



Original Article

Advanced paternal age is associated with lower facial attractiveness



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ABSTRACT

In view of disease risk, Kong et al. (2012) demonstrated that most of the new mutations are explained by the age of the father at conception. Accordingly, paternal age effects have been found for a variety of offspring traits, from physical and mental health to intelligence. Here, we investigated whether facial attractiveness is significantly associated with paternal age. We used the Wisconsin Longitudinal Study ($n = 4018$ male and 4416 female high school graduates) to analyze the association between an individual's father's age at birth and that individual's facial attractiveness (estimated by rating the high school yearbook photographs from 1957), controlling for sex, age as well as mother's age. We find that subject's facial attractiveness decreased with advancing paternal but not maternal age, suggesting that facial attractiveness might be a cue of an individual's new mutation load.

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1. Introduction

In recent years, growing evidence shows that advanced paternal age at conception is linked with an increased risk of a wide range of neuropsychiatric disorders, including schizophrenia (Brown et al., 2002; Malaspina, 2001; Sipos et al., 2004), autism spectrum disorder (Hultman, Sandin, Levine, Lichtenstein, & Reichenberg, 2011; Reichenberg et al., 2006), bipolar disorder (Frans et al., 2008), and epilepsy (Vestergaard, Mork, Madsen, & Olsern, 2005) as well as Mendelian disorders (Crow, 2000) and aspects of physical health (Bray, Gunnell, & Smith, 2006). Higher paternal age also predicts lower intelligence (Cannon, 2009) and a higher risk of obesity (Eriksen, Sundet, & Tambs, 2013). This association of higher risk for disease and paternal but not maternal age is explained by the fact that women are born with their full supply of eggs, whereas men continue with sperm production throughout reproductive life (Crow, 2000). In the egg, all cell divisions are completed before birth, whereas the number of cell divisions and chromosome replications that sperm cells have gone through increase with the age at which the sperm is produced. As a consequence, a sperm undergoes many more germline cell divisions than an egg, the difference increasing with advancing age (Crow, 2000). Accordingly, Kong et al. (2012) demonstrated that a much higher number of mutations are transmitted by the father than the mother to their children, and that it is the age of the father which explains nearly all of the new mutations in a child.

A vast body of work has been published about cues, preferences and significance of facial attractiveness (e.g., Fink & Penton-Voak, 2002; Hume & Montgomerie, 2001; Rhodes, 2006; Thornhill &

Gangestad, 1999; Weeden & Sabini, 2005). Only little is known, however, about whether facial attractiveness has a genetic basis. Yet, two very recent papers by Mitchem et al. (2013) and Lee et al. (2013) showed heritable genetic influences on facial attractiveness, and Liu et al. (2012) reported on 5 genes influencing facial morphology.

This is the first study investigating whether facial attractiveness is associated with the father's age at conception, which would suggest that new mutations in the father's sperm are expressed in offspring attractiveness. This view is in line with mutation-selection balance theory and fitness-indicator theory. Mutation-selection balance theory proposes that a balance of forces between constantly arising mildly harmful mutations and selection causes variation in genetic quality and phenotypic condition (Keller, 2008; Miller, 2000). Mutation-selection balance is assumed to be particularly important in traits influenced by many genetic loci; this assumption is reasonable for a complex trait such as facial attractiveness because these traits provide a larger target size for mutations (Keller, 2008). Fitness indicator theory proposes that traits can function as reliable indicators of an individual's genetic quality and/or phenotypic condition. A fitness indicator serves as a signal of viability, fertility as well as genetic quality in terms of low mutation load and low genetic inbreeding, to potential mates, rivals, or allies (Arden, Gottfredson, & Miller, 2009; Haselton & Miller, 2006; Keller, 2008). Reliable fitness indicators cannot be faked because they are costly and demonstrate an ability to resist perturbations by genetic mutations and/or environmental hazards (Sefcck, Brumbach, Vasquez, & Miller, 2007).

In view of these hypotheses, we would expect that facial attractiveness is sensitive to mutations, and we therefore predict that facial attractiveness should decline with paternal age at conception. We analyzed the association of an individual's father's age at birth and that individual's facial attractiveness, controlling for sex, age as well as mother's age. We used the Wisconsin Longitudinal

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Table 1
Bivariate correlation matrix of key variables.

	Sex (1 = m, 2 = f)	Year of birth (1937–1940)	Father's age at subject's birth	Mother's age at subject's birth
Year of birth (1937–1940)	0.097***			
Father's age at subject's birth	0.021	0.047***		
Mother's age at subject's birth	0.037**	0.053***	0.773***	
Subject's facial attractiveness	−0.039**	0.026*	−0.074***	−0.035*

Values are Spearman R.

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

Study for these analyses because it is one of the most comprehensive longitudinal studies tracing the life of several thousand individuals. Moreover, the suitability of this dataset for research on attractiveness has been recently demonstrated (Jokela, 2009).

2. Material and methods

The Wisconsin Longitudinal Study (WLS) is a long-term study of a random sample of 10,317 men and women who graduated from Wisconsin high schools in 1957, born in the years 1937–1940. Yearbook photos from 1957, when the subjects were on average 18 years of age, were rated in 2004 and 2008 by judges recruited from roughly the same cohort as the WLS participants and thus aged between 63 to 91 years. Each yearbook photo was rated by six men and six women using a photo-labeled 11-point rating scale ranging from "not at all attractive" (=1) to "extremely attractive" (=11). With a Cronbach alpha value of 0.83, calculated based on the raw rating scores of the 12 raters, inter-rater reliability was good. The mean (SD) attractiveness raw score for all 12 raters was 5.5 (2.05) for male and 5.36 (2.13) for female subjects. As a measure of attractiveness, we used the mean of the "normed average coder rating" (further termed "facial attractiveness") from all 12 raters. According to Wisconsin Longitudinal, norming effectively removed coder fixed effects. Norming by Wisconsin Longitudinal was done by subtracting the mean from the original values and then dividing the resulting values by the standard deviation. We used the 2nd release of the rating data. Due to some minor errors in processing prior to this 2nd release, Wisconsin Longitudinal removed cases with less than 11 ratings and added approximately 5500 new cases in the 2nd release.

Additionally, we included the following variables, surveyed by the WLS, in the analyses: year of birth, sex (1 = male, 2 = female), as well as age of the subject's father (mean = 31.55, SD = 6.8) and mother (mean = 27.77, SD = 5.90) at the time of the subject's birth. To take into account potential effects of father's attractiveness (which we do not know) on subject's attractiveness, we divided father's age at subject's birth into two fractions, namely age at birth of the subject's eldest sibling (if there is any), and time span between birth of the subject's eldest sibling and birth of the subject ("time to subject's birth"). The reason is that, firstly, it may take longer for less attractive fathers to find a mate, so that they would start reproduction later compared to more attractive fathers. Secondly, attractiveness may to some degree be heritable. If both are true, then any association between father's age at subject's birth and subject's attractiveness could also reflect father's attractiveness.

We used SPSS 19 and R 3.0.2 for statistical analysis. In addition to bivariate Spearman correlations between the key variables, we calculated a general linear model (GLM), regressing the subject's father's and mother's age at time of the subject's birth, respectively, as

well as the subject's sex and year of birth (1937–1940) on the subject's facial attractiveness. To take into account potential confounding effects of father's attractiveness, we further calculated a GLM, regressing the subject's father's age at birth of the subject's eldest sibling, time to the subject's birth, as well as the subject's sex and year of birth on the subject's attractiveness. Initially, we included all two-way interactions with father's age at subject's birth and father's age at birth of the subject's eldest sibling and time to subject's birth, respectively, and then reduced the models stepwise by excluding all non-significant interactions. Sample sizes vary because some data are missing.

3. Results

The subject's facial attractiveness decreased significantly more strongly with increasing father's age at subject's birth than with increasing mother's age at subject's birth (Test of difference between correlated correlations, $t = 4.09$, $p < 0.001$) (Table 1, Fig. 1). In a multivariate model including both father's and mother's age at subject's birth as well as subject's sex and year of birth, only the effect of father's age at subject's birth remained highly significantly negative, whereas the effect of mother's age at subject's birth even turned significantly positive, subject's sex exerting a significant negative and birth year a significant positive effect (Table 2).

By splitting father's age at subject's birth into father's age at birth of the subject's eldest sibling and time to subject's birth, both father's age at birth of the subject's eldest sibling and time to subject's birth exerted significantly negative effects on graduate's attractiveness. In addition, sex exerted a significant negative and year of birth a significant positive effect (Table 3).

The results remained essentially unchanged by analyzing male and female subjects in separate models (Supplementary Online Material, Table S1 a, b, available on the journal's website at www.ehbonline.org). In both male and female subjects, facial attractiveness decreased significantly with advancing paternal age but increased marginally significantly with maternal age. In addition, in female but not in male subjects, facial attractiveness increased significantly with year of birth.

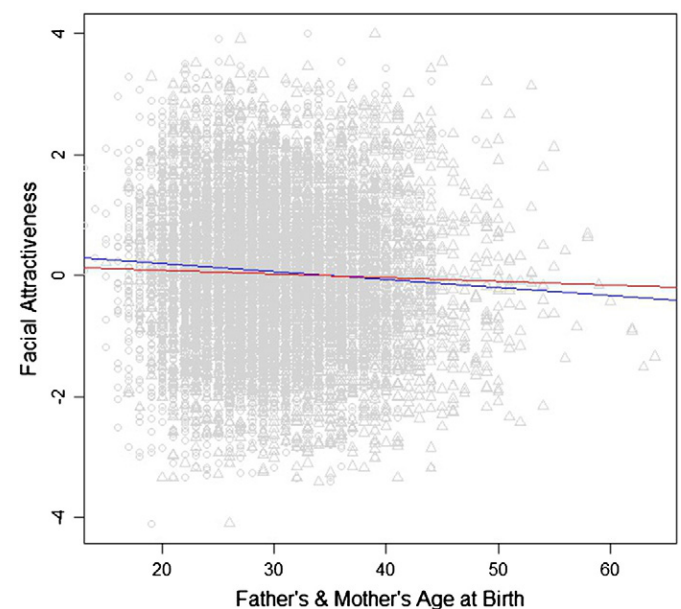


Fig. 1. Scatter plot and linear regression on subject's facial attractiveness of father's age at subject's birth (blue line, triangles; Pearson $r = -0.071$, $p < 0.001$) and mother's age at subject's birth (red line, circles; Pearson $r = -0.029$, $p = 0.038$).

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