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2 **WOMEN’S ATTRACTIVENESS IS LINKED TO EXPECTED AGE AT**  
3 **MENOPAUSE**

4 (WOMEN’S ATTRACTIVENESS AND AGE AT MENOPAUSE)

5  
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23 Abstract

24 A great number of studies have shown that features linked to immediate fertility explain a  
25 large part of the variance in female attractiveness. This is consistent with an evolutionary  
26 perspective, as men are expected to prefer females at the age at which fertility peaks (at least  
27 for short-term relationships) in order to increase their reproductive success. However, for  
28 long-term relationships, a high residual reproductive value (the expected future reproductive  
29 output, linked to age at menopause) becomes relevant as well. In that case, young age AND  
30 late menopause are expected to be preferred by men. However, the extent to which facial  
31 features provide cues to the likely age at menopause has never been investigated so far. Here,  
32 we show that expected age at menopause is linked to facial attractiveness of young women.  
33 As age at menopause is heritable, we used the mother's age at menopause as a proxy for her  
34 daughter's expected age of menopause. We found that men judged faces of women with a  
35 later expected age at menopause as more attractive than those of women with an earlier  
36 expected age at menopause. This result holds when age, cues of immediate fertility and facial  
37 ageing were controlled for. Additionally, we found that the expected age at menopause was  
38 not correlated with any of the other variables considered (including immediate fertility cues  
39 and facial ageing). Our results show the existence of a new correlate of women's facial  
40 attractiveness, expected age at menopause, which is independent from immediate fertility cues  
41 and facial ageing.

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46 Key words: humans, sexual selection, mate choice, female attractiveness, face, menopause,  
47 residual reproductive value, fertility

48 1. Introduction

49 Why some women are more attractive than others has been the focus of many studies, and it  
50 has been repeatedly shown that features linked to immediate fertility (i.e. fertility at a given  
51 time) explain a large part of the variance in attractiveness (see Rhodes 2006 for a review).  
52 Cues of immediate fertility can be found in body shape, voice pitch, or facial features; in fact,  
53 all traits linked to sexual maturity, age and parity or substantially influenced by sex hormones  
54 (which are factors influencing immediate fertility) have the potential to influence physical  
55 attractiveness (see, for example, Symons 1995; Henss 2000; Singh 2002; Jasienska et al.  
56 2004; Feinberg et al. 2005; Law Smith et al. 2006; Pipitone and Gallup 2008; Singh et al.  
57 2010; Little et al. 2011; Puts et al. 2012, 2013; Pfluger et al. 2012; Jones 2014; Mondragón-  
58 Ceballos et al. 2015; Sugiyama 2015; Butovskaya et al. 2017 but see Marcinkowska et al.  
59 2014, 2015 for some modulations of these preferences). To increase their reproductive  
60 success, males should prefer females of the age at which age-specific fertility peaks, at least  
61 for short-term mates (Maestripieri et al. 2014). For long-term relationships such as marriage,  
62 however, residual reproductive value - the expected future reproductive output - becomes  
63 pertinent too. In humans, this trend is strengthened by the existence of reproductive  
64 senescence or menopause (i.e., the permanent cessation of menstruation), associated with the  
65 ultimate cessation of child-bearing potential, long before the somatic senescence.

66 Consequently, for long-term relationships, the number of offspring produced by the couple  
67 will depend in part on the number of years before the woman reach menopause, particularly in  
68 natural fertility populations where reproduction could theoretically extend until menopause.

69 Thus, men can increase their reproductive success by choosing a long-term mate with  
70 a longer reproductive window (i.e. higher residual reproductive value). The first criterion of a  
71 long reproductive window is of course age. And indeed, youth is one of the most important  
72 factor of women's attractiveness (Buunk et al. 2001). Then, for a given age, the temporal  
73 reproductive window will vary according to the age at menopause, which is highly variable  
74 both across and within populations (Avis et al. 2001; Thomas et al. 2001; Velde et al. 2002;

75 Dratva et al. 2009; Morris et al. 2011; Stepaniak et al. 2013). If the future age at menopause is  
76 somehow detectable in young adults, it could contribute substantially to mate choice and thus  
77 influence female attractiveness. It is possible that previously identified components of  
78 immediate fertility are also informative of female residual reproductive value: reproductive  
79 value at a young age and later in life could be positively correlated due to some common  
80 underlying factors, or negatively correlated as a result of a biological trade-off (Hamilton  
81 1966; Wood et al. 2001; Carter and Nguyen 2011). Alternatively, future age at menopause  
82 could be independent of immediate fertility cues, and thus a correlate of attractiveness that has  
83 not yet been identified.

84 In this study, we investigated whether expected age at menopause is related to the  
85 attractiveness of young women's faces. As age at menopause is heritable (heritability between  
86 0.42 and 0.72 depending on the study: Snieder et al. 1998; de Bruin et al. 2001; van Asselt et  
87 al. 2004; Murabito et al. 2005; Morris et al. 2011), mother's age at menopause was used as a  
88 proxy for the daughter's expected age of menopause. To better understand how the residual  
89 reproductive value could be facially detectable, immediate fertility cues were included in the  
90 model as possible explanatory variables. It could also be speculated that women who reach  
91 menopause later have an overall slower life history trajectory, with a slower general physical  
92 ageing, and may look younger, at the same age, than women who will experience menopause  
93 at an earlier age (in line with this idea, a later age at menopause is associated with a longer  
94 life expectancy, for a review see Gold 2011). To see if general physical ageing could mediate  
95 the relationship between facial attractiveness and expected age at menopause, we included  
96 facial ageing (measured as the difference between actual age and perceived age) as another  
97 explanatory variable.

98

## 99 2. Materials and Methods

100 **2.1 Ethics Statement.** The protocol used to recruit participants and collect data was approved  
101 (#1226659) by the French National Committee of Information and Liberty (CNIL). For each

102 participant, the general purpose of the study was explained (“a study on the determinants of  
103 mate choice”) and a written voluntary agreement was requested for a statistical use of data  
104 (private information and photographs). Data were analysed anonymously.

105 **2.2 Stimuli.** A total of 97 women between 25 and 35 years of age were recruited by social  
106 networks and advertising in Montpellier, France. Sixty-eight Caucasian women whose mother  
107 had a natural and known age at menopause constituted our final stimuli sample (mean age =  
108 28.4, age range: 25-35, see table S4). Volunteers were instructed to come to the lab after  
109 collecting information about their mother’s and (when possible) grandmothers’ menopause  
110 (menopause was defined as the first full year without any menstruation) and without wearing  
111 any make-up. For each woman, the following information was collected: date and place of  
112 birth for themselves, their parents and grandparents; monthly income (divided into ten classes  
113 from less than 760€ to more than 4705€) for themselves and their parents; education level;  
114 and age at menopause for their mother and grandmothers. A facial photograph was taken with  
115 the same digital still camera (Canon EOS 20D) at a distance of 1 m using the same general  
116 settings. Each woman was asked to have a neutral facial expression, to remove any glasses or  
117 earrings, and to wear a hairband (to make sure that all the face was visible). All photographs  
118 were electronically processed using Adobe Photoshop CS3 to normalise size (photographs  
119 were aligned on eyes position, with a fixed distance between eyes and chin), colour balance,  
120 contrast and luminosity (using the Photoshop auto-corrections tools). Hairstyle was cropped,  
121 and the background was replaced by a uniform grey colour (see figure 1). A compensation of  
122 20€ was provided for the subjects’ participation.

123 **2.3 Procedure.** A Delphi-based computer program was generated to present randomly drawn  
124 pairs of photographs of the 68 women (see figure 1). For each pair, the rater was instructed to  
125 click on the photograph depicting the woman he found the most attractive (the outcome  
126 measure of our study). The position of the photograph on the screen (left or right) was  
127 randomly ascribed. Each rater had 30 distinct pairs of photographs to assess, corresponding to  
128 60 different women. If the rater knew one of the women he had to judge, the trial was

129 removed. Also, the first pair seen by each participant was not used for the analyses, because  
130 the task could require some habituation. Three pairs, randomly chosen from among those  
131 previously viewed, were presented again at the end to estimate judgement reliability.

132 **2.4 Raters.** A total of 156 male raters assessed the relative attractiveness of these women.  
133 Volunteer raters were recruited in public places in Montpellier (France) and were unaware of  
134 the purpose of the study when assessing the pairs of pictures. For each rater, the following  
135 information was collected: date and place of birth, grandparents' origins, monthly income,  
136 occupation, house ownership, taxability, education level, and sexual orientation. Only data  
137 from Caucasian and heterosexual raters were used for the analyses. Assessments of unreliable  
138 raters (i.e., with more than one incorrect answer during the test of judgement reliability) were  
139 removed. A total of 119 raters were retained in the final sample, with a mean age of 36.2 (age  
140 range: 17-72, see table S4). Each woman was observed, on average, by 101.1 raters (range:  
141 93-108).

142 **2.5 Immediate fertility cues.** We collected 3 physical features hypothesised to be linked to  
143 women's immediate fertility: the waist-to-hip ratio (the ratio between body circumference at  
144 the waist and the hips or WHR, Singh 1993; Jasienska et al. 2004; Singh and Randall 2007;  
145 Lassek and Gaulin 2007; Mondragón-Ceballos et al. 2015; Butovskaya et al. 2017; but see  
146 Nenko and Jasienska 2009), the fundamental frequency of the voice (F0, Harries et al. 1998;  
147 Abitbol et al. 1999; Feinberg 2008; Evans et al. 2008; Abend et al. 2014) and the facial  
148 femininity (Farkas 1987; Johnston and Franklin 1993; Perrett et al. 1998; Fink and Neave  
149 2005; Law Smith et al. 2006; Little et al. 2011; Pfluger et al. 2012; Jones 2014). The WHR  
150 was measured in the lab by the investigator. To measure the F0, women were recorded reading  
151 the French version of a standard text ("La bise et le soleil") using a Tascam DR-07 MKII  
152 digital recorder. Across each recording, the fundamental frequency (F0, the acoustic correlate  
153 of pitch) was measured using Praat software (Boersma and Weenink 2013). To generate  
154 morphological facial femininity scores, a geometric morphometric analysis of the faces was

155 used following methods described in Scott et al. 2010; Lee et al. 2014; Dixson et al. 2017:  
156 First, the coordinates of 142 landmarks (anatomical points present in all individuals, e.g. the  
157 corners of the lips) and semi-landmarks (sliding points positioned along some anatomical  
158 curves, such as the bow of the eyebrow) were delineated for each female face, as well as for  
159 26 male facial photographs retrieved from another database. These 26 additional men were  
160 recruited according to the same criteria as for the women's recruitment: heterosexuality,  
161 Caucasian origin, 25-35 years old. The delineation of the landmarks and semi-landmarks were  
162 done using Psychomorph (Tiddeman et al. 2005). The R package Geomorph (version 3.0.3)  
163 was used to carry out a Procrustes superimposition of the landmark and semi-landmark data,  
164 which removes non-shape information such as translation, size, and rotational effects  
165 (Zelditch et al. 2012, 2013). A Principal Component Analysis (PCA) was conducted on the  
166 Procrustes-registered landmarks and semi-landmarks data of the 26 male faces and 26 female  
167 faces randomly drawn from this study dataset, matching the age distribution of the 26 men.  
168 This PCA produced shape variables which are a decomposition of the landmark coordinates of  
169 the male and female faces (see figure S1). The values on the factors of the PCA were  
170 computed for the remaining 42 female faces (not used to create the PCA). Then, a linear  
171 discriminant analysis (LDA) incorporating the two first components of the PCA was used to  
172 discriminate between male and female faces. The resulting analysis provided correct sex  
173 classification for 92.6% of faces. Discriminant function scores were therefore used as an  
174 index of facial femininity, with high scores indicating a more feminine facial morphology  
175 scores (Scott et al. 2010; Lee et al. 2014; Dixson et al. 2017). All analyses were performed  
176 using R software, version 3.4.2.

177 **2.6 Estimation of facial ageing.** It could be speculated that women who reach menopause  
178 later have an overall slower life history trajectory, with a slower general physical ageing, and  
179 may look younger, at the same age, than women who will experience menopause at an earlier  
180 age. To control for this possibility, a second Delphi-based computer program was generated to  
181 present the facial photographs of the 68 women to 136 raters. For each photograph, the rater



182 was instructed to estimate the age of the woman (see figure S2). Each rater had 20 distinct  
183 photographs to assess, randomly drawn among the 68 pictures. Three photographs, randomly  
184 chosen among those previously viewed, were presented again at the end to estimate  
185 judgement reliability. For each rater, information about sex and age was collected. The  
186 reliability of raters was assessed by computing the sum of absolute differences between the 3  
187 first estimations and the corresponding repetitions. Raters with values higher than 15 years  
188 were removed (a more stringent threshold of 9 years, or no threshold, did not change  
189 qualitatively the results). A total of 107 facial ageing raters (including 61 women) were  
190 retained in the final sample, with a mean age of 35.1 (age range: 16-65). Each woman was  
191 observed, on average, by 31.2 raters (range: 24-43). For each woman, the difference between  
192 their real age and the mean age given by the raters was calculated. This variable represents the  
193 facial ageing of the women, a critical explanatory variable for the analysis of attractiveness.

194 **2.7 Statistical analyses.** Logistical regressions were used to analyse raters' attractiveness  
195 preferences. The binary response variable corresponded to being chosen or not for the focal  
196 woman (arbitrarily the woman presented at the left position) during the presentation of each  
197 pair. Women and attractiveness raters were considered random samples from a larger  
198 population of interest and were thus random-effect variables. Therefore, generalised linear  
199 mixed models with a binomial error structure were used. For each choice made by a rater, the  
200 difference between the ages at menopause of the focal and the non-focal woman's mothers  
201 was calculated. The value of this difference was integrated into the model as the main variable  
202 of interest. To control for potential confounding effects, the differences between the focal and  
203 the non-focal woman's ages and socio-economic status (SES, a PCA combination of  
204 education level and the woman's and her parents' monthly incomes) were introduced into the  
205 model. Because the subjects displayed a perceptible smile in some photographs, a qualitative  
206 variable describing this aspect was also introduced (this binary variable was coded by three  
207 independent raters, blind to the other characteristics of the women). Variables concerning the  
208 raters' characteristics were also included in the model as potential confounding effects. These

209 variables were the rater's age and SES (a PCA combination of the variables "monthly  
210 income", "occupation", "house ownership", "taxability", and "education level"). All variables  
211 were standardized for the analysis. In a second model, the difference between the two women  
212 for cues of immediate fertility (facial femininity, WHR and F0), and facial ageing were  
213 included as explanatory variables. Indeed, these variables, which may be linked to expected  
214 age at menopause, could potentially mediate the relationship between expected age at  
215 menopause and facial attractiveness.

216 Linear regression was used to analyse the mother's age at menopause according to the  
217 maternal grandmother's age at menopause. The "one-parent - one child" regression coefficient  
218 represents half the heritability ( $h^2$ ) of the trait (Lynch and Walsh 1998). Pearson correlations  
219 were used to analyse relationships between each woman's measured traits: expected age at  
220 menopause, immediate fertility cues, facial ageing, age, and SES. All statistical analyses were  
221 performed using R software, version 3.4.2.

222

### 223 3. Results

224 **3.1 Attractiveness, age at menopause and immediate fertility.** The variable expected age at  
225 menopause (estimated by mother's age at menopause) had a significant positive effect on the  
226 probability of a woman being chosen as the most attractive: Men tend to prefer women who  
227 are likely to reach menopause later ( $\beta = 0.22$ ,  $SE = 0.053$ ,  $P < 0.001$  see model 1 in table 2).  
228 This result holds when immediate fertility cues and facial ageing are controlled for ( $\beta = 0.24$ ,  
229  $SE = 0.053$ ,  $P < 0.001$ , see model 2 in table 1 and figure 2), showing that the effect of  
230 expected age at menopause on attractiveness is not due to know cues of immediate fertility  
231 cues or facial ageing. Additionally, the 3 cues of immediate fertility had a significant effect on  
232 the probability of being chosen: men tend to prefer more feminine faces ( $\beta = 0.4$ ,  $SE = 0.057$ ,  
233  $P < 0.001$ , see model 2 in table 1), and the faces of women who have a higher (i.e. more  
234 feminine) F0 ( $\beta = 0.2$ ,  $SE = 0.058$ ,  $P = 0.001$ ). In contradiction with our prediction, men also

235 tend to prefer the faces of women who had a higher (i.e. more masculine) WHR ( $\beta = 0.13$ , SE  
236 = 0.057,  $P = 0.02$ ). Facial ageing had a negative effect on the probability to be chosen ( $\beta = -$   
237 0.56, SE = 0.06,  $P < 0.001$ ): Independently of their actual age, women who look younger than  
238 their actual age were preferred by men. Women's age and smile demonstrated a significant  
239 effect on the probability of being chosen: men preferred women who were younger ( $\beta < -0.2$ ,  
240  $P < 0.001$ , see models 1 and 2 in table 1) and smiled more ( $\beta > 0.27$ ,  $P < 0.001$ , see models 1  
241 and 2 in table 1). The socio-economic status of the woman had a negative effect on the  
242 probability to be chosen as the more attractive, but this result was significant only in model 2  
243 ( $\beta = -0.17$ , SE = 0.057,  $P = 0.003$ ). The raters' age and socio-economic level had no  
244 significant effect on their choices (all  $P > 0.5$ , see models 1 and 2 in table 1).

245 **3.2 Menopause and other women's features.** There was no significant correlation between  
246 expected age at menopause and immediate fertility cues (facial femininity, F0 and WHR),  
247 facial ageing, woman's age or socio-economic status (all  $P > 0.1$ , see table 2), showing that  
248 expected age at menopause is capturing a distinct correlate of facial attractiveness. There was  
249 no significant correlation between the other variables, except a negative correlation between  
250 facial ageing and SES ( $r = -0.29$ ,  $P = 0.021$ , see table 2).

251 **3.3 Heritability of age at menopause.** To help establish the validity of our sample, we  
252 measured the heritability of age at menopause, for comparison with previous studies done  
253 with various samples and methods (Snieder et al. 1998; de Bruin et al. 2001; van Asselt et al.  
254 2004; Murabito et al. 2005; Morris et al. 2011). Here we used the regression between grand-  
255 mother and mother, without controlling for possible shared environments (this is not crucial  
256 for the present study, as the main purpose here is to establish the validity of the mothers' age  
257 at menopause as a proxy for the daughters' expected age at menopause). Among the 97  
258 women, 42 completed information about both their mother's and maternal grandmother's  
259 menopause. The mean age at menopause was 51.0 (range: 42-58) for the mothers and 50.3  
260 (range: 39-60) for the grandmothers. The maternal grandmother's age at menopause had a

261 significant effect on the mother's age at menopause ( $\beta = 0.275$ ,  $SE = 0.11$ ,  $P = 0.016$ , see  
262 figure 3). This implies a heritability of age at menopause from the maternal side of 27.5% and  
263 thus an overall heritability  $h^2 \sim 55\%$  ( $SE = 0.22$ ).

#### 264 4. Discussion

265 Here, we show that expected age at menopause is significantly related to the facial  
266 attractiveness of young women. This result holds when variables potentially linked to  
267 immediate fertility (age, facial femininity, voice pitch and WHR), facial ageing and socio-  
268 economic status are controlled for. Additionally, immediate fertility cues and facial ageing  
269 were not correlated with the expected age at menopause. Thus, the expected age at menopause  
270 seems to be linked to independent facial information, which is not deducible from previously  
271 documented components of facial attractiveness linked to immediate fertility or facial ageing.

272 Results classically found in the literature were replicated in this study, suggesting that  
273 this sample of young females is not different from those described elsewhere. First, our  
274 sample provided an heritability estimate for age at menopause of 0.55, consistent with  
275 previous values ranging from 0.42 to 0.72 (Snieder et al. 1998; de Bruin et al. 2001; van  
276 Asselt et al. 2004; Murabito et al. 2005; Morris et al. 2011). Moreover, immediate fertility  
277 cues were positively correlated with facial attractiveness, as in previous studies: men in our  
278 sample preferred more feminine faces as in Cunningham et al. 1995; Perrett et al. 1998;  
279 Rhodes et al. 2003; Koehler et al. 2004; Little et al. 2011, and facial attractiveness was  
280 positively correlated to pitch voice ( $F_0$ ), consistent with Collins and Missing 2003; Feinberg  
281 et al. 2005; Wheatley et al. 2014; Smith et al. 2016. Also, attractive faces were rated younger  
282 than their true age, as in the study of Kwart (2012). However, two variables had significant  
283 effects on attractiveness, but in the opposite direction than expected. First, men in our sample  
284 had a preference for faces of women who have a higher (i.e. more masculine) WHR, which is  
285 in contradiction with the idea that face and body would signal one same quality. However, our  
286 results go in the same direction than results of Thornhill and Grammer (1999), who found a

287 positive but insignificant correlation between facial attractiveness and WHR. Further studies  
288 are needed to investigate if face and WHR are signaling different aspects of female mate  
289 quality. Secondly, we found that socio-economic status of the women had a negative effect on  
290 facial attractiveness. We were expecting a positive correlation, as a higher socio-economic  
291 status is related to less stress during development, better nutrition, less unhealthy behavior,  
292 etc. (Adler et al. 1994; Kalick et al. 1998). But here again, even if counterintuitive, our results  
293 are in the same direction than a previous study showing a negative correlation between facial  
294 attractiveness and SES for female (Hume and Montgomerie 2001). We cannot speculate on  
295 this result, as the variance of SES in our female sample is very narrow (women were all  
296 students at the university). However, we can suggest that it deserves more study (a lot of  
297 research focused on the effect of attractiveness on SES, but less on the reverse relationship).

298         Spurious significant results may sometimes arise following model simplification  
299 (Whittingham et al. 2006). This statistical bias is unlikely in this study, as all terms were kept  
300 and no model simplification was performed. However, it is still possible that a confounding  
301 variable, which remains to be identified, explains the link between expected age at menopause  
302 and facial attractiveness. Moreover, further study is needed to specify the facial cues used by  
303 men to detect residual reproductive value in young women (in this respect, figure S3 shows  
304 the differences in face shape between women of high and low expected age at menopause).  
305 Here, we investigated the mediating role of immediate fertility cues and facial ageing, as  
306 residual reproductive value could potentially be linked to these two traits (Wood et al. 2001;  
307 Gold 2011). The next step would be to consider a large range of facial features such as facial  
308 symmetry, averageness, adiposity, skin colour, skin homogeneity, hair, etc., in an exploratory  
309 attempt to detect the facial cues linked to expected age at menopause. Also, age at menopause  
310 could additionally be assessed with more objective methods than self-report, for example by  
311 using the serum antimüllerian hormone concentration (Disseldorp et al. 2008), or through  
312 genetic analysis (He et al. 2009, 2010). Assuming that preferences reflect actual mate choice  
313 (which remains to be established for this trait), men's preference for women signalling a late

314 age at menopause - and thus a longer temporal reproductive window - could suggest a  
315 current selection towards a later menopause, at least in Western societies. Interestingly, a  
316 secular trend of increased menopausal age has recently been observed (vanNoord et al. 1997;  
317 Rodstrom et al. 2003; Dratva et al. 2009). This suggests that the social, familial and cultural  
318 conditions found today in Western societies are promoting current selection towards a later  
319 menopause in women. As a consequence, studies carried out in these societies are probably  
320 not adequate to empirically test evolutionary hypotheses on the ancestral selection on the  
321 emergence or maintenance of an extensive post-reproductive life-span in the human lineage  
322 (Thouzeau and Raymond 2017). Our results also suggest that sexual selection should be  
323 included in studies investigating the evolution of menopause in humans.

324 Somatic senescence, or ageing, is readily detectable in a face through wrinkles, skin  
325 texture and colouration, etc. (for a review, see Rhodes 2009). Those traits are specifically  
326 targeted by cosmetic changes when a younger appearance is desirable. Facial traits correlated  
327 with reproductive senescence have yet to be identified, and it remains to be determined  
328 whether they can be, or are already, manipulated to increase attractiveness by signalling a  
329 later menopause.

### 330 References

- 331 Abend P, Pflüger LS, Koppensteiner M, et al (2014) The sound of female shape: a redundant  
332 signal of vocal and facial attractiveness. *Evol Hum Behav* 36:174–181. doi:  
333 10.1016/j.evolhumbehav.2014.10.004
- 334 Abitbol J, Abitbol P, Abitbol B (1999) Sex hormones and the female voice. *J Voice* 13:424–  
335 446. doi: 10.1016/s0892-1997(99)80048-4
- 336 Adler NE, Boyce T, Chesney MA, et al (1994) Socioeconomic status and health: The  
337 challenge of the gradient. *Am Psychol* 49:15–24. doi: 10.1037/0003-066X.49.1.15
- 338 Avis NE, Stellato R, Crawford S, et al (2001) Is there a menopausal syndrome? Menopausal  
339 status and symptoms across racial/ethnic groups. *Soc Sci Med* 52:345–356. doi:  
340 10.1016/S0277-9536(00)00147-7
- 341 Boersma P, Weenink D (2013) Praat: doing phonetics by computer.
- 342 Butovskaya M, Sorokowska A, Karwowski M, et al (2017) Waist-to-hip ratio, body-mass  
343 index, age and number of children in seven traditional societies. *Sci Rep* 7:1622. doi:

- 344 10.1038/s41598-017-01916-9
- 345 Buunk BP, Dijkstra P, Kenrick DT, Warntjes A (2001) Age preferences for mates as related to  
346 gender, own age, and involvement level. *Evol Hum Behav* 22:241–250.
- 347 Carter AJ, Nguyen AQ (2011) Antagonistic pleiotropy as a widespread mechanism for the  
348 maintenance of polymorphic disease alleles. *BMC Med Genet* 12:160. doi:  
349 10.1186/1471-2350-12-160
- 350 Collins SA, Missing C (2003) Vocal and visual attractiveness are related in women. *Anim*  
351 *Behav* 65:997–1004. doi: 10.1006/anbe.2003.2123
- 352 Cunningham MR, Roberts AR, Wu CH, et al (1995) Their Ideas of Beauty Are, on the Whole,  
353 the Same as Ours - Consistency and Variability in the Cross-Cultural Perception of  
354 Female Physical Attractiveness. *J Pers Soc Psychol* 68:261–279.
- 355 de Bruin JP, Bovenhuis H, van Noord PAH, et al (2001) The role of genetic factors in age at  
356 natural menopause. *Hum Reprod* 16:2014–2018. doi: 10.1093/humrep/16.9.2014
- 357 Disseldorp J van, Faddy MJ, Themmen APN, et al (2008) Relationship of Serum  
358 Antimüllerian Hormone Concentration to Age at Menopause. *J Clin Endocrinol Metab*  
359 93:2129–2134. doi: 10.1210/jc.2007-2093
- 360 Dixson BJW, Lee AJ, Sherlock JM, Talamas SN (2017) Beneath the beard: do facial  
361 morphometrics influence the strength of judgments of men’s beardedness? *Evol Hum*  
362 *Behav* 38:164–174. doi: 10.1016/j.evolhumbehav.2016.08.004
- 363 Dratva J, Real FG, Schindler C, et al (2009) Is age at menopause increasing across Europe?  
364 Results on age at menopause and determinants from two population-based studies.  
365 *Menopause- J North Am Menopause Soc* 16:385–394.
- 366 Evans S, Neave N, Wakelin D, Hamilton C (2008) The relationship between testosterone and  
367 vocal frequencies in human males. *Physiol Behav* 93:783–788. doi:  
368 10.1016/j.physbeh.2007.11.033
- 369 Farkas L (1987) Age-and sex-related changes in facial proportions. *Anthr Facial Proportions*  
370 *Med Springf Charles C Thomas P* 29–56.
- 371 Feinberg DR (2008) Are human faces and voices ornaments signaling common underlying  
372 cues to mate value? *Evol Anthropol* 17:112–118. doi: 10.1002/evan.20166
- 373 Feinberg DR, Jones BC, DeBruine LM, et al (2005) The voice and face of woman: One  
374 ornament that signals quality? *Evol Hum Behav* 26:398–408.
- 375 Fink B, Neave N (2005) The biology of facial beauty. *Int J Cosmet Sci* 27:317–325. doi:  
376 10.1111/j.1467-2494.2005.00286.x
- 377 Gold EB (2011) The Timing of the Age at Which Natural Menopause Occurs. *Obstet Gynecol*  
378 *Clin North Am* 38:425–440. doi: 10.1016/j.ogc.2011.05.002
- 379 Hamilton WD (1966) The moulding of senescence by natural selection. *J Theor Biol* 12:12–  
380 45. doi: 10.1016/0022-5193(66)90184-6
- 381 Harries M, Hawkins S, Hacking J, Hughes I (1998) Changes in the male voice at puberty:  
382 vocal fold length and its relationship to the fundamental frequency of the voice. *J*  
383 *Laryngol Otol* 112:451–454.

- 384 He C, Kraft P, Chasman D, et al (2010) A large-scale candidate gene association study of age  
385 at menarche and age at natural menopause. *Hum Genet* 128:515–527. doi:  
386 10.1007/s00439-010-0878-4
- 387 He C, Kraft P, Chen C, et al (2009) Genome-wide association studies identify loci associated  
388 with age at menarche and age at natural menopause. *Nat Genet* 41:724–728. doi:  
389 [http://www.nature.com/ng/journal/v41/n6/supinfo/ng.385\\_S1.html](http://www.nature.com/ng/journal/v41/n6/supinfo/ng.385_S1.html)
- 390 Henss R (2000) Waist-to-hip ratio and female attractiveness. Evidence from photographic  
391 stimuli and methodological considerations. *Personal Individ Differ* 28:501–513.
- 392 Hume DK, Montgomerie R (2001) Facial attractiveness signals different aspects of “quality”  
393 in women and men. *Evol Hum Behav* 22:93–112.
- 394 Jasienska G, Ziomkiewicz A, Ellison PT, et al (2004) Large breasts and narrow waists indicate  
395 high reproductive potential in women. *Proc R Soc B-Biol Sci* 271:1213–1217.
- 396 Johnston VS, Franklin M (1993) Is Beauty in the Eye of the Beholder. *Ethol Sociobiol*  
397 14:183–199.
- 398 Jones BC (2014) Agreement and Individual Differences in Men’s Preferences for Women’s  
399 Facial Characteristics. In: *Evolutionary Perspectives on Human Sexual Psychology*  
400 *and Behavior*. Springer, New York, NY, pp 87–102
- 401 Kalick SM, Zebrowitz LA, Langlois JH, Johnson RM (1998) Does Human Facial  
402 Attractiveness Honestly Advertise Health? Longitudinal Data on an Evolutionary  
403 Question. *Psychol Sci* 9:8–13. doi: 10.1111/1467-9280.00002
- 404 Koehler N, Simmons LW, Rhodes G, Peters M (2004) The relationship between sexual  
405 dimorphism in human faces and fluctuating asymmetry. *Proc R Soc B-Biol Sci*  
406 271:S233–S236.
- 407 Kwart DG, Foulsham T, Kingstone A (2012) Age and beauty are in the eye of the beholder.  
408 *Perception* 41:925–938.
- 409 Lassek WD, Gaulin SJC (2007) Menarche is related to fat distribution. *Am J Phys Anthropol*  
410 133:1147–1151. doi: 10.1002/ajpa.20644
- 411 Law Smith MJ, Perrett DI, Jones BC, et al (2006) Facial appearance is a cue to oestrogen  
412 levels in women. *Proc R Soc B-Biol Sci* 273:135–140.
- 413 Lee AJ, Mitchem DG, Wright MJ, et al (2014) Genetic Factors That Increase Male Facial  
414 Masculinity Decrease Facial Attractiveness of Female Relatives. *Psychol Sci* 25:476–  
415 484. doi: 10.1177/0956797613510724
- 416 Little AC, Jones BC, DeBruine LM (2011) Facial attractiveness: evolutionary based research.  
417 *Philos Trans R Soc B Biol Sci* 366:1638–1659. doi: 10.1098/rstb.2010.0404
- 418 Lynch M, Walsh B (1998) *Genetics and analysis of quantitative traits*. Sinauer Associates,  
419 Sunderland
- 420 Maestripieri D, Klimczuk ACE, Traficante DM, Wilson MC (2014) A greater decline in  
421 female facial attractiveness during middle age reflects women’s loss of reproductive  
422 value.
- 423 Marcinkowska UM, Dixson BJ, Kozlov MV, Rantala MJ (2015) Men’s Preferences for



- 424 Female Facial Femininity Decline With Age. *J Gerontol B Psychol Sci Soc Sci*. doi:  
425 10.1093/geronb/gbv077
- 426 Marcinkowska UM, Kozlov MV, Cai H, et al (2014) Cross-cultural variation in men's  
427 preference for sexual dimorphism in women's faces. *Biol Lett*. doi:  
428 10.1098/rsbl.2013.0850
- 429 Mondragón-Ceballos R, Garcia Granados MD, Cerda-Molina AL, et al (2015) Waist-to-Hip  
430 Ratio, but Not Body Mass Index, Is Associated with Testosterone and Estradiol  
431 Concentrations in Young Women.
- 432 Morris DH, Jones ME, Schoemaker MJ, et al (2011) Familial concordance for age at natural  
433 menopause: results from the Breakthrough Generations Study. *Menopause* 18:956–  
434 961.
- 435 Murabito JM, Yang Q, Fox C, et al (2005) Heritability of age at natural menopause in the  
436 Framingham Heart Study. *J Clin Endocrinol Metab* 90:3427–3430.
- 437 Nenko I, Jasienska G (2009) Fertility, body size, and shape: An empirical test of the covert  
438 maternal depletion hypothesis. *Am J Hum Biol* 21:520–523. doi: 10.1002/ajhb.20938
- 439 Perrett DI, Lee KJ, Penton-Voak I, et al (1998) Effects of sexual dimorphism on facial  
440 attractiveness. *Nature* 394:884–887.
- 441 Pfluger LS, Oberzaucher E, Katina S, et al (2012) Cues to fertility: perceived attractiveness  
442 and facial shape predict reproductive success. *Evol Hum Behav* 33:708–714.
- 443 Pipitone RN, Gallup GG (2008) Women's voice attractiveness varies across the menstrual  
444 cycle. *Evol Hum Behav* 29:268–274.
- 445 Puts DA, Bailey DH, Cardenas RA, et al (2013) Women's attractiveness changes with  
446 estradiol and progesterone across the ovulatory cycle. *Horm Behav* 63:13–19.
- 447 Puts DA, Jones BC, DeBruine LM (2012) Sexual Selection on Human Faces and Voices. *J*  
448 *Sex Res* 49:227–243. doi: 10.1080/00224499.2012.658924
- 449 Rhodes G (2006) The evolutionary psychology of facial beauty. In: *Annual Review of*  
450 *Psychology*. Annual Reviews, Palo Alto, pp 199–226
- 451 Rhodes G, Chan J, Zebrowitz LA, Simmons LW (2003) Does sexual dimorphism in human  
452 faces signal health? *Proc R Soc Lond B Biol Sci* 270:S93–S95. doi:  
453 10.1098/rsbl.2003.0023
- 454 Rhodes MG (2009) Age Estimation of Faces: A Review. *Appl Cogn Psychol* 23:1–12.
- 455 Rodstrom K, Bengtsson C, Milsom I, et al (2003) Evidence for a secular trend in menopausal  
456 age: a population study of women in Gothenburg. *Menopause- J North Am*  
457 *Menopause Soc* 10:538–543.
- 458 Scott IML, Pound N, Stephen ID, et al (2010) Does Masculinity Matter? The Contribution of  
459 Masculine Face Shape to Male Attractiveness in Humans.
- 460 Singh D (1993) Body Shape and Women's Attractiveness - the Critical Role of Waist-to-Hip  
461 Ratio. *Hum Nat- Interdiscip Biosoc Perspect* 4:297–321.
- 462 Singh D (2002) Female mate value at a glance: Relationship of waist-to-hip ratio to health,

- 463 fecundity and attractiveness. *Neuroendocrinol Lett* 23:81–91.
- 464 Singh D, Dixon BJ, Jessop TS, et al (2010) Cross-cultural consensus for waist-hip ratio and  
465 women's attractiveness. *Evol Hum Behav* 31:176–181.
- 466 Singh D, Randall PK (2007) Beauty is in the eye of the plastic surgeon: Waist-hip ratio  
467 (WHR) and women's attractiveness. *Personal Individ Differ* 43:329–340. doi:  
468 10.1016/j.paid.2006.12.003
- 469 Smith HMJ, Dunn AK, Baguley T, Stacey PC (2016) Concordant Cues in Faces and Voices:  
470 Testing the Backup Signal Hypothesis. *Evol Psychol*. doi:  
471 10.1177/1474704916630317
- 472 Snieder H, MacGregor AJ, Spector TD (1998) Genes Control the Cessation of a Woman's  
473 Reproductive Life: A Twin Study of Hysterectomy and Age at Menopause. *J Clin*  
474 *Endocrinol Metab* 83:1875–1880. doi: 10.1210/jcem.83.6.4890
- 475 Stepaniak U, Szafraniec K, Kubinova R, et al (2013) Age at natural menopause in three  
476 Central and Eastern European urban populations: The HAPIEE study. *Maturitas*  
477 75:87–93.
- 478 Sugiyama LS (2015) Physical Attractiveness: An Adaptationist Perspective. In: *The*  
479 *Handbook of Evolutionary Psychology*. John Wiley & Sons, Inc.,
- 480 Symons D (1995) Beauty is in the adaptations of the beholder: The evolutionary psychology  
481 of human female sexual attractiveness. *Sex Nat Sex Cult* 80–118.
- 482 Thomas F, Renaud F, Benfice E, et al (2001) International variability of ages at menarche  
483 and menopause: Patterns and main determinants. *Hum Biol* 73:271–290.
- 484 Thornhill R, Grammer K (1999) The Body and Face of Woman: One Ornament that Signals  
485 Quality? *Evol Hum Behav* 20:105–120. doi: 10.1016/S1090-5138(98)00044-0
- 486 Thouzeau V, Raymond M (2017) Emergence and maintenance of menopause in humans: A  
487 game theory model. *J Theor Biol* 430:229–236. doi: 10.1016/j.jtbi.2017.07.019
- 488 Tiddeman B p., Stirrat M r., Perrett D i. (2005) Towards Realism in Facial Image  
489 Transformation: Results of a Wavelet MRF Method. *Comput Graph Forum* 24:449–  
490 456. doi: 10.1111/j.1467-8659.2005.00870.x
- 491 van Asselt KM, Kok HS, Pearson PL, et al (2004) Heritability of menopausal age in mothers  
492 and daughters. *Fertil Steril* 82:1348–1351.
- 493 vanNoord PAH, Dubas JS, Dorland M, et al (1997) Age at natural menopause in a population-  
494 based screening cohort: The role of menarche, fecundity, and lifestyle factors. *Fertil*  
495 *Steril* 68:95–102.
- 496 Velde T, R E, Pearson PL (2002) The variability of female reproductive ageing. *Hum Reprod*  
497 *Update* 8:141–154. doi: 10.1093/humupd/8.2.141
- 498 Wheatley JR, Apicella CA, Burriss RP, et al (2014) Women's faces and voices are cues to  
499 reproductive potential in industrial and forager societies. *Evol Hum Behav* 35:264–  
500 271. doi: 10.1016/j.evolhumbehav.2014.02.006
- 501 Whittingham MJ, Stephens PA, Bradbury RB, Freckleton RP (2006) Why do we still use  
502 stepwise modelling in ecology and behaviour? *J Anim Ecol* 75:1182–1189.

- 503 Wood JW, O'Connor KA, Holman DJ, et al (2001) The evolution of menopause by  
504 antagonistic pleiotropy. Cent Stud Demogr Ecol Work Pap 1–4.
- 505 Zelditch ML, Swiderski DL, Sheets HD (2012) Geometric Morphometrics for Biologists: A  
506 Primer. Academic Press
- 507 Zelditch ML, Swiderski DL, Sheets HD (2013) A Practical Companion to Geometric  
508 Morphometrics for Biologists: Running analyses in freely-available software.
- 509

510 Tables and figures captions

511 **Table 1.** Effects of the different variables on the probability to be chosen during the test of  
 512 attractiveness (male raters had to choose the woman found to be the most attractive between  
 513 two facial photographs).  $N = 3439$  observations (119 male raters and 68 female faces). Model  
 514 1 only includes the variable of interest (mother's age at menopause), and the control  
 515 variables. Model 2 also includes cues of immediate fertility and facial ageing as explanatory  
 516 variables. Significance codes: \*\*\*  $p < 0.001$ ; \*\*  $p < 0.01$ ; \*  $p < 0.05$ .

	Model 1				Model 2				
	Estimate	Std. Error	z value	Pr(> z )	Estimate	Std. Error	z value	Pr(> z )	
(Intercept)	0.092	0.121	0.762	0.446	0.096	0.112	0.861	0.389	
Mother's age at menopause <sup>†</sup>	0.217	0.053	4.129	< 0.001 ***	0.240	0.053	4.516	< 0.001 ***	
WHR <sup>†</sup>	-	-	-	-	0.132	0.057	2.321	0.020 *	
Facial femininity <sup>†</sup>	-	-	-	-	0.404	0.057	7.148	< 0.001 ***	
FO <sup>†</sup>	-	-	-	-	0.200	0.058	3.469	0.001 **	
Age <sup>†</sup>	-0.204	0.053	-3.883	< 0.001 ***	-0.271	0.058	-4.683	< 0.001 ***	
Facial ageing <sup>†</sup>	-	-	-	-	-0.563	0.060	-9.350	< 0.001 ***	
Smile <sup>†</sup>	0.335	0.053	6.364	< 0.001 ***	0.271	0.058	4.662	< 0.001 ***	
Socio-economic status <sup>†</sup>	-0.067	0.052	-1.302	0.193	-0.170	0.057	-3.009	0.003 **	
<i>Raters' characteristics</i>									
Age	-0.033	0.061	-0.548	0.584	-0.041	0.063	-0.642	0.521	
Socio-economic status	-0.015	0.061	-0.252	0.801	-0.012	0.063	-0.187	0.852	

517 <sup>†</sup>For each of these variables, the difference between the two women presented was integrated  
 518 into the model.

519 **Table 2.** Pearson's correlations between measures in the female sample ( $N=68$  women).

520 Significance codes: \*\*\*  $p < 0.001$ ; \*\*  $p < 0.01$ ; \*  $p < 0.05$ .

	Age	Mother's age at menopause	FO	WHR	Facial femininity	Facial ageing
Mother's age at menopause	0.07					
FO	-0.10	0.07				
WHR	0.22	-0.04	0.01			
Facial femininity	-0.20	-0.13	0.03	-0.01		
Facial ageing	-0.23	-0.08	-0.13	-0.03	0.24	
Socio-economic status	0.05	0.13	0.08	0.20	-0.18	-0.29*

521

522 **Figure 1.** Example of screenshot during the evaluation of women's facial attractiveness by the  
523 raters. For each pair of women, which was randomly chosen, the rater was instructed to click  
524 on the photograph of the woman that he found the most attractive. Photographs reproduced  
525 with permission.

526 **Figure 2.** Predicted probability to be chosen during the test of attractiveness, according to the  
527 difference in expected age at menopause (unstandardized values) between the focal and the  
528 non-focal women, controlling for all the other variables of model 2. Circle areas are  
529 proportional to the number of choices made by the raters: chosen (1) or not (0) as the most  
530 attractive woman. 95% confidence interval is represented by the dotted lines.

531 **Figure 3.** Relationship between age at menopause of mothers and maternal grandmothers.  
532 Plain line represents the linear regression with all points ( $\beta = 0.275$ ,  $SE = 0.11$ ,  $P = 0.016$ ,  
533 corresponding to a heritability of age at menopause  $h^2 = 0.55$ ). 95% confidence interval in  
534 grey.

535

### 536 Supporting Information

537 **Figure S1.** Results of the Principal Component Analysis (PCA) conducted on the Procrustes-  
538 registered landmarks and semi-landmarks data. This PCA produced shape variables which are  
539 a decomposition of the landmark coordinates of the female (black dots) and male (grey dots)  
540 faces. Only the two first components (or shape variables) are represented here.

541 **Figure S2.** Example of screenshot during the evaluation of women's age by the raters. The  
542 rater was instructed to estimate the women's age. The age appearing by default for each  
543 picture was randomized. For each woman, the difference between their real age and the mean  
544 age given by the raters was calculated. This variable represents the facial ageing of the  
545 women. Photograph reproduced with permission.

546 **Figure S3.** *Top:* Shape differences of a low expected reproductive value face (average face of  
547 the 7 women with the earlier expected age at menopause in our sample) relative to the average  
548 face (average of all the women's face in our study), on a Thin-Plate Spline (TPS) grid.

549 *Bottom:* shape differences of a high expected reproductive value face (average face of the 7  
550 women with the later expected age at menopause) relative to the average face. For both, the  
551 shape deformation has been magnified by 2. Figure created using R package Geomorph 3.0.3.

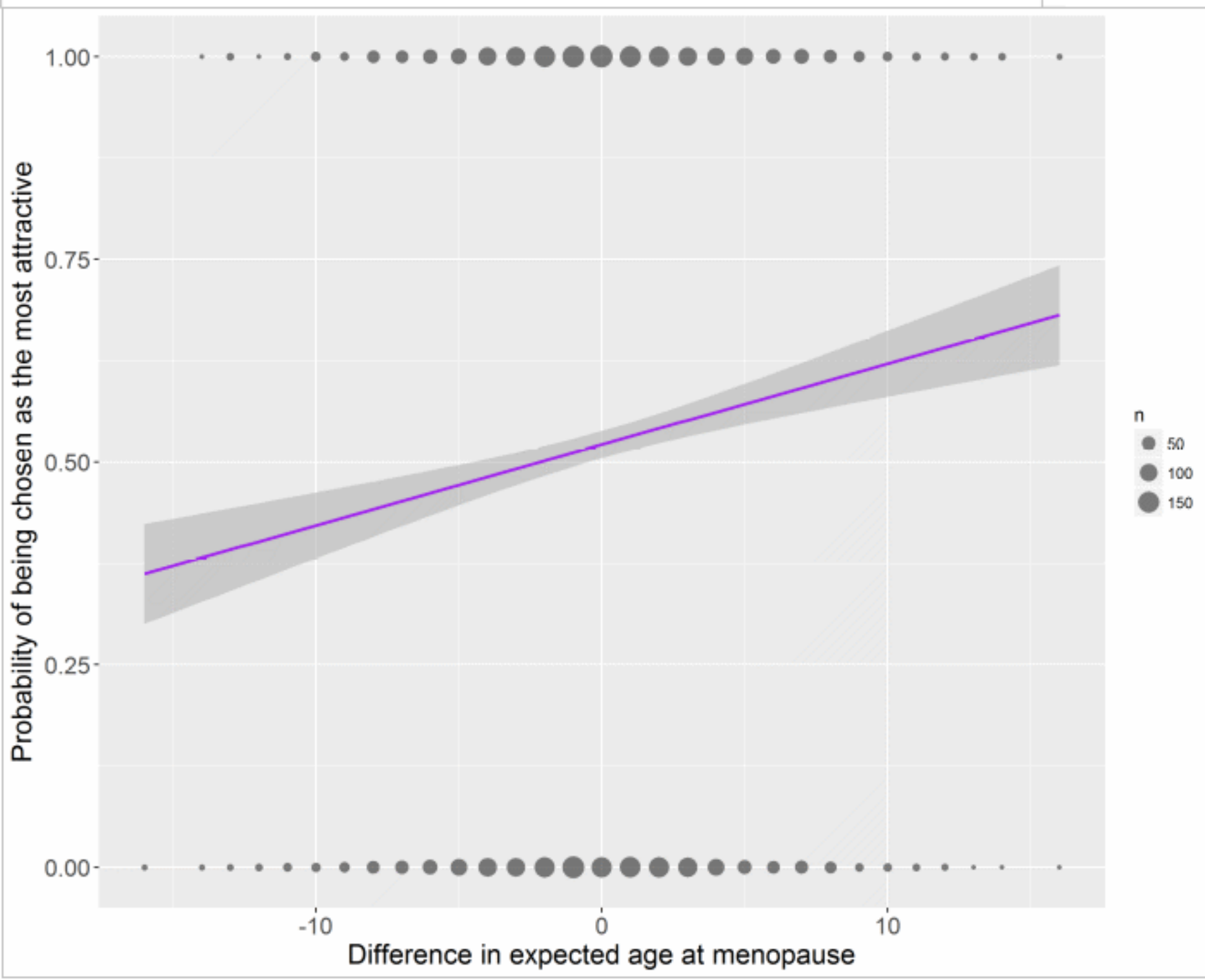
552

553 **Table S4.** Descriptive statistics

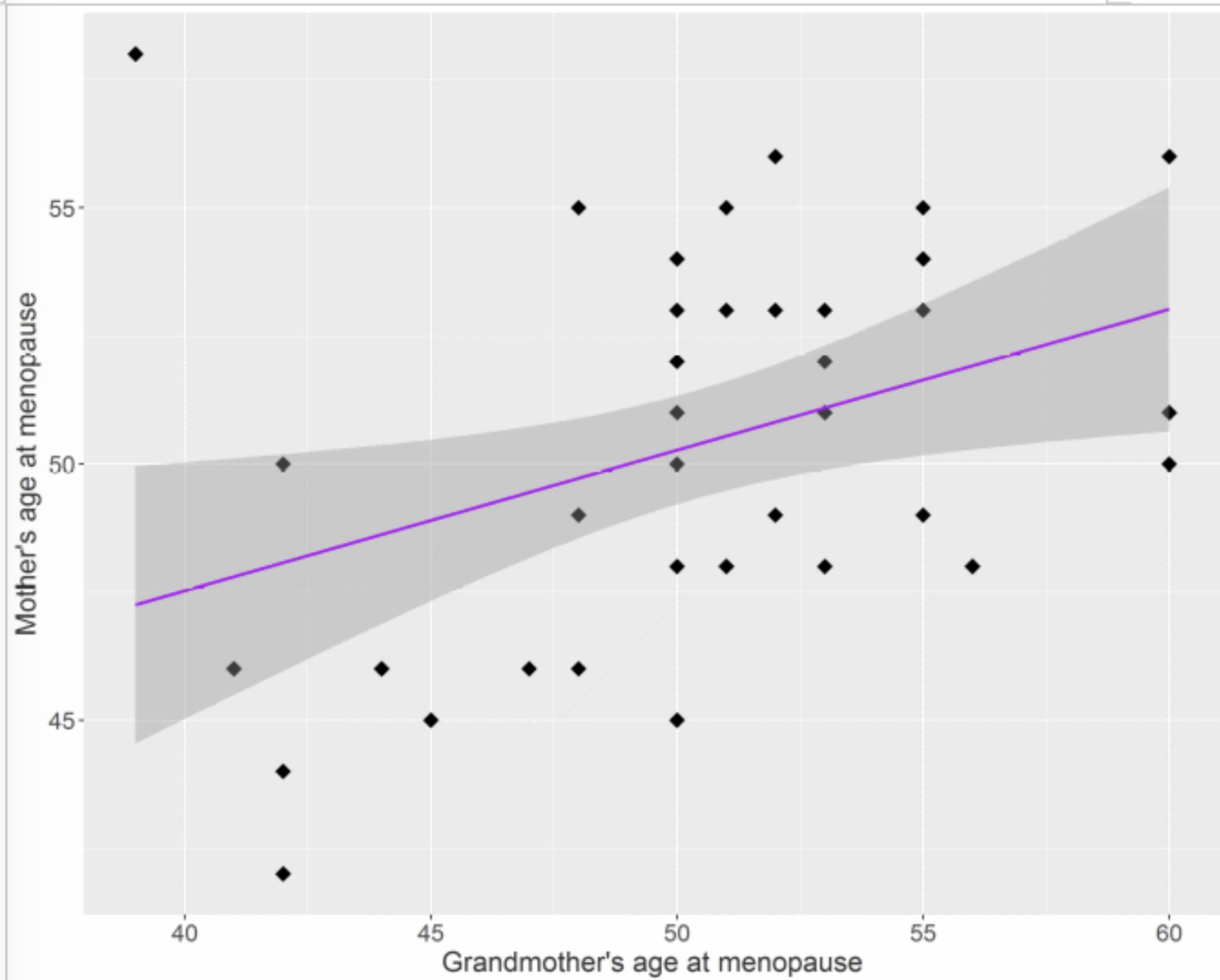
Variable	N	Mean	St. Dev.	Min	Max
Mother's age at menopause (year)	68	50.97	3.22	42	58
WHR (ratio)	68	0.73	0.04	0.62	0.83
Facial femininity (index)	68	0.78	0.98	-1.71	3.33
F0 (Hz)	68	203.28	19.94	142.50	243.70
Age (year)	68	28.43	3.00	25	35
Facial ageing (years)	68	1.34	3.90	-5.57	12.71
Smile (binary)	68	0.31	0.47	0	1
Socio-economic status (PCA coordinate)	68	0.07	0.75	-1.23	2.08
<i>Raters' characteristics</i>					
Age (year)	119	36.23	12.25	17	72
Socio-economic status (PCA coordinate)	119	0.02	0.72	-0.99	1.98

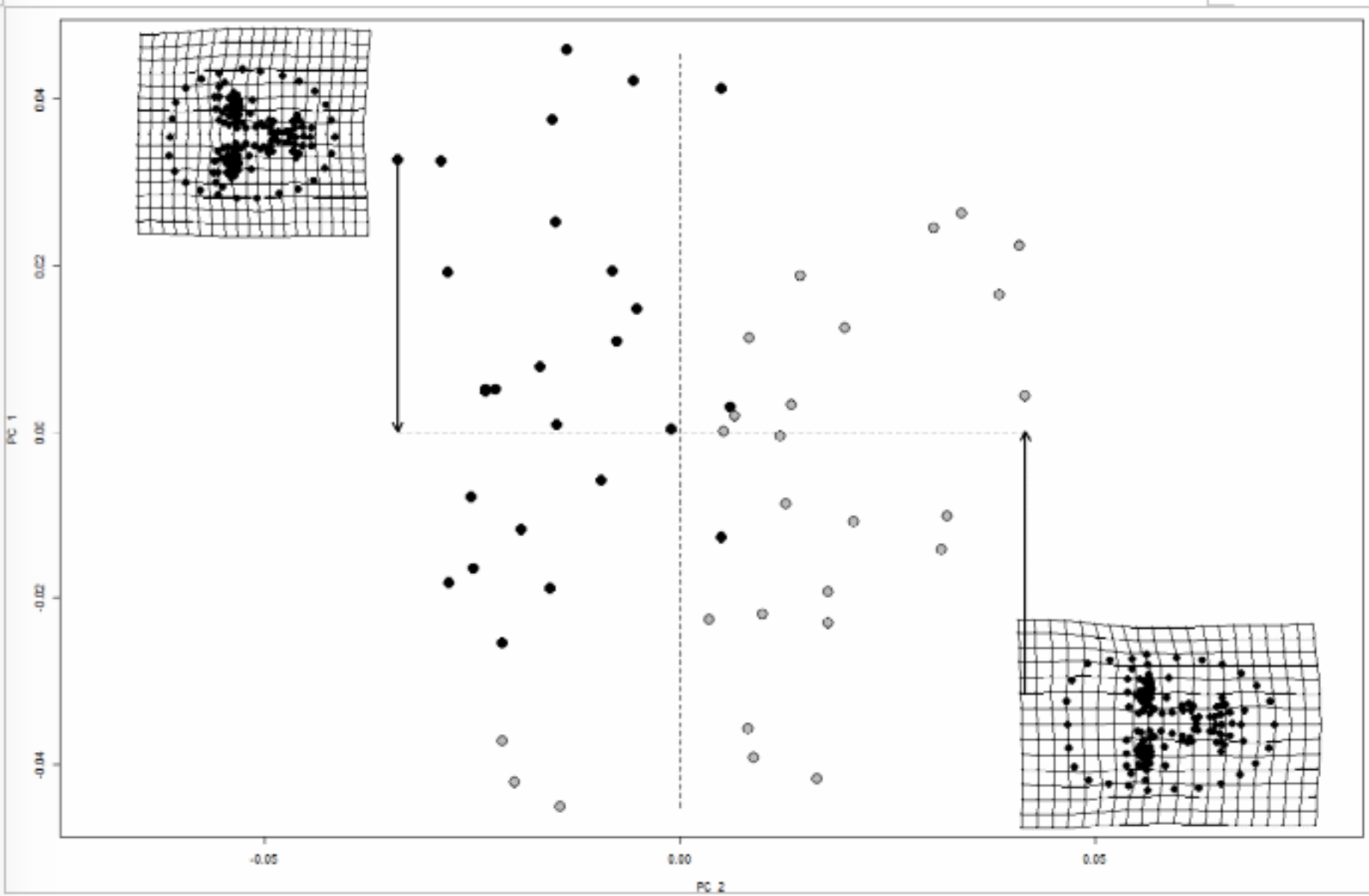
554













Age:

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Next

I know this person

How old is she ?

