Evolutionary Psychology
October-December 2017: 1–11

DOI: 10.1177/1474704917742807
journals.sagepub.com/home/evp
SAGE

Adaptive Memory: Remembering Potential Mates

Josefa N. S. Pandeirada[1,2], Natália Lisandra Fernandes[1], Marco Vasconcelos[3], and James S. Nairne[2]

Abstract

According to the adaptive memory perspective, memory should function more efficiently in fitness-relevant domains. The current work explored whether there is a mnemonic tuning in a fundamental domain for human evolution: reproduction. In two experiments, female participants assessed how desirable potential male candidates (represented by a face and a short descriptor) would be in the context of a long-term mating relationship or in the context of a long-term work relationship. Then, after a short distractor task, participants performed a recognition task for the faces and a source memory task. Finally, they were asked to recall the descriptors presented during encoding. Experiment 1 used a between-subjects design, whereas Experiment 2 employed a within-subject design. In both experiments, participants remembered the faces best when they were encoded in the mating condition. Also, in Experiment 1, source memory performance was better in the mating condition than in the working condition with the reverse being true for free recall of the descriptors. The latter difference was not observed in Experiment 2. These results suggest a potential mnemonic tuning for the faces of potential mate partners.

Keywords

adaptive memory, mating, recognition, human faces, source memory

Date received: July 13, 2017; Accepted: September 28, 2017

The idea that memory reflects the selection pressures humans encountered throughout evolution has become known as "adaptive memory." Over the past decade, empirical evidence has been accumulating for better memory performance in fitness-relevant domains, that is, situations related to survival and/or chances of reproduction. Nairne, Thompson, and Pandeirada (2007) described for the first time a mnemonic advantage for information processed in a survival context. In their experiments, participants rated the relevance of items to an imagined situation in which they had to find food resources, shelter, and protection from potential predators (survival scenario). Free recall performance for the items was better after survival processing than after a set of control conditions (e.g., pleasantness rating task or relevance rating to a moving scenario). This result has been replicated against many encoding conditions well-known to boost memory performance (Nairne, Pandeirada, & Thompson, 2008) as well as with a variety of control scenarios, type of material, memory tasks, and retention intervals (for an overview, see Nairne & Pandeirada, 2016).

Less attention, however, has been devoted to the involvement of memory on what is considered to be the driving wheel of evolution: reproduction (Miller, 2001; Smith, 2017). Although this connection is by no means new—many theories of mate choice in nonhumans suggest that memory is crucial in the mating process (Bateson & Healy, 2005), it has rarely been tested in humans. Some studies have used a procedure similar to the survival paradigm: Participants are asked to rate the relevance of random words with respect to mating-related scenarios and then memory is tested for those words. Sandry, Trafimow, Marks, and Rice (2013) asked participants to rate the relevance

[1] Department of Education and Psychology, CINTESIS.UA, University of Aveiro, Aveiro, Portugal
[2] Department of Psychological Sciences, Purdue University, West Lafayette, IN, USA
[3] Department of Education and Psychology, CESAM, University of Aveiro, Aveiro, Portugal

Corresponding Author:
Josefa N. S. Pandeirada, Department of Education and Psychology, University of Aveiro, Campus Universitário de Santiago, 3810-193 Aveiro, Portugal.
Email: josefa@ua.pt

of words to searching for a partner who would satisfy them sexually, to identifying any potential relatives in order to avoid incest, to identifying potential rivals for their partners, and to confirming their spouse's infidelity. In Klein (2013), participants rated the relevance of words to selecting a mate. None of these conditions yielded a memory advantage relative to controls.

In a recent study, Derringer, Scofield, and Kostic (2017) had participants rate the relevance of trait adjectives to a set of different conditions. Their argument was that trait adjectives that described potential mates would be more relevant to selecting a mate than object nouns (the stimuli used in previous studies). In Experiment 1, participants rated how desirable the traits would be in a romantic partner or in a coworker; in Experiments 2a and 2b, participants rated the traits on their relevance to predicting whether their partner would engage in different types of infidelity (sexual and emotional infidelity). In the last experiment, participants rated the relevance of objects either to a romantic date scenario or to a housewarming party. In all experiments, a pleasantness rating condition was also used as a control condition. Even though, in Experiments 1 and 3, the mating-related conditions produced better recall than the pleasantness rating condition, suggesting some mnemonic benefit when thinking about reproduction, the former did not differ from the scenario-based nonfitness conditions. No differences among conditions were found in Experiment 2. In sum, studies in which participants rated the relevance or desirability of verbal information have failed to provide convincing evidence for a mnemonic sensitivity for reproduction-related matters.

Other studies used a different approach to tackle the issue exploring how the presence of sexually dimorphic characteristics—physical characteristics signaling the mate value of individuals—influence memory. For example, male voices with lower pitches are indicative of reproductive success (e.g., Apicella, Feinberg, & Marlowe, 2007). Smith, Jones, Feinberg, and Allan (2011) had females observe objects presented on the screen while the objects' names were simultaneously presented aloud via headphones. The key manipulation was the nature of the voices which varied in sex (male or female voices) and in pitch (lowered or raised to become more or less masculinized, respectively). Objects presented by a masculinized male voice were better recognized than those presented by a feminized male voice, whereas the female voice manipulation had no effect.

The mate selection context (seeking a short- vs. long-term relationship) also seems to impact how different characteristics are valued, a prediction derived from the idea that humans faced different selection pressures in these contexts (e.g., Buss & Schmitt, 1993). In particular, signs indicative of genetic quality ought to be favored in short-term contexts, whereas those related to being a good provider ought to be more important for long-term relations (e.g., Buss, 2006). Horgan, Broadbent, McKibbin, and Duehring (2016) had female participants observe a video of a male introducing himself after being prompted to think of him as a potential short- or long-term mate. A later surprise memory task revealed that participants prompted for the short term remembered more of the physical aspects, whereas those prompted for the long term remembered more of the personal information verbally presented by the male in the video. Females with stronger preferences for short-term relations were also better at identifying the context in which a more masculinized male face was presented, whereas those more inclined to long-term relations remembered more details of the less masculine faces' context (Smith, Jones, & Allan, 2013). Overall, the evidence from studies exploring the mate selection context (short vs. long term) suggests that memory performance is enhanced for information presented along with cues consistent with the current mating goals (i.e., short vs. long term).

The Current Experiments

As just reviewed, studies showing that memory is sensitive to the presence of sexually dimorphic cues have typically used artificially manipulated stimuli (e.g., more masculinized or feminized voices or faces). In addition, these studies have not directly compared mating against nonmating conditions or assessed whether memory performance is enhanced for the information that is directly related to the candidates' mate value (e.g., objects vs. the mate-relevant faces themselves; for an exception, seen Horgan, Broadbent, McKibbin, & Duehring, 2016). To explore a possible reproduction memory benefit for stimuli of direct relevance to mating (nonmanipulated faces and mate descriptors), the current experiments used a procedure that resembles the survival processing paradigm (Nairne et al., 2007). Participants processed and remembered exactly the same information—what differed was whether it was considered in a mating context or not.

In two experiments, females were asked to rate how desirable candidates (represented by faces and a short descriptor) would be if they were looking for a long-term mate (mating condition) or for a long-term coworker (control condition). This task forced participants to assess explicitly the mate/coworker value of the candidate. The final surprise memory tests (recognition and source memory [SM]) focused on the faces of the candidates given that visual recognition is one of the most immediate ways to identify previously encountered potential mates. We expected memory performance to be better when faces were considered in the mating condition. We also tested memory for the short descriptors that were presented along with the faces. Here, the predictions were less clear because findings in the literature are mixed. Some studies have failed to find enhanced retention for verbal materials in a mating context (Klein, 2013; Sandry, Trafimow, Marks, & Rice, 2013), whereas others have found mating-related effects for verbal information when comparing different mating contexts (short- vs. long-term mating context; Horgan et al., 2016). Memory performance for the descriptors will also inform whether memory for the candidate increases as a whole or if the (potential) boost in memory performance is restricted to face recognition. Importantly, everyone was asked to remember exactly the same information (faces and descriptors); what differed was the encoding context (mating or working). The first experiment used a between-subjects design and the second a within-subject design.

Experiment 1

In the first experiment, female participants viewed male faces (a candidate) accompanied by a short descriptive sentence. Their task was to rate how desirable each candidate would be if they were looking for a long-term mating partner or for a long-term coworker. A face could be presented with a desirable, a neutral (i.e., neither desirable nor undesirable), or an undesirable descriptor (e.g., "is an honest person," "has two brothers," or "is envious," respectively). After a series of rating trials, and after a short distractor period, participants performed an old/new recognition task for the faces; when a face was recognized as "old," participants were asked to identify whether that candidate had been considered desirable, neutral, or undesirable (SM task). Finally, participants were asked to recall all the descriptors presented during the task.

Method

Participants

Seventy-two young-adult females ($M_{age} = 21.31$ years, $SD = 2.92$) attending the University of Aveiro (Portugal) participated in exchange for course credit or for a small monetary compensation. They were randomly assigned to the "mating" and "working" conditions (both groups with $n = 36$). A power analysis conducted using G*Power (Version 3.1.9.2; Faul, Erdfelder, Lang, & Buchner, 2007) showed that this sample size ($N = 72$) had sufficient power ($1 - \beta = .80$) to detect a medium effect size ($f = 0.33$) at a significance level of $\alpha = .05$. Informed consent was obtained from all participants and all procedures conformed to the Declaration of Helsinki. Debriefing was provided at the end of the experiment.

Material

Two types of material were used: descriptive sentences and faces.

Descriptive sentences. A list of 99 characteristics was drawn from a previous study that collected characteristics considered desirable, neutral, or undesirable when looking for a long-term mate partner or a long-term working partner (Pandeirada, Fernandes, Marinho, & Vasconcelos, 2015). In a pilot study, sixty females ($M_{age} = 21.43$, $SD = 3.26$; $n = 30$ in each group) were asked to rate the desirability of these characteristics for each context (see scenarios below) using a rating scale ranging from −3 (*highly undesired*) to +3 (*highly desired*); a value of 0 corresponded to "neither desirable nor undesirable" characteristics (neutral). We then selected 36 descriptors that were rated as equally desirable, neutral, and undesirable for the two scenarios (12 descriptors of each type). Table 1 presents the selected descriptors along with their mean rating values for each scenario. Three extra characteristics to be used in the practice trials were selected using the same criteria. The use of characteristics spanning from desirable to undesirable compelled participants to spread their ratings and find some candidates that would be more desirable and others that would be less desirable. This variability also served as a control to check whether participants were performing the encoding task as intended.

Face stimuli. Seventy-two frontal-view male faces displaying a neutral emotional expression were used (+3 to be used in practice trials). These were selected from an initial pool of 122 male faces to have an average level of attractiveness ($M = 3.22$, $SD = 0.68$; scale 1–7), according to a previous norming study (Pandeirada, Fernandes, & Vasconcelos, 2014). The selected faces were then divided in two sets of similar attractiveness, absolute $t(35) < 1$, to be presented as targets and as distractors in a counterbalanced manner across participants. Each of these sets was further divided into three subsets of 12 faces of similar attractiveness to be assigned to the desirable, neutral, and undesirable characteristics during encoding; this assignment was also counterbalanced across participants. The pairing of the descriptors with the faces was determined randomly within each of the assigned subsets.

Procedure

Each session included groups of up to six participants and lasted approximately 30 min. On arrival at the laboratory, participants were randomly assigned to one of the conditions (long-term mating or long-term working) and to one of the experiment versions. Each participant was tested separately on an individual computer with all experimental events controlled via *E-prime 2.0 Professional* (Schneider, Eschman, & Zuccolotto, 2002).

At the beginning of the experiment, participants were told they would be rating a set of stimuli in one of the following conditions:

Mating condition. "In this experiment, we would like you to imagine that you are looking for a partner with whom you wish to establish a long-term relationship. You aim to create a family and spend the rest of your life with this person, so it is very important that you make the right choice!"

Working condition. "In this experiment, we would like you to imagine that you are looking for a worker to join the company you work for, with whom it would be desirable to establish a long-term contract. You aim to create a team to develop a number of important projects for the company which will include this person, so it is very important that you make the right choice!"

Also, would it be possible to maintain the same formatting as the previous instruction paragraphs in this additional set of instructions?

In both conditions, the instructions continued as follows:

> Next you will see a set of male faces presented along with a brief description. Please rate how desirable each person would be, considering both the person's face and the description, as a potential partner with whom to establish this long-term relation / long-term contract. Some people might be more desirable than others; it's up to you to decide who best corresponds to what you are looking for in a long-term partner / long-term co-worker.

Table 1. Descriptors Used in Experiments 1 and 2 Along With the Mean Values (and *SD*s) Obtained for Each Descriptor as Well as the Mean Values for the Sets Used in Each Experiment.

Undesirable			Neutral			Desirable		
Descriptor	Mate	Coworker	Descriptor	Mate	Coworker	Descriptor	Mate	Coworker
Lies frequently	−2.90 (0.31)	−2.77 (0.63)	Has tattoos[a]	−0.03 (1.07)	0.00 (1.23)	Has good sense of humor	2.33 (0.76)	2.00 (0.91)
Is rude	−2.83 (0.46)	−2.73 (0.52)	Has two brothers[a]	0.00 (0.79)	−0.13 (1.41)	Is nice[a]	2.33 (0.80)	2.40 (0.67)
Is racist	−2.77 (0.68)	−2.63 (0.85)	Lives in a busy street	0.00 (0.59)	0.03 (1.33)	Values friendship	2.37 (0.72)	2.10 (0.99)
Is always in a bad mood	−2.73 (0.52)	−2.50 (0.78)	Wears glasses[a]	0.00 (0.64)	0.10 (0.99)	Is hard worker	2.40 (0.62)	2.77 (0.57)
Is a fake person	−2.67 (0.96)	−2.40 (1.16)	Practices riding[a]	0.03 (0.85)	−0.10 (1.16)	Is humble[a]	2.47 (0.68)	2.57 (0.68)
Has poor hygiene	−2.60 (0.62)	−2.27 (0.87)	Likes short coffee	0.03 (1.33)	0.23 (1.30)	Is attentive[a]	2.50 (0.86)	2.43 (0.73)
Is selfish[a]	−2.57 (0.57)	−2.43 (0.94)	Has a white t-shirt	0.10 (0.71)	0.10 (0.88)	Is an honest person	2.57 (0.73)	2.83 (0.38)
Is sexist[a]	−2.47 (0.94)	−2.33 (1.09)	Was born in a maternity	0.10 (0.40)	0.17 (0.95)	Is responsible	2.67 (0.61)	2.73 (0.52)
Is envious	−2.43 (0.63)	−2.57 (0.73)	Prefers to write with a pencil	0.10 (0.31)	0.20 (1.06)	Is understanding[a]	2.70 (0.60)	2.17 (1.12)
Usually causes conflicts	−2.43 (0.82)	−2.47 (0.86)	Likes his steak cooked rare	0.20 (0.81)	−0.03 (1.05)	Is respectful	2.70 (0.60)	2.67 (0.66)
Is not sociable[a]	−2.27 (0.83)	−2.40 (0.72)	Has a gray coat	0.27 (0.87)	0.17 (1.23)	Works to achieve his goals	2.77 (0.50)	2.77 (0.43)
Is never on time[a]	−1.83 (1.14)	−2.93 (0.37)	Likes to eat tuna	0.30 (0.95)	0.13 (1.04)	Is a person we can trust	2.83 (0.53)	2.83 (0.46)
Undesirable	Mate	Coworker	Neutral	Mate	Coworker	Desirable	Mate	Coworker
Mean Exp. 1	−2.54 (0.29)	−2.54 (0.20)	Mean Exp. 1	0.09 (0.11)	0.07 (0.12)	Mean Exp. 1	2.55 (0.18)	2.52 (0.30)
Mean Exp. 2	−2.68 (0.17)	−2.54 (0.17)	Mean Exp. 2	0.14 (0.11)	0.12 (0.09)	Mean Exp. 2	2.58 (0.19)	2.59 (0.34)

Note. These data were obtained in the pilot study using an independent sample.
[a]Descriptors used in Experiment 1 only.

The desirability scale was as described in the pilot study (from −3 to +3) and participants were asked to use all the values in the scale. During encoding, each trial began with the presentation of the face and the question "How desirable would this person be for a long-term mating/working relation?" The descriptor was added 2 s later for another 4.5 s. The rating scale was then displayed along with the face and the descriptor, and participants were allowed 2.5 s to select their rating; if no response was given within the 2.5 s limit, the trial ended and a 250 ms intertrial interval started (see Figure 1 for a schematic representation of the encoding procedure). Three initial practice trials allowed familiarization with the rating task. Stimuli were presented in a random order for each participant.

After rating the 36 stimuli, participants performed simple math problems for approximately 3 min (distractor task). In the surprise recognition that followed, the 36 target and 36 distractor faces were randomly presented and participants had to indicate whether the face was old or new. In case of an "old" response, participants were asked to indicate if that person had been previously considered "undesirable," "neither desirable nor undesirable," or "desirable"; this second decision corresponds to the SM task in this experiment. In case of a "new" response, the program advanced to the next face. In the final surprise free recall task, participants were given 5 min to recall as many descriptors as they could from the encoding task by typing them directly on the computer. Finally, participants responded to a set of demographic questions.

Data Analysis

The dependent variables of main interest were the memory measures: recognition and SM for the faces as well as free recall of the descriptors. Of secondary interest were the ratings and response times. The former will indicate if participants performed the encoding task as instructed to and will also be relevant to the discussion of congruity as a possible proximate mechanism. The later will inform about differences in the time taken to provide a rating response which could influence memory performance. Analyses of variance were used as the main statistical tests. The level of statistical significance was set at .05 (two tailed). The results of this experiment are available at http://evo.psych.purdue.edu/datasets/

Results and Discussion

Desirability Ratings

Stimuli were rated as more desirable in the working condition ($M = 0.12$, $SD = 0.35$) than in the mating condition ($M = -0.35$, $SD = 0.55$), $F(1,70) = 18.92$, $MSE = .211$, $p < .001$, $\eta_p^2 = .213$. Overall, stimuli were rated in agreement

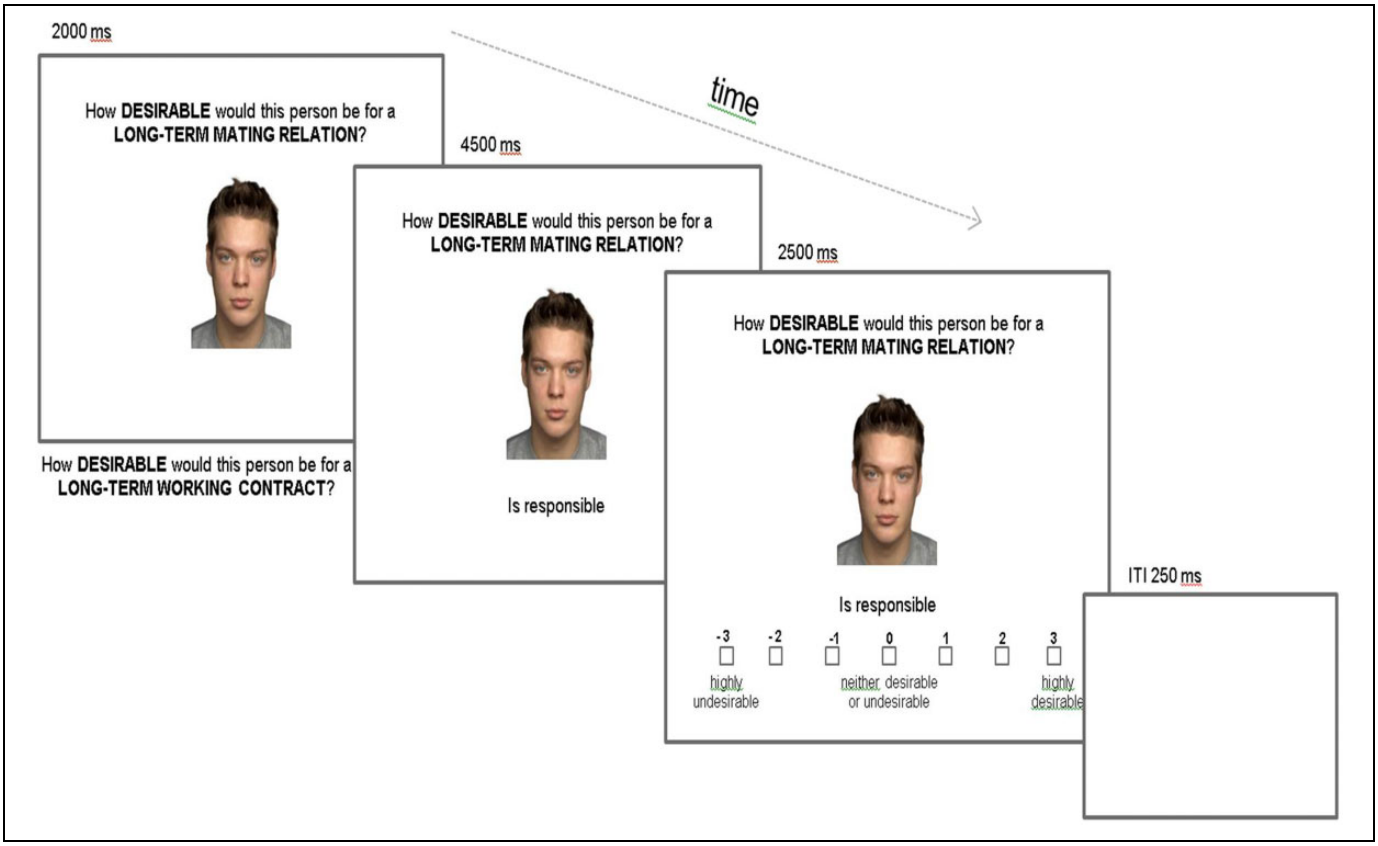

Figure 1. Schematic representation of the encoding procedure.

Table 2. Mean Rating Values (and *SD*s) Obtained in Each Experiment for Each Condition and Type of Stimuli.

Experiment / Condition	Undesirable	Neutral	Desirable
Experiment 1			
Mate	−2.16 (0.59)	0.02 (0.59)	1.15 (0.92)
Coworker	−2.11 (0.61)	.0.52 (0.55)	1.95 (0.35)
Experiment 2			
Mate	−2.32 (0.83)	−0.09 (0.84)	1.18 (0.96)
Coworker	−2.24 (0.72)	0.35 (0.78)	1.85 (0.78)

with our initial classification of the descriptors: Stimuli including the desirable descriptors were rated as more desirable than those presented with "neutral" descriptors which, in turn, were rated as more desirable than those containing undesirable descriptors (see Table 2). The percentage of stimuli classified by participants was mostly in agreement with the classification obtained in our pilot study.[1] In spite of a tendency for a higher classification agreement in the working than in the mating condition ($M_{\text{mating}} = .73$, $SD = .17$; $M_{\text{working}} = .80$, $SD = .13$), the difference was not statistically significant, $F(1,70) = 3.56$, $MSE = .024$, $p = .063$, $\eta_p^2 = .048$. This information confirms that participants were largely encoding the stimuli as intended. The number of nonrated items was low and similar in the two conditions ($M_{\text{mating}} = 1.3$, $SD = 1.30$; $M_{\text{working}} = 1.3$, $SD = 1.45$), $F(1,70) < 1$.

Response Times During Encoding

On average, participants took about 1 s to rate the stimuli during the encoding task in both conditions ($M_{\text{mating}} = 1{,}003.74$, $SD = 195.01$; $M_{\text{working}} = 974.46$, $SD = 172.35$), $F(1,70) < 1$.

Recognition Performance

Participants in the mating condition were significantly better at recognizing previously presented faces (recognition Hits) than participants in the working condition, $F(1,70) = 8.85$, $MSE = .022$, $p = .004$, $\eta_p^2 = .112$ (see Figure 2). The proportion of false alarms (FA) was similar between groups, $F(1,70) < 1$. These conclusions were further supported by analyses of discriminability (d') and of response bias (Criterion C). Regarding the first, participants in the mating condition were significantly more successful at discriminating old from new faces ($d' = 1.64$, $SD = 0.72$) than participants in the working condition ($d' = 1.19$; $SD = 0.52$), $F(1,70) = 9.34$, $MSE = .390$, $p = .003$, $\eta_p^2 = .118$. The response bias did not differ between conditions ($c_{\text{mating}} = 0.48$, $SD = 0.40$ vs. $c_{\text{working}} = 0.55$, $SD = 0.35$), $F(1,70) < 1$.

Source Memory

Recognition "old" responses were followed by a SM task, wherein participants had to identify if that face had been

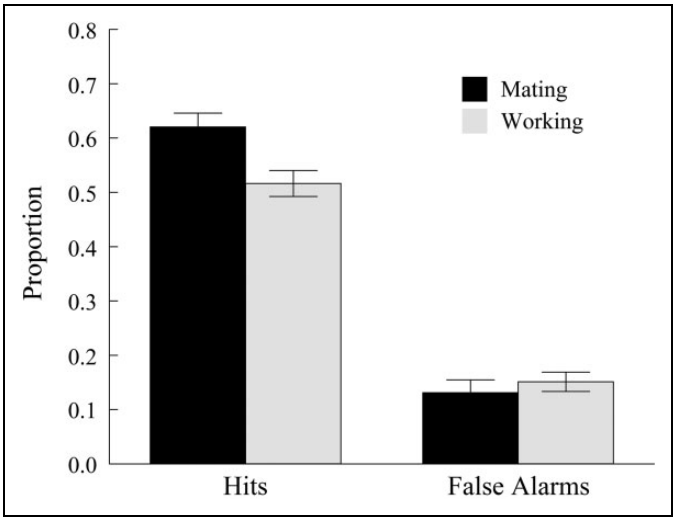

Figure 2. Mean proportion of recognition Hits and False Alarms per condition in Experiment 1. The error bars represent ± 1 standard error of the mean.

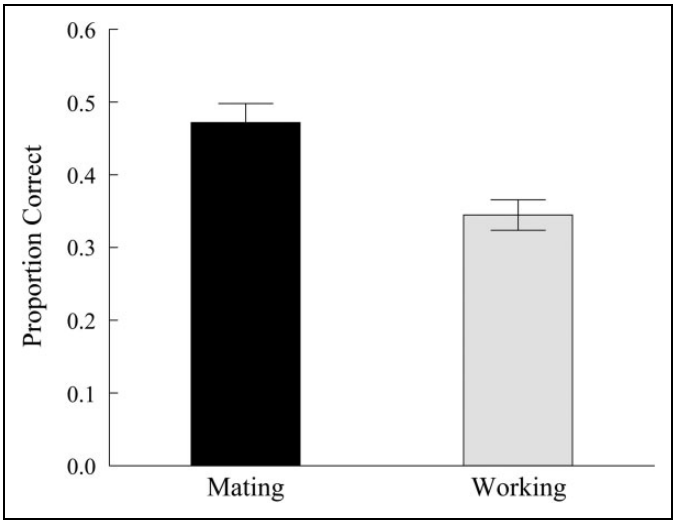

Figure 3. Mean proportion of source memory correct responses for recognition hits per condition in Experiment 1. The error bars represent ± 1 standard error of the mean.

classified as a desirable, neutral, or undesirable candidate; the classification assigned by each participant to each stimulus during encoding was considered. SM performance corresponds to the conditional source identification scores, which are calculated as the proportion of studied items recognized as old that were attributed to the correct source.

Participants in the mating condition performed better in this task than participants in the working condition, $F(1,70) = 14.51$, $MSE = .020$, $p < .001$, $\eta_p^2 = .172$ (see Figure 3). If participants were responding at chance, each possible SM response (desirable, neutral, or undesirable) would be selected about 33% of the time. Note that the overall SM performance was significantly higher than chance in the mating condition, $t(35) = 5.52$, $p < .001$, but not in the working condition, absolute $t(35) < 1$.

Free Recall of the Descriptors

Participants in the working condition recalled significantly more descriptors than those in the mating condition ($M_{working} = .36$, $SD = .087$; and $M_{mating} = .31$, $SD = .097$), $F(1,70) = 5.66$, $MSE = .008$, $p = .02$, $\eta_p^2 = .075$. Participants in the working condition also tended to produce more intrusions than participants in the mating condition ($M_{working} = 1.33$, $SD = 1.35$; $M_{mating} = .94$, $SD = 1.07$), but the difference was not statistically significant, $F(1,70) = 1.83$, $MSE = 1.48$, $p = .180$.

Faces of potential candidates (recognition task), as well as their previous desirability classification (SM task), were better remembered when encoded in the context of a long-term mating than in the context of a long-term worker relation. Participants in the working condition were more successful at remembering the descriptors associated with the faces during encoding, although there was also a tendency for those participants to commit more intrusions. From the perspective of an adaptive memory system, the results for the descriptors are puzzling given that verbal information processed in a survival context is remembered particularly well. This discrepancy is mitigated by the fact that in the typical survival context experiments, only verbal material is presented, whereas in this experiment, such material competed with face stimuli for attentional resources. Still, our findings are in line with previous studies that failed to produce a memory advantage for verbal material (e.g., object names) processed in a mating context as compared to control conditions (e.g., Sandry et al., 2013). They also suggest that the enhanced face recognition in the mating condition is unlikely to have been driven by an overall better memory for the whole stimuli (faces and descriptors).

Experiment 2

Our second experiment was designed to replicate the findings from Experiment 1 and to explore whether this mnemonic advantage would occur in a within-subject design as well. Some memory phenomena are known to depend on the type of experimental procedure (within vs. between; e.g., emotionality effects; see McDaniel & Bugg, 2008). In this experiment, each participant rated potential candidates in both the mating and the coworker contexts across different blocks of trials. A final recognition test for the previously seen faces was then presented. The SM task that followed each "old" response in the recognition test differed, however, from the one used in Experiment 1. Rather than asking people to identify the desirability classification previously assigned to the candidates, we asked participants to indicate if the face had been previously considered in the mating or the coworker context. The task ended with the free recall test for the descriptors.

Method

Participants

Forty young-adult females attending the University of Aveiro (Portugal) participated in exchange either for course credit or for a small monetary compensation ($M_{age} = 20.8$ years, $SD = 2.04$). This sample size allows us to detect a medium effect size (Cohen's $f = .23$), assuming a power of .80 and an α level of .05, as calculated using G*Power (Version 3.1.9.2; Faul et al., 2007). As before, all procedures conformed to the Declaration of Helsinki; all participants consented to participate and were fully debriefed at the end of the experiment.

Material

Descriptive sentences. Twenty-four descriptors were selected from the set of descriptors used in Experiment 1 (see Table 1). The descriptors that produced similar ratings between conditions in Experiment 1 were selected for this experiment.

Face stimuli. Forty-eight male faces were drawn from the set used in Experiment 1 ($M_{attractiveness} = 3.52$, $SD = 0.61$, scale 1–7). As before, this set of faces was divided into two sets of similar attractiveness to be presented as targets and as distractors in a counterbalanced manner across participants, absolute $t(46) < 1$.

Procedure. Groups of up to six females participated in each session which lasted about 30 min. Participants performed the task on individual computers with all experimental events controlled by *E-prime 2.0 Professional* (Schneider, et al., 2002). The initial instructions informed the participants that they would be presented with faces along with short descriptors and that they would have to rate each person according to different contexts. Four different blocks of items were then presented in an alternated manner, two assigned to the mating and the other two to the worker condition. Half of the participants performed the tasks in the order working—mating—working—mating and the other half in the order mating—working—mating—working; participants were randomly assigned to one of the versions before starting the experiment. Three practice trials preceded the first block for each condition to familiarize participants with the encoding task. At the beginning of each encoding block, the scenario was fully presented as described in Experiment 1. The selection of stimuli for each block was random with the constraint that each had to contain 2 items of each type of descriptor (desirable, neutral, and undesirable). The remaining procedural details were as described for Experiment 1 with the exception of the SM and final surprise free recall tasks. In this SM task, for each "old" recognition response, participants had to identify the context in which the face had been presented (mating or working)—that is, was the face previously considered in the mating or in the working condition? The free recall task lasted 3 minutes and participants were asked to write down on paper all the descriptors they could remember irrespective of the condition in which they appeared.

Data analysis. The dependent variables here analyzed were as in Experiment 1. Repeated-measure analyses of variance were used as the main statistical tests; as before, the level of statistical significance was set at .05 (two tailed). The main results of this experiment are available at http://evo.psych.purdue.edu/datasets/

Results and Discussion

Desirability Ratings

As in Experiment 1, participants rated the potential coworkers as more desirable than the potential mates ($M_{coworker} = -0.03$, $SD = 0.54$; and $M_{mate} = -0.41$, $SD = 0.55$), $F(1,39) = 16.86$, $MSE = .166$, $p < .001$, $\eta_p^2 = .302$. Importantly, the stimuli were rated as expected: Those that contained descriptors considered desirable and undesirable in our pilot study were classified as more and less desirable by participants, respectively (see Table 2). Applying the same scoring method as in Experiment 1, the consistency in the classification was again high in the two conditions, but it was now significantly higher in the working condition than in the mating condition ($M_{working} = .82$, $SD = .17$; and $M_{mating} = .73$, $SD = .23$), $F(1,39)$, $= 7.30$, $MSE = .02$, $p = .01$, $\eta_p^2 = .158$.

Response Times During Encoding

Participants took approximately 1 s to rate the stimuli during the encoding task in both conditions ($M_{mating} = 1{,}075.36$, $SD = 195.50$; $M_{working} = 1{,}075.95$, $SD = 207.84$), $F(1,39) < 1$.

Recognition Performance

The percentage of Hits was significantly higher for faces originally processed in the mating condition than for faces processed in the working condition, $F(1, 39) = 4.19$, $MSE = .017$, $p = .048$, $\eta_p^2 = .097$ (see Figure 4). On average, participants produced 2.63 FA during the recognition task (about 11%); the within-subject procedure prevents us from contrasting the FAs between the two conditions. Overall, these results replicate the mnemonic advantage of processing faces in the mating context.

Source Memory

When participants correctly recognized an "old" face, they were asked to identify the condition in which the stimuli had been previously considered (i.e., mating or working). Even though correct identification was above chance (50%) in both conditions, lowest $t(39) = 3.37$, $p = .002$, for the mating condition, participants were significantly more accurate at identifying the items from the working condition ($M = .68$, $SD = .15$) than those from the mating condition ($M = .59$, $SD = .17$), $F(1, 39) = 5.01$, $MSE = .029$, $p = .031$, $\eta_p^2 = .114$. Also of interest are the SM responses when the "old" responses were in fact FA, as these could be indicative of potential response biases; in other words, considering the

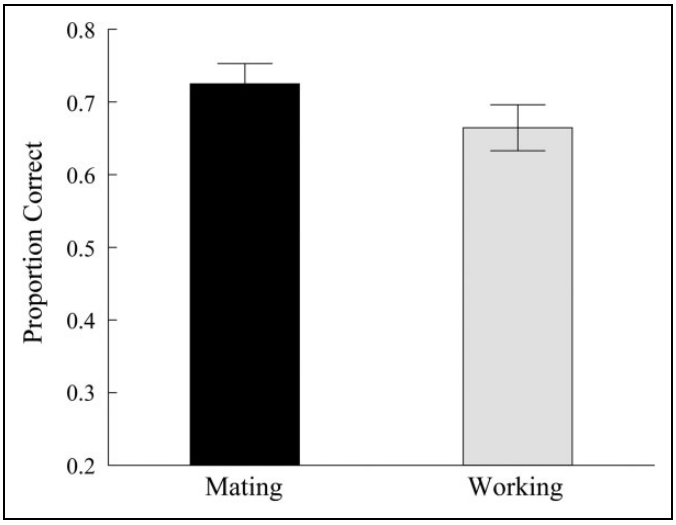

Figure 4. Mean proportion of recognition Hits per condition in Experiment 2. The error bars represent ± 1 standard error of the mean.

total number of FA committed by each participant, what proportion was classified as mating or working? Eight participants who did not commit FA were not included in this analysis. Interestingly, participants were also significantly more likely to attribute the incorrectly recognized distractors to the working condition ($M = .66$, $SD = .34$) than to the mating condition ($M = .34$, $SD = .34$), $F(1, 31) = 7.35$, $MSE = .231$, $p = .011$, $\eta_p^2 = .192$, suggesting a bias to assign faces to the working condition.

Free Recall of the Descriptors

Two participants were excluded from this analysis because they failed to follow instructions for this task. The remaining participants recalled on average a little over four descriptors per condition ($M_{mating} = 36\%$, $SD = 12.8$; and $M_{working} = 34\%$, $SD = 15.0$), with a repeated-measures analyses of variance confirming the absence of a significant difference between them, $F(1, 37) < 1$.

General Discussion

Is reproduction one of the evolutionary-relevant domains for which human memory is biased or tuned? The studies that have used the survival paradigm to address this question have failed to obtain evidence for such a reproduction-related tuning. In such studies, participants were invited to rate the relevance of random words to selecting a mate (Klein, 2013), to some other mating-related activity (Sandry et al., 2013), to whether object nouns could be used as gifts to be given on a romantic date (Derringer, Scofield, & Kostic, 2017), or participants rated trait adjectives in the context of considering a romantic partner or of predicting infidelity (Derringer et al., 2017). Memory for the rated words or adjectives was then tested. Each study failed to obtain evidence for a mating-related mnemonic advantage. Yet, other studies adopting different procedures have shown that memory is indeed sensitive to reproduction-related aspects. One potentially important difference between these approaches is that, whereas in the former the assessment of random words or objects provided no explicit information relevant to solving the adaptive problem of selecting a mate, in the latter, there is always some element of the encoding task that affords information about the mating value of the candidate, such as sexually dimorphic characteristics (Smith, Jones, Feinberg, & Allan, 2011). Still, these latter studies usually probed memory only for arbitrary stimuli previously associated with reproduction-relevant characteristics and have not contrasted mating against nonmating related conditions.

In the experiments reported here, which used faces rather than objects, during encoding participants had to directly evaluate how desirable potential candidates would be to establish a long-term mating (i.e., determine their mating value) or a long-term working relationship (i.e., determine their coworker value). Given that females rely on various indicators to evaluate a potential mate partner (Buss, 2006), male faces were presented along with short descriptions of behaviors or characteristics usually considered by females to be desirable, neutral, or undesirable in a long-term partner. Additionally, our memory task tapped one of the most common forms of identifying people: Face recognition of the candidates. In both experiments, recognition accuracy of the faces was higher in the mating than in the working condition.

Interestingly, the typical survival effect does not seem to occur when faces are used as stimuli, as shown by Savine, Scullin, and Roediger (2011). In their experiments, participants rated how helpful the person would be in a survival and/or in a control scenario (e.g., helping the participant in a bank robbery, moving home, among others). At face value, these findings contrast with the ones reported here, but important procedural variations may underlie these apparent discrepancies. For instance, whereas we used color pictures, Savine and colleagues used computer generated (Experiment 1) or Black and White faces (Experiments 2–5). Besides the evident difference in ecological validity, the color of the face is known to provide relevant information about the health status of individuals (e.g., Carrito et al., 2016). One could also speculate whether the faces used in Savine et al.'s study afforded sufficient and relevant information vis-à-vis the decision participants were required to make. Moreover, it is possible that different fitness-relevant contexts afford memory tunings to different sorts of information, particularly to those that are more informative or relevant to the adaptive problem at hand.

In Experiment 1, participants in the mating condition were also better at identifying the desirability classification previously assigned to the candidates (SM task)—that is, people in the mating condition were better at recognizing whether the person was previously considered a potentially desirable, undesirable, or neither desirable nor undesirable candidate. Being able to remember such information correctly when having to select among potential mates, or even in future encounters, would greatly aid the decision process. In Experiment 2, the

SM task requested a different decision from participants; here, participants were asked to identify the encoding context, that is, during encoding, was the face considered as a potential mate partner or as a coworker? In this task, participants were significantly more likely to respond "coworker" for the correctly identified old faces but also for the falsely recognized new faces. Such a result suggests that the SM working advantage for correctly recognized faces might be due to a response bias. Although we have no explanation for the failure to obtain a mating advantage for SM in Experiment 2, it is worth noting that prior work on survival processing also failed to find a survival advantage when the task required identification of the encoding context (see Bröder, Krüger, & Schütte, 2011; Nairne, Pandeirada, VanArsdall, & Blunt, 2015).

For recall of the descriptors, participants in Experiment 1 recalled a significantly larger number of descriptors in the working condition, but they also tended to generate more intrusions. In Experiment 2, the difference in recall between conditions was nonsignificant. Previous studies comparing memory for verbal information processed in a mating-related versus a control condition, such as those using the survival processing paradigm, have reported similar null findings (Derringer et al., 2017; Klein, 2013; Sandry et al., 2013). Yet, as shown by Horgan et al. (2016), females' memory for descriptive information can be influenced by the mating context (long vs. short term), suggesting that memory is tuned to the particular features germane to the fitness-relevant task at hand (see also Fitzgerald, Horgan, & Himes, 2016, for results with male participants, and Smith, 2017, for a discussion of this topic). Note, however, that this study did not compare the mating conditions (long and short term) with a control (nonfitness) condition which limits the comparison with our results.

The current experiments provide a relatively stringent test for the mating and memory hypothesis because our control condition—looking for a long-term working partner—could arguably have fitness consequences over the long term. The selection of a good coworker would likely have an effect on the company's success which, in turn, would impact the participant's ability to acquire more resources for his and her offspring. Also, working teams can function as coalitional groups with potential benefits to the members (e.g., Bugental, 2000).

One of the recurring questions underlying the adaptive memory framework relates to the proximate mechanisms, that is, what are the underlying processes that support a fitness-relevant tuning? (Nairne & Pandeirada, 2016). Congruity, or the fit between the encoded items and the encoding context, is one possibility. It is argued that richer and more elaborated memory traces are created when the item is more compatible with the encoding context making them easier to retrieve (Moscovitch & Craik, 1976; Nairne & Pandeirada, 2011). In the current experiments, we attempted to keep the overall level of congruity similar between the two conditions by presenting descriptors that would be equally desirable, neutral, or undesirable to both conditions; according to our pilot study, this was the case. However, when paired with faces, participants considered that the stimuli were more congruent (desirable) in the working than in the mating condition in both experiments. According to this account, this difference should have favored retention of information in the working condition. Also, the Derringer et al. (2017) findings indicate that rating values seem to have no effect in recall. Hence, it is unlikely for congruity to underlie the mating advantage we observed.

Self-reference is another element that could be contributing to this mating effect. Indeed, thinking about a potential mating partner could arguably be more relevant to the self than thinking about a potential coworker. Yet, previous studies have failed to find a mating effect when participants had to rate the relevance of words (objects and traits) to a mating context (as compared to various control conditions), a task that is presumably more self-relevant than the controls used (e.g., Derringer et al., 2017; Klein, 2013; Sandry et al., 2013). These findings suggest that self-relevance is not a major contributor to the mnemonic efficiency found in fitness-relevant domains in general and to our findings in particular, although further research is clearly needed.

Another possibility is that people simply pay more attention to facial characteristics when considering the desirability of a mate, as compared to when considering a potential coworker. In other words, the facial characteristics of a coworker might be less important than those of a mate, which may account for the mating advantage in face recognition. However, facial attractiveness has been shown to be a potent factor in memory for female faces but not for male faces of the type used in the current experiments (e.g., Anderson et al., 2010). In addition, facial characteristics (namely, attractiveness) have been reported to play an important role in coworker selection as well (e.g., Hosoda, Stone-Romero, & Coats, 2003; Pfeifer, 2011). Furthermore, we did not observe differences in the encoding response times between conditions in either of our experiments. Therefore, it seems unlikely that differential attention to the physical characteristics of the faces can explain the current results. Nevertheless, additional research is necessary before definitive conclusions can be reached.

Over the last decade, a set of studies started to establish that memory functioning is tuned to respond to the adaptive challenges faced during evolution. In addition to the survival processing advantage (Nairne & Pandeirada, 2016), it has been shown that memory is sensitive to potential contaminants (Fernandes, Pandeirada, Soares, & Nairne, 2017; Nairne, 2015) and to animacy (Nairne, VanArsdall, & Cogdill, 2017), both with evident adaptive significance (Nairne, Pandeirada, & Fernandes, 2017). The experiments reported here explored another fitness-relevant topic: reproduction. Our results join those of the studies that have showed that, when the encoding task includes elements or processes informative of the mate value of potential partners, participants' memory can be improved. The generality of the advantage remains unclear at this point, though, given the differential mnemonic effects that mate processing seems to have for different kinds of information (e.g., faces and descriptors). Further studies are needed to explore this new phenomenon.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: The Portuguese Foundation for Science and Technology provided support for Josefa N. S. Pandeirada (FCOMP-01-0124-FEDER-029610—PTDC/MHC-PCN/5274/2012; IF/00058/2012/CP0172/CT0002), and Natália L. Fernandes (SFRH/BD/109775/2015). Preparation of this work was also supported, in part, by a grant from the National Science Foundation awarded to James S. Nairne (BCS-1532345).

ORCID iD

Josefa N. S. Pandeirada http://orcid.org/0000-0001-7116-4609

Notes

1. To calculate the agreement between our initial classification and that provided by participants, stimuli that were assigned negative values by the participants were considered undesirable, those assigned positive values were considered desirable, and those assigned a "0" were considered neutral.

References

Anderson, U. S., Perea, E. F., Becker, D. V., Ackerman, J. M., Shapiro, J. R., Neuberg, S. L., & Kenrick, D. T. (2010). I only have eyes for you: Ovulation redirects attention (but not memory) to attractive men. *Journal of Experimental Social Psychology*, *46*, 804–808. doi:10.1016/j.jesp.2010.04.015

Apicella, C. L., Feinberg, D. R., & Marlowe, F. W. (2007). Voice pitch predicts reproductive success in male hunter-gatherers. *Biology Letters*, *3*, 682–684. doi:10.1098/rsbl.2007.0410

Bateson, M., & Healy, S. D. (2005). Comparative evaluation and its implications for mate choice. *Trends in Ecology & Evolution*, *20*, 659–664. doi:10.1016/j.tree.2005.08.013

Bröder, A., Krüger, N., & Schütte, S. (2011). The survival processing memory effect should generalise to source memory, but it doesn't. *Psychology*, *2*, 896–901. doi:10.4236/psych.2011.29135

Bugental, D. B. (2000). Acquisition of the algorithms of social life: A domain-based approach. *Psychological Bulletin*, *126*, 187–219. doi:10.1037//0033-2909.126.2.187

Buss, D. M. (2006). Strategies of human mating. *Psychological Topics*, *15*, 239–260. doi:159.913:159.942

Buss, D. M., & Schmitt, D. P. (1993). Sexual strategies theory: An evolutionary perspective on human mating. *Psychological Review*, *100*, 204–232. doi:10.1037/0033-295X.100.2.204

Carrito, M. d. L., Santos, I. M. B. d., Lefevre, C. E., Whitehead, R. D., Silva, C. F. d., & Perrett, D. I. (2016). The role of sexually dimorphic skin colour and shape in attractiveness of male faces. *Evolution and Human Behavior*, *37*, 125–133. doi:10.1016/j.evolhumbehav.2015.09.006

Derringer, C. J., Scofield, J. E., & Kostic, B. (2017). Investigations of a reproductive processing advantage in memory. *Memory & Cognition*, 1–19. doi:10.3758/s13421-017-0709-0

Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, *39*, 175–191. doi:10.3758/BF03193146

Fernandes, N. L., Pandeirada, J. N. S., Soares, S. C., & Nairne, J. S. (2017). Adaptive memory: The mnemonic value of contamination. *Evolution and Human Behavior*, *38*, 451–460. doi:10.1016/j.evolhumbehav.2017.04.003

Fitzgerald, C. J., Horgan, T. G., & Himes, S. M. (2016). Shaping men's memory: The effects of a female's waist-to-hip ratio on men's memory for her appearance and biographical information. *Evolution and Human Behavior*. doi:10.1016/j.evolhumbehav.2016.05.004

Horgan, T. G., Broadbent, J., McKibbin, W. F., & Duehring, A. J. (2016). Show versus tell? The effects of mating context on women's memory for a man's physical features and verbal statements. *Journal of Social and Personal Relationships*, *33*, 733–750. doi:10.1177/0265407515590279

Hosoda, M., Stone-Romero, E. F., & Coats, G. (2003). The effects of physical attractiveness on job-related outcomes: A meta-analysis of experimental studies. *Personnel Psychology*, *56*, 431–462. doi:10.1111/j.1744-6570.2003.tb00157.x

Klein, S. B. (2013). Does optimal recall performance in the adaptive memory paradigm require the encoding context to encourage thoughts about the environment of evolutionary adaptation? *Memory & Cognition*, *41*, 49–59. doi:10.3758/s13421-012-0239-8

McDaniel, M. A., & Bugg, J. M. (2008). Instability in memory phenomena: A common puzzle and a unifying explanation. *Psychological Bulletin & Review*, *15*, 237–255. doi:10.3758/PBR.15.2.237

Miller, G. (2001). *The mating mind: How sexual choice shaped the evolution of human nature*. New York, NY: Anchor Books.

Moscovitch, M., & Craik, F. I. M. (1976). Depth of processing, retrieval cues, and uniqueness of encoding as factors in recall. *Journal of Verbal Learning and Verbal Behavior*, *15*, 447–458. doi:10.1016/S0022-5371(76)90040-2

Nairne, J. S. (2015). Adaptive memory: Novel findings acquired through forward engineering. In D. S. Lindsay, C. M. Kelley, A. P. Yonelinas, & H. L. Roediger (Eds.), *Remembering: Attributions, processes, and control in human memory: Papers in honor of Larry L. Jacoby* (pp. 3–14). New York, NY: Psychology Press.

Nairne, J. S., & Pandeirada, J. N. S. (2011). Congruity effects in the survival processing paradigm. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *37*, 539–549. doi:10.1037/a0021960

Nairne, J. S., & Pandeirada, J. N. S. (2016). Adaptive memory: The evolutionary significance of survival processing. *Perspectives on Psychological Science*, *11*, 496–511. doi:10.1177/1745691616635613

Nairne, J. S., Pandeirada, J. N. S., & Fernandes, N. L. (2017). Adaptive memory. In J. H. Byrne (Ed.), *Learning and memory: A comprehensive reference* (pp. 279–293). Oxford, England: Academic Press.

Nairne, J. S., Pandeirada, J. N. S., & Thompson, S. R. (2008). Adaptive memory: The comparative value of survival processing. *Psychological Science*, *19*, 176–180. doi:10.1111/j.1467-9280.2008.02064.x

Nairne, J. S., Pandeirada, J. N. S., VanArsdall, J. E., & Blunt, J. R. (2015). Source-constrained retrieval and survival processing. *Memory & Cognition*, *43*, 1–13. doi:10.3758/s13421-014-0456-4

Nairne, J. S., Thompson, S. R., & Pandeirada, J. N. S. (2007). Adaptive memory: Survival processing enhances retention. *Journal of*

Experimental Psychology: Learning, Memory, and Cognition, *33*, 263–273. doi:10.1037/0278-7393.33.2.263

Nairne, J. S., VanArsdall, J. E., & Cogdill, M. (2017). Remembering the living: Episodic memory is tuned to animacy. *Current Directions in Psychological Science*, *26*, 22–27. doi:10.1177/0963721416667711

Pandeirada, J. N. S., Fernandes, N. L., Marinho, P. I., & Vasconcelos, M. (2015). *What do people (un)desire when looking for a mate partner?* Paper presented at the International Convention of Psychological Science, Amsterdam, the Netherlands.

Pandeirada, J. N. S., Fernandes, N. L., & Vasconcelos, M. (2014). *Normas portuguesas de atratividade para faces humanas*. Paper presented at the 9th National Meeting of the Portuguese Association for Experimental Psychology, Covilhã, Portugal.

Pfeifer, C. (2011). Physical attractiveness, employment and earnings. *Applied Economics Letters*, *19*, 505–510. doi:10.1080/13504851.2011.587758

Sandry, J., Trafimow, D., Marks, M. J., & Rice, S. (2013). Adaptive memory: Evaluating alternative forms of fitness-relevant processing in the survival processing paradigm. *PLoS One*, *8*, e60868. doi:10.1371/journal.pone.0060868

Savine, A. C., Scullin, M. K., & Roediger, H. L. (2011). Survival processing of faces. *Memory & Cognition*, *39*, 1359–1373. doi:10.3758/s13421-011-0121-0

Schneider, W., Eschman, A., & Zuccolotto, A. (2002). *E-Prime user's guide*. Pittsburgh, PA: Psychology Software Tools.

Smith, D. S. (2017). Commentary: Shaping men's memory: The effects of a female's waist-to-hip ratio on men's memory for her appearance and biographical information. *Frontiers in Psychology*, *8*. doi:10.3389/fpsyg.2017.00157

Smith, D. S., Jones, B. C., & Allan, K. (2013). Socio-sexuality and episodic memory function in women: Further evidence of an adaptive "mating mode." *Memory & Cognition*, *41*, 850–861. doi:10.3758/s13421-013-0301 -1

Smith, D. S., Jones, B. C., Feinberg, D. R., & Allan, K. (2011). A modulatory effect of male voice pitch on long-term memory in women: Evidence of adaptation for mate choice? *Memory and Cognition*, *40*, 135–144. doi:10.3758/s13421-011-0136-6