RESEARCH ARTICLE

"Survival Processing of the Selfish Gene?": Adaptive Memory and Inclusive Fitness

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Abstract

The survival processing advantage in memory is the finding that items encoded in survival scenarios are remembered better than words encoded in survival-irrelevant scenarios or in deep encoding situations (e.g., pleasantness). Whether this mnemonic advantage, which is generally found in scenarios involving *personal* survival, can also be observed in scenarios involving the survival of *other people*, and in particular, *genetically related others*, has received little attention. In the present study, we asked nulliparous women to imagine being stranded in the grasslands of a foreign land without any basic survival items and to consider either their personal survival, the survival of their biological child, or the survival of an orphan. Compared to a pleasantness (control) condition, a survival processing advantage was found for the child survival group, which did not differ reliably from personal survival. Both the child and the personal survival conditions yielded better recall than the orphan condition, which did not reliably differ from the pleasantness condition. These findings provide further evidence for the view that memory has been sculpted by evolutionary processes such as inclusive fitness.

Keywords Adaptive memory · Survival processing advantage · Inclusive fitness

The evolutionary approach to human cognition is based on the idea that our brain has evolved in the same way as other parts of our body to solve recurrent survival and reproduction issues faced by our ancestors in the distant past. Indeed, our hunter-gatherer ancestors were regularly faced with the problems of finding food, drinking water, and protection from predators. Our cognitive capabilities, including memory, have been sculpted by such evolutionary pressures. The adaptive memory view is precisely the view that episodic memory, in particular, involves processing characteristics that are the result of confronting these evolutionary challenges (Nairne 2010; Nairne and Pandeirada 2008; Nairne and Pandeirada 2010;

Nairne et al. 2017a). There are several types of evidence for the adaptive memory view. Contamination effects in memory constitute one type. It has recently been found that items processed in relation to contamination, or that contaminated things themselves, are remembered better than items not processed in relation to contamination, or than healthy things (Bonin et al. 2019a; Fernandes et al. 2017; Henriques da Silva et al. 2019). Also, animates are remembered better than inanimates (Bonin et al. 2014; Bonin et al. 2015; Gelin et al. 2017; Nairne et al. 2013) and the reason why an animacy advantage in memory is found is according to evolutionary psychologists that animates have a higher fitness value than inanimates since they can be predators, prey, or potential sexual partners (Nairne et al. 2017b). However, most evidence in favor of the adaptive memory view comes from the *survival processing advantage* which is the focus of the present paper.

The survival processing advantage is the observation that information processed in relation to survival and/or to reproduction is remembered better than information not processed for its fitness value. Nairne et al. (2007) were the first to show that words processed for their relevance in a survival scenario are memorized better than words processed in a non-survival scenario, such as moving to a foreign land, or than words encoded deeply (e.g., rating words for their pleasantness).

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This memory effect has been replicated a number of times and is therefore robust (see for reviews: Bonin and Bugaiska 2014 and Kazanas and Altarriba 2015; see for a meta-analysis: Scofield et al. 2018). It has been qualified as "(…) one of the best—if not *the* best—encoding procedures yet identified in human memory research (…)" (Nairne et al. 2008, p. 180).

Until now, one issue that has received only little attention in the literature is whether the survival processing effect is found only when survival scenarios involve the self or whether this memory effect can also be extended to scenarios in which the survival situation concerns other people. In the present study, we addressed more precisely the issue of whether a survival processing advantage can be found when items are processed in situations involving personal survival, the survival of a biological child, and that of a non-biological child (an orphan). As we shall review below, evidence showing that the survival processing advantage is not confined to survival situations involving the self, but can also be found in survival situations involving other people, is mixed. This is an important issue because the ultimate goal of reproduction in sexual species does not strictly speaking concern individuals but their genes. The idea that natural selection operates at the level of the genes has been one major refinement to Darwin's (1859) natural selection theory and has been popularized by Dawkins (1976) as "the selfish gene" view. Dawkins (1976) put forward the idea that "we are the vehicle of our genes," and thus genes, not phenotypes, ultimately survive to continue to exist in the future. According to the "inclusive fitness theory" (Hamilton 1964) or "kin selection theory" (Smith 1964), not only is it possible to ensure the survival of our genes by means of direct reproduction (by having children), but also by ensuring the survival of the genes that we share with our kin. Behaviors intended to help genetic relatives, even at a cost to oneself, will be favored by evolution if these behaviors increase net genetic fitness (Hamilton 1964). Relatives are vehicles of an individual's genes but they differ in fitness value. For example, we are 50% related to our parents, children, and siblings; 25% related to our grandparents, uncles, and aunts; and 12.5% related to our first cousins. Therefore, adaptations to help kin in proportion to their genetic relatedness should have been favored by selection (see below for empirical evidence), even though altruistic behaviors can evolve under conditions of low, or even in the absence of genetic relatedness (e.g., reciprocal altruism, Trivers 1971; signal of mate quality, Farrelly et al. 2016). As proposed by Buss (2019), it follows from the inclusive fitness theory that selection should favor mechanisms, including memory mechanisms, which are tuned to help close kin more than distant kin or unrelated people. From an evolutionary point of view, one straightforward hypothesis is that we should observe a survival processing advantage, not only when "we" are faced with survival issues, but also when such issues involve our close kin, for instance our children, since we share half of our genes

with them. Also, the survival processing advantage should be less important when survival processing is directed to distant kin or to unrelated kin as in the case of an orphan.

In the literature on altruistic behaviors, it has been found that helping behaviors are not indifferentially directed to others. As one example, most people would not give the same amount of money to a child begging in the street as they would to their own child. Indeed, several studies have shown that individuals take care more of their kin than of unrelated others (strangers). Burnstein et al. (1994) asked participants to imagine being involved in different kinds of scenarios in which they had to help people who varied in their degree of genetic relatedness (.50 vs. .25 vs. .125). The hypothetical scenarios also varied in the cost of the helping behaviors that were required. In some scenarios, helping was substantial—life-or-death scenarios such as rescuing certain people in a burning house—whereas in other scenarios, helping was less costly, involving, for example, giving someone some money to help pay for a car or loading furniture during a move. The findings were clear-cut: Willingness to help in these hypothetical scenarios decreased as a function of the degree of genetic relatedness, especially in the life-or-death scenarios, with the result that .50 relatives were helped more than .25 relatives who were, in turn, helped more than .125 relatives (see also Fitzgerald and Whitaker 2009; Stewart-Williams 2007, 2008). In a more recent study (Antfolk et al. 2017), willingness to invest in children belonging to different categories—direct offspring, nieces/nephews, stepchildren, and friends' children—was assessed in a large population of adults. It turned out that they reported more willingness to invest in their own biological children than in other related children (nieces and nephews), or in stepchildren and friends' children in hypothetical scenarios (e.g., willingness to give a kidney, half of a month's salary). Importantly, altruistic behaviors have also been assessed in real-life situations and not only in the form of stated intentions. Likewise, it has been found that costly helping behaviors are directed more to close relatives than to distant relatives. The helping behaviors in question can take the form of bequeathing material wealth (Smith et al. 1987), gift giving (Tifferet et al. 2018; Saad and Gill 2003), enduring physical pain due to a physical exercise that results in a material benefit (Madsen et al. 2007).

For the great majority of our history as a species, we lived in small groups of nomadic gatherers and hunters. We are therefore a social species, and given our cooperative nature (De Waal 2015), the survival processing advantage in memory should be found not only in scenarios in which people must survive alone but also when groups of people have to survive. However, at the same time, as claimed by Klein (2012): "few things are more self-relevant than one's own survival" (p. 2). In the adaptive memory literature, only very few studies have investigated whether survival effects can be found when survival processing is directed to people other than the self, and moreover, the findings have turned out to be inconsistent.

Evidence that survival effects extend to people other than the self was provided by Weinstein et al. (2008). These authors compared first and third person (a friend) survival encoding scenarios—in the grasslands or in a city—and found a similar survival processing advantage in these conditions compared to a control non-survival scenario—moving to a new home in a foreign land. Also, and interestingly, Kang et al. (2008) found a survival effect in memory even when a cartoon character was the target of the survival encoding. Finally, Kostic et al. (2012) compared a scenario in which participants had to imagine being stranded at sea alone with a scenario where they were with a group of friends. Memory performance was better in the two survival scenarios than in the pleasantness condition but, importantly, the group and isolation conditions did not differ. These studies suggest therefore that the survival processing advantage extends to other people, and is not restricted to personal survival situations.

In contrast, the idea that the survival processing advantage is restricted to the self is supported by the studies by Leding and Toglia (2018) and Cunningham et al. (2013). Leding and Toglia (2018) asked their participants to imagine being stranded in the grasslands, going on a space mission, or moving to a foreign land while alone or with a group of friends. In an incidental recall test, the survival processing advantage was found only in the isolated condition and not in the group condition. Also, in a repeated-measures experiment, Cunningham et al. (2013) had participants rate the usefulness of items in the context of their own survival in a grasslands context, or that of the survival of a familiar other person (David Cameron). A semantic encoding task was used as a control task (rating whether items can be found in the city, in the natural world or sometimes in both contexts). In this study, no survival-processing effect was found on recognition performance when the words were rated in the context of the survival of a familiar other person, thus leading Cunningham et al. (2013) to claim that "(…) human memory systems may well have been tuned for survival (Nairne et al. 2007), but that this tuning is functionally specific to the continued existence of the self." (p. 240). At the same time, later in the paper, Cunningham et al. (2013) made the interesting suggestion that: "(…) if participants in the current experiment had been asked to encode information in the context of their mother's survival, the pattern of recognition memory performance would have been more in line with self than David Cameron." (p. 242).

Krause et al. (2019) have investigated the survival processing effect in different survival scenarios involving the survival of self ("you"), of kin (experiment 1: "you and your family"; experiment 2: "your close family members"), and other social categories (experiment 1: "you and several unrelated people"; experiment 2: "people who are unrelated"). The control condition was pleasantness. In both experiments, there were similar levels of recall across the kin, non-kin and self-conditions,

with all the survival conditions yielding higher recall rates than the pleasantness control condition. Given that in both experiments, the instructions did not indicate specific individuals such as a sibling, a fourth experiment was performed in which the kin condition took the form of "your youngest blood relative." Two other survival conditions were "a friend" and "a famous person." The control condition was again pleasantness. There were similar recall rates in the "kin," "friend," and "famous" groups, all of which yielded higher recall rates than the control group. Taken overall, the findings did not provide evidence that the survival of "kin" had a specific memory advantage compared to non-kin. As acknowledged by Krause et al. (2019), it remains possible that their study was not adequately designed to isolate an effect of kin selection. We agree, and thus, in our study, we again tested an effect of kin selection in memory by considering a different type of kin and non-kin relation, namely biological children and orphans. Finally, and directly related to the issue addressed here, Seitz et al. (2018) provided evidence for a reproduction-processing effect in memory: Compared to a pleasantness condition, a mnemonic advantage was found when rating words for their relevance to raising one's offspring ("your baby") in an ancestral environment. Importantly, this effect was comparable to that of the original (personal) survival-processing effect.[1]

Our study expands upon the adaptive memory literature and the altruistic kin literature. We designed one study to test the hypothesis that the survival processing advantage in memory should vary as a function of genetic relatedness (1 vs. .50 vs. .00). This makes sense because the ancestral survival scenario (Nairne et al. 2007) is an instance of a life-or-death scenario and, as reviewed earlier, the willingness to behave altruistically in life-or-death scenarios varies as a function of genetic distance among kin (Burnstein et al. 1994; Fitzgerald and Whitaker 2009; Stewart-Williams 2007, 2008). According to the adaptive memory view (Nairne 2010, 2015; Nairne and Pandeirada 2016; Nairne et al. 2017a), memory is tuned to remember items that are processed in relation to survival issues better than items that are not processed in this way, as instantiated by the survival processing advantage, which has proven to be a robust effect (Scofield et al. 2018). From an evolutionary perspective, a survival processing advantage should also be obtained when the scenario involves the survival of a biological child because offspring are a kind of vehicle for parents in that they permit their parents' genes to be transmitted through future generations (Buss 2019). From a gene perspective, the survival of an individual is worthless without children.

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[1] However, the authors did not find a reproduction processing advantage when the scenario emphasized finding a mate (see also Derringer et al. 2017; Sandry et al. 2013; but see Pandeirada et al. 2017 for a mnemonic advantage in the mating domain).

Importantly, in accordance with inclusive fitness theory (Hamilton 1964) and certain findings in the altruistic kin literature, the survival advantage in memory, if any, should be less when the recipient of helping behaviors is a non-biological child, namely an orphan.

Only nulliparous women were involved in the present study. We decided to focus on women, and not on men, because certain studies suggest that women are more likely than men to allocate resources directly to their children (e.g., Bossong 2001). Depending on the group, participants had to rate words for their relevance in three survival scenario conditions: "self," "biological child," or "orphan." Pleasantness was used as a control condition. It is a deep encoding condition that has often been used to evaluate the potential presence of a survival processing advantage (e.g., Bonin et al. 2019b; Kazanas and Altarriba 2017; Nairne and Pandeirada 2010; Olds et al. 2014; Seitz et al. 2018). Finally, because empathic concern has been found to be related (in part) to willingness to help (Maner and Gailliot 2007), we decided to assess dispositional empathy among our participants using the French version of the Basic Empathy Scale (Carré et al. 2013). The questionnaire was given after the memory experiment.

Method

Participants

Two hundred forty nulliparous female students (mean age 19.5 years) at the University of Bourgogne took part. They were divided into four groups ($n = 60$ in each group) that differed in encoding condition. All were native speakers of French, received course credits for their participation, and none were taking medication known to affect the central nervous system. The number of participants per condition was chosen on the basis of Scofield et al.'s (2018) meta-analysis of the survival-processing advantage in memory. The set of studies with between-subjects designs included in their analysis had a mean of 37.5 participants per group. If we consider the average effect size η_p^2 given by Scofield et al. (2018)—estimated between .06 and .09—power was more than .91 in our experiment[2] at an η_p^2 of .06, which is the lower bound of the interval.

Stimuli

The word list was created based on the criteria used by Nairne et al. (2007) to draw up their word list. We selected 30 words

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taken from 30 different semantic categories as given by the Bueno and Megherbi (2009) database (we used exactly the same semantic categories as Nairne et al. 2007).

Procedure

The participants were tested individually and were seated comfortably in a quiet room. They were randomly assigned to one of the four encoding conditions: personal survival in the grasslands, biological child survival in the grasslands, orphan survival in the grasslands, or pleasantness. For the "personal survival grasslands" condition, the instructions used were taken verbatim from Nairne et al. (2007):

Personal survival grasslands: "In this task, we would like you to imagine that you are stranded in the grasslands of a foreign land, without any basic survival materials. Over the next few months, you'll need to find steady supplies of food and water and protect yourself from predators. We are going to show you a list of words, and we would like you to rate how relevant each of these words would be for you in this survival situation. Some of the words may be relevant and others may not—it's up to you to decide."

Two additional scenarios were created from the personal survival grasslands scenario. However, they differ from it in mentioning that survival related either to a biological child or to an orphan. More precisely, the "biological child survival grasslands" scenario read as follows:

In this task, we would like you to imagine that you are stranded in the grasslands of a foreign land and that you are the mother of a young child. It turns out your child is very weak and needs you. In the coming months, you will have to take care of your child, to find her/him food, drinking water and ensure her/his protection. We are going to show you a list of words, and we would like you to rate how relevant each of these words would be for you in this situation of helping your child. Some of the words may be relevant and others may not—it's up to you to decide.

The scenario in the orphan condition was worded in the same way as the biological child scenario:

In this task, we would like you to imagine that you are stranded in the grasslands of a foreign land and that you have gathered a young orphan. It turns out this orphan is very weak and needs you. In the coming months, you will have to take care of this child, to find her/him food, drinking water and ensure her/his protection. We are going to show you a list of words, and we would like

you to rate how relevant each of these words would be for you in this situation of helping this child. Some of the words may be relevant and others may not—it's up to you to decide.

In the pleasantness condition, the participants had to rate the words for their pleasantness. The instructions were exactly the same as in Nairne et al. (2007). For the survival conditions, the participants were told that they would be given an imaginary scenario and that they would have to rate the relevance of each item in that scenario on Likert scales, with 1 indicating that the word was "totally irrelevant" to 5 indicating that the word was "extremely relevant." The scenarios were provided both orally by the experimenter and also presented on the computer screen. For the pleasantness condition, a Likert scale was used, with 1 corresponding to the response "very unpleasant" and 5 to "very pleasant." The words to be rated were presented one-by-one, centered on the screen. The stimulus presentation was self-paced, that is to say each presented word remained on the screen until the participant's response. However, a limit of 5 seconds was set, after which the next word was presented. Different random orders for word presentation were used across participants.

The ratings were made by pressing a key (labeled l to 5) on the keyboard. After the encoding task, the participants had to perform two interference tasks that lasted about three minutes: the "X-O" letter-comparison task (Salthouse et al. 1997) and the "plus-minus" task from Jersild (1927) and Spector and Biederman (1976). The surprise recall test took place immediately after the two interference tasks. The participants had five minutes to write down the previously presented words in any order they liked. After the recall task, the participants were given the French version of the Basic Empathy Scale (BES) (Carré et al. 2013). The BES is a tool that has been used to assess empathy in young people and adolescents on the basis of a dual-component conception of empathy: an affective and a cognitive component (Jolliffe and Farrington 2006). The BES comprises 20 items for which participants have to give ratings on 5-point Likert scales (1: strongly disagree; 2: disagree; 3: neither agree nor disagree; 4: agree; 5: strongly agree). The BES consists of 9 items for the cognitive empathy subscale (e.g., "I find it hard to know when my friends are frightened") and 11 for the affective empathy subscale (e.g., "My friends' emotions don't affect me much"). This scale has been translated into French by D'Ambrosio et al. (2009) who also validated it among French adolescents. Importantly, this scale has also been validated in French adults (Carré et al. 2013). In addition, Carré et al. (2013) have proposed an alternative classification of the items on the basis of three factors: emotional contagion (6 items, e.g., "I get caught up in other people's feeling easily"), cognitive empathy (8 items, e.g., "I have trouble figuring out when my friends are happy"),

and emotional disconnections (6 items, e.g., "I am not usually aware of my friend's feelings").

Design

The experiment was a 4 (scenario: personal survival grasslands, biological child survival, orphan survival, pleasantness) between-subjects design.

Results

The mean encoding times and the mean ratings (together with their standard deviations), and number of extra-list intrusions are reported in Table 1.

Encoding Times (msec) and Relevance Ratings As far as the time taken to rate the words is concerned, there was a significant effect of the type of encoding factor ratings, $F(3, 236) = 2.65$, $p = .049$, $\eta_P^2 = .033$. The encoding times were shorter for the pleasantness group than in the orphan survival condition: $q(4, 236) = 3.76$, $p = .041$, $\delta = -.049$[3]. The differences between the other conditions were not reliable (all $ps > .1$).

There was also a significant effect of the type of encoding factor on the relevance ratings, $F(3, 236) = 23.23$, $p < .001$, $\eta_P^2 = .228$. The mean ratings were higher in the pleasantness condition than in all other conditions: personal survival: $q(4, 236) = 11.35$, $p < .001$, $\delta = 1.47$; child survival: $q(4, 236) = 7.52$, $p < .001$, $\delta = .97$; orphan survival: $q(4, 236) = 8.29$, $p < .001$, $\delta = 1.07$. The ratings in the personal survival scenario were also lower than in the child condition, $q(4, 236) = 3.84$, $p = .034$, $\delta = -.50$. No other difference was reliable (all $ps > .1$).

Recall Rates A reliable effect of type of encoding was found, $F(3, 236) = 8.92$, $p < .001$, $\eta_P^2 = .102$ (see Fig. 1). More words were recalled in the personal survival scenario than in the orphan survival and pleasantness conditions, $q(4, 236) = 4.99$, $p = .003$, $\delta = .64$ and $q(4, 236) = 5.77$, $p < .001$, $\delta = .74$. Also, more words were recalled in the child survival group than in either the orphan survival, $q(4, 236) = 4.5$, $p = .009$, $\delta = .58$, or pleasantness, $q(4, 236) = 5.28$, $p = .001$, $\delta = .68$, groups. Moreover, the difference between the personal and child survival scenarios was not significant, $q(4, 236) = .49$, $p = .986$, $\delta = .06$, as was also the case for the difference between the orphan survival scenario and the pleasantness condition, $q(4, 236) = .78$, $p = .947$, $\delta = .10$. It is worth noting that the pattern of results was the same irrespective of whether encoding times or relevance ratings were included as covariates in the model.

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[3] δ was computed as the ratio of the difference between the observed means over the square root of the mean square error.

Table 1 Mean (M) and standard deviations (SD) of encoding times (in msec), ratings (1–5), and number (proportion in brackets) of extra-list intrusions as a function of the different encoding conditions

	Personal survival		Child survival		Orphan survival		Pleasantness	
	M	SD	M	SD	M	SD	M	SD
Encoding times	2187	528	2192	536	2256	662	1992	421
Ratings	2.70	.46	2.89	.44	2.85	.35	3.27	.29
Intrusions	1.22	2.08	.85	1.04	1.55	1.92	.47	.77
	[.07]	[.11]	[.06]	[.07]	[.11]	[.13]	[.04]	[.06]

Proportions of intrusions are computed as the number of extra-list items divided by the total number of items reported by the participant

As far as the numbers of extra-list intrusions are concerned (Table 1), these differed reliably across the different encoding conditions, $F(3, 236) = 5.41$, $p = .001$, $\eta_P^2 = .064$. There were significantly more intrusions in the orphan survival condition than in the pleasantness scenario, $q(4, 236) = 5.39$, $p = .001$, $\delta = .70$. There was also a higher number of intrusions in the personal survival scenario than in the pleasantness condition, $q(4, 236) = 3.73$, $p = .044$, $\delta = .48$. None of the other differences was significant.

The analyses performed with the Basic Empathy Scale (Carré et al. 2013) revealed no significant differences between the experimental conditions, either when considering the two-factor model, cognitive empathy: $F(3, 236) = .92$, $p = .434$, $\eta_P^2 = .011$; affective empathy: $F(3, 236) = 1.10$, $p = .349$, $\eta_P^2 = .014$; or the three-factor model, cognitive empathy: $F(3, 236) = 1.57$, $p = .198$, $\eta_P^2 = .020$; emotional contagion: $F(3, 236) = 1.37$, $p = .252$, $\eta_P^2 = .017$; emotional disconnection: $F(3, 236) = 1.02$, $p = .384$, $\eta_P^2 = .013$.[4] Given these results, it is not surprising that including the empathy dimensions as covariates in the analysis of the recall rates did not change the pattern of results. In addition, it is worth noting that there were significant positive effects of affective empathy and emotional disconnection on recall rates in the two-factor and three-factor models respectively, that is to say more words were recalled by more affective empathetic and less disconnected individuals.

Discussion

Anecdotal evidence suggests that we do not provide the same level of help to strangers as we do to our relatives. It is hard to imagine a world in which parents faced with a life-or-death situation, such as a shipwreck in which the number of lifeboats is limited, would hesitate to save the life of their own

biological child rather than that of an unrelated child. To our knowledge, such a world does not exist: We do not behave altruistically in an undifferentiated manner (Buss 2019). Helping has been found to vary as a function of genetic relatedness (Burnstein et al. 1994; Fitzgerald and Whitaker 2009; Stewart-Williams 2007, 2008). That being said, human beings belong to a highly cooperative species since we have lived in small and interdependent groups for most of our evolution (Hrdy 2009). Social species exhibit an impressive array of altruistic behaviors, some of which are directed to unrelated others (e.g., reciprocal altruism, Trivers 1971), and such altruistic behaviors have perhaps evolved to solve issues related to group living (Marsh 2016).

Turning to the adaptive memory literature, the survival processing advantage initially discovered by Nairne et al. (2007) is now a well-established finding. However, the question of whether this memory advantage extends to the survival of other people (Kostic et al. 2012; Krause et al. 2019; Seitz et al. 2018; Weinstein et al. 2008) or is restricted to personal survival (Cunningham et al. 2013; Leding and Toglia 2018) is a matter of debate because of discrepant findings in the literature. In the present study, we put forward the hypothesis that a survival processing advantage should be observed with an imaginary scenario involving the survival of a biological child because, from an evolutionary perspective, offspring are vehicles for their parents' genes (Buss 2019). More importantly, we also hypothesized that, in line with the inclusive fitness and kin-selection theories (Hamilton 1964), the survival effect in memory, if any, should be smaller when the recipient of helping behaviors is a non-biological child, namely an orphan. The findings were clear-cut. First of all, we were able to replicate the original survival processing advantage (Nairne et al. 2007): Encoding words in relation to a personal survival situation yielded better memory performance than rating words for their pleasantness. It should be remembered that pleasantness has often been used as a control condition to evaluate survival processing because it is a deep processing task (e.g., Kazanas and Altarriba 2017; Nairne and Pandeirada 2010; Olds et al. 2014). When survival was directed to a biological child, a survival processing advantage was also found. In line with Seitz et al.'s (2018) parenting scenario involving the

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[4] At the item level, a significant difference was found for only one item, i.e., item number 9, which corresponded to the statement "When someone is feeling 'down' I can usually understand how they feel", $F(3, 236) = 3.17$, $p = .025$, $\eta_P^2 = .039$. However, no pairwise comparisons reached significance with the Tukey tests (lowest $p = .09$).
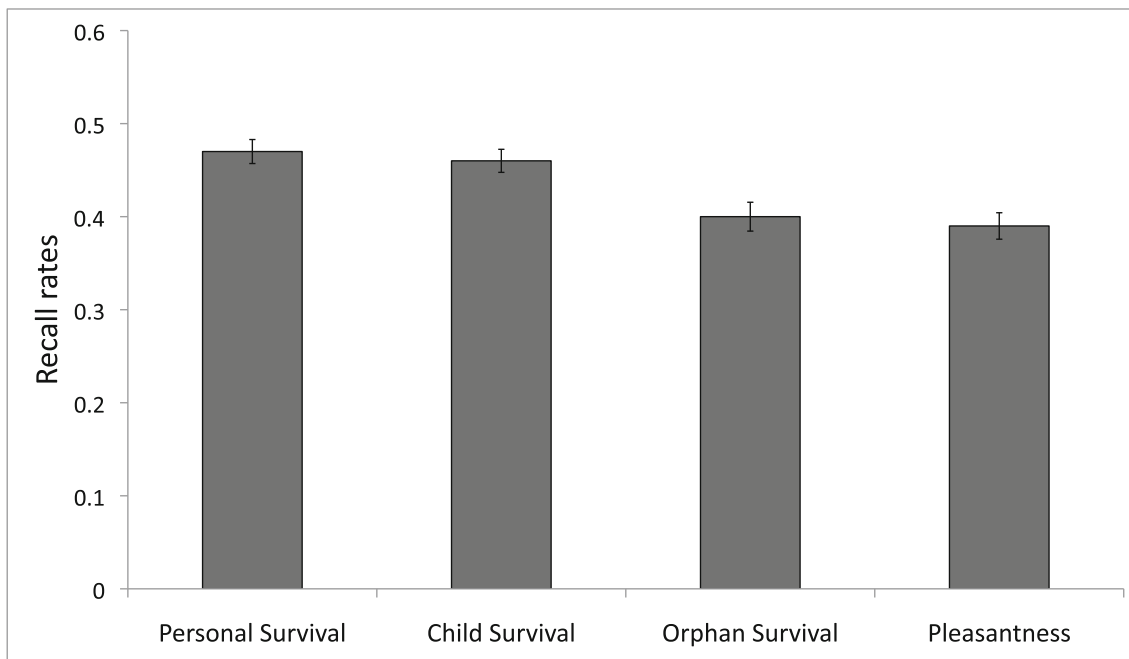
Fig. 1 Correct recall rates as a function of the different encoding conditions. The bars correspond to standard errors of correct recall

survival of the participants' babies in the grasslands, we found a reproductive advantage in memory that did not differ reliably from a personal survival advantage. More importantly, in accordance with the inclusive fitness theory (Hamilton 1964) and kin selection theory (Smith 1964), the level of recall varied as a function of genetic relatedness: More words were recalled in a survival situation involving a biological child than in a survival situation involving an orphan, and the latter condition did not differ reliably from the pleasantness condition.

From this pattern of findings, a critical question arises. Why did Krause et al. (2019) fail to find a differential survival processing advantage in their experiments comparing different types of kin vs. non-kin conditions? In Krause et al.'s research, different survival conditions were compared: personal survival, survival of family members, a youngest blood relative, unrelated people. It should be remembered that the authors found that compared to the pleasantness control group, the recall rates were similar across the "kin," "friend," and "famous" groups. Thus, the pattern of recall did not show that the survival of kin produced a memory advantage compared to that of non-kin. It remains possible that the social relationships that Krause et al. took into account were not specific enough for differential effects on memory performance to emerge. Finally, it cannot be excluded that our scenarios and Krause et al.'s scenarios are too different to be compared directly. In effect, Krause et al. modified the original survival scenario only slightly, and the different

scenarios were similar, whereas in the current study, more modifications were made to the original survival scenario. The strength of our study is that we took care to be specific by comparing children who are biologically related to their mothers with children who are not biologically related (we did not therefore include a generic "unrelated other" condition such as "strangers"). Moreover, we decided to include only female participants because it has been found that, in general, women are more interested in children than men are (Cárdenas et al. 2013; Charles et al. 2013; Maestripieri and Pelka 2002), and they also take more time to care for them (Babchuk et al. 1985; Buss 2007).

Some readers might be concerned about the finding that no survival processing advantage occurred with an orphan. Does this finding mean that people do not behave "altruistically" towards orphans? Certainly not. First of all, our findings concern memory performance and tell us nothing about the emotional responses people may have towards orphans. As suggested by Marsh (2016): "Parental care is such an ordinary phenomenon that we often fail to think of it as altruism. But it clearly meets the definition, which is a behavior that improves the welfare of another individual at the expense of the altruist." (p. 62). Parental care is often provided to distantly related children or to unrelated children (Hrdy 2009), including children who are adopted. According to Marsh (2016), care-based altruism results from the co-option of systems that initially evolved to support parental care. Here, we have shown that there are differences at a cognitive level in the way things are

remembered when they have been processed in a survival situation involving a biological child compared to a biologically unrelated child. Second, if we take a closer look at the memory performance, we observe that the words processed in a survival situation in the orphan condition were recalled well because they were recalled at the same level as the words that were encoded deeply, that is for their pleasantness. One important aspect worth noting is that the words in the orphan condition were not recalled less well than the words in the pleasantness condition—a deep encoding condition. Thus, there is still some level of altruistic behavior at a cognitive level that is deployed in the case of orphans.

Our findings have strong theoretical implications since they show for the first time that the survival processing advantage has to do with inclusive fitness and kin selection (Hamilton 1964; Smith 1964). From a general standpoint, they reinforce the evolutionary view of memory according to which our memory is still peculiarly attuned toward processing issues that our ancestors faced during the distant past, such as finding food, drinking water, and protection from predators both for themselves and also for their kin, and in particular for their children. It is already clear that more work will be needed to investigate further whether human memory is tuned to encode things better for different types of kin relationships such as sibling, parental, and grandparental relationships. We are aware of the fact that having only nulliparous women as participants constitutes a limitation of our study. Perhaps a different pattern of results would have been found if our participants had been mothers. Furthermore, it remains an avenue for future research to conduct the same study on young men. It is possible to anticipate that different findings will emerge because men and women faced different reproductive issues in the distant past. While women are 100% sure of their parenthood, ancestral men were (and indeed modern men still are) confronted with the problem of paternity uncertainty due to cryptic ovulation (Buss 2019). This reproductive problem faced specifically by men would account for their lesser interest (e.g., Cárdenas et al. 2013; Charles et al. 2013; Maestripieri and Pelka 2002) and investment in children compared to women (e.g., Babchuk et al. 1985; Buss 2007). Based on these findings, we anticipate that men will recall more words in both the personal survival scenario and child scenario than in the pleasantness condition, but that even when the risk of not being the biological father is low, men will recall less words in the child condition than will nulliparous women. However, in a survival scenario in which men have to imagine that there is a high risk that the child they must take care of is not their biological

child, our prediction is that the recall rate will be close to that found here in the orphan condition. Finally, in the future, it would be interesting to test whether grandparents' memory for items in survival situations involving their grandchildren differs as a function of the certainty of genetic relatedness. Likewise, a maternal grandmother is more genetically certain of her grandchildren than a paternal grandfather and, as found by DeKay (1995, reported by Buss 2019), maternal grandmothers are closer to and invest more resources in the grandchild than paternal grandfathers.

The question of the proximate mechanisms that underpin the survival processing advantage in memory is an issue which has given rise to a large number of studies. Different proximate mechanisms have been put forward and, according to Krause (2015), at least eight candidate mechanisms could contribute to the survival memory advantage. Although it was not the aim of our study to address this issue, our findings nevertheless suggest that self-reference, even though it certainly plays a role in this memory effect (Cunningham et al. 2013), is not the sole proximate mechanism involved. Indeed, if this were the case, survival-processing effects should have been restricted to the personal survival condition, unless biological children are considered to be part of the parents' self. In line with the latter claim, the literature on the self-reference effect reports that the mnemonic difference between self-reference and other-reference conditions is attenuated or eliminated when the other-reference conditions correspond to a parent or to a best-friend (Bower and Gilligan 1979; Symons and Johnson 1997).

Elaboration is a basic memory mechanism which certainly plays a role in the survival processing effect as suggested by certain studies (e.g., Bell et al. 2015; Röer et al. 2013; Wilson 2016). Nairne et al. (2017a, b) initially reported that survival processing increases not only true memories but also false memories. Here also, we found a higher number of extra-list intrusions in the personal survival scenario than in the pleasantness condition. This type of finding—namely an increase in both true and false memories—was later extended by Howe and Derbish (2010, 2014) and Otgaar and Smeets (2010), while other studies have failed to find significant effects of survival processing on extra-list intrusions (Bonin et al. 2019b; Gelin et al. 2017). According to Howe and Derbish (2014), because elaboration is known to increase both true and false memories, the effect of survival processing sometimes found on both true and false memories may be due to the need for greater levels of elaboration in order to rate words for their survival values. Interestingly, in the current study, we found that the greatest number of extra-list intrusions occurred in the orphan condition. Overall, the current pattern of findings

accords with the idea that elaboration underpins (at least in part) the survival processing advantage.[5]

As found in some previous studies (e.g., Seitz et al. 2018), mean relevance ratings were higher in the pleasantness condition than in any of the other conditions. However, and more specifically, recall performance was higher for both the personal and the child survival scenario than for the pleasantness control condition. It is also interesting to note that the ratings in the child condition were significantly higher than in the personal survival, but this difference did not translate into a recall difference between these two conditions. The pattern of findings for relevance ratings and recall rates suggests that the overall difference in recall rates across conditions was not a result of differences in depth of processing or in congruity, since it is generally accepted that words that are processed at a deeper level (Craik and Tulving 1975) or that are more congruent in a given encoding context (Butler et al. 2009; Craik 2002) are often recalled more accurately than words that are processed more superficially or that are rated as being less congruent (Seitz et al. 2018).

There are studies which suggest a relationship between empathy and altruistic behaviors (Marsh 2016). However, the analyses performed with the scores obtained from the Basic Empathy Scale (Carré et al. 2013) did not reveal that this dispositional trait played a role in the memory performance observed in the different encoding conditions that we considered. Emotional closeness has been found to be a proximal cause of altruism that partially mediates the impact of genetic relatedness on the willingness to act altruistically (Korchmaros and Kenny 2001). In the current study, we did not assess our participants' willingness to help as a function of different types of social relationship in an ancestral survival situation. However, because we were interested in knowing whether willingness to help an orphan versus a biological child would mirror memory performance as indexed by recall rates, as described in more detail in the Supplementary Material, we designed a questionnaire using LimeSurvey (www.limesurvey.org) and this was completed online by a pool of 84 undergraduates (only nulliparous women were taken into account). We collected ratings using Likert scales of willingness to help in a survival situation—by providing food, drinking water, and protection for both an orphan and a biological child who were said to be weak. In addition, we collected ratings for other types of kin (e.g., mother, sister, cousin) and non-kin (friend, neighbor, stranger) relationships. The findings (see the Results section in the Supplementary Material) turned out to be in line with those reported in the literature on altruistic behaviors (e.g., Burnstein et al. 1994; Fitzgerald and Whitaker 2009; Stewart-Williams 2007, 2008), that is to say, in a hypothetical survival scenario, women were more willing to aid close kin (e.g., child, mother) than distant kin (e.g., cousin), more willing to help distant kin than neighbors, "acquaintances," or "strangers" (see Figure 1A in the Supplementary Material). Interestingly, the level of help for "friend" was comparable to that of "cousin" (Figure 1A). More importantly, as far as the comparison between biological child and orphan is concerned, women chose to help their biological child more than an orphan. However, the level of help for "orphan" was close to that for "cousin" (Figure 1A).

To conclude, Krause et al. (2019) made the strong claim that kin selection is one more fitness-relevant scenario that has been found to be either unrelated or irrelevant to the survival processing advantage. The findings from the present study suggest just the contrary, namely that the survival processing advantage varies as a function of genetic relatedness, at least when the kin in question are biological children who, from an evolutionary point of view, ensure the perpetuation of our genes. Thus, our findings are in agreement with the claim put forward by Nairne et al. (2007) that "mnemonic processes likely operate more efficiently when dealing with fitness-relevant problems."

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[5] As stressed by Nairne et al. (2017a), the question of whether survival processing is due to the involvement of proximate mechanisms such as elaboration (e.g., Erdfelder and Kroneisen 2014) should not be conceived as ruling out an evolutionary account of this effect because, as these authors have convincingly argued, adaptations often mobilize basic processes to achieve their functions.

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