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Timing of natural menopause covaries with timing of birth of a first daughter: Evidence for a mother–daughter evolutionary contract?

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ABSTRACT

Age at natural menopause is characterized by significant variability, but the factors responsible for this observed variation are still not well recognized. Humans are cooperative breeders and non-reproducing grandmothers play important roles in raising children. We propose an evolutionary "mother–daughter contract" hypothesis that suggests that the oldest daughter helps her mother to raise younger siblings but, in return, expects her mother to cease her reproduction, shifting energy and time once her daughter's children are born.

Data were collected by a questionnaire from 914 Polish post-menopausal women. From among those, 506 women, 44–98 years old, who had at least one child and who went through a natural menopause were included in the analysis. A woman's age at menopause was sensitive to the age at which she had her first daughter. The age of giving birth to the first daughter, even when she was not her first child, positively correlated with the age of the mother's menopause ($N = 332$, $p < 0.02$), while the age of giving birth to a first son did not have a statistically significant effect ($N = 332$, $p = 0.36$). Results of our study suggest that research on the menopausal transition should take into account mother–daughter relationships as potentially important determinants of the timing of menopause.

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Introduction

Women differ in the age at which they enter menopause, but only a limited number of factors responsible for this variation are recognized. Some reproductive and general lifestyle factors are associated with an earlier age at natural menopause, i.e. nulliparity and smoking (Sievert, 2006). Due to the fact that substantial variation remains unexplained, we are still not able to predict the reproductive lifespan for an individual (Coxworth and Hawkes, 2010).

Menopause is a phenomenon unique to humans – a universally occurring and complete cessation of fertility long before the end of life is unknown in any other species (Emery Thompson et al., 2007). Several hypotheses have been proposed to explain the appearance of menopause in the course of human evolution. Recently, the reproductive conflict hypothesis proposed that women exhibit an extraordinarily low level of generational reproductive overlap, much lower than is the case for females of other primates, to minimize reproductive competition between generations over resources in cooperatively breeding family (Cant and Johnstone, 2008; Lahdenperä et al., 2012).

In hunter–gatherers the mean reproductive overlap between generations is close to zero (Cant and Johnstone, 2008). In some societies, when a mother lives in the same household as her daughter, only one of them reproduces (Flinn, 1989). In pre-industrial Finns, overlapping reproduction of two generations of women was associated with up to 66% reduced survival of offspring from mothers of both generations (Lahdenperä et al., 2012), Moreover, Mace and Alvergne (2012) have shown that mothers cease reproduction when their daughters start to reproduce even if daughters do not coreside with their mothers. It is possible that this phenomenon of non-overlapping reproduction by two generations of women does not result only from cultural norms or a social suppression by other females, as previously suggested.

The grandmother hypothesis, an alternative hypothesis which explains the appearance of menopause and women's long postreproductive live span in the course of human evolution, focuses on intergenerational cooperation rather than competition. This hypothesis suggests that due to a diminishing probability of older women giving birth to a healthy child, a better strategy to transfer copies of their genes may be to cease direct reproduction and instead help raise grandchildren (Hawkes, 2003; Hill and Hurtado, 1991).

Humans are cooperatively breeding species and important roles in raising children are played by non-breeding helpers. Previous studies have shown that grandchildren primarily benefit from the presence and help of maternal rather than paternal grandmothers (for review see Sear and Mace, 2008). Therefore, we hypothesize that a woman's age at menopause should be sensitive to the age at which she gives birth to her first daughter. The earlier a woman has her first daughter, the earlier, on the average, this daughter enters the reproductive age and has offspring herself, therefore, the earlier a grandmother should cease her own reproduction. This paper does not attempt to explain the evolution of menopause or the evolution of a post-menopausal lifespan of human females, but points to an additional, previously unconsidered factor that may help to explain the variation in menopausal age. In addition, our paper contributes to understanding the phenomenon of extremely low levels of reproductive overlap between mothers and daughters observed in humans.

Materials and methods

We conducted a survey of 914 urban and rural women from Poland. Participating women answered a self-administered, anonymous questionnaire about their reproductive history and birthdates of their children. The age at menopause was considered the age of woman's last menstrual period followed by at least 12 months of amenorrhoea. We excluded 313 women who had surgical ($N = 119$) or other unnatural (i.e. radiation therapy, chemotherapy) causes ($N = 38$) of menstrual cessation, and/or reported using hormone replacement therapy ($N = 240$). It should be noted that some women had more than one reason for exclusion. In the remaining sample ($N = 601$), the mean age at natural menopause was 50.7 years, and the median age was 51 years. Non-parous women reported a significantly earlier mean age at natural menopause (mean 49.7 years; $N = 95$) than parous women (mean 50.9 years; Student's t-test, $t = 2.69$; $df = 558$; $p < 0.01$).

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The sample was further reduced to 465 women, aged 44–98 years (mean 68.3 years; $SD = 10.60$), to include only those who had children (mean 2.64; $SD = 1.84$). Mean age at birth of the first child was 24.4 years ($SD = 4.53$). Mean age at birth of a first daughter, regardless of birth order (that is, it was possible that a mother already had one or more sons before giving a birth to a daughter) was 25.8 years ($SD = 4.9$) and of a first son, regardless of birth order, was 25.7 years ($SD = 4.8$). All analyses were performed with Statistica version 10.0.

Results

In a simple linear regression model that included women who had at least one daughter, the age at birth of a first daughter, even when she was not a first child, was positively correlated with the age at menopause ($N = 332$, $\beta = 0.12$ years, $SD = 0.05$, $t = 2.21$, $p = 0.027$; *R2 for the model* = 0.02), with an earlier birth leading to the earlier menopause. The same type of model that included women with at least one son showed that the age at birth of a first son, regardless of birth order, did not have a statistically significant relationship with maternal menopausal age ($N = 332$, $\beta = 0.05$ years, $SD = 0.05$, $t = 0.91$, $p = 0.36$). There was also no significant relationship between the age at birth of a first child and the age at maternal menopause (simple regression model, $N = 456$, $\beta = 0.06$ years, $SD = 0.04$, $t = 1.45$, $p = 0.14$) Further, there was no statistically significant difference in the age at menopause between those women whose first child was a son (mean 51.0 years) or a daughter (mean 50.8 years, Student's t-test, $t = -0.46$; $df = 460$; $p = 0.65$).

In a subsequent multiple regression model that included women with at least one daughter and at least one son ($N = 241$), we found that only the age at birth of a first daughter, regardless of birth order, influenced the age of maternal menopause ($\beta = 0.17$ years, $SD = 0.07$, $t = 2.46$, $p = 0.014$). The age of giving birth to a first son did not have a statistically significant effect ($\beta = -0.034$ years, $SD = 0.07$, $t = -0.46$, $p = 0.64$; *R2 for the model* = 0.03). The relationship between the age at having a first daughter and the age at maternal menopause was still statistically significant when the birth year of the mother was added to the model ($N = 208$, age at birth of a first daughter: $\beta = 0.17$ years, $SD = 0.07$, $t = 2.40$, $p = 0.017$; age at birth of a first son: $\beta = -0.04$ years, $SD = 0.07$, $t = -0.61$, $p = 0.54$; year of birth of the mother: $\beta = -0.17$ years, $SD = 0.07$, $t = -2.50$, $p = 0.013$; *R2 for the model* = 0.06).

Discussion

Our results suggest that the age a woman gives birth to her first daughter is one of the determinants of the age at menopause. These findings could explain why reproductive overlap between generations is such a rare phenomenon (Cant and Johnstone, 2008). We interpret this as tentative evidence in favour of an evolutionary contract between a daughter and her mother.

A woman following a strategy of having a first daughter early in life acquires a valuable 'helper at the nest'. In some populations, the sole help of an older sister increases the survival probability of younger siblings (Sear and Mace, 2008). On the other hand, when first daughter enters the reproductive age it is beneficial for her reproductive success when her mother does not compete with her for resources, but ceases her own reproduction earlier and devotes time and resources to raising her grandchildren. In an alternative scenario, a woman following a strategy of having a first daughter later in life may lack help in raising children, but can reproduce longer herself.

The existence of the proposed mother–daughter contract is supported by research indicating an important role of maternal grandmothers in women's reproduction. In several populations, the presence of the maternal (but not paternal) grandmother shows a positive correlation with the survival and nutritional status of grandchildren (Sear et al., 2000; Sear and Mace, 2008). It is worth noting that this relationship is not universal, and that the positive impact seems to appear only when the grandmother herself is not reproducing (Sear and Mace, 2008).

The relationship observed in our study between age at giving birth to a first daughter and subsequent age at menopause, while statistically significant, explains a very low fraction of variation in menopausal age. In addition, we were not able to control for potentially confounding factors that are known to influence the age at menopause, such as smoking or socioeconomic status (Sievert, 2006). Several possible explanations may be provided in an attempt to understand the low explanatory power

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of our analyses. Firstly, help received by grandmothers when raising children may have been important in ancestral environments, but it is likely than in a modern setting, especially in contemporary populations with unrestricted access to nutritional resources, grandmothers do not have an important influence on grandchildren's well-being. Moreover, in modern societies where resources are easily accessible, competition between successive generations over resources becomes less intense, therefore, it is less important for mother–daughter reproductive scheduling. The presented finding could be just a remnant of past evolutionary strategies.

Secondly, it is possible that a mother–daughter contract functions only when a mother and her daughter reside together or at least have frequent physical contact. Unfortunately, information about co-residence and mother–daughter interactions was not available in our study. However, Mace and Alvergne (2012) have shown that mothers are willing to cease reproduction to avoid reproductive conflict and help their daughters reproduce even though they do not reside together. Finally, our results suggest that a woman's age at menopause tends to be sensitive to the age at which she gives birth to her first daughter rather than synchronized with this age. It is likely that a stronger correlation would be present between a woman's age at menopause and the age when her oldest daughter starts her own reproduction.

Proximately, menopause occurs when the number of follicles in the ovary declines below a threshold level, which depends both on initial number of follicles at birth and the rate of follicular atresia (Sievert, 2006). The rate of atresia is influenced by the ovarian environment created by chemical, immunological and hormonal factors. Potential mechanisms through which demographic, socioeconomic, lifestyle and reproductive factors influence ovarian environment and thus influence the rate of follicular atresia and, subsequently, age at menopause are not well understood (Jasienska, 2013).

In addition to factors related to adult life, developmental conditions, both during prenatal life and during childhood, have also emerged as potentially important determinants of menopausal age (Tom et al., 2010). Indeed, reproductive function in women, especially levels of reproductive hormones, seems to be under the influence of nutritional status during foetal (Jasienska et al., 2006a, 2006b, 2006c) and childhood periods (Núñez-de la Mora et al., 2007). Thus it is plausible that physiological and metabolic events occurring during development, including being pregnant with a female foetus, also influence the rate of follicular atresia. Interestingly, a female foetus affects the mother's physiology differently than a male foetus, as indicated by the observation that female foetuses have, on average, lower rates of intrauterine growth and that levels of human chorionic gonadotropin in maternal serum are significantly higher in the presence of a female foetus (Yaron et al., 2002).

The existence of physiological mechanisms leading to the menopausal transition in women in response to the onset of reproduction of their daughters has not been well documented. However, in many social species, including humans, the reproductive physiology of females can be influenced by other females in a group, which results in reproductive suppression (Clutton-Brock et al., 2006), or synchronization of menstrual cycles (McClintock, 1971). Sievert et al. (2001) suggested that the age at menopause might be also partially determined by the presence of other family members. Pheromonal influence by a husband living in the household has been suggested to account for frequently observed later age at menopause in married women. The study presented here cannot confirm our hypothesis, but our results suggest that research on determinants of menopausal transition should also include data on social and family interactions, especially mother–daughter relationships.

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