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WOMEN'S ATTRACTIVENESS IS LINKED TO EXPECTED AGE AT MENOPAUSE

(WOMEN'S ATTRACTIVENESS AND AGE AT MENOPAUSE)

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Abstract

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

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

1. Introduction

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

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

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

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

2. Materials and Methods

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

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

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

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

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

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

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

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

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

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

3. Results

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

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

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

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

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

4. Discussion

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

Results classically found in the literature were replicated in this study, suggesting that this sample of young females is not different from those described elsewhere. First, our sample provided an heritability estimate for age at menopause of 0.55, consistent with previous values ranging from 0.42 to 0.72 (Snieder et al. 1998; de Bruin et al. 2001; van Asselt et al. 2004; Murabito et al. 2005; Morris et al. 2011). Moreover, immediate fertility cues were positively correlated with facial attractiveness, as in previous studies: men in our sample preferred more feminine faces as in Cunningham et al. 1995; Perrett et al. 1998; Rhodes et al. 2003; Koehler et al. 2004; Little et al. 2011, and facial attractiveness was positively correlated to pitch voice (F0), consistent with Collins and Missing 2003; Feinberg et al. 2005; Wheatley et al. 2014; Smith et al. 2016. Also, attractive faces were rated younger than their true age, as in the study of Kwart (2012). However, two variables had significant effects on attractiveness, but in the opposite direction than expected. First, men in our sample had a preference for faces of women who have a higher (i.e. more masculine) WHR, which is in contradiction with the idea that face and body would signal one same quality. However, our results go in the same direction than results of Thornhill and Grammer (1999), who found a

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

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

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

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

References

Abend P, Pflüger LS, Koppensteiner M, et al (2014) The sound of female shape: a redundant signal of vocal and facial attractiveness. Evol Hum Behav 36:174–181. doi: 10.1016/j.evolhumbehav.2014.10.004

Abitbol J, Abitbol P, Abitbol B (1999) Sex hormones and the female voice. J Voice 13:424–446. doi: 10.1016/s0892-1997(99)80048-4

Adler NE, Boyce T, Chesney MA, et al (1994) Socioeconomic status and health: The challenge of the gradient. Am Psychol 49:15–24. doi: 10.1037/0003-066X.49.1.15

Avis NE, Stellato R, Crawford S, et al (2001) Is there a menopausal syndrome? Menopausal status and symptoms across racial/ethnic groups. Soc Sci Med 52:345–356. doi: 10.1016/S0277-9536(00)00147-7

Boersma P, Weenink D (2013) Praat: doing phonetics by computer.

Butovskaya M, Sorokowska A, Karwowski M, et al (2017) Waist-to-hip ratio, body-mass index, age and number of children in seven traditional societies. Sci Rep 7:1622. doi:

10.1038/s41598-017-01916-9

Buunk BP, Dijkstra P, Kenrick DT, Warntjes A (2001) Age preferences for mates as related to gender, own age, and involvement level. Evol Hum Behav 22:241–250.

Carter AJ, Nguyen AQ (2011) Antagonistic pleiotropy as a widespread mechanism for the maintenance of polymorphic disease alleles. BMC Med Genet 12:160. doi: 10.1186/1471-2350-12-160

Collins SA, Missing C (2003) Vocal and visual attractiveness are related in women. Anim Behav 65:997–1004. doi: 10.1006/anbe.2003.2123

Cunningham MR, Roberts AR, Wu CH, et al (1995) Their Ideas of Beauty Are, on the Whole, the Same as Ours - Consistency and Variability in the Cross-Cultural Perception of Female Physical Attractiveness. J Pers Soc Psychol 68:261–279.

de Bruin JP, Bovenhuis H, van Noord PAH, et al (2001) The role of genetic factors in age at natural menopause. Hum Reprod 16:2014–2018. doi: 10.1093/humrep/16.9.2014

Disseldorp J van, Faddy MJ, Themmen APN, et al (2008) Relationship of Serum Antimüllerian Hormone Concentration to Age at Menopause. J Clin Endocrinol Metab 93:2129–2134. doi: 10.1210/jc.2007-2093

Dixson BJW, Lee AJ, Sherlock JM, Talamas SN (2017) Beneath the beard: do facial morphometrics influence the strength of judgments of men's beardedness? Evol Hum Behav 38:164–174. doi: 10.1016/j.evolhumbehav.2016.08.004

Dratva J, Real FG, Schindler C, et al (2009) Is age at menopause increasing across Europe? Results on age at menopause and determinants from two population-based studies. Menopause- J North Am Menopause Soc 16:385–394.

Evans S, Neave N, Wakelin D, Hamilton C (2008) The relationship between testosterone and vocal frequencies in human males. Physiol Behav 93:783–788. doi: 10.1016/j.physbeh.2007.11.033

Farkas L (1987) Age-and sex-related changes in facial proportions. Anthr Facial Proportions Med Springf Charles C Thomas P 29–56.

Feinberg DR (2008) Are human faces and voices ornaments signaling common underlying cues to mate value? Evol Anthropol 17:112–118. doi: 10.1002/evan.20166

Feinberg DR, Jones BC, DeBruine LM, et al (2005) The voice and face of woman: One ornament that signals quality? Evol Hum Behav 26:398–408.

Fink B, Neave N (2005) The biology of facial beauty. Int J Cosmet Sci 27:317–325. doi: 10.1111/j.1467-2494.2005.00286.x

Gold EB (2011) The Timing of the Age at Which Natural Menopause Occurs. Obstet Gynecol Clin North Am 38:425–440. doi: 10.1016/j.ogc.2011.05.002

Hamilton WD (1966) The moulding of senescence by natural selection. J Theor Biol 12:12–45. doi: 10.1016/0022-5193(66)90184-6

Harries M, Hawkins S, Hacking J, Hughes I (1998) Changes in the male voice at puberty: vocal fold length and its relationship to the fundamental frequency of the voice. J Laryngol Otol 112:451–454.

He C, Kraft P, Chasman D, et al (2010) A large-scale candidate gene association study of age at menarche and age at natural menopause. Hum Genet 128:515–527. doi: 10.1007/s00439-010-0878-4

He C, Kraft P, Chen C, et al (2009) Genome-wide association studies identify loci associated with age at menarche and age at natural menopause. Nat Genet 41:724–728. doi: http://www.nature.com/ng/journal/v41/n6/suppinfo/ng.385_S1.html

Henss R (2000) Waist-to-hip ratio and female attractiveness. Evidence from photographic stimuli and methodological considerations. Personal Individ Differ 28:501–513.

Hume DK, Montgomerie R (2001) Facial attractiveness signals different aspects of "quality" in women and men. Evol Hum Behav 22:93–112.

Jasienska G, Ziomkiewicz A, Ellison PT, et al (2004) Large breasts and narrow waists indicate high reproductive potential in women. Proc R Soc B-Biol Sci 271:1213–1217.

Johnston VS, Franklin M (1993) Is Beauty in the Eye of the Beholder. Ethol Sociobiol 14:183–199.

Jones BC (2014) Agreement and Individual Differences in Men's Preferences for Women's Facial Characteristics. In: Evolutionary Perspectives on Human Sexual Psychology and Behavior. Springer, New York, NY, pp 87–102

Kalick SM, Zebrowitz LA, Langlois JH, Johnson RM (1998) Does Human Facial Attractiveness Honestly Advertise Health? Longitudinal Data on an Evolutionary Question. Psychol Sci 9:8–13. doi: 10.1111/1467-9280.00002

Koehler N, Simmons LW, Rhodes G, Peters M (2004) The relationship between sexual dimorphism in human faces and fluctuating asymmetry. Proc R Soc B-Biol Sci 271:S233–S236.

Kwart DG, Foulsham T, Kingstone A (2012) Age and beauty are in the eye of the beholder. Perception 41:925–938.

Lassek WD, Gaulin SJC (2007) Menarche is related to fat distribution. Am J Phys Anthropol 133:1147–1151. doi: 10.1002/ajpa.20644

Law Smith MJ, Perrett DI, Jones BC, et al (2006) Facial appearance is a cue to oestrogen levels in women. Proc R Soc B-Biol Sci 273:135–140.

Lee AJ, Mitchem DG, Wright MJ, et al (2014) Genetic Factors That Increase Male Facial Masculinity Decrease Facial Attractiveness of Female Relatives. Psychol Sci 25:476–484. doi: 10.1177/0956797613510724

Little AC, Jones BC, DeBruine LM (2011) Facial attractiveness: evolutionary based research. Philos Trans R Soc B Biol Sci 366:1638–1659. doi: 10.1098/rstb.2010.0404

Lynch M, Walsh B (1998) Genetics and analysis of quantitative traits. Sinauer Associates, Sunderland

Maestripieri D, Klimczuk ACE, Traficonte DM, Wilson MC (2014) A greater decline in female facial attractiveness during middle age reflects women's loss of reproductive value.

Marcinkowska UM, Dixson BJ, Kozlov MV, Rantala MJ (2015) Men's Preferences for

Female Facial Femininity Decline With Age. J Gerontol B Psychol Sci Soc Sci. doi: 10.1093/geronb/gbv077

Marcinkowska UM, Kozlov MV, Cai H, et al (2014) Cross-cultural variation in men's preference for sexual dimorphism in women's faces. Biol Lett. doi: 10.1098/rsbl.2013.0850

Mondragón-Ceballos R, Garcia Granados MD, Cerda-Molina AL, et al (2015) Waist-to-Hip Ratio, but Not Body Mass Index, Is Associated with Testosterone and Estradiol Concentrations in Young Women.

Morris DH, Jones ME, Schoemaker MJ, et al (2011) Familial concordance for age at natural menopause: results from the Breakthrough Generations Study. Menopause 18:956–961.

Murabito JM, Yang Q, Fox C, et al (2005) Heritability of age at natural menopause in the Framingham Heart Study. J Clin Endocrinol Metab 90:3427–3430.

Nenko I, Jasienska G (2009) Fertility, body size, and shape: An empirical test of the covert maternal depletion hypothesis. Am J Hum Biol 21:520–523. doi: 10.1002/ajhb.20938

Perrett DI, Lee KJ, Penton-Voak I, et al (1998) Effects of sexual dimorphism on facial attractiveness. Nature 394:884–887.

Pfluger LS, Oberzaucher E, Katina S, et al (2012) Cues to fertility: perceived attractiveness and facial shape predict reproductive success. Evol Hum Behav 33:708–714.

Pipitone RN, Gallup GG (2008) Women's voice attractiveness varies across the menstrual cycle. Evol Hum Behav 29:268–274.

Puts DA, Bailey DH, Cardenas RA, et al (2013) Women's attractiveness changes with estradiol and progesterone across the ovulatory cycle. Horm Behav 63:13–19.

Puts DA, Jones BC, DeBruine LM (2012) Sexual Selection on Human Faces and Voices. J Sex Res 49:227–243. doi: 10.1080/00224499.2012.658924

Rhodes G (2006) The evolutionary psychology of facial beauty. In: Annual Review of Psychology. Annual Reviews, Palo Alto, pp 199–226

Rhodes G, Chan J, Zebrowitz LA, Simmons LW (2003) Does sexual dimorphism in human faces signal health? Proc R Soc Lond B Biol Sci 270:S93–S95. doi: 10.1098/rsbl.2003.0023

Rhodes MG (2009) Age Estimation of Faces: A Review. Appl Cogn Psychol 23:1–12.

Rodstrom K, Bengtsson C, Milsom I, et al (2003) Evidence for a secular trend in menopausal age: a population study of women in Gothenburg. Menopause- J North Am Menopause Soc 10:538–543.

Scott IML, Pound N, Stephen ID, et al (2010) Does Masculinity Matter? The Contribution of Masculine Face Shape to Male Attractiveness in Humans.

Singh D (1993) Body Shape and Women's Attractiveness - the Critical Role of Waist-to-Hip Ratio. Hum Nat- Interdiscip Biosoc Perspect 4:297–321.

Singh D (2002) Female mate value at a glance: Relationship of waist-to-hip ratio to health,

fecundity and attractiveness. Neuroendocrinol Lett 23:81–91.

Singh D, Dixson BJ, Jessop TS, et al (2010) Cross-cultural consensus for waist-hip ratio and women's attractiveness. Evol Hum Behav 31:176–181.

Singh D, Randall PK (2007) Beauty is in the eye of the plastic surgeon: Waist-hip ratio (WHR) and women's attractiveness. Personal Individ Differ 43:329–340. doi: 10.1016/j.paid.2006.12.003

Smith HMJ, Dunn AK, Baguley T, Stacey PC (2016) Concordant Cues in Faces and Voices: Testing the Backup Signal Hypothesis. Evol Psychol. doi: 10.1177/1474704916630317

Snieder H, MacGregor AJ, Spector TD (1998) Genes Control the Cessation of a Woman's Reproductive Life: A Twin Study of Hysterectomy and Age at Menopause. J Clin Endocrinol Metab 83:1875–1880. doi: 10.1210/jcem.83.6.4890

Stepaniak U, Szafraniec K, Kubinova R, et al (2013) Age at natural menopause in three Central and Eastern European urban populations: The HAPIEE study. Maturitas 75:87–93.

Sugiyama LS (2015) Physical Attractiveness: An Adaptationist Perspective. In: The Handbook of Evolutionary Psychology. John Wiley & Sons, Inc.,

Symons D (1995) Beauty is in the adaptations of the beholder: The evolutionary psychology of human female sexual attractiveness. Sex Nat Sex Cult 80–118.

Thomas F, Renaud F, Benefice E, et al (2001) International variability of ages at menarche and menopause: Patterns and main determinants. Hum Biol 73:271–290.

Thornhill R, Grammer K (1999) The Body and Face of Woman: One Ornament that Signals Quality? Evol Hum Behav 20:105–120. doi: 10.1016/S1090-5138(98)00044-0

Thouzeau V, Raymond M (2017) Emergence and maintenance of menopause in humans: A game theory model. J Theor Biol 430:229–236. doi: 10.1016/j.jtbi.2017.07.019

Tiddeman B p., Stirrat M r., Perrett D i. (2005) Towards Realism in Facial Image Transformation: Results of a Wavelet MRF Method. Comput Graph Forum 24:449–456. doi: 10.1111/j.1467-8659.2005.00870.x

van Asselt KM, Kok HS, Pearson PL, et al (2004) Heritability of menopausal age in mothers and daughters. Fertil Steril 82:1348–1351.

vanNoord PAH, Dubas JS, Dorland M, et al (1997) Age at natural menopause in a population-based screening cohort: The role of menarche, fecundity, and lifestyle factors. Fertil Steril 68:95–102.

Velde T, R E, Pearson PL (2002) The variability of female reproductive ageing. Hum Reprod Update 8:141–154. doi: 10.1093/humupd/8.2.141

Wheatley JR, Apicella CA, Burriss RP, et al (2014) Women's faces and voices are cues to reproductive potential in industrial and forager societies. Evol Hum Behav 35:264–271. doi: 10.1016/j.evolhumbehav.2014.02.006

Whittingham MJ, Stephens PA, Bradbury RB, Freckleton RP (2006) Why do we still use 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.

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Tables and figures captions

Table 1. *Effects of the different variables on the probability to be chosen during the test of attractiveness (male raters had to choose the woman found to be the most attractive between two facial photographs). N = 3439 observations (119 male raters and 68 female faces). Model 1 only includes the variable of interest (mother's age at menopause), and the control variables. Model 2 also includes cues of immediate fertility and facial ageing as explanatory 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†	0.217	0.053	4.129	< 0.001	***	0.240	0.053	4.516	< 0.001	***
WHR†	-	-	-	-		0.132	0.057	2.321	0.020	*
Facial femininity†	-	-	-	-		0.404	0.057	7.148	< 0.001	***
F0†	-	-	-	-		0.200	0.058	3.469	0.001	**
Age†	-0.204	0.053	-3.883	< 0.001	***	-0.271	0.058	-4.683	< 0.001	***
Facial ageing †	-	-	-	-		-0.563	0.060	-9.350	< 0.001	***
Smile†	0.335	0.053	6.364	< 0.001	***	0.271	0.058	4.662	< 0.001	***
Socio-economic status†	-0.067	0.052	-1.302	0.193		-0.170	0.057	-3.009	0.003	**
Raters' characteristics										
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	

†*For each of these variables, the difference between the two women presented was integrated into the model.*

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

Significance codes: *** p < 0.001; ** p < 0.01; * p < 0.05.

	Age	Mother's age at menopause	F0	WHR	Facial femininity	Facial ageing
Mother's age at menopause	0.07					
F0	-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*

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

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

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

Supporting Information

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

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

Figure S3. *Top*: Shape differences of a low expected reproductive value face (average face of the 7 women with the earlier expected age at menopause in our sample) relative to the average face (average of all the women's face in our study), on a Thin-Plate Spline (TPS) grid. *Bottom*: shape differences of a high expected reproductive value face (average face of the 7 women with the later expected age at menopause) relative to the average face. For both, the shape deformation has been magnified by 2. Figure created using R package Geomorph 3.0.3.

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
Raters' characteristics					
Age (year)	119	36.23	12.25	17	72
Socio-economic status (PCA coordinate)	119	0.02	0.72	-0.99	1.98

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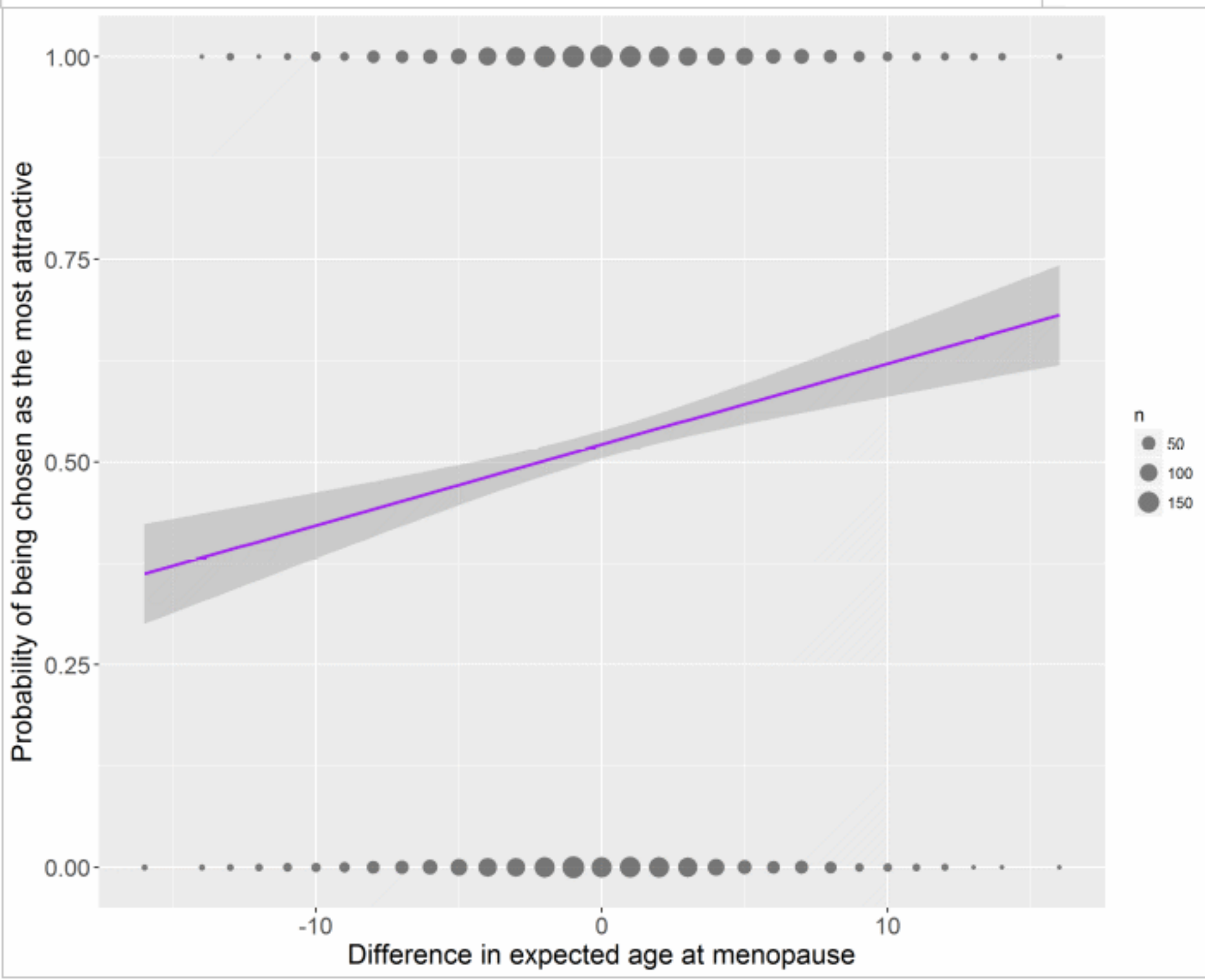
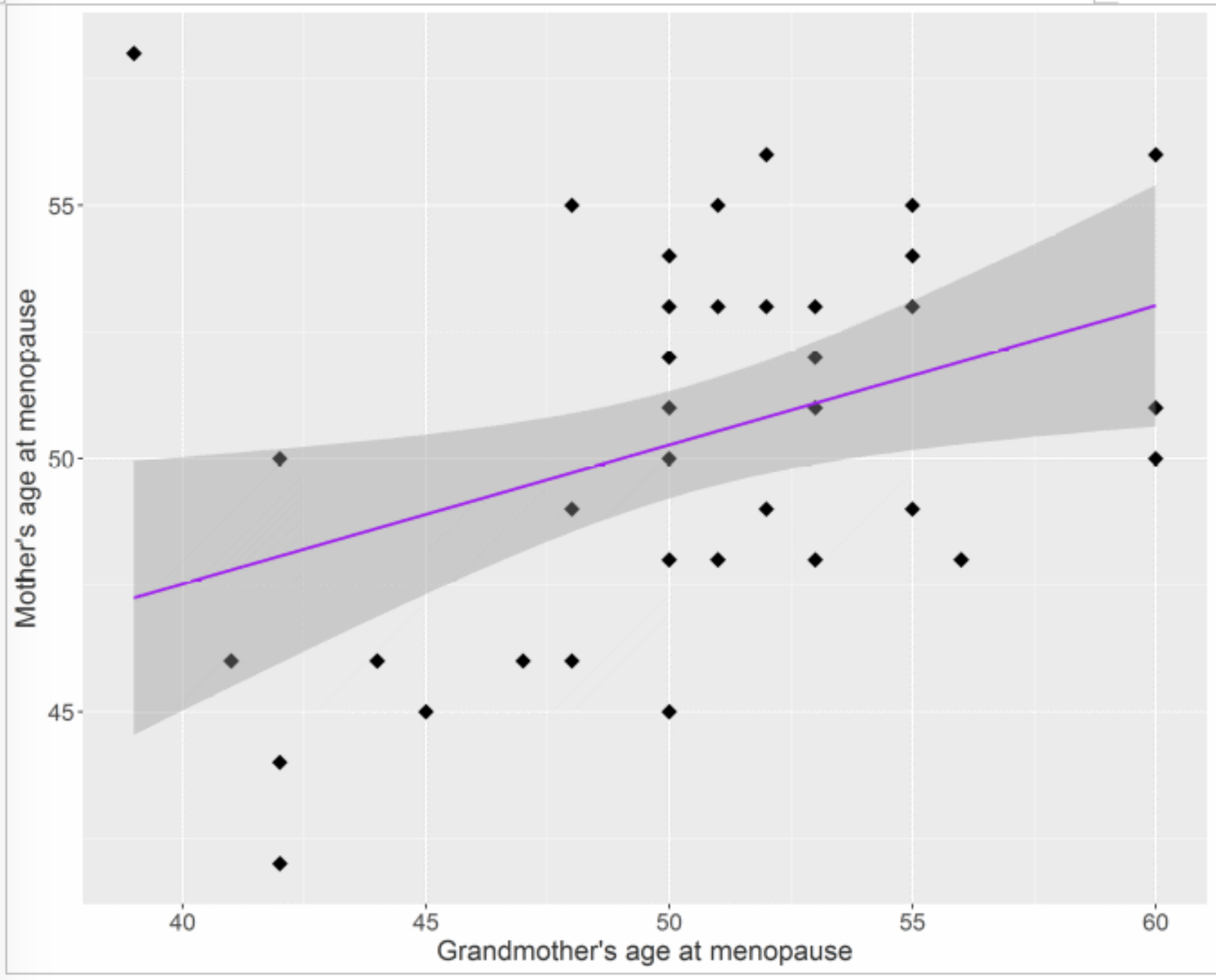
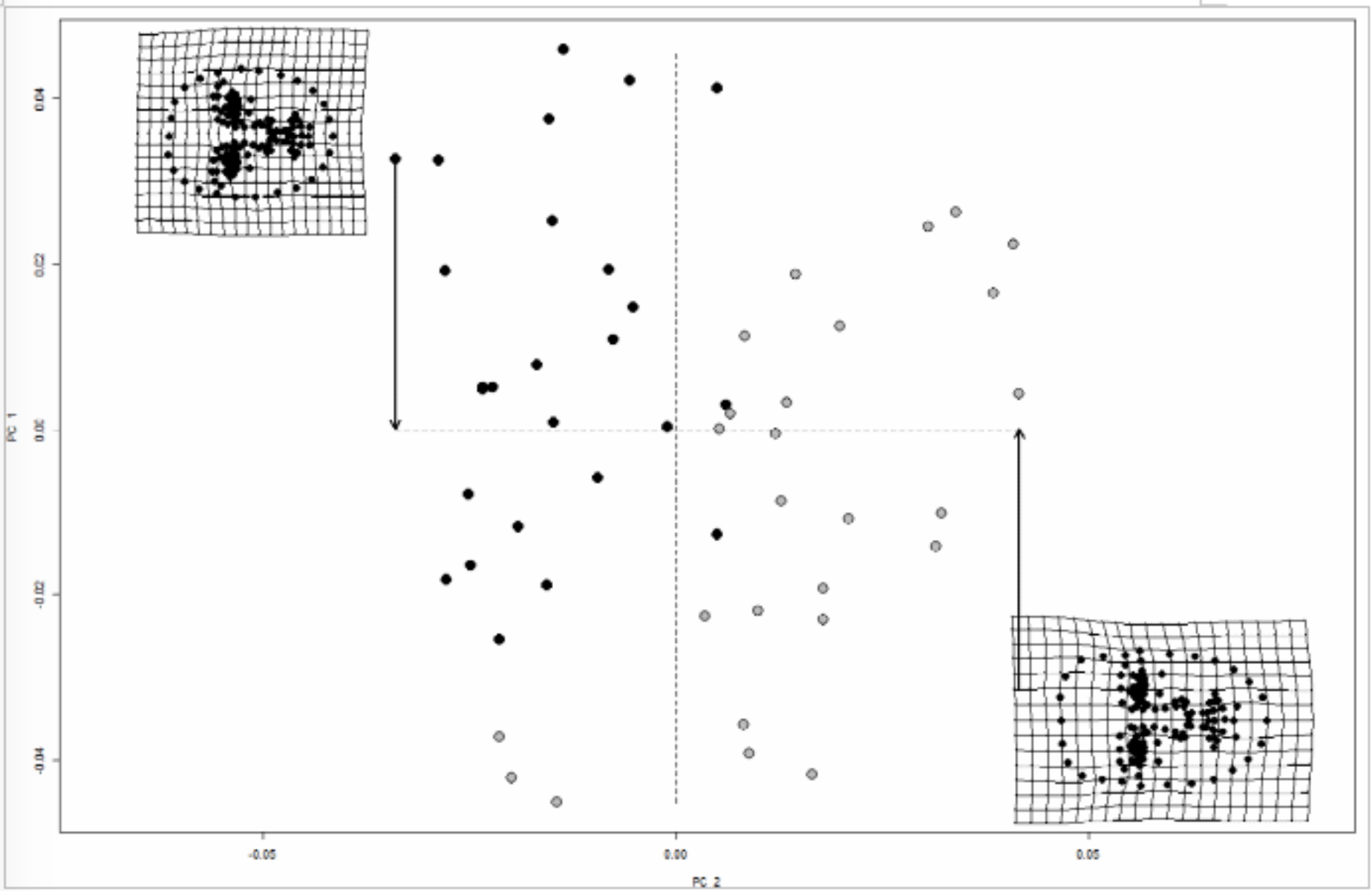

1.00
0.75
0.50
0.25
0.00
Probability of being chosen as the most attractive
-10
0
10
Difference in expected age at menopause
n
50
100
150


Mother's age at menopause
55
50
45
40
45
50
55
60
Grandmother's age at menopause


0.04
0.02
0.00
-0.02
-0.04
PC 1
-0.05
0.00
0.05
PC 2

Age:

28
29
30
31
32
33
34
35

Next

I know this person

How old is she ?