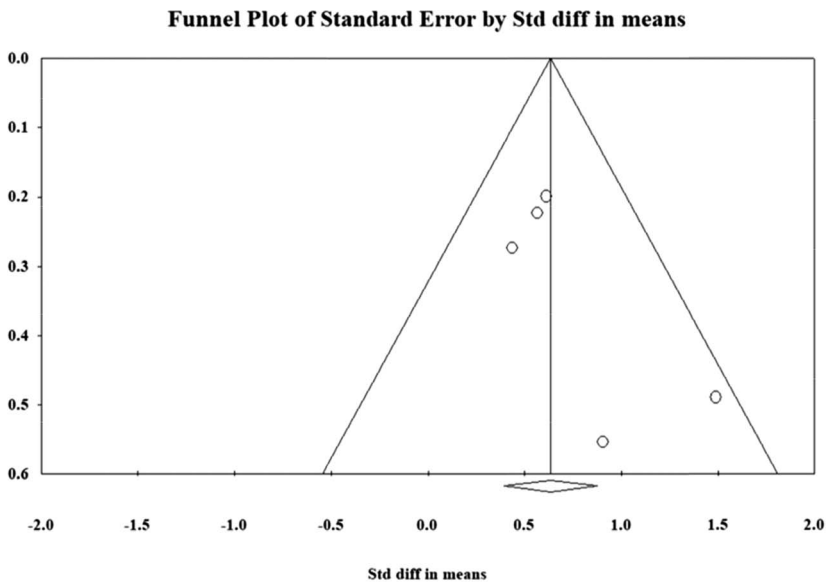


Figure 2. Forest plot of survival effect vs. control meta-analysis.



(a) Contextual effect



(b) Survival effect

Figure 3. Funnel plots showing potential publication biases for contextual and survival effects.

metaregression analysis for the relationship between effect size and year of publication. The analysis revealed that contextual effect diminished over the years, $\beta = -0.08$, $Z = -2.45$,

$p = .01$, but not for survival effect, $\beta = 0.68$, $Z = 1.74$, $p = .08$. It is noteworthy that no effect size outliers were identified for both contextual and survival effect, based on sample-

adjusted meta-analytic deviance (Beal, Corey, & Dunlap, 2002; Huffcutt & Arthur, 1995), and a cutoff criterion of four (Blume, Ford, Baldwin, & Huang, 2010; Steel, 2007).

Qualitative Review: Contextual Effect

We found that the grassland context contribution to the SPE is mixed. Closer scrutiny of the studies revealed that the experiments generally controlled for the presence of survival threats. Thus, the effect on memory can be attributed to the context. However, it is noteworthy that survival threat per se (i.e., context neutral), led to equitable memory compared to the typical grassland scenario (Klein, 2013), suggesting that the presence of survival threat in itself generated as much mnemonic advantage as a scenario that contained both the grassland context and survival threat. To clarify whether contextual effects contribute to memory performance, we examined the nature of the contexts that were used as control conditions to which the grassland context was compared to. In particular, we examined whether the contexts are related to the Environment of Evolutionary Adaptedness (EEA) for humans. The EEA refers to the evolutionary period, and environmental and social conditions in which the human brain evolved (Cosmides & Tooby, 1997; Nairne & Pandeirada, 2008b). As such, contexts that are similar to the EEA would logically induce more efficient cognitive processing compared to contexts dissimilar to the EEA. Three subtypes of contexts were found for the control conditions: EEA related (e.g., desert, sea, jungle), modern non-EEA related (e.g., foreign city, cruise), and novel non-EEA related (e.g., space). There were no discernible differences in terms of the effect sizes across the three subtypes of contexts. Generally, although our review of these studies suggests there appear to be minimal grassland context contribution to the SPE, the mixed findings preclude definitive conclusions related to contextual effect on memory.

Qualitative Review: Survival Effect

In general, we found that the presence of survival threats in the survival processing paradigm is vital in producing the SPE. Notably, scenarios that contained low survival threat (i.e., lacking water only) did not induce any

memory advantage compared to scenarios that contained high survival threats (i.e., predators, and the lack of food and water). This indicates that SPE is predicated on a combination of internal (i.e., food and water) and external threats (i.e., predators).

The survival effect may overlap with other survival related processing. Particularly, studies that compare survival processing with thoughts of death observed mixed findings. It has been argued that survival processing may involve both mortality salience and potential to survive (Bugajska, Mermillod, & Bonin, 2015). The present review suggests that there may indeed be some degree of overlap between the concepts of survival and death.

Secondary Findings

The remaining studies that did not specifically investigate the contextual or survival effect generally revealed that scenarios depicting the grassland context showed SPE compared to other control conditions. Specifically, among these studies, only eight studies did not find the SPE, and three did not explicitly include the grassland survival scenario.

Closer scrutiny of these studies revealed that the nongrassland scenarios (i.e., moving to a foreign city) used as control conditions mostly did not contain any survival threat and/or the comparisons were made with conditions that did not contain contexts (e.g., pleasantness rating, relevance to self). As such, it is not clear from these studies whether the SPE emerged from the grassland context or the presence of survival threats per se.

In addition, we observed that the 37 studies focused on proximate mechanisms. As such, the context and survival threat are not controlled as studies normally would when examining either of these effects specifically. It is noteworthy that studies did not find the SPE when proximate mechanisms such as planning (Klein, Robertson, & Delton, 2011) was used or found partial support for the SPE when stimuli other than English words, such as pictures (Otgaar, Howe, Smeets, & Garner, 2014) or Japanese words (Nouchi, 2013), were used.

Caveats

There are caveats pertaining to the SPE that emerged from the present review. First, signif-

icant findings for the SPE were generally for incidental memory. In particular, participants were not explicitly told that their memory for the items they were rating would be tested. As such, the SPE may not be observed for other types of memories such as intentional memory (e.g., Seamon et al., 2012). Second, the SPE observed for verbal stimuli appears to generalize to some types of nonverbal stimuli such as valent pictures (Otgaar et al., 2010). However, it should be noted that only three of the 56 studies reviewed used nonverbal stimuli.

Discussion

In this meta-analytic and qualitative review, we attempted to distinguish between the influence of survival threats and grassland contexts in the survival processing paradigm. Our findings indicate that survival threat is a significant contributor to enhanced memory in the survival processing paradigm, and the grassland context generally has some additive effect on memory. Specifically, we found that (a) including control conditions that have contexts similar to a grassland (e.g., desert) are less likely to demonstrate the SPE, (b) the presence of survival threats alone can lead to memory enhancement, (c) the memory advantage induced by the survival threats may share common underlying mechanisms activated by similar primes like mortality salience (Burns, Hart, & Kramer, 2014), and (d) SPEs observed in some studies may have emerged from the lack of survival threat in the control conditions. The present review is the first to systematically examine the relative contributions of the contextual and survival effects in the SPE paradigm. Broadly, the meta-analytic analysis supplemented by a qualitative review suggest that while both contextual and survival effects contribute to the SPE, survival effects appear to be the stronger of the two.

The Role of Contextual Effect in SPE

Consistent with a functional-evolutionary view, enhanced memory for threatening stimuli may be most adaptive when remembering such stimuli is not entirely dependent on the context. Particularly, survival threats were mostly found in savannah grasslands, as well as in nongrassland environments. In particular, research suggests that human ancestors may have lived in

nongrassland areas such as mountains (Yang et al., 2014) and deserts (Kostic et al., 2012). Thus, a memory system that is sensitive to survival threats that is independent of the type of environment the threats occur in would be adaptive. Indeed, the presence of a stronger survival-processing advantage, as we found, is consistent with the fact that survival threats are ubiquitous across contexts and would have been present over longer periods of time in human evolutionary history than the local threats in any one environment that might characterize that specific ecology.

However, this does not mean that context is irrelevant. With reference to the encoding specificity principle (Tulving & Thomson, 1973), memory for adaptively relevant stimuli associated with the encoding context may be adaptive. Remembering a survival threat that repeatedly presents itself in a specific context can be important for survival. For example, a lioness (*Panthera leo*) may return repeatedly to the same watering hole to both drink and hunt Thompson's gazelle (*Eudorcas thomsonii*). Gazelles that learn to associate the watering hole with potential threats will survive better than those who lack such a memory bias. Thus, an item is more likely to be retained for a specific context if the context is relevant to the survival threat, particularly when the context boosts elaboration or the distinctiveness for the items (Otgaar et al., 2014). This explains the additive effect of the grassland context and clarifies the absence of SPE when there is a lack of cues signaling survival threat observed in the current review. Consequently, a combination of both grassland context and survival threats tends to yield greater memory benefits compared to those that are attenuated on one of the two factors. For instance, the only study (we know of) that concurrently examined both contextual (i.e., grassland vs. city) and survival effects (i.e., easy vs. moderate vs. difficult) showed that grasslands with the greatest survival threat (i.e., difficult) produced the highest memory advantage (Olds et al., 2014). This suggests that the grassland context provides an additive effect over and above the survival effect even though it may be incapable of producing SPE by itself.

Studies examining the SPE typically did not control for survival threats sufficiently. Even though some studies controlled for the presence

of survival threat, the type of survival threats were not identical. Although attackers were commonly used in the city scenario, predators were typically used as the survival threat in the grassland scenario. Because the survival threat posed by attackers and predators are qualitatively different, the degree and meaning of the threats may also differ. As such, future studies should equate the survival threats in their experiments so the degree of contribution to memory from the contextual effect could be more accurately assessed. For instance, attackers can be used for both the grassland and city scenarios.

Meanings Associated With Survival Threats

It is unclear what the implicit meanings are that underlie the association between the survival threats and the to-be-remembered items. This is important in consideration of future research that seeks to examine other stimuli such as emotional pictures and faces using the survival processing paradigm. Thus far, survival processing research has presumed that objects that were rated for their relevance were rated in accordance to their relative use given the context (e.g., grassland, city) and the associated survival threats (e.g., predators). We found that apart from facial stimuli, the SPE seems to generalize to other nonverbal stimuli such as emotion inducing pictures. As such, it may be revealing to consider the SPE in terms of the meaning between the survival and the to-be-remembered items in terms of the survival-utility match. Specifically, survival threat may be construed differently with respect to memory for other types of stimuli like faces. The association between an object (e.g., common noun) with the survival threat may be stronger than the association between a face and the survival threat. This can explain the absence of SPE for facial stimuli. Taking this into consideration, properties inherent in a face such as its sex or emotional expression may be more relevant to the survival threats. For instance, research demonstrates that cognitive mechanisms are tuned toward angry men (compared to angry women, and happy men and women) because it offers protection from physical harm (Becker, Mortensen, Anderson, & Sasaki, 2014; Maner, Miller, Moss, Leo, & Plant, 2012; Tay, 2015). As such, emotional male and female faces may

be more relevant in a survival processing paradigm compared to emotionally neutral faces (cf. Savine, Scullin, & Roediger, 2011). It may be that context allows people to more effectively and efficiently process relatively ambiguous emotions, and potential threats.

Taken further, we suggest that the survival effect can potentially be dissociated from the contextual effect. In addition, the meaning underlying the survival threats and the to-be-remembered items is partially derived from the context it exists in, and survival threat that is not in concordance with its context may lead to an attenuation of the SPE because its meaning is not clearly construed based on its context. For instance, a predator in the grassland primes a different meaning compared to a predator in a foreign city (e.g., a lion in the savannah compared to one in Manhattan). Hence, one would expect SPE in the grassland context but not in the foreign city. This notion may be clarified by a consideration of the proximate mechanisms involved in SPE. For instance, it is conceivable that item-specific processing may be related more to the presence of survival threats in the scenario. Particularly, thinking of the relevance of an individual item for fending off predators or obtaining food and water may induce item-specific processing (Burns, Hart, Griffith, & Burns, 2013). On the other hand, the context (e.g., savannah grassland) may provide a background for relational processing where items related by their relevance to the context are associated in the memory. This implies that considering the proximate mechanisms can illuminate the reasons for inconsistent findings in the survival processing literature by dissociation of the mechanisms driven by the survival vis-à-vis the contextual effect.

Implications for Adaptive Memory

Parts of human cognition like memory are a limited resource. Memory systems that indiscriminately remember all stimuli are unlikely to be adaptive as they do not focus attention on important information given the plethora of information passing through our attentional systems. Findings from SPE research suggest that cognitive systems are sensitive to information in relation to the physical environment and the survival value of the stimuli. This information guides memory processes that ul-

timately promote survival or reproductive fitness. As such, the physical environment and stimuli properties interact to determine which stimuli are important to commit to memory. However, because the human brain evolved in the EEA (Cosmides & Tooby, 1997; Nairne & Pandeirada, 2008b), inherent properties of the stimuli are likely to be oriented toward those found in the ancestral environment rather than those exclusively found in the modern environment (Cook et al., 1986; Craik & Tulving, 1975; Öhman & Mineka, 2001). As such, human memory is adaptive to the extent that both the context and the stimuli resemble the ancestral environments. Extending on these notions, adaptive memory is likely to be influenced by what meaning people make of the stimuli they encounter. As such, individual differences may come into play in adaptive memory. For instance, although remembering hunting routes might be important to ancestral men, remembering the location for objects in a smaller area might be more relevant for ancestral women (Coolidge & Wynn, 2009; Silverman, Choi, & Peters, 2007; Silverman & Eals, 1992). SPE studies that found enhanced memory for stimuli when they are personally relevant lend support to this notion (Klein, 2012; Weinstein et al., 2008). Thus far, SPE research appears to be lacking in this area. Taken together, our understanding of adaptive memory is likely to be enhanced when the physical environment/context, the survival value that is contingent on the inherent properties of the stimuli, and individual differences (e.g., sex, personality) of the perceiver are examined within the same framework.

Our review indicates that the mnemonic advantage that emerged from the context is weaker compared to that of survival threat and may involve different cognitive processes. As such, future research can be conducted with greater rigor by controlling both the contextual and survival effects. Based on the insights gleaned from the current review, we propose that future research ensure that the presence, type, and quantity of survival threat be controlled between the experimental and control scenarios. In addition, it may be necessary to include scenarios that contain only the context or the survival threat to determine if either of

the two factors contributes to memory advantage.

Conclusion

The present review provides the first comprehensive analysis on the relative contribution of contextual versus survival effects in the SPE paradigm. Given that investigations of survival processing almost always confound both context and survival threat within the same scenario, our findings provide a preliminary explication of the complex relationship between the context and survival effects. Studies that reported significant findings for SPE may be problematic because the survival threat is not controlled for in the control scenarios.

As suggested above, the current conceptual considerations have vital implications for future research on the SPE. Specifically, the underlying cognitive processes that drive the effect cannot be ascertained without first dissociating the effect between the context and survival threat or at least examining the relative contribution between the context and survival threat as outlined above. By dissociating survival and contextual effects, the mechanisms that underlie each effect can be delineated more precisely. Consequently, our understanding of what constitutes adaptive memory can be enhanced.

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