



## Original Article

# Did sexual selection shape human music? Testing predictions from the sexual selection hypothesis of music evolution using a large genetically informative sample of over 10,000 twins



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## ABSTRACT

Although music is a universal feature of human culture, little is known about its origins and functions. A prominent theory of music evolution is the sexual selection hypothesis, which proposes that music evolved as a signal of genetic quality to potential mates. The sexual selection hypothesis offers several empirically testable predictions. First, musically skilled and active individuals should have greater mating success than less-skilled individuals. Second, if musical ability functions as an indicator of genetic quality, it is expected to be associated with other traits putatively related to genetic quality. Third, associations as per the first and second predictions are expected to be at least partly due to overlapping genetic influences. We tested these predictions in a large genetically informative sample of 10,975 Swedish twin individuals aged between 27 and 54 years ( $M = 40.1$ ,  $SD = 7.7$ ), using musical aptitude and music achievement as measures of musical ability. To assess mating success we examined number of sex-partners, age of first intercourse, sociosexuality, and number of offspring. General intelligence, simple reaction time, and height were used to investigate relationships with traits putatively related to genetic quality. Twin modeling showed moderate genetic influences on musical aptitude for both sexes (heritability estimates were 38% for males and 51% for females). Music achievement was also moderately influenced by genetic influences in males (heritability = 57%), but the genetic influences were low and nonsignificant for females (heritability = 9%). Contrary to predictions, the majority of phenotypic associations between musical ability and music achievement with mating success were nonsignificant or significant in the other direction, with those with greater musical ability scoring lower on the measures of mating success. Genetic correlations between these measures were also nonsignificant. Most correlations of musical aptitude and music achievement with genetic quality measures were significant, including correlations with general intelligence, simple reaction time, and, in females, height (but only for aptitude). However, only the correlation between musical aptitude and general intelligence in men was significantly driven by overlapping genetic influences. Our findings provide little support for a role of sexual selection in the evolution of musical ability. Alternative explanations and limitations are discussed.

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## 1. Introduction

Music or musicality—"a natural, spontaneously developing trait based on and constrained by our cognitive system" (p. 4; [Honing & Ploeger, 2012](#))—is a universal feature of human culture which, in most cultures, developed independently and can be traced back more than 40,000 years (based on an old bone "flute" found in Slovenia; [Kunej &](#)

[Turk, 2000](#); [McDermott & Hauser, 2005a, 2005b](#)). Music forms part of many cultural events such as weddings and funerals, and individuals invest a considerable amount of time (and resources) in listening to music or learning to play an instrument. Further, music can evoke emotions and therefore has become a central part of the advertisement and entertainment industries ([DeNora, 2001](#)). However, despite its importance in human culture, little is known about the origins and functions of music. Why do humans make music although it appears not to aid survival? Why do humans spend resources (e.g. time, energy, money) on music which could be spent on more obvious contributions to fitness? While some argue that music may be a byproduct of more general purpose mechanisms, e.g. the auditory or language system ([Pinker, 1997](#)), others

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believe that music may be a biological adaptation (e.g. Darwin, 1871; Miller, 2000a), suggesting that music has evolved through natural or sexual selection.

### 1.1. Music as a biological adaptation

An important criterion for an adaptationist explanation of music, apart from being universal across cultures and history, is that aspects of music (e.g. skills involved in music perception and production) are genetically based, since adaptations are necessarily encoded in the DNA. Evidence shows that some basic cognitive components underlying musicality such as relative pitch, tonal encoding of pitch, beat induction and metrical encoding of rhythm may be universal and develop spontaneously and early during child development (for a detailed review see McDermott & Hauser, 2005a). Further, a common operationalization of music ability is sensory discrimination of auditory musical stimuli of various types (Seashore, 1960). Performance on such discrimination tests shows substantial associations with music practice and is consistently better among professional musicians compared to non-musicians (Schellenberg & Weiss, 2013). It recently has been shown that such auditory discrimination abilities—rhythm, melody and pitch discrimination—are moderately heritable suggesting that 50, 59, and 12–30% of the variance, respectively, could be explained by genetic influences (Ullén, Mosing, Holm, Eriksson, & Madison, 2014). Another study reported an even higher heritability of 80% for musical discrimination using the distorted tones test (DTT), which requires the participant to identify incorrect pitches from melodic stimuli (Drayna, Manichaikul, de Lange, Snieder, & Spector, 2001). In addition, genome-wide linkage and association studies have identified specific genetic polymorphisms apparently associated with musical aptitude (Oikkonen et al., 2014; Ukkola, Onkamo, Raijas, Karma, & Järvelä, 2009; Ukkola-Vuoti et al., 2013).

### 1.2. Sexual selection theory

A variety of functional hypotheses for the origins of musicality as an adaptation have been developed in recent years, such as enhancing parent and child bonding (Dissanayake, 2008), promotion of mental and social development (Cross, 2007), increasing social cohesion (Merker, 2000), or play beneficial to cognitive functions (music resulting from exaptation; Honing, 2011). The most prominent adaptationist theory of music evolution, though, is Darwin's (Darwin, 1871) sexual selection hypothesis—later refined by Miller (2000a)—suggesting that music has evolved for the purpose of signaling genetic quality to potential mates and thus increasing mating success. The theory is based on Darwin's well-established idea that bird songs function as (primarily male) courtship displays to attract sexual mates (primarily choosy females) (Darwin, 1871) and has proven the most useful hypothesis for understanding the functions of insect stridulation, bird, and whale song, and lots of other complex auditory signaling in other species. The sexual selection theory of music evolution (Miller, 2000d) proposes that genetic mutations accumulated over many generations (i.e. mutation load) have deleterious downstream effects on general functioning (Houle, 1998; Keller & Miller, 2006), and that cognitive ability is an especially sensitive indicator of mutation load because brain function depends on a very large proportion of the genome and will thus be affected by a large proportion of random mutations (Sandberg et al., 2000). As such, cognitive ability has been hypothesized to be a fundamental indicator of good genes (Miller, 2000c, 2000d). However, variation in cognitive ability (as measured by intelligence tests) is not directly observable, but can only be indirectly communicated through exhibition of complex behavior, such as music production (Miller, 2000a, 2000d). As such, the theory proposes that musical production has been used to advertise such traits and humans have evolved to utilize the information such display conveys about the performer (Miller, 2000a). Accordingly, musicality would be an indicator of high genetic quality promising indirect

benefits of mate choice in the form of genetic benefits to the offspring. Based on this framework, there are several predictions which can be tested.

### 1.3. Predictions of sexual selection hypothesis

First, if music production evolved as a sexual display, it follows that more musically skilled individuals should have quantitatively greater mating success (e.g. more sex-partners) than less-skilled individuals (Miller, 2000a). To the extent that women have been more choosy than men (see Stewart-Williams & Thomas, 2013 and commentaries for a discussion), the link between sexual display and mating success could be expected to be stronger in men. Second, if musical ability functions as display of cognitive ability and, more generally, of genetic quality, we expect positive associations of musical ability with cognitive ability and other traits putatively reflecting genetic quality, such as reaction speed and height (specifically for males; Stulp, Buunk, & Pollet, 2013). Third, the associations between musical ability and putative genetic quality traits are expected to be genetically based (i.e. positive genetic correlations) because each trait is an imperfect index of the same underlying “mutation load.” Further, if musical ability is causally influencing mating success because of its role as an indicator of genetic quality, a positive genetic correlation is expected between the two. This is because when a heritable trait (musical ability in this case) causally influences a second trait, the genes affecting the first trait will necessarily affect the second trait as well, resulting in a genetic correlation between the traits.

Here we test these predictions using a large genetically informative sample of Swedish twins.

## 2. Methods

### 2.1. Participants

The data were collected with two Web-based surveys from a large cohort of Swedish twins with approximately 32,000 twin individuals born between 1959 and 1985—the STAGE cohort (Lichtenstein et al., 2006). The first survey, conducted between 2005 and 2006, included questions about body height and sexuality (number of sex-partners, age at first intercourse) and had a total of 11,229 male and 14,096 female participants ( $M = 33.7$  years,  $SD = 7.7$ ; Långström, Rahman, Carlström, & Lichtenstein, 2010). The second survey was conducted between 2012 and 2013 (for further detail on this survey see Mosing, Madison, Pedersen, Kuja-Halkola, & Ullén, 2014; Ullén et al., 2014) and contained, among others, measures of musical ability, IQ and simple reaction time, as well as the Mini-K questionnaire and number of children (see below). Data from the first survey were matched to the participants of the second survey, i.e. participation in the second survey determined inclusion in the present study. The final sample consisted of 11,543 participants aged 27–54 at time of the second survey ( $M = 40.7$ ,  $SD = 7.8$ ) with a score for at least one of the traits studied here. Single twins were included as they contribute to the estimation of means and variances. Around 28% of the participants reported that they play or have played a musical instrument (including singing). Choir singing is commonly offered as an extra-curricular school activity in Sweden, and some schools offer in addition a basic orientation in instrumental playing. Further, 18% of the musically active reported having participated in special musical education also outside of school.

Zygosity was determined based on questions about intra-pair resemblance. In the STR, this method has been shown to be more than 98% accurate when zygosity status was confirmed using genotyping (Lichtenstein et al., 2002). For further details on the STAGE cohort and zygosity determination in the Swedish Twin Registry see Lichtenstein et al. (2002, 2006). The present study received approval from the Regional Ethics Review Board in Stockholm (Dnr 2011/570-31/5, 2012/1107/32, 2012/2172-32).

## 2.2. Measures

### 2.2.1. Measures of musical ability

**2.2.1.1. Musical aptitude.** Musical aptitude was measured using the Swedish Musical Discrimination Test (SMDT; Ullén et al., 2014). The SMDT consists of three sub-tests measuring pitch, melody, and rhythm discrimination. Internal consistencies and split-half reliabilities of the three subscales were excellent (0.79–0.89) and inter-correlations were moderate and positive ( $r$  values 0.27–0.41). For a more detailed description and psychometric validation see Mosing et al. (2014) and Ullén et al. (2014). The pitch test consisted of 27 trials presenting two successive tones that differed in pitch. The frequency of one of the tones was always 500 Hz, whereas the frequency of the other tone varied in the range 501–517 Hz. The participant indicated whether the second tone was lower or higher than the first. The melody test consisted of 18 trials with two isochronous sequences of four to nine tones. The pitch of one randomly selected tone was altered in the second stimulus (i.e. an A might be replaced by a C#), without altering the melodic contour of the sequence. The participant indicated which tone in the second sequence differed from the first. For rhythm (18 trials), the participant indicated whether two rhythmical sequences of five to seven tones (all with the same pitch) were the same or different. The two sequences in a trial differed in that one note was moved in time in the second stimulus as compared to the first stimulus or that a different starting point in the sequence was used. Number of correct trials for each domain was summed, resulting in a score for rhythm, melody, and pitch discrimination. Here, overall musical ability was taken as the mean of the standardized subscale scores (if participants had valid scores on all subtests).

**2.2.1.2. Music achievement.** Music achievement was measured using an adapted and translated version of the Creative Achievement Questionnaire (CAQ; Carson, Peterson, & Higgins, 2005), a self-report inventory addressing involvement in different arts and science domains. Here, only the music item was used which consisted of seven statements about music achievement, ranging from (1) 'I am not engaged in music at all' via (4) 'I have played or sung, or my music has been played in public concerts in my home town, but I have not been paid for this' to (7) 'I am professionally active as a musician and have been reviewed/featured in the national or international media and/or have received an award for my musical activities'. Given the very large sample size, the variable was analyzed continuously, despite only seven categories and a positively skewed distribution. Music achievement correlated moderately with musical aptitude ( $r = 0.47$ ).

### 2.2.2. Mating measures

**2.2.2.1. Lifetime number of sex partners.** Individuals were asked how many partners they had sexual intercourse with in their lifetime. Twins that were mostly homosexual (defined as having had only same-sex partners, or having had up to five opposite-sex partners with more than three times as many same-sex partners), were excluded from analyses.

**2.2.2.2. Age at first intercourse.** Individuals were asked how old they were when they first voluntarily had sexual intercourse.

**2.2.2.3. Sociosexuality.** Two items of the Swedish translation of the Mini-K, a 20 item short form of the Arizona Life History Battery (Figueroa et al., 2006) were used to estimate sociosexuality (orientation towards short-term versus long-term relationships). The items were: 'I'd rather have one than several sexual relationships at the same time' and 'I need to feel affection and closeness to someone before it feels good to have sex', rated on a seven point Likert scale, ranging from 'I disagree strongly' (1), over 'I don't know' (4), to 'I agree strongly' (7). The two response scores were reverse coded and summed.

**2.2.2.4. Number of children.** Individuals were asked how many children they have, with response options ranging from 1 (zero children) to 11 (ten or more children). Individuals under 40 years of age were classified as missing on this variable because of the higher chance they were yet to complete reproduction. It has previously been shown in a Swedish population study that an age cut-off of 40 gives a very good estimate of lifetime reproductive success and longer-range fitness (Zietsch, Kuja-Halkola, Walum, & Verweij, 2014).

### 2.2.3. Putative genetic quality traits

**2.2.3.1. Intelligence.** Psychometric intelligence (IQ) was measured with the Wiener Matrizen-Test (WMT; Formann & Piswanger, 1979). The WMT is a visual matrix test similar in construction to and correlating highly with Raven's standard progressive matrices ( $r = 0.92$ ) (Formann & Piswanger, 1979). Participants were given the recommended 25 minutes to complete the test. The WMT has been shown to have good reliability in both paper-and-pencil and online administrations (Cronbach's  $\alpha = 0.81$ ; Formann & Piswanger, 1979; Ullén et al., 2012). The test consists of 24 multiple choice items. Correctly answered items are summed to yield the test score.

**2.2.3.2. Simple reaction time.** Simple auditory reaction time was measured with a computer-based task in which participants were asked to press the space bar on their computer as fast as possible after hearing a cowbell sound. The response-to-stimulus intervals between consecutive trials varied randomly (rectangular distribution) between 2.5 and 4.0 s. Measured reaction times were corrected for variability pertaining to different software versions, including operating systems. For our analyses we took the median reaction time of 25 trials. Extreme outliers were treated as missing.

**2.2.3.3. Height.** Individuals were asked to indicate their body height in centimeters.

All continuous variables described above were standardized separately by sex and winsorized at three standard deviations from the mean. Also, the measures were corrected for potential mean effects of age in all analyses by including age as a covariate.

## 2.3. Statistical analyses

All analyses were conducted using maximum likelihood procedures in the statistical package Mx (Neale, Boker, Xie, & Maes, 2006), taking into account the relatedness of the sample. Variables were analysed as raw data. In maximum-likelihood modelling, the goodness-of-fit of a model to the observed data is distributed as chi-square ( $\chi^2$ ), and the number of unknown parameters (those to be estimated) is reflected by the degrees of freedom ( $df$ ). By testing the change in chi-square ( $\Delta\chi^2$ ) against the change in degrees of freedom ( $\Delta df$ ), we were able to test whether dropping model parameters, or constraining them to be equal, significantly worsened the model fit.

### 2.4. Testing predictions based on the sexual selection hypothesis

#### 2.4.1. Prediction 1. The association between musical ability and mating measures

Using maximum likelihood procedures, we tested whether musical aptitude and music achievement are associated with a mating advantage by determining their correlation with number of sex-partners and age at first intercourse. Note that age at first intercourse can only be affected by music achievement if individuals started playing an instrument before their age of first intercourse. In our sample, the mean age individuals started to play an instrument was 9.0 years ( $SD = 5.0$ ), considerably younger (on average 8.8 years,  $SD = 4.3$ ) than the mean age at first intercourse (we do not have information about when individuals started to play in public). Additionally we tested

whether a higher score on each of the two measures of musical ability is associated with higher sociosexuality (more orientated towards short-term relationships, which would be expected if musical ability can be used to increase number of partners), and having more children.

#### 2.4.2. Prediction 2. Musical ability as an indicator of genetic quality

We tested whether musical ability serves as a 'mental fitness indicator', i.e. an observable display that signals an individual's high-functioning brain and therefore high genetic quality, by determining whether musical aptitude and music achievement are correlated with general intelligence. In addition, we also tested whether these two measures of musical ability covaried with two other putative indicators of genetic quality, simple reaction time and height. Reaction time is an index of processing speed and has been found to be negatively correlated with general intelligence and increases from the age of 20 (Hultsch, MacDonald, & Dixon, 2002). Height is reduced by inbreeding (McQuillan et al., 2012; Verweij et al., 2014) and shares in part the same genes as IQ (Keller et al., 2013); both observations are consistent with height being related to genetic quality, though the evidence at this point is indirect.

#### 2.4.3. Prediction 3. Genetic overlap between musical ability and mating and genetic-quality measures

If musical ability is used as a sexual display and reflects high genetic quality, we would not only predict correlations between musical ability and the other genetic quality traits, but also that these correlations are partly due to overlapping genetic influences (i.e. underlying mutation load). If high musical ability (and associated low mutation load) caused greater mating success and more short-term orientation, this would also entail genetic correlations, i.e. between musical aptitude, music achievement and the mating measures.

By applying the classical twin design we determined the extent to which covariation of the two measures of musical ability with the mating measures and genetic quality indicators is due to overlapping genetic and/or overlapping environmental variance. In this way we obtained the correlation between the genetic influences on both traits (i.e. genetic correlation). In the classical twin design the variance in a trait and the covariance between traits are decomposed into additive genetic (A), shared environmental (C), and residual (E) influences. Additive genetic variance includes the influence of the summed allelic effects. Shared environmental variance results from environmental influences shared within twin pairs, making twins more similar to each other (e.g. home environment and socioeconomic status). Residual variance represents variance not shared within twin pairs (including idiosyncratic experiences, stochastic biological effects, but also measurement error).

Partitioning of variance into genetic and environmental components can be achieved because identical (monozygotic, MZ) twins share 100% of their genes, whereas non-identical (dizygotic, DZ) twins share on

average 50% of their segregating genes. Therefore if A were the only source of variance in a trait we would expect a twin correlation of 1 for identical pairs and 0.5 for non-identical pairs. In contrast, if C were the only source of variance in a trait, we would expect a twin correlation of 1 for both identical and non-identical pairs. Finally, if all variance were due to E we would expect a twin pair correlation of 0 for both identical and non-identical twin pairs. Hence, A, C, and E influences predict different patterns of MZ and DZ twin pair correlations, and structural equation modeling can be used to determine which combination best matches the observed data.

Using bivariate twin models, the cross-twin cross-trait correlations (e.g. correlation between musical aptitude of one twin and IQ of the other twin) enable the partitioning of the covariance between traits into A, C, and E in the same way as for the variance in a single trait. Accordingly, we estimated the extent to which the observed correlation between variables is due to overlap in genetic influences, shared environmental influences, or residual factors. Additional information on the classical twin design can be found elsewhere (Neale & Cardon, 1992; Posthuma et al., 2003).

We first fitted univariate twin models to the musical ability, mating and genetic quality measures to determine the proportion of variance accounted for by A, C, and E influences. We then ran bivariate models to look at the contribution of A, C, and E to the correlation between the musical ability measures and the other variables of interest (note that this was done only if the phenotypic correlation between the measures was significant). We report the genetic correlation ( $r_A$ ), which measures the overlap in the genetic influences on each trait. A genetic correlation of zero indicates no overlap in genetic variance and a genetic correlation of 1 indicates complete overlap. Note that a high genetic correlation does not necessarily imply that genes explain a large proportion of the covariation between the two traits, as the latter is also a function of the heritabilities of the two traits (see supporting information in Zietsch et al. (2014): 'Using the classical twin design to decompose the covariance between two traits'). For that reason we also report the bivariate heritability, which is the contribution of genetic influences to the phenotypic correlation between the traits. For example, a phenotypic correlation of 0.6 could be made up of a genetic contribution of 0.2 (bivariate heritability), a shared environmental contribution of 0.1 and a non-shared environmental contribution of 0.3. Variance components were estimated separately for males and females. In all analyses age and sex effects on the means were taken into account.

### 3. Results

#### 3.1. Descriptive statistics

After excluding twins with unknown zygosity ( $n = 368$ ), and twins which were mostly homosexual ( $n = 200$ ), the study sample contained

**Table 1**  
Descriptive statistics.

	Males ( $n = 4609$ )			Females ( $n = 6366$ )			Sex-difference	
	$n$	$M$ (SD)	Range	$n$	$M$ (SD)	Range	Cohen's $d$	$p$ -Value
Musical aptitude <sup>a</sup>								
Rhythm	2747	15.4 (2.2)	4–18	3780	15.3 (2.2)	5–18	0.08	<0.01
Melody	2704	6.8 (3.0)	0–18	3734	6.6 (2.8)	0–17	0.06	0.03
Pitch	2670	18.7 (5.1)	1–27	3700	17.8 (4.6)	1–27	0.18	<0.001
Music achievement	2685	2.0 (1.5)	1–7	3800	2.1 (1.4)	1–7	−0.07	<0.001
Number of sex-partners	2876	9.7 (21.1)	0–500	4503	6.6 (7.5)	0–100	0.20	<0.001
Age at first intercourse	2908	18.1 (3.3)	8–38	4935	17.4 (2.8)	11–39	0.24	<0.001
Sociosexuality	3259	6.0 (3.2)	2–14	4579	4.4 (3.0)	2–14	0.50	<0.001
Number of children	1801	1.8 (1.2)	0–10 <sup>b</sup>	2563	1.9 (1.1)	0–10 <sup>b</sup>	−0.05	0.03
IQ	3361	13.6 (5.4)	0–24	4693	12.3 (5.1)	0–24	0.25	<0.001
Simple reaction time (ms)	2803	239.2 (47.5)	106–490	3873	243.8 (47.0)	107–499	−0.10	<0.001
Height (cm)	3725	181.0 (6.8)	145–205	5648	167.1 (5.9)	137–197	2.18	<0.001

Note.  $M$  = mean;  $SD$  = standard deviation. Significance of mean differences between the sexes was tested using a  $t$ -test in IBM-SPSS version 22.

<sup>a</sup> The Musical ability variable is a composite measure of standardized scales scores of rhythm, melody and pitch. Therefore we provided the descriptives only for the separate sub-tests.

<sup>b</sup> Note there was one male and one female with 10 or more children; we treated their value as 10.



**Table 2**

Phenotypic correlations (95% confidence intervals) of musical aptitude and music achievement with number of sex partners, age at first intercourse, sociosexuality and number of children.

	Musical aptitude		Music achievement	
	Males <i>r</i> (95% CIs)	Females <i>r</i> (95% CIs)	Males <i>r</i> (95% CIs)	Females <i>r</i> (95% CIs)
Number of sex-partners	0.02 (−0.03; 0.07)	0.00 (−0.04; 0.04)	−0.01 (−0.06; 0.03)	−0.07 (−0.10; −0.03)***
Age at first intercourse	0.07 (0.02; 0.11)**	0.12 (0.09; 0.16)***	0.04 (0.00; 0.08)	0.17 (0.13; 0.20)***
Sociosexuality	−0.09 (−0.12; −0.05)***	−0.11 (−0.14; −0.08)***	−0.05 (−0.08; −0.01)*	−0.10 (−0.13; −0.07)***
Number of children	0.04 (−0.01; 0.09)	−0.02 (−0.06; 0.03)	0.09 (0.04; 0.14)***	0.01 (−0.03; 0.05)

\*  $p < 0.05$ .\*\*  $p < 0.01$ .\*\*\*  $p < 0.001$ .

10,975 individuals. This included 2759 complete twin pairs (818 MZM, 450 MZF, 481 DZM, 303 DZF, and 707 DZ-opposite sex (DZOS) pairs) and 5457 single twins whose co-twin did not participate (795 MZM, 898 MZF, 822 DZM, 912 DZF, 779 DZOS-M, and 1251 DZOS-F twin individuals). Note that sample sizes differ per variable, see Table 1. Fifty-eight percent of the sample was female and the mean age was 40.7 years ( $SD = 7.7$ ). 21.5% of the males and 24.9% of the females had played music in public (either paid or unpaid), corresponding to a score of 4 or higher on the music achievement scale. Sample descriptives for all variables (before standardizing and winsorizing) as well as the standardized effect size of the sex difference can be found in Table 1. Sex differences, especially on the music measures, are mostly (very) small [see Hyde (2014) for a review of sex-differences in human behavior]. Males scored somewhat higher than females on the musical aptitude subtests, but females scored a little higher on Music Creative Achievement (Cohen's  $d$  between 0.06 and 0.18). Furthermore, males performed better than females on the IQ and reaction time tests, and reported more sex-partners, fewer children, and a higher age at first intercourse (Cohen's  $d$  between 0.05 and 0.25). The largest sex-differences were found for sociosexuality and height, with males scoring substantially higher (Cohen's  $d = 0.50$  and 2.18, respectively).

### 3.2. Testing predictions based on the sexual selection hypothesis

#### 3.2.1. Prediction 1. The association between musical ability and mating measures

Phenotypic correlations are shown in Table 2. Consistent with predictions, men with higher music achievement had more children; however, this association was not found for men with higher musical aptitude and there were no significant associations of the two musical ability measures with number of children in women. All other associations were either not significant (i.e. musical aptitude with number of sex partners in both sexes and music achievement with number of sex partners and age at first intercourse in males), or they were in the opposite direction to predictions (i.e. significant negative correlations of the two musical ability scales with sociosexuality in both sexes; positive correlations of musical aptitude with age at first intercourse in males and females; and significantly fewer sex partners and a higher age at first intercourse in musically high achieving women).

#### 3.2.2. Prediction 2. Musical aptitude as an indicator of genetic quality

Consistent with predictions, there were significant positive correlations of musical aptitude and music achievement with general intelligence as well as negative correlations with simple reaction time (Table 3). There was also a significant positive correlation between musical aptitude and height for women, but not for men. Associations between music achievement and height were not significant in either sex.

#### 3.2.3. Prediction 3. Genetic overlap between musical ability and mating and genetic-quality measures

Before modeling the A, C, and E variance components, we tested the effects of age and zygosity on the means and variances ( $\alpha = 0.01$ ) and estimated the twin pair correlations for each of the traits (see Supplementary Material—Genetic modeling—Preliminary analyses, and Supplementary Table S1, respectively). For each trait, the MZ twin pair correlations were higher than the corresponding DZ twin pair correlations, suggesting genetic influences on the traits. The opposite-sex twin pair correlations were significantly lower than the DZ same-sex twin pair correlations for musical ability ( $\chi^2_1 = 8.60$ ,  $p < 0.01$ ) and age at first intercourse ( $\chi^2_1 = 19.81$ ,  $p < 0.001$ ), indicating differences in the source of genetic and/or shared environmental variation in males and females. For this reason we did not include opposite-sex twins in subsequent genetic modeling, as we are unable to determine whether it is the genetic and/or the shared environmental effects that differ between sexes.

In line with the sexual selection hypothesis of music and consistent with previous studies (Drayna et al., 2001; Ullén et al., 2014), univariate modeling showed that musical aptitude is moderately heritable (38% for males and 51% for females). Music achievement was also moderately heritable for males (57%), but the heritability for females was low and nonsignificant (9%). Shared environmental influences also played a role in musical aptitude (33% for males and 20% for females), and music achievement (13% for males and 46% for females). All other variables were also partly influenced by genes, although the heritability estimates were not significant for sociosexuality in either sex, nor for number of children or simple reaction time in males. Estimates of the A, C, and E variance components for all variables can be found in Supplementary Table S2.

Table 4 shows the genetic correlations as obtained from the bivariate twin models, as well as the bivariate heritabilities. Musical aptitude was

**Table 3**

Phenotypic correlations (95% confidence intervals) of musical aptitude and music achievement with putative genetic-quality indicators (IQ, simple reaction time, and height).

	Musical aptitude		Music achievement	
	Males <i>r</i> (95% CIs)	Females <i>r</i> (95% CIs)	Males <i>r</i> (95% CIs)	Females <i>r</i> (95% CIs)
IQ	0.37 (0.33; 0.40)***	0.33 (0.30; 0.35)***	0.15 (0.11; 0.18)***	0.16 (0.13; 0.19)***
Simple reaction time	−0.10 (−0.14; −0.06)***	−0.09 (−0.12; −0.06)***	−0.05 (−0.09; −0.01)**	−0.05 (−0.08; −0.01)**
Height	0.03 (−0.01; 0.07)	0.06 (0.03; 0.10)***	0.01 (−0.03; 0.06)	0.01 (−0.02; 0.04)

\*\*  $p < 0.01$ .\*\*\*  $p < 0.001$ .

**Table 4**  
Genetic correlations ( $r_A$ ) and bivariate heritabilities ( $Biv h^2$ ) of musical aptitude and music achievement with measures of mating success and putative indicators of genetic quality.

	Musical aptitude						Music achievement					
	Males			Females			Males			Females		
	$r_A^a$	$Biv h^2$	$p$ -Value	$r_A^a$	$Biv h^2$	$p$ -Value	$r_A^a$	$Biv h^2$	$p$ -Value	$r_A^a$	$Biv h^2$	$p$ -Value
Number sex-partners <sup>a</sup>	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.06	0.01	0.80
Age of first intercourse	−0.12	−0.05	0.70	−0.06	−0.03	0.75	NA	NA	NA	0.29	0.06	0.46
Sociosexuality	−0.66	−0.17	0.10	0.98	0.07	0.27	−0.10	−0.03	0.88	−0.09	−0.01	0.82
Number of children	NA	NA	NA	NA	NA	NA	0.41	0.14	0.19	NA	NA	NA
IQ	0.56	0.24	<0.01	0.31	0.14	0.05	0.12	0.06	0.50	0.77	0.14	0.06
Simple reaction time	−0.63	−0.18	0.07	−0.12	−0.04	0.58	0.09	0.03	0.73	0.80	0.11	0.20
Height	NA	NA	NA	−0.03	−0.02	0.87	NA	NA	NA	NA	NA	NA

Parameters were only estimated when there was a significant phenotypic correlation between the two traits (otherwise NA).

<sup>a</sup> Note that a genetic correlation can be high without explaining a significant part of the phenotypic covariation between two variables (as indicated by the bivariate heritability and the  $p$ -value).

genetically correlated with IQ ( $p < 0.01$  and  $p = 0.05$  for males and females). None of the other genetic correlations were significant. [The shared environmental ( $r_C$ ) and residual ( $r_E$ ) correlations can be found in Supplementary Table S3].

#### 4. Discussion

The sexual selection hypothesis of music evolution proposes that music has evolved for the purpose of signaling genetic quality to potential mates and increasing mating success. This is the first study empirically testing several predictions based on this hypothesis using a genetically informative sample.

The first prediction was that, if music production evolved as sexual display, musically skilled individuals would have a mating advantage compared to musically less skilled individuals. We found that, consistent with our expectations, men with higher scores on the music achievement scale had more children. However, all other associations between musical ability and the mating measures were either nonsignificant or were significant in the opposite direction to predictions: females who scored higher on music achievement had fewer sex-partners, and males and females with higher scores on the aptitude test, and females with higher achievement scores, had a higher age at first intercourse. Finally, males and females who scored higher on the musical aptitude or music achievement measures scored lower on sociosexuality. Importantly, genetic correlations between musical aptitude and the measures of mating success were all nonsignificant.

Next, we tested predictions regarding the feasibility of musical ability being an indicator of genetic quality. The most straightforward prediction here is that musical ability should be phenotypically and genetically correlated with intelligence, which has been hypothesized to be a fundamental indicator of good genes (Miller, 2000b). This reasoning assumes that musical ability depends on general intelligence and its underlying genetic variation; consistent with this we confirmed that musical aptitude is moderately heritable and is phenotypically and genetically correlated with intelligence (although the genetic correlation in females did just not reach significance, with a  $p$ -value of 0.05). However, music achievement was only significantly heritable in males and although positive phenotypic correlations with IQ were significant, genetic correlations were not (for either sex). Further, mutation load is thought to have deleterious downstream effects on various fitness-increasing traits, since mutations tend to disrupt the optimal development of the organism. As such, different traits reflecting mutation load are expected to correlate positively with respect to fitness. Simple reaction time and height are potentially two such traits, hence the predictions that they would be significantly phenotypically and genetically correlated with musical ability. Although we found the predicted correlations of musical aptitude and music achievement with reaction time (both sexes) and of musical aptitude with height (only in females), we did not detect significant genetic components to these correlations.

Whether this is due to insufficient power or the true absence of genetic correlations is unclear.

Although basic musical skill is associated with general cognitive ability (which is in line with previous findings; Lynn, Wilson, & Gault, 1989; Schellenberg & Weiss, 2013) and may therefore serve as a mental fitness indicator, our findings show that higher musical aptitude or achievement does not lead to increased sexual success (quantitatively). However, there are other possible explanations that are at least partly in line with our findings and to some extent still consistent with the sexual selection hypothesis. First, given the importance of mutual mate choice (Stewart-Williams & Thomas, 2013), pair-bonding, and bi-parental investment in humans, it could be that more musically skilled individuals attract higher quality sex partners (rather than greater quantity; Miller, 2013; Stewart-Williams & Thomas, 2013). Second, it has been suggested that women may make trade-offs in mating along two dimensions—good gene fitness indicators (as suggested above) but also good investment indicators (Gangestad & Simpson, 2000), the latter including resource acquisition potential but also warmth, emotional stability and kindness—potential indicators of being a ‘good dad’ or a ‘good partner’ (Buss & Shackelford, 2008; Miller, 2013). Rather than musical ability being a good genes indicator, it may serve as a good-dad or good-partner indicator signalling discipline, conscientiousness, and openness (traits known to predict music practice; Corrigan, Schellenberg, & Misura, 2013) and potentially emotional stability or kindness (playing an instrument has been associated with emotional competence; Theorell, Lennartsson, Mosing, & Ullen, 2014). Both explanations are in accordance with the mutual mate choice model rather than the male compete/females choose model and emphasize long-term mating and mate quality over quantity (Stewart-Williams & Thomas, 2013), which would be in line with our findings of more offspring (but not more sex-partners) in musically high achieving males and a stronger focus towards a long-term partner in higher skilled and achieving individuals (lower sociosexuality). However, the first explanation would still regard musical ability as an indicator of high genetic quality, which is in line with our finding of a significant genetic correlation of musical aptitude and IQ, but not with the nonsignificant genetic associations between musical aptitude and reaction time and height and between music achievement and all three genetic fitness indicators. The second explanation does not necessarily suggest superior genetic quality but rather increased fitness through superior parenting investment/skills. If true, this would imply that common genetic mechanisms underlie the—at least in males—present phenotypic correlation between music achievement and number of children. However, we did not find a significant genetic correlation between these variables. Also, there was no significant association between musical aptitude and number of children. This suggests that although both explanations fit our data better than the sexual selection hypothesis under the males compete/women choose model (lending support to the mutual mate choice model), neither of them perfectly can explain our findings. To further

test these explanations and sexual selection in a mutual mate choice society, future studies would need to establish whether musically talented individuals indeed (i) possess superior parenting skills/show higher parental investment and (ii) attract higher quality mates. Investigating this would require information also on fitness indicators of the participants' partners.

However, our finding that higher musical ability does not lead to increased sexual success are also compatible with the idea that musicality may not be a direct target of selection, but rather may be co-opted from mechanisms that evolved for other functions that were more directly selected for (i.e. music as a by-product rather than a direct product of selection) as suggested by Pinker (1997) and Patel (2010). This would be in line with the finding that most if not all brain areas involved in music serve other purposes as well (for a review see Marcus, 2012b). One such function which has been selected for could be language. Musical aptitude has been shown to be correlated with linguistic abilities, such as phonological awareness, pronunciation, and reading, even when controlling for general intelligence (Milovanov & Tervaniemi, 2011; Schellenberg & Weiss, 2013). Further, many studies have shown that there is overlap between the regions of the brain that process speech and those that process music (Koelsch et al., 2004; Peretz & Zatorre, 2005; Zatorre & Gandour, 2008).

There are several limitations to the study. First, the predictions were tested in a modern developed society that is unlike those of our evolutionary history. In today's society occupational roles are highly specialized and mass communication (radio, TV, internet, portable media players and CDs etc.) allow for very wide distribution of music so that a small number of exceptional musicians can reach an extremely large number of listeners. As such, the competition and incentive structure for learning and performing music are very different to the kind of circumstances in which music probably evolved. Also, it is unclear to what extent number of children or number of sex-partners of individuals in modern societies (with birth control, family planning, assisted conceptions, and low birth and death rates) reflects fitness as it would have manifested in ancestral societies. Further, based on the number of children question we could not distinguish between adopted and biological children, which may introduce some small error to the variable.

Second, here we tested basic auditory musical aptitude (sensory discrimination of musical stimuli) rather than objective measures of performance skills (i.e. playing an instrument or singing). Successfully playing a musical instrument (or singing) clearly requires more than just auditory skills (although auditory skills are essential for any musician), such as (1) the understanding and interpretation of auditory input or feedback of the music/notes heard, (2) representation of the notes the musician wants to play, (3) the representation of those notes on the instrument played, and (4) fine motor control of finger movements in time and space to produce the required sounds (Marcus, 2012a). Unfortunately we did not have measures of all these skills available. Further, it could be that only a successful combination of all these skills including the willingness to practice and display them (in public) would lead to an increase in mating success. Although our measure of music achievement should provide an indication of musical ability and the willingness to show off one's skills, we did not have an objective measure of their music production ability. However, given that a large and genetically informative sample is needed to test many of the hypotheses of the sexual selection theory it would be hard to derive objective ratings of musical ability in terms of music production and popularity. More generally, for the majority of the variables we used in this study we relied on self-report data, which is subject to response-biases such as socially desirable responding.

In line with this, because we used an existing dataset we had to work with the variables available from the sample, which were not always optimal for the hypotheses we tested here. Future studies should include more targeted measures of musicality and musical success as well as mating and genetic quality measures to replicate our findings and test other predictions based on the sexual selection hypothesis of

music evolution. Measures of parental investment as well as of potential fitness indicators of partners should be included. Finally, the methods applied here illustrate how future studies can illuminate sexual selection hypotheses about other mental fitness indicators and establish further whether sexual selection might indeed work through increasing mating success in term of quality rather than quantity. However, it is also important to keep in mind that the explanations mentioned above are not mutually exclusive.

In summary, the present study is the first to test several predictions based on the sexual selection hypothesis of music evolution in a genetically informative sample. The findings provided little support for a role of sexual selection in the evolution of music. Individuals with higher musical ability were generally not more sexually successful (at least not quantitatively), although men scoring higher on the music achievement scale did have more offspring. Musical aptitude was correlated with other potential indicators of fitness, such as general intelligence, simple reaction time, and—for females—height. However, the genetic components of these associations were not significant with the exception of the genetic covariation between musical aptitude and general intelligence. The evolutionary basis of music remains unclear. Future studies are needed to test alternative characterizations of the sexual selection hypothesis as well as other theories of music evolution.

### Supplementary Materials

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.evolhumbehav.2015.02.004>.

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