Original Article

Vocal fundamental and formant frequencies are honest signals of threat potential in peripubertal males

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Fundamental and formant frequencies influence perceived pitch and are sexually dimorphic in humans. The information content of these acoustic parameters can illuminate the forces of sexual selection shaping vocal sex differences as well as the mechanisms that ensure signal reliability. We use multiple regression to examine the relationships between somatic (height, adiposity, and strength) and acoustic (fundamental frequency [F_0], formant position [P_f], and fundamental frequency variation [F_0-SD]) characteristics in a sample of peripubertal Bolivian Tsimane. Results indicate that among males—but not females—strength is the strongest predictor of F_0 and P_f and that F_0 and P_f are independent predictors of strength when height and adiposity are controlled. These findings suggest that listeners may attend to vocal frequencies because they signal honest, nonredundant information about male strength and threat potential, which are strongly related to physical maturity and which cannot be ascertained from visual or other indicators of height or adiposity alone.

Key words: **costly signaling, formants, fundamental frequency, pitch, voice.**

INTRODUCTION

Two acoustic attributes—fundamental frequency (F_0) and formant structure (formant dispersion and formant position; Fitch 1997; Puts et al. 2012)—appear particularly salient in mammalian vocal communication. Low F_0 and low, narrow formant structure contribute to the auditory perception of a deeper-sounding voice. The length and mass of the vocal folds are developmentally responsive to testosterone (Pedersen et al. 1986) and jointly determine F_0 (Titze 1994), which is the primary determinant of perceived pitch. The dimensions of the supralaryngeal vocal tract (including the pharynx, nasal cavities, and mouth) determine the formants (Fitch 1997), which are energy peaks in the harmonic spectrum (Fitch 1997). Lower and more closely spaced formants give a deeper, more "resonant" character to the voice—analogous to the fuller and deeper resonance of a tuba versus a trumpet. Both anatomical clusters, and hence F_0 and formant structure, are sexually dimorphic in humans (Gonzalez 2004; Rendall et al. 2005; Puts et al. 2012). Recent research suggests that variation in F_0 (F_0-SD) might also be sexually dimorphic (Puts et al. 2012) and sexually selected (Hodges-Simeon et al. 2010, 2011), with dominant males speaking in a monotone manner with less variable F_0 (Puts et al. 2012).

Researchers studying nonhuman primate vocalizations (Rendall et al. 2005; Ey et al. 2007) and the human voice (Pedersen et al. 1986; Titze 1994; Fitch 1997; Evans et al. 2006; Sell et al. 2010; Puts et al. 2012) have speculated about the information content of these masculine vocal parameters. Such auditory features may convey honest information about a signaler if either the costs of production are high ("handicaps") (Zahavi 1975) or the signal is constrained by other aspects of the phenotype ("indices") (Fitch 1997; Fitch and Giedd 1999). When vocalizations honestly convey fitness-relevant information, conspecific listeners benefit by attending to them (Searcy and Nowicki 2005). Thus, to clarify how selection has shaped sexually dimorphic vocal features—both anatomical and acoustical—one must determine the information content and honesty of the associated signals (Fitch 1997; Rendall et al. 2005; Evans et al. 2006; Ey et al. 2007; Sell et al. 2010; Puts et al. 2012). Research on pandas (Charleton et al. 2010, 2011), red deer (Reby and McComb 2003; Reby et al. 2005), elephant seals (Sanvito et al. 2007), and primates (Rendall et al. 2005; Ey et al. 2007), among other species, suggests that conspecifics attend to fundamental and formant frequencies in courtship and competitive interactions as honest indicators of fitness-relevant characteristics such as age, sex, body size, or hormonal status.

As a basis for an index-based mechanism of signal reliability among humans, initial approaches to the information content of F_0 and formant structure suggested a possible allometry between overall body size and vocal tract dimensions. Such a relationship

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would make vocal signals partly redundant with visual observation of height and/or weight. Although inconclusive, previous research suggests the allometry assumption may be incorrect: Although several studies have found associations between height (Graddol and Swann 1983; Puts et al. 2012) or weight (Evans et al. 2006) and F_0, more have reported no significant association between measures of overall body size and this vocal parameter (e.g., Collins 2000; Gonzalez 2004; Rendall et al. 2005). Research on the relationship between body size and formant structure is similarly inconclusive: Several studies have reported positive associations (Gonzalez 2004; Evans et al. 2006; Puts et al. 2012), but others have not (Collins 2000; Rendall et al. 2005; Sell et al. 2010). Recently, Puts et al. (2012) proposed a new calculation of formant structure, formant position, which may improve on previous measures and thus clarify the relationship between format structure and body size.

The focus on body size in the human and nonhuman literatures arises from an assumed relationship between size and threat potential among males. Because greater height and weight are often associated with success in physical contests (e.g., Sanvito et al. 2007), competitors can adaptively base fight-or-flight decisions on assessments of body size (Maynard Smith and Parker 1976). Although larger size has advantages in combat (Reilly and Secher 1990; Katic et al. 2005), Sell et al. (2010) suggest that body size often usefully reveals fighting ability because it is reliably associated with muscular strength. In humans, upper-body strength predicts a history of fighting better than height or weight; in addition, perceptions of fighting ability from photographs track strength better than they track height or weight (Sell et al. 2009). For these reasons, vocal parameters may have evolved to signal threat potential via their association with fighting ability, which is more strongly related to strength (Sell et al. 2009; Puts et al. 2012) than to body size. Puts et al. (2012) examined US and Hadza adult males, finding an association between formants and strength in the US sample only, and between F_0 and strength among the Hadza only. Sell et al. (2010) found relationships between perceptions of strength and both acoustic dimensions, but no associations with actual strength.

Here, we attempt to identify the information content of sexually dimorphic human vocal parameters by examining relationships among somatic variables (height, adiposity, and upper-body strength) and 3 sexually dimorphic acoustic characteristics (F_0, formant position, and F_0-SD) in a sample of male and female peripubertal Tsimane. Most studies target adult men (e.g., Evans et al. 2006; Sell et al. 2010; Puts et al. 2012); but puberty heralds a dramatic change in both acoustic and somatic characteristics (Hodges-Simeon et al. 2013). If male vocal parameters honestly signal physical formidability, then vocal and anatomical characteristics should change in parallel with measures of physical formidability—such as height, weight, and strength—during and after puberty. This period also offers a greater range in vocal frequencies, sizes and strengths than can be found in adult samples, more accurately reflecting the range of these parameters found in natural human groups. Because physical formidability may be more dependent on strength than on mere size, we expect low male voice to better predict strength than it predicts height or weight.

METHODS

Participants

Seventy-nine male and 76 female Tsimane (age 8–23; M = 13.6, SD = 3.3) participated. The Tsimane are forager-horticulturalists living in central Bolivia (Gurven et al. 2007). Research was approved by the Human Subjects Committee at the University of California, Santa Barbara. All procedures were conducted in accordance with ethical standards, including assent by all participants and informed consent by their parents.

Ages were estimated using participants' stated age and birth date, which were verified against the Tsimane Health and Life History census. When the 2 ages were in conflict, the census age was used (see Gurven et al. 2007; Hodges-Simeon et al. 2013 for detailed age-assignment methods). Because the onset and length of pubertal development can vary widely across individuals and populations (Bogin 1999), a liberal age range was used to capture all potential peripubertal somatic and vocal variation. Analyses are performed on the full sample as well as a more limited age range (11–19; see Results).

Anthropometric measures

Body and strength measurements were collected by CHS using standard anthropometric protocols (Frisancho 1990). Right-side measurements were recorded in duplicate and averaged for analyses. Grip strength was measured to the nearest 0.5 psi using a Baseline bulb pneumonic hand dynamometer. Flexed-biceps size was recorded to the nearest 0.2 cm using an anthropometric tape measure. Triceps and subscapular skinfolds were measured to the nearest 0.2 mm using a Harpenden caliper. Skinfolds were used to calculate adiposity using the Slaughter formula for peripubertal individuals (Slaughter et al. 1988); arm fat area (another measure of adiposity; Frisancho 1990) was substituted for Slaughter adiposity into all models without any appreciable change in the results. We used adiposity instead of weight in our analyses due to the high correlation ($r = 0.95$) and multicollinearity (variation inflation factor [VIF] > 10) between weight and height. A composite strength measure was created by averaging standardized grip strength and flexed-bicep circumference; this composite has been used to index upper-body strength in previous voice research (Sell et al. 2009; Puts et al. 2012).

Voice measurement and analysis

Participants were shown 5 photographs of common objects in Tsimane life (cat, dog, plantains, soccer ball, and frog) and asked to name each object in sequence. The spoken sample was analyzed as one single voice sample. These words were selected because they terminate in 5 different vowel sounds (míshi: "ee"; açhuj: "oo"; pe're: "ā"; perota: "ah"; and ococo: "oh"). Because each vowel sound has a different formant profile, the full voice clip for each participant represents a normal range of formant values. A Sony PCM-M10 digital audio recorder with a sampling rate of 44 100 Hz and 16-bit quantization recorded voice samples in mono. A headset-mounted Audio-Technica lavalier microphone was placed 5 cm from the lips for each participant. Recordings were saved as high-quality uncompressed linear PCM.wav files.

For each participant's recording, mean F_0 (and standard deviation; F_0-SD) and formant structure (P_f) were measured in Hertz (Hz) using Praat voice analysis software (Version 5.1.37; Boersma and Weenik 2010). Formants were obtained using methods described by Puts et al. (2012); however, formant ceilings were adjusted for different developmental groups (see below; Boersma and Weenik 2010). Participants completed the Pubertal Development Scale (Petersen et al. 1988), a self-report scale that has been shown to be a reliable approximation of the Tanner stages (Brooks-Gunn et al. 1987; Petersen et al. 1988; Coleman and Coleman 2002). The Tanner stages are 5 stages of reproductive development based on genital

and pubic hair maturation and are widely used to mark pubertal development (Brooks-Gunn et al. 1987; Petersen et al. 1988; Coleman and Coleman 2002). Males and females in stages 1 and 2 (mean age = 10.9 ± 1.6) were measured using a formant ceiling of 7000 Hz. Females in stages 3, 4, and 5 (mean age = 15.4 ± 2.7) and males in stage 3 (mean age = 15 ± 1.5) were measured using a formant ceiling of 6000 Hz. And males in stages 4 and 5 (mean age = 18.2 ± 2.3) were measured with a formant ceiling of 5000 Hz. F1 through F4 were measured at each glottal pulse, targeting voiced speech only, and then averaged for analyses (mean number of glottal pulses per file = 527 ± 273). In order to calculate P_f, the first 4 formants were standardized using between-sex means and standard deviations (Puts et al. 2012).

RESULTS

Although males were the primary targets of our analyses, we conducted parallel analyses on females in order to provide a comparative baseline. A log transformation adequately corrected for nonnormality in the distributions of height, strength, age, F_0, P_f, and F_0-SD. Height, adiposity, and strength were entered together into separate multiple regression models to predict F_0, P_f, F_0-SD (Table 1, Models 1, 2, 3). For males only, strength was a significant predictor of F_0 (β = −0.62, P < 0.01); height (β = −0.25, ns) and adiposity (β = 0.04, ns) were both nonsignificant. Strength was the only significant predictor of male P_f (β = −0.70, P < 0.01), and height was the only significant predictor of female P_f (β = −0.53, P < 0.01). Both adiposity (β = −0.47, P < 0.01) and height (β = 0.63, P < 0.05) were significant predictors of F_0-SD for females. Effect sizes were large. Height, adiposity, and strength explained 71% of the variance in male F_0 and 68% of the variance in male P_f. These 3 variables explained 21% of the variance in female F_0 and 62% of the variance in female P_f.

Having established that strength is associated with F_0 and P_f among males, we explored whether vocal characteristics explain unique variance in strength that is not explained by height and adiposity. Thus, F_0, P_f, F_0-SD, age, height, and adiposity were used to predict strength. In this model, F_0 (β = −0.17, P < 0.01), F_0-SD (β = 0.10, P < 0.05), height (β = 0.61, P < 0.001), and adiposity (β = 0.09, P < 0.05) were statistically significant (Table 1, Model 4). P_f approached significance (β = −0.11, P = 0.07). Among females, none of the vocal parameters explained any additional variance in strength beyond the effects of height (β = 0.56, P < 0.001) and adiposity (β = 0.20, P < 0.01). This model explained 93% of the variance in male strength and 88% of the variance in female strength.

Because the boundaries of pubertal development vary across populations, all analyses (Models 1 through 4) were rerun with a narrower age range: 11–19 (N = 63 for both males and females). Results remained largely unchanged (i.e., only small changes in beta and P values). In only Model 4, the P value for one predictor, F_0-SD, changed from P < 0.05 to P = 0.07.

DISCUSSION

For peripubertal males, but not females, aspects of voice pitch provide additional information about strength that is not revealed by height or adiposity. Controlling for these 2 size variables as well as age, males with lower voices (as indicated by low F_0 and P_f) were significantly stronger than males with higher voices. This study is the first to show that both F_0 and P_f signal additive, nonredundant information to the listener about male strength that cannot be gained from information about height or adiposity. These findings also suggest that listeners can make accurate assessments of strength, and hence probably physical dominance, when they attend to low F_0 or P_f (cf., Puts et al. 2007; Hodges-Simeon et al. 2010) in peripubertal males.

Table 1

Multiple regression models

	Males			Females		
	Standardized beta coefficients (t statistic)	Zero-order correlations r	Partial correlations	Standardized beta coefficients (t statistic)	Zero-order correlations r	Partial correlations
1. Predicting F_0[a]						
Height	−0.25 (−1.28)	−0.82***	−0.15	−0.02 (−0.07)	−0.42***	−0.01
Adiposity	0.04 (0.50)	−0.34**	0.06	0.04 (0.50)	−0.41**	−0.10
Strength	−0.62 (−3.19**)	−0.84***	−0.34**	−0.32 (−1.15)	−0.45***	−0.13
2. Predicting P_f[b]						
Height	−0.17 (−0.87)	−0.79***	−0.10	−0.53 (−3.06**)	−0.78***	−0.34**
Adiposity	0.08 (1.17)	−0.29**	0.13	−0.11 (−0.88)	−0.64***	−0.10
Strength	−0.70 (−3.41**)	−0.82***	−0.36**	−0.19 (−0.99)	−0.75***	−0.12
3. Predicting F_0-SD[c]						
Height	−0.62 (−1.81†)	−0.18	−0.20†	0.63 (2.47*)	0.13	0.27*
Adiposity	−0.08 (−0.62)	−0.12	−0.07	−0.47 (−2.64**)	−0.15	−0.30**
Strength	0.48 (1.38)	−0.12	0.16	−0.17 (−0.61)	0.03	−0.07
4. Predicting strength[d]						
Height	0.61 (8.15***)	0.87***	0.70***	0.56 (6.31***)	0.91***	0.60***
Adiposity	0.09 (2.56*)	0.33***	0.29*	0.20 (2.90**)	0.80***	0.33**
F_0	−0.17 (−2.23**)	−0.84***	−0.30**	−0.05 (−1.07)	−0.45***	−0.13
P_f	−0.11 (−2.02†)	−0.82***	−0.21†	−0.02 (−0.26)	−0.75***	−0.03
F_0-SD	0.10 (2.80*)	−0.12	0.31**	−0.02 (−0.45)	0.03	−0.05
Age	0.11 (2.00)	0.87***	0.18	0.21 (2.80**)	0.81***	0.32**

Males: [a]$F(3,79)$ = 62.00***; R^2 = 0.71. [b]$F(3,79)$ = 54.60***; R^2 = 0.68. [c]$F(3,79)$ = 1.72; R^2 = 0.06. [d]$F(6,79)$ = 156.85***; R^2 = 0.93. Females: [a]$F(3,76)$ = 6.47**; R^2 = 0.21. [b]$F(3,76)$ = 39.24***; R^2 = 0.62. [c]$F(3,76)$ = 4.17**; R^2 = 0.15. [d]$F(6,76)$ = 81.90***; R^2 = 0.88.
†P < 0.08, *P < 0.05, **P < 0.01, ***P < 0.001.

The signal content of fundamental and formant frequencies has been of continuing interest (Graddol and Swann 1983; Fitch and Giedd 1999; Collins 2000; Sanvito et al. 2007; Sell et al. 2009). Across many mammals (e.g., Sanvito et al. 2007), vocalizations mediate access to resources and mates (Maynard Smith and Parker 1976; Searcy and Nowicki 2005). Theory suggests that vocalizations should be ignored unless they carry honest information about the vocalizer's phenotype—information useful to competitors or potential mates. Our findings suggest that both F_0 and P_f signal strength, providing additive information about potential competitors' formidability.

Previous research on the value of fundamental and formant frequencies for intrasexual competition among humans has been mixed (Graddol and Swann 1983; Collins 2000; Gonzalez 2004; Rendall et al. 2005; Evans et al. 2006; Puts et al. 2012). We improve on past research in 2 ways. First, with a few exceptions (Sell et al. 2010; Puts et al. 2012), past studies measure height and weight, but not strength. By examining multiple measures of threat potential, it is possible to identify which features best predict vocal frequencies and to examine the unique contributions of different acoustic parameters to strength measures. Second, we target peripubertal ages rather than adulthood. This age group provides valuable information on this topic, as tremendous change in both vocal and somatic features occurs during puberty (Hodges-Simeon et al. 2013). In addition, because mating competition intensifies during this period, attention to signals of dominance should be particularly high.

Contrary to predictions, F_0-SD was positively associated with strength when other vocal parameters were controlled. That is, males with less monotone, more variable F_0 were stronger than those with less variable F_0. This finding is in contrast to conclusions made in previous research on the value of F_0 variation for dominance signaling (Hodges-Simeon et al. 2010, 2011). That is, F_0 variation may leak information on autonomic activation (i.e., nervousness and arousal) and therefore may only be useful during ecologically relevant social interactions (e.g., Hodges-Simeon et al. 2010, 2011). Clearly, more research on F_0 variation is needed.

Signaling systems are vulnerable to cheaters and will be evolutionarily stable only if constraints ensure reliability (Grafen 1990; Searcy and Nowicki 2005). Fitch and Giedd (1999) argue that formant structure is an index of height; that is, allometry with linear dimensions assures honesty. If such developmental constraints dominated, formant structure would scale with linear growth and this vocal feature would be a redundant indicator of height. Although P_f and F_0 are correlated with height in both sexes, the results presented here show that when both strength and body size (i.e., height and adiposity) are entered simultaneously into a multiple regression, strength is the only significant predictor of P_f and of F_0. These results support the hypothesis that vocal frequencies signal physical formidability, which is more strongly related to strength than to body size.

A potential concern is whether these findings generalize to other populations. The Tsimane live in an energetically demanding, highly infectious environment, and it is possible that our results may not extend to other populations. However, because the Tsimane ecology more closely aligns with the environment in which humans evolved, these data may provide a closer representation of the selective forces on male vocal anatomy than data from industrialized countries (Henrich et al. 2010). This is the first study to examine the relationships among peripubertal strength, body size, and sexually dimorphic vocal parameters in a nonindustrialized population. By targeting interpopulation variation in somatic and acoustic characteristics, future studies will reveal the extent to which ecology influences the information content of vocal parameters.

A further consideration is the extent to which these results generalize beyond puberty. Many studies have examined the relationship between body size (height and weight) and vocal characteristics among adult men, with mixed results (Graddol and Swann 1983; Collins 2000; Gonzalez 2004; Rendall et al. 2005; Evans et al. 2006; Puts et al. 2012). A question of continuing interest is why adult listeners assign larger size (i.e., greater height and weight) to lower-sounding vocalizations if the empirical relationship between them is so weak. Rendall et al. (2007) propose 3 hypotheses to address this question: 1) listeners overgeneralize from age- and sex-based classifications, 2) listeners overgeneralize from broader environmental sound-size associations, or 3) the voice is closely aligned with other dimensions of a speaker and that these associations intrude on our perceptions of size. For instance, F_0 and P_f appear to be linked with testosterone (Pedersen et al. 1986; Dabbs and Mallinger 1999), which itself may affect traits like strength. Several studies have examined the association between strength and vocal parameters; however, like height and weight, the results have been inconclusive (Sell et al. 2010; Puts et al. 2012).

The results of the present study support Rendall's first and third hypotheses. In addition, these findings suggest an additional explanation: Listeners may attend to low-voiced speakers because it provides a record of energetic condition and formidability during pubertal development. In a previous study using these data, modeling the developmental trajectory of vocal characteristics showed that individuals in better condition have an earlier voice change and a faster rate of change than those in poorer condition. This precocious developmental trajectory may lead to a lower voice in adulthood (Hodges-Simeon et al. 2013), suggesting that adult vocal characteristics may reveal pubertal condition. This may be useful information to potential mates and competitors if it co-occurs with characteristics such as heritable quality or coalitional strength. These are questions for future research.

In summary, our findings indicate that both F_0 and P_f contribute nonredundant, additive information about physical strength, beyond what is revealed by height or adiposity, in peripubertal males. These results suggest that humans attend to these auditory characteristics because, on average, they indicate something about male formidability that cannot be ascertained from visual inspection of height or adiposity. Because contest competition is far less intense in women than in men (Daly and Wilson 1983; Puts 2010), this information is less useful to females; accordingly, F_0 and P_f contribute no additional information about female strength. The relationship between strength and vocal parameters suggests that sexual selection may have targeted F_0 and P_f in the evolution of men's voices.

FUNDING

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