Universidade de
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Dissertação apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Mestre em Psicologia da Saúde e Neuropsicologia, realizada sob a orientação científica da Doutora Josefa N. S. Pandeirada, equiparada a investigadora principal do Departamento de Educação e Psicologia da Universidade de Aveiro, e coorientação da Doutora Mariana de Lurdes Carrito, investigadora da Faculdade de Psicologia e Ciências da Educação da Universidade do Porto.

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A todos vocês, a minha eterna gratidão.

**palavras-chave**

memória adaptativa, reprodução, coloração dos cartotenoides

**resumo**

A evolução humana depende da reprodução. No entanto, ainda não está claro qual o papel que a memória desempenha em contextos relacionados à reprodução. Os poucos estudos que investigam esta questão apresentam resultados mistos: alguns afirmam benefícios mnemónicos relacionados com o processamento relacionado com a reprodução, enquanto outros não mostram efeitos. Este estudo visa fornecer mais dados a esta discussão e ao mesmo tempo investigar a importância de uma característica ainda pouco considerada na literatura: a coloração dos carotenóides. Essa característica pode ser considerada uma pista diagnóstica do valor do companheiro, pois está relacionada à aparência saudável e à atratividade de faces. Essa coloração da pele também pode estar associada a vários indicadores importantes, incluindo maior sucesso reprodutivo, fotoproteção e defesa imunológica mais forte. Para o efeito, e mimetizando o procedimento utilizado por Fitzgerald et al. (2016), foram apresentadas a participantes do sexo feminino informações descritivas sobre diferentes potenciais parceiros. A memória foi então testada para esta informação descritiva. É importante destacar que, entre participantes, cada face masculina foi apresentada com a sua coloração alta/baixa em teor de carotenoides. Previmos que a memória seria melhor quando a face que acompanha a descrição apresentasse alto teor de carotenoides. Os resultados mostraram que um alto nível de coloração de carotenóides foi percebido como mais atraente, em consonância com a literatura. No entanto, não conseguimos obter evidências da influência dos níveis de carotenoides na memória para a informação descritiva apresentada com a face. Os resultados são discutidos à luz do que tem sendo investigado no campo da reprodução e da memória.

**keywords** adaptive memory,reproduction, carotenoid coloration

**abstract**

Human evolution depends on reproduction. However, it is still unclear what role memory plays in reproduction-related contexts. The few studies investigating this subject present mixed findings: some claim mnemonic benefits related to reproduction-related processing whereas others show no effects. This study aims to provide further data into this discussion while also investigating the importance of a characteristic still scarcely considered in the literature: carotenoid coloration. Such characteristic might be considered a diagnostic cue of mate value as it relates to healthy appearance and attractiveness of faces. This skin color may also be linked to several important indicators, including enhanced reproductive success, photoprotection, and stronger immune defense. To that end, and mimicking the procedure employed by Fitzgerald et al. (2016), female participants were presented with descriptive information regarding different males. Memory was then tested for that descriptive information. Importantly, across participants, a given male face was presented with its high/low carotenoid coloration. We predicted memory would be best when the face accompanying the description showcased the high coloration. The results showed that a high level of carotenoid coloration was perceived as more attractive. However, no influence of the face carotenoid coloration was obtained on memory performance for the descriptive information presented with the face. The results are discussed in light of what has been investigated in the field of reproduction and memory.

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## Introduction

A functional approach to memory predicts that its functioning should be regulated to increase humans' chances of survival and reproduction – a notion known as “adaptive memory” (Nairne & Pandeirada, 2008), and has turned into a rich research program over the past decade. Indeed, several phenomena related to such goals have been proposed; These include better memory for information processed in a survival context, as research discovered that items processed in a survival scenario promoted better retention than in other contexts (Nairne et al., 2007). This effect is called "survival processing advantage" and has been replicated numerous times (Nairne et al., 2007, 2008; Yildirim et al., 2022).

Additionally, there is evidence indicating the mnemonic advantage in other fitness-relevant domains (that is, those that impact our chances of survival and/or reproduction), such as contamination. In this case, researchers showed that individuals recall and recognize better items coded as potential sources of contamination compared to items processed in relation to non-contamination (Bonin et al., 2019; da Silva et al., 2019; Fernandes et al., 2017, 2021). The fitness-relevant character of contamination for memory is notorious, since it can assist people in preventing and avoiding potential contamination, and thus impact their chances of survival (Bonin et al., 2019; da Silva et al., 2019; Fernandes et al., 2017, 2021).

Animacy is another domain relevant to fitness, which has been revealed to influence memory through the "animacy effect," the finding that people remember animate (living) items better than inanimate (non-living) items (Félix et al., 2019; Gelin et al., 2015; Nairne et al., 2013, 2017). Animates have a unique status in memory because they are important environmental stimuli that can influence an individual's chances of survival and reproduction; for example, they can be potential sexual partners, cooperators, rivals, predators, or preys (Félix et al., 2019; Gelin et al., 2015; Nairne et al., 2013, 2017).

Another plausible candidate to be subject to a mnemonic advantage is reproduction, considering that evolution was driven not only by survival but also by reproduction success (Nairne & Pandeirada, 2008). Enhanced memory for traits that indicate a high-quality potential partner can assist individuals in making better decisions when selecting a mate and may provide them with the best opportunities for reproductive success, which is a key factor in evolutionary success (Nairne & Pandeirada, 2008).

Many theories of reproduction in nonhumans advocate that memory is important in the mating process because it can help in comparing the fitness value of potential mates (Bateson & Healy, 2005). For example, the peacock blenny females memorize cues and locations of previously encountered potential mates and use this information to make mating decisions (Locatello & Rasotto, 2017). Despite that, this topic has rarely been studied in humans, and the few existing studies are inconclusive.

Currently, studies on memory and reproduction cover various aspects of human reproductive success, such as mate selection, mate retention, and kin selection (Yildirim et al., 2022). Some studies in this domain have used a processing paradigm, where participants rate the relevance of random words in mating-related scenarios, and then memory for the rated words is evaluated. For example, in the study of Sandry et al. (2013) participants rated the relevance of words to search for a partner in several mating-related activities, including mate-detection and jealousy. In Klein (2013), participants were asked to rate the relevance of random words in selecting a mate. Derringer et al. (2017) used trait adjectives in the context of romantic partners and infidelity. Later, Seitz et al., (2018) compared memory performance for words studied in different scenarios including survival, ancestral reproduction, and others. However, no indication of a systematic mnemonic advantage related to mating has been found in these studies.

In another type of studies, particular attention has been devoted to characteristics of potential mates that might inform about their mate value. From an evolutionary view, potential partners' appearance and personal statements, among other useful cues, signal to the observer both desirable and undesirable mate qualities, allowing them to make judgments about potential partners (Horgan, 2020). The selection pressures faced by our ancestors led to the development of genetic properties that favor attraction to high-value mates because it likely increased reproductive success (Sugiyama, 2016). Attractiveness may improve an individual’s reproductive success, as it allows the identification of high-quality mates through detecting and assessing cues indicative of mate value (Garza, 2022).

In this line, the study of Pandeirada et al. (2017), in which participants judged the desirability of faces presented along with short descriptor traits in a mating or a working context showed that women remember better male faces considered in a mating (vs. a non-mating) context. Moreover, research that has manipulated cues to convey information about a potential partner's mate value or desired qualities in a mate, such as sexually dimorphic characteristics (bodily features, voice, or face) demonstrated evidence in favor of a mnemonic benefit for reproduction (Baker et al., 2015; Fitzgerald et al., 2016; Horgan et al., 2016; Pandeirada et al., 2017). For example, studies found that a lower-pitched male voice is linked to reproductive success. Accordingly, studies have revealed that females tend to remember best objects previously associated with masculinized (vs. feminized) male faces (Apicella et al., 2007; Puts et al., 2016; Smith et al., 2012). Similarly, in another study, while listening to a story, participants (of both sexes) viewed 10 opposite-sex faces that were highly attractive or with an average level of attractiveness. Memory was then tested for the details of the story. Men were found to remember more descriptive details about females when previously exposed to highly (vs. average) attractive faces (Baker et al., 2015).

Further, in the studies of Fitzgerald and collaborators (2016), men showed better memory for women with a body characteristic indicative of greater reproductive potential, namely a waist-to-hip ratio (WHR) closer to the ideal. Participants were shown one of the variations of the image of a woman which was digitally manipulated to display WHR between 0.50 and 0.90. The image was presented along with a paragraph of biographical information (e.g., woman's name, college major, job, favorite places to visit, etc.). Then, free recall and recognition tasks were used to evaluate the participants' memory for the appearance and details of the potential partner. The results revealed that participants remembered more details about the female potential partner when her image displayed a WHR of around 0.70, compared to those who viewed the image displaying WHR of 0.50 or 0.90.

Until recently, most studies on reproduction have focused on non-color-related body characteristics and facial traits, such as averageness and symmetry. Recently, the color appearance of human faces has gained increasing attention, with some studies suggesting it plays a significant role in the perception of attractiveness (Carrito et al., 2016; Lefevre & Perrett, 2015). Research in this line has shown that carotenoid coloration imparts the skin an orange-yellow color that is perceived as healthy and attractive (Foo et al., 2017; Lefevre & Perrett, 2015; Pezdirc et al., 2018; Stephen et al., 2011).

Such skin coloration might be considered a diagnostic cue of mate value as it relates to several important indicators, including visual acuity, photoprotection of the skin, stronger immunity characteristics, and reproductive health in humans (Alexander et al., 1985; Dowling & Simmons, 2009; Tan & Stephen, 2019; Vinkler & Albrecht, 2010). Interestingly, we know that this coloration influences mate selection in many non-human species, including birds and fish, as it relates to several important health factors, such as fertility and improved immune function (Stephen et al., 2011). In several species of birds, females prefer males with carotenoid-based plumage. One example is the female Mallards, Anas platyrhynchos, known to produce eggs with a heavier texture and larger size after breeding with males that have artificially augmented carotenoid coloration (Giraudeau et al., 2011).

Carotenoid coloration is associated with increased fruit and vegetable consumption (Ip et al., 2019). The carotenoids dietary is positively related to skin yellowness (Stephen et al. 2011) and has been shown to produce visible changes in a short period. For example, Whitehead et al. (2012) reported visible changes occurring within six weeks of increased intake of fruit and vegetables. Other studies have also shown increased yellowing and redness within eight weeks of taking daily beta-carotene supplements (Coetzee et al., 2014; Stephen et al., 2011) and a more recent study that reported similar changes in individuals who took smoothies with high levels of carotenoids for six weeks (Tan et al., 2015).

Although melanin-associated coloration also increases the perception of health (Stephen et al., 2009, 2011), previous work shows a direct preference for carotenoid-associated coloration over melanin coloration (Lefevre & Perrett, 2015; Stephen et al., 2011). This preference is present even in ethnicities where the individual tends to perceive tanning and melanin coloration as attractive (Pezdirc et al., 2018). For instance, Lefevre & Perrett (2015) found that faces with high carotenoid coloration are significantly more attractive than faces with high melanin coloration. Additional evidence supports this result, like the study of Pezdirc et al. (2018) that showed that Australian observers when asked to manipulate the facial color to enhance healthy appearance, commonly increased carotenoid coloration over melanin coloration.

Carotenoid coloration is strongly preferred and may be universal (Ip et al., 2019). The preference for this skin color properties in faces has been proven in different cultures, including Caucasian (Lefevre & Perrett, 2015; Pezdirc et al., 2018; Stephen et al., 2011), African (Coetzee et al., 2014; Stephen et al., 2012), Malaysian Chinese (K. W. Tan et al., 2017, 2018), and Hong Kong Chinese (Ip et al., 2019).

Previous research has only examined the role of carotenoid skin coloration on perceived health, healthy diet, perceived age, and attractiveness, all of which are indicative of the person's mate value (Lefevre & Perrett, 2015; Pazda et al., 2016; Stephen et al., 2009, 2012; Thorstenson et al., 2017). However, no research has yet explored the potential effect of carotenoid coloration on mating decisions and/or memory.

Because human memory evolved to preferentially encode information of greater adaptive value (Nairne & Pandeirada, 2008), people may exhibit enhanced memory for a potential mate partner who displays enhanced carotenoid skin coloration. Such superior memory would afford more mating opportunities with more fit partners, thus ensuring higher reproductive success (Nairne & Pandeirada, 2008).

Given the above, this work aims to contribute to the still limited literature regarding the involvement of memory in reproduction, focusing on the potential significance of carotenoid coloration as an indicator of mate value. To that end, and mimicking the procedure employed by Fitzgerald, we presented to female participants descriptive information regarding different males. Memory was then tested for that descriptive information. Importantly, across participants, a given male face was presented with its high carotenoid coloration or with its low carotenoid coloration. We predicted that memory would be best when the face accompanying the description showcases the high carotenoid coloration.

## Pilot Study

Before moving on to the actual study, it was necessary to determine the amount of increase in carotenoid coloration that produces optimal attractiveness in faces. The results of this phase allowed us to select the stimuli (faces) for our following Experimental study. This was achieved through an interactive task procedure, where participants adjusted the face color level according to their preferences (Carrito et al., 2016; Perrett et al., 1998). Based on previous literature in this area, we predicted that participants would prefer high carotenoid coloration than low carotenoid coloration when looking for the most attractive appearance of faces. This study was pre-registered (AsPredicted #132215). Our studies have been approved by the Research Ethics Committee of the ISPA – Instituto Universitário.

# Method

## Participants

The sample size was estimated according to the effect sizes reported in the area's most recent and relevant studies (Jones, 2018; Study 2). A total sample of 112 participants was recruited from an online running platform (Prolific), at university, and through other media sharing means (e.g., Facebook). Participants recruited through Prolific were paid for their participation. As pre-registered, the inclusion criteria were age between 18 and 35, cisgender identity, Caucasian ethnicity, heterosexual, having English or Portuguese as a first language, and reporting no vision or color vision impairment. The application of the aforementioned criteria did not result in any participant exclusion.

Some additional exclusion criteria were pre-registered, namely: having performance that 3SDs below the overall sample mean, responding faster than what would be considered acceptable for the task at hand (e.g., less than 2 seconds for the color-interactive task), or indicating their data should not be considered reliable (e.g., in response to an honesty question). The application of the aforementioned criteria resulted in no exclusions. However, during the data analysis phase, we decided to also exclude those participants with at least 20% missing values. This resulted in the exclusion of fifteen participants (six English and nine Portuguese). Thus, our final sample included 103 participants (54 male). Of these, 50 English participants (26 male, mean age = 28.3 years, age range = 19–35 years) took part in the online version, and 53 Portuguese participants (28 male, mean age = 21.2 years, age range = 18–33 years) completed the task in the laboratory.

## Material

Ten composite female faces and ten composite male faces were used for perceptual judgments - each one was an average of three different faces of the same sex. These sets of three faces were selected at random from the 102 adult images in the open-access Face Research Lab London Set (DeBruine & Jones, 2021). All images exhibit neutral emotional expressions, and similar mean attractiveness levels (between 2.9 to 3.9, on a 1-7 scale ranging from "much less attractiveness than average" to "much more attractive than average"). Similar to another experiment (Carrito et al., 2016), the averaging procedure was employed to diminish individual disparities in the color and shape of the face stimuli. To attain this, on every face image, one hundred and ninety-two landmarks were denoted to specify the facial attributes targeted for transformation.

Following earlier research, these face images were then manipulated using Psychomorph (Tiddeman et al., 2001), in accordance with the color difference between two endpoint color masks, representing the high and low carotenoid coloration as performed elsewhere (Lefevre & Perrett, 2015). A sequence of 21 images was obtained for each face, ranging from -200 to +200% carotenoid coloration, with the original composite face as the middle image. The color continua represented a total range of ±1.1 L* units, ±1.45 a* units, and ±3.8 b* units (indicated units consider the CIE L*a*b* color space, which is commonly used in human perceptual studies (Stephen et al., 2009). An oval white mask was later applied to occlude part of the neck and background of all versions of each face.

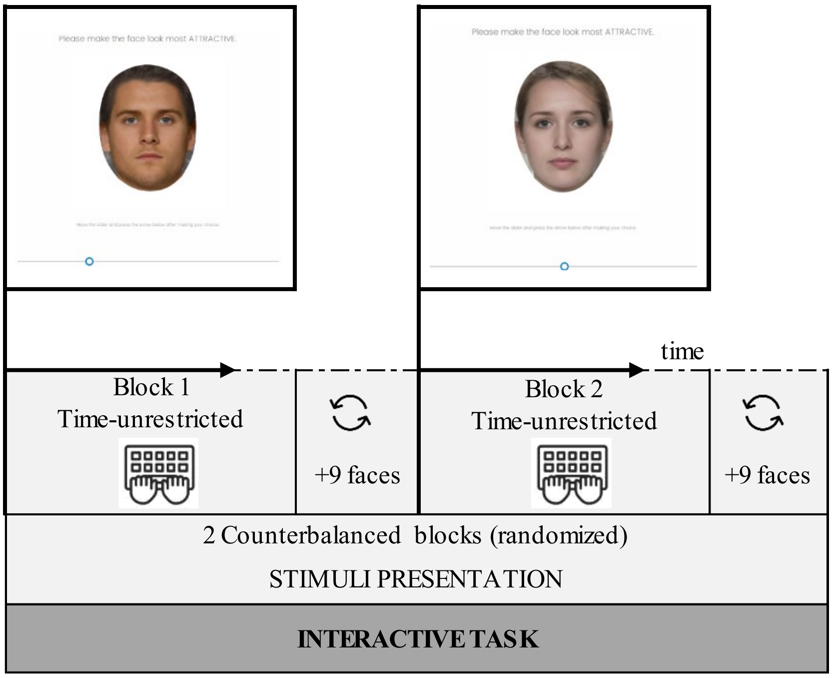
**Procedure**

The procedures of this Pilot study were implemented using the Qualtrics platform. About half of the participants conducted the experiment using individual computers in groups of one to six persons at the University of Aveiro's EvoCogLab facility. The other half performed the experiment online on their personal computers through the Prolific platform. The hybrid data collection method was driven by convenience.

After providing their informed consent, participants were presented with a short demographic questionnaire. Subsequently, they performed a self-paced interactive task, where they were instructed to “make the face look as attractive as possible” (see Appendix A and Fig 1). The task consisted of adjusting the skin color along the carotenoid axis to enhance the attractiveness of the faces from the range available. Similar to other experiments (Carrito et al., 2016; Carrito et al., 2020), participants could alter the color of the shown face by moving horizontally a sliding scale.

Two counterbalanced blocks of ten faces, divided by the face's sex, were displayed in a random order. Each face's presentation was also randomized in both same-sex blocks. Participants choose the point along the color axis by moving their mouse cursor horizontally. The starting point and direction of the slider (moving left or right, increasing, or decreasing color) were all pseudo-randomized. In both versions, participants were instructed to adjust the monitor's color calibration to ensure an accurate representation of colors. Finally, participants were asked to answer a question regarding if they paid attention and answered honestly to the task, and whether we should consider their data in the analyses. The debriefing information was presented on the last page. Participants took approximately 10 minutes to complete the task.

**Figure 1.** *A scheme of the Pilot Study procedure.*




**Data Analysis**

Data were analyzed using IBM SPSS Statistics (Version 29). The dependent variable was the average amount of preferred carotenoid coloration, representing optimal attractiveness. Data from this study is primarily descriptive. One sample t-test was employed to explore whether the chosen level of carotenoid coloration is significantly different from no change in coloration (i.e., 0% color manipulation). Analyses of variance were also applied. The statistical significance level was set at $p < 0.05$ (two-tailed) for all analyses.

## Results

The mean degree of carotenoid coloration for each participant was calculated for the male and female faces separately (see Table 1). A significant preference for carotenoid coloration was found for male faces (one sample t-test against no change in skin color, $t(52) = 91.51$, $p < .001$, $d = 57.41$), and for female faces ($t(52) = 102.30$, $p < .001$, $d = 43.43$) for the Portuguese participants. Similarly, increased carotenoid choices were shown to be greater than chance for male faces ($t(49) = 95.36$, $p < .001$, $d = 45.81$) and for female faces ($M = t(49) = 95.56$, $p < .001$, $d = 48.34$) for the English participants.

A 3-way mixed ANOVA (between-subjects factor: language and sex of participant; within-subjects factor: sex of the faces) revealed a non-significant main effect of sex of the face, $F(1, 99) = 1.66$, $p = .199$, $\eta_{p^2} = .017$. The effect of the sex of the participant did not reach statistical significance, $F(1, 99) =3.71$, $p = .057$, $\eta_{p^2} = .036$ Similarly, the language main effect was non-significant, $F(1, 99) = 0.02$, $p = .887$, $\eta_{p^2} < .001$. The interaction between the sex of the face and the sex of the participant, as well as between the language and the sex of the face, were non-significant, $F(1, 99) = .364$, $p = .548$, $\eta_{p^2} = .004$, and $F(1, 99) = 1.42$, $p = .236$, $\eta_p^2 = .014$, respectively. The three-way interaction between language, the sex of the face, and the sex of the participants was also found to be non-significant, $F(1, 99) = 3.34$, $p = .070$, $\eta_p^2 = .033$.

**Table 1.** *Mean degrees of carotenoid coloration (and SDs) for male and female faces by sex and language of participants.*

| | **Male Faces** | | **Female Faces** | | **Overall** | |
|---|---|---|---|---|---|---|
| | **Portuguese** | **English** | **Portuguese** | **English** | **Portuguese** | **English** |
| **Female participants** | 101.86 (51.95) | 105.11 (42.56) | 102.07 (49.5) | 110.56 (42.96) | 101.96 (43.85) | 107.84 (43.85) |
| **Male participants** | 82.25 (61.32) | 86.36 (47.66) | 102.51 (38.12) | 81.72 (49.66) | 92.38 (43.85) | 84.04 (43.85) |
| **Overall participants** | 91.5 (57.41) | 95.36 (45.81) | 102.3 (43.43) | 95.56 (48.34) | 97.17 (43.92) | 95.94 (43.88) |

## Discussion

In the Pilot Study, we aimed to determine the amount of increase in carotenoid coloration that produces optimal attractiveness in faces. Consistent with the results reported earlier, participants showed a significant preference for increased carotenoid coloration to maximize attractive appearance of both male and female Caucasian faces. These outcomes provide strong evidence that those with increased levels of carotenoid coloration, whether male or female, are rated as more attractive. Also, this finding aligns with other research that employed interactive tasks wherein participants were directed to adjust the carotenoid coloration appearance of a stimulus face to make it appear healthier (Pezdirc et al., 2018; Stephen et al., 2011). There was no interaction with the sex and language of the observer, suggesting that the preferences found here are probably independent of mate choice mechanisms exclusive to one sex and consistent for both English and Portuguese participants.

## Experimental Study

The present study aimed to investigate if the color of the face influences the memorability of information that is associated with the face. For this purpose, and mimicking the procedure employed by Fitzgerald (Fitzgerald et al., 2016), female participants were shown opposite-sex faces with high carotenoid coloration or with low carotenoid coloration, in addition to descriptive information of such individuals. After a short distractor task, participants were asked to recall the descriptive information and rate the desirability of each face presented. We predicted that participants would remember better descriptive information associated with the face presented with the high coloration. This study was pre-registered (AsPredicted #149531).

## Method

### Participants

A power analysis using G*Power 3.1.9.2 software (Faul et al., 2007) indicated that a sample size of 76 participants had sufficient power ($1-\beta = .85$) at a significance level of $\alpha = .05$ to detect a small to medium effect size (dz = 0.35) on a paired t-test, the effect we aimed to obtain in the study based on the subject analysis. A total sample of 76 participants was recruited at the university and through other media sharing means (e.g., Facebook). As pre-registered, the inclusion criteria were age between 18 and 35, female, cisgender identity, Caucasian ethnicity, heterosexual, speaking Portuguese as a first language, and normal (or corrected) color vision. The application of the aforementioned criteria did not result in any participant exclusion.

Some additional exclusion criteria were pre-registered, namely: recalling at least one piece of information on each potential mate partner; having performance that 3SDs below the overall sample mean or indicating their data should not be considered reliable (e.g., in response to an honesty question). The application of the aforementioned criteria did not result in any participant exclusion. Thus, our final sample included 76 participants (mean age = 20 years, age range = 18–32 years).

## Material

Two types of material were used: face stimuli and descriptive information.

**Face stimuli**. Four composite male faces from the pilot study were used for perceptual judgments. These face images were selected based on the lowest average color variability chosen by female Portuguese participants. Then, using Psychomorph (Tiddeman et al., 2001), two new versions of each original face image were created, one with color changes toward its high carotenoid coloration and one with color changes toward its low carotenoid coloration (see Figure 2). The average coloration applied by female Portuguese participants to male faces in the pilot study was used to determine the amount of transformation.

**Descriptive information.** A list of 36 characteristics considered desirable (e.g., "is responsible"), neutral (e.g., "wear glasses"), or undesirable (e.g., "envious") (12 descriptors of each type) was drawn from a previous study (Pandeirada et al., 2017). Four groups of nine (3 of each) characteristics rated as desirable, neutral, and undesirable were then formed based on the mean rating values reported in the previously mentioned study. This helps to ensure that the memory for the descriptive information is more likely to be related to the features of the faces and less influenced by the desirability of the descriptors. These groups of characteristics were then supplemented with additional information, such as name and more details about each descriptor, creating the four descriptive pieces of information that accompanied the face images.

**Figure 2.** *Coloration applied to faces along the extremes of carotenoid color axis – the left image represents the low carotenoid color (poor diet) and the right image represents the high carotenoid color (good fruit and veg intake).*

**Procedure**

The procedure of this Experimental study was implemented using the Qualtrics platform. Participants conducted the experiment using individual computers in groups of one to six persons at the University of Aveiro's EvoCogLab facility. They started by answering the informed consent, followed by a short demographic questionnaire. Subsequently, participants were shown a cover story (see Appendixes B e C), which explained that they were taking part in the initial testing of a new student information system intended to promote the development of relationships between students and reduce situations of isolation and/or integration challenges among first-year university students. Additionally, it was disclosed to the participants that the university administration wanted to determine whether the new system helped students remember details about their classmates to improve their relationships. The participants were also instructed to imagine that they are actively looking for a partner with whom to begin a romantic relationship and think about each person presented as a potential mate. Next, it was stated that they would initially see the face image of each person; then the face would remain visible along with the text that gave general, positive, and negative descriptive information about that person. Participants were also instructed to remember as much information as possible about each person. They were allowed to read the cover story at their own pace, without time restriction.

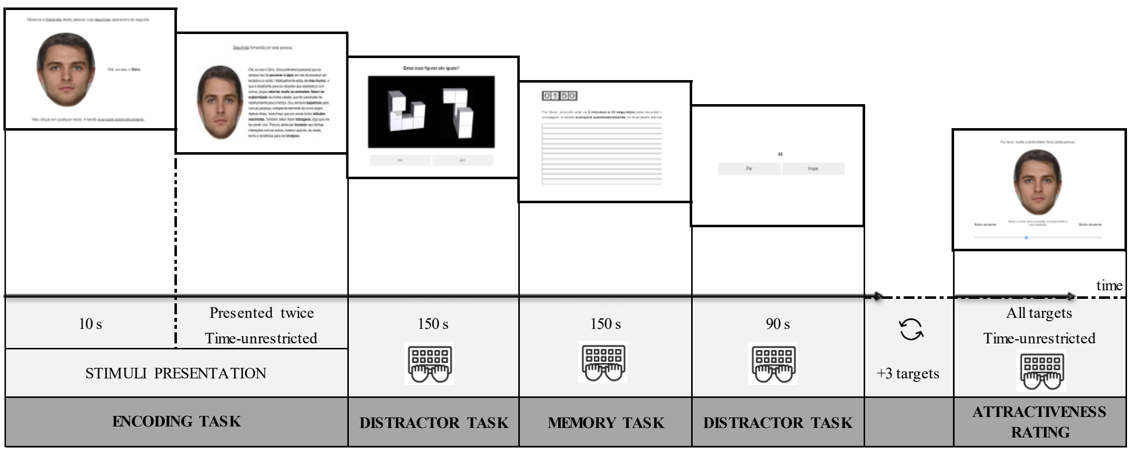
After reading the cover story, four images of potential mate partners (targets) were presented to participants, one at a time. For each participant half of the face images displayed a high carotenoid coloration, and the other half displayed a low carotenoid coloration (this was counterbalanced across participants). Across participants, each face image was presented in the same order and an equal number of times in its high/low carotenoid coloration. Descriptive information about each of the potential mates was presented on the right side of the face image. All participants were shown the same descriptive information for each face image in its high/low carotenoid coloration.

Each trial of the encoding task started with the presentation of the person's name and face image (total of 10s), see Appendix D. Subsequently, descriptive information about that person was presented along with the face image (see Appendix E). Participants were asked to read and press the “next” button to continue once they finished reading the story for the first time. Then, they were given a second opportunity to read the story without any time restrictions. After reading the information twice, participants responded to a short distraction task (total of 150 s), in which two figures were presented simultaneously, and participants had to discriminate if they were the same image or not, considering their rotation. The figures were presented in the center of the screen and participants should press the “YES” or “NO” button to respond to the question “Are they the same figure?”. After the distractor task, participants were asked to recall the descriptive information about the target that had been presented.

Participants were given 150 seconds to recall as much information as they could from the encoding task by typing them directly on the computer. The free recall task was then followed by another distractor task (total of 90 s) which consisted on discriminating if the single-digit numbers were odd or even. The numbers were presented in the center of the screen and participants should click with the mouse on the “ODD” or “EVEN” response options. This sequence of procedures (face presentation + 2 readings of description + mental rotation distractor task + free recall task + even/odd distractor task) was repeated four times, one for each target (see Figure 3 for an illustration of the procedure).

After completing the same tasks for each of the four face images and the corresponding descriptive information, participants were asked to rate the attractiveness of each face presented on a 100-point sliding scale (see Figure 3). Finally, participants were asked to indicate whether they paid attention, provided truthful responses, and agreed that their data should be considered in the analyses. On the final page, the debriefing information was displayed. The task took each participant around 40 minutes to finish.

**Figure 3.** *A scheme of the Experimental Study procedure.*



## Data Analysis

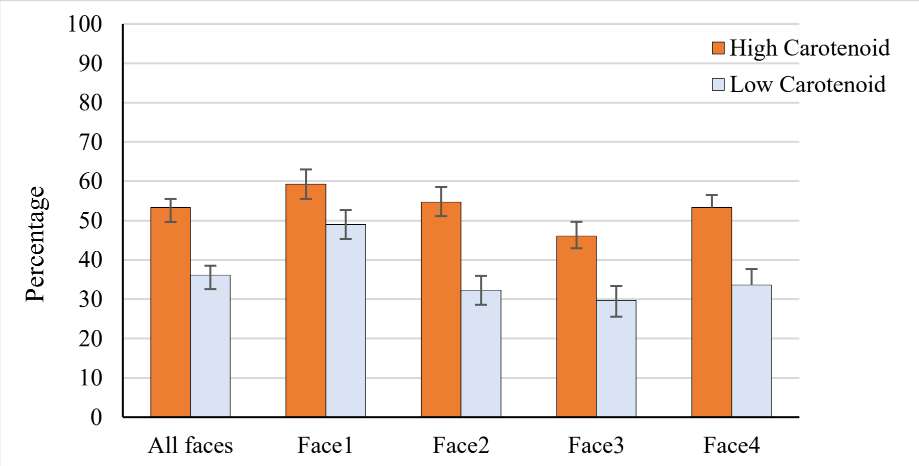
Data were analyzed using IBM SPSS Statistics (Version 29). The level of carotenoid coloration of the face is the independent variable. The dependent variable of main interest is the mean amount of descriptive information correctly remembered. To analyze the possible impact of carotenoid coloration (high vs low) on the proportion of correctly recalled information, t-tests were employed. These were conducted based on the subject (paired t-test) and on the item data (independent t-tests). To confirm the effect of the carotenoid manipulation on the evaluations of attractiveness, attractiveness ratings were compared between the high and the low levels of carotenoid coloration. The attractiveness ratings were also considered (e.g., as co-variables) when analyzing the effect of the coloration on the amount of descriptive information correctly remembered. Additional exploratory analyses were conducted on secondary variables that could be informative for interpreting the recall data (e.g., descriptive information reading time, attractiveness ratings response time). The level of statistical significance was set at .05 (two-tailed) in all analyses.

# Results

## Attractiveness Rating

Face stimuli were rated as more attractive in their high carotenoid coloration than in the low carotenoid coloration ($t(75) = 7.64$, $p < .001$, $d_z = 0.88$). Regarding each face stimulus, the influence of coloration manipulation was consistent across faces (see Figure 4). This result was highly significant in all faces except for face 1 for which the difference was only marginally significant ($p = 0.051$).

**Figure 4**. *Overall mean percentage of attractiveness ratings for all faces and for each face stimuli in its high and low carotenoid coloration. The error bars represent ±1 standard error of the mean.*

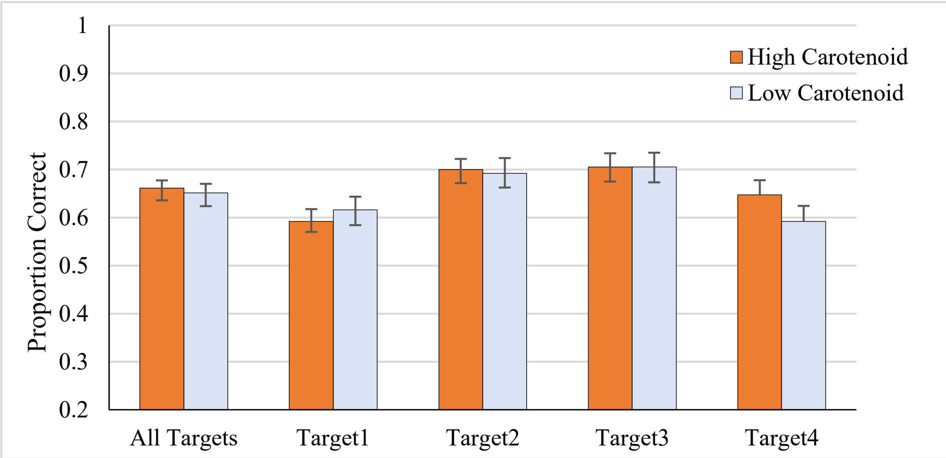



**Recall of target biographic information**

T-tests were employed to analyze the correctly recalled biographic information of the targets as a function of high/low carotenoid coloration. We considered as correct responses the recall of the desirable, neutral, and negative descriptors that were embedded in each text (total of 9) as well as the name of the target, totaling a possible maximum of 10 correct answers. Responses that raised questions were examined by three independent judges; only those that reached full agreement were considered correct.

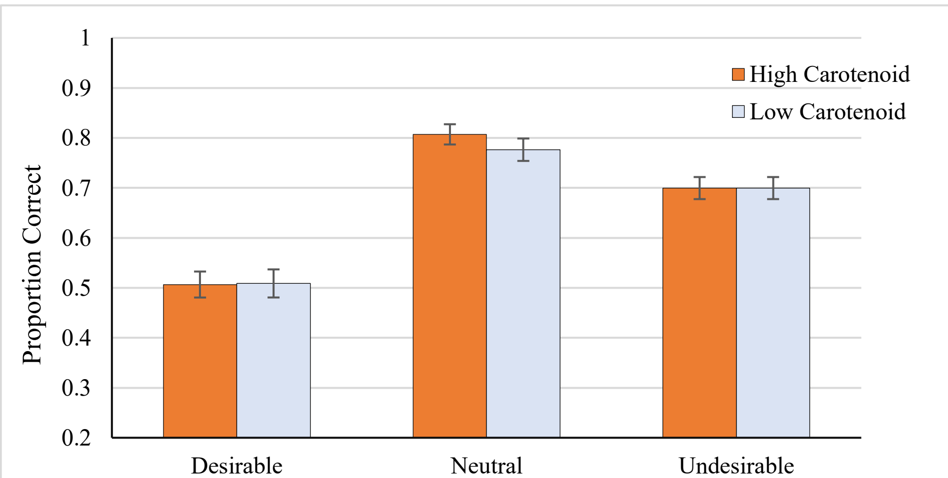
The overall results, as well as those per target, are depicted in Figure 5. Overall, there was no significant difference in the proportion of information correctly recalled depending on whether such information was presented with a face with high carotenoid coloration or a low carotenoid coloration ($t(75) = 0.70$, $p = 0.49$, $d_z = 0.08$). Regarding each story, in two of the cases (targets 2 and 4), there was a tendency for better recall when it was presented with the face in its high coloration in comparison to the low coloration, there was one tie (target 3) and another case with the reverse tendency (target 1) (see Figure 5). However, none of these differences were revealed to be statistically significant (lowest p-value for target 4; $p = 0.21$).

**Figure 5.** *Overall mean proportion of recall of target information, and for each target. The error bars represent ±1 standard error of the mean.*




As this was the first study investigating the possible influence of carotenoid coloration on memory for the associated information, we conducted a series of exploratory analyses to enrich our understanding of this manipulation. First, we explored if there were differences depending on the type of descriptor (positive, negative, and neutral) present in the stories. On average, participants recalled a higher proportion of neutral descriptors, as compared to the desirable and undesirable descriptors (see Figure 6); this pattern was similar irrespectively of the coloration condition.

**Figure 6**. *Mean proportion of recall by type of descriptor. The error bars represent ±1 standard error of the mean.*



In addition, we noticed some participants recalled physical aspects of the targets' faces (e.g., the color of the eyes or the hair). Recall of these elements was quite low (on average, each participant recalled fewer than one physical aspect per target) and did not differ depending on coloration condition ($M_{\text{high}}$ = 0.37, *SD* = 0.97; $M_{\text{low}}$ = 0.49, *SD* = 1.23), $t(75) = 1.44$, $p = .15$, $d_z = 0.17$).

We also explored the time participants spent reading each story. On average, they took about 74 s to read the target biographic information for both high and low carotenoid coloration, $t(75) = 0.84$, $p = 0.40$, $d_z = .096$. Additionally, a non-significant difference was seen in the reading times for each of the stories depending on the high and low carotenoid versions of each face stimulus (lowest $p = 0.06$, for face 1). Regarding the response times taken to rate the attractiveness of the face stimuli, on average, participants spent about 8.7 seconds, and this did not differ depending on the carotenoid condition of the faces, $t(75) = 0.12$, $p = 0.91$, $d_z = 0.01$ (see Table 2). The attractiveness rating times for the high and low versions of each face stimulus were also not different (lowest $p = 0.54$, for face 3).

**Table 2.** *Response times (and SDs) for the story reading times and the attractiveness rating task.*

| | **Reading Times** | | **Attractiveness Rating times** | |
|---|---|---|---|---|
| | **High Carotenoid** | **Low Carotenoid** | **High Carotenoid** | **Low Carotenoid** |
| **All Faces** | 72.69 (3.61) | 74.72 (3.96) | 8.70 (0.42) | 8.76 (0.5) |
| **Face1** | 54.39 (3.05) | 63.12 (3.4) | 12.23 (0.86) | 13.09 (1.5) |
| **Face2** | 78.85 (5.11) | 76.59 (5.22) | 8.99 (0.62) | 9.18 (0.87) |
| **Face3** | 79.80 (6.72) | 76.16 (6.02) | 7.00 (0.63) | 6.52 (0.46) |
| **Face4** | 77.72 (6.16) | 83.03 (8.48) | 6.59 (0.63) | 6.25 (0.48) |

Additionally, we conducted Pearson correlations to examine the relationship between overall reading time and the overall amount of biographical information recalled in the high and low carotenoid coloration conditions. We found a moderately positive and significant correlation between the two variables in both conditions (see Table 3). For both coloration levels of the faces (high and low) and respective associated stories, as reading time increases, the amount of biographical information recalled also increases.

**Table 3.** *Pearson correlation coefficients between the overall reading times and overall recall of biographic information.*

| | | Recall of Target Biographic Information | |
|---|---|---|---|
| | | **High Carotenoid (all faces)** | **Low Carotenoid (all faces)** |
| **Reading Times** | **High Carotenoid (all faces)** | .442** | |
| | **Low Carotenoid (all faces)** | | .462** |

Also, when examining the relationship between the attractiveness ratings and recall, we found a relatively low but statistically significant positive correlation between the two variables. Such relation suggests participants tended to recall more information when it was presented with faces rated as more attractive ($r = .250$, $p < 0.05$).

## Discussion

Human evolution depends on reproduction (Nairne & Pandeirada, 2008). However, it is still unclear what role memory plays in reproduction-related contexts. The few studies investigating this subject have presented mixed findings: some claim mnemonic benefits related to reproduction-related processing, whereas others show no effects. Some studies in the domain of reproduction have used a processing paradigm, where participants rate the relevance of random words in mating-related scenarios; no indication of a systematic mnemonic advantage related to mating has been found in these studies (Derringer et al., 2017; Klein, 2013; Sandry et al., 2013; Seitz et al., 2018).

However, research that has manipulated cues to convey information about a potential partner's mating value has demonstrated the opposite. For example, women remember more male faces considered in a mating (vs. a non-mating) context (Pandeirada et al., 2017). Also, females tend to remember best objects that were previously associated with masculinized (vs. feminized) male faces (Smith et al., 2012). Moreover, men showed better memory for women with highly (vs. average) attractive faces (Baker et al., 2015), and a waist-to-hip ratio closer to ideal (Fitzgerald et al., 2016). Furthermore, people's mating preferences (short- vs. long-term relationships) seem to influence these memory tunings (Horgan et al., 2016). These tunings are towards characteristics indicative of higher mate value and support evolutionary theories that propose that our preferences have been determined by selection pressure to help select high-quality mates.

However, these studies have tested memory for only a few physical cues indicative of potential mate value (voice, face, and body characteristics), and the importance of carotenoid coloration—a trait that also serves as an indicator of mate value—has not been yet investigated. Such characteristic might be considered a diagnostic cue of mate value as it relates to several important indicators, including reproductive success, healthy appearance, and attractiveness of faces (Foo et al., 2017; Lefevre & Perrett, 2015; Pezdirc et al., 2018; Thomas & Stewart-Williams, 2018).

In the present work, we aimed to examine how facial carotenoid coloration of potential mates affects participants' memory for descriptive information about such mates. Following previous research on reproduction and memory (Fitzgerald et al., 2016), we predicted that information would be remembered better when the face accompanying the description showcases high carotenoid coloration. To accomplish this, we conducted two experiments, a pilot study to determine the amount of increase in carotenoid coloration that produces optimal attractiveness in faces. We predicted that participants would prefer high carotenoid coloration to low carotenoid coloration when looking for the most attractive appearance of faces. In the experimental study, female participants were presented with descriptive information regarding different males while we manipulated the carotenoid level of the faces that accompanied such information. Memory was then tested for that descriptive information. Additionally, participants were asked to evaluate the attractiveness of the potential partners. Importantly, across participants, a given male face was presented with its high carotenoid coloration or with its low carotenoid coloration.

In the pilot study, results were in line with our hypothesis that participants would prefer high carotenoid coloration to low carotenoid coloration when looking for the most attractive appearance of faces. Consistent results were found in the experimental study: Participants rated the high carotenoid versions of the face targets as significantly more attractive than when they were in the low carotenoid versions, validating our manipulation. This result was consistent across all faces (only for face 1 the difference did not reach conventional levels of significance).

The results from both tasks also suggest that like in other animal species (Stephen et al., 2011), carotenoid coloration may play a role in human mate selection, to the extent that attractiveness influences mating success (Rhodes et al., 2005). The carotenoid coloration of the skin may serve as a mate quality signal because it correlates with a healthier appearance and leads to the perception of increased attractiveness (Foo et al., 2017; Lefevre & Perrett, 2015; Pezdirc et al., 2018; Stephen et al., 2011).

For the recall of the descriptors of the targets, contrary to our prediction, on average, as well for each story, participants did not show better memory for the biographic information associated with the high carotenoid coloration of the faces. Still, we found a tendency for better recall when the story was presented with the face in its high coloration in comparison to the low coloration in two of the cases, but the differences were nonsignificant. Notably, face 1 was rated as the most attractive and had the lowest level of recall. On the other hand, for the other faces rated as less attractive, more descriptive information was recalled associated with the high carotenoid coloration of those faces, except for face 3, for which there was a tie. Therefore, there was a slight tendency to better recall the descriptive information when the face was viewed as less attractive but exhibited its high (vs. its low) carotenoid coloration. This suggests that, for faces that may be less attractive from a morphological stance, skin color may be more readily used as a mate value cue.

Regarding the story reading times, it is important to mention that participants did not have a limited time to read the stories; they saw the face stimuli and the biographic information twice and took as much time as they wanted to read the story. Interestingly, the coloration condition did not influence the time spent reading the stories. One could expect that, when facing the high coloration face (the most attractive) they would devote more time reading the story to improve the recallability of the associated information. Furthermore, no significant difference was found on the attractiveness rating times as a function of high/low carotenoid coloration.

Nevertheless, we obtained a moderate positive correlation between the reading time and the amount of biographical information recalled in both coloration conditions. By providing as much time as wanted to read the stories, participants were able to maximize the retention of information and one might have limited the extent to which the carotenoid manipulation influenced such retention. Also, in real life, one usually has limited time to apprehend information of potential partners. Thus, it is possible that constraining the reading time would provide a more "ecologically-valid" situation and would afford a clearer influence of our carotenoid manipulation on memory for the presented information. This idea could be explored in future work.

Given this was the first study exploring the potential impact of carotenoid coloration of potential partners on memory for their associated information, it is challenging to compare them to previous studies. However, the results raise questions that could inspire future work and there are still other variables that could play a role in this problem. For example, it is known that distinct mating preferences (short-term vs. long-term relationships) influence the memory tuning to different types of information, especially for those that are more pertinent to the specific adaptive issue. For example, Horgan et al. (2016) showed that females' memory for a man's physical features and verbal statements can be influenced by the mating strategy (short-term vs. long-term relationship). Females who considered a male target as a short-term partner remembered more physical aspects, while those who considered a male target as a long-term partner recalled more verbally presented personal information. However, comparison with our data is limited because we did not manipulate these different mating conditions (long-term and short-term) nor had a clear set of physical and descriptive information to remember. Additionally, because we did not specify the mating strategy participants should be considering while considering the potential partners, they may have considered them in a short-term context. According to the just presented study, such should have increased memory for physical rather than for biographic information. If this were the strategy adopted by our participants, it could help to explain the failure to obtain a recall advantage for the targets' story when they were associated with the higher mate value condition (high carotenoid coloration). On the other hand, given that physical cues are more important when selecting short-term mates, one would expect carotenoid coloration to have a greater influence in this context. This explanation aligns with the significant preference for high carotenoid coloration when rating the attractiveness of face stimulus. These considerations should inspire further studies.

Even though our color manipulation did not influence the recall of the descriptive information, it would be interesting to explore if it would influence the recall of physical information and/or of faces themselves. For example, one could use a face recognition task for the presented faces, since visual recognition is a more immediate way to identify potential partners (Pandeirada et al., 2017). Furthermore, in the present study, we only used two levels of manipulation (high and low) which might not generalize to other variations; so, different coloration levels should be explored. Also, other measures, such as eye-tracking could help to determine which elements of the stimuli participants are attending to more preferentially. If the assertions presented above are correct, we would predict that when considering targets as short-term potential mates, participants should preferentially attend to the physical characteristics of the faces, such as skin coloration.

Other aspects of this paradigm would also be interesting to explore in future work. For instance, memory for opposite-sex faces increased in prior experiments when they were processed as potential mates, in comparison to a non-mating context (Pandeirada et al., 2017). In that study, the memory test came as a surprise to participants (i.e., encoding was incidental) whereas in our case, participants were intentionally memorizing the information. It would be interesting to investigate whether a general memory advantage would occur using our general mating-related procedure as compared to a non-mating context. This would reveal whether any potential advantages associated with the ideal level of carotenoid coloration would be specifically related to mating or merely represent a general preference for high carotenoid coloration (Lefevre & Perrett, 2015).

A functional approach to memory predicts that its functioning should be regulated to increase individuals' chances of survival and reproduction. Indeed, several phenomena related to such goals have been proposed; These include better memory when information is processed for survival (Nairne & Pandeirada, 2016), for contaminated (vs. non-contaminated) items (Fernandes et al., 2017), and for animates (vs. inanimates) (Nairne et al., 2017). The experiment reported here explored another plausible candidate within this reasoning: reproduction. Although we were unable to obtain evidence of such reproduction tuning related to carotenoid coloration, our data confirmed that the high level of this skin carotenoid coloration is perceived as more attractive. Therefore, the innovation of this study and its suggestions for improvement should be considered in future studies for a full understanding of the importance of this variable in reproduction and memory.

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## Appendix

**Appendix A** – Encoding Instructions of the Pilot Study

**Instructions**

A set of faces will be presented to you. You can control the attractiveness of each face by slowly moving the slider that is presented below the image. Please make the face look as attractive as possible. When you have chosen the most attractive appearance, press the arrow button.

**Appendix B** – Encoding Instructions of the Experimental Study – Screen 1

**Por favor, leia atentamente as instruções seguintes.**

Os serviços administrativos da Universidade pretendem desenvolver um sistema que procura promover o estabelecimento de relações entre os estudantes e diminuir situações de isolamento e/ou dificuldades na sua integração. Para tal, pediram aos novos estudantes que se descrevessem, indicando aspetos **positivos**, **negativos**, e outros mais **genéricos**.

Nesta fase inicial, os serviços pretendem avaliar se este sistema permitirá ajudar os estudantes a recordarem-se de informações sobre os seus colegas, no sentido de facilitar os seus relacionamentos.

Clique em **"SEGUINTE"** para continuar.

**Appendix C** – Encoding Instructions of the Experimental Study – Screen 2

**Por favor, leia atentamente as instruções seguintes.**

Adicionalmente, pedimos que imagine que, neste momento, procura ativamente um parceiro com quem pretende estabelecer uma relação amorosa. Considere cada uma das pessoas apresentada como sendo um **potencial parceiro** com quem poderia estabelecer essa relação.
De seguida, ser-lhe-ão apresentadas **quatro pessoas**.

Inicialmente, irá ver a **fotografia** de cada uma delas. Deve prestar atenção a essa fotografia para poder, em possíveis interações futuras, identificá-la.

Depois, juntamente **com a fotografia**, será apresentada uma **descrição da pessoa** correspondente. Procure memorizar o máximo de informações sobre essa pessoa para depois as poder recordar.

Clique em **"SEGUINTE"** para continuar.

**Appendix D** – Presentation of the person's name and face image

Observe a fotografia desta pessoa cuja descrição aparecerá de seguida.

Olá, eu sou o **Gino**.

Não clique em qualquer tecla. A tarefa avançará automaticamente.

**Appendix E** – Presentation of the person's descriptive information and face image

Descrição fornecida por esta pessoa:

Olá, eu sou o Gino. Uma preferência pessoal que eu sempre tive foi **escrever a lápis** em vez de escrever em teclados ou ecrãs. Habitualmente estou de **mau-humor**, o que é desafiante para as relações que estabeleço com outros, já que **valorizo muito as amizades. Nasci na maternidade** da minha cidade, que foi construída há relativamente pouco tempo. Sou sempre **respeitoso** para com as pessoas, independentemente de como sejam. Apesar disso, reconheço que por vezes tenho **atitudes machistas.** Também adoro fazer **tatuagens**, algo que me faz sentir vivo. Procuro ainda ser **honesto** nas minhas interações com os outros, mesmo quando, às vezes, tenho a tendência para ser **invejoso**.

Clique em **"SEGUINTE"** para continuar.