Evolution and Human Behavior 39 (2018) 602–610

Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.elsevier.com/locate/ens

Do men with more masculine voices have better immunocompetence?

Steven Arnocky[a,*], Carolyn R. Hodges-Simeon[b], Danielle Ouellette[c], Graham Albert[b]

[a] Department of Psychology, Nipissing University, Canada
[b] Department of Anthropology, Boston University, USA
[c] Medical Sciences, Northern Ontario School of Medicine, Canada

ABSTRACT

The human voice is often considered to be a secondary sexual characteristic that signals underlying information about the immunocompetence of the speaker (i.e. the immunocompetence handicap hypothesis; ICHH). However, no studies have yet shown a relationship between vocal characteristics and biomarkers of immune function or self-reported health. In a sample of 108 men, we examined correlations between masculine vocal characteristics [i.e. relatively low fundamental frequency (F_0), low F_0 variability (F_0-*SD*), low formant position (P_f), and high vocal tract length (VTL)] in relation to salivary immunoglobulin-A (sIgA; a marker of mucosal immunity), testosterone (T), and well-validated measures of self-reported health status. Results showed that sIgA correlated with masculinized F_0, P_f, and VTL. Self-report health correlated with masculinized P_f and VTL. Anticipated future health correlated negatively with F_0-*SD* and sick role propensity (less interference of illness in daily life) correlated positively with VTL. Perceived susceptibility to infection correlated with more feminized F_0 and F_0-*SD*. Our results demonstrated a small relationship between men's vocal characteristics and one putative indicator of mucosal immunity along with self-identified health status. We suggest that more research is warranted to determine whether the masculinity of men's voices may serve as an indicator of their phenotypic quality.

1. Introduction

The voice is among the most sexually-dimorphic of human traits (e.g., Puts et al., 2016). Sex differentiation of fundamental frequency (which corresponds perceptually to perceived pitch), standard deviation (variability in pitch), and formant frequencies (overtones, which create the perception of timbre and correspond to vocal tract length) primarily occurs during puberty, when males experience an increase in testosterone (T) production causing the vocal folds to thicken and the vocal tract to lengthen. This produces a more masculine voice, characterized by lower F_0, F_0-*SD* and formants (Butler et al., 1989; Harries, Hawkins, Hacking, & Hughes, 1998; Harries, Walker, Williams, Hawkins, & Hughes, 1997). Among adults, evidence suggests that vocal masculinity may also be correlated with T levels (Cartei, Bond, & Reby, 2014; Dabbs & Mallinger, 1999; Evans, Neave, Wakelin, & Hamilton, 2008; Jenkins, 2000; Puts, Apicella, & Cárdenas, 2012; Titze, 1994; but see Skrinda, Krama, Kecko, et al., 2014).

The immunocompetence handicap hypothesis (ICHH) suggests that male secondary sex characteristics, including some sexually-selected vocal characteristics, honestly signal immunological condition to others due to the immunosuppressive effects of the androgens (notably, T) necessary for their production and/or maintenance (Folstad & Karter, 1992; Furman et al., 2014; Muehlenbein & Bribiescas, 2005; Simmons & Roney, 2009; Zahavi, 1975). Consistent with the ICHH, evidence suggests that exogenously administered T suppresses immune function (Duffy, Bentley, Drazen, & Ball, 2000; Furman et al., 2014). In addition, T has been shown to decrease in production following an energetically-costly immune challenge (i.e. vaccine; Simmons & Roney, 2009). Therefore, the cost of developing and maintaining energetically-expensive phenotypic signals is more easily incurred by those who are of the highest quality and thus have higher overall energy budgets (Folstad & Karter, 1992; Zahavi, 1975). This may lead to positive correlations between endogenous T and some markers of immune function (i.e. phenotypic correlation; Muehlenbein & Bribiescas, 2005).

Within the context of the ICHH, sexually-dimorphic signals that convey superior genetic quality and immunocompetence should generally be more attractive to members of the opposite sex; although the strength of these preferences varies contextually and as a function of various individual differences (e.g., DeBruine, Jones, Crawford, Welling, & Little, 2010). For instance, Feinberg, Jones, Little, Burt, and Perrett (2005) found that male voices manipulated to be lower in F_0 were rated as more attractive (see also: Collins, 2000). Other research

* Corresponding author at: Department of Psychology, Nipissing University, 100 College Drive, North Bay, ON P1B 8L7, Canada.
E-mail address: stevena@nipissingu.ca (S. Arnocky).

https://doi.org/10.1016/j.evolhumbehav.2018.06.003
Received 15 March 2017; Received in revised form 7 June 2018; Accepted 7 June 2018

has demonstrated greater mating success among males with lower F_0-*SD* (Hodges-Simeon, Gaulin, & Puts, 2011) as well as greater preferences among women for lower formants in men's voices (Pisanski & Rendall, 2011). Additionally, women demonstrate a stronger preference for men's voices with lower-than-average F_0 during the fertile phase of their menstrual cycles (Hodges-Simeon, Gaulin, & Puts, 2010; Puts, 2005). Recent research suggests that lower voice pitch may ultimately predict reproductive success among hunter-gatherers (Apicella, Feinberg, & Marlowe, 2007). Considering that sexually-dimorphic, T-dependent vocal traits are likely associated with immunosuppressive endogenous hormones, and that such vocal traits are preferred by members of the opposite sex, many researchers have considered some characteristics of the human voice to be costly signals of underlying immunocompetence (see Feinberg, 2008 and Puts, Jones, & DeBruine, 2012 for review).

1.1. Immunocompetence handicapping hypothesis and vocal characteristics

A large literature relies on the ICHH to support evolutionary research on the origins of vocal sexual dimorphism (e.g. Apicella et al., 2007; Collins, 2000; Evans et al., 2008; Feinberg, 2004; Feinberg et al., 2005; Hodges-Simeon, Gurven, & Gaulin, 2015; Puts et al., 2016; Puts, Apicella, & Cárdenas, 2012). Yet few studies have actually examined human immunocompetence in relation to vocal characteristics. Of those that have, most have relied solely on *indirect* (e.g. T-voice associations) rather than direct biomarkers of immune functioning or self-reported health. For instance, Cartei et al. (2014) found that men who were taller and had higher salivary testosterone levels also had lower F_0, and formant spacing (i.e. lower, more closely spaced formants, which is measured by formant dispersion or formant position), and were in turn rated as more masculine by women. Several other studies have demonstrated links between testosterone and F_0 (Akcam et al., 2004; Dabbs & Mallinger, 1999; Puts et al., 2016; Puts, Apicella, & Cárdenas, 2012), although some studies have failed to observe a relationship between testosterone and F_0 (e.g., Bruckert, Liénard, Lacroix, Kreutzer, & Leboucher, 2006; Harries et al., 1997; Skrinda et al., 2014) and formants (e.g., Cartei et al., 2014; Evans et al., 2008).

Hughes, Harrison, and Gallup (2002) also found links between men's vocal attractiveness and bilateral symmetry – a putative indirect marker of underlying phenotypic quality. Similarly, Hill et al. (2017) found that fluctuating asymmetry (FA) related negatively to vocal attractiveness across samples collected from both Western industrialized as well as hunter-gatherer (Hadza) participants. However, when examining vocal pitch specifically, the researchers found that objective vocal pitch measures were unrelated to symmetry, as well as with second-to-fourth digit ratio – a potential sign of prenatal androgen exposure (Hughes, Pastizzo, & Gallup, 2008). This body of research suggests that some acoustic parameters likely co-vary with FA. However, because FA may not be a precise measure of developmental instability (Dongen, 2006), and only modestly reflects immunocompetence (Thornhill & Gangestad, 2006), reliance on such indirect markers of phenotypic quality in relation to vocal parameters precludes the ability to make direct conclusions about the specific role of voice as a marker of immunocompetence. Indeed, when considering research on other putative markers of masculinity, such as facial characteristics, within the context of immunocompetence handicapping, Skrinda et al. (2014) found a positive relationship between men's rated facial masculinity and their antibody response to a Hepatitis-B vaccine. Rantala et al. (2012) found that male testosterone was positively related to both immune responsiveness to a vaccine, and to their facial attractiveness as rated by women, and that these relationships were strongest among men who were simultaneously low in cortisol, supporting a stress-linked immunocompetence handicapping model of sexual selection. Conversely, other more recent research has found no evidence of a CxT interaction predicting facial attractiveness (Kandrik et al., 2017). Interestingly, recent research has also demonstrated that lower cortisol and higher T predicted lower F_0 in two samples of men (Puts et al., 2016).

When examining links between markers of immunocompetence and voice directly, Skrinda et al. (2014) found no links between testosterone or antibody response to a hepatitis-B vaccine and either F_0 or formants. Hodges-Simeon et al. (2015) sampled 91 Tsimane' (Bolivian hunter-horticulturalist) males ranging in age from childhood through adolescence, using BMI and secretory immunoglobulin-A (an antibody produced by white blood cells that is secreted at the mucosal surfaces; sIgA) as indicators of physical condition, such that higher scores on each represented better health. Results showed empirical support for a model whereby T mediated links between condition (BMI and sIgA) and vocal masculinization. At the bivariate level, sIgA correlated positively with T, and modestly and positively with body fat, but did not correlate directly with F_0, F_0-*SD*, or formant structure. However, other research has found no links between T and sIgA in men (van Anders, 2010).

1.2. Present study

In the present study, our aim is to move beyond the reported links between *indirect* measures of immunocompetence (e.g., T, BMI, bilateral symmetry) and vocal sexual dimorphism, which have shown inconsistent findings. Instead, we examine *directly* whether biological (sIgA) and self-report measures of actual health status correlate with sexually-dimorphic vocal characteristics in post-pubertal (i.e. young adult) males living in Canada.

Immunocompetence was measured using biological and self-report measures. Following Hodges-Simeon et al. (2015), we assayed secretory immunoglobulin-A (sIgA) as a marker of adaptive mucosal (and perhaps systemic; Brandtzaeg, 2007) immunity. In mammals, production of sIgA exceeds all other isotypes, comprising 70% of mucosal antibodies (Macpherson, McKoy, Johansen, & Brandtzaeg, 2008). Salivary IgA is produced by plasma B cells residing within salivary glands. It is secreted into the saliva, providing an initial defense against pathogens (Brandtzaeg, 2009; Macpherson et al., 2008). Men have been shown to be higher in sIgA than women in community samples, making it a potentially important target for investigation in studies of immune-androgen interactions (Evans et al., 2000; Hodges-Simeon, Gurven, & Gaulin, 2018). Further, several studies suggest that sIgA is positively associated with T (Gettler, McDade, Agustin, Feranil, & Kuzawa, 2014; Hodges-Simeon et al., 2018). Low levels of sIgA have previously been linked to increased infection (Fahlman & Engels, 2005; Nakamura, Akimoto, Suzuki, & Kono, 2006; Volkmann & Weekes, 2006). In a 19-year-long prospective longitudinal study of men and women, Phillips, Carroll, Drayson, and Der (2015) found that sIgA negatively correlated with mortality, particularly from cancer and respiratory diseases.

Well-validated self-report measures of (1) general overall health status; (2) perceptions of prior, current, and anticipated future health, disease resistance, concern about health, sickness orientation, rejection of the sick role, and attitude toward doctor visits; and (3) risk of infection and germ avoidance, are also expected to correlate with vocal characteristics. Specifically, if the human voice indeed evolved as a costly signal of phenotypic quality, men who score higher on biological and self-report health measures are expected to express voices that are lower in F_0, F_0-*SD*, and formant frequencies and higher in VTL relative to less healthy men.

We specifically target men in this report for three reasons. First, the ICHH was formulated to explain the conspicuous secondary sexual traits that characterize mammalian males (Folstad & Karter, 1992). Second, it is currently unclear whether the female voice has been the target of sexual selection. Very high female voices are rated as unattractive, as they may sound child-like (Borkowska & Pawlowski, 2011; but see Feinberg, DeBruine, Jones, & Perrett, 2008). Nevertheless, we did also collect a corresponding female sample from which results are available upon request.

2. Method

2.1. Participants

Participants were 108 undergraduate men between the ages of 17 and 29 (M_{age} = 20.62 (17–29), *SD* = 2.39; n = 100 Caucasian/White, n = 3 Black, n = 2 Asian, n = 1 South Asian, n = 1 First Nations/Aboriginal, n = 1 Arab). Participants were recruited from a small university and college in Northern Ontario using the campus online research participation system and recruitment stations in common areas.

2.2. Materials and procedure

Participants were instructed not to eat, drink (except water), smoke, or exercise for at least 2 h prior to their testing session. Prior to testing, all participants reported being free of medications affecting hormone concentrations and having no history or diagnosis of a psychiatric illness or drug dependency. Participants were led to a private and quiet testing room. As part of a larger study on mating behavior, they provided a saliva sample via passive drool into a transparent 5 ml polystyrene culture tube, provided a vocal sample, and subsequently completed a self-report paper and pencil questionnaire. Participants were remunerated with research credit or $5CAD.

2.2.1. Immunoglobulin-A (sIgA) concentrations

Saliva samples were stored at −60 °C until assayed using commercially available enzyme immunoassay kits (DRG International, NJ, USA). Samples were assayed in duplicate for sIgA whereby the average of the duplicates (log transformed) was used for all statistical analyses. Average intra- and inter-assay coefficients of variation were below 6%. Previous research has shown that salivary flow rate corresponds to measurable sIgA levels (Eliasson, Österberg, & Carlén, 2006). Consistent with this, in the present study, flow rate (volume ml/provision time in minutes) was negatively correlated with sIgA ($r(108) = -0.21$, $p = .01$). Time of sample provision (ranging from 9:02 to 20:05, M = 13:12, *SD* = 2:43) did not correlate with sIgA ($r(108) = -0.01$, $p = .45$). Accordingly, flow rate was controlled for in analyses involving sIgA.

2.2.2. Testosterone concentrations

For T, samples were assayed in duplicate using commercially available enzyme immunoassay kits (DRG International, NJ, USA). The average of the duplicates (log transformed) was used for all statistical analyses. Average intra- and inter-assay coefficients of variation were below 11%. Testosterone levels correlated with the sample provision time of day ($r(108) = -0.24$, $p = .01$). Accordingly, time of day was controlled for when examining links between T and other study variables.

2.2.3. General health status

Following Mossey and Shapiro (1982), general health status was assessed using the single self-report item, "In general, for your age, would you say your health is excellent/very good/good/fair/poor?" This measure has been shown to correlate with an index of objective health status (diagnosed medical condition) and mortality among older adult Canadians, over and above other prominent risk indices such as socioeconomic status and gender (Mossey & Shapiro, 1982). In a review of twenty-seven international studies examining global self-rated health, this measure was an independent predictor of mortality in nearly all reports, even after controlling for numerous other health status indicators and relevant covariates (Idler & Benyamini, 1997).

2.2.4. Self-report health perceptions

Participants also completed the Health Perceptions Questionnaire, Form II (HPQ; Ware, 1976). The HPQ is a frequently used measure consisting of 32 items rated using a five-point Likert-type scale ranging from 1 = *Definitely False* to 5 = *Definitely True*. The HPQ measures eight facets of perceived health: (1) Current health status (e.g., "*According to the doctors I've seen, my health is now excellent*") where high scores indicate better current health, (2) prior health status (e.g., "*I was so sick once I thought I might die*," reverse coded) where high scores indicate better prior health, (3) outlook (anticipated future health status; e.g., "*In the near future, I expect to have better health than other people I know*") where high scores indicate better perceived future health, (4) disease resistance (e.g., "*My body seems to resist illness very well*") where high scores indicate greater perceived resistance, (5) worry about health (e.g., "*My health is a concern in my life*," reverse coded) where high scores indicate less worry/concern, (6) sick orientation (e.g., "*I accept that sometimes I'm just going to be sick*" reverse coded) where higher scores indicate a belief that sickness is not likely to be a part of their life, (7) rejecting the sick role (e.g., "*When I'm sick I try to just keep going as usual*") where higher scores indicate less illness interference with life, and (8) attitude toward doctor visits (e.g., "*It doesn't bother me to go to the doctor*") where high scores indicate greater comfort with seeing a doctor. Previous factor analytic work has demonstrated that these components load well onto three distinct factors, with components 1–2 loading onto a factor termed *Present/Prior Health*, components 3–6 loading onto a factor termed *Future Health*, and components 7–8 loading on a factor termed *Sick Role Propensity*. It is these three overarching health factors that were of interest to the present study. Previous research has shown that the scales are reliable, valid, and stable over time and across populations (Ware, 1976). In the present study, internal consistency was acceptable for *Present/Prior Health* (α = 0.72) and *Future Health* (α = 0.69), but was low for *Sick Role Propensity* (α = 0.48).

2.2.5. Perceived vulnerability to disease

Participants completed the 15-item Perceived Vulnerability to Disease questionnaire, which assesses concerns regarding one's potential for contracting infectious diseases. The measure provides scores on two subscales: (1) *infectability* concerns beliefs about one's own susceptibility to infectious diseases (e.g., "*I am more likely than the people around me to catch an infectious disease*"); (2) *germ aversion* concerns emotional discomfort in contexts that indicate an especially high potential for pathogen transmission ("*It does not make me anxious to be around sick people*," reverse coded). Items were rated using a seven-point Likert-type scale ranging from 1 = *Strongly Disagree* to 7 = *Strongly Agree*. Previous research has shown that the measure demonstrates good convergent, discriminate, and predictive validity (e.g., Duncan, Schaller, & Park, 2009). In the present study, both the infectability (α = 0.86) subscale and germ avoidance subscale (α = 0.68) showed acceptable internal consistency.

2.2.6. Vocal characteristics

We recorded participants speaking five monophthong vowel sounds (i.e. *eh* as in '*bet*', *ee* as in '*see*', *ah* as in '*father*', *oh* as in '*note*', *oo* as in '*boot*') into a Samson Meteorite USB Condenser microphone, positioned approximately 20 cm from the participants' mouths. Recordings were made in a quiet room. Participant's voices were recorded using Goldwave version 6.10 software in mono with a sampling rate of 44.1 kHz and 16-bit quantization. The voice recordings were saved as high quality uncompressed wav files. All voice recordings were analyzed using Praat voice analysis software version 5.4.22 (Boersma & Weenink, 2014). We used the autocorrelation method to determine the F_0 of each vowel sound within the utterance. The pitch floor was set to 60 Hz and the pitch ceiling was set to 300 Hz. F_0-*SD* was determined by calculating the standard deviation of F_0 across the five vowel sounds. To calculate the formant frequencies, the vowel sounds were initially extracted (i.e. to exclude sporadic background noise, microphone pops, and accidental fricatives) by the Praat Vocal Toolkit Extract Vowels plug-in (Corretge, 2012). We then used Praat's Burg linear predictive coding algorithm. The maximum formant value was set to 5 kHz, the time step between the two analysis frames was set to 0.01 s, and the

window length was set at 0.025 s. Formants were not manually adjusted according to best visual fit with Pratt's estimation. Formant frequencies were obtained for the first four formants of the five vowels. P_f was calculated by averaging standardized measures of F1–F4 (formants standardized using between-sex means and standard deviations) (Puts, Apicella, & Cárdenas, 2012), and VTL was based on an algorithm provided by Kalashnikova, Carignan, and Burnham (2017) (see also: Fitch & Giedd, 1999). F_0-*SD* and P_f were not normally distributed and thus were log transformed.[1] Descriptive statistics for all study variables presented in Table 1.

3. Results

3.1. Analytic plan

We anticipated vocal variables to correlate positively with measures of immunocompetence and negatively with the measure of infectability. Therefore, we employed one-tailed tests of statistical significance in our correlation analyses. The analytic plan yielded thirty-two correlations of interest between each of testosterone, sIgA, and five self-report health variables in relation to each of the four vocal parameters: F_0, F_0-*SD*, P_f, and VTL. We therefore employed the Benjamini-Hochberg procedure to correct for multiple comparisons (Benjamini & Hochberg, 1995). Given the exploratory nature of this initial study and the potential cost of a false negative in terms of failing to identify potential relationships for further examination, we elected to employ a false discovery rate of 0.20 to correct for multiple comparisons (McDonald, 2014). This correction did not alter the interpretation of statistical significance/non-significance for any *p*-values in this study using the conventional benchmarks. Therefore, we report conventional *p*-values and interpretations of statistical significance throughout. However, it should be noted that using a more restrictive false discovery rate, or a more restrictive correction for multiple comparisons such as the Bonferroni correction, would lead to the reported relationships being interpreted as non-significant.

3.2. Salivary testosterone and sIgA

Given previous studies which have demonstrated a positive relationship between T and sIgA concentrations in Filipino men (Gettler et al., 2014) and in Tsimane pre-adolescents and adolescent males (Hodges-Simeon et al., 2015; Hodges-Simeon et al., 2018), we first examined interrelation among the two biological markers sIgA and T. Results showed that controlling for flow rate and time of sample provision, salivary T was correlated with sIgA ($r(103) = 0.18$, $p = .03$), suggesting that men with higher T concentrations also had higher concentrations of one marker of mucosal immunity (see Table 2).

3.3. Salivary testosterone and vocal characteristics

Contrary to previous research (e.g., Dabbs & Mallinger, 1999; Evans et al., 2008), we did not find a relationship between men's T concentrations and any of the measured vocal parameters. T concentration was not correlated with F_0 ($r(105) = 0.02$, $p = .41$), F_0-*SD* ($r(105) = -0.08$, $p = .21$), P_f ($r(105) = -0.10$, $p = .15$), or VTL ($r(105) = 0.03$, $p = .40$) (see Table 2).

3.4. Salivary sIgA and vocal characteristics

Results indicated that sIgA correlated negatively with F_0 ($r(104) = -0.21$, $p = .01$) and P_f ($r(104) = -0.16$, $p = .05$), positively with VTL ($r(104) = 0.17$, $p = .04$ (see Fig. 1), and modestly with F_0-*SD* ($r(104) = -0.13$, $p = .09$). Together, these findings suggest that men with deeper, more monotone voices may express higher levels of one marker of immunocompetence (see Table 2).

[1] Results did not change meaningfully when examining the untransformed vocal parameters.

Table 1
Descriptive statistics for study variables. Note that here we present raw scores for F_0-*SD*, D_f, P_f, sIgA (ng/ml), and T (pg/ml) values, which were subsequently Log transformed.

	N	Min.	Max.	Mean	SD
1. F1	108	409.1	811.3	513.1	56.3
2. F2	108	1316.0	1883.9	1556.2	139.0
3. F3	108	2292.4	2899.8	2599.0	120.7
4. F4	108	3044.4	4171.4	3410.2	270.2
5. F_0	108	71.95	154.29	111.82	15.52
6. F_0-*SD*	108	4.95	57.83	17.56	10.73
7. P_f	108	−1.28	2.62	0.00	0.70
8. VTL	108	14.44	18.70	16.90	0.91
9. sIgA	108	6.08	105.25	37.80	22.27
10. Testosterone	108	7.38	149.10	48.86	23.90
11. Infectability	107	1.00	5.57	3.04	0.96
12. Germ avoidance	107	1.13	5.75	3.31	0.99
13. Gen. Health	108	2.00	5.00	3.63	0.82
14. Current Health	108	2.08	4.67	3.51	0.58
15. Future Health	106	2.07	4.36	3.29	0.45
16. Sick Role	107	1.67	5.00	3.60	0.58

3.5. Self-report indices of health and vocal characteristics

Next, we examined F_0, F_0-*SD*, P_f, and VTL in relation to (1) general health status, (2) perceived vulnerability to disease scores on the infectability and germ avoidance subscales, and (3) Health Perceptions Questionnaire scores on the present/prior health, future health, and sick role propensity subscales. Results showed that general health status correlated negatively with P_f ($r(108) = -0.20$, $p = .02$), positively with VTL ($r(108) = 0.23$, $p = .01$, and modestly with F_0-*SD* ($r(108) = -0.15$, $p = .06$), but not with F_0 ($r(108) = -0.09$, $p = .17$). We targeted the relationship between vocal characteristics and perceived vulnerability to disease. Infection risk was correlated with F_0 ($r(108) = 0.17$, $p = .04$) and F_0-*SD* ($r108) = 0.18$, $p = .03$), but only modestly with P_f ($r(108) = 0.12$, $p = .10$), and VTL ($r(108) = -0.14$, $p = .07$), (Fig. 2). Conversely, germ avoidance was unrelated to any of the voice variables. Scores on the Health Perceptions Questionnaire present/prior health subscale correlated positively with VTL $r(108) = 0.19$, $p = .03$), and modestly with P_f ($r(108) = -0.15$, $p = .066$). The future health subscale correlated negatively with F_0-*SD* ($r(106) = -0.16$, $p = .05$) and modestly with F_0 ($r(106) = -0.14$, $p = .07$). The sick role subscale correlated positively with VTL ($r(107) = 0.18$, $p = .03$). However, there were two individuals who scored notably low on the sick role measure (2-3SD below the mean; see Fig. 2); with these scores windsorized to the next lowest acceptable score, the strength of this relationship with VTL became reduced ($r(107) = 0.13$, $p = .08$).

4. Discussion

The primary goal of the current study was to investigate the relationship between men's vocal masculinity and their immunocompetence using a direct biomarker of immune function as well as measures of self-perceived health. We found that men's salivary sIgA concentrations were negatively correlated with both their F_0 and their P_f (also modestly negative with F_0-SD) and positively with VTL. These findings yield some tentative support for the ICHH (Folstad & Karter, 1992; Zahavi, 1975) by demonstrating that those men who are higher on a single marker of immunological condition exhibit more masculinized vocal features. In other words, males with lower voices and with lower and more closely spaced formant frequencies had levels of functionally protective antibodies that confer lower risk of infection

Table 2
Correlations among study variables.

	F_0	F_0-SD	P_f	VTL	T	sIgA	Infect.	Germ avoid	Gen. Health	Cur. Health	Fut. Health
1. F_0	–										
2. F_0-SD	.32***	–									
3. P_f	0.01	0.05	–								
4. VTL	−0.09	−0.10	−.94***	–							
5. Testosterone (T)	0.02	−0.08	−0.10	0.03	–						
6. sIgA	−.21*	−.13†	−.16*	.17*	.18*	–					
7. Infectability	.17*	.18*	12†	−.14†	0.08	−0.05	–				
8. Germ avoid	0.05	0.09	0.08	−0.05	0.11	−.14†	.27**	–			
9. Gen. Health	−0.09	−.15†	−.20*	.23**	0.01	0.05	−.39***	−0.12	–		
10. Cur. Health	−0.07	−0.06	−.15†	.19*	−.18*	−0.01	−.36***	−.15†	.60***	–	
11. Fut. Health	−.14†	−.16*	−0.02	0.05	−0.04	0.01	−.63***	−.28**	.40***	.34***	–
12. Sick Role	0.01	−0.04	−0.11	.18*	−0.04	0.03	−0.04	−.14†	0.05	0.07	−0.03

Note. For salivary immunoglobulin-A (sIgA), we report partial correlations controlling for salivary flow rate. For testosterone, partial correlations control for time of day.

† $p < .10$.

* $p < .05$.

** $p < .01$.

*** $p < .001$ (1-tailed).

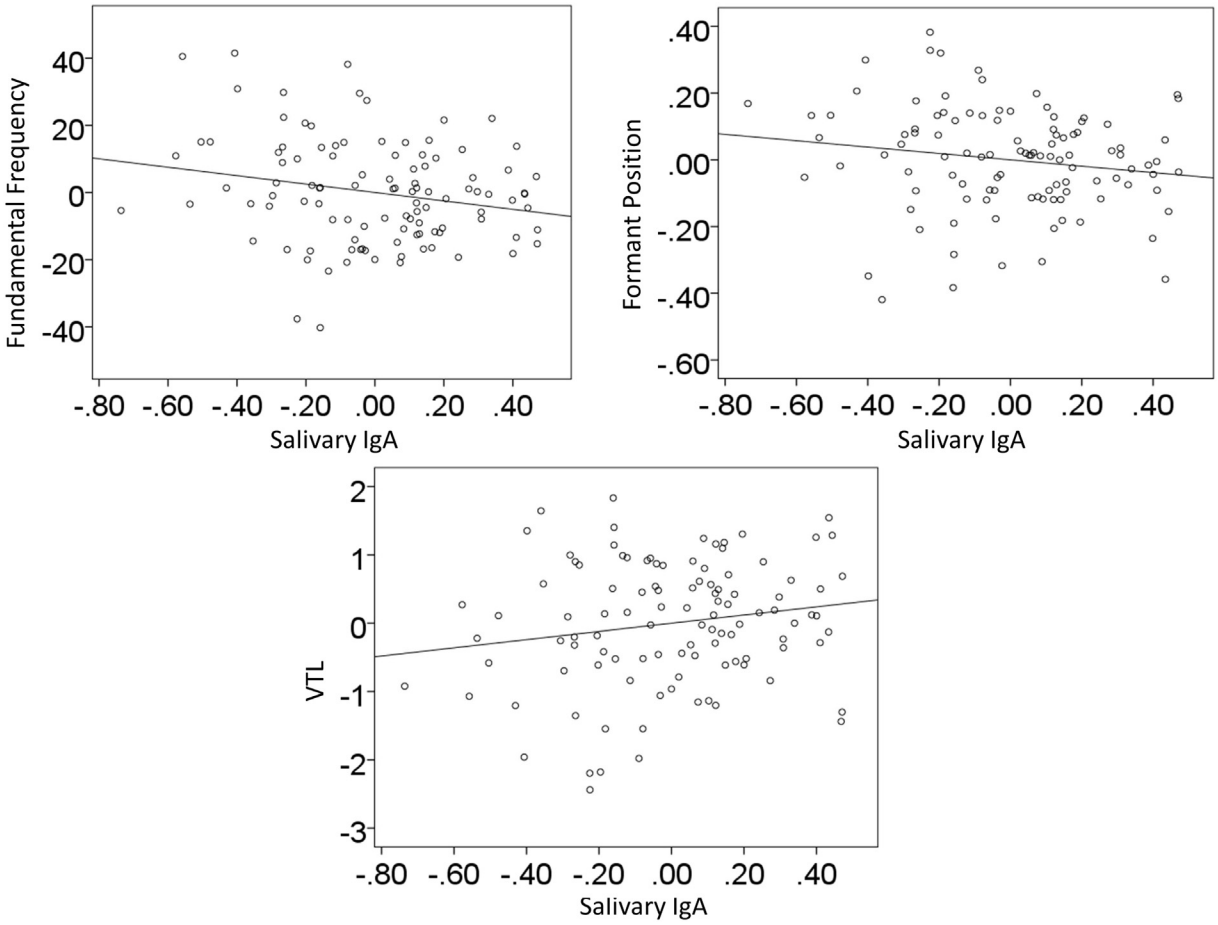

Fig. 1. Partial regression plots showing statistically-significant ($p < .05$) partial relations (controlling for flow rate) between salivary immunoglobulin-A (sIgA) and vocal characteristics.

and illness (Drummond & Hewson-Bower, 1997; Fahlman & Engels, 2005; Nakamura et al., 2006; Phillips et al., 2015; Volkmann & Weekes, 2006). sIgA also demonstrated a modest partial correlation in the same direction with F_0-SD.

Although several studies have reported a link between indirect health measures (i.e. bilateral symmetry and 2D:4D ratio) and T-dependent traits (e.g., Hughes, Dispenza, & Gallup, 2004; Hughes et al., 2002), very few have demonstrated a relationship between such traits and direct measures of health. Skrinda et al. (2014) found a positive relationship between men's rated facial masculinity and their antibody response to a Hepatitis-B vaccine, and Rantala et al. (2012) found that T mediated the relationship between facial attractiveness and response to a Hepatitis-B vaccine. However, the authors did not find a relationship between men's immunocompetence and their rated vocal attractiveness.

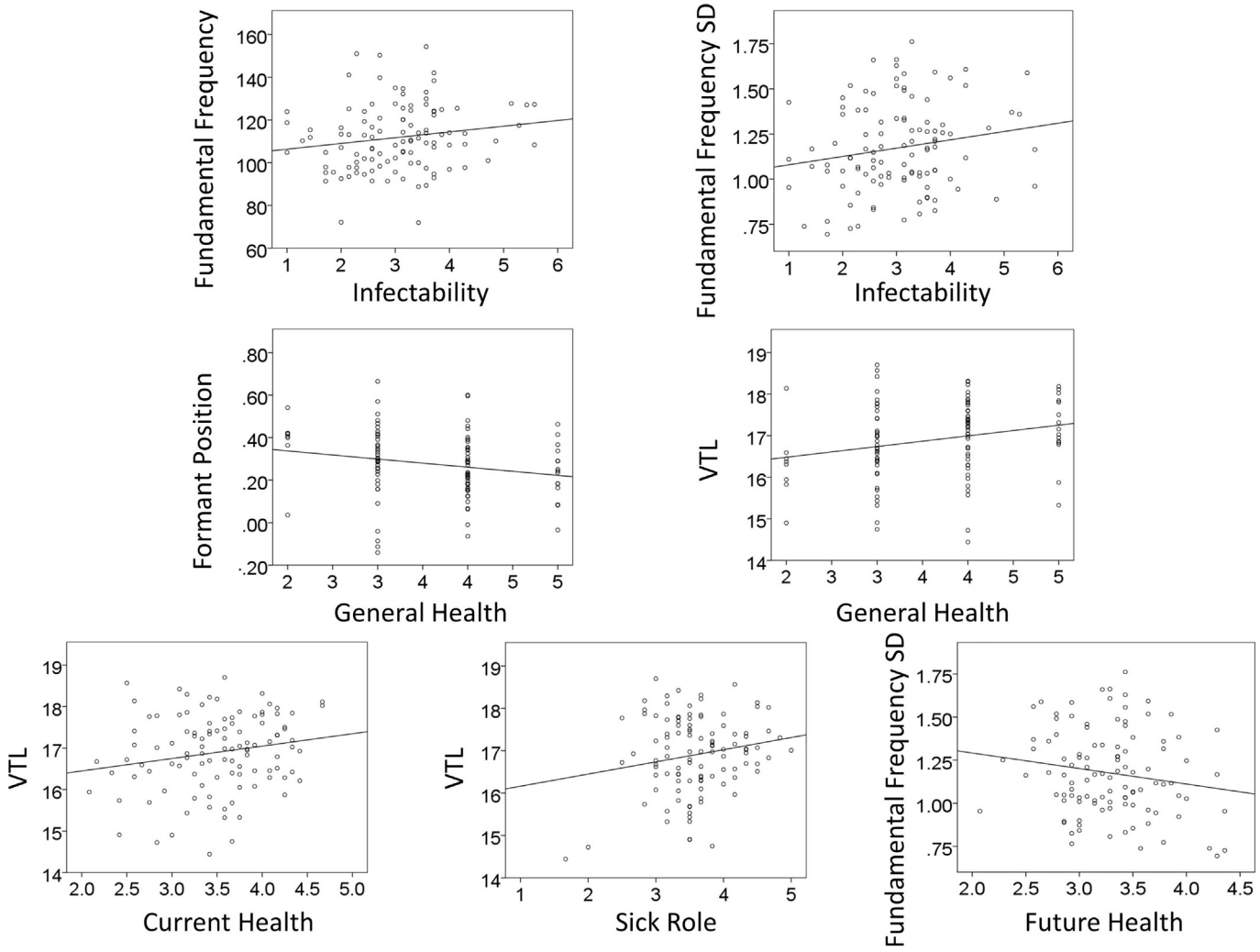

Fig. 2. Scatterplots showing statistically-significant ($p < .05$) relations between self-report health measures and vocal characteristics.

The current study extended previous findings by demonstrating a relationship between men's voice pitch and a putative marker of physical health, providing some initial evidence that men's voice pitch may act as a signal of immunocompetence to listeners.

Additionally, we found that men with lower rates of self-perceived infectability had lower F_0 and F_0-SD relative to men who perceived themselves as being more infectable. Men who believed themselves to be in better general health had lower P_f and longer estimated VTL relative to men who believed themselves to have generally worse health. Similarly, both men's reported prior/current health and sick role propensity (e.g., fewer doctor visits) correlated with VTL such that men with more masculinized VTL's reported greater health on these scales, whereas better future anticipated health was associated with a more masculinized F_0-*SD*.

Together these findings suggest some initial support for the hypothesis that healthier men exhibit more masculine vocal characteristics. However, we note that 1) the pattern of relationships was not consistent for each vocal variable, whereby different health measures emerged differentially for the vocal variables, 2) that the correlation coefficients coupled with visual examination of the scatterplots suggest that the magnitude of the effect is small, and 3) employing a more restrictive *p*-value correction, such as the Bonferroni procedure, or a more restrictive false discovery rate using the Benjamini-Hochberg procedure (0.15 or lower), would weaken the findings to statistical non-significance. It is largely held that the Bonferroni adjustment is problematic (e.g., Perneger, 1998); however, future research with larger sample sizes should be performed on the relationship between indicators of immunocompetence and vocal characteristics before any conclusions are made about the stability of the relationship between male immunocompetence and vocal characteristics.

Results also showed a significant positive relationship between sIgA and T. Several other studies have found a link between sIgA and T, which suggests that this association deserves additional empirical attention. Gettler et al. (2014) found that longitudinal increases in T were significantly associated with concomitant increases in sIgA among Filipino adult males. The authors found that men with lower levels of T and sIgA experienced more cold/flu symptoms, which may suggest that men in poorer condition were unable to mount a mucosal defense that is necessary for effective pathogen resistance. Hodges-Simeon et al. (2018) showed a positive association between sIgA and T in adolescent males. Finally, administration of T increases sIgA secretion in male rats (Sullivan & Allansmith, 1987). van Anders (2010) failed to find an association between T and sIgA in adult males; however flow rate was not controlled for in the analyses. Future research should continue to examine potential links between sIgA and T.

Despite evidence linking a masculine voice and T among adult males (Dabbs & Mallinger, 1999; Evans et al., 2008; Jenkins, 2000; Puts, Apicella, & Cárdenas, 2012; Titze, 1994; but see Skrinda et al., 2014), and the present empirical associations between T and sIgA and between sIgA and a masculine voice, we were surprised to find no relationship between T and any vocal parameter in the present study. T—as a biomarker of male mating effort—is often oversimplified in

behavioral research. T-behavior relationships are known to be dynamic (Dabbs, 1993), reciprocal (Mazur & Booth, 1998), non-linear (e.g. Moffat & Hampson, 1996), and dependent on social and intraindividual factors (Archer, 1991; Dabbs, 1993; Mazur & Booth, 1998). However, in spite of our efforts to control for some of these problems through research design (i.e. random sampling of participants) and statistic controls for time of day, we were unable to find a relationship between T and the vocal characteristics of interest. It may be that a single salivary assay of T is simply unreliable for identifying links to vocal parameters. Previous studies have found that relationships between high T levels and vocal masculinity (low F_0, Puts et al., 2016) or immune function (Rantala et al., 2012) are strongest for men with low cortisol levels. This could be because infection upregulates cortisol levels (Sapolsky, Romero, & Munck, 2000), which might ultimately affect the extent to which circulating testosterone levels affect tissue (e.g. Burnstein, Maiorino, Dai, & Cameron, 1995). Given that the present study did not examine cortisol levels, it could also be the case that these participants had stress hormone levels that affected this relationship (see Puts et al., 2016). Future research should consider collecting multiple samples across days in attempting to assess trait T.

4.1. Limitations and future directions

The present study has several limitations, which suggest avenues for future research. First, the use of a single biomarker provides only a narrow window into overall immune function. Research on immune-endocrine associations suggests a complex immunomodulatory role for T (Trumble et al., 2016); therefore, future studies may benefit from inclusion of biomarkers of both cellular and humoral immunity. Nevertheless, even as a single marker of immune function, sIgA has been shown to have important consequences for human health and mortality. Low sIgA is associated with increased risk of infections, particularly those of the respiratory tract (Drummond & Hewson-Bower, 1997; Fahlman & Engels, 2005; Nakamura et al., 2006; Volkmann & Weekes, 2006). Critically, low sIgA has been linked to higher mortality, especially from cancer and respiratory illness (Phillips et al., 2015).

Second, participants for the present research were drawn exclusively from a healthy, “WEIRD” (Western, educated, industrialized, rich and democratic) population (Henrich, Heine, & Norenzayan, 2010). Future studies would benefit from sampling populations that inhabit an environment more closely aligned with the selection pressures that yielded the predictions of the ICHH—namely, non-industrialized, small-scale societies with energy limitations and significant immunological burdens. For instance, research has shown that T is significantly lower in hunter-gatherer males than in North American males (e.g. Bribiescas, 1996), and that these populations carry substantially larger pathogen burdens (e.g. Martin, Blackwell, Gurven, & Kaplan, 2013). Initial evidence suggests, however, that data from these types of populations may yield similar findings; Tsimane post-pubertal adolescent males with higher sIgA had higher T (Hodges-Simeon et al., 2018). Surprisingly, however, sIgA was not associated with any vocal characteristics in this population (using both pre- and post-pubertal males) after controlling for age (Hodges-Simeon et al., 2015).

Third, in the present study T did not correlate with any vocal variables. This contrasts with a growing body of evidence linking T to lower F_0 (Cartei et al., 2014; Evans et al., 2008; Hodges-Simeon et al., 2015; Markova et al., 2016; Puts, Apicella, & Cárdenas, 2012; Puts et al., 2016). Puts et al. (2016) recently showed that T interacts with low cortisol to predict lower F_0, which might help to explain the lack of direct relationship between these variables.

Finally, the correlational nature of the present study was not designed to assess causal relationships between the variables under investigation. Future research might better address causality by examining longitudinally links between immunocompetence in childhood and subsequent vocal development following puberty. It would also be beneficial to explore the extent to which increased markers of mucosal immunity among men with lower F_0's actually puts them at a lower risk of infection, illness, and death (Drummond & Hewson-Bower, 1997; Fahlman & Engels, 2005; Nakamura et al., 2006; Phillips et al., 2015; Volkmann & Weekes, 2006). When listeners make judgments of health, dominance, or attractiveness using attributes of the voice (e.g., Feinberg, 2004; Feinberg et al., 2005; Jones, Feinberg, DeBruine, Little, & Vukovic, 2010; Puts, Hodges, Cárdenas, & Gaulin, 2007), they are presumably doing so in line with predictions derived from signalling theory (Albert et al., 2018; Searcy & Nowicki, 2005); that is, listeners attend to those characteristics that honestly reveal the signaler's immunocompetence. Future rating studies of vocal perception may focus on listeners' ability to accurately rate the immunocompetence of speakers.

5. Conclusion

The immunocompetence handicap hypothesis—as an explanation for the existence and maintenance of sexual dimorphism—is one of the most widely cited theories in evolutionary biology (Roberts, Buchanen, & Evans, 2004). Because the human voice is so sexually-dimorphic, many researchers have assumed that a masculine voice must be an honest, reliable signal of male immune quality. However, no previous studies had yet shown a direct relationship between vocal characteristics and measures of immunocompetence. Here we report preliminary evidence supporting the ICHH for the human voice. We found a general trend linking more masculinized vocal characteristics with one measure of immune function as well as self-perceptions of health. However, the observed effects were small and inconsistent. Further research using larger samples and more diverse biological markers of immunocompetence are necessary before making any firm conclusions about the link between vocal masculinity and immunocompetence.

References

Akcam, T., Bolu, E., Merati, A. L., Dermus, C., Gerek, M., & Ozkaptan, Y. (2004). Voice changes after androgen therapy for hypogonadotrophic hypogonadism. *The Laryngoscope, 114*(9), 1587–1591. http://dx.doi.org/10.1097/00005537-200409000-00016.

Albert, G., Pearson, M., Arnocky, S., Wachowiak, M., Nicol, J., & Murphy, D. R. (2018). Effects of masculinized and feminized male voices on men and women's distractibility and implicit memory. *Journal of Individual Differences*. http://dx.doi.org/10.1027/1614-0001/a000259.

Apicella, C. L., Feinberg, D. R., & Marlowe, F. W. (2007). Voice pitch predicts reproductive success in male hunter-gatherers. *Biology Letters, 3*(6), 682–684. http://dx.doi.org/10.1098/rsbl.2007.0410.

Archer, J. (1991). The influence of testosterone on human aggression. *British Journal of Psychology, 82*(1), 1–28. http://dx.doi.org/10.1111/j.2044-8295.1991.tb02379.x.

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society, Series B, 57*(1), 289–300. http://dx.doi.org/10.2307/2346101.

Boersma, P., & Weenink, D. (2014). Praat: doing phonetics by computer [computer program]. Version 5.4.22. Retrieved from http://www.praat.org/.

Borkowska, B., & Pawlowski, B. (2011). Female voice frequency in the context of dominance and attractiveness perception. *Animal Behaviour, 82*(1), 55–59. http://dx.doi.org/10.1016/j.anbehav.2011.03.024.

Brandtzaeg, P. (2007). Do salivary antibodies reliably reflect both mucosal and systematic immunity? *Annals of the New York Academy of Sciences, 1098*, 288–311. http://dx.doi.org/10.1196/annals.1384.012.

Brandtzaeg, P. (2009). Mucosal immunity: Induction, dissemination, and effector functions. *Scandinavian Journal of Immunology, 70*(6), 505–515. http://dx.doi.org/10.1111/j.1365-3083.2009.02319.x.

Bribiescas, R. G. (1996). Testosterone levels among ache hunter/gatherer men: A functional interpretation of population variation among adult males. *Human Nature, 7*(2), 163–188. http://dx.doi.org/10.1007/BF02692109.

Bruckert, L., Liénard, J., Lacroix, A., Kreutzer, M., & Leboucher, G. (2006). Women use voice parameters to assess men's characteristics. *Proceedings of the Royal Society B: Biological Sciences, 273*, 83–89. http://dx.doi.org/10.1098/rspb.2005.3265.

Burnstein, K. L., Maiorino, C. A., Dai, J. L., & Cameron, D. J. (1995). Androgen and glucocorticoid regulation of androgen receptor cDNA expression. *Molecular and Cellular Endocrinology, 115*(2), 177–186.

Butler, G. E., Walker, R. F., Walker, R. V., Teague, P., Riad-Fahmy, D., & Ratcliffe, S. G. (1989). Salivary testosterone levels and the progress of puberty in the normal boy. *Clinical Endocrinology, 30*(5), 587–596. http://dx.doi.org/10.1111/j.1365-2265.

1989.tb01431.x.
Cartei, V., Bond, R., & Reby, D. (2014). What makes a voice masculine: Physiological and acoustical correlates of women's ratings of men's vocal masculinity. *Hormones and Behavior, 66*(4), 569–576. http://dx.doi.org/10.1016/j.yhbeh.2014.08.006.
Collins, S. A. (2000). Men's voices and women's choices. *Animal Behaviour, 60*(6), 773–780. http://dx.doi.org/10.1006/anbe.2000.1523.
Corretge, R. (2012). Praat Vocal Toolkit. Retrieved from http://www.praatvocaltoolkit.com.
Dabbs, J. M. (1993). Salivary testosterone measurements in behavioral studies. *Annals of the New York Academy of Sciences, 694*(1), 177–183. http://dx.doi.org/10.1111/j.1749-6632.1993.tb18351.x.
Dabbs, J. M., & Mallinger, A. (1999). High testosterone levels predict low voice pitch among men. *Personality and Individual Differences, 27*(4), 801–804. http://dx.doi.org/10.1017/S0191-8869(98)00272-4.
DeBruine, L. M., Jones, B. C., Crawford, J. R., Welling, L. L., & Little, A. C. (2010). The health of a nation predicts their mate preferences: Cross-cultural variation in women's preferences for masculinized male faces. *Proceedings of the Royal Society of London B: Biological Sciences, 277*(1692), 2405–2410. http://dx.doi.org/10.1098/rspb.2009.2184.
Dongen, S. V. (2006). Fluctuating asymmetry and developmental instability in evolutionary biology: Past, present and future. *Journal of Evolutionary Biology, 19*(6), 1727–1743. http://dx.doi.org/10.1111/j.1420-9101.2006.01175.x.
Drummond, P. D., & Hewson-Bower, B. (1997). Increased psychosocial stress and decreased mucosal immunity in children with recurrent upper respiratory tract infections. *Journal of Psychosomatic Research, 43*(3), 271–278. http://dx.doi.org/10.1016/S0022-3999(97)00002-0.
Duffy, D. L., Bentley, G. E., Drazen, D. L., & Ball, G. F. (2000). Effects of testosterone on cell-mediated and humoral immunity in non-breeding adult European starlings. *Behavioral Ecology, 11*(6), 654–662. http://dx.doi.org/10.1093/beheco/11.6.654.
Duncan, L. A., Schaller, M., & Park, J. H. (2009). Perceived vulnerability to disease: Development and validation of a 15-item self-report instrument. *Personality and Individual Differences, 47*(6), 541–546. http://dx.doi.org/10.1016/j.paid.2009.05.001.
Eliasson, L., Österberg, B. D., & Carlén, A. (2006). Minor salivary gland secretion rates and immunoglobulin A in adults and the elderly. *European Journal of Oral Sciences, 114*(6), 494–499. http://dx.doi.org/10.1111/j.1600-0722.2006.00413.x.
Evans, P., Der, G., Ford, G., Hucklebridge, F., Hunt, K., & Lambert, S. (2000). Social class, sex, and age differences in mucosal immunity in a large community sample. *Brain, Behavior, and Immunity, 14*(1), 41–48. http://dx.doi.org/10.1006/brbi.1999.0571.
Evans, S., Neave, N., Wakelin, D., & Hamilton, C. (2008). The relationship between testosterone and vocal frequencies in human males. *Physiology & Behavior, 93*(4), 783–788. http://dx.doi.org/10.1016/j.physbeh.2007.11.033.
Fahlman, M. M., & Engels, H. J. (2005). Mucosal IgA and URTI in American college football players: A year longitudinal study. *Medicine & Science in Sports & Exercise, 37*(3), 374–380.
Feinberg, D. R. (2004). Fundamental frequency perturbation indicates perceived health and age in male and female speakers. *The Journal of the Acoustical Society of America, 115*(5), http://dx.doi.org/10.1121/1.4784735.
Feinberg, D. R. (2008). Are human faces and voices ornaments signaling common underlying cues to mate value? *Evolutionary Anthropology, 17*(2), 112–118. http://dx.doi.org/10.1002/evan.20166.
Feinberg, D. R., Debruine, L. M., Jones, B. C., & Perrett, D. I. (2008). The role of femininity and averageness of voice pitch in aesthetic judgments of women's voices. *Perception, 37*(4), 615–623. http://dx.doi.org/10.1068/p5514.
Feinberg, D. R., Jones, B. C., Little, A. C., Burt, D. M., & Perrett, D. I. (2005). Manipulations of fundamental and formant frequencies influence the attractiveness of human male voices. *Animal Behaviour, 69*(3), 561–568. http://dx.doi.org/10.1016/j.anbehav.2004.06.012.
Fitch, W. T., & Giedd, J. (1999). Morphology and development of the human vocal tract: A study using magnetic resonance imaging. *The Journal of the Acoustical Society of America, 106*(3), 1511–1522. http://dx.doi.org/10.1121/1.427148.
Folstad, I., & Karter, A. J. (1992). Parasites, bright males, and the immunocompetence handicap. *American Naturalist, 139*(3), 603–622. http://dx.doi.org/10.2307/2462500.
Furman, D., Hejblum, B. P., Simon, N., Jojic, V., Dekker, C. L., Thiébaut, R. et al. Davis, M. M. (2014). Systems analysis of sex differences reveals an immunosuppressive role for testosterone in the response to influenza vaccination. *Proceedings of the National Academy of Sciences, 111*(2), 869–874. http://dx.doi.org/10.1073/pnas.1321060111.
Gettler, L. T., McDade, T. W., Agustin, S. S., Feranil, A. B., & Kuzawa, C. W. (2014). Testosterone, immune function, and life history transitions in Filipino males (*Homo sapiens*). *International Journal of Primatology, 35*(3–4), 787–804. http://dx.doi.org/10.1001/s10764-014-9749-5.
Harries, M., Hawkins, S., Hacking, J., & Hughes, I. (1998). Changes in the male voice at puberty: Vocal fold length and its relationship to the fundamental frequency of the voice. *The Journal of Laryngology and Otology, 112*(05), 451–454. http://dx.doi.org/10.1017/S0022215100140757.
Harries, M. L. L., Walker, J. M., Williams, D. M., Hawkins, S., & Hughes, I. A. (1997). Changes in the male voice at puberty. *Archives of Disease in Childhood, 77*(5), 445–447. http://dx.doi.org/10.1136/adc.77.5.445.
Henrich, J., Heine, S. J., & Norenzayan, A. (2010). The weirdest people in the world? *Behavioral and Brain Sciences, 33*, 61–135. http://dx.doi.org/10.1017/S0140525X0999152X.
Hill, A. K., Cárdenas, R. A., Wheatley, J. R., Welling, L. L. M., Burriss, R. P., Claes, P. et al. Puts, D. A. (2017). Are there vocal cues to human developmental stability? Relationships between facial fluctuating asymmetry and voice attractiveness. *Evolution and Human Behavior, 38*(2), 249–258. http://dx.doi.org/10.1016/j.evolhumbehav.2016.10.008.
Hodges-Simeon, C. R., Gaulin, S. J., & Puts, D. A. (2010). Different vocal parameters predict perceptions of dominance and attractiveness. *Human Nature, 21*(4), 406–427. http://dx.doi.org/10.1007/s12110-010-9101-5.
Hodges-Simeon, C. R., Gaulin, S. J., & Puts, D. A. (2011). Voice correlates of mating success in men: Examining "contests" versus "mate choice" modes of sexual selection. *Archives of Sexual Behavior, 40*(3), 551–557. http://dx.doi.org/10.1007/s10508-010-9625-0.
Hodges-Simeon, C. R., Gurven, M., & Gaulin, S. J. C. (2015). The low male voice is a costly signal of phenotypic quality among Bolivian adolescents. *Evolution and Human Behavior, 36*(4), 294–302. http://dx.doi.org/10.1016/j.evolhumbehav.2015.01.002.
Hodges-Simeon, C. R., Gurven, M., & Gaulin, S. J. C. (2018). *Sex steroid hormones and mucosal immunity in Amazonian adolescents: A test of the immunocompetence-handicap hypothesis.* (Under review).
Hughes, S. M., Dispenza, F., & Gallup, G. G., Jr. (2004). Ratings of voice attractiveness predict sexual behavior and body configuration. *Evolution and Human Behavior, 25*(5), 295–304. http://dx.doi.org/10.1016/j.evolhumbehav.2004.06.001.
Hughes, S. M., Harrison, M. A., & Gallup, G. G., Jr. (2002). The sound of symmetry: Voice as a marker of developmental instability. *Evolution and Human Behavior, 23*(3), 173–180. http://dx.doi.org/10.1016/S1090-5138(01)00099-X.
Hughes, S. M., Pastizzo, M. J., & Gallup, G. G., Jr. (2008). The sound of symmetry revisited: Subjective and objective analyses of voice. *Journal of Nonverbal Behavior, 32*(2), 93–108. http://dx.doi.org/10.1007/s10919-007-0042-6.
Idler, E. L., & Benyamini, Y. (1997). Self-rated health and mortality: A review of twenty-seven community studies. *Journal of Health and Social Behavior, 38*(1), 21–37. http://dx.doi.org/10.2307/2955359.
Jenkins, J. S. (2000). The lost voice: A history of the castrato. *Journal of Pediatric Endocrinology and Metabolism, 13*(Supplement), 1503–1508. http://dx.doi.org/10.1515/jpem-2000-s625.
Jones, B. C., Feinberg, D. R., Debruine, L. M., Little, A. C., & Vukovic, J. (2010). A domain-specific opposite-sex bias in human preferences for manipulated voice pitch. *Animal Behaviour, 79*(1), 57–62. http://dx.doi.org/10.1016/j.anbehav.2009.10.003.
Kalashnikova, M., Carignan, C., & Burnham, D. (2017). The origins of babytalk: Smiling, teaching or social convergence? *Royal Society Open Science, 4*(8), 170306. http://dx.doi.org/10.1098/rsos.170306.
Kandrik, M., Hahn, A. C., Han, C., Wincenciak, J., Fisher, C. I., Debruine, L. M., & Jones, B. C. (2017). Does the interaction between cortisol and testosterone predict men's facial attractiveness? *Adaptive Human Behavior and Physiology, 3*(4), 275–281. http://dx.doi.org/10.1007/s40750-017-0064-1.
Macpherson, A. J., McKoy, K. D., Johansen, F. E., & Brandtzaeg, P. (2008). The immune geography of IgA induction and function. *Mucosal Immunology, 1*, 11–22. http://dx.doi.org/10.1038/mi.2007.6.
Markova, D., Richer, L., Pangelinan, M., Schwartz, D. H., Leonard, G., ... Perron, M. Paus (2016). Age- and sex-related variations in vocal-tract morphology and voice acoustics during adolescence. *Hormones & Behavior, 81*, 84–96. http://dx.doi.org/10.1016/j.yhbeh.2016.03.001.
Martin, M., Blackwell, A. D., Gurven, M., & Kaplan, H. (2013). Make new friends and keep the old? Parasite coinfection and comorbidity in *Homo sapiens*. In J. Brinkworth, & K. Pechenkina (Eds.). *Primates, pathogens, and evolution* (pp. 363–387). New York: Springer.
Mazur, A., & Booth, A. (1998). Testosterone and dominance in men. *Behavioral and Brain Sciences, 21*(3), 353–397. http://dx.doi.org/10.1017/S0140525X98001228.
McDonald, J. H. (2014). *Handbook of biological statistics* (3rd ed.). Baltimore, Maryland: Sparky House Publishing.
Moffat, S. D., & Hampson, E. (1996). A curvilinear relationship between testosterone and spatial cognition in humans: Possible influence of hand preference. *Psychoneuroendocrinology, 21*(3), 323–337. http://dx.doi.org/10.1016/0306-4530(95)00051-8.
Mossey, J. M., & Shapiro, E. (1982). Self-rated health: A predictor of mortality among the elderly. *American Journal of Public Health, 72*(8), 800–808. http://dx.doi.org/10.2105/AJPH.72.8.800.
Muehlenbein, M. P., & Bribiescas, R. G. (2005). Testosterone-mediated immune functions and male life histories. *American Journal of Human Biology, 17*, 527–558.
Nakamura, D., Akimoto, T., Suzuki, S., & Kono, I. (2006). Daily changes of salivary secretory immunoglobulin A and appearance of upper respiratory symptoms during physical training. *Journal of Sports Medicine and Physical Fitness, 46*(1), 152–157.
Perneger, T. V. (1998). What's wrong with Bonferroni adjustments. *BMJ, 316*(7139), PMC1112991. http://dx.doi.org/10.1136/bmj.316.7139.1236.
Phillips, A. C., Carroll, D., Drayson, M. T., & Der, G. (2015). Salivary immunoglobulin A secretion rate is negatively associated with cancer mortality: The West of Scotland twenty-07 study. *PLoS ONE, 10*(12), e0145083. http://dx.doi.org/10.1371/journal.pone.0145083.
Pisanski, K., & Rendall, D. (2011). The prioritization of voice fundamental frequency or formants in listeners' assessments of speaker size, masculinity, and attractiveness. *The Journal of The Acoustical Society of America, 129*(4), 2201–2212. http://dx.doi.org/10.1121/1.3552866.
Puts, D. A. (2005). Mating context and menstrual phase affect women's preference for male voice pitch. *Evolution and Human Behavior, 26*(5), 388–397. http://dx.doi.org/10.1016/j.evolhumbehav.2005.03.001.
Puts, D. A., Apicella, C. L., & Cárdenas, R. A. (2012). Masculine voices signal men's threat potential in forager and industrial societies. *Proceedings of the Royal Society B: Biological Sciences, 279*(1728), 601–609. http://dx.doi.org/10.1098/rspb.2011.0829.
Puts, D. A., Hill, A. K., Bailey, D. H., Walker, R. S., Rendall, D., Wheatley, J. R. et al. Jablonski, N. G. (2016). Sexual selection on male vocal fundamental frequency in humans and other anthropoids. *Proceedings of the Royal Society B: Biological Sciences, 283*(1829), 20152830.

Puts, D. A., Hodges, C. R., Cárdenas, R. A., & Gaulin, S. J. (2007). Men's voices as dominance signals: Vocal fundamental and formant frequencies influence dominance attributions among men. *Evolution and Human Behavior, 28*(5), 340–344. http://dx.doi.org/10.1016/j.evolhumbehav.2007.05.002.

Puts, D. A., Jones, B. C., & DeBruine, L. M. (2012). Sexual selection on human faces and voices. *Journal of Sex Research, 49*(2–3), 227–243. http://dx.doi.org/10.1080/00224499.2012.658924.

Rantala, M. J., Moore, F. R., Skrinda, I., Krama, T., Kivleniece, I., Kecko, S., & Krams, I. (2012). Evidence for the stress-linked immunocompetence handicap hypothesis in humans. *Nature Communications, 3*, 694. http://dx.doi.org/10.1038/ncomms1696.

Roberts, M. L., Buchanen, K. L., & Evans, M. R. (2004). Testing the immunocompetence handicap hypothesis: A review of the evidence. *Animal Behaviour, 68*(2), 227–239. http://dx.doi.org/10.1016/j.anbehav.2004.05.001.

Sapolsky, R. M., Romero, L. M., & Munck, A. U. (2000). How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocrine Reviews, 21*(1), 55–89. http://dx.doi.org/10.1210/edrv.21.1.0389.

Searcy, W. A., & Nowicki, S. (2005). *The evolution of animal communication: Reliability and deception in signaling systems.* Princeton: Princeton University Press.

Simmons, Z. L., & Roney, J. R. (2009). Androgens and energy allocation: Quasi-experimental evidence for effects of influenza vaccination on men's testosterone. *American Journal of Human Biology, 21*(1), 133–135. http://dx.doi.org/10.1002/ajhb.20837.

Skrinda, I., Krama, T., Kecko, S., et al. (2014). Body height, immunity, facial and vocal attractiveness in young men. *Naturwissenschaften, 101*(12), 1017–1025. http://dx.doi.org/10.1007/s00114-014-1241-8.

Sullivan, D. A., & Allansmith, M. R. (1987). The effect of aging on the secretory immune system of the eye. *Immunology, 63*(3), 403–410.

Thornhill, R., & Gangestad, S. W. (2006). Facial sexual dimorphism, developmental stability, and susceptibility to disease in men and women. *Evolution and Human Behavior, 27*(2), 131–144. http://dx.doi.org/10.1016/j.evolhumbehav.2005.06.001.

Titze, I. R. (1994). *Principles of voice production.* Englewood, N.J.: Prentice Hall.

Trumble, B. C., Blackwell, A. D., Stieglitz, J., Thompson, M. E., Suarez, I. M., Kaplan, H., & Gurven, M. (2016). Associations between male testosterone and immune function in a pathogenically stressed forager-horticultural population. *American Journal of Physical Anthropology, 161*, 494–505. http://dx.doi.org/10.1002/ajpa.23054.

van Anders, S. M. (2010). Gonadal steroids and salivary IgA in healthy young women and men. *American Journal of Human Biology, 22*(3), 348–352. http://dx.doi.org/10.1002/ajhb.20997.

Volkmann, E. R., & Weekes, N. Y. (2006). Basal SIgA and cortisol levels predict stress-related health outcomes. *Stress and Health, 22*(1), 11–23. http://dx.doi.org/10.1002/smi.1077.

Ware, J. E. (1976). Scales for measuring general health perceptions. *Health Services Research, 11*(4), 396–415.

Zahavi, A. (1975). Mate selection—A selection for a handicap. *Journal of Theoretical Biology, 53*(1), 205–214. http://dx.doi.org/10.1016/0022-5193(75)90111-3.