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Voice Cues: Intersexual Selection



Katarzyna Pisanski (b^{1,2,3} and David Puts (b⁴)¹CNRS French National Centre for Scientific Research, DDL Dynamics of Language lab, University of Lyon, Lyon, France ²ENES Bioacoustics Research Lab, Jean Monnet

University of Saint-Etienne, Saint-Etienne, France

³Institute of Psychology, University of Wrocław, Wrocław, Poland

⁴Department of Anthropology, The Pennsylvania State University, Pennsylvania, PA, USA

Synonyms

Deceptive Signals; Formant Frequencies; Fundamental Frequency; Mate Choice; Nonverbal Communication; Reproductive Fitness; Secondary Sexual Characteristic; Sexual Selection; Vocal Attractiveness; Voice Modulation; Voice Pitch

Definition

Acoustic features of the voice, including fundamental and formant frequencies, communicate qualities of the vocalizer. The preferences of potential mates may have shaped these vocal parameters in both sexes over human evolution,

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contributing not only to large sexual dimorphisms but also to patterns of vocal modulation that leverage mate preferences.

Sexual Selection on the Human Voice and Vocal Attractiveness

In the human evolutionary sciences, men's voices are often compared to the magnificently ornamented tail of a male peacock or the imposing antlers of a red deer stag. While the resemblances may not be immediately apparent, these traits share a key attribute: They have been shaped by sexual selection, a type of natural selection favoring traits that increase mating success. Charles Darwin proposed two forms of sexual selection: intrasexual selection, in which same-sex competitors are the agents of selective pressures, often involving contests between males over mates and resources, and intersexual selection, in which potential mates are the agents of selection, most often involving mate choice of males by females (Darwin, 1859, 1871). Darwin recognized that these powerful processes can produce sexual dimorphism in phenotypic traits, including visual and vocal signals.

Converging evidence strongly suggests that key nonverbal properties of the human voice have been shaped by sexual selection, including the most salient vocal parameter, fundamental frequency (f_o), perceived as pitch. Not only is human voice pitch sexually dimorphic, but also

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this dimorphism is more extreme in humans than in any other extant great ape species (Puts et al., 2016). These sex differences in voice pitch emerge at puberty following a testosterone surge in males that enlarges the larynx and lengthens the vocal folds, causing the folds to vibrate more slowly (Titze, 1994), and leading to a modal f_0 among adult men that is about 75% lower than that of women (Pisanski et al., 2014). Such pubertal masculinization points to sexual selection on men's vocal anatomy and implicates testosterone as a key driver of sexual dimorphism in the human voice, as it is for other androgen-mediated secondary sexual characteristics in the face and body (Feinberg, 2008). While a low f_0 is a relatively weak predictor of body size and physical strength within adults of each sex (Aung & Puts, 2020; Pisanski et al., 2014 for meta-analyses), men with lower-pitched voices have higher testosterone and lower cortisol levels, and this may indicate a healthy underlying condition and perhaps superior immune function (Aung & Puts, 2020; Puts et al., 2016; Schild et al., 2020).

Ultimately, the greatest power of voice pitch may lie in its perceptual effects on listeners. Regardless of the information content of voice pitch, hundreds of studies show that listeners associate low pitch with large size, physical strength, dominance, and masculinity (Pisanski & Bryant, 2019 for review). Low pitch also communicates a sense of power, leadership, authority, and competence in both sexes (Aung & Puts, 2020 for review; Klofstad et al., 2012) and is often perceived as attractive in men's voices (Pisanski & Feinberg, 2019 for review). The mechanisms driving these perceptual effects and the degree to which they reflect honest signals or deception remain debated (Feinberg et al., 2018; Pisanski & Reby, 2021; Puts & Aung, 2019), as do the relative but not mutually exclusive contributions of same-sex contests versus mate choice in the evolution of male and female vocal signals (Kordsmeyer et al., 2018; Puts, 2010; Puts et al., 2012; Puts & Aung, 2019). Nevertheless, there now exists ample empirical evidence that both intrasexual and intersexual selection operated to some extent on men's voices, particularly on voice pitch, to intimidate rivals and attract mates.

The vast majority of research on human sexual selection has focused on men's rather than women's traits as sexual ornaments and/or displays of threat and formidability. This is likely because sexual selection operates more strongly on male than female traits in most mammals (Andersson, 1994), as males tend to invest less in offspring and are capable of monopolizing the investment of multiple females (Trivers, 1972). Deep voices in men are generally preferred by heterosexual women, and in turn, men with lower-pitched voices tend to have higher social status and mating success compared to men with higher-pitched voices (Aung & Puts, 2020; Pisanski & Feinberg, 2019; Schild et al., 2020 for reviews). However, women's preferences for deep male voices appear adaptively flexible (Puts et al., 2012 for review). For example, heterosexual women show stronger preferences for low voice pitch and for other masculine, sexually dimorphic characteristics in men's voices, faces, body shapes, and body odors in the context of shortterm compared to long-term mating (Little et al., 2011; Puts, 2005; Schild et al., 2020). This flexibility may reflect contextual shifts in the costs and benefits of mating with masculine males. Namely, masculine men may not only confer superior genes or immunocompetence to their offspring, but may also pose a higher risk of infidelity and lower investment in those offspring, which can be particularly disadvantageous to women in a longterm relationship (O'Connor et al., 2014). Such costs may also help to explain why women's preferences for low voice pitch have their limits, with hypermasculinized voices being relatively dis-preferred (Puts et al., 2012 for review).

Women also show preferences for low formant frequencies and thus a deep timbre in men's voices (Pisanski & Feinberg, 2019 for review). While formants are also sexually dimorphic, sex differences in formants are less extreme than in fundamental frequency, and women's formant preferences are less consistently replicated than are those for voice pitch (e.g., Schild et al., 2020). Formants are resonances of the vocal tract that affect perceptions of vocal timbre. Because formants scale allometrically with height owing to anatomical constraints on skull size and vocal tract length (Fitch, 2000), their relative spacing moderately predicts body size both between and within the human sexes (Pisanski et al., 2014). A resonant voice with densely spaced formants may therefore sound attractive in men because it can signal tall stature, which itself predicts social and sexual success in men across a range of industrialized countries (Stulp & Barrett, 2016). At the same time, female preferences for deep and sonorous male voices may have shaped men's neurocognition and vocal anatomy to exploit such preferences. For example, selection may have favored a capacity in men to dynamically lower f_{o} and formants, thereby exaggerating the impression of physical formidability and other traits linked to mate quality, as described in the following section (see Voice modulation for trait exaggeration).

Fewer studies have examined men's preferences for women's voices, and so what makes a woman's voice attractive, and why, is still not entirely clear. Early experimental research pointed to a general preference for vocal femininity, suggesting that a relatively higher pitch is perceived as attractive in women's voices (Pisanski & Feinberg, 2019; Puts et al., 2012 for reviews). A preference for high voice pitch may be linked to a general preference for youth and fertility in female partners, often expressed by heterosexual men (Buss & Schmitt, 2019), if women's voice pitch reliably indicates current fertility or potential future reproduction. Women's voices change systematically across the life span, including becoming lower pitched during menopause, and so may indeed indicate general reproductive potential. However, the extent to which dynamic fluctuations in fertility can be gauged from vocal signals remains poorly understood (Kreiman & Sidtis, 2011 for review).

A handful of more recent studies suggest that men sometimes prefer relatively *lower* pitch in women's voices. For example, in a real-life speed dating paradigm, Pisanski et al. (2018) found that heterosexual men preferred women who spoke with a lower pitch, with women's f_o explaining as much as 55% of the variance in men's mate preferences. In turn, women spoke with a lower-pitched voice on dates with men they preferred and who were also most often desired by the other women. This aligns with studies on intentional voice modulation showing that women lower their voice f_0 when instructed to sound sexy (Hughes et al., 2014). Two possible explanations are that dynamically lowering pitch can communicate maturity, competence, and social dominance in women much as it does in men, traits that could theoretically be beneficial and attractive among women in some modern sociocultural contexts. Lowering f_0 may also communicate sexual interest. Evidence that men sometimes prefer lower pitch in women's voices also corroborates research on men's preferences for femininity/masculinity in women's faces, where some degree of variability is likewise observed (Puts et al., 2012).

Adding to the mixed findings regarding preferences for high versus low pitch in women's voices, a large correlational study found that natural variation in female voice pitch did not predict attractiveness judgments when other acoustic parameters were statistically controlled (Puts et al., 2016). In sum, the underlying acoustic predictors of voice attractiveness in women remain an open question. The answer may lie in a broader constellation of nonverbal vocal parameters that have received comparatively little research attention relative to pitch. Another possibility is that voice preferences are dynamic - varying by social context, audience, and/or the intention of the vocalizer. The human capacity to voluntarily and often deceptively modulate our voices to influence how others perceive us, including with the intention to attract a potential mate, may thus offer critical insight into how sexual selection has operated on vocal signals, and on our ability to control them.

Voice Modulation for Trait Exaggeration

Deceptive signals are common in the animal kingdom (Searcy & Nowicki, 2005). In most communication contexts, including mate choice and same-sex contests, the interests of signalers and receivers do not entirely overlap or may even be opposed. In acoustic communication, selection thus often favors the evolution of vocal signals that can manipulate the responses of receivers to the potential benefit of the deceptive signaler, while simultaneously minimizing the risks of deception such as reputational and retaliation costs. At the same time, selection operates on listeners to detect and evade deceptive signals. This honest signaling paradigm forms the foundation of an evolutionary arms race in which both the vocalizer and the listener are expected to behave in ways that increase their own reproductive fitness (Dawkins & Krebs, 1978).

Deceptive signaling via voice modulation appears to have played a role in the evolution of human vocal communication (Leongómez et al., 2021 for theme issue), including in mating contexts (Hughes & Puts, 2021). For example, although voice pitch explains little variation in men's actual heights (Aung & Puts, 2020; Pisanski et al., 2014), men with deeper voices are perceived as substantially taller (Puts et al., 2016), and lowering voice pitch makes men sound taller still (Pisanski & Reby, 2021). This perceptual "low is large" bias may be critical to understanding the communicative power and attractiveness of deep voices in men. This is because large size is a key predictor of male resource holding potential and reproductive success in a range of species (Andersson, 1994), including humans. Indeed a host of benefits are linked to human height, particularly among men (Stulp & Barrett, 2016 for review), suggesting that the capacity to exaggerate size may increase mating success in men as it does in many other male animals (Searcy & Nowicki, 2005). Moreover, humans possess superior neural control over the vocal anatomy compared to other terrestrial mammals, including other primates, and are therefore particularly adept at voluntarily modulating vocal output (Ackermann et al., 2014; Pisanski et al., 2016). Taken together, this suggests that vocal size exaggeration may be common in our species.

Another strategy to exaggerate body size observed across the animal kingdom is to lower the resonances of the vocal tract, reducing formant spacing. Owing to anatomical constraints that impose a degree of honesty, formants can reliably signal true body size in many terrestrial mammals (Fitch & Hauser, 2003), including humans (Pisanski et al., 2014). Yet animals have evolved an impressive array of anatomical adaptations to lower their formants and give the impression of a larger size (Charlton & Reby, 2016; Fitch & Hauser, 2003). Red deer stags, for example, have descended larynges that they pull down even lower into their vocal tracts during competitive roaring contests with other males to further decrease their formant frequencies. Not only does this deter rivals, but it also attracts hinds (Taylor et al., 2016 for review). When asked to "sound larger," humans volitionally lower both their f_{o} (pitch) and formants (Pisanski et al., 2016b). Human listeners can often detect such deceptive size exaggeration, and they recalibrate their height judgments when they do, but remain biased in their body size assessments when deception goes undetected, suggesting that vocal size exaggeration is effective on average (Pisanski & Reby, 2021).

Beyond sounding bigger, can humans also make themselves sound more socially dominant, competent, or attractive? This too could prove to be an advantageous strategy to increase one's success in the mating market. Lab-based studies indicate that human vocalizers can indeed manipulate how dominant, masculine/feminine, authoritative, and intelligent they sound, "on demand," in part by modulating their fundamental and formant frequencies; however, increasing vocal attractiveness appears more difficult (Cartei et al., 2012; Fraccaro et al., 2013; Hughes et al., 2014; Sorokowski et al., 2019). Perception studies further suggest that listeners can often detect such deceptive voice modulation, such as when vocalizers attempt to sound more attractive (Leongómez et al., 2014) or physically larger than their true body size (Pisanski & Reby, 2021). Nevertheless, listeners in these experiments still tended, on average, to perceive deceptive vocalizers as respectively more attractive and as larger, especially when deception went undetected (Leongómez et al., 2014; Pisanski & Reby, 2021). This suggests that while selection is likely to have operated on listeners to detect deception in order to mitigate its costs, deceptive signals still bias listeners' judgments on the whole in ways that may benefit the signaler, and thus a degree of deception may still pay off. Ultimately, the extent to which voice modulation offers an effective mating strategy in humans will require more data regarding the real-world costs and benefits of this behavior, such as real-life mate choice decisions (Pisanski et al., 2018) or actual competition outcomes (Cheng et al., 2016).

Although vocal deception in a mating context is often achieved by manipulating the nonverbal parameters of speech, for example, during conversations with potential mates or rivals (Hughes & Puts, 2021 for review), this can also be achieved through the production or modulation of nonverbal vocalizations such as agonistic roars (Raine et al., 2019) or pleasure moans and groans (Brewer & Hendrie, 2011). While human nonverbal vocalizations remain remarkably understudied compared to speech, they are excellent candidates for amplifying mate-relevant information in part due to their cross-cultural universality, lack of linguistic constraints, and robust form-function mappings (Pisanski et al., 2022 for review). Volitional roars, for example, maximize the perceived strength and size of humans more effectively than does neutral or emotional speech (Raine et al., 2019), largely owing to a higher proportion of harsh-sounding nonlinear phenomena that signal aggression while also lowering the perceived voice pitch of the vocalizer (Anikin et al., 2021). In humans, vocal attractiveness can also be communicated through the singing voice (Valentova et al., 2019).

Conclusion and Future Directions

There now exists ample and converging evidence that nonverbal parameters of men's voices have been shaped by sexual selection to communicate or exaggerate fitness-related qualities of the vocalizer. Fundamental frequency and formant frequencies represent two particularly sexually dimorphic and salient vocal parameters that together explain a substantial proportion of variance in listeners' voice-based perceptions and preferences. For example, despite the relatively weak associations between f_0 and size or strength within sexes, listeners consistently perceive men and women with low-pitched voices as relatively larger and stronger. Lower pitch is in turn typically preferred in men's voices and has been found to predict men's social and reproductive success, with the important caveat that women's preferences vary adaptively in ways that are likely to maximize the benefits and limit the costs of choosing a mate with a masculine, deep voice. The limited body of research on women's voice attractiveness has produced contradictory results suggesting that heterosexual men sometimes prefer a relatively higher voice pitch, and sometimes a relatively lower voice pitch, with few studies examining other acoustic correlates of women's vocal attractiveness. The evolutionary and sociocultural mechanisms driving variance in voice preferences, and their real-world outcomes on men's and women's reproductive fitness, warrant further investigation.

As prime candidates for acoustic parameters shaped by sexual selection, fundamental and formant frequencies have received almost exclusive attention in voice attractiveness research. More work is needed to uncover other nonverbal vocal parameters or speech patterns that may predict mate choice decisions. Bottom-up approaches have, for example, shown that amplitude, breathiness, and speed of speech can influence the attractiveness of both men and women's voices (Babel et al., 2014). The remarkable capacity in humans to readily control and alter all of these nonverbal parameters also implies that voice modulation may be a promising strategy to exaggerate traits, from size and social dominance to competence and trustworthiness, in order to adaptively increase a speaker's perceived attractiveness and mate quality (Hughes & Puts, 2021; Pisanski et al., 2016a). While deception has been extensively studied in animal signaling systems (Searcy & Nowicki, 2005), voice modulation is a relatively recent and burgeoning area of research in the human voice sciences that promises to offer ample insight into the evolution and functions of vocal communication (Leongómez et al., 2021).

The logic of studying sexual selection of men's traits and women's preferences for those traits is well grounded in evolutionary theory (Buss &

Schmitt, 2019; Darwin, 1871; Trivers, 1972), but modern humans are socially and culturally complex. Mate preferences and same-sex competition are expressed, to some extent, by both men and women, perhaps in part because men invest more in their offspring than is typical among male mammals. Thus, men's preferences for women's voices and same-sex competition between women may have also contributed to sexual dimorphism in the human voice, albeit to a lesser extent than did women's preferences for men's traits and male-male contests (Hughes & Puts, 2021; Puts et al., 2012 for reviews). Human sexual relationships also span a variety of nontraditional and nonheterosexual forms that have been largely neglected in research on human mate preferences (but see Valentová et al., 2013; Zhang et al., 2018). Mate preferences furthermore vary, sometimes considerably, across human populations as a function of variable ecological conditions and sociocultural norms that impose differential costbenefit trade-offs in mate choice decisions, highlighting an urgent need to study voice preferences across diverse cultures (Bryant, 2021; Pisanski & Feinberg, 2013 for reviews). A comprehensive account of how the human voice has been shaped by sexual selection must inevitably consider all of this complexity and variability.

Cross-References

- Cross-cultural Comparisons: Intersexual Selection
- Good Genes Hypothesis
- Intrasexual Mate Competition (Men): Testosterone and Formidability
- Intrasexual Mate Competition (Women)
- ► Testosterone: Male Reproductive Health
- ► Voice Pitch: Formidability
- Vocal Pitch: Infidelity

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