Total sexual selection on men's voices

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Abstract

Previous correlational research indicates sexual selection in the evolution of vocal masculinity. There is a lack of experimental research on pitch variation when compared to two other sexually dimorphic vocal parameters- pitch and formant structure. We experimentally manipulated male pitch variation. Pitch variation is quadratically related to perceptions of attractiveness and dominance. We report a larger body of correlational research examining the relationships between pitch, pitch variation, and formant position with both attractiveness to women and dominance to men in naturally occurring speech. Pitch is linearly and formant position is quadratically related to attractiveness. Pitch and formant position linearly predict dominance. Pitch variation does not predict sexual selection relative to pitch and formant position.

Introduction

The human voice is well-suited to study the relative contributions of mate choice and contest competition mechanisms of sexual selection. The human voice shows large sexual dimorphism (differences between men and women) - as it relates to the vocal parameters of pitch (fundamental frequency or F0), formant position (timbre), and within-utterance standard deviation of pitch (F0-SD)(see (D.A. Puts, Apicella, & Cardenas, 2011) for F0-SD dimorphism)(Hodges-Simeon, Gaulin, & Puts, 2010a). Mating success is associated with vocal characteristics(Hodges-Simeon et al., 2010a). A 2005 paper, demonstrated within a North American sample that men with lower voice pitch self-reported more sexual partners in the last year (David A. Puts, 2005). In the Hadza, men with lower voice pitch reported a higher number of surviving offspring (Apicella, Feinberg, & Marlowe, 2007).

Voice traits are implicated in both mate choice and contest competition (Hodges-Simeon et al., 2010a). Male mate choice was probably central in women's mating competition, especially since ancestral females could not constrain the choices of larger and more aggressive males (David A. Puts, 2010).Therefore, female voices have been

primarily shaped by male preferences (D.A. Puts, Barndt, Wlling, Dawood, & Burriss, 2011).

By contrast, intrasexual competition may have been a more salient factor in the evolution of male vocal traits (David A. Puts, 2010). For instance, in a 2011 paper, dominant linguistic content predicted mating success, however, attractive linguistic content did not (Hodges-Simeon et al., 2010a). Men's traits are better designed for contest competition than for other mechanisms of sexual selection and contest competition overrides other mechanisms of sexual selection (David A. Puts, 2010). If men can exclude competitors from mating opportunities by force or threat of force, there is no opportunity for other mechanisms, such as mate choice, to occur.

While mate choice and contest competition usually favor the evolution of different traits, over the course of human evolution male monopolization of females was imperfect. This allowed other mechanisms, such as female mate choice to also contribute in shaping men's traits (David A. Puts, 2010). This may explain why many male traits that seemed designed for combat such as strength and muscularity are also favored by women (Hodges-Simeon et al., 2010a). However, even when a trait is favored under both mechanisms of selection, it will typically have a greater impact on one or the other, suggesting the primary selection pressure in the evolution of that trait. For instance, masculine musculature, voice, and facial features have a greater impact on contest competition (as measured by perceptions of dominance by other men) than mate choice (as measured by perceptions of attractiveness to women)(David A. Puts, 2010).

Both sexes seem to attend to vocal cues to assess the threat potential of intrasexual competitors (see (D.A. Puts, Barndt, et al., 2011) for women, and (D.A. Puts, Apicella, et al., 2011) for men). However, when it comes to vocal masculinity in particular, men and women may pay more attention to different vocal parameters. When judging men's attractiveness, women attend strongly to mean F0, whereas when assessing men's dominance, men attend strongly to pitch variation (F0-SD) (Hodges-Simeon et al., 2010a).

Assessing Sexual Selection in Humans

To understand the influence of sexual selection researchers look to determine how various traits influence reproductive success. One way to quantify reproductive success is to measure the number of viable offspring left behind by an individual. However, modern social conventions such as birth control and socially imposed monogamy make it difficult to interpret reproductive outcomes from an evolutionary perspective in industrialized, modern societies.

Because of this difficulty, researchers use measures of copulatory success, such as the number of sexual partners in the last year, as a proxy to reproductive success. This type of research assumes that over the course of human evolution increased access to mating opportunities has been significantly correlated with more traditional measures of reproductive success. This approach has "yielded many insights into the force of sexual selection in humans"(Hodges-Simeon et al., 2010a).

Researchers have used measures of copulatory success to assess the relative contributions of the two most salient mechanisms by which humans compete for mates of the opposite sex: intersexual mate choice and intrasexual contest competition. While both of these mechanisms have played a role over the course of human evolution, they will often favor the evolution of different types of traits.

Traits that are involved in intrasexual (typically male) contest competition are weapon-like, increasing reproductive success by allowing their bearers to use force or threat of force to exclude same-sex competitors from mating opportunities. Traits that are involved in intersexual

mate choice are charms or ornaments, increasing the reproductive success of their bearers by making them more attractive to members of opposite sex. (David A. Puts, 2010).

Examples of these two different selection pressures are found throughout nature. The hallmark example of mate choice selection is the peacock's tail feather. While a large, symmetrical, and brightly colored tail feather will not aid the peacock in survival (ecological fitness), it signals heritable genetic quality (reproductive fitness) to peahens that have developed a preference for this trait. Contest competition favors the production of size, strength, armaments, and aggression. A classic example of this intrasexual selection can be found in elephant seals, in which a dominant alpha male will attempt to monopolize an entire beachhead of females, using intimidation and/or force to ward off the advances of other males. Which mechanism is the source of the greatest selection pressure will vary between species and often between sexes within a species.

In humans, men's copulatory success can often be predicted by measuring traits involved in male contests and female choice (Hodges-Simeon et al., 2010a). Traits that make men more attractive to women, such as a lowered voice pitch are associated with variance in the number of sexual partners a man has (David A. Puts, Gaulin, & Verdolini, 2006) and the number of viable offspring sired (Apicella et al., 2007). Traits that are associated with status in male hierarchies can also predict increased mating success.

Recently, research has looked to evaluate the relative contributions of these two types of sexual selection to the evolution of human vocal parameters. Perceptions of dominance and attractiveness are used by researchers to assess which mode of sexual selection was predominant in the evolution of sexually dimorphic traits (traits that differ between males and females of the same species). Some traits are perceived as primarily as attractive to the opposite sex, suggesting that the trait evolved primarily through mate choice. However, other traits have a greater effect on how dominant its possessor is perceived to be by same-sex competitors, conveying the prominence of contest competition in the evolution of the trait.

Temporal mating strategies and male hierarchies

Sexual strategies theory has provided critical evidence demonstrating that mate preferences differ in predictable ways depending on a temporal context(Buss & Schmitt, 1993). These differences "seem tailored to solving particular adaptive problems" that are faced in long-term and short-term circumstances (Buss & Schmitt, 1993). For this reason it is important to distinguish between how monotonicity influences short-term attractiveness as compared to long-term attractiveness as it relates to intersexual selection (mate choice).

Researchers have also differentiated two distinct types of male superiority (Johnson, Burk, & Kirkpatrick, 2007).Men who are physically dominant achieve access to mates and resources through aggression or threats of aggression(David A. Puts et al., 2006). Prestige, however, is freely conferred deference that may be a mechanism for enhancing the benefits of cultural transmission (Henrich & Gil-White, 2001). It is therefore essential to assess how pitch variation differentially influences perceptions of physical dominance and prestige attributions made by other men.

In a 2011 study, F0 variation significantly predicted copulatory success. In that study fundamental frequency or voice pitch, a well-studied trait correlated with attractiveness

(and thus implicating mate choice selection) did not. This suggests the primacy of contest competition in the evolution of male vocal masculinity (Hodges-Simeon et al., 2010a)This was the first study to show that F0 variation was associated with mating success (Hodges-Simeon et al., 2010a).

F0 variation has been significantly correlated with self-reported physical aggressiveness, again suggesting its salience in assessing threat potential, a perception relevant to dominance attributions (D.A. Puts, Apicella, et al., 2011)In another study, F0 variation predicted ratings of attractiveness by non-fertile females rating short term attractiveness, fertile females rating long term attractiveness, and ratings of physical dominance by men (Hodges-Simeon, Gaulin, & Puts, 2010b).

Few studies on sexual selection and pitch variation have been experimental (Riding, Lonsdale, & Brown, 2006). Previous research has demonstrated a relationship between F0 variation and perceptions relevant to sexual selection. In the first study an experiment was conducted, manipulating only pitch variation to test how five different levels of pitch variation effect perceptions of attractiveness and dominance.

The second study was conducted to examine the influence of pitch variation on sexual selection relative to pitch and formant position in naturally occurring speech. Total sexual selection on male voices was examined through the relationships between three vocal parameters associated with variance in mating success: pitch, pitch variation, and formants and relative sexual selection were examined. Previous correlational research looking at multiple acoustic parameters in men and perceptions relevant to sexual selection have typically not included pitch variation, not examined perceptions relevant to contest competition (i.e. dominance), and have not looked for quadratic relationships (Collins, 2000).

Study 1

Methods

Voice Recording, Analysis, and Manipulation

Six male undergraduates from Michigan State University were recorded reading the first sentence of the "Rainbow Passage," a passage used commonly in phonetics research. The rainbow passage includes many sounds from the English language and their combinations (Fairbanks, 1960). Participants read, "When the sunlight strikes raindrops in the air, they act as a prism and form a rainbow," in an anechoic, soundproof booth using a Shure SM58 vocal cardioid microphone. A curved wire projection from the microphone stand kept each participant's mouth approximately 9.5 cm from the microphone. Voices were recorded into a computer using Goldwave software. Recordings were made in mono at a sampling rate of 44,100 Hz and 16-bit quantization. All files were saved as uncompressed ".wav" files.

Each recording was analyzed using Praat software (version 5.2.27). Praat determines pitch using acoustic periodicity detection on the basis of autocorrelation, the correlating of a time-domain signal with itself (Boersma & Weenik, 2011). This technique is more accurate, noise-resistant, and robust, than alternative methods such as those based on cepstrum or combs (Boersma & Weenik, 2011). A pitch floor of 75 Hz and a pitch ceiling of 300 Hz were used in accordance with the programmers' recommendations (Boersma & Weenik, 2011) for male

voices. All frequency (F0) and frequency variation (F0SD) values were converted from Hz (cycles per second) to ERB (equivalent rectangular bandwidth). The greater linearity between ERB and psychosocial auditory perception allows for a much more uniform manipulation across voice recordings from different speakers.

Using a Praat script mean F0 (mean pitch) is used in the formula meanPitch + ((x - meanPitch) * w) to manipulate each file, where x is the F0 of each point in the accompanying pitch tier, and w is the amount of manipulation to F0-SD (intonation factor) across the utterance. W values >1 result in more dynamic or less monotone voices. W values between 0 and 1 result in more monotone voices. Each voice was manipulated in Praat by increasing and decreasing the F0-SD of each voice stimulus by both one and two within-sex standard deviations in this variable.

Raters

One hundred sixty-five adults (n=165) participated in this Institutional Review Board approved study over the course of two trials. Male and female undergraduates between the ages of 18 and 25 (mean age= 20.38 years, range=18-26, SD= 1.261) from the Pennsylvania State University were recruited for the study. The sample includes eighty females and twenty-four males (n=104). A second round of data collection was conducted between April 16, 2012 and April 20, 2012. That sample includes forty-two females and nineteen males (n=61). The second trial was conducted to increase the number of participants as well as to determine the influence of upgraded headphones. Overall, voices were rated by one-hundred twenty-two females and forty-three males. Raters identified as 72.7 percent white, 9.7 percent Black or African American, 8.5 percent Asian, 4.8 percent Hispanic or Latino, 3.6 percent other, and 0.6 percent (1 rater) American Indian or Alaska Native. 93.3 percent of raters self-identified as heterosexual based on the attraction element of a demographic survey (i.e. responded that they are exclusively attracted to the other sex or almost exclusively attracted to the opposite sex).

Participants for the first trial were recruited from large lecture classes in anthropology and psychology. Participants received extra-credit compensation. Participants were scheduled for half-hour sessions.

All participants completed a demographic survey which included an item related to sexual orientation. Women were also asked to complete a menstrual cycle survey. Research has demonstrated cyclic variation in women's preferences for masculine voices (David Andrew Puts, 2006). For instance, Puts found that predicted progesterone and prolactin levels predicted preferences for vocal masculinity in normally cycling women (those not using a hormonal contraceptive).

Menstrual cycle information was used to estimate risk of conception at the time of the trial. First, the distance from the mid-cycle peak in days was calculated (e.g., -3 signifies 3 days before, 3 signifies 3 days after). This calculation was made by first estimating the onset of the participant's next menstrual bleeding. This estimate is based on the participant's self-reported last day of menstrual bleeding and self-reported average cycle length. Ovulation status was then determined by assuming that the Luteinizing hormone peak associated with ovulation occurs 15 days prior to the onset of menses (Bakos, Lundkvist, Wide, & Bergh, 1994). The distance from the mid-cycle peak (representing the number of days away from ovulation) is rounded to the nearest day. A corresponding conception risk

is assigned based on weighted averages (based on sample size) of data from Schwartz et al. (1980), Wilcox et al. (1980), and Columbo and Masarotto (2000)(D. Puts, personal communication, June 12, 2012).

Procedure

Participants sat at an isolated computer station and wore headphones (Sony MDR-V250 headphones for the first trial and Sennheisser HD 280, 64 ohm headphones for the second trial) during the experiment. Each rater listened to four manipulations and one original sample from six different voices, for a total of 30 samples per trial. Samples were presented one at a time via SuperLab stimuli presentation software. The order of stimuli presentation was randomized. After listening to each sample the participant was asked to rate the voice on a ten button Likert scale with only the ends labeled. The same ten button Likert design was used for all rating tasks. Men were asked to rate each voice for physical dominance on a scale from not dominant at all to extremely dominant. Men were also asked to rate each voice for prestige on a scale from no prestige to extremely high prestige. Women were asked after each voice to assign a rating for attractiveness in a short-term mating context on a scale from not attractive at all to extremely attractive. Women were also asked to rate each voice for long-term mating desirability on a scale from not attractive at all to extremely attractive.

Each participant listened to each voice and rated it on one perception and then repeated the trial for the other perception. Male raters were randomly assigned to either the physical dominance question asked first group or the prestige question asked first group. Likewise, women were randomly assigned to either the short-term mating question first or long-term mating question first group.

Defining short-term attractiveness, long-term attractiveness, dominance, and prestige

A definition of the dependent variable was presented with each rating task. Short-term attractiveness was defined as attractiveness for a "short-term, purely sexual relationship such as a one night stand". Long term attractiveness was defined as desirability for a "long-term, committed relationship such as steady dating or marriage."

Definitions were also provided to male participants with each rating. Physical dominance was defined as "capability of winning physical contests, such as sports and physical fights". Prestige, the most nuanced of thee perceptions was defined by explaining that someone high in prestige "is respected, admired, and held in high esteem. People consider him an expert, talented and likely to be successful in some areas, value his opinion and want to be like him". This definition represents all of the variables that loaded onto the prestige principal component in a 2009 study (Cheng, Tracy, & Henrich, 2010).

Data analysis

To examine the effect of the manipulations, while controlling for variability in ratings due to differences between the voices, the difference in rating from the unmanipulated stimuli rating was calculated for each participant's rating of each manipulation of each voice.

Manipulations generally made the voices sound less attractive, dominant, or prestigious. The slightly less monotone manipulation was more prestigious than the unmanipulated, and the

slightly less monotone manipulation was less attractive for raters rating for long-term attractiveness. This tendency creates a convex, parabolic relationship between pitch variation and all four attributes. (Figure A.)

Multivariate analysis of variance was conducted to test for significant effects of pitch variation on mean differences in the attributes physical dominance and prestige for male raters. A separate multivariate analysis was conducted to test for significant effects of pitch variation on mean differences in the attributes short-term attractiveness and long-term attractiveness for female raters. In the presence of a significant variance, tests of between subject effects are reported along with multiple comparisons performed using the Bonferroni procedure at the $\alpha = 0.05$ significance level.

To further characterize the influence of pitch variation on selection, curve estimation was performed.

All data analyses were performed in IBM SPSS version 20.

Results

Multivariate analysis of variance (MANOVA) revealed a significant effect of pitch variation on mean difference in perceptions related to male-male competition (i.e. physical dominance and prestige) (Pillai's Trace $(8,2570)=0.031$, F=5.058, p=<0.001). Levene's test suggested unequal variances for physical dominance (F(4,1285)=79.445, p=<0.001) and prestige (F(4,1285)=84.667, p=<0.001). However, analysis of variance (ANOVA) is robust against unequal variances considering the equality of sample sizes. So, ANOVAs are reported with an $\alpha=0.025$. Tests of between-subjects effects reveal a significant effect of pitch variation on both physical dominance (F(4)=5.097, p=<0.001) and prestige (F(4)=4.940, p=0.001). Multiple comparisons using the Bonferroni method can be found in Appendix A1.

An independent MANOVA analysis revealed a significant effect of pitch variation on mean difference in perceptions related to female mate choice (i.e. short-term and long-term attractiveness)(Pillai's Trace(8,7310)=0.028, F=12.750, p=<0.001). Levene's test suggested unequal variances for short-term attractiveness (F(4,3655)=214.926, p=<0.001) and long-term attractiveness (F(4,3655)=198.341, p=<0.001). ANOVAs are reported with an $\alpha=0.025$. Tests of between-subjects effects reveal a significant effect of pitch variation on both short-term attractiveness (F(4)=13.431, p=<0.001) and long-term attractiveness (F(4)=13.584, p=<0.001). Multiple comparisons using the Bonferroni method can be found in Appendix A2.

Curve estimation revealed that pitch variation significantly predicts short-term attractiveness variance quadratically (R2=0.013, F(2,3657)=23.382, p=<0.001). The relationship can be described by the equation:

$$y = -1.272 + 0.743x - 0.117x^2$$

Curve estimation revealed that although pitch variation is linearly related to long-term attractiveness (R2=0.002, F(1,3658)=5.910, p=0.015), more variation in attractiveness is explained more significantly by the quadratic function (R2=0.014, F(2,3657)=26.795, p=<0.001). This function can be described by the equation:

$$y = -1.225 + 0.769x - 0.120x^2$$

Curve estimation revealed that pitch variation significantly predicts physical dominance variation quadratically ($R^2=0.014$, $F_{(2,1287)}=8.861$, $p=<0.001$). The relationship can be described by the equation:

$$y = -1.026 + 0.635x - 0.109x^2$$

Curve estimation revealed that although pitch variation is linearly related to prestige ($R^2=0.003$, $F_{(1,1288)}=4.172$, $p=0.041$), more variation in prestige is explained more significantly by the quadratic function ($R^2=0.014$, $F_{(2,1287)}=9.333$, $p=<0.001$). This function can be described by the equation:

$$y = -1.114 + 0.697x - 0.105x^2$$

Study 2

Methods

Participants

One-hundred seventy-five self-identified heterosexual Michigan State University undergraduate male students (mean age= 20.9 years, range=18-26, SD= 1.725) participated in this IRB-approved study. Participants identified as 90.3 percent White, 3.4 percent Asian, 2.3 percent Black or African American, 2.3 percent Hispanic or Latino, 0.6 percent American Indian or Alaska Native, and 1.1 percent other.

Voice recording and measurements

Men scheduled one, one-hour morning session (starting times between 8:20 and 10:00 h) and one, one-hour evening session (starting times between 17:20 and 19:00 h). There was a week in between sessions. Voice recordings were made at each session.

Male participants were recorded reading an excerpt of the rainbow passage, a standard passage used in phonetics research (Fairbanks, 1960). Participants were recorded in an anechoic, soundproof booth using a Shure SM58 carioid dynamic microphone. A curved wire projection was used to keep participants' mouths approximately 9.5 cm from the capsule of the microphone. Voices were digitally recorded using Goldwave software. Mono, uncompressed wav audio files with a sampling rate of 44,100 Hz and 16 bit quantization were created for all voices.

Each recording (duration mean (SD) = 5.33 (0.69) seconds) was analyzed using Praat, a free software program for doing phonetics research on computers. Each recording was measured for pitch or fundamental frequency (F0)(mean(SD)= 112.52(14.61) Hz), pitch variation or monotonicity (F0SD)(mean (SD)=15.87(4.49)Hz), and four formant frequencies (F1- F4)(mean (SD)= 444.23(30.12)Hz for F1, 1512.60(64.50)Hz for F2, 2397.47(82.95)Hz for F3, & 3,388.57(113.71)Hz for F4). A pitch floor of 75 Hz and a pitch ceiling of 500 Hz were used in accordance with the programmer's recommendation for male voices (Boersma & Weenik, 2011). Default settings were used for all other program parameters.

Formants, F1 through F4 were measured at each glottal pulse (automatically detected by Praat) and averaged across measurements. This calculated formant measurements for the entire utterance- sampling a greater range of vocal tract configurations when compared with only measuring individual vowels. This method only measures voiced speech. It avoids fricatives, which regress apparent vocal tract length because the fricative originates in oral turbulence, not vocal fold vibration (Baken, 1987).

Praat sometimes shifts formants (e.g. calculating F2 as F1). Because of this tendency, formant measurements from glottal pulses for which any value exceeded a predetermined threshold (less than 2% of pulses) were omitted. Published data was used to determine thresholds for formant measurements (Rendall, Kolias, Ney, & Lloyd, 2005). Thresholds for men were 1000, 2850, 2750 and 4500 Hz for F1-F4.

All measurements were then converted from cycles per second (Hz) to equivalent-rectangular bandwidths (ERB). The greater linearity between ERB measurements and auditory perception allows for a more meaningful interpretation of data throughout the range of human vocal parameters. To convert from Hz to ERB we used the formula described by Glasberg and Moore (Glasberg & Moore, 1990),

$$ERB = 21.4 * \log(0.00437 * Fc + 1)$$, where Fc is frequency in Hz.

Formant position (Pf) was then calculated. Formant position was defined as the standardized between session mean of standardized formant values for the first n formants, where formants are standardized using between-sex means and standard deviations. Thus,

$$P_f = \frac{\sum_{i=1}^{n} F_i'}{n}$$

, where F_i' the standardized ith formant, and n is the number of formants measured. Essentially, this method assigned each standardized formant a unit weight rather than, for example, a beta weight obtained via regressing formants on sex or height. This approach was used following Cohen (Cohen, 1990).Cohen suggested that unit weights have better predictive power than beta weights derived from moderate-sized samples.

Pitch (F0) and pitch variation (F0SD) were also averaged together for both sessions to create composite measures of pitch and pitch variation (referred to in the analysis simply as pitch and variation). Data from one session was used in lieu of means for participants who only had one session of data. Twenty-three participants had only first session ratings. One of these participants does have second session measurements averaged into pitch and variation. Three participants had only second session voice measurements and ratings. One participant had only first session ratings but was not rated for dominance. Therefore, there is one less mean dominance score (N= 174).

Rating procedures

Voice recordings were rated by 568 men (mean age: 19.4 ± 1.8 years) and 558 women (mean age: 19.1 ± 2.4 years) from a large northeast U.S. University. Each rater assessed 24.9 ± 2.6 voice recordings. Raters listened to the voices in this sample as well as the voices of male siblings and female participants not included in this sample. No rater assessed a voice more than once. Using 7-point Likert scales, voices were rated for short-term and long-term attractiveness by women and physical dominance by men. The order in which the rating tasks were completed was randomized (e.g. short- or long-term first). The order of stimulus presentation was also randomized. The first fifteen ratings obtained for each voice for each type of rating were averaged to produce mean short-term attractiveness, long-term attractiveness, and physical dominance ratings.

Data analysis

Pearson's correlation was also used to examine the relationship between short-term attractiveness and long-term attractiveness to determine the feasibility of creating a composite measure, attractiveness. Pearson's correlation indicates a near perfect correlation between long-term and short-term attractiveness ($r(173)=0.958$, $p=<0.0001$). A new variable, attractiveness (i.e. mean attractiveness), was used in further analysis.

To quantify the strength and form of sexual selection regression techniques were used following the work of Hunt et al. (John Hunt, Breuker, Sadowski, & Moore, 2009). First, trait values for pitch (mean F0), variation (F0SD), and formants (Pf) were standardized, $\left[z_i = \frac{(x_i - \mu_i)}{\sigma_i} \right]$

. Then selection (i.e. attractiveness and dominance) was converted to relative selection (ω) by dividing individual selection by mean selection for the population, $\left(\omega = \frac{W}{\overline{W}} \right)$.

Examination of the zero-order linear relationships between acoustic measurements (standardized trait values) and relative sexual selection (relative attractiveness and relative dominance) was performed using Pearson's correlation.

Correlations- Relative Selection and Vocal Measurements (ERB)		Formant Position	Pitch	Variation	Relative Attractiveness	Relative Dominance
Formant Position	Pearson Correlation	1	.039	.157*	-.131	-.361**
	Sig. (2-tailed)		.610	.037	.085	.000
	N	175	175	175	175	174
Pitch	Pearson Correlation	.039	1	.541**	-.324**	-.427**
	Sig. (2-tailed)	.610		.000	.000	.000
	N	175	175	175	175	174
Variation	Pearson Correlation	.157*	.541**	1	-.187*	-.321**
	Sig. (2-tailed)	.037	.000		.013	.000
	N	175	175	175	175	174
Attractiveness	Pearson Correlation	-.131	-.324**	-.187*	1	.644**
	Sig. (2-tailed)	.085	.000	.013		.000
	N	175	175	175	175	174
Dominance	Pearson Correlation	-.361**	-.427**	-.321**	.644**	1
	Sig. (2-tailed)	.000	.000	.000	.000	
	N	174	174	174	174	174
*. Correlation is significant at the 0.05 level (2-tailed).						
**. Correlation is significant at the 0.01 level (2-tailed).						

Multiple regressions were used to calculate linear selection gradients:
$$\omega = \alpha + \beta z_1 + \beta z_2 + \beta z_3 + \varepsilon$$

Alpha (α) is the regression intercept, Betas (βs) are the partial regression coefficients and epsilon (ε) is the random error component. The partial regression coefficients are the standardized linear selection gradients and estimate the contribution of a particular trait to fitness while holding the effects of the other traits constant. Beta therefore represents the direction of the greatest incline from the population average on that particular fitness surface (John Hunt et al., 2009; Lande & Arnold, 1983)

Nonlinear forms of selection are then estimated by running separate regressions that include quadratic (zii2) and cross-product ($z_i z_j$) terms:

$$\omega = \alpha + \beta z_1 + \beta z_2 + \beta z_3 + \frac{\gamma}{2} z_1^2 + \frac{\gamma}{2} z_2^2 + \frac{\gamma}{2} z_3^2 + \gamma z_1 z_2 + \gamma z_1 z_3 + \gamma z_2 z_3 + \varepsilon$$

The linear terms (β) are not interpreted from this equation. Instead, the equation is used with higher order terms to indicate how selection influences the variances and covariances of traits when the effects of linear selection are removed (Hunt et al., 2009 & Lande & Arnold, 1983). The γ coefficients associated with the squared terms of each standardized variable reflect the direct effects of nonlinear selection on the trait variances, characterizing the shape of curvature of the fitness surface along the individual traits axes (z1-z3) (Hunt et al., 2009 & Lande & Arnold, 1983). A negative γ indicates convex (i.e. downwardly curved) selection while a positive γ indicates concave (i.e. upwardly curved) selection. The γ coefficients for cross-products represent the direct effects of correlational selection for traits to become positively (positive γ) or negatively (negative γ) correlated (John Hunt et al., 2009).

Hunt cautions that interpretation of nonlinear selection can be troublesome as the number of individual traits being examined increases (John Hunt et al., 2009). When only a few traits show nonlinear forms of selection, the multiple-regression approach provides an adequate description and quantification (J Hunt, Wolf, & Moore, 2007). Since the current analysis only involves three traits, canonical analysis was not employed.

All data analyses were performed in IBM SPSS Statistics version 20.

Results

Pearson's correlation calculated significant correlations between formant position and variation (r(173) = 0.157, p= 0.037) and formant position and relative dominance(r(172) = -0.361, p= <0.001). The correlation between formant position and relative attractiveness neared significance (r(173) = -0.131, p= .085). There are significant correlations between pitch and variation (r(173) = 0.541, p=<0.001), pitch and relative attractiveness (r(173) =-0.324, p=<0.001), and pitch and relative dominance (r(172) = -0.427, p=<0.001). Variation is also significantly correlated with relative attractiveness (r(173) =-0.187, p=0.013) and relative dominance (r(172) =-0.321, p=<0.001). Finally, relative dominance and relative attractiveness are significantly correlated (r(172) = 0.644, p=<0.001).

A linear regression revealed that formants, variation, and pitch predict a significant proportion of the variance in attractiveness (R2=0.119, F(3,171)=7.694, p=<0.001). However, pitch was found to be the only significant linear predictor of attractiveness (β=-0.323, t(171)=-3.775, p=<0.001). A second linear regression including quadratic and interaction terms (R2=0.173, F(9,165)=3.847, p=<0.001) indicates that formant position (formant position2) is significantly, negatively, quadratically related to relative attractiveness (β=-0.175, t(165)=-2.347, p=0.02).

A linear regression revealed that formants, variation, and pitch predict a significant proportion of the variance in relative dominance (R^2=0.304, $F(3,170)$=24.735, p=<0.001). Both formant position and pitch are significant linear predictors of dominance (β=-0.337, $t(170)$=-5.190, p=<0.001 for formant position and β=-0.383, $t(170)$=-5.013, p=<0.001 for pitch). A second linear regression including quadratic and interaction terms (R^2=0.584, $F(9,164)$=9.410, p=<0.001) indicates that pitch (mean pitch2) is significantly, negatively, quadratically related to relative dominance (β=0.176, $t(164)$=2.165, p=0.032). Curve estimation revealed that although pitch is quadratically related to dominance (R^2=0.190, $F(2,171)$=20.088, p=<0.001), the variation in dominance may more accurately be described as a linear function (R^2=0.182, $F(1,172)$=38.375, p=<0.001). This function can be described by the equation:

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$$y = 1.000 - 0.098$$

Discussion

Multivariate analysis of variance indicates that pitch variation has a significant effect on perceptions relevant to both mate choice and contest competition modes of sexual selection.

Curve estimation indicates that a convex quadratic function significantly describes the relationship of between pitch variation and short-term attractiveness as well as pitch variation and physical dominance. A convex quadratic function also more significantly describes the relationships between pitch variation and long-term attractiveness as well as pitch variation and prestige than a linear function.

Pitch negatively linearly predicts relative attractiveness; however formant position and pitch variation do not. This result supports current research suggesting that women may primarily use pitch as cue to vocal masculinity and judge men with lower pitched voices to be more attractive. Formants are negatively, quadratically related to relative attractiveness (convex selection). This suggests that men's voices are under stabilizing selection, such that voices near the within-sex mean in formant position are the most attractive. Pitch variation is not quadratically related to attractiveness, when controlling for the influence of pitch and formant structure.

Pitch and formant position linearly predict relative dominance; however pitch variation does not. This supports research correlating pitch with other measures of physical dominance such as height, weight, arm strength, and testosterone levels and suggests that men's voice have been influenced by selection to evolve masculine voice pitch as an indicator of threat potential. Pitch is also positively, quadratically related to relative dominance (concave selection), but the relationship is predominately linear in nature (see Relative Dominance curve fit plot)

Conclusions

Study 1 suggests that pitch variation definitely affects dominance and attractiveness perceptions curvilinearly. This result indicates that pitch variation has played a role in the perception of vocal masculinity for both men and women.

Study 2 suggests that pitch variation is not an important contributor to total sexual selection in male voices, relative to pitch and formant position in naturally-varying speech. Pitch important to attractiveness and dominance, but more important to dominance. This result that selection for low pitched voices is both intrasexual (related to contest competition) and

intersexual (related to mate choice). It also suggests a predominance (even if marginally) of contests competition in the evolution of masculine voice pitch.

Study 2 also suggests that formant position is negatively, curvilinearly related to attractiveness and negatively linearly to dominance. This result supports research correlating sexually dimorphic formant measurements (i.e. masculine vocal timbre) with attractiveness to women and indicators of physical dominance such as upper body strength, height, weight, and fighting abilities. That a linear nature describes the relationship between formant position and dominance while a quadratic relationship describes the relationship between formant position and attractiveness may suggest that masculine vocal timbre plays a role in assessing the life history and health status of conspecifics. This may help explain why men masculine vocal timbre is correlated physical dominance attributions by men, and women use it to predict age. In comparison, formant structure has a more significant influence on dominance, again suggesting the primacy of contest competition in the evolution of vocal masculinity.

The current study demonstrates that while correlational research can suggest the need to investigate a trait experimentally, experimental results need to be interpreted in the context of related traits in naturally occurring stimuli. In general, we also present evidence of stronger selection on men's voices through male contests than female choice. More research is needed, designed explicitly to answer this question. Finally, future research will also determine if selection via contests in other traits associated is directional while selection via female choice on other traits demonstrates stabilizing selection on men's traits, as this is one of the first studies to examine quadratic relationships between sexually dimorphic vocal parameters and sexual selection.

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