VOCAL ATTRACTIVENESS

David R. Feinberg

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews

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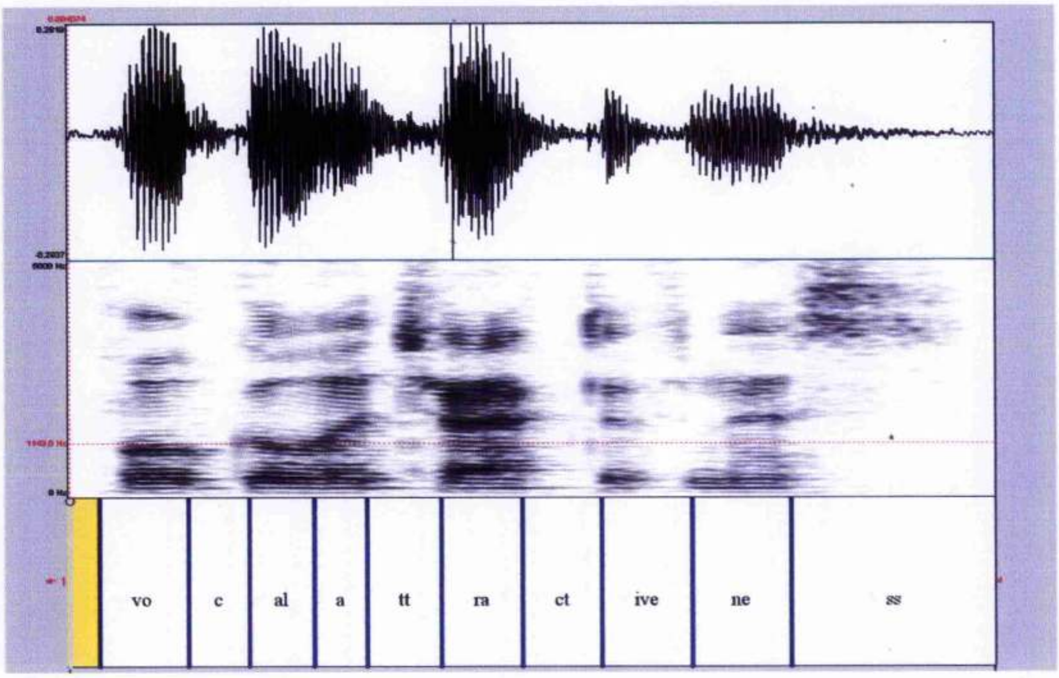
Vocal Attractiveness



David R. Feinberg

October 2005

A thesis submitted to the University of St Andrews for the degree of Doctor of Philosophy in the School of Psychology

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Publication list/author roles

Parts of this thesis are adapted from the publications listed below:

Chapter 5 adapted from
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Chapter 6 adapted from:
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Author roles:
Feinberg, DR: experimental design, recorded voices, stimuli generation, acoustic analysis, running of participants, statistical analysis, wrote paper
Jones, BC: edited paper, running of participants, aided in stimuli calibration
Little, AC: aided in statistical analysis, edited paper
Burt, DM: programmed stimuli presentation software
Perrett, DI: theoretical input, edited published paper

Chapter 8 adapted from:
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Author roles:
Feinberg, DR: experimental design, recorded voices, stimuli generation, acoustic analysis experiment setup, running of participants, statistical analysis, writing

Jones, BC: aided in menstrual cycle classification, running of participants, editing of published paper
Law Smith, MJ: aided in interpreting hormone assays, running of participants
Moore, FR: Programmed HTML code for diary data, running of participants
DeBruine, LM: running of participants, editing of published paper
Cornwell, RE: running of participants
Hillier, SG: Hormone assays
Perrett, DI: theoretical input, aided in menstrual cycle classification, editing of published paper

Chapter 10 adapted from:
Feinberg DR, Jones BC, DeBruine LM, Moore FR, Law Smith MJ, Cornwell RE, Tiddeman BP, Boothroyd, LM, Perrett DI. (2005) The voice and face of woman: one ornament that signals quality? Evolution and Human Behavior. 26, 398-408.

Author roles

Feinberg, DR: experimental design, recording of UK voices, UK photography, acoustic analysis, measuring UK facial-metric femininity, averaged faces, ran UK participants, statistical analysis, wrote paper
Jones, BC: recording of Canadian voices, Canadian photography, editing paper
DeBruine, LM: Canadian photography, recording of Canadian voices, delineating Canadian faces, measuring Canadian facial-metric femininity, editing paper
Moore, FR: HTML code for online experiment, running participants
Law Smith: running participants
Cornwell, RE: Deliniating UK faces, running participants
Tiddeman, BP: programming face morphing software, coding software for facial-metric measurements
Boothroyd, LM: running participants on raw face experiment
Perrett, DI: theoretical input, editing published paper

Also, in chapter 9, Martin Sharpe and Emad Al-Dujaili analysed testosterone and cortisol.

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Abstract

In this thesis, I aimed to explore vocal attractiveness from an evolutionary perspective: how listener's preferences for vocal qualities of potential partners could increase mating success and reproductive success. Chapters 1-4 outline the background to the thesis, reviews acoustics, sexual selection theory, and human mate-choice.

In chapter 5, I correlated attributions made to voices to the acoustic properties of the voices. In men's voices, pitch negatively predicted vocal attractiveness. Attributions of masculinity, size, age, health and vocal attractiveness were all positively correlated. In women's voices, pitch, formant dispersion and perceived health positively predicted vocal attractiveness. Masculinity, size and age negatively predicted vocal attractiveness.

In chapter 6, I measured the effect of manipulating fundamental and/or formant frequencies (apparent vocal-tract length) on vocal attributions. Women found men's voices with lowered voice pitch and decreased formant dispersion more attractive, masculine, large, older and healthier. Women's size predicted preference for male vocal-tract length.

In chapter 7, I explored attitudes to voices speaking vowels and whole sentences using a correlation design and acoustic manipulations. Women's self-rated attractiveness positively predicted vocal masculinity preferences.

Most of the remaining studies focus on how hormones relate to vocal production and perception. Women with less oestrogen showed the biggest menstrual cycle shifts in vocal masculinity preferences, preferring masculinity most in the fertile phase (chapter 8). Men's testosterone levels predicted the size of changes in attributions of dominance to men's voices (chapter 9). Women's voice pitch correlated with facial-metric masculinity and facial attractiveness (chapter 10). Men preferred women's voices with raised pitch to lowered pitch at multiple levels of starting pitch (chapter 11). These findings indicate men preferred femininity to averageness. In chapter 12, I relate the work in this thesis to other work and the broader evolutionary perspective.

Chapter 1

General introduction

1 Different strokes for different folks

There are many psychological approaches one can take to study vocal attractiveness. Vocal attractiveness through a social psychological perspective focuses on how vocal stereotypes are formed (Berry & Hansen, 2000; Berry, Hansen, Landrypester, & Meier, 1994; Tusing & Dillard, 2000; Zuckerman & Driver, 1989; Zuckerman, Miyake, & Elkin, 1995). A neuroscientific approach to vocal attractiveness studies how and where sound is represented in the brain, and what types of sound activate different brain regions differently (Walpurger, Pietrowsky, Kirschbaum, & Wolf, 2004; Wang, Lu, Snider, & Liang, 2005). A cognitive approach, explores how voices are processed (Bedard & Belin, 2004; Belin, Zatorre, Lafaille, Ahad, & Pike, 2000; Fecteau, Armony, Joanette, & Belin, 2005). An evolutionary approach to studying vocal attractiveness takes into account how voice qualities might be perceived in a mating and/or competitive context (Collins & Missing, 2003; Collins, 2000; Feinberg & Jacobson, 2001; Hughes, Dispenza, & Gallup, 2004; Hughes & Gallup, 2003; Hughes, Harrison, & Gallup, 2002; Puts, 2005).

2 The chosen path

In this thesis, I predominantly take an evolutionary approach to vocal attractiveness. Studies from social psychology have identified that stereotypes of which types of voices are attractive can form at a young age (Berry et al., 1994). Other social psychology studies have shown that certain socially relevant stereotypes such as dominance (Tusing & Dillard, 2000), maturity (Zuckerman et al., 1995) and a pro-social attitude (Zuckerman & Driver, 1989) may influence vocal attractiveness. The social psychological explanation does a good job of explaining what stereotypes are attractive, but does not explain how and why certain stereotypes are attractive. On the other hand, a cognitive approach studies how voices are processed (see Bedard & Belin, 2004; Burton & Bonner, 2004; Fecteau et al., 2004). Thus, the cognitive approach answers the question of how certain voice types might be attractive because of the way they are represented in the brain. An evolutionary approach is unique in that can combine research on how voices are processed and encoded (cognitive psychology and behavioural neuroscience), with research on what stereotypes are formed (social psychology), and attempt to explain why certain types of voices are attractive. This is normally done by applying frameworks provided by evolutionary theory.

2.1 An evolutionary perspective

According to Andersson (1994) the most studied sexually selected trait in the animal kingdom is some aspect of a vocalisation (in terms of number of publications and positive results). Andersson (1994) tallies 81 species (mostly anurans, birds and insects) in which some aspect of animal vocalisations are used as displays related to sexual selection. Thus studying the relationship between animal vocalisations and mate choice has been a fruitful enterprise.

To try to understand how acoustic properties of the human voice relate to mate choice decisions, one can look around the animal kingdom to find similarities and differences between species in terms of what different acoustic features signal, and what about the animals' ecologies and mating systems change how they are interpreted by perceivers.

The mammalian species that has been studied in a way most like how humans have been studied, in terms of vocal production and how the same vocal features relate to mate choice is red deer (*Cervus elaphus*). Red deer are a species that have ruts, or breeding seasons, usually every autumn (McComb, 1987). During the rut, males advertise their status to females through roar vocalisations. Deer roar vocalisations are special signals, whereas the signals studied in human vocalisations occur in all voiced speech (Collins 2000; Collins 2003). Nevertheless, the impact of frequency components of anuran and avian vocalisations have been studied extensively (see see Fitch & Hauser, 2002; Hauser, 1996, for reviews).

McComb (1991) found that roaring rate of male red deer predicted how attractive males were to females. In this experiment, McComb (1991) also manipulated the fundamental frequency of male red deer roars, but observed no systematic effect on female mate choice. Reby & McComb (2003) discovered that formant frequencies (the resonant frequencies of the vocal-tract) were a more salient cue to body size (i.e. body weight) in red deer than fundamental frequency was (Reby & McComb, 2003). Indeed, male red deer with large body size (weight) and large vocal-tracts enjoy the highest reproductive success (Reby & McComb, 2003).

Playback studies have shown that male red deer, whose roars were manipulated to have large apparent vocal-tracts (indicative of large body size), drew more attention from other males than male red deer whose roars were manipulated to have small apparent vocal-tract lengths. This suggests that roaring is not only used in female choice, but male-male competition (Reby et al., 2005).

Humans on the other hand, show a different pattern in terms of which acoustic properties of the male voice are attractive to females. Collins (2000) demonstrated that women prefer men with low fundamental frequencies, not large vocal-tracts. So, one can ask, why are particular acoustic properties of the voice attractive in some species, but not others? The answer may lie in what physical parameters these acoustic properties of the voice relate to, and how the different ecologies and mating systems of the animals influence how different species use different signals of mate quality.

For example, fundamental frequency does not relate to body size in adult humans (Lass & Brown, 1978) or red deer (Reby & McComb, 2003). By contrast, fundamental frequency predicts men's testosterone levels, testicle size throughout puberty (Harries, Hawkins, Hacking, & Hughes, 1998; Harries, Walker, Williams, Hawkins, & Hughes, 1997) and testosterone at adulthood (Dabbs & Mallinger, 1999). This later finding indicates that either pubertal testosterone level correlates with adult testosterone level or there is some behavioural relationship between voice pitch and testosterone in adult men. Nevertheless, testosterone related traits may be attractive in men because they may be cues to dominance (Mazur & Booth, 1998), long-term health (Rhodes, Chan, Zebrowitz, & Simmons, 2003) and heritable immunity to infection (Folstad & Karter, 1992; see chapters 3 & 4 for review). Fundamental frequency might also relate to prenatal testosterone as prenatal testosterone is involved in setting up testosterone receptors for use later in life (see Manning, Brundred, & Flanagan, 2002; Manning, Bundred, Newton, & Flanagan, 2003; Newman, Butler, Hammond, & Gray, 2000), although this has not yet been empirically demonstrated. It is unknown if voice pitch (fundamental frequency) of red deer relates to hormonal qualities.

On the other hand, formant frequencies (acoustic features tied to vocal-tract length) predict body size (height and/or weight) in both red deer and humans (Reby & McComb, 2003; Collins & Missing, 2003). In male red deer, vocal-tract length is positively related to reproductive success. In humans, females have not yet been shown to exhibit systematic preferences for vocal-tract length. In both species, body size is a likely indicator of access to resources and status. Red deer appear to use vocal-tract length as an indicator of status (Reby et al., 2005). By contrast, humans may be using the wrong vocal signals to determine body size. Studies have shown that humans misuse fundamental frequency as a cue to body size in adults, when fundamental frequency may only relate to body size throughout physical development (Huber, Stathopoulos, Curione, Ash, & Johnson, 1999) and between sexes (Childers & Wu, 1991; Rendall, Kollias, Ney, & Lloyd, 2005). Thus people seem to overextend the perception of low pitch as being associated with large body size to adults (Collins, 2000; Fitch 1994; Fitch & Hauser, 1995; Smith et al., 2005). Thus inaccurate attributions of body size to voice pitch may overshadow accurate perceptions of size given by formant frequencies, especially in mate-choice relevant decisions (Collins, 2000; Fitch, 1994; Fitch & Hauser 1995).

2.2 Here we go

The goal of this thesis is to explore vocal attractiveness from an evolutionary perspective. I focus primarily on how hormones influence vocal qualities and how hormones influence how voices are perceived. I utilise correlational and experimental methodologies. Using correlations, I attempt to identify specific acoustic cues to attractiveness and other attributions that are mate-choice relevant. Then, using manipulations, I test the role of specific acoustic parameters (in isolation) on attractiveness. Whilst I am not able to administer exogenous hormones (and may not want to as they can act differently than endogenous hormones by stopping the production of endogenous hormones), by utilising natural variation in hormone levels, such as menstrual cycle in women and diurnal shifts in testosterone and cortisol in men, I am able to conduct natural experiments investigating the effects of hormonal variation on voice perception. I do have data concerning hormone levels and voice qualities; however, due to constraints of space and time, they will not be reported in this thesis. Briefly, I have found, however, that among women, within a menstrual cycle phase, level of urinary oestrogen metabolite is positively related to fundamental frequency and formant dispersion. I have also found that among women, within a menstrual cycle phase, urinary progesterone metabolite is positively related to jitter. I found that within women, across the menstrual cycle, jitter is elevated in the luteal (high progesterone) menstrual cycle phase. No other measured acoustic properties (i.e. fundamental frequency, formant dispersion and shimmer) changed over the menstrual cycle. Among men, testosterone was negatively related to fundamental frequency and this relationship was much stronger than that reported in Dabbs & Mallinger (1999). In this study, unfortunately, voices were only recorded in the afternoon. Thus, tracking diurnal shifts in vocal features was not possible.

First, in chapter 2, I outline how speech signals are represented physically and produced and interpreted aurally. Next, in chapter 3, I present a short review of topics in sexual selection relating to sexual dimorphism. In chapter 4, I present a review of topics relevant to this thesis in the area of human mate choice. These chapters provide a background for the empirical work on human attraction to vocal characteristics in the remainder of the thesis.

In chapter 5, I test for correlations between vocal attributes and acoustic properties of the men and women's voices. Vocal attributions include men's and women's ratings of attractiveness, masculinity/femininity, size, age and health made to peer-aged opposite sex voices (speaking monopthong vowel sounds). Acoustic measurements include fundamental frequency (pitch), formant dispersion (apparent vocal-tract length), and jitter and shimmer (periodic variation in the fundamental frequency and in the amplitude of the fundamental frequency).

The purpose of chapter 5 is to identify specific acoustic correlates of vocal attractiveness. The purpose of chapter 6 is to isolate acoustic properties of the voice by utilising manipulations of fundamental and formant frequencies applied to vowel sounds. Here I test the effect of direct manipulations of single and multiple acoustic features on perceptions of attractiveness, masculinity, size, age and health. I also investigate how age, height and weight of listeners might affect how listeners perceive different voice qualities.

The purpose of chapter 6 is to identify individual differences in preferences for male voices. There are other potential factors involved in human mate choice decisions that have not yet been investigated. In other species that paternally invest, such as sticklebacks and guppies, female condition predicts the strength of their preferences for sexual dimorphism in male guppies (Bakker, Kunzler, & Mazzi, 1999; Lopez, 1999). In humans, similar variation in female preferences for male facial symmetry and facial masculinity has been observed (Little, Burt, Penton-Voak, & Perrett, 2001; Penton-Voak et al., 2003). This variation in preferences may reflect that men with high testosterone are less likely to be in committed relationships and invest in offspring than men with low testosterone are likely to be (Burnham et al., 2003; Gray, 2003; Gray, Campbell, Marlowe, Lipson, & Ellison, 2004; Gray, Chapman et al., 2004; Gray, Kahlenberg, Barrett, Lipson, & Ellison, 2002). Little et al. (2001) and Penton-Voak et al (2003) found that attractive women (as rated by themselves and by others) and women with feminine waist-to-hip ratios had stronger preferences for masculine male face shape than less attractive and masculine bodied women. This effect was most pronounced when women considered male faces as long-term partners. Therefore, attractive and feminine women are thought to have the strongest preferences for male masculinity because they might secure masculine men as long-term mates. To the best of my knowledge there is no published data showing that feminine and attractive women *do* secure masculine men as long-term mates, a study by DeBruine et al. (unpulished data) supports this hypothesis. If testosterone is reflected in measures of facial (Penton-Voak & Chen, 2004) and vocal (Dabbs & Mallinger, 1999) masculinity, than how attractive women consider themselves to be should also predict preferences for masculinity in men's voices. I test this hypothesis in chapter 7. Also in chapter 7, I test if fundamental frequency and perceived masculinity influence the attractiveness of men's voices when speaking sentences instead of vowel sounds. This is an attempt to examine previous work (see chapters 5 & 6) in a situation more representative of real life.

High roaring rate (a correlate of male quality) of male red deer advances the date of oestrus in female red deer (McComb, 1987). Regarding reproductive cycles in humans, women appear to prefer masculinity more at fertile parts of the menstrual cycle, as opposed to less fertile stages (Johnston, Hagel, Franklin, Fink., & Grammer, 2001; Penton-Voak & Perrett, 2000b; Penton-Voak et al., 1999). Similarly, if masculinity of faces and voices reflect common underlying qualities, the menstrual cycle should also shift women's preferences for masculinity in men's voices. Combining predictions from chapter 7 and those from menstrual cycle studies of face preferences, if women with features reflecting higher oestrogen levels (i.e. attractive faces and feminine body shapes) can secure masculine men as long-term mates, women with lower oestrogen levels should show the strongest menstrual cycle shifts in attraction to masculinity in men's voices. I test these hypotheses in chapter 8.

All of my own studies that I have mentioned investigate attraction to voices from the opposite sex. Another important factor in sexual selection is dominance and male-male competition. Manipulations of apparent vocal-tract length in male red deer have been shown to alter their apparent dominance to other male red deer (Reby et al., 2005). Manipulations of fundamental and formant frequencies should also alter the apparent dominance of human voices. Attributions of dominance, however, may rely on the hormonal state of the perceiver. Testosterone changes diurnally and is higher in the morning than in the afternoon (Dabbs, 1990). As testosterone increases self perceived dominancė (see Salvador, 2005, for review), men may rate voices (particularly subordinate voices) as less dominant when the listener's own testosterone is raised. I test these hypotheses in chapter 9.

Except chapter 5, the studies of mine that I mentioned only encompass women's attraction to men's voices. I return to women's voices in chapter 10. Collins & Missing (2003) found that female vocal and facial attractiveness were intercorrelated. Kamachi et al. (2003) found that people were able to correctly match the identity of faces and voices with reasonable accuracy. Neither study, however, has identified a potential mechanism by which these judgements are made. Individual identity in voices can be discriminated with striking accuracy using fundamental and formant frequencies (Bachorowski & Owren, 1999) –both potential acoustic correlates of femininity and attractiveness of women's voices (Collins & Missing, 2003). Femininity also plays a strong role in differentiating individual faces (O'Toole et al., 1998) and in facial attractiveness (Perrett et al., 1998; Rhodes, Hickford, & Jeffery, 2000). Thus, the degree to which femininity is expressed in the face and voice may explain why attractiveness correlates within and between the two modalities and why identity in the face can be matched to the identity of the voice at rates significantly above chance level. One reason facial and vocal femininity may be expressed to a similar degree is that that both facial femininity (Law Smith et al., In Press) and women's voice pitch (Abitbol, Abitbol, & Abitbol, 1999; Chae, Choi, Kang, Choi, & Jin, 2001) may be positively related to oestrogen levels. In chapter 10, I explore the potential relationships between voice pitch and an objective measure facial femininity, and if voice pitch can predict the attractiveness of faces.

In chapter 10, I test how cross-modal indices of femininity were related, and if vocal femininity predicted facial attractiveness. Evidence that femininity of the voice is attractive, however, is limited. Average configurations of faces (Langlois & Roggman, 1990), non-face visual objects (Halberstadt & Rhodes, 2000, 2003) and music (Repp, 1997) have been found attractive. Nonetheless, preferences for facial femininity have been shown to supersede preferences for averageness in female faces (Perrett et al., 1998; Perrett, May, & Yoshikawa, 1994). Although Collins & Missing (2003) found that fundamental frequency of the voice positively predicted vocal attractiveness, they did not report whether the voice pitch in their sample was representative of that of the general population. Thus if the mean voice pitch from the sample utilised in Collins & Missing (2003) was lower than the population mean, any observed preferences for high voice pitch in Collins & Missing (2003) could have reflected preferences for averageness. In Chapter 11, this topic will be investigated using fundamental frequency manipulations of women with high, average and low starting fundamental frequencies (voice pitch). If men prefer averageness in women's voices, adding femininity (raising voice pitch) to already high-pitched voices increases their attractiveness will make them less attractive. Another aim of this study is to examine if fundamental frequency, in isolation, is a salient cue to female vocal attractiveness.

Lastly, in chapter 12, I will relate my findings to other's work and the broader evolutionary perspective on vocal attractiveness.

Chapter 2

Acoustics review

1. Differences between human and non-human primate vocal apparatus

At rest, the adult human larynx is positioned lower in the neck than in non-human primates (see Fitch, 2000a, for review). The epiglottis of human infants, along with non-human primates contacts the nasal passages, allowing breathing and swallowing at the same time. As infants age the larynx drops such that by puberty, the female larynx is nearly at its final position. The male larynx, however, descends further during puberty. After infancy, the larynx is descended enough in both sexes such that people cannot swallow and breathe at the same time. In humans, the lower position of the larynx in the neck, the larger pharyngeal cavity and positioning of the tongue allow for a greater range of phonation than in other animals (Fitch, 2000a, 2000b), although many other animals appear to move their larynx during vocalisations (Fitch, 2000b; Fitch & Reby, 2001). It has been suggested that across species, descending the larynx during vocalisation exaggerates vocaliser size (Fitch & Hauser, 1995; Fitch & Reby, 2001; Ohala, 1983, 1984). See figure 2-1 for illustration of vocal-tract differences among some primates.

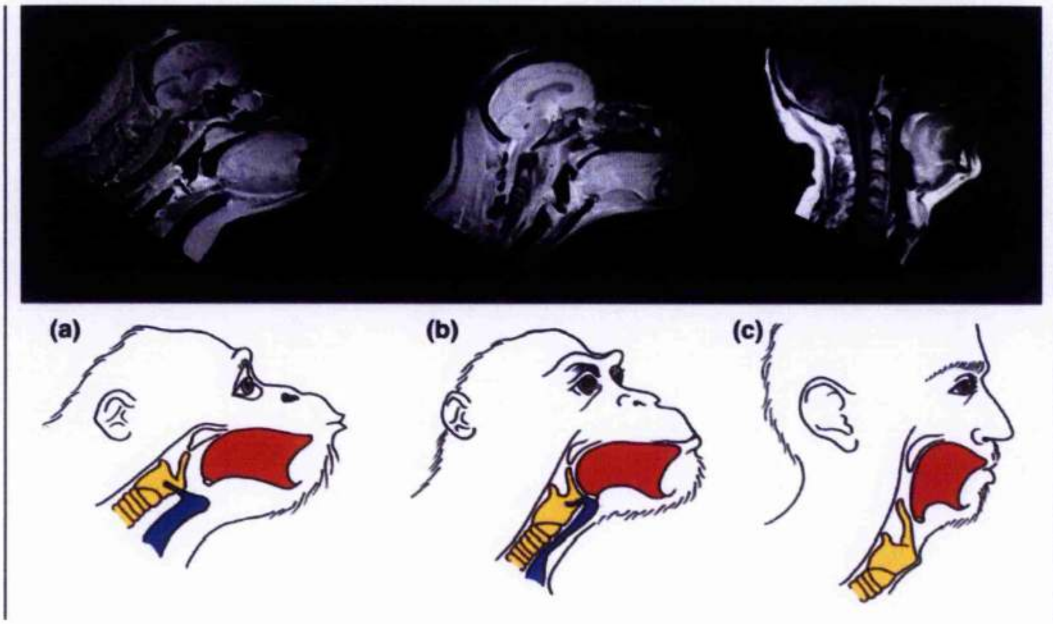


Figure 2-1 (from Fitch, 2000a). **Comparison of vocal apparatus across some primate species.** Humans (c) have longer and lower positioned vocal-tracts (yellow) and larger pharyngeal cavities than chimpanzees (b) and orang-utans (a). Note also that in the human, there is no air-sac (blue).

2. Some very basic anatomy of the human larynx

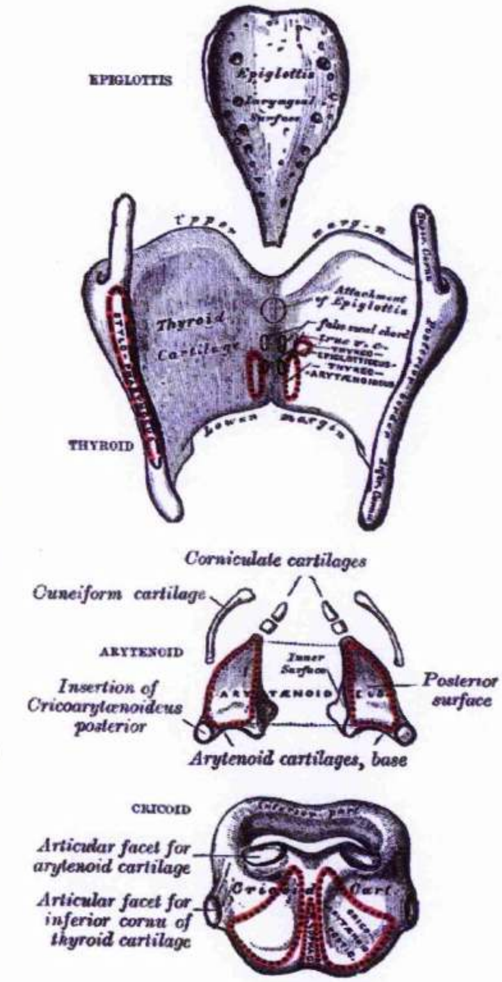
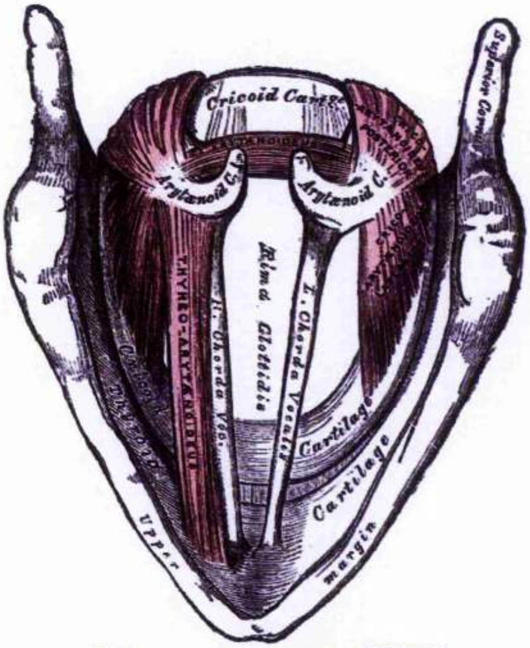


Figure 2-2. The laryngeal cartilages (Gray, 1918)

Titze (1994) outlined the anatomy of the larynx. Here I present a simplified version of that outline as the intricacies are beyond the scope of this thesis. Here I focus on a few anatomical structures of the larynx that are most relevant to speech production. One important factor about the larynx is that the larynx is suspended in the neck and can move up and down in position. Furthermore, as the larynx is comprised of cartilages, muscles and other soft tissue, the larynx can grow freely and independently from the rest of the body and the rest of the vocal-tract.

At the bottom of the larynx is the cricoid cartilage. This cartilage is signet ring shaped. The anterior end is thin and short, and the posterior end is wide and tall. The posterior end of the cricoid cartilage looks like a hexagonal plate with a medial ridge. Above the anterior cricoid cartilage are the thyroid cartilages. The thyroid cartilage has vertically plate-like shapes that form an angle between 90° and 120° at the anterior end. At the anterior end, there is a notch. The angle of the thyroid cartilage determines the size of the "Adam's Apple" (the notch in the thyroid). The smaller the angle of the thyroid cartilage is, the larger the projection or "Adam's Apple" is. At the posterior ends of the thyroid cartilage, there are superior and inferior projections.

Figure 2-3. Top-down view of the laryngeal cartilages and muscles (Gray, 1918).



Atop the posterior end of the cricoid cartilage, sits the arytenoid cartilages (pyramid shaped). Stretched between the arytenoid cartilage and the anterior thyroid cartilage are the vocal cords.

The anterior inferior end of the thyroid cartilage connects to the cricoid cartilage via the cricothyroid muscle. The cricothyroid muscle changes the length and tension of the vocal cords by narrowing or enlarging the cricothyroid space, which moves thyroid cartilage towards or away from the arytenoid cartilage. This raises or lowers pitch (see section on vocal fold mechanics). The thyroarytenoid muscle attaches the anterior thyroid cartilage and the arytenoid cartilage. The thyroarytenoid muscle is divided into two sections: the vocalis and the muscularis. Although the full function of the

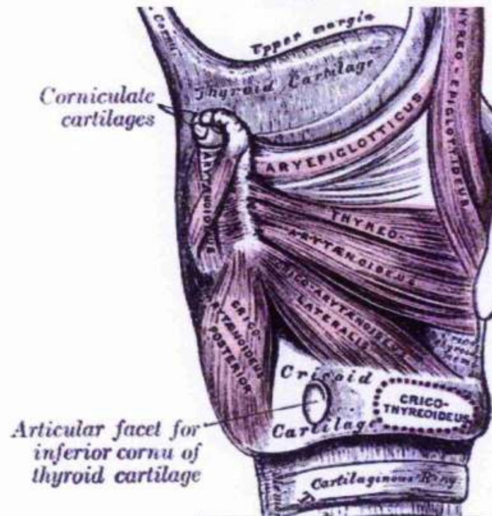


Figure 2-4. Lateral view of the laryngeal cartilages and muscles (Gray, 1918).

thyroarytenoid muscle is still debated, contraction of the thyroarytenoid muscles may shorten and thicken the vocal folds (see Titze, 1994).

3. Vocal fold mechanics

The myoelastic-aerodynamic theory of vocal-fold vibration (van den Burg, 1958) stated that coupling of airflow to the vocal folds (which have elastic properties) produces sustained oscillation. Voiced speech is caused by vocal-fold vibration (formants are caused by air vibrating; more will follow on formants later). Vocal folds must start close enough together such that they can vibrate. Otherwise, whispers will be produced. The vocal folds, however, do not have to touch at each glottal pulse for phonation to occur, as happens during breathy speech. Positive acceleration of the air helps to drive the vocal folds outward. When the vocal folds are closing, acceleration of airflow is negative, thus helping to close the vocal folds. A key factor in allowing sustained oscillation is the asymmetry in pressure between the opening and closing of the vocal folds. Furthermore, the vocal folds are not uniform in mass. This leads to a convergent vocal fold shape while the vocal folds open and a divergent vocal fold shape when vocal folds close. The motion of vibrating vocal-folds is like a ribbon and its degrees of freedom correspond to the natural modes of vocal-fold vibration (see Fitch & Hauser, 2002; Titze, 1994, for review). Multiple mass models or ribbon models of vocal-fold vibration allow for an excised larynx to vibrate as long as air is forced through it.

1.1 Fundamental frequency

We can derive the fundamental frequency from the length, density and stress of the vocal folds. Fundamental frequency is inversely proportional to vocal fold length. Vocal folds will have a constant density and vocal-fold stress is regulated by vocal fold mass (e.g. thicker rubber bands are more tense when stretched than thinner rubber bands are) and length (stretched rubber bands have more stress on them than un-stretched rubber bands) (Titze, 1994). Thus the variable factors involved in the calculation of the fundamental frequency can be reduced to the density (which is constant within an individual at a given time), stress and length of the vocal folds. Therefore, we can construct the equation $F = \frac{1}{L}\sqrt{\frac{\sigma}{\rho}}$, where F=fundamental frequency, L=the length of the vocal folds, σ=stress and ρ=density (Titze, 1994).

1.2 Harmonics

Harmonic frequencies are produced at integer multiples of the fundamental frequency (see figure 2-5 and Titze, 1994).

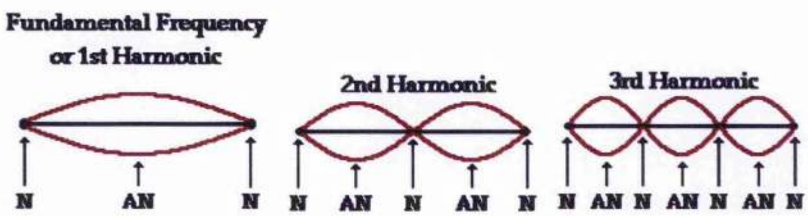


Figure 2-5. Harmonics. Endpoints are nodes (N), at which the wave appears to not vibrate. At antinodes (AN), the pressure difference is greatest. (www.physicsclasroom.com)

If the amplitude and frequencies of the harmonics are plotted, the amount of energy lost at the glottis determines the slope of a regression between harmonics frequencies and their amplitudes (Titze, 1994). This creates either "fluty" (weak harmonics) or "brassy" sounding voices (strong harmonics) (Fitch & Hauser, 1995).

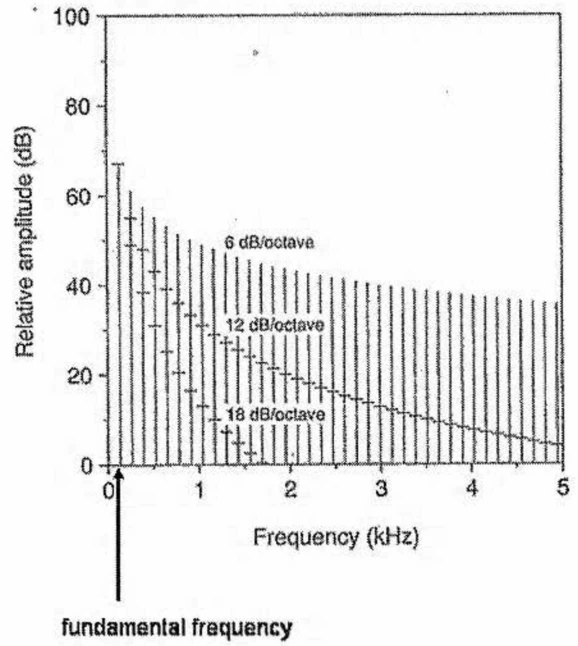


Figure 2-6. Illustration of different spectral slopes. Here an amplitude/frequency spectrum displays 3 spectral slopes of a waveform with fundamental frequency of 130Hz (From Titze, 1994, pg 119). The leftmost frequency is the fundamental frequency and frequencies to the right (of the fundamental) are harmonics. Increased spectral slope can result from incomplete closure of the vocal folds during vibration. Incomplete vocal-fold closure increases the amount of energy lost at the glottis, therefore increasing the spectral slope (Hanson & Chuang, 1999).

3. Formant frequencies

Waveforms generated at the glottis are formed by forced oscillation. Objects also have natural oscillations, which have frequencies that the object will vibrate at when disturbed. When the frequency of forced oscillation is synchronised with the natural frequency, resonance occurs. This is why the vocal-tract has resonant frequencies, which "selectively" attenuate certain harmonics (see Titze, 1994).

Titze (1994) outlined how to derive formant frequencies from a given length of tube. Consider a length of tube uniform in length. The following equations derive formant frequencies from length of tube L. Let t_0=the length of time a propagated wave takes to make a return journey from one end of the tube to the other and back again (transit time). Thus T (the period,) $=\frac{1}{F}=\lambda$ (wavelength)=$2t_0$ and $\frac{T}{2}=t_0$.

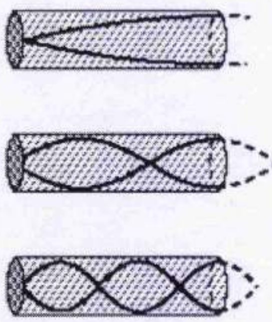


Figure 2-7. The first three resonances of an open-closed tube. (www.hyperphysics.phy-ast.gsu.edu)

The rest of the formula involves algebraic replacement involving the equation velocity=distance/time. Let velocity be c, the speed of sound (350m/s in the vocal tract) and distance be 2L (double the length of the tube). Hence, $t_0=\frac{2L}{c}$. Then, substituting $\frac{T}{2}$ for t_0, yields $\frac{T}{2}=\frac{2L}{c}$. Then replacing T with $\frac{1}{F}$, gives the formula: $\frac{\frac{1}{F}}{2}=\frac{2L}{c}$. Then multiplying each side by 2, yields $\frac{1}{F}=\frac{4L}{c}$. Then inverting the fractions gives the formula: $F=\frac{c}{4L}$.

The above equation set solved the first formant frequency given a length of tube. Formants can be calculated depending on whether the tube is closed on both ends, open on both ends or closed on one end and open on the other end. If the tube is closed on both ends, formants occur at consecutive integer multiples because as the wave propagates from one end to another, pressure doubles at both ends of the tube, creating component frequencies at all natural modes of the tube. If a tube is open on both ends, formants are resonated at even integer multiples. If the tube is open at one end and closed on the other (as the most common model of the human vocal-tract), formants occur only at odd number integer multiples because pressure always doubles at the closed end (the node, see section on harmonics) but is cancelled when air propagates out of the open end. Thus, we add a factor that produces odd number integers (2n-1) into the above equation $F_n=(2n-1)\left(\frac{c}{4L}\right)$, where n=formant number. F=1/λ(wavelength), $\lambda=4L$, or $L=\frac{1}{4}\lambda$, hence the name *quarter wave resonator* is given to an open-closed tube.

4. Formant dispersion

Classical formant dispersion is the average distance between successive formants (Fitch 1997). If we take an open-closed tube with a length of 17.5cm, the above equation yields formants 500Hz, 1500Hz, 2500Hz and 3500Hz. Thus, in a tube of 17.5cm, the distance between formants is always 1000Hz. A tube of length 15.5cm, yields formants at 564.5Hz, 1693.5Hz, 2822.6Hz and 3951.6 Hz (rounding off to the nearest 10^{th}). Thus, the distance between formants is always 1129Hz. Thus, formant dispersion is inversely related to vocal-tract length.

Fitch & Hauser (2002) explain that although the open-closed tube approximation provides a model of the vocal-tract that is easily understandable, the glottis opens and closes many times during phonation. Furthermore, as mentioned earlier when discussing spectral slopes, the glottis may not always close completely. Therefore, the vocal-tract also is open on two ends during portions of phonation. In an open-closed tube model, a 17.5cm vocal-tract would produce its formant frequencies at 500Hz, 1500Hz, 2500Hz and 3500Hz (see above) whereas if the same vocal-tract length were open on both ends would produce formants at 1000Hz, 2000Hz, 3000Hz and 4000Hz. Thus, if using raw formant frequencies or the average formant frequency as our indicator of vocal-tract length, we could have wildly different estimates depending on whether we caught the glottis in an open or closed state. By using formant dispersion, the aforementioned caveat can be avoided because in both cases (open-closed and open-open), the average distance between formants is the same (in this case, at VTL=17.5cm, formant dispersion=1000Hz).

5. Hearing

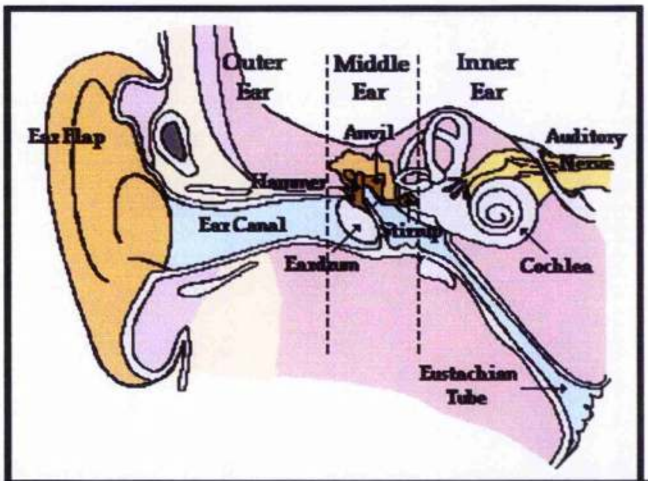


Figure 2-8. Anatomy of the human ear. Image from: http://www.glenbrook.k12.il.us

The human ear consists of many parts. Vibrating air enters the ear through the outer ear and passes through the ear canal (Stevens, 1998). The moving air vibrates the tympanum (eardrum) (Stevens, 1998). The tympanum passes the vibration of the sound wave onto the ear bones (hammer, anvil, and stirrup), which amplify the acoustic signal (Stevens, 1998). The movement of the stirrup impacts on the oval window which then vibrates the fluid inside the cochlea, creating a compression wave (Stevens, 1998). The nerve cells inside the cochlea are hair-like, each tuned to a particular characteristic frequency (Robles & Ruggero, 2001; Stevens, 1998). Cochlear hair cells are arranged tonotopically (Robles & Ruggero, 2001). In other words, different positions on the basal membrane are most responsive to certain frequency ranges. One advantage to a tonotopic arrangement of cells is that in cases where the frequency of sound is faster than the reset speed of cochlear hair cells, neighbouring cells will respond such that frequency and temporal resolution is not diminished in fast moving and high frequency sounds (Robles & Ruggero, 2001). The compression wave in the fluid inside the cochlea stimulates the cochlear nerve cells (Stevens, 1998). The cochlear nerve cells then send electrical signals that are passed on to the auditory nerve and then into the brain for processing (Stevens, 1998).

Hearing is not linear in relation to frequency (Hz). Weber's law states that higher frequency sounds will need greater differences to be perceived than lower frequency sounds do (actually, Weber's law applies to all perceptions). Thus, perceptual scales of pitch have been created: bark, semitone, equivalent rectangular bandwidth (ERB) and mel (Stevens, 1998; Traunmüller, 1990), but see others for criticism of the mel scale (Greenwood, 1997).

6. Voice processing

Perceptual biases in voice processing could influence preferences because of the manner by which they are processed. Here, I outline some perceptual biases.

Wang et al. (2005) showed that in the auditory cortex marmosets (*Callithrix jacchus*), sustained firing of neurons was maintained for prolonged periods of time after preferred auditory stimuli were presented, whereas neuronal firing rates dissipated more rapidly when non-preferred auditory stimuli were presented. If this result extrapolates to humans, then neurons in the auditory cortex may sustain firing more for attractive than unattractive voices. Further support for the idea that voices (or perhaps attractive voices) have special neural representation comes from Belin et al. (2000), who showed that the superior temporal sulcus (STS) selectively responded to voices (of adults, children, infants and elderly) more than matched controls. The STS has also been shown to be a face-selective area, but also responding preferentially to stimuli that individuals are highly trained upon (see Perrett, Hietanen, Oram, & Benson, 1992, for review).

Following neurological evidence for voice selectivity over non-voice sounds, and for special neurological representation of preferred sounds, there appears to be a voice inversion effect (Bedard & Belin, 2004). What this means is that when a spectrum is inverted over a particular frequency, the ability to discriminate between voices is reduced. Similar effects have been found in detection of facial symmetry of inverted faces (Little & Jones, 2003). This suggests that the brain represents faces and voices differently than other stimuli.

Burton & Bonner (2004) showed that people were able to make sex classifications based on voice alone quicker if they were familiar with the stimuli than if they were not familiar with the stimuli. This suggests that people remember identity cues in voices, and use this information to aid in discrimination of sex. Evidence that familiarity effects extend to vocal preferences comes from infants (Barker & Newman, 2004). Infants prefer the sound of their mother's voices to that of strangers and their fathers. Infants also prefer sounds that they were exposed to in the womb over novel sounds (see Barker & Newman, 2004, for review). What is interesting here is that father's voices were not preferred over strangers voices, suggesting that familiarity alone cannot account for the increased preference for mothers' voices. Perhaps there is an interaction between familiarity and stimulus-reward value (e.g. mothers provide infants with food rewards via lactation).

Next I will review some theory on sexual selection that will be pertinent to this thesis.

Chapter 3

Sexual selection

1 Natural selection and sexual selection

Selection is the differential survival of genes. Genes code for proteins, which can in turn produce physical or behavioural traits. Natural selection favours traits that enhance survival, but are not directly related to reproduction. Examples of naturally selected traits are body characteristics that suit the environment (e.g. the shape of a bird's beak or a prehensile tail in certain new world primates). Sexual selection favours traits that are not necessarily favoured by natural selection, but, nonetheless enhance reproductive success. Examples of sexually selected traits are deer antlers (see Andersson, 1994, for review) and peacock's trains (Petrie, 1994). There is an interaction between natural selection such that traits can evolve via sexual selection to larger sizes only to the extent to which they do not cause the organism to fail to reproduce. For example, deer antlers may be sexually selected to be larger in each subsequent generation. If antlers get too large, however, the animal possessing the antlers may not be able to lift its head and may therefore die before it is able to reproduce. Therefore, an equilibrium between natural and sexual selection is often established (see below for review of directional, disruptive and stabilising selection). There are also many traits where natural selection and sexual selection overlap (see Cartwright, 2000, for review). For example, natural selection and sexual selection can favour resistance to pathogens. An organism needs to be resistant to pathogens to survive to reproduce. Also, if resistance to pathogens is inheritable, members of the opposite sex might preferentially choose to mate with individuals who have traits that signal that an individual is resistant to pathogens. Evolution, however, can only build upon pre-existing structures. This may explain why for example, humans do not have antlers, but do have variation in voice pitch between the sexes.

2 Types of selection: stabilising, directional and disruptive

2.1 Stabilising selection

Stabilising selection is selection against the extremes a particular trait such that the average trait is maintained (Trivers, 1985). In humans, an example of stabilising selection may be body weight. If an individual (either male or female) is too thin or to fat, they may not survive to reproduce, or their reproductive potential could be compromised because of physiological or social reasons.

2.2 Directional selection

Directional selection is selection against one extreme of a trait, such that the mean value of the trait shifts away from the extreme that was selected against (Trivers, 1985). One example of directional selection in humans is brain size. Throughout the evolution of *Homo sapiens sapiens*, brain size has increased over the past 3 million years. There must have been selection against humans with smaller brains in each generation for this to have occurred. Nevertheless, average human brain size has not changed since a slight reduction in size at the time in history when domesticated animals appeared in the fossil record. Therefore, brain size may be currently under the force of stabilising selection, where extremely large and extremely small brains are selected against, thus maintaining the average brain size.

2.3 Disruptive selection

Disruptive selection selects against the mean trait, such that a bimodal distribution in the trait is established (Trivers, 1985). Sex differences are often created and maintained by disruptive selection, whereby the androgynous form is selected against. Therefore, one example of disruptive selection in humans may be voice pitch. If at some time in our evolutionary past, men and women (or their progenitors) had similar voice pitch, disruptive selection acted selected against androgynous voice pitch such that today, men have lower voice pitch than women (see Childers & Wu, 1991). Whether or not voice pitch, within each sex, is currently undergoing stabilising selection, disruptive or directional selection is a topic investigated in this thesis.

3 Secondary sexual characteristics

Sexually dimorphic characteristics can be modifications of primary sexual characteristics (organs are involved directly in reproduction e.g. penis and vagina). Secondary sexual characteristics, however, are primarily traits that are not necessary for reproduction. In humans, most secondary sexual characteristics appear at puberty or undergo intense growth at puberty or both (e.g. beards in men and breasts in women).

4 Sex differences in reproductive rates

In general, males reproduce at a faster rate than females. For example, in humans, women can produce roughly one child per year (barring twins), whereas men can potentially inseminate upwards of more than 5 women per day. Not all men actually inseminate 5 women per-day (in fact, few probably do). Nevertheless, as females reproduce at slower rates than males do and are more limited in the number of offspring they can produce, there is a larger cost of mating with individuals of low mate value (e.g. low phenotypic quality and, low parental investment (in investing species)) for females than males.

5 Intensity of intrasexual competition & sexual dimorphism

Intrasexual competition is competition between members of the same sex for access to mates. While there are many factors that can lead to sexual dimorphism (e.g. pleiotropic genetic effects, ecological niche partitioning, males as unsuitable prey for predators, sex discrimination, intrasexual selection, intersexual selection, and more, Andersson, 1994), here I focus on intrasexual competition and intersexual selection. Intrasexual competition leads to an arms race where evolution favours adaptations that aid in intrasexual competition such as large body size, weaponry and defensive organs (Cartwright, 2000). Here I outline key factors that influence the intensity of intrasexual competition.

5.1 Operational sex ratio

Operational sex ratio is defined as the ratio of males to females who are ready to mate at a given time (see Andersson, 1994; Cartwright, 2000; Kvarnemo & Ahnesjö, 1996; Low, 2000; Trivers, 1985, for reviews). The sex with the larger number of individuals ready to mate at a given time generally competes more for access to members of the opposite sex. As the operational sex ratio moves further from 1, sex differences in the intensity of intrasexual competition increase (see figure 3-1).

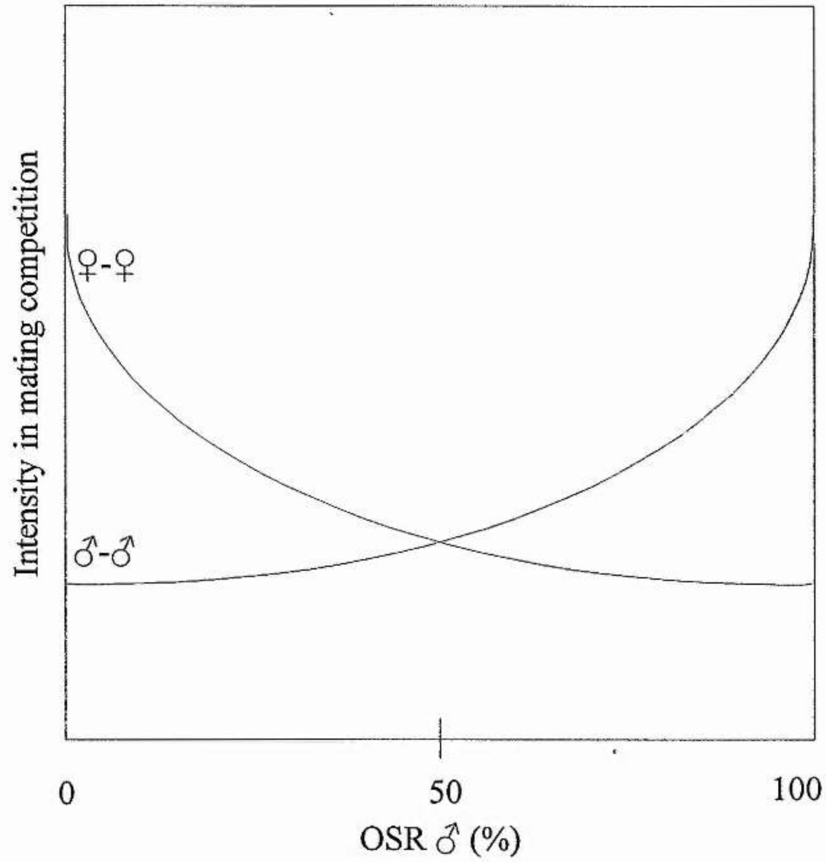


Figure 3-1 (adopted from Kvarnemo & Ahnesjö, 1996). **Operational sex ratio and intensity of competition.** When there are more females than males, intensity of female-female competition over males is high, whereas intensity of male-male competition for females is low. When there are equal numbers of males and females, intensity of mate

competition between males and females is equal. When there are more males than females, intensity of male-male competition over females is high, whereas intensity of female-female competition for males is low.

The operational sex ratio (of men to women) in Scotland, estimated for the year 2004, for the age range that I predominantly study in this thesis (18-25) is 1.02 (http://www.gro-scotland.gov.uk/). In Fife, where the University of St Andrews is located, the operational sex ratio of males to females from the ages 18-25 is 1.03 (http://www.gro-scotland.gov.uk/). This age range does not cover the full operational sex-ratio of the population, but is tailored towards undergraduate student age. This ratio also does not cover pregnancy or hormonal contraceptives that would further drive the operational sex ratio to have more males than females than reported above. There are slightly more males than females in the age range of 18-25 in Scotland and in Fife. Thus, male-male competition should be higher than female-female competition in the population predominantly studied in this thesis.

There are many factors which may affect operational sex ratios and how they interact with intensity of sexual selection (see Ahnesjö, Kvarnemo, & Merilaita, 2001; Kvarnemo & Ahnesjö, 1996, for reviews). There are sex differences in potential reproductive rate. What this means is if a man and a women each have unprotected, heterosexual sex with a different person each night (if all of the women were in their late-follicular, fertile menstrual cycle phase) for a period of 10 nights, the man has the potential to have sired 10 offspring whereas the woman has the potential to have produced only 1 offspring. Sex differences in reproductive rates lead to sex differences in mating strategies. If females have a lower potential reproductive rate than males, then females may be more choosey in terms of with whom they mate then males because the cost of choosing a mate of poor quality may be higher for females than males.

There are sex differences in the age at which sexual maturity is reached. Men tend to reach sexual maturity a few years later than women. Thus, if all else were equal, there would be more women than men ready to mate at a given time. This last point is also related to sex differences in length of reproductive careers. Women have reproductive careers that span roughly 20-40 years, whereas men are able to produce sperm for a much longer amount of time than women produce eggs for. Thus, if all else were equal, given sex differences in potential reproductive rates and sex differences in length of reproductive career, there would be more males than females ready to mate at a given time.

Migration and spatial distribution of mates also influences operational sex ratios. Depending on the sex that migrates, the spatial distribution of mates will vary. This in turn affects the operational sex ratio. In Scotland, it is common for both men and women to leave their parents' house as early as the age of 16. In Scotland, there is probably a fairly even spatial distribution of mates.

Finally, mortality during the mating season or throughout a mating career (for species such as humans that do not have mating seasons) affects operational sex ratios. Daly & Wilson (2001) provide an extensive review that shows that men are more likely to engage in risk-taking behaviour than women. Thus, men are more likely to engage in behaviour that will reduce their probability of reproducing than women (see also Booth, Johnson, & Granger, 1999; Trivers, 1985, for reviews). Thus, if all else were equal, differential mortality between the sexes could sway the operational sex ratio towards women.

In humans, there are modern examples of how operational sex ratios affect the intensity of intrasexual competition. For example, in China in the next 10-20 years there will be more males than females ready to reproduce. Thus, intensity of male-male competition should be higher than female-female competition. During World War II in the United States, many men of reproductive age were away at war. Thus, in America, there were more females than males ready to reproduce. At this time, female-female competition was higher than male-male competition (Cartwright, 2000).

5.2 Variance in reproductive success

One key principal that is related to mating systems is variance in reproductive success. Bateman (1948) showed that in drosophila, males had greater variance in reproductive success than females. Furthermore, males who copulated more had higher reproductive success, but female mating success did not increase reproductive success. This result has also been demonstrated again in many other polygamous species (see Wilson, 1975, for review). Bateman further explained that sex differences in the variance in reproductive success were due to sex differences in the variance in the energy invested in their sex cells. Female sex cells are larger and less motile than male sex cells and therefore have a higher metabolic cost, limiting their production in comparison to male sex cells (as sperm are metabolically cheaper than eggs to produce). Female reproductive success in limited by the ability to produce eggs, whereas male reproductive success is limited by the ability to fertilise eggs (Bateman, 1948; Trivers, 1972). Later I will describe how sex differences in parental investment are implicated in sexual selection.

The amount of variance in reproductive success within a sex is related to the type of mating system (polygamy, monogamy, or polyandry). Polygamy usually is found when there is high variance in male reproductive success and low variance in female reproductive success. Here, male-male competition should be higher than female-female competition as some males will mate with multiple females, whereas some males will not mate at all. Nearly all females, however, will have an equal probability of mating. Monogamy is usually found when variance in reproductive success is relatively equal. Given an equal operational sex ratio and a monogamous mating system, male-male and female-female competition should be relatively equal in intensity. Polyandry is usually found when there is higher variance in female reproductive success than male reproductive success. Here, if there are more females than males and more variance in female reproductive success than male reproductive success, there should be more intense intrasexual competition among females than among males.

5.3 Parental investment

Trivers (1972, pg. 139) stated that parental investment is: "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring." Therefore, at one level, anisogamy, or sex differences in sizes of gametes may constitute initial investment. Eggs are often more energetically costly to produce than sperm, but the term investment also includes behaviour such as feeding and guarding young. By definition, the term investment does not include energy expended in mate search or intrasexual competition that aided in producing the offspring in question because these variables do not effect the survival of *future* offspring (except in special cases, Trivers 1972). Energy may not be the best measure of parental investment. For example, a bird sitting and guarding its offspring in a nest expends very little energy whilst sitting and guarding. If the parent bird, however, becomes a victim of predation, the consequences for the offspring are high. Thus, investment can be high whilst energy expended is low. Therefore, investment may be difficult to quantify.

Trivers (1972) proposed that the sex that invests the least will compete more for the sex that invests the most, whereas the sex that invests most may incur the biggest loss if a mate of poor quality is chosen. Differential parental investment, along with operational sex ratios, influences sex differences in mating behaviour. The sex that invests more, and the sex that has lower variance in reproductive success due to operational sex ratios, is usually more choosey about with whom they mate than the sex that invests less is. The sex that invests least, however may still invest, and may therefore also incur losses if a mate of poor quality is chosen. Trivers (1972) also theorised that the payoff for desertion is greater for the sex that invests less or the sex with greater variance in reproductive success. Kokko & Jennoins (2003) explain that Trivers's argument left out the fact that if there are more males than females available to mate at a given time, it may be difficult for a male that has deserted to find an available female. Thus, the payoff for desertion may also be contingent upon the male's ability to secure mates and the availability of potential mates. I discuss this in further detail in section 5.4.

5.4 Mating effort

Margath & Komdeur (2003) reviewed the topic of mating effort. Mating effort can be defined as any energy expended with the goal of obtaining mates. Mating effort can be physiological, such as the production of secondary sexual characteristics or behavioural, such as vocal advertisements, status displays and territory defence. Sex differences in mating effort depend on the dynamics of the mating system. In polygamous situations, males may have higher mating effort than females because the operational sex ratio is male-biased. Thus, competition for mates is higher for males than females, so males may have a higher payoff of increased mating effort than females may have. In monogamous situations, or situations in which the operational sex ratios are equal, there may be relatively equal mating effort between males and females, because the level of competition for mates is equal across sexes. Thus both males and females will benefit from increased mating effort. In polyandrous situations, or situations in which the operational sex ratio is biased towards females, there may be more female mating effort than male mating effort because the level of female competition for mates will be higher than the level of male competition for mates.

Mating effort is often studied in the context of whether it is beneficial to increase mating effort after offspring have been produced. This can take the form of extra mating effort occurring simultaneously (e.g. extra-pair copulations) or sequentially (e.g. serial monogamy or desertion) with parental investment. As each individual has a fixed amount of energy, there is a trade-off between energy expended in mating effort, parental investment and somatic growth and maintenance. The payoff for additional mating effort at the cost of decreased parental and somatic investment should be positively correlated with own mate value (e.g. phenotypic quality, status and resource availability) and the number of members of the opposite sex that are ready to mate. Also, the payoff for additional mating effort may also be influenced by the mate value of the current mate. For example, if one is pair-bonded with a very high quality mate, it may be costly to seek extra pair copulations and risk losing further mating opportunities with the current, high quality mate. Furthermore, guarding the current mate from other potential mates can also potentially increase reproductive success.

Research in birds (Van Roo, 2004) and humans (Burnham et al., 2003; Gray, 2003; Gray et al., 2004; Gray, Kahlenberg, Barrett, Lipson, & Ellison, 2002) show that testosterone is associated negatively with paternal investment and related positively to mating effort (Magrath & Komdeur, 2003) and possibly phenotypic qualities such as dominance and good immune function (see Folstad & Karter, 1992). Thus there may be a trade-off between selecting a male with good genes for dominance and good immune function and paternal investment. In monogamous species, "personality" compatibility becomes an issue if long-term pair bonds are established.

As females are often limited in the number of offspring they can produce, female's level of parental investment is often higher than male's level of parental investment. Males, however, are limited in the number of offspring they produce by their ability to fertilise females. Therefore, male parental strategies range from no paternal investment to equal investment than females. Occasionally there is greater male parental investment than female parental investment, for example in pipefish and seahorses.

Another factor related to the amount of paternal investment is paternity certainty. In highly polygamous species (or situations) there is often little to no paternal investment. In monogamous species paternal investment is higher than in polygamous species and paternity certainty is higher than in polygamous species (although the direction of causality may not be clear).

6 Competition

Intrasexual competition can take the form of competition for resources between the sexes (amongst other forms). In many species, competition for resources can drive sexual dimorphism via niche partitioning (for example), where males and females inhabit different ecological niches. For example, in humans, it is not uncommon for men and women to apply for the same jobs. Nevertheless, an analysis of over 1000 societies showed that in humans, there is evidence of sexual division of labour (Low, 2000), thus reducing intrasexual competition for resources. If there was sexual division of labour when humans evolved (e.g. men hunting and women gathering), there may have been selection pressure for males to choose the best gatherers and women to select the best hunters.

7 Selection

Intersexual selection is the process by which individuals from one sex choose to mate with individuals from the other sex. If individuals possess a certain inheritable trait, and members of the opposite sex choose to mate with individuals possessing that trait over individuals that do not possess that trait, the frequency of the trait will increase in subsequent generations. Intersexual selection does not have to be independent of intrasexual selection or natural selection. Traits can have many functions. Here, I outline some mechanisms of intersexual competition from the point of view of female selection of males; however, these mechanisms can also be implicated in male selection of females.

7.1 Direct vs. indirect benefits

Price et al. (1993) mathematically modelled how direct and indirect benefits can affect reproductive success. Indirect benefits can be constituted as benefits to one's reproductive success that are not realised immediately, but benefit subsequent offspring. Indirect benefits can be genetic or not. For example, there can be an indirect benefit of mating with a person with inheritable immunity to infection and an indirect benefit of mating with someone who is wealthy (if the wealth is passed on to offspring). Direct benefits of mating can increase one's reproductive success, and are realised immediately. Direct benefits can include mating with healthy individuals (to avoid contagion), mating with intervals who provide nuptial gifts, protection from predators, resources and others. There can be overlap between direct and indirect benefits, such as in the case of health (if there are inheritable and non-inheritable components) and wealth (wealth can be spent on the mate and the offspring).

7.2 Fisherian or runaway selection

Females may have a preference for a male trait. As the trait increases in size, quality, intensity etc., females may prefer the trait in question more and more, thus, self-reinforcing selection for the trait (Fisher, 1930). Fisherian selection can result in elaborate traits that may hurt the individual's fitness in terms of natural selection. For example, a peacock's train is large and elaborate, and highly attractive to females, but carries the cost of making it difficult for males to evade predators. Nevertheless, as mentioned earlier, sexual selection and natural selection tend to reach a state of equilibrium (see Andersson, 1994; Cartwright, 2000; Low, 2000; Trivers, 1985, for reviews).

7.3 The good genes hypothesis

The good genes hypothesis states that females should choose males with traits that honestly indicate that they have good genes (e.g. genes for inheritable immunity to infection, dominance, etc.) so that their offspring may inherit these good genes.

7.3.1 The handicap hypothesis

Zahavi (1975, pg. 213) stated that "The handicap principle as understood here suggests that the marker of quality should evolve to handicap the selected sex in a character which is important to the selecting sex, since the selecting sex tests, through the handicap, the quality of its potential mate in characters which are of importance." In other words, females, for example, should choose a male that displays a trait that is costly to its own fitness because the male has survived thus far with the handicap. Another example is that in terms of money, richer individuals can afford to give away more money than poorer individuals.

7.3.2 Hamilton-Zuk hypothesis

The Hamilton-Zuk hypothesis suggests that females select male traits that indicate heritable resistance to parasites. Hamilton & Zuk (1982) showed that in birds, brightness of colouration in both sexes and high quality male song were negatively related to parasite load.

7.3.3 Immunocompetence hypothesis

A development of the Hamilton-Zuk hypothesis (1982) is the immunocompetence hypothesis (Folstad & Karter, 1992). Foltad & Karter (1992) argued that testosterone is a steroid that suppresses the immune system. Therefore, traits that reflect expression of testosterone also should display parasite resistance. Hence, females should choose males with traits that signal high levels of testosterone because they may have high immunocompetence.

7.3.4 Qualifications to the handicap and immunocompetence hypotheses

Recent research shows that testosterone is not the only steroid involved in suppression of immune function. In humans, after dominance related contests, both testosterone and cortisol are often elevated more in the winners than in the losers, but cortisol is sometimes suppressed in winners also (see Salvador, 2005, for review). Thus, if dominant males often have higher testosterone than subordinate males, but cortisol in dominant males can be either higher or lower than in subordinate males, there are two possible implications for immunocompetence. First, if cortisol is higher in dominant males, then cortisol may be handicapping dominant males, such that they can afford higher cortisol levels than subordinate males can, without detriment to immune function. Second, if cortisol is higher in subordinate males than in dominant individuals, then dominant males may not be handicapped by cortisol as much as subordinate males, but may be handicapped by testosterone (sensu Folstad & Karter, 1992). Thus, in both cases, we can look for a positive association between testosterone and immune function (see Creel 2001, for review).

A recent review of empirical demonstrations of the immunocompetence hypothesis found conflicting evidence for the immunocompetence hypothesis across species (Roberts, Buchanan, & Evans, 2004). Getty (2002) gives further insight as to why evidence in support of the immunocompetence hypothesis is equivocal.

Getty (2002) challenged the idea of counting parasites as a method of assessing the Hamilton-Zuk hypothesis (1982) and the immunocompetence hypothesis (Folstad & Karter, 1992). The idea is that in order for the parasite-counting method to be valid, each host must have been exposed to the same number of parasites. If a host with low resistance to parasites was exposed to very few parasites, it may be able to produce elaborate ornamentation. Conversely, if a host with high parasite resistance was exposed to a very high number of parasites, its ornamentation may suffer. Thus, individuals can have similar levels of ornamentation, but different parasite loads. Another caveat to using parasite load as a measure of health is that there may be differential effects of parasites on individuals with equal overall immunocompetence (e.g. different individuals could be immune to different pathogens, but have the same total immunocompetence), such that a big signaller can handle a large parasite load and still be healthy. Therefore, females can choose males with high parasite loads *and* are healthy. Thus, counting parasites is not a valid measure to use when assessing the immunocompetence hypothesis (Folstad & Karter, 1992), the Hamilton-Zuk hypothesis (1982) or the handicap hypothesis (Zahavi, 1975).

7.4 Access to resources/parental investment

Females may choose males who have higher levels of resources, traits that indicate likelihood of the male having higher resources, males that are willing to commit to relationships and invest in offspring, and males with traits that indicate the likelihood of commitment to mates and investment in offspring. The sexy son hypothesis was formulated to encompass cases when attractive traits do not signal the amount of resources available to an individual.

7.4.1 The sexy son hypothesis

The sexy son hypothesis specifically states that if an attractive male does not have a large territory, then the female that mated with this male will initially have relatively lower reproductive success. If, however, the offspring inherit some of the attractive characteristics of the father, the mother will eventually have relatively higher reproductive success (Weatherhead & Robertson, 1979). More generally, the sexy son hypothesis notes that attractive traits need not in themselves be linked to any particular function. Their attractiveness in their own right can ensure benefit to female reproductive success.

8 Intersexual selection meets intrasexual selection

Dominant males often have higher reproductive success than subordinate males do. There is a point where intersexual selection and intrasexual competition meet. Selection of dominant males can take many forms. Females can select for dominant males (or any trait/behaviour crossing between intrasexual competition or intersexual selection) when females have seen dominance bouts and know which males are dominant, or they may have learned that there is an association between a particular trait and the probability of winning dominance interactions, and thus select males possessing the trait in question. Alternatively, males may also mate with females via forced copulation (or rape). A controversial account of evolutionary explanations of rape can be found in Thornhill & Palmer (2001).

8.1 Benefits of selecting dominant males

Dominant males often have enhanced sexually dimorphic characteristics. As mentioned above, enhanced sexually dimorphic characteristics may be cues to heritable immunity to infection and the ability to survive predation given that they have a trait that may be detrimental to their fitness. Furthermore, as many sexually dimorphic characteristics require extra nutrition to produce, they may signal the individual's potential to procure resources. Dominant males may have dominant offspring because of inherited behavioural or physical status passing between generations or resources or both. If dominant males have the highest reproductive success (in some cases the most dominant males do not have the highest reproductive success because they spend more time trying to maintain dominance status than copulating, see Mueller & Mazur, 1998), then their offspring may also have high reproductive success. Dominant males may also have more resources (e.g. larger territories, more money) and be able to defend their resources against other conspecifics and/or predators. Also, males displaying traits associated with dominant behaviour may also be displaying inheritable immunity to infection (see Booth et al., 1999; Chen & Parker, 2004; Creel, 2001; Folstad & Karter, 1992; Getty, 2002; Salvador, 2005).

In the next chapter I will relate this chapter to what is known about sexual selection in humans.

Chapter 4

Human mate choice

In this chapter, I review what qualities we should choose in mates (given evolutionary theory), what affects these qualities, how these qualities are assessed, and what about the assessor changes what qualities are sought. First, I discuss non-vocal mate choice relevant qualities and then I discuss vocal mate-choice relevant qualities.

1 What qualities should we choose in mates?

Given that the operational sex ratio in Scotland, at the age range that I predominantly study in this thesis (18-25) is biased towards males (http://www.gro-scotland.gov.uk), there should be higher intrasexual competition among men than among women. This figure does not include the full age range of the operational sex-ratio, or pregnancy and hormonal contraceptive use. Including these factors would bias the sex ratio even more towards men and increasing the intensity of intrasexual competition among men. Humans have sex differences in potential reproductive rates. Women potentially reproduce at much slower rates than men. Hence, there should be higher variance in men's reproductive success than in women's reproductive success.

So are people polygamous, monogamous or polyandrous? Given the male biased operational sex ratio and sex differences in potential reproductive rate, it can be predicted that humans are polygamous. Although in many societies, there is the rule of one marriage at a time, or a social convention that cheating on a partner is taboo, some biological definitions of polygamy and monogamy do not allow for "serial monogamy" (e.g. Low, 2000). Although serial monogamy often occurs in humans, I will consider this as a form of polygamy. This topic, however, may be open for debate (the debate itself, as it is a matter of semantic classification, is outside the scope of this thesis). Thus, I will consider that humans are predominantly a polygamous species. There are many cases of monogamy and polyandry in humans, however, 83% of all studied cultures are polygamous (Low, 2000). Indeed, men are more likely to re-marry and have children with subsequent wives after divorce than women are. Men are more likely to have more wives than women are to have more husbands in societies where multiple marriages are legal or permitted by society (Low, 2000).

Given that humans, in general are polygamous, it has been predicted that in general, women should choose dominant men that displaying high status and health as these are important qualities for women to seek in men regardless of paternal investment (see Buss, 1989; Greenlees & McGrew, 1994, for examples, but there are many others who also hypothesised the same). Humans also invest in offspring. Women's parental investment is normally high, whereas men's parental investment can range from 0% to 100%. It has been predicted that particularly for long term relationships, women should choose not only men that are dominant and healthy, but also men signalling their willingness to invest (see Fink & Penton-Voak, 2002; Penton-Voak & Perrett, 2000, for reviews; Thornhill & Gangestad, 1999). Men on the other hand might choose women who display cues to fertility (e.g. physical attractiveness), health and potentially resources. Also, men might prefer women displaying good maternal behaviour. Indeed in a monogamous bird species (Japanese quail, *Coturnix japonica*), males prefer females displaying maternal brooding behaviour over those not displaying maternal brooding behaviour and those with chicks (Ruscio & Adkins-Regan, 2003).

Another factor in terms of long-term relationships, for both sexes is compatibility on personality traits. Men reach sexual maturity later than women do. Therefore, women should choose men older than themselves and men should choose women younger then themselves. As men's paternity certainty is lower than women's maternity certainty, men should value chastity more than women.

1.1 Lonely hearts advertisements

Studies of lonely hearts advertisements examined whether 1) men and women advertise what is predicted to be attractive to the opposite sex based on sexual-selection theory; and 2) what each sex is looking for in the opposite sex. In nearly every study, similar results were found (see Campos, Otta, & Siqueira, 2002; Greenlees & McGrew, 1994; Koziel & Pawlowski, 2003; Pawlowski & Koziel, 2002; Smith & Stillman, 2002; Strassberg & Holty, 2003; Waynforth & Dunbar, 1995, but there are many other studies showing similar results). Men seek physical appearance more than women do. Women advertise physical appearance more than men do. Women seek resources more than men do. Men advertise resources more than women do. Men advertise maturity more, whereas women advertise youth more. The strength of preferences for either appearance (in men's preferences for women) or commitment (in women's preferences for men) appears to change with age. As men age, they become more demanding, whereas when women age, they become less demanding (Campos et al., 2002). This suggests that as men accumulate status through age, they can afford to be choosier, or men's preferences for youth and physical appearance seem to get stronger because the relative age between older men and younger women is larger. As women approach the end of their reproductive careers, they may not be able to afford to be as choosy as they once were because their own mate value has declined in the eyes of men.

1.2 Self-report questionnaires

Buss (1989) examined self-reports from 37 cultures of what people were looking for in potential mates. Buss found consistently that women were more interested in financial potential in men than men in women were. Men were more interested in physical appearance than women were. Women were more interested in ambition than men were. Men were more interested in chastity than women and men preferred women younger than themselves, whereas women preferred men older than themselves. Kenrick and Keefe (1992) replicated most of Buss's findings, although they found that preferences for age were not contingent on participants' ages.

Thus, evidence from self-reports and lonely hearts advertisements generally support predictions about human mate choice drawn from evolutionary theory.

2 What affects qualities such as fertility, dominance, resources and health?

2.1 Age

Age seems to be the key factor influencing the aforementioned qualities. I will explain further.

2.1.1 Fertility

Both men and women are not able to produce offspring until puberty. After puberty, women's are fertile until menopause. Men's fertility also drops with age. The older men are when they conceive children and the larger the age difference between men and women at conception, the more likely the mother is to miscarry (de La Rochebrochard & Thonneau, 2002).

2.1.2 Dominance and resources

Logically, older men and women have had more time to acquire resources and climb social ladders than younger men and women. So, on average, older men and women should be more dominant and have higher resources than younger men. Indeed, a meta-analysis found that age (independent of height, weight and gender), was positively related to income and workplace success (Judge & Cable, 2004). Age also may be related to physical dominance, as older people (comparing for example, sexually mature to sexually immature people) will have had more time do develop musculature and stamina than younger men. These effects however, will decline as people get older. Pawlowski & Dunbar (1999) showed that male market value increased with respect to age (reflecting increasing wealth), but decreased with respect to age (as life expectancy decreased). As knowledge accumulates over time, age maybe positively related to knowledge (until such stage as age is related to mental decline). Each of these factors may relate to one's dominance and status.

2.1.3 Health

The interaction between health and age is less straightforward. Obviously, both men and women tend to get ill more as they approach old age and death. The difference between men and women in the speed at which sexual maturity is reached may relate to health as well. If just after puberty, men and women are in peak physical condition, then slightly younger young adult women and slightly older young adult men should be the healthiest.

2.2 Height

2.2.1 Fertility

Height in men is positively correlated with testicular volume, and hence sperm production capacity (Ku, Kim, Jeon, Lee, & Park, 2002). As mentioned in chapter 3, however, male reproductive success is more closely tied to the ability to fertilise eggs, than it is related to sperm production (although there may be an interaction between the two). Indeed, taller men do have higher reproductive success (Mueller & Mazur, 2001; Pawlowski, Dunbar, & Lipowicz, 2000). Shorter women have higher reproductive success than very tall or very short women have (Nettle, 2002a, 2002b). In terms of women's fertility, research proposes a trade-off between energy used to promote somatic growth and energy used to promote reproductive development (Nettle, 2002a, 2002b). Therefore, taller women may reach full sexual maturity after shorter women. Thus, in a young-adult age bracket, shorter women may be more fertile than taller women.

2.2.2 Dominance and resources

In a recent meta-analysis of both men and women, height was positively related to income and workplace success, independently of age, weight and sex (Judge & Cable, 2004). Height was also correlated with other measures of socio-economic status (see Mueller & Mazur, 2001, for review). Height may also positively relate to physical dominance. Also, there is a cross-cultural twin study showing that height is positively related to educational achievement (Silventoinen et al., 2004). This study showed that differences between the positive relationship between height and educational achievement between monozygotic and dizygotic twins were not systematic. This suggests that the relationship between height and educational achievement is more due to environmental factors than genetic factors (although height has a heritable component, Chatterjee & Das, 1995).

2.2.3 Health

In both men and women, height is related to health generally because growth is stunted by poor nutrition (although there are also genetic components to height, see above), and nutrition is positively linked to health. In both men and women, being too tall can have detrimental effects on health (see Mueller & Mazur, 2001, for review).

3 Hormonal profile (masculinity/femininity)

3.1 Women

3.1.1 Fertility

At puberty, increases in oestrogen and progesterone levels coincide with the start of women's menstrual cycles and hence their reproductive careers (Alonso & Rosenfield, 2002). Within the menstrual cycle (e.g. state concentration of sex hormones) progesterone and oestrogen levels are positively associated with increased conception rates and success of pregnancy (Baird et al., 1999; Lipson & Ellison, 1996; Stewart, Overstreet, Nakajima, & Lasley, 1993). High oestrogen levels (within the normal, healthy range) are associated with egg survival rates, follicle size, endometrial thickness (Dickey, Olar, Taylor, Curole, & Matulich, 1993; Eissa et al., 1986) and cervical perfusion (Roumen, Doesburg, & Rolland, 1982). Without progesterone, endometrial cells cannot fully mature in the luteal menstrual cycle phase (Chaffkin, Luciano, & Peluso, 1993; Santoro et al., 2000).

3.1.2 Dominance and resources

One study suggests that at times of the menstrual cycle characterised by high oestrogen, women derogate other potential female competitors (Fisher, 2004). Fisher (2004), however, did not measure oestrogen levels, so this result remains controversial. Women's facial attractiveness is positively related to oestrogen levels (Law Smith et al., In Press). A meta-analysis showed that women with attractive faces also tended to get hired more often and make more money than women with less attractive faces did (Hosoda, Stone-Romero, & Coats, 2003). Therefore, there may be a link between oestrogen level and resource acquisition ability in women.

3.1.3 Health

Oestrogen and progesterone have positive and negative associations with health. For example, at menopause, oestrogen replacement therapy may be associated with higher incidence of colorectal and ovarian cancers (Csizmadi, Collet, Benedetti, Boivin, & Hanley, 2004; Drew, 2001). Conversely, Thornhill & Gangestad (1999) argue that oestrogen production may utilise resources that the body needs for immune function and somatic repair. Therefore, they argue that oestrogen may be a handicapping hormone, much like testosterone may be in men (see Folstad & Karter, 1992, but also see chapter 3 for further discussion). More research should be conducted to clarify the role of oestrogen in immune function.

3.2 Men

3.2.1 Fertility

Gonadal testosterone levels are positively linked to sperm production (Hiort, 2002). Interestingly, new male contraceptives (currently not yet on the market) are testosterone based because administration of exogenous testosterone feeds back into the pituitary gland and sends a signal to the gonads to stop producing testosterone, which in turn stops sperm production (Grimes, Gallo, Grigorieva, Nanda, & Schulz, 2005; Ly, Liu, & Handelsman, 2005).

3.2.2 Dominance and resources

Mazur & Booth (1998) state that testosterone is related to dominant behaviour. They define dominant behaviour as "[actions with the] apparent intent to achieve or maintain high status, or to obtain power, influence or valued prerogatives – over a conspecific" (pg. 21). Mazur & Booth (1998) define aggressiveness as "[actions with the] apparent intent to inflict physical injury on a member of its species (pg. 21). Thus, as many dominant behaviours in humans are not aggressive by definition (e.g. arguments and board games), Mazur & Booth claim that testosterone relates to aggressive behaviour in as much as the aggressive behaviour is implicated in seeking dominance in a particular instance. In chapter 3, I mentioned the relative roles of testosterone and cortisol in immunocompetence. Classically, testosterone has been shown to be positively related to spatial-cognitive abilities, but negatively related to verbal abilities (Burton, Henninger, & Hafetz, 2005; Hooven, Chabris, Ellison, & Kosslyn, 2004; Tan, Okuyan, Albayrak, & Akgun, 2003). A recent study, however, shows that on its own, testosterone does not necessarily relate to cognitive performance on mental rotation tasks and verbal fluency tasks, but interacts with the status of the individual (Newman, Sellers, & Josephs, 2005). Individuals with high testosterone's spatial and verbal cognitive abilities were enhanced when put in a high status position, but were impaired when put in a low status position.

Testosterone also relates to questionnaire-based assessments of dominant-related behaviour and mood (Archer, Birring, & Wu, 1998; O'Connor, Archer, Hair, & Wu, 2001; O'Connor, Archer, & Wu, 2004; O'Connor, Archer, & Wu, 2001).

Testosterone influences the growth of male secondary sexual characteristics (Hiort, 2002). Thus, testosterone may be related to dominant appearance (see Swaddle & Reierson, 2002). More of this will be explained later when I outline what traits signal qualities relating to intra and intersexual competition.

3.2.3 More on testosterone and health

Regardless of testosterone's role in immune function (see chapter 3), testosterone may be positively related to risk-taking, and antisocial behavioural patterns (Booth et al., 1999; Daly & Wilson, 2001). Furthermore, testosterone is higher in violent and sexual criminals than testosterone is in matched controls (Studer, Aylwin, & Reddon, 2005). Testosterone (within normal limits) is positively associated with incidence of sexually transmitted disease and trauma (Booth et al., 1999). Conversely, testosterone is negatively related to the incidence of colds, depression, cardiovascular disease and obesity (Booth et al., 1999). Thus, testosterone may have positive associations with health, even given the behavioural handicap whereby men with high testosterone take more risks than men with low testosterone.

4 How are mate-choice relevant qualities signalled and assessed?

If a preference for a trait is to be adaptive, the perception of the trait must be accurate. Only honest signalling conveys benefits to future offspring. Here I review characteristics that relate to attractiveness and their adaptive functions.

4.1 Women

4.1.1 Facial attractiveness

4.1.1.1 Averageness

Initially, research reported that female facial attractiveness was solely predicted by facial averageness because these faces would be more face-like (Langlois & Roggman, 1990). Facial averageness may also be a cue to general genetic heterozygosity (Thornhill & Gangestad, 1999). Heterozygousity may be beneficial because it may indicate reduced inbreeding or a diverse HLA profile (human leukocye antigen, also known as human MHC or major histocompatability complex) (Thornhill & Gangestad, 1999). Perrett et al. (1994) showed that adding the face shape of highly attractive women to faces with average configuration increased their attractiveness. Furthermore, adding the difference in face shape between average and highly attractive women's faces to highly attractive women's faces (caricaturing their attractiveness) increased the attractiveness of already attractive faces (Perrett et al., 1994). Highly attractive women's faces in the aforementioned study, had characteristics that were female typical such as a smaller facial size, larger eyes, and fuller lips (Perrett et al., 1994).

4.1.1.2 Symmetry

Fluctuating asymmetry (random deviations from perfect bilateral symmetry) is thought to be an indicator of developmental stability (Van Valen, 1962). Deviations from perfect bilateral symmetry are thought to be caused by developmental perturbations. Fluctuating asymmetry is therefore a highly studied trait in the research area of human mate choice. Women with symmetrical faces (Perrett et al., 1999) and symmetrical bodies (Gangestad, Thornhill, & Yeo, 1994) were rated as more attractive than their relatively asymmetrical counterparts.

4.1.1.3 Femininity

Enhanced femininity in manipulated female faces has been shown to increase attractiveness ratings (Perrett, Lee, Penton-Voak, Rowland, Yoshikawa, Burt, Henzi, Caltles et al., 1998; Rhodes, Hickford, & Jeffery, 2000). This suggests that physical markers of femininity, rather than markers of averageness should be most attractive. Neoteny is the retention of juvenile characteristics in the adult form (www.dictionary.com). Many feminine facial features are associated with neoteny, and faces retaining these charateristics have been found attractive (Jones, 1995). Ratings of facial femininity do correspond with differences in face shape between men and women (Perrett et al., 1998), and thus may be considered accurate attributions. Preferences for facial femininity may be adaptive because facial femininity (and facial attractiveness) is positively correlated with oestrogen levels, which are in turn related to reproductive health (see above for review).

4.1.1.4 Age

Indeed many studies demonstrated that men prefer women younger than themselves and younger women in general (Buss, 1989; Kenrick & Keefe, 1992). Jones (1995) also showed cross-culturally that men preferred faces of women that were manipulated to look younger than they actually were. Furthermore, faces manipulated to have increased shape femininity were rated more attractive and younger than faces manipulated to have increased shape masculinity (Perrett et al. 1998). Perrett et al. (2002) found that by transforming faces based on facial averages of older and younger women, men had significant preferences for younger women's faces. Later, I will review qualifications to this result.

4.1.1.5 Health

Feminine and younger looking faces appear to be healthier looking (Law Smith et al., In Press) and healthy looking faces are considered more attractive than relatively unhealthy looking faces (Jones, Little et al., In Press; Jones et al., 2005).

4.1.1.6 Appearance of skin

It has been suggested that men prefer women with lighter skin because lighter skin may signal youth and/or fertility (Darwin, 1871; Frost, 1988; Van den Berghe & Frost, 1986). This may have some merit as skin colour becomes lightest at the late-follicular menstrual cycle phase (Frost, 1988). By contrast, skin darkens when women are on oral contraceptives and when pregnant, which are hormonally characterised by high progesterone (Steinberger, Rodriguez-Rigau, Smith, & Held, 1981).

Law Smith et al. (In Prep) found that different colours corresponded to different levels of testosterone, cortisol, oestrogen and progesterone. Topographic analyses of faces produced maps of where each hormone was related to each particular skin colour on the face. Then, these pixels were manipulated on each colour dimension (in essence manipulating the relationship between hormone level and skin colour). Men preferred women's faces with colour that indicated low cortisol, high oestrogen and high progesterone. These preferences may be adaptive because cortisol is increased by stress and has detrimental effects on immune function (Chen & Parker, 2004). Oestrogen and progesterone are related to reproductive health (see above for review).

Smoothness of skin also appears to contribution to attractiveness. Fink, Grammer and Thornhill (2001) found that smooth skin texture (measured by separate analysis of red, green and blue channels via hue, saturation and value pixel analysis) was positively related with men's attractiveness ratings of women's faces.

4.1.1.7 Body shape

Jasienska et al. (2004) found that low waist-to-hip ratio was associated with high oestrogen and progesterone. Studies using line drawings (Singh, 1993; Singh & Young, 1995) have shown that women with low waist-to-hip ratios were more attractive than women with high waist-to-hip ratios. These studies were confounded because altering the waist-to-hip ratios also altered the body-mass-index of the images (Tovée & Cornelissen, 2001). Later I will discuss cross-cultural preferences for waist-to-hip ratios.

The preference for men to prefer women who are not too thin, and not too heavy is potentially adaptive because the ability to carry pregnancy to full term (as opposed to spontaneous abortion) is reduced when women are emaciated (Kirchengast & Huber, 2004) and obese (Bellver, Bosch, & Pellicer, 2004; Bellver et al., 2003). Furthermore, Moran et al. (1999) and Zaadastra et al. (1993) found in women that high levels of upper-body body fat were indicative of a lack of ovulatory cycles.

Body-mass-index has been shown to contribute to female body attractiveness more so and independently from waist-to-hip ratio (Tovée, Emery, & Cohen-Tovée, 2000; Tovée, Reinhardt, Emery, & Cornelissen, 1998). The relationship between body-mass-index and attractiveness is a negative quadratic function (Tovée et al., 1998), with the vertex below the population mean. In other words, within the healthy range of body mass index (20-24 kg/m^2) there is a linear relationship between body attractiveness and body-mass-index.

As research has progressed, novel measures of body attractiveness such as waveform analyses (Tovée, Hancock, Mahmoodi, Singleton, & Cornelissen, 2002) and volume-height index (Fan, Liu, Wu, & Dai, 2004) claim to be the best measures of attractiveness of body shape. These measures are yet to be shown to predict sex hormone levels, but may as the aforementioned measures encompass elements of waist-to-hip ratio and body mass index.

4.1.2 Interrelationships between measures of mate quality

There are a few theories as to how multiple traits that signal quality evolved and are maintained (Candolin, 2003). Perhaps the most relevant case/theory to this thesis is when multiple traits signal the same quality they may be back-up signals. Each signal will have a degree of error, thus assessment of multiple signals will reduce this error. Thus, if multiple traits are influenced by sex hormone levels, then the extent to which these traits are expressed should be related (Thornhill & Grammer, 1999).

4.1.2.1 Face & body

Among women, perceived femininity of women's faces (Law Smith et al., In Press) is positively related to oestrogen and among women, waist-to-hip ratio is negatively related to oestrogen levels (Jasienska, Ziomkiewicz, Ellison, Lipson, & Thune, 2004). Enhanced femininity in women's faces (Perrett et al., 1998; Rhodes et al., 2000) and low waist-to-hip ratio has been found attractive have been rated as attractive by men (Singh, 1993, 1995a, 1995b). Evidence for a link between body and facial symmetry is equivocal (Gangestad & Thornhill, 2003), although 3D symmetry is traditionally measured on 2D images, potentially reducing the power of the measurement technique (Jones et al., 2003). Nevertheless, facial attractiveness is positively related to facial and body symmetry (Gangestad et al., 1994; Perrett et al., 1999). Furthermore, it has been found that women with attractive faces have been shown to have attractive bodies (Thornhill & Grammer, 1999).

4.1.2.2 Face & smell

HLA heterozygousity at 3 or more loci, rather than less than 3 loci is associated with facial attractiveness in men (Roberts et al., 2003). Indeed, women tend to prefer the smell of men with dissimilar HLA configurations to their own (Wedekind, Seebeck, Bettens, & Paepke, 1995). It can be surmised that this would also extend to men's preferences for women. Thus, if (1) HLA is tied to odour production (Wedekind et al., 1995), (2) HLA is tied to adrenal androgen production (Chen & Parker, 2004), (3) oestrogen synthesis is tied to androgen production (Abitbol, Abitbol, & Abitbol, 1999), (4) oestrogen is related to body shape (Jasienska et al., 2004) and facial attractiveness (Law Smith et al., In Press), then attractiveness of body odour may relate to facial attractiveness. Indeed, Rikowski & Grammer (1999) found just that. Women with attractive body odours also had attractive faces. Their reasoning, however, was different than described above. Rikowski & Grammer (1999) suggested that the relationship between facial attractiveness was based on both signalling common information reflecting individual fluctuating asymmetry, but found no support for this hypothesis in women. Nonetheless, there was an observed correlation between the attractiveness of two disparate traits: face and odour. Furthermore, male preference strength for femininity in female faces was found to correlate with male preference strength for female-typical putative pheromones (Cornwell et al., 2004).

4.2 Men

4.2.1 Face

4.2.1.1 Masculinity

Ratings of facial masculinity are related to testosterone in real and composite (averaged) faces (Penton-Voak & Chen, 2004). Thus, ratings of facial masculinity relate to hormone levels, as well as the differences between men and women's faces (Penton-Voak & Chen, 2004; Perrett et al., 1998). Also, faces masculinised by transforming faces by the differences between men and women's faces tend to be rated as older and more dominant, but less warm, less emotional, less honest, less cooperative and poorer quality parents (Perrett et al., 1998). Thus, facial masculinity appears to signal positively, certain qualities that should relate to mate quality (e.g. age and dominance), but also signals negatively, other attributes that should relate to mate quality (e.g. warmth, emotionality, honesty, cooperativeness, and quality as a parent). These findings led others to theorise that there is a theoretical trade-off between good genes for dominance and heritable immunity to infection (Johnston, Hagel, Franklin, Fink., & Grammer, 2001; Little, Burt, Penton-Voak, & Perrett, 2001; Little, Jones, Penton-Voak, Burt, & Perrett, 2002; Penton-Voak & Perrett, 2000; Penton-Voak et al., 1999) and good genes for parental investment. There seems to be some empirical evidence for this trade-off. In general, testosterone seems to enhance immune function (Booth et al., 1999; Chen & Parker, 2004), but also is associated with behaviour that leads to ill health and risk taking (Booth et al., 1999). There is also an interaction between cortisol, testosterone and health, but this relationship remains unclear (Salvador, 2005). Furthermore, testosterone is negatively associated with investment in children and long-term relationships (Burnham et al., 2003; Gray, 2003; Gray et al., 2004; Gray et al., 2002). Thus, as facial masculinity appears to signal disparate information relating to mate quality, it is not surprising that evidence that facial masculinity is attractive (in general) is equivocal. Perrett et al. (1998) and Rhodes et al. (2000) found that faces manipulated in the shape differences between men's and women's faces were more attractive when slightly feminised. Johnston et al. (2001) found that slightly masculinised faces were more attractive than feminised faces. Cornwell et al. (2003) found that faces with average level of masculinity in shape were attractive. Nonetheless, as I will review later, lack of consistency in general preferences for masculinity may reflect within and between individual differences relating to state and trait hormone levels, fertility status, degree of feminisation, self-image and ecological conditions.

4.2.1.2 Dominance

Ratings of facial dominance do relate to the size of sexually dimorphic facial characteristics (Perrett et al., 1998) and facial characteristics thought to reflect how the face changes at puberty (Swaddle & Reierson, 2002). So, apparent facial dominance may be a valid signal to traits that might enhance physical dominance. Dominant looking faces, however, are not consistently judged as the most attractive by women (Perrett et al., 1998; Swaddle & Reierson, 2002). Rated facial dominance also appears to relate to social dominance. Dominance ratings facial photographs from graduating West-Point Cadets have been shown to positively correlate with terminal rank in the men's military careers. Furthermore, military rank positively predicts reproductive success (as measured by number of children) and attractiveness of the men's partners (Mazur & Mueller, 1996; Mueller & Mazur, 1996).

4.2.1.3 Age

Face shape changes with age (Enlow & Moyers, 1971). As men age, they become more masculine, particularly at puberty. Perrett et al. (unpublished data) found that women preferred men's faces that were manipulated to look older, rather than younger.

4.2.1.4 Health

Women prefer healthy looking men's faces (Jones, Little et al., In Press; Jones, Little, Feinberg et al., 2004; Jones et al., 2001; Jones et al., 2005). A recent study by Law Smith et al. (In Prep) shows that attributions of health in the face relate to cortisol levels, which change depending on stress and illness (Chen & Parker, 2004).

4.2.1.5 Skin

Attractiveness ratings of small patches of men's cheek skin correlates positively with the attractiveness of the whole face (Jones, Little, Burt, & Perrett, 2004). Furthermore, men with attractive looking skin (as evaluated from these cheek patches) are more likely to be heterozygous at 3 HLA loci than men with unattractive looking skin (who are more likely to be heterozygous at <3 HLA loci, Roberts et al., 2003). Therefore, ratings of attractiveness given to faces manipulated upon the dimension of perceived health are likely to reflect actual differences in immunocompetence.

4.2.1.6 Body

Maisey et al. (1999) has shown that women prefer men's bodies that have low waist-to-shoulder ratios more than men's bodies with high waist-to-shoulder ratios, independently of body-mass-index. Waist-to shoulder ratio is theoretically related to testosterone levels. Other studies use shoulder-to hip ratio as another index of body masculinity (Hughes et al., 2004).

4.2.2 Interrelationships between measures of quality

4.2.2.1 Facial symmetry and health

Jones et al. (2004) showed by making composites of symmetrical men's faces and asymmetrical men's faces in the domains of colour and texture, but not shape, that men with symmetrical faces look healthier and more attractive than men with asymmetrical faces do.

4.2.2.2 Symmetry and other measures of quality

In men, fluctuating asymmetry is a well studied putative indicator of mate quality in relation to other indicators of quality. Low fluctuating asymmetry is related to high developmental stability. Correlates of fluctuating asymmetry include, but are not limited to: IQ (Furlow, Armijo-Prewitt, Gangestad, & Thornhill, 1997), facial masculinity (Gangestad & Thornhill, 2003), semen quality (Firman, Simmons, Cummins, & Matson, 2003), vocal attractiveness (Feinberg & Jacobson, 2001; Hughes, Harrison, & Gallup, 2002); incidence of female orgasm as reported by women (Shackelford et al., 2000) and men (Thornhill, Gangestad, & Comer, 1995), body size (height and weight, Trivers et al., 1999), number of reported extra-pair copulations (Gangestad & Thornhill, 1997) etc. (this list is not exhaustive, but evidence enough that symmetry is well studied and relates to other indices of mate quality).

5 Individual differences in what is attractive

5.1 Age

Little et al. (2001) found that women's age positively predicted their preferences for masculinity of men's face shape. This finding may relate to the fact that manipulations of facial masculinity also alter perceptions of age (Perrett et al., 1998), thus older women were selecting older looking men than younger women were. Perrett et al. (unpublished data) show that indeed, that age correlates with preferences for faces manipulated on the dimensions of actual and perceived age.

5.2 Relationship status, hormonal contraceptives and temporal context

Little et al. (2002b) and Johnston et al. (2001) found that when women rated men's faces that were manipulated in shape masculinity, preferences for masculinity were stronger when women evaluated these faces as a potential short-term partner than when they rated the faces as a potential long-term partner. Furthermore, women in committed relationships who were not on hormonal contraceptives had stronger facial masculinity preferences than women who were not currently in committed relationships (Little et al., 2002b). This latter pattern was reversed (but not significant) for women who were taking hormonal contraceptives. These findings suggest that women are judging faces in such a way that they have learned (unconsciously perhaps) that men with higher testosterone have more masculine faces than men with lower testosterone (Penton-Voak & Chen, 2004), men with higher testosterone invest less in offspring and are less likely to be in committed relationships than men with lower testosterone (Burnham et al., 2003; Gray, 2003; Gray et al., 2004; Gray et al., 2002). Also, women decrease their self-reported commitment to relationships at fertile parts of the menstrual cycle (Jones et al., 2005). See section 5.4 for more on menstrual cycle and preference changes.

5.3 Attractiveness/femininity

Two studies have shown, using different methods, that femininity of women's body shape, and attractiveness of the face (as rated by themselves and by others) positively predicts women's preferences for masculinity in men's faces (Little et al., 2001; Penton-

Voak et al., 2003). This effect was largest when women judged faces as potential long-term partners and more attractive and more feminine women differed less in their attractiveness judgements between relationship contexts than less attractive and more masculine women did. The authors suggest that attractive and feminine women may be able to secure masculine men as long-term mates more easily than less attractive, more masculine women can. Thus, less attractive and more feminine women adjust their preferences accordingly.

5.4 Menstrual cycle

5.4.1 Facial masculinity preferences

Studies have shown that women's facial masculinity preferences are strongest at the late-follicular, most fertile menstrual cycle phase and weakest at other times of the menstrual cycle (Penton-Voak et al., 1999; Penton-Voak & Perrett 2002; Johnston et al., 2001). These shifting preferences have been theoretically linked to a trade-off between women being able to obtain either men possessing dominance and inheritable immunity to infection (masculine men) or men who will invest in offspring (feminine men, see Penton-Voak et al., 1999; Penton-Voak & Perrett 2002;. Johnston et al., 2001). This theoretical trade-off is somewhat supported by empirical data showing that testosterone in men is negatively linked to investment in offspring and commitment to relationships (Burnham et al., 2003; Gray, 2003; Gray et al., 2004; Gray et al., 2002).

5.4.2 Preferences for height

Pawlowski & Jasienska (2005) reported that women preferred line drawings with a taller ratio between male and female height at the fertile (late-follicular) menstrual cycle phase than at other times of the menstrual cycle. They theorised that this reflects the trade-off between women being able to either obtain dominant men and inheritable immunity to infections from men, or men who will invest in offspring (see above).

5.4.3 Preferences for healthy looking faces

Jones et al., (2005) showed that during the luteal menstrual cycle phase, pregnancy and hormonal contraceptive use (each characterised by high progesterone), women were more adverse to unhealthy looking faces than at other times of the menstrual cycle, when not pregnant and when not on oral contraceptives (each characterised by low progesterone). Initially, this report seemed to contradict evidence that menstrual cycle shifts in masculinity preferences reflect a trade-off between inheritable immunity to infection and parental investment. Nonetheless, as Getty (2002) mentioned, current health status is not necessarily an accurate indicator of inheritable immunity to infection. Thus, the two results are not in opposition. Menstrual cycle shifts in preferences for healthy looking faces appear to mirror menstrual cycle shifts (and differences between pregnant and non-pregnant women) in sensitivity to disgusting stimuli and food types (Fessler, 2003; Fessler & Navarrete, 2003).

5.5 Psychological condition

Women's psychological condition (as measured by an anxiety and depression inventory) is associated with preference for apparent health in faces (Jones et al., In Press). Women who scored high on anxiety and depression measures had the weakest preferences for apparent health in faces (of both men and women).

5.6 Ecology

5.6.1 Body

Cross-cultural studies of preferences for waist-to-hip ratio showed that in rural Jamaica, men preferred line drawings of women with more masculine waist-to-hip ratios (Manning, Trivers, Singh, & Thornhill, 1999). This was thought to be because women with masculinised bodies might have more male children. This has been challenged. The first challenge stated that waist-to-hip ratio does not cause more male children, but is a result of having more male children (Tovée, Brown, & Jacobs, 2001; Yu & Shepard, 1999). Second, the line drawings used also varied on body-mass-index (Tovée & Cornelissen, 1999). Nevertheless, there is cultural variation in preferences for waist-to-hip ratio and/or body-mass index.

5.6.2 Face

In rural Jamaica, where there is little paternal investment in offspring (men usually care for their sister's children, rather than their own) and higher parasite loads than the US or UK, women had stronger facial masculinity preferences than women in the UK, suggesting that Jamaican women preferred cues to dominance and heritable immunity to infection over cues to paternal investment (Penton-Voak, Jacobson, & Trivers, 2004).

6 What physical characteristics do acoustic properties of the voice relate to?

6.1 Women

6.1.1 Hormones

6.1.1.1 Testosterone

6.1.1.1 Pitch

In both men and women, prenatal testosterone sets up the number and sensitivity of testosterone receptors that will be used later in life (Manning et al., 2003). Thus, prenatal testosterone should relate to adult voice pitch in women, particularly after puberty and menopause. The ratio of finger lengths of the second and fourth digits is a marker of prenatal testosterone is (Lutchmaya, Baron-Cohen, Raggatt, Knickmeyer, & Manning, 2004; Manning et al., 2004). Only one published study has investigated the relationship between digit ratios and voice pitch and did not reveal a significant relationship (Putz, Gaulin, Sporter, & McBurney, 2004). Nevertheless, I have unpublished data showing that digit ratios do indeed correlate with voice pitch.

A study of female to male transsexuals who have received exogenous testosterone showed that after testosterone administration, voice pitch drops (Van Borsel, De Cuypere, Rubens, & Destaerke, 2000). This is most likely due to a thickening of the vocal folds, thus the process is irreversible without surgery.

As testosterone is a masculinising hormone and oestrogen is a feminising hormone, and since testosterone and oestrogen may influence women's voice pitch, it can be hypothesised that women with higher pitched voices should be rated as more feminine than women with lower pitched voices.

6.1.1.2 Vocal-tract length

Fitch & Geidd (1999) found that sex differences in vocal-tract length were greater than what could be accounted for by sex differences in height alone. Therefore, they hypothesised that vocal-tract length would relate to testosterone. As hypothesised for voice pitch, because testosterone is a masculinising hormone, and it has been hypothesised that women's vocal-tract length may be related to testosterone (Fitch & Geidd, 1999), women with relatively longer vocal-tract lengths may be rated as more masculine than women with relatively shorter vocal-tract lengths.

6.1.1.2 Oestrogen and progesterone

6.1.1.2.1 Pitch

Abitbol et al. (1999) suggested that because oestrogen is a testosterone antagonist, and testosterone lowers voice pitch, oestrogen should be positively related to voice pitch. As women receive an oestrogen surge at puberty, voice pitch in women may be a marker of pubertal oestrogen levels (Alonso & Rosenfield, 2002). If adult and pubertal oestrogen levels are correlated, and pubertal and adult voice pitches are correlated, adult oestrogen levels should also correlate with adult voice pitch.

6.1.1.2.2 Vocal-tract length

If oestrogen is a testosterone antagonist, and Fitch & Geidd (1999) hypothesised that vocal-tract length might correlate positively with testosterone, vocal-tract length may correlate negatively with oestrogen levels.

6.1.1.2.3 Jitter and shimmer

Jitter and shimmer are periodic variation in the fundamental frequency and the amplitude thereof (respectively). Jitter and shimmer, perceptually correspond to voice roughness. As blood flow and hydration levels change over the menstrual cycle, it is possible to hypothesise that jitter and shimmer may also change over the menstrual cycle. In samples of women who experience pre-menstrual tension (syndrome) and in samples of women where these data were not recorded, during the luteal menstrual cycle phase (characterised by high progesterone), women's levels of jitter and shimmer were elevated (Abitbol et al., 1999; Amir & Kishon-Rabin, 2004; Amir, Kishon-Rabin, & Muchnik, 2002; Chae, Choi, Kang, Choi, & Jin, 2001). Coincidentally, women on birth control pills (usually characterised by high doses of progesterone) have lower in jitter and shimmer than women not on hormonal contraceptives (Amir & Kishon-Rabin, 2004; Amir et al., 2002). Women's faces are more attractive when fertile (Roberts et al., 2004), and jitter and shimmer are lower when women are more fertile (excluding data on hormonal contraception), men might rate women with less jitter and shimmer as more attractive.

6.1.2 Body characteristics

6.1.2.1 Waist-to-hip ratio

If voice pitch is positively related to oestrogen levels and waist-to-hip ratio is negatively correlated with oestrogen levels, among women, voice pitch should correlate negatively with waist-to-hip ratio. Collins & Missing (2003) found that a composite score of body-mass-index, weight, hip circumference and waist circumference correlated with voice pitch, such that smaller bodied women had higher pitch of voice. A separate, composite score of height and waist-to-hip ratio did not correlate with voice pitch. It is possible that no relationship between waist-to-hip ratio and voice pitch was found because it was grouped statistically with height. The findings in Collins & Missing (2003) still suggest that there is a relationship between waist-to-hip ratio and voice pitch because the composite score containing raw waist and hip measurements did correlate with voice pitch.

6.1.2.2 Height and weight

6.1.2.2.1 Pitch

Fundamental frequency and height are not related among adult women (Lass & Brown, 1978). Fundamental frequency does, however decrease with age throughout development, so through ontogenetic development, fundamental frequency does relate to height (Huber et al., 1999; Linders, Massa, Boersma, & Dejonckere, 1995). Furthermore, fundamental frequency can predict the difference in height between groups of adult men and adult women (Rendall et al., 2005). As height is correlated with weight, it can be hypothesised that variance in pitch accounted for by height may also be explained by weight (but only through weight's association with height). Even though among adult women, pitch may not relate to height and weight, people may still incorrectly extend the association between pitch and height among children to adults. Thus, women with high pitched voices may be rated as being larger (taller and heavier) than women with low pitched voices may be rated. Indeed Fitch (1994) and Smith et al. (2005) found that voices with higher pitch were rated as coming from larger (the rating was size, not height and/or weight) people than voices with lower pitch.

6.1.2.2.2 Vocal-tract length

Fitch & Geidd (1999) found that vocal-tract length (as measured via magnetic resonance imaging - MRI) was correlated positively with height and weight. They explained that the association between weight and vocal-tract length was due to the positive association between weight and height, and that the relationship between weight and vocal-tract length might diminish in emaciated and obese people. There are mixed results that formant dispersion (Fitch, 1997), an acoustic correlate of vocal-tract length (formant dispersion is negatively correlated with vocal-tract length, see Chapter 2 for full explanation), is correlated negatively with height in women. Collins & Missing (2003) and Gonzalez (2004) found a negative correlation between height and formant dispersion, whereas others (Rendall et al., 2005) did not find such a relationship. Rendall et al. (2005) theorised that they did not find such a link due to changes in formant structure over the menstrual cycle, but did not record menstrual cycle data, or that formant dispersion is a poor correlate of body size Clearly, if formant dispersion correlates with vocal-tract length and vocal-tract length correlates with body size, if researchers fail to find such relationships, it may be due to measurement or sampling error, rather than formant dispersion being a poor correlate of vocal-tract length and body size (height and weight). Indeed, Fitch (1994) and Smith et al. (2005) found that voices with lower and more closely spaced formants were rated as larger (not taller or heavier) than voices with higher and further spaced formants.

6.1.2.2.3 Jitter

In young girls, jitter has been shown to be negatively related to height (Linders et al., 1995). This is thought to be due to growth stabilising either structure and/or control of the vocal folds. Thus, girls with less jitter might sound smaller than girls with more jitter.

6.1.3 Age

6.1.3.1 Pitch and vocal-tract length

Voice pitch becomes lower and the vocal-tract gets longer though development (Fitch & Giedd, 1999; Huber et al., 1999). Women's voice pitch drops by about 33% at puberty (Abitbol et al., 1999), and changes in vocal-tract length may correspond to growth spurts at puberty. Thus, pitch and vocal-tract length may be used to discriminate age in pre-pubertal women and between sexually mature and sexually immature women. Furthermore, women's voice pitch drops drastically at menopause (Abitbol et al., 1999).

6.1.3.2 Jitter and shimmer

As jitter and shimmer are related to vocal fold quality (e.g. health, see below), and like most body parts, vocal folds degrade in quality as age increases (Titze, 1994), jitter and shimmer can also be used as indices of age. Indeed research has shown that jitter and shimmer are positively related to age (Ramig, Scherer, & Titze, 1984).

6.1.4 Health

6.1.4.1 Fundamental frequency

If fundamental frequency in women is related to oestrogen and testosterone (Abitbol et al., 1999; Van Borsel et al., 2000), and in turn, testosterone and oestrogen may be related to immune function (Chen & Parker, 2004; Thornhill & Gangestad, 1999) women with high voice pitch may be healthier than women with low voice pitch.

6.1.4.2 Vocal-tract length

If vocal-tract length is negatively related to testosterone (see Fitch & Geidd, 1999, for hypothesis), then vocal-tract length may be negatively related to health in women.

6.1.4.3 Jitter & Shimmer

Jitter and shimmer are produced by imperfect, asynchronous vocal-fold vibration (Titze, 1994). This has been shown experimentally in living humans where magnetic stimulation of unilateral vagus nerve implants caused increased voice perturbation (Kersing, Dejonckere, van der Aa, & Buschman, 2002). Jitter and shimmer have been used to discriminate voices with pathologies (e.g. unilateral vocal-fold paralysis; cancer; Parkinson's disease) from healthy voices (Hertrich & Ackermann, 1995; Kotby, Titze, & Saleh, 1991; Parsa & Jamieson, 2000; Wolfe & Martin, 1997). Thus, vocal-fold health is likely to be an indicator of overall health.

6.1.4.4 Facial attractiveness

Facial attractiveness and perceived facial femininity are positively related to oestrogen levels among women (Law Smith et al., In Press). Voice pitch may also be positively related to oestrogen levels among women (Abitbol et al., 1999). Therefore, voice pitch may be related to facial attractiveness and facial femininity.

6.2 Men

6.2.1 Hormones (testosterone)

6.2.1.1 Prenatal testosterone

As mentioned earlier, prenatal testosterone influences the amount and sensitivity of testosterone receptors present later in life. Therefore, prenatal testosterone may relate to voice pitch. Putz et al. (2004) found no link between digit ratio (an indicator of prenatal testosterone) and voice pitch. It should be noted, however, that a null result does not prove that the phenomenon does not exist (especially in the study by Putz et al. 2004, where each vocaliser spoke different words in different hypothetical situations) and therefore, further studies should be done to determine if there is a link between prenatal testosterone and voice pitch. As mentioned earlier, I do have unpublished data indicating there is a link between digit ratio and voice pitch.

6.2.1.2 Pubertal testosterone

Longitudinal studies have shown that testosterone is negatively related to voice pitch throughout puberty (Harries et al., 1997; 1998). This is most likely due to testosterone enlarging the larynx at puberty, lengthening and thickening the vocal-folds (Kahane, 1978, 1982).

6.2.1.3 Adult testosterone

Dabbs & Mallinger (1999) found that adult testosterone levels are negatively related to voice pitch. I have unpublished data showing a negative correlation between pitch and testosterone that is double the strength of that from Dabbs & Mallinger (1999). As voice pitch is relatively static after puberty, Dabbs & Mallinger (1999) offered two explanations as to why voice pitch correlates with adult testosterone. First, pubertal testosterone is related to adult testosterone, thus explaining the relationship between a marker of pubertal testosterone (voice pitch) and adult testosterone levels. Alternatively, the link between adult voice pitch and adult testosterone levels may be explained in terms of behaviour: men with higher testosterone may speak with a lower pitch and men with lower testosterone speak with a higher pitch. More research is needed to determine the nature of this relationship.

6.2.2 Body characteristics

6.2.2.1 Height

6.2.2.1.1 Pitch

As mentioned above, pitch of voice is negatively related to height as a function of age, in pre-pubertal males (Huber et al., 1999). Furthermore, pitch of voice predicts height differences between men and women (Rendall et al., 2005), but not within each sex (Lass & Brown, 1978).

6.2.2.1.2 Vocal-tract length

Like in women, vocal tract length is positively related to height and weight in men (Fitch & Geidd, 1999). Again, the sex difference in vocal-tract length is greater than what can be accounted for by sex differences in height alone (Fitch & Geidd, 1999). Rendall et al. (2005) found a negative correlation between height and formant dispersion (an acoustic parameter negatively related to vocal-tract length) in men.

6.2.2.2 Chest hair

The appearance of chest hair at puberty is associated with increased androgen levels (Hiort, 2002). Thus in adulthood, voice pitch may be negatively related to the amount of chest hair a man has. Collins (2000) found that women thought men with low frequency voices had more chest hair than men with high frequency voices.

6.2.2.3 Age

6.2.2.3.1 Pitch

Pitch of voice lowers through development, and drops rapidly at puberty, and then is relatively fixed until old age (Titze, 1994; Huber et al., 1999; Childers & Wu, 1991). Therefore voice pitch in men is a likely to be an accurate indicator of age until adulthood. Nonetheless, (Collins 2000) failed to find a significant relationship between perceived and actual age of young adult men.

6.2.2.3.2 Vocal-tract length

Like voice pitch, the vocal-tract length gets longer as men age, and (resting position) is fixed at puberty (see Fitch & Geidd, 1999; Huber et al, 1999). Therefore, apparent vocal-tract length (or formant dispersion) is likely to be an accurate indicator of age until adulthood. Again, Collins (2000) found no link between formant frequency properties and perceived age. These frequency configurations, however, were based on principal components analysis but also included formant dispersion. Thus, these measures may have been too weak to detect such a relationship because of the principal components analysis.

6.2.2.3.3 Jitter

Jitter is highest at young and old ages, and lowest from puberty until mid-age (Linders et al., 1995; Linville, 1985). Therefore, jitter may indicate age between children and younger adults and between younger adults and older adults.

6.2.4 Health

6.2.4.1 Pitch

If testosterone is related to health both positively through immune system promotion (Chen & Parker, 2004) and negatively (Booth et al., 1999) through risk taking behaviour (thus men with higher testosterone may be able to afford this risk-taking behaviour, see Zahavi, 1975, but see chapter 3 for discussion of the possible role of cortisol in immunocompetence), and voice pitch is negatively related to pre-natal testosterone (speculatively), pubertal testosterone (Harries, Hawkins, Hacking, & Hughes, 1998;

Harries, Walker, Williams, Hawkins, & Hughes, 1997) and adult testosterone (Dabbs & Mallinger, 1999), voice pitch may be negatively related to actual and perceived health.

6.2.4.2 Vocal-tract length

In a similar fashion to the hypothesis drawn above between voice pitch and health, if testosterone is related to vocal-tract length (see Fitch & Geidd, 1999 for hypothesis), and vocal-tract length is related to body size (height and weight, Fitch & Geidd, 1999), which is in turn related to nutritional status through development, then men with larger vocal-tract lengths may be and sound healthier than men with smaller vocal-tract lengths.

6.2.4.3 Jitter and shimmer

As mentioned above when discussing the relationship between jitter and shimmer and health in women, jitter and shimmer indicate vocal-fold health (Hertrich & Ackermann, 1995; Kotby et al., 1991; Parsa & Jamieson, 2000; Wolfe & Martin, 1997), which is tied to incidence of disease. Therefore, vocal-fold health is probably an indicator of overall health. Voices with high jitter and shimmer may be perceived as less healthy than voices with low jitter and shimmer.

7 What is attractive in the voice and what does vocal attractiveness relate to?

7.1 Vocal attributes and acoustic properties of the voice

7.1.1 Pitch

7.1.1.1 Women's voices

Fundamental frequency of the voice (pitch) has been shown to correlate positively with attractiveness ratings (Collins & Missing, 2003). In this study, women's voices that had higher fundamental frequencies were also rated as sounding younger than women's voices with lower fundamental frequencies. Smith et al. (2005) found that voices manipulated to have higher pitch were judged as smaller (this was not an assessment of height or weight, but an assessment of body size) than voices manipulated to have lower pitch were. Smith et al. (2005) did not report whether the participants speaking were male or female, or what age they were. This is important, especially in a psychophysics study such as Smith et al. (2005), because although stimuli were manipulated to have the fundamental frequencies of men, women and children, other acoustic properties of the voice, such as spectral slope, are sexually dimorphic and change with age (Hanson & Chuang, 1999; Linville, 1985), and may therefore interact with perceptions of body size.

7.1.1.2 Men's voices

Collins (2000) found that pitch of voice correlated negatively with vocal attractiveness, perceptions of weight, age, muscularity and presence of chest hair in men. Fitch (1994) found that voices synthesised to have male-typical fundamental frequencies were rated smaller (not shorter or thinner, but smaller) when fundamental frequency was 150Hz, than when fundamental frequency was 100Hz. Smith et al. (2005) found that voices manipulated to have lower fundamental frequencies were rated as larger (not taller or heavier) than voices manipulated to have higher fundamental frequencies. Age and sex, however, of these original voices was not reported.

7.1.2 Formant frequencies

7.1.2.1 Women's voices

High fundamental frequency and high formant dispersion have been shown to relate negatively to perceived age (Collins & Missing, 2003).

Smith et al. (2005) found that voices manipulated to have large apparent vocal-tract lengths were rated larger (not taller or heavier, but actually rated larger) than voices manipulated to have smaller apparent vocal-tract lengths were (see above for potential caveats in the study by Smith et al., 2005). Fitch (1994) synthesised voices to have formant frequency properties of large and small adult women, but with fundamental frequency characteristics of adult men. Nevertheless, synthetic voices with larger apparent vocal-tract lengths were rated larger (again, size was the attribution used, *not* height or weight) than voices with smaller apparent vocal-tract lengths were.

7.1.2.2 Men's voices

Collins (2000) failed to find a relationship between formant qualities and perceived height and weight, although Fitch (1994) and Smith et al. (2005) did find that apparent vocal-tract length was related positively to perceived size (not height and weight specifically, but size). Thus far, no link between formant frequencies and vocal attractiveness in men's voices has been found.

Jitter and shimmer have been associated positively with perceived age (Linville & Fisher, 1985). This perception may be accurate as jitter and shimmer are correlated positively with real and perceived age (Linville & Fisher, 1985; Ramig et al., 1984).

7.2 Vocal attractiveness and non-vocal, characteristics

7.2.1 Symmetry

Hughes et al. (2002) found that both women and men with attractive voices had more symmetrical bodies (see also, Feinberg & Jacobson, 2001). Hughes et al. (2002) suggest that these disparate signals are correlated because they may both reflect genetic quality. In this study, Hughes et al. (2002) failed to find a significant relationship between second to fourth digit ratio and vocal attractiveness.

7.2.2 Body Shape

Attractiveness ratings of women's voices correlated negatively with waist-to-hip ratio (Hughes et al., 2004). Attractiveness ratings of men's voices were positively correlated with shoulder-to-hip ratio (Hughes et al., 2004). Nonetheless, associations between vocal attractiveness and body shape in men and women were non-significant when controlling for body-mass-index and age.

7.2.3 Perceived age

Collins & Missing (2003) found that younger sounding women's voices were judged by men to be more attractive than older sounding men's voices.

7.2.4 Facial attractiveness

Collins & Missing (2003) found that women with attractive faces had attractive voices, but reported that in unpublished data they had found no such relationship in men. Nevertheless, although not peer-reviewed, one news article does report findings from a study showing that men's facial and vocal attractiveness were correlated positively (http://www.news-medical.net/?id=8403).

7.3 Vocal attractiveness and other attributions

Men and women with attractive voices have reported more sexual partners, started having sex earlier, cheated on a partner more times and were the person whom someone cheated on their partner with more than women with relatively unattractive voices (Hughes et al., 2004). Thus, either these self-reports are true, or people with attractive voices are biased to report higher numbers on socio-sexual inventories than people with less attractive voices.

7.4 Individual differences in voice perception

One study (Puts, 2005) claims that between-subjects, menstrual cycle and relationship context (whether women rated voices as a potential long-term partner or potential short-term partner) affects women's preferences for men's voice pitch. Women in the fertile (late-follicular) menstrual cycle phase and women judging voices as potential short-term partners showed the highest preferences for male voices that Puts (2005) claimed were lowered in pitch. Puts (2005), however, did not *only* manipulate pitch of voice, but rather manipulated the *entire* sound spectrum, changing both pitch and formant frequencies. Thus it is unknown if the findings from Puts, (2005) reflect perceptions of pitch or vocal-tract length or both.

Pawlowski (2003) found that women's height predicted their preference for relative height in a potential partner (by using assessments of line drawings). Thus, women's height may predict their preferences for male apparent vocal-tract length.

The remainder of this thesis is dedicated to testing how acoustic properties of the voice relate to mate-choice relevant attributions and characteristics, and what about perceivers changes mate choice relevant decisions.

Chapter 5

Correlations between acoustic properties of the voice and attributions to voices

The purpose of the following studies is to explore possible associations between perceptual attributions and acoustic properties of young adult men's and young women's voices.

Study 1 – Men's voices

1 Rationale

Collins (2000) conducted a correlational study (utilising vowel sounds) that investigated how attributions made to the voices (i.e. attractiveness and characteristics related to masculinity such as amount of chest hair, weight, body type – slim or muscular, age and height) related to acoustic properties of the voice (fundamental and formant frequencies, peak frequencies and harmonic frequencies). Collins (2000) utilised principal components analysis (PCA) to group acoustic variables that were intercorrelated. Collins (2000) tested the relationship between statistical constructs (PCA factors) and the aforementioned attributions. Men's voices were split into three groups of 10 and were rated by three different groups of women. Two groups of female listeners had about 20 raters and the third group contained 11 raters. Voices were not presented in random orders, but statistical measures were taken to account for this.

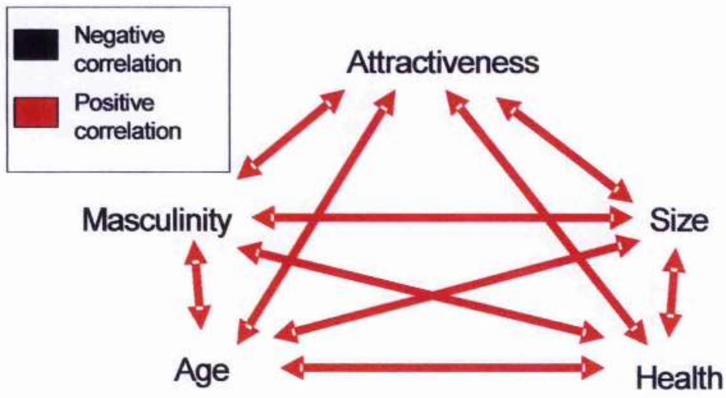
Collins (2000) found that fundamental, harmonic and peak frequencies loaded onto the same PCA factor. This is to be expected as harmonic frequencies are multiples of the fundamental and thus are multiple measures of the same acoustic phenomena (Ladefoged, 1996). Nevertheless, multiple measures of the same acoustic phenomenon may help overcome potential measurement error. The PCA factor associated with low fundamental frequency and low harmonics was positively associated with vocal attractiveness, attributions of masculinity, age and weight in each group of voices/listeners. Attributions of height, muscularity and chest hair, however, were correlated positively with the PCA factor associated with low fundamental frequency in only one group of stimuli/raters each. Thus, low-pitched voices in men were perceived as attractive, and arguably, from large, masculine men.

The other PCA factors in the study by Collins (2000) represented a mixture of different formant frequency configurations from different vowels. Surprisingly, none of these 3 PCA factors associated with formant frequency configurations were correlated with any of the aforementioned attributions. Nevertheless, other studies have shown that formant frequencies and formant frequency dispersion are negatively associated with perceptions of large body size (here attributions were body size, not height and/or weight, Fitch, 1994; Smith et al., 2005). It is possible that the Collins (2000) did not find relationships between formant qualities and perceived size because here, formants were grouped into orthogonal categories that vary independently (principal components), rather than ran through algorithms constructed to reflect how formants are produced (see Fitch &

Hauser, 2002, and chapter 2 for explanation of why formant dispersion is a better measure correlate of vocal-tract length than raw or average formants).

Collins (2000) found positive associations between masculine vocal features, attributions related to masculinity and attractiveness. Furthermore, Buss (1989) and Kenrick & Keefe (1992) found that women prefer older men and men that were older than themselves. Therefore, I predicted that attributions of masculinity and age would positively predict attractiveness of men's voices. In general, height and weight are sexually dimorphic. The attribution of body size is a combination of height and weight. Barring overweight and underweight individuals, height and weight are positively related (see Fitch & Geidd, 1999; chapter 6). Previous studies (Fitch 1994; Smith et al., 2005) have used body size as an attribution to voices varying in formant qualities (see also definition section for further detail). Therefore, to reduce the number of variables measured, throughout this thesis I used the attribution of body size instead of height and weight as individual variable. Collins (2000) found that perceived height and weight correlated positively with vocal attractiveness (although this relationship was thought to be dependent on the PCA factor related to harmonics). Therefore I predicted that vocal attractiveness would correlate positively with perceived size. If perceptions of health are accurate, healthy sounding voices should also be attractive as this will aid in contagion avoidance. Furthermore, I predicted that voices that were perceived as more masculine would also be perceived larger and older. Figure 5-1 is a diagram showing predictions for correlations between attributes in men's voices.

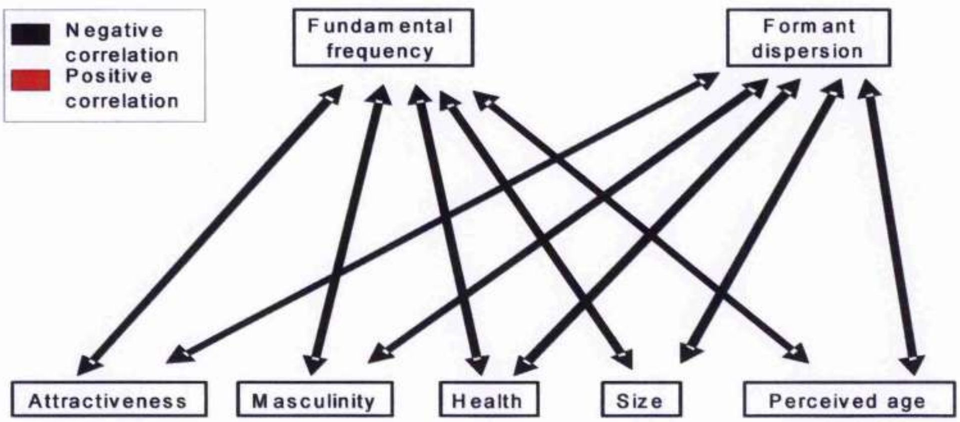
Figure 5-1. Predicted correlations among attributes in men's voices



I sought to replicate the finding by Collins (2000) that fundamental frequency negatively predicted male vocal attractiveness, perceived body size, perceived masculinity and perceived age. Rhodes (2003) found that rated facial masculinity in men was positively related to long-term medical health. Accordingly, I hypothesised that fundamental frequency, a masculine vocal characteristic (Collins 2000), would be negatively related to perceived health.

Fitch (1994) and Smith et al. (2005) found that apparent vocal-tract length was positively related to perceptions of vocaliser size (not specifically height and/or weight). Therefore I predicted that formant dispersion would be negatively correlated with attributions of body size. Body size (i.e. height and weight) is sexually dimorphic. I therefore predicted that formant dispersion would correlate negatively with perceived masculinity. Vocal tract length and formant frequencies (and their dispersion) lower with age until adulthood (Huber et al., 1999). Hence, I predicted that formant dispersion would correlate negatively with perceived age. Growth can be stunted by poor nutrition. Consequently, I predicted that formant dispersion would also correlate negatively with perceived health. Also, because height is positively associated with reproductive success in men (Mueller & Mazur, 2001; Pawlowski et al., 2000), I predicted that formant dispersion would negatively predict attractiveness ratings. Figure 5-2 illustrates predictions for correlations between fundamental frequency, formant dispersion and attributes to men's voices.

Figure 5-2. Predicted relationships among acoustic features and vocal attributes in men's voices.



Two other acoustic properties of the voice may also relate to attractiveness. There is support for the idea that increased perturbation of the fundamental frequency, and the amplitude thereof (jitter and shimmer, respectively) of human voices indicates poor vocal fold health and can discriminate between healthy and ill individuals (Hertrich & Ackermann, 1995; Kotby et al., 1991; Parsa & Jamieson, 2000; Pinto & Titze, 1990; Wolfe & Martin, 1997). Healthy appearance has been found to be a strong predictor of facial attractiveness (Jones, Little et al., In Press; Jones, Little, Feinberg et al., 2004; Jones et al., 2001; Jones et al., 2005). As a result, acoustic properties of the voice that measure health (i.e. jitter and shimmer) should also be associated with attractiveness. To the best of my knowledge, it has not yet been shown, if jitter and shimmer are associated with perceived health.

Jitter and shimmer have been associated positively with real and perceived age (Linville, 1985; Ramig et al., 1984). These studies (Linville, 1985; Ramig et al., 1984) utilised broad age ranges and surmised that jitter related to age because at older ages, the vocal folds degrade in quality. In the current study, age is more likely a variable associated with sexual maturity because I study young adults. Jitter and shimmer may predict positively, attractiveness in men's voices through its association with age. Furthermore, jitter and shimmer may relate to attractiveness because jitter has been associated positively with negative affect (Bachorowski & Owren, 1995, 1996; see also Fitch, Neubauer, & Herzel, 2002, for review and predictions). Positive affect (smiling) increases the attractiveness of faces (Otta, Abrosio, & Hoshino, 1996). Attractive faces increase activation of a brain region associated with stimulus-reward (the medial orbitofrontal cortex, O'Doherty et al., 2003). Smiling further enhances brain activation in the aforementioned brain region (O'Doherty et al., 2003). Thus, one could predict that low jitter and shimmer (through their association with affect) may relate to vocal attractiveness, and mediate the reward-value of already attractive voices.

2 Methods

2.1 Voice recordings

Fifty-seven male (aged 18-33 M=21.8, S.D.=2.8) undergraduates at the University of St Andrews were recorded speaking the monopthong vowels: eh as in bet (ɛ), ee as in see (i), ah as in father (a), oh as in note (oʊ), oo as in boot (Y↔) (symbols in parentheses are International Phonetic Alphabet symbols). Monopthong vowels were chosen because the equation for formant dispersion assumes a constant vocal-tract area (Fitch, 1997) and monopthongs contain less formant variation (hence less variation in vocal-tract area) than dipthongs do. Sounds were recorded with an Audio-Technica AT4041 cardioid condenser microphone (*see* http://www.audio-technica.com) in a quiet room. Research by Titze & Winholtz (1993) validates the use of cardioid condenser microphones in voice perturbation studies. Vowel sounds were recorded directly onto computer hard disk and were encoded at 44.1 kHz sampling rate, at 16 bit-quantisation, and saved as uncompressed "wav" files. A 44.1 kHz sampling rate was used for recording and playback throughout this thesis unless otherwise indicated because humans can hear frequencies between 20 Hz and 20 kHz (Ladefoged, 1996). At 44.1 kHz, the maximum frequency captured by the recording is 22.05 kHz (the Nyquist frequency, Ladefoged

1996), which may be the reason why the standard sampling rate for compact disks is 44.1 kHz. All acoustic measurements and normalisations were performed with Praat software (Boersma & Weenink, 2001).

2.2 Stimuli generation

As loud sounds are perceived as higher in pitch than soft sounds (Stevens, 1998), I normalised the root-mean-squared amplitude (RMS) of each sound to 87.5dB with a low pass anti-aliasing filter. Fast sounds (e.g. fast pulses) are also perceived as higher pitched than slow sounds (e.g. slow pulses, Stevens, 1998). I have run two pilot studies one in which I did not control for differences in duration and the other in which I extracted the middle 0.2s (2/3 the duration of the shortest vowel sound in my sample) from each vowel sound. I have observed few differences in the relationships among attributions and acoustic properties of the voice among the two pilot studies and the current studies. Upon debriefing during the pilot studies, many participants noted that they thought the voices that were normalised in duration by extracting the middle 0.2s sounding strange and unnatural, which is why I used the pitch-synchronous overlap add (PSOLA) manipulation to normalise duration in the current experiment. Voices were normalised to 500 ms in duration with the pitch-synchronous overlap add (PSOLA) algorithm (Boersma & Weenink, 2001; Charpentier & Moulines, 1989). Table 5-1 displays the amount that the voices were manipulated in duration. The PSOLA manipulation had a minimal effect on between-voice variation in jitter and shimmer. The average correlation coefficient between each measure of jitter and shimmer of the original voices, as compared to time altered voices was 0.8. Nevertheless, all measurements reported here are from the time and amplitude normalised voices to ensure that the fundamental frequency perturbation measured reflected the fundamental frequency perturbation heard by listeners. Fundamental and formant frequencies were unaffected by the time and amplitude normalisations.

Table 5-1. Descriptive statistics of how much voices were altered in duration

Men's Voices				
Values reported in seconds	**Min**	**Max**	**Mean**	**S.D.**
Sum across vowels	-1.09	12.66	3.49	3.76
Mean across vowels	-0.22	2.53	0.70	0.75
|Sum| across vowels	0.01	12.66	3.60	3.66
|Mean| across vowels	0.00	2.53	0.72	0.73

2.3 Playback

For each vocaliser, vowels were played back in the order: "ah", "ee", "eh", "oh", "oo". The order in which each vocaliser's set of vowels was played was randomised. Therefore, order of stimuli could not have systematic effects on vocal attributions. Vowel sounds were played back to 10 female raters who listened to the sounds via Sennheiser HD280 headphones (www.sennheiser.com). Headphones were used so that vocal attributions could not reflect a consensus view between raters. Voices were assessed on a computer screen using 7 point scales (1=very unnattractive/unealthy/feminine/small, 7=very attractive/healthy/masculine/large), except for age, which was rated on a chronological 40-point scale from ages 10 to 50. Each attribution was assessed on screen at the same time, in the same block. Raters were allowed *ad-libitum* repetitions of each voice at an adjustable volume. Male voices were assessed by female raters. Age of raters ranged from 18-25. Playback sampling rate was 44.1 kHz.

2.4 Acoustical analysis

Each vowel sound was analysed separately using Praat software (Boersma & Weenink, 2001). Prior to measurement and manipulations, Praat automatically re-samples sounds to 11.025 kHz (producing a maximum frequency of 5.5 kHz, which is approximately the maximum value of human adult formant frequencies, Ladefoged 1996) to increase frequency resolution.

2.4.1 Fundamental frequency (pitch)

Initially, the mean fundamental frequency of each vowel sound was measured using Praat's periodic auto-correlation algorithm (Boersma & Weenink, 2001). Fundamental frequency of each male voice was searched for between 75 and 300 Hz, whereas female fundamental frequency's were searched for between 100 and 600 Hz. Goodness of fit was visually assessed by overlaying the predicted fundamental frequency over the 8^{th} harmonic of an independently produced, spectrogram with Gaussian shaped window of 0.05 seconds in length. If the predicted fundamental frequency was suspected of corruption (i.e. did not overlay well on top of the harmonic, usually in cases where the fundamental was close to the extremes of the algorithms input parameters), fundamental frequencies were re-measured with different maximum and minimum fundamental frequency values until the visual assessment was satisfactory. Descriptive statistics of fundamental frequency are displayed in table 5-2.

2.4.2 Fundamental frequency perturbation (jitter and shimmer)

Periods were identified in the fundamental frequency of each vowel sound using Praat's periodic cross-correlation algorithm (Boersma & Weenink, 2001). This fundamental frequency was also visually assessed as above. Jitter (periodic variation in the fundamental frequency) was calculated using the following algorithms: DDP, which calculates the absolute difference between differences of consecutive periods; local, which measures the mean absolute difference between consecutive periods, divided by the average period; local absolute, which measures mean absolute difference between consecutive periods; PPQ5, which is a 5-point period perturbation quotient, and RAP, which is the relative average perturbation.

Shimmer (periodic variation in the amplitude of the fundamental frequency) was calculated using the following algorithms: DDA, which calculates the absolute difference between difference of amplitude of consecutive periods; local, which measures the mean absolute difference between amplitudes of consecutive periods; local dB, which measures the mean absolute difference between log base 10 amplitudes of consecutive periods; APQ3, which is a 3-point amplitude perturbation quotient; APQ5, which is a 5-point amplitude perturbation quotient; & APQ11 which is an 11-point amplitude perturbation quotient (see Boersma & Weenink, 2001, for detailed descriptions of algorithms).

Multiple measures of jitter and shimmer were used here because of the general disagreement in the literature over a standardised measurement technique (Pinto & Titze, 1990), and to ascertain the robustness of the findings. For each vocaliser, mean jitter and shimmer values were calculated by averaging jitter and shimmer values across vowels. Descriptive statistics on jitter and shimmer are reported in table 5-2.

2.4.3 Formant frequencies

The first (lowest) four formant frequencies of each vowel sound were measured in order to obtain estimates of vocal-tract length. Formant frequencies were measured using the Burg Linear Predictive Coding algorithm. The first set of predictions (using Praat's default input parameters) was plotted as dots overlaid on frequency-time spectrograms. Subsequently Praat's input parameters (maximum formant value and number of formants to search for) were adjusted to obtain the best visual fit of the predicted formants onto the observed formants. The algorithm produced a mean formant frequency, averaged across voiced windows of each vowel sound. Formant dispersion (the average distance between successive formants, Fitch, 1997) was used to estimate vocal-tract length. Formant dispersion (from Fitch, 1997) was calculated as [(F4-F3)+(F3-F2)+(F2-F1)]/3 where F1-F4 represent the first 4 formant frequencies. As per fundamental frequency, formant dispersion was averaged across vowels for each vocaliser. Table 5-2 displays descriptive statistics for formant frequencies and formant dispersion.

Table 5-2. Descriptive statistics of fundamental frequency, jitter and shimmer in men's voices.

Male voices N=56	Minimum	Maximum	Mean	S.D.
Fundamental frequency	85	145	111	14
F1	363	712	439	33
F2	1495	2114	1492	87
F3	2529	3344	2536	104
F4	3494	4527	3534	160
Fdisp	1013	1319	1032	54
% Jitter local	.021520	.077300	.053558	.012323
% Jitter local absolute	.000024	.000140	.000054	.000023
% Jitter RAP	.001160	.005980	.002453	.001014
% Jitter PPQ5	.001540	.007440	.003412	.001435
% Jitter DDP	.003480	.017880	.007348	.003037
% Shimmer local	.021520	.077300	.053558	.012323
% Shimmer local dB	.189360	.739900	.522611	.119933
% Shimmer APQ 3	.010140	.039140	.024521	.006539
% Shimmer APQ 5	.013260	.050920	.032250	.008735
% Shimmer APQ 11	.020040	.072240	.046594	.011739
% Shimmer DDA	.030420	.117460	.073564	.019614

2.5 Statistical Analysis

All statistical analyses were conducted using SPSS v11.0. As analyses are exploratory, and weak relationships were expected, results were not corrected for multiple comparisons. Two tailed probability estimates were used.

2.5.1 Principal components analysis (PCA) of jitter and shimmer

Because there were 5 measures of jitter, 6 measures of shimmer and disagreement in the literature as to which measurement to use (Pinto & Titze, 1990), a principal components analysis (PCA) was conducted to reduce the number of variables, and find a value representative of commonalities between the multiple measures. A PCA was conducted with all 11 measures simultaneously. Varimax rotation was used to reduce covariance between factors. This analysis revealed 2 PCA factors per sex. The first factor explained 71% of the variance in men's voices and was more associated with shimmer than jitter (see table 5-3). Thus, this factor was labelled shimmer. The second factor explained 21% of the variance in men's voices and was explained more by jitter than shimmer (see table 5-3). This factor was labelled jitter. See table 5-3 for factor loadings. Here one male voice was removed because it was a statistical outlier ($p < 0.05$ using Grubbs test from http://www.graphpad.com).

Table 5-3. Loadings of variables on factors after varimax rotation (men's voices).

Perturbation measure	Factor 1 (Shimmer)	Factor 2 (Jitter)
% Jitter local	**.955**	.274
% Jitter local absolute	.329	**.881**
% Jitter RAP	.239	**.963**
% Jitter PPQ5	.344	**.887**
% Jitter DDP	.237	**.963**
% Shimmer local	**.995**	.274
% Shimmer local dB	**.890**	.166
% Shimmer APQ 3	**.907**	.319
% Shimmer APQ 5	**.894**	.378
% Shimmer APQ 11	**.888**	.306
% Shimmer DDA	**.907**	.319

2.5.2 Inter-rater agreement

Inter-rater agreement on perceptual attributes was estimated using Cronbach's Alpha test. All alpha values were > 0.7. Therefore, mean ratings reported here should reflect a group consensus (Bohrnstedt, 1970).

2.5.3 Normality tests

Each variable (acoustic measures and ratings) was tested for normal distribution using the one sample Kolmogorov-Smirnov test. It was determined that each variable had a normal distribution, as all p-values were above 0.05.

3 Results

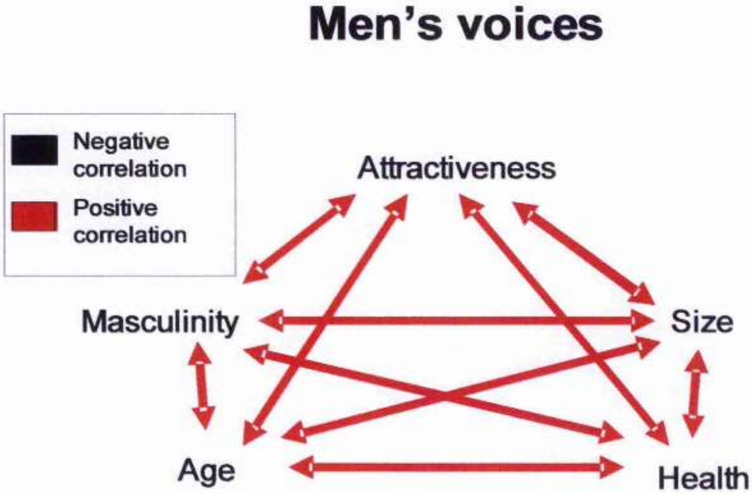
3.1 Zero-order correlations

As predicted, all perceptual attributes were significantly and positively intercorrelated. Fundamental frequency was negatively correlated with all ratings except for perceived health. Unexpectedly, formant dispersion was only significantly related to attributions of size and age. Perceived age was more closely related to other perceptual attributions and vocal traits than real age. Table 5-4 displays inter-correlations between measured variables. Figure 5-3 illustrates these results. Jitter was positively related to real age and shimmer was negatively related to fundamental frequency. Thus, subsequent partial correlations were performed to control for effects of fundamental frequency (see section 3.3).

Table 5-4. R values of Pearson correlations among variables in men.

N=56	Attractiveness	Health	Masculinity	Size	Perceived age	Real age	F_0	Fdisp	Jitter
Health	0.66**								
Masculinity	0.63**	0.48**							
Size	0.46**	0.53**	0.82**						
Perceived age	0.27*	0.30*	0.65**	0.72**					
Real age (n=36)	0.213	0.34*	0.41*	0.55**	0.38**				
F_0	-0.56**	-0.21	-0.65**	-0.51**	-0.48**	-0.24*			
Fdisp	0.07	0.005	0.19	-0.29*	-0.31**	-0.43**	-0.08		
Jitter	-0.034	-0.095	0.046	0.137	0.360**	-0.078	-0.179	0.122	
Shimmer	-0.023	-0.124	0.100	0.081	0.194	0.289*	-0.366**	0.038	<0.001

*denotes significance at $p<0.05$, **denotes significance at $p<0.01$
F_0=Fundamental frequency (pitch), Fdisp=Formant dispersion, Jitter=PCA factor related to jitter, Shimmer=PCA factor related to shimmer. Correlations excluding the 1 participant whose age was 33 revealed no qualifications to the results displayed in table 5-4.



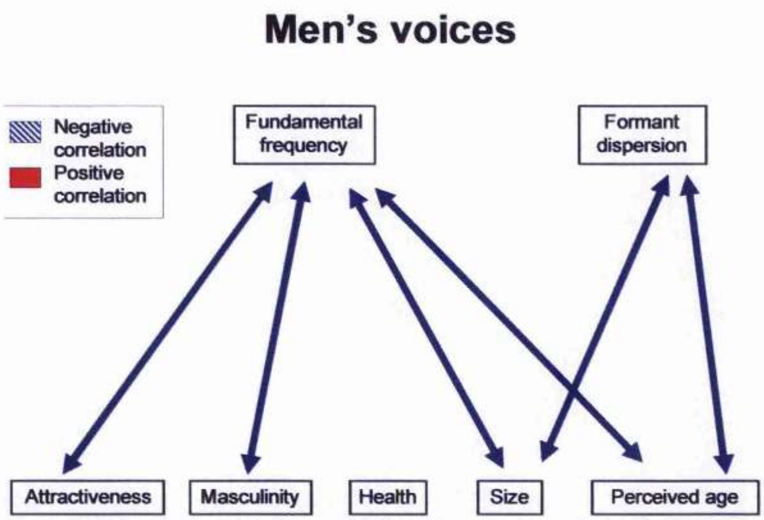


Figure 5-3. Interrelationships among attributions to men's voices and acoustic measurements.

3.2 Effects of time normalisations on relationships among variables

To control for the possibility that attributions were influenced by the amount that duration of each voice was manipulated, I calculated the total time and mean time (across vowels) that each voice was manipulated. I also calculated the absolute value of total time and mean time that each voice was manipulated to create an unsigned value of how much each voice was manipulated in time. Next I re-analysed the aforementioned analysis several times whilst controlling for signed and unsigned total time and mean time that each voice was manipulated (each control separately). Although the strength of the correlations changed, most of the aforementioned relationships remained significant. No relationships that were previously not significant became significant after controlling for the amount of time each voice was manipulated. The only zero-order correlation that changed from significant to non-significant whilst controlling for the amount of time that each voice was manipulated in duration was relationship between perceived health and real age (in each type of control for amount of time that each voice was altered in duration: R_{54}=0.263, p=0.081).

3.3 Partial correlations

Controlling for fundamental frequency and formant dispersion, ratings of attractiveness were found to be negatively associated with shimmer (R_{52}=-0.305, p=0.025). The relationship between shimmer and attractiveness became non-significant when controlling for the amount of time that each voice was manipulated by. Perceived age was positively associated with jitter (R_{52}=0.383, p=0.004). No other correlations were significant (all $|R_{52}| < 0.224$, all p>0.113). The relationship between perceived age and jitter remained significant after controlling for the amount of time that each voice was manipulated by. Voice perturbation thus related positively to age. Controlling for jitter and shimmer revealed no qualifications to the analysis using zero-order correlations.

4 Discussion

4.1 Attributions to men's voices

I predicted that women would be attracted to relatively masculine sounding, older sounding, healthier sounding and larger sounding men's voices. My results supported my predictions. Women found men's voices that sounded relatively more masculine, older, healthier and larger to be relatively more attractive. These results support those found by Collins (2000) who also found that voices with masculine related attributions were rated more attractive than feminine sounding voices. Also in agreement with Collins (2000) is the finding that voices that sounded like they came from taller men were more attractive than voices that sounded like they came from shorter men. In the current study, the finding that relatively healthy sounding voices were more attractive than relatively unhealthy sounding voices was novel. This finding suggests that women use men's voices as cues to health. If perceived health relates to real health then choosing healthy mates has the direct benefit of reduced exposure to contagion. If attributions of masculinity, size and age are accurate (real age was related significantly to perceived age and attributions of masculinity were associated with sexually dimorphic acoustic properties of the voice), then choosing masculine, larger and older mates can have direct and indirect benefits. If resources are shared directly with a mate then one direct benefit of choosing relatively more masculine, larger and older mates is that they may have more resources than relatively more feminine, smaller and younger mates (Judge & Cable, 2004; see chapter 4 for review). Possible indirect benefits of choosing relatively more masculine, larger and older mates can also include long-term medical health (Rhodes, Chan, Zebrowitz, & Simmons, 2003) and inherited resources and status (Judge & Cable, 2004).

I also hypothesised that relatively masculine sounding voices would be perceived as coming from relatively larger sounding, relatively older sounding and relatively healthier men. My results supported my hypotheses. I found that women positively associated perceived masculinity with perceived age, perceived health and perceived size. This finding may reflect that as men go through puberty, their male-typical (masculine) traits develop and men grow.

I predicted that relatively healthy sounding voices would also sound relatively masculine. Perceived health was positively correlated with perceived masculinity. In face research, a new study shows that faces manipulated in shape masculinity do not alter perceptions of health, whereas faces manipulated on the dimension of perceived health do vary in apparent masculinity (Boothroyd et al., 2005). This result is puzzling, however, it may be due to the fact that there is more information about masculinity than face shape alone (i.e. colour and texture information) which was not included in the masculinity manipulation. When facial colour and textural cues that relate to perceived health were manipulated, apparent masculinity was altered. Thus, the finding that masculine sounding voices are perceived as healthier is somewhat supported by the face literature (Boothroyd et al., 2005). It is yet to be determined if perceived health of the face and voice relate to actual health because actual health is difficult to objectively and quantitatively assess. If perceived voice health is related to actual health, then women are using men's voices as an accurate indicator of current health status.

4.2. Vocal attributes and acoustic properties of the voice

4.2.1 Fundamental frequency

Fundamental frequency was correlated negatively with vocal attractiveness men, supporting findings by Collins (2000). Women's preferences for low fundamental frequency in men are potentially adaptive as fundamental frequency is negatively related to testosterone levels and testicular volume at puberty (Harries et al., 1998; Harries et al., 1997) and testosterone in adulthood (Dabbs & Mallinger, 1999). Testosterone may in turn related to perceived and actual dominance status (Mazur & Booth, 1998; O'Carroll, 1998; Schaal, Tremblay, Soussignan, & Susman, 1996; Swaddle & Reierson, 2002) and with its interaction with cortisol and behaviour related to immunocompetence (Booth et al., 1999; Creel, 2001; Folstad & Karter, 1992, see chapters 3 & 4 for review).

Fundamental frequency negatively predicted perceived age and perceived size, supporting findings by Collins (2000), Fitch (1994) and Smith et al. (2005). This was expected as fundamental frequency lowers with age throughout growth and development (Huber et al., 1999). Although fundamental frequency is not related to body size in adults (Lass & Brown, 1978), people may over generalise the relationship between fundamental frequency and body size found throughout development and between sexes to adults within one sex. This later point is extremely important because perceived size is related to fundamental frequency and attractiveness, but actual height and weight are not related to fundamental frequency in adults (Lass & Brown 1978). Therefore, when using voices in isolation from visual cues to size, women appear to be inferring size from the wrong acoustic parameter. Nevertheless, outside of the laboratory, accept for blind and deaf people, it will probability be a rare occasion when auditory and visual information are not used in conjunction when making *final* decisions on whether or not to mate with an individual. Even in modern society with telephones, non-blind people may have to see each other at least briefly before mating. Therefore, because visual cues can confirm or negate auditory cues, it may be unlikely that this misuse of fundamental frequency as an indicator of body size in men has a great influence on sexual selection in humans. Nevertheless, it is mysterious why this misuse of fundamental frequency as an indicator of body size still remains. Some attempts have been made to determine why this inaccurate attribution remains (Fitch, 2000a; Fitch & Hauser, 1995, 2002). The relationship between fundamental frequency and body size is present between immature and mature animals and between men and women (Fitch & Hauser 1995; Rendall et al. 2005). Furthermore, Fitch & Hauser (1995) argue that although there are many exceptions to the rule, in general, across species, larger animals produce lower pitched calls than smaller animals (Hauser, 1993). Thus, women may over generalise the relationships noted above to adult men. As humans may have a great capacity for learning audio-visual associations, it remains unclear why humans do not learn that pitch is not associated with body size.

4.2.2 Formant dispersion

I observed no relationship between formant dispersion and attractiveness ratings in men's voices. Perhaps the relationship between fundamental frequency and attractiveness overshadowed a potential relationship between formant dispersion and attractiveness.

Formant dispersion negatively predicted perceived masculinity and perceived age. This finding was expected as vocal-tract length is sexually dimorphic (Fitch & Giedd, 1999), and formant dispersion lowers through development (Huber et al., 1999).

4.2.3 Jitter and Shimmer

Shimmer relates to vocal fold health and can discriminate pathological (e.g. Parkinson's disease, vocal-fold paralysis and cancer) and non-pathological populations (Hertrich, Lutzenberger, Spieker, & Ackermann, 1997; Kotby et al., 1991; Parsa & Jamieson, 2000; Wolfe & Martin, 1997). High levels of voice perturbation also indicate negative affect (Bachorowski & Owren, 1995, 1996). Therefore high levels of shimmer should theoretically be unattractive. I did find that shimmer was negatively correlated with attractiveness. This relationship, however, was influenced by the duration manipulation. Therefore, this finding should be treated with caution and investigated further with better controls for duration. Voice perturbation also increases as people age (Ramig et al., 1984). I found that jitter was related to perceived age. This relationship was not affected by the duration manipulation. Thus, my results extend previous findings that age relates to voice perturbation to a sample with a relatively small, young adult age range.

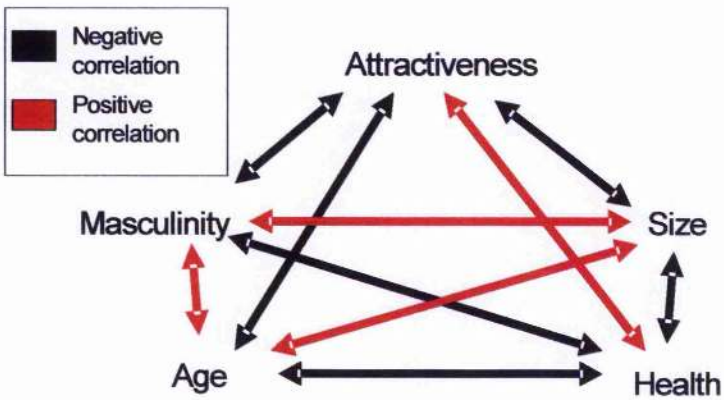
Study 2 – Women's voices

1 Rationale

Collins & Missing (2003) conducted a correlational study (utilising vowel sounds) to determine the relationship between attractiveness, acoustic properties of the voice and real and perceived age (amongst other qualities such as body shape and facial attractiveness, discussed in chapters 4 and 10). Collins & Missing (2003) found that vocal attractiveness was predicted positively by fundamental frequency, and predicted negatively by formant dispersion and perceived age in young adult women.

The purpose of the following study was to explore further, the acoustic correlates of perceptual attributions to young adult women's voices. Collins & Missing (2003) found feminine and neotenous vocal features (high voice pitch and small vocal-tracts) and feminine vocal attributes (relatively young perceived age and relatively lower perceived height) were attractive. Thus, I predicted that vocal attractiveness would be positively associated with ratings of femininity, and negatively associated with perceived age. Studies show that perceived health is positively associated with facial attractiveness (Jones, Little, Boothroyd, Feinberg et al., In Press; Jones et al., 2005). Therefore I predicted that perceived health of the voice would also be positively associated with vocal attractiveness. Collins & Missing (2003) formant dispersion was positively correlated with attractiveness ratings. Furthermore, Nettle (2002a; 2002b) found that women who were shorter than the population mean had higher reproductive success. Therefore, I predicted that ratings of body size would negatively predict vocal attractiveness. Figure 5-4 shows predictions for correlations among attributes in women's voices.

Figure 5-4. Predicted correlations among attributes in women's voices.

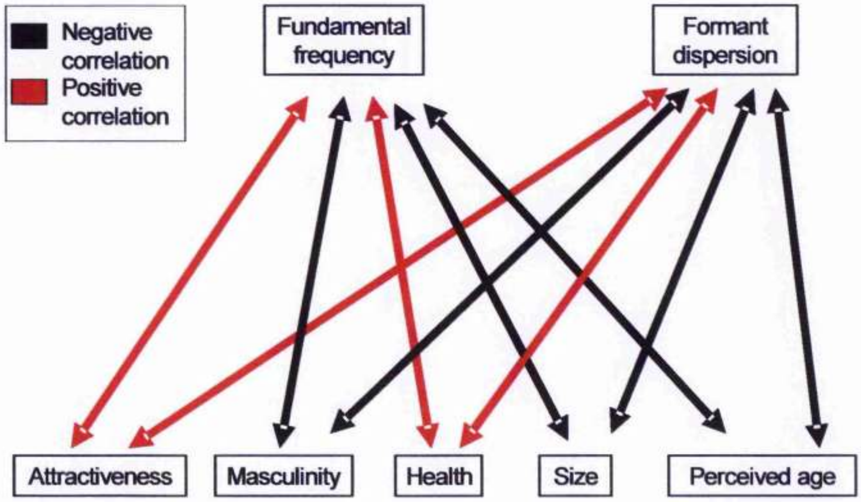


I sought to replicate the finding by Collins & Missing (2003) that fundamental frequency is positively associated with vocal attractiveness and associated negatively with perceived age. Fundamental frequency is not necessarily related to body size (height and weight) in adults (Lass & Brown, 1978). Surprisingly, studies have found that perceptions of body size and weight were positively associated with low fundamental frequency (Collins, 2000; Fitch, 1994; Smith et al., 2005). Therefore, I predicted that people would rate voices with low fundamental frequencies as larger. As fundamental frequency is positively associated with oestrogen levels (Abitbol et al., 1999) and is sexually dimorphic, being higher in women than men (Childers & Wu, 1991), high fundamental frequency should be positively associated with perceived femininity and health. Collins

& Missing (2003) found that fundamental frequency was negatively related to age. I therefore predicted that fundamental frequency would correlate negatively with real and perceived age.

I also sought to replicate findings by Collins & Missing (2003) that formant dispersion was associated positively with vocal attractiveness. Large apparent vocal-tract length (low formant dispersion) has been found to be associated positively perceived body size in women (Fitch, 1994; Smith et al., 2005). Thus, I predicted that I would also find a negative relationship between formant dispersion and perceived body size. If height is associated negatively with attractiveness, and attractiveness is associated positively with perceived health, formant dispersion should be associated positively with perceived health. As mentioned above, formant frequencies lower as people grow & age (Huber et al., 1999). Therefore, I predicted that formant frequencies would be associated negatively with perceived age. Figure 5-5 illustrates predictions for correlations among fundamental frequency, formant dispersion and attributes to women's voices.

Figure 5-5. Predicted relationships among fundamental frequency, formant dispersion and attributes to women's voices.



Jitter and shimmer are associated negatively with perceived health and real and perceived age (Kotby et al., 1991; Linville & Fisher, 1985; Parsa & Jamieson, 2000; Parsa & Jamieson, 2001; Ramig et al., 1984). Hence, I predicted that jitter and shimmer would be associated negatively with attractiveness and perceived health, and associated positively with perceived age.

2 Methods

All methods were identical to those in study 1 unless otherwise noted. Participants included 106 female undergraduates at the University of St Andrews (aged 17-27 M=20.6, S.D.=1.9).

2.1 Voice Recordings

Voices were recorded using identical methods to study 1.

2.2 Stimuli generation

Stimuli were generated in an identical fashion to study 1. Table 5-5 shows descriptive statistics on how much voices were altered in duration.

Table 5-5. The amount to which women's voices were altered in duration

Women's Voices				
Values reported in seconds	**Min**	**Max**	**Mean**	**S.D.**
Sum across vowels	-1.05	18.05	3.52	3.59
Mean across vowels	-0.21	3.61	0.70	0.72
|Sum| across vowels	0.00	18.05	3.58	3.52
|Mean| across vowels	0.00	3.61	0.71	0.70

2.3 Playback

Playback methods were identical to study 1 except that vowel sounds were played back to 10 male raters. Voices were assessed in two equal sized blocks by the same raters because of the large number of female voices. Order of stimuli and order of blocks were randomised. Age of raters ranged from 18-25.

2.4 Acoustic measurements

2.4.1 Fundamental frequency

Fundamental frequency of women's voices was searched for between 100 and 600 Hz. All other methods were identical to study 1.

2.4.2 Formant frequencies

Methods of formant frequency measurement and calculation of formant dispersion were identical to study 1.

2.4.3 Jitter and shimmer

Input parameters were to search for jitter and shimmer between 100 and 600 Hz. All other methods were identical to study 1. Table 5-6 shows descriptive statistics of acoustic measurements.

Table 5-6. Descriptive statistics of measured acoustic features of women's voices.

Women's voices n=106	Minimum	Maximum	Mean	S.D.
Fundamental frequency	170	273	207	21
F1	364	712	525	55
F2	1495	2114	1779	130
F3	2529	3344	2923	146
F4	3495	4527	4072	192
Formant dispersion	1014	1319	1182	61
% Jitter local	.019100	.083880	.03560912	0.01
% Jitter local absolute	.000009	.000270	.00003331	.000035
% Jitter RAP	.001120	.034720	.00384140	.004390
% Jitter PPQ5	.001300	.036380	.00396754	.004326
% Jitter DDP	.003300	.104120	.01152035	.013166
% Shimmer local	.019100	.083880	.03560912	.010177
% Shimmer local dB	.166160	.887400	.32736509	.097777
% Shimmer APQ 3	.010380	.042900	.01853825	.005607
% Shimmer APQ 5	.011140	.057800	.02135228	.006522
% Shimmer APQ 11	.014320	.072500	.02740105	.008670
% Shimmer DDA	.031080	.128700	.05561596	.016820

2.5 Statistical analysis

2.5.1 Principal components analysis (PCA) of jitter and shimmer

A PCA was conducted with all 11 measures simultaneously. Varimax rotation was used to reduce covariance between factors. This analysis revealed 2 PCA factors. The first factor explained 81% of the variance in women's voices and was more associated with shimmer than jitter (see table 5-7). Thus, this factor was labelled shimmer. The second factor explained 15% of the variance in women's voices and was explained more by jitter than shimmer (see Table 5-7). This factor was labelled jitter. See table 5-7 for factor loadings. Here two female voices were removed, as they were statistical outliers (both $p < 0.05$ using Grubbs test from http://www.graphpad.com).

Table 5-7. Loadings of variables on factors after varimax rotation (women's voices)

Women's voices (n=106)		
Acoustic measurement	**Factor 1 (Shimmer)**	**Factor 2 (Jitter)**
% Jitter local	**.969**	.223
% Jitter local absolute	.228	**.928**
% Jitter RAP	.196	**.972**
% Jitter PPQ5	.221	**.995**
% Jitter DDP	.196	**.972**
% Shimmer local	**.969**	.233
% Shimmer local dB	**.861**	.403
% Shimmer APQ 3	**.954**	.183
% Shimmer APQ 5	**.970**	.184
% Shimmer APQ 11	**.904**	.218
% Shimmer DDA	**0.95**	0.18

2.5.2 Inter-rater agreement

Inter-rater agreement on perceptual attributes was estimated using Cronbach's Alpha test. All alpha values were > 0.7. Therefore, mean ratings reported here should reflect a group consensus (Bohrnstedt, 1970).

2.5.3 Normality tests

Each variable (acoustic measures and ratings) was tested for normal distribution using the one sample Kolmogorov-Smirnov test. It was determined that each variable had a normal distribution, as all p-values were above 0.05.

3 Results

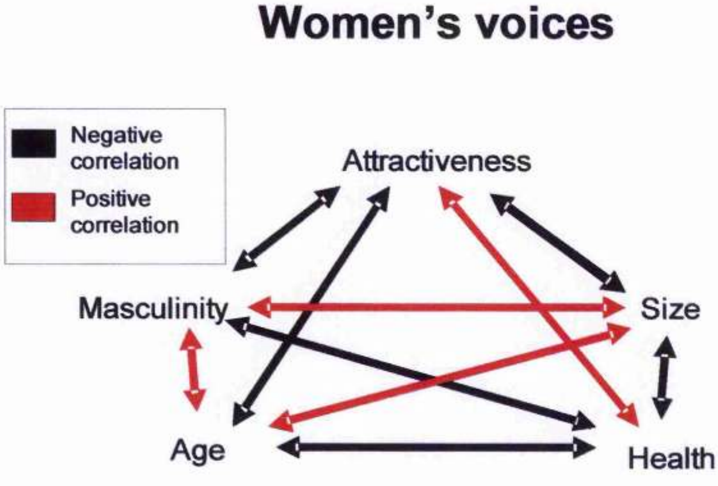
3.1 Zero-order Correlations

Table 5-8 displays correlations between objective and subjective variables. Figure 5-6 illustrates these results. All perceptual attributes were intercorrelated in their predicted directions. Fundamental frequency correlated with each vocal attribute in its predicted direction. Formant dispersion predicted all perceptual attributions except for masculinity, in the direction predicted. Surprisingly, jitter and shimmer were correlated with formant dispersion in opposite directions. Also surprisingly, shimmer was positively related to vocal attractiveness. Subsequent analyses, partialling out fundamental frequency and formant dispersion were conducted to investigate this phenomenon.

Table 5-8. R values of Pearson correlations among variables in women's voices.

*denotes significance at $p<0.05$, **denotes significance at $p<0.01$
F_0=Fundamental frequency (pitch), Fdisp=Formant dispersion, Jitter=PCA factor related to jitter, Shimmer=PCA factor related to shimmer

N=112	Attractiveness	Health	Masculinity	Size	Perceived age	Real age	F_0	Fdisp	Jitter
Health	0.7**								
Masculinity	-0.55**	-0.4**							
Size	-0.61**	-0.46**	0.41**						
Perceived age	-0.39**	-0.4**	0.28**	0.61**					
Real age	-0.14	-0.10	-0.17	0.22*	0.38**				
F_0	0.28**	0.32**	-0.24*	-0.54**	-0.67**	-0.27*			
Fdisp	0.23*	0.33**	-0.12	-0.38**	-0.29**	-0.43**	0.174		
Jitter	-0.065	-0.163	-0.129	0.106	0.124	0.187*	-0.171	-0.333**	
Shimmer	0.199*	0.132	-0.06	-0.170	0.017	0.039	-0.13	0.316**	<0.001



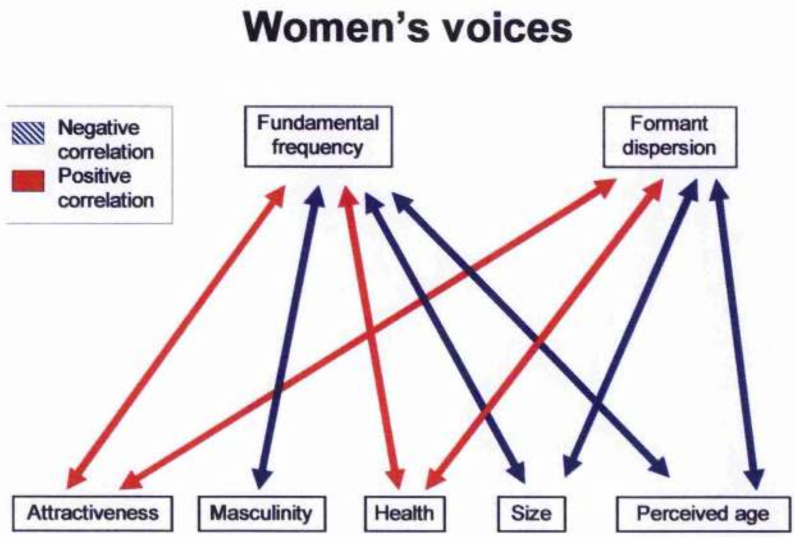


Figure 5-6. Interrelationships among attributions to women's voices and acoustic measurements.

As was done for men's voices, I re-ran the aforementioned analyses whilst controlling for the amount of time each voice was manipulated. Again, I used the variables: total time and mean time (across vowels) that each voice was manipulated and their absolute values.

3.2 Controlling for the duration manipulation

The following is a list of items that changed significance level when controlling for the duration manipulation.

Controlling for signed total time that each voice was manipulated:

- Attractiveness and shimmer (R_{106}=0.112, p=0.249)
- Perceived size and real age (R_{106}=0.181, p=0.06)

Controlling for signed mean time that each voice was manipulated

- Attractiveness and formant dispersion (R_{106}=0.079, p=0.417)
- Perceived size and real age (R_{106}=0.181, p=0.06)
- Perceived age and formant dispersion (R_{106}=-0.185, p=0.055)

Controlling for unsigned total time that each voice was manipulated

- Attractiveness and shimmer (R_{106}=0.119, p=0.221)
- Perceived size and real age (R_{106}=0.185, p=0.056)

Controlling for unsigned mean time that each voice was manipulated

- Attractiveness and formant dispersion (R_{106}=0.088, p=0.363)
- Perceived size and real age (R_{106}=0.185, p=0.056)
- Perceived age and formant dispersion (R_{106}=-0.189, p=0.05)

3.3 Partial correlations

As in study 1, partial correlations were employed to investigate possible relationships between jitter and shimmer and attributions to voices, independent from the effects of fundamental frequency and formant dispersion. Conversely, relationships between fundamental frequency, formant dispersion and attributions were explored whilst controlling for the effects of jitter and shimmer.

Controlling for fundamental frequency and formant dispersion, ratings of attractiveness were found to be positively associated with shimmer (R_{108}=0.199, p=0.037). For women's voices, the findings were opposite to those in men's voices. Voice perturbation was positively related to attraction. Shimmer also correlated negatively with perceived size (R_{108}=-190, p=0.047). The relationship between shimmer and attractiveness became non-significant when additionally controlling for the amount of time that each vowel was manipulated by. Shimmer had no further significant associations and jitter was not significantly related to any variables (all $|R_{108}| < 0.97$, all p>0.311).

4 Discussion

4.1 Attributions to women's voices

I hypothesised that men would prefer the voices of women that sounded relatively feminine, small, young and healthy. My results supported my hypotheses. Men's ratings of attractiveness of women's voices correlated with positively with ratings of femininity and health and negatively with ratings of size and age. These results are consistent with Collins & Missing (2003), who found negative correlations between vocal attractiveness and perceived height. Male preferences for femininity and youth in women are potentially adaptive because femininity and youthful traits may be accurate indicators of reproductive health (Alonso & Rosenfield, 2002). Here, perceived age was positively correlated with actual age. Furthermore, if perceived size relates to actual size, male preferences for voices of women with small apparent size are potentially adaptive because women shorter than the population mean (but not extremely tall or short) enjoy the highest reproductive success (Nettle, 2002a, 2002b) and because obesity is related to infertility (Moran et al., 1999).

4.2 Vocal attributes and acoustic properties of the voice

4.2.1 Fundamental frequency

I predicted that men would find women with high fundamental frequencies feminine, healthy, small, younger and attractive sounding. My results supported my predictions. Fundamental frequency was positively correlated with perceptions of attractiveness, femininity and health. Fundamental frequency was negatively correlated with perceived size, perceived age and real age. These findings are in agreement with Collins & Missing (2003), who found that attractiveness of women's voices correlated positively with fundamental frequency. Men's preferences for high fundamental frequency are women is potentially adaptive because high fundamental frequency may be associated with high oestrogen levels (Abitbol et al., 1999), an indicator of reproductive health (Baird et al., 1999; Dickey et al., 1993; Eissa et al., 1986; Lipson & Ellison, 1996; Roumen et al., 1982; Stewart et al., 1993). Also, the perception that high fundamental frequency is indicative of femininity and youth may be because fundamental frequency is sexually dimorphic (Childers & Wu, 1991) and lowers with age (Huber et al., 1999). The relationship between fundamental frequency and perceived size may not be accurate because fundamental frequency and height are not correlated in adults (Lass & Brown 1978). Nevertheless, men use fundamental frequency as an indicator of body size. The implications of this were discussed in study 1, when the misuse of fundamental frequency was found when women listened to men's voices. Fundamental frequency also correlated positively with perceived health. This supports findings in faces that femininity and perceived health are highly related (Law Smith et al., In Press).

4.2.2 Formant dispersion

I predicted that formant dispersion would correlate positively with attractiveness and perceptions of femininity, size, age and health. My results supported my hypotheses. The finding that attractiveness was positively related to formant dispersion, however, was influenced by the duration manipulation. Thus, the role of formant dispersion in attractiveness of women's voices remains unclear because Collins & Missing did find a positive correlation between formant dispersion and attractiveness, but did not control for duration of voices, whereas the positive correlation between formant dispersion and attractiveness in the current study was confounded by the duration manipulation (in each type of control for the duration manipulation). Nevertheless, I do have unpublished data showing that direct manipulations of formant dispersion (independent of fundamental frequency and duration) do affect attractiveness ratings. Men preferred the voices of women that were manipulated to have shorter apparent vocal-tract lengths (higher formant dispersion). Male preferences for women with smaller vocal-tract lengths, indicating smaller body size (Collins & Missing, 2003; Fitch & Giedd, 1999) are potentially adaptive because women who were shorter than the population average had higher reproductive success than tall or very short women (Nettle, 2002a; 2002b).

In the current study, formant dispersion was correlated negatively with perceived size and perceived age. These findings support Collins & Missing (2003) who found that formant dispersion was correlated negatively with perceived height. The perceptions that large formant dispersion is related to small size and youth may be fairly accurate because formant dispersion is negatively related to vocal-tract length (Fitch 1997) which is in turn negatively correlated with height and weight (Fitch & Geidd 1999). Formant frequencies also lower with age throughout development (Huber et al., 1999).

4.2.3 Jitter and Shimmer

I predicted that men would prefer women's voices that contained relatively low levels of jitter and shimmer. My results did not support my hypotheses. Initial analyses revealed that attractiveness ratings were positively correlated with shimmer. At first this presented a complicated, confusing explanation because in both men and women, shimmer relates to vocal fold health and can discriminate pathological (e.g. Parkinson's disease, vocal-fold paralysis and cancer) and non-pathological populations. Therefore high levels of shimmer should theoretically be unattractive. Upon closer inspection, I found a more parsimonious explanation. When controlling for the amount of time that each voice was manipulated by, the relationship between shimmer and attractiveness in women's voices became non-significant. This suggests that the time normalisation affected the relationship between shimmer and attractiveness, and this relationship should be treated with caution or disregarded completely.

5 General discussion

5.1 Directional selection

Men preferred women with high fundamental frequencies, whereas women preferred men with low fundamental frequencies. There is evidence that men and women with attractive voices report higher mating success (Hughes et al., 2004). Thus, if the report by Hughes et al. (2004) is valid, and fundamental frequency is heritable (Debruyne, Decoster, Van Gijsel, & Vercammen, 2002), I may have observed evidence for disruptive selection of fundamental frequency at the species level (i.e. selection against androgynous voices in both sexes). Whilst the design of this study cannot determine if this selection pressure will result in increased sexual dimorphism over time, it does show that there is directional selection pressure (within each sex) to at least maintain current levels of sexual dimorphism in human fundamental frequency.

5.2 Direct benefits

Both men and women preferred relatively healthy sounding voices to relatively unhealthy sounding voices. The primary direct benefit of choosing healthy mates is contagion avoidance. Thus, one would expect that people would also choose to associate with healthy sounding same-sex individuals. Women choosing relatively larger and older male mates may gain direct benefits of resource acquisition because taller and older men generally have higher income than shorter and younger men (Judge & Cable 2004). Furthermore, masculine, larger and older men may be more dominant and could offer the direct benefit of physical protection to women.

5.3 Indirect benefits

Women preferred men's voices that had relatively low fundamental frequencies, relatively large apparent size, and relatively high perceived masculinity. Each of these traits may be related to dominance status and resource availability (taller men generally have higher income than shorter men, Judge & Cable 2004; and men with face shapes characterised by high testosterone at puberty are perceived as more dominant than men with faces characterised by low testosterone at puberty, Swaddle & Rierson, 2002). Thus, if accurate, these attributions may convey the indirect benefit of inherited dominance status and resources to offspring. Indeed, perceived facial dominance does relate to actual status (Mueller & Mazur, 1996).

High levels of cortisol, caused by illness and/or stress, inhibit testosterone production (Chen & Parker 2004). Thus, if an individual has relatively high testosterone, it may be an indicator that the individual is healthy. Fundamental frequency is an indicator of pubertal and adult (and possibly pre-natal) testosterone levels (Harries et al. 1997; 1998; Dabbs & Mallinger 1999). Therefore, low vocal fundamental frequency of men's voices may indicate low incidence of illness during puberty. As testosterone is 50% heritable from fathers to sons (Harris, Vernon, & Boomsma, 1998), the offspring of women selecting for men with low fundamental frequencies may enjoy the indirect benefit of enhanced dominance and/or enhanced immunocompetence.

Men preferred women with relatively high pitched voices to women with relatively low pitched voices. Voice pitch is positively related to oestrogen levels (Abitbol et al. 1999). Oestrogen is positively related to reproductive health (Alonso & Rosenthal 2002). Thus, men choosing women with high pitched voices may be selecting women with increased reproductive health, which in turn could increase their reproductive success.

5.4 Pitfalls

There were fewer significant correlations in men's voices than women's voices. This most likely reflects that the sample size in men was about ½ that of women's. Another caveat is that there were a large number of comparisons, increasing the likelihood of false positive results. The results were not corrected for multiple comparisons because this was an exploratory study, and weak relationships were expected.

To control for differences in duration of vowels I manipulated each vowel to a standard length. By doing so I introduced a new potential confound. Each voice was manipulated in time by a different amount. In general, the manipulations of duration did not affect the relationships among attributions and relationships among attributions. In both men's voices, the relationship between shimmer and attractiveness was influenced by the duration manipulation. Furthermore, in women's voices, correlations between attractiveness and formant dispersion were also influenced by the duration manipulation. In women's voices, the relationships between perceived size and real age and perceived age and formant dispersion were weakened when controlling for the duration manipulation. As these relationships remained as trends $p<0.6$, it is possible that these relationships were weak to begin with and that the reduction in power from partial correlations drove them from significance to non-significance, rather than being influenced unduly by the duration manipulation. For future studies, I propose that manipulating the specific acoustic variables in question (e.g. fundamental frequency and formant dispersion), while holding duration constant might be a method with fewer potential confounds than normalising duration.

There are advantages and disadvantages to using correlational methodologies. Correlational studies are useful to explore the relationships between variables. Correlational studies, however, may not reveal effects that are masked by different, stronger relationships. No relationship between formant dispersion and male vocal attractiveness was observed in this study or in Collins (2000). Hence, from correlational studies, it cannot be known if this is because the two variables are unrelated, or their relationship is overshadowed by cues that are more salient. Thus, only direct manipulation of variables can establish causal relationships and reduce confounds from other variables (Perrett et al., 1999). Therefore, guided by results from the current study, direct manipulations of fundamental and formant frequencies will be utilised in later studies.

5.5 Conclusion

In conclusion, my data supported most of my hypotheses. I found that men preferred women with high fundamental frequencies and high formant dispersion. Men attributed increased femininity, good health, small body size and young age to these voices. By contrast, I found that women preferred men with low fundamental frequencies. This suggests that there is now and possibly was in our evolutionary past, disruptive selection acting on fundamental frequency at the species level to drive sexual dimorphism to its current levels and that there is currently directional selection acting to at least maintain current levels of sexual dimorphism in voice pitch within each sex.

Chapter 6

Manipulations of fundamental and formant frequencies influence the attractiveness of human male voices

1 Rationale

McComb (1991) manipulated the fundamental frequency (pitch) of red deer stag roars and found it had no impact on female attraction. McComb (1991) discussed these results in light of the fact that pitch of voice in deer is not known to be related to any physical attribute that predicts mate value. As reviewed in chapters 3 and 4, low pitch of voice in men is associated with high testosterone throughout development and in adulthood and testicular volume (but not same sex adult body size). Indeed, Collins (2000) showed that male voices with lower peak frequencies, lower fundamental frequency and smaller harmonic spacing were more attractive. Due to the correlational nature of chapter 5 and Collins (2000) it is unknown if the findings in chapter 5 and Collins (2000) reflected the effects of fundamental frequency or the influence of unmeasured acoustic parameters (including, but not limited to jitter, shimmer and duration). Thus direct manipulations are necessary to validate these findings.

As reviewed in Chapter 4, formant dispersion is an acoustic correlate of height and weight in humans (amongst many other species). Collins (2000) & chapter 5 found no relationship between formant qualities and vocal attractiveness in men. Due to the correlational nature of these studies, it is possible that the effects of formant frequencies on male vocal attractiveness were overshadowed by other vocal parameters. Moreover, it is probable that formant dispersion will affect attractiveness as manipulations of formant dispersion affect perceived size (Fitch, 1994; Smith et al., 2005).

Here I investigated the relationship between sexually dimorphic acoustic properties of the voice and vocal attractiveness by using real voices with frequency manipulations. Direct manipulations of acoustic properties allow potential mate quality cues in male voices to be evaluated without confounds from other variables (see Perrett et al., 1999; Thornhill & Gangestad, 1999). First, I manipulated (i.e. raised and lowered) fundamental frequency of male voices by 20Hz. I hypothesised that lowering the fundamental frequency would increase attractiveness as women appear to show preferences for masculine aspects of male voices (see Collins, 2000).

Second, I increased and decreased the apparent vocal tract length of male voices to change apparent vocaliser size (i.e. apparent height and weight). Here I hypothesised that women would prefer the voices of larger-sounding men as male size is positively linked to reproductive (Mueller & Mazur, 2001; Pawlowski et al., 2000). Finally, fundamental frequencies and apparent vocal tract lengths were manipulated simultaneously to values of 16-year-old men and 20-year-old men (see Huber et al., 1999). As many studies have grouped all adult men into one fundamental frequency category and because of the relatively subtle changes that happen to the male voice after puberty (Childers & Wu, 1991; Huber et al., 1999) I chose to explore the difference between mature and immature male voices. As Buss (1989) and Kenrick & Keefe (1992) reported female preferences for older men, I hypothesised that women would prefer the older-sounding male voices.

Regardless of the role of cortisol in immunocompetence (see chapters 3 & 4, for review), testosterone is negatively related to incidence of illness, but positively related to risky behaviour (Booth et al., 1999). Thus, there may be a behavioural handicap associated with high testosterone, whereby only the men with high testosterone can afford risky behaviour. Therefore, men with low voice pitch may be perceived as healthier than men with high voice pitch.

Collins (2000) suggests that because there is general agreement amongst raters, it is important to determine overall preferences. Recently, individual differences in preference strength have been investigated. Pawlowski (2003) has shown that female's own height predicts preferences for relative height of opposite sex partners. This study investigates whether female raters' height and weight predict the strength of their preference for male voices manipulated to have acoustic properties that indicate increased or decreased body size.

2 Methods

Participants included 10 men from Rutgers University aged 20-22 (mean 20.4, s.d. 0.84) and 71 women aged 18-24 (mean 20.4, s.d. 2.21) from the University of St Andrews. Both the University of St Andrews and Rutgers University ethics committees approved the protocol for this study. Participants gave informed consent and were paid £4 or $10, respectively, for participating. Male participants were Caucasian, and female participants were of mixed ethnicities (61 Caucasian and 7 non-Caucasian). Female participants' height (cm) and weight (kg) were recorded. Sexual orientation was self-reported.

Ten male voices were recorded speaking the common English vowels [common English spelling in "", IPA spelling in ()] "A" (ε□) "E" (ι) "I" (α□)"O" (oY)and "U" (φυ) with a north-eastern American accent (mean duration = 0.64 s, s.d. = 0.14) using a Rode NT 2 cardioid microphone (*see* http://www.rode.com). The vowel "U" was excluded because in 6 participants the vowel "U" was distorted by offset noise, as it was the final vowel spoken. The vocal stimuli were encoded with Digidesign's ProTools software at CD quality (18 bit external audio-digital conversion, 16 bit quantisation, and a 41.1 kHz sampling rate. All recordings were re-sampled to 11.025 kHz sampling rate with a low-pass anti-aliasing filter. Re-sampling to 11.025 kHz creates a Nyquist frequency of 5.5 kHz, which is roughly the maximum formant frequency for adult human speech, hence re-sampling reduces extraneous information in the sound file, not produced by the voice and increases frequency resolution of measurements (see Ladefoged, 1996).

2.1 Acoustic measurements

All acoustic measurements were performed in an identical fashion to chapter 5.

2.2 Acoustic manipulations

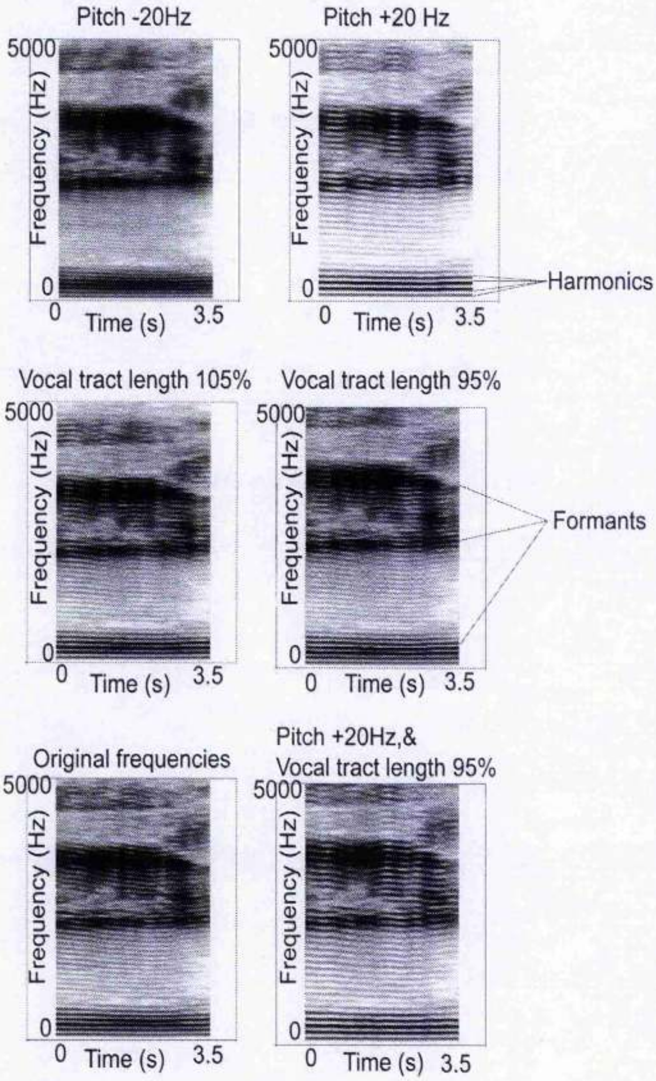
The fundamental frequencies (*see* Fig. 6-1, upper section), of five male voices were raised and lowered by 20 Hz with the Pitch-Synchronous Overlap and Add method (PSOLA) (Boersma & Weenink, 2001; Charpentier & Moulines, 1989). This method allows for a fundamental frequency manipulation (and corresponding harmonics), while preserving apparent vocal tract length (formant dispersion) and *vice versa*. Ten novel voices (5 increased fundamentals, 5 decreased fundamentals), each speaking a series of vowels, were created from the five original voices.

Apparent vocal tract lengths were manipulated by modifying the formant frequencies, using the PSOLA method (*see* Fig. 6-1, middle section). Initially the entire sound spectrum was raised such that the apparent vocal tract-length would be 95% or 105% of the original. Subsequently, fundamental frequencies were manipulated back to their original values using the PSOLA manipulation. The same original 5 voices used in the fundamental frequency manipulation were used to create 10 novel voices (5 with lengthened, 5 shortened vocal tract lengths).

A third 'combined' manipulation transformed the fundamental (harmonic) and formant frequencies simultaneously for 5 separate voices (aged 20-22) speaking the same series of vowels (*see* Fig 6-1, lower section). Five new voices were modified so that familiarity with the voices from previous trials would not influence ratings. This manipulation was used to create voices with fundamental and formant frequencies of the average 16-year-old as described by Huber et al. (1999) (*see Table 6-1 for target frequencies*). To create voices with 16-year-old characteristics, the previous two manipulations were combined. Simultaneously, the fundamental frequency was raised 20 Hz and the apparent vocal tract length decreased by 5%. To create voices with acoustic properties of 20-year-olds, the manipulated series of vowels (from the 16-year-old transform) were additionally manipulated back to their original frequencies. This manipulation was done to avoid the possibility that the 20-year-old voices would be more attractive because they were not manipulated.

The amplitude of all vocal stimuli was normalized to 87.5 dB RMS before playback. Transformed values are given in Table 6-1. Examples of voice transforms can be heard at http://www.perceptionlab.com/manipulated_voices/manipulated_voices.html. Figure 6-1 contains spectrograms of the vowel "e" before and after manipulation.

Figure 6-1. Spectrograms of vowel "e" before and after each manipulation



Time is on the x-axis, frequency is on the y-axis, and amplitude is represented by shading (louder is darker). The fundamental frequency manipulation can be seen by noting the change in the position of the first harmonic (the fundamental frequency) and the harmonic spacing (the spacing of the horizontal striations in the plot). The vocal tract length manipulation can be seen by noting the change in formant spacing (the spacing of the 4 dark broad bands of acoustic energy in the plot).

2.3 Procedure

All series of vowels were presented in the order A, E, I, O (see above for IPA spellings) at a constant interval (0.5 seconds). The order in which the vocal stimuli were played was randomised. Participants listened to vocal stimuli via Sennheiser HD280-Pro headphones with a flat frequency response from 20 Hz to 20 kHz (the range of human hearing) (*see* http://www.sennheiser.com).

2.3.1 Masculinity, size, health and age judgements

In one experimental block, 12 female participants, recruited through advertisements posted in the school of psychology, University of St Andrews, listened to each of the 30 male voices each speaking the series of vowels (18 women rated voices for health). This block was run as a stimuli calibration, separate from attractiveness ratings. Each female assessed each voice, with *ad-libitum* repetitions of individual voices, in a random order. Each participant recorded apparent masculinity on a scale from 1 to 7 (1=very feminine, 4=neutral, 7=very masculine), size (1=very small, 4=medium, 7=very large), health (1=very unhealthy, 4=-neutral, 7=very healthy) and age (within the range 13-26 years) of the vocaliser, simultaneously, in each trial. An explanation of the use of perceived size is found in chapter 5 and in the definitions section.

2.3.2 Attractiveness judgments

Three separate experimental blocks were created for attractiveness ratings of the 3 types of stimuli. Each block contained 10 novel vocal stimuli created from 5 original male voices. A computer program presented both the blocks and stimuli within blocks, in a random order. Sixty-eight women listened to and assessed vocaliser attractiveness. Voices were presented one at a time, and participants recorded assessments on the screen on a scale from 1 to 7 (1 = very unattractive, 4 = neutral, 7 = very attractive).

2.4 Acoustic analysis

The resultant fundamental frequencies after acoustic manipulations were considered to be within the male vocal range because the mean adult male fundamental frequency is 124.6 Hz (s.d. = 20.5). The mean adult female fundamental frequency is about 225 Hz (s.d. = 27.4) (Childers and Wu, 1991). The total transformed voice sample reported here had fundamental frequencies with a mean of 109 Hz (SD = 16.0). Table 6-1 shows descriptive statistics for fundamental and formant frequencies of original and manipulated voices.

Table 6-1. Mean fundamental and formant frequencies (Hz) & formant dispersion
F0 =Fundamental Frequency
F_n=Formant (n)
Formant Dispersion = ((F4-F3)+(F3-F2)+(F2-F1))/3

Each value was derived from 5 voices, except for the original row, which was calculated from all 10 voices.

	Mean F0	*F1*	*F2*	*F3*	*F4*	*Formant Dispersion*
Original voices	115	837	2049	3078	3894	1019
Lowered fundamental	96	751	1950	2960	3859	1036
Raised fundamental	135	745	1937	2944	3866	1040
Vocal tract lengthened	116	778	1955	2948	3772	998
Vocal tract shortened	116	820	2061	3071	3990	1057
Age reduced	130	507	1289	1926	2674	722
Age restored (original)	110	503	1295	1893	2620	706
16 Year old Target*	120	670	1273	2442	N/A	577
20 Year old Target*	106	666	1232	2585	N/A	563

*Target Values from (Huber et al., 1999)
*formant dispersion calculated as: ((F3-F2)+(F2-F1))/2
Standard deviation reported in parentheses ()

2.5 Statistical analysis

Participants were excluded from analysis if they reported hearing problems, and/or non-heterosexuality (n=3). All analyses used two-tailed probability estimates.

2.5.1 Inter-rater agreement

Inter-rater agreement was estimated for raw scores using Cronbach's Alpha. Since inter-rater reliability was very high, ($\alpha > 0.9$ in all cases), I consider that in general women agree on assessments (Bohrnstedt, 1970).

2.5.2 Paired comparisons

Mean scores were calculated for each female participant by averaging ratings of each voice, for each type of acoustic manipulation. The analysis compared preferences across listeners. Thus, the degrees of freedom reported in the t-tests reflect female participant sample size, rather than number of male voices heard. Here, difference scores were not used (see subsequent section). Therefore, paired sample t-tests were used rather than 1-sample t-tests.

2.5.3 Individual differences and preference scores

For each female listener and acoustic manipulation, preference scores were created by subtracting the mean of 5 attractiveness ratings of the series of vowels with one direction of manipulation from the mean of the 5 ratings of the opposite direction of manipulation (e.g. attractiveness of lowered fundamental frequencies minus attractiveness of raised fundamental frequencies). Preference scores were used only in correlational analyses not paired comparisons. This is why I used paired-sample t-tests for paired comparisons. Preference scores were not created for the other attributions (attributions other than attractiveness) because I analysed their relationships using paired-sample t-tests, not one-sample t-tests or correlations. The only reason I created preference scores was to correlate preferences for each manipulation type with listeners' height, age and weight. Also, if I did create preference scores for other variables, and then used 1-sample t-tests, I would get identical results as if I used paired sample t-tests on average ratings of each manipulation type.

3 Results

3.1 Masculinity, size, health and age

Paired sample t-tests of mean ratings of masculinity, size and age tested the effect that the manipulations had on female listeners' assessments. The t-tests reported here compare a mean rating from each female for each vocal group. Voices with increased apparent vocal tract lengths ratings were rated larger (t_{11}=4.5, $p<0.001$), more masculine (t_{11}=4.8, $p<0.001$) and older (t_{11}=5.7, $p<0.0001$) than voices with decreased apparent vocal tract lengths (see Table 6-2). Voices with lowered fundamental frequencies were rated larger (t_{11}=2.6, p=0.024), more masculine (t_{11}=5.7, $p<0.0001$), healthier (t_{17}=3.9, p=0.001) and older (t_{11}=6.3, $p<0.0001$) than voices with raised fundamental frequencies. Voices with the combined manipulation of reconstructed original fundamental frequencies and vocal tract lengths were rated larger (t_{11}=5.7, $p<0.0001$), more masculine (t_{11}=7.8, $p<0.0001$), healthier (t_{17}=2.9, p=0.01) and older (t_{11}=4.6, $p<0.001$) than voices with the combined manipulation of raised fundamental frequencies and increased apparent vocal tract lengths.

Table 6-2. Paired sample t-test results for attractiveness, masculinity, size, age and health by female

Assessment	*Manipulation*	*Mean Difference*	*SD Difference*	*Paired sample t-value*	*P value*
Size	VTL	0.93	0.73	4.5 (d.f. 11)	.001
Size	F_0	0.80	1.06	2.6 (d.f. 11)	.024[1]
Size	Combined	1.28	0.78	5.7 (d.f. 11)	.0001
Masculinity	VTL	1.18	0.85	4.8 (d.f. 11)	.001
Masculinity	F_0	1.83	1.12	5.7 (d.f. 11)	.0001
Masculinity	Combined	1.92	0.85	7.8 (d.f. 11)	.0001
Age	VTL	2.25	1.40	5.5 (d.f. 11)	.0002
Age	F_0	2.90	1.59	6.3 (d.f. 11)	.0001
Age	Combined	2.93	2.19	4.6 (d.f. 11)	.001
Health	VTL	-0.2	0.88	-0.97 (d.f. 17)	.346
Health	F_0	0.7	0.74	3.9 (d.f. 17)	.0001
Health	Combined	0.37	0.54	2.89 (d.f. 17)	.01
Attractiveness	VTL	0.08	0.84	0.7 (d.f. 67)	.457 (n.s.)
Attractiveness	F_0	0.72	0.95	6.2 (d.f. 67)	.0001
Attractiveness	Combined	0.40	0.80	4.1 (d.f. 67)	.0001

[1]Not significant after bonferroni correction

F_0=Fundamental frequency

VTL=Vocal-tract length

3.2 Attractiveness

Voices with lowered fundamental frequencies were preferred to voices with raised fundamental frequencies (*see* Table 6-2 for paired sample t-tests, comparing across female participants the mean attractiveness ratings of raised and lowered fundamental frequency manipulated voices, t_{68}=6.2, p<0.0001). Attractiveness assessments of voices with increased apparent vocal tract lengths showed no significant difference from voices with decreased apparent vocal tract lengths (t_{68}=0.7, p=0.46). Voices with combined fundamental frequencies raised and apparent vocal tract lengths decreased were rated less attractive compared to voices with original fundamental frequencies and vocal tract length characteristics (t_{68}=4.1, p<0.0001, *see* table 6-2).

3.3 Individual differences and preference scores

Women's height and weight were positively correlated with each other (r_s=0.419, n=68, p=0.0003). Height and weight of female participants also correlated positively with preference scores for voices with manipulated apparent vocal tract lengths (height: r_s =0.241, n=68, p=0.048; weight: r_s=0.291, n=68, p=0.016) but not with preference scores for voices with only manipulated fundamental frequencies (height: r_s=0.09, n=68, p=0.47; weight: r_s=0.16, n=68, p=0.20) or preference scores for voices with the combined manipulation (height: r_s=0.004, n=68, p=0.97; weight: r_s=0.02, n=68, p=0.88). Thus larger (taller and heavier) women preferred voices of men manipulated to increase apparent size.

There was no evidence of assortment in preferences of apparent vocaliser age. Indeed, listeners' own ages did not significantly correlate with preference scores for any manipulation: fundamental frequency decrease (r_s=0.11, n=68, p=0.35), and apparent vocal tract length increase (r_s=0.10, n=68, p=0.40) or combined manipulation that simulates vocaliser age change (r_s=0.04, n=68, p=0.74).

4 Discussion

4.1 Fundamental frequency

The manipulation of fundamental frequency revealed a female preference for male voices with lowered fundamental frequencies as compared to raised fundamental frequencies. This relationship is in agreement with Collins (2000) who found that fundamental frequency is a correlate of male vocal attractiveness. The present study provides explicit evidence for the relationship between fundamental frequencies and attractiveness of male voices because the selective manipulation allowed other potential acoustic confounds (e.g. formant dispersion and duration of each vowel) to be held constant.

This preference for low fundamental frequency suggests a preference for traits related to high testosterone and high masculinity. As masculine traits have been linked to aspects of male quality (e.g. health, dominance) (Johnston et al., 2001; Rhodes et al., 2003; Rhodes et al., 2000) the preference for men with low fundamental frequencies is potentially adaptive. Additionally, this finding suggests a female preference for male voices that sound larger, although fundamental frequency may not be a valid cue of size of adult men.

4.2 Size preference

I hypothesised that women would prefer the voices of larger-sounding men because male size is positively linked to reproductive success (Mueller & Mazur, 2001; Pawlowski et al., 2000). The current study offered no support for this hypothesis. The acoustic manipulation designed to increase the apparent vocal tract length produced a significant increase in the perception of vocaliser size. This manipulation, however, did not significantly affect the overall attractiveness ratings of the voices. Although the modest apparent vocal tract length manipulation was strong enough to drive other attributions, perhaps a larger difference in vocal tract length is needed to affect overall attractiveness ratings. Alternatively, apparent vocal-tract length is not used as a cue to vocal attractiveness. Further research involving manipulations to more levels of apparent vocal-tract length than used here should be conducted to determine if apparent vocal-tract length is related to general vocal preferences.

Acoustic manipulation of apparent vocal tract lengths did affect vocal attractiveness ratings at a more subtle level. Listeners' weight and height correlated positively with preference for voices with increased apparent vocal tract lengths. Taller and heavier women preferred male voices with increased apparent vocal tract lengths. While the results reported here are not directly comparable to those of Pawlowski (2003), both studies show that female height influences preferences for male body size. Although formant dispersion is related to height and weight (i.e. the relationship between vocal-tract length and weight should be weaker when considering obese people, Fitch & Giedd, 1999), female weight influenced preferences for male voices manipulated to have acoustic properties that reflect a change in body size more than female height did. It is possible that the weight and size preference correlation is driven by the fact that in this sample, female height and weight were highly correlated. Women may also be associating an increase in height with an increase in weight. Female weight may also affect preferences for real and apparent weight in men (see chapters 4 & 12 for reviews). Possible reasons for the observed assortative preference may be that they have learned over time that they may only secure mates with people of relatively equal body size, thus adjusting their preferences accordingly. Assortment for size also has potential benefits as mismatched couples have increased risk of abnormal pregnancy (see Mueller & Mazur, 2001, for review).

4.3 Age preference

The combined manipulation of fundamental frequency and apparent vocal tract length was designed to decrease apparent age of vocalisers. The acoustic manipulation produced the intended effect on perceived vocaliser age and in addition it altered vocaliser attractiveness. Peer aged women found voices transformed to sound relatively younger, less attractive. This female preference for male voices with the combined manipulation indicate that age, or perhaps sexual maturity, are important factors in female mating preferences. This finding is in accordance with Buss (1989) and Kenrick & Keefe (1992) who showed that, in general, women prefer older men. The preference for voices with increased apparent vocal tract lengths and lowered fundamental frequencies could potentially be driven solely by lowering the fundamental frequency, as increasing only apparent vocal tract length had no overall effect on attractiveness. It is relevant in this context that Reby and McComb (2003), found that formant frequencies, rather than fundamental frequency predicted reproductive success in red deer. As ecological constraints differ across species, and what different traits signal can differ across species, one cannot expect the same trait to be selected for in every species.

Unlike the assortative preferences for apparent vocaliser size, there was no relationship between age of the listener and the age preference score: i.e. in the sample studied older women did not show a stronger preference for older sounding male voices. This finding may not generalise to samples with larger age ranges.

4.4 Acoustic transforms and attributions to voices

Vocal tract length is related to body size (height & weight) in humans and many other animals (for review, see chapter 4). The findings that men with increased apparent vocal tract lengths were rated as larger supports other studies that show that manipulations of apparent vocal-tract length alter perceptions of height (Fitch, 1994; Smith et al., 2005).

Research indicates that fundamental frequencies are independent of height and weight within adult humans (Lass & Brown, 1978). In the current study, women rated male voices with lowered fundamental frequencies as larger. For adult male voices, fundamental frequency appears to be used inappropriately by listeners as a cue to vocaliser size (perceived height and weight and perceived size), as others have observed (Collins, 2000; Fitch, 1994; Fitch & Giedd, 1999; Fitch & Hauser, 1995; Smith et al., 2005). As noted by Fitch & Hauser (1995), the perception that fundamental frequency relates to size may arise because fundamental frequency changes with growth steadily until puberty. In addition, height and fundamental frequency are sexually dimorphic (men are taller and have lower fundamental frequencies than women, Childers & Wu, 1991;

Rendall et al., 2005). Thus fundamental frequency does carry information about likely sex and stage of development and hence the size of an individual. Nonetheless the listeners may over-generalize the relationship between fundamental frequency and size when judging adult male voices.

Women rated men with increased apparent vocal tract lengths as more masculine. As body size is sexually dimorphic, apparent vocal tract lengths should act as a cue to male-female differences and may hence be a valid cue to masculinity. Fundamental frequency and vocal tract length manipulations are both components of the combined manipulation, and naturally change with age. This may explain why independent manipulations of fundamental frequency and vocal tract length both had an effect on perceived vocaliser age. Additionally, pitch contour and mean pitch of voice may indicate dominance status and assertiveness (Ohala, 1983, 1984). It is also possible that other vocal features such as tone of voice indicate dominance.

In chapter 5, fundamental frequency did not correlate with perceived health. Here, using a direct manipulation, fundamental frequency was associated negatively with perceived health. This type of finding demonstrates the utility of direct manipulations of acoustic features. In the current study, only manipulations involving fundamental frequency altered health perception. This may reflect the fact that fundamental frequency has been explicitly linked to testosterone. If testosterone is negatively related to incidence of disease, but positively related to risky behaviour, then men with high testosterone may be able to afford this risky behaviour and signal health via voice pitch (see chapters 3 & 4 for reviews). Although testosterone may actually relate to health, women may be associating health with dominance, rather than thinking that men with low pitched voices have high testosterone and are therefore healthy. In other words, people may not know why they give certain voices certain attributions.

Clear conclusions as to which vocal feature is more important in influencing different attributions cannot be drawn from the data presented here because it is unknown if different manipulations were equally discriminable.

In summary, this is the first study to manipulate sexually dimorphic acoustic parameters of voices and measure their impact on male vocal attractiveness. The methods employed here allowed the isolation of independent contributions of two acoustic cues to attractiveness (fundamental frequency and apparent vocal-tract length). Natural human male voices manipulated to have lowered fundamental frequencies were rated as more attractive than voices with raised fundamental frequencies. Male voices with decreased apparent vocal tract lengths were more attractive only to taller and heavier women. Male voices manipulated to sound younger (by raising fundamental frequency and decreasing apparent vocal tract length) were perceived as less attractive than older sounding male voices. This study lends support to the hypothesis that testosterone dependent secondary sexual characteristics, such as pitch of voice are used as cues to mate value.

Chapter 7

Self-rated attractiveness positively predicts women's preferences for masculine men's voices

1 Rationale

In adult men, testosterone levels are related positively to ratings of facial masculinity (Penton-Voak & Chen, 2004) and vocal masculinity (i.e. low voice pitch, Dabbs & Mallinger, 1999). Testosterone is also related positively to dominance in humans (see Salvador, 2005, for review). Perceptions of dominance are related to testosterone-related facial (Swaddle & Reierson, 2002) and vocal features (see chapters 8 & 9; Ohala, 1983, 1984). Facial dominance (Mueller & Mazur, 1996) and height (also related positively to testosterone, Notelovitz, 2002; Tremblay et al., 1998) are each associated positively with reproductive success (Mueller & Mazur, 2001; Pawlowski et al., 2000). Men with masculine faces also have better long-term medical health than men with feminine faces (Rhodes et al., 2003). Men with high testosterone however, are less likely to be in committed relationships and invest less in offspring than men with low testosterone (Burnham et al., 2003; Gray, 2003; Gray, Chapman et al., 2004; Gray et al., 2002). Whilst masculinity and dominance are not the same trait, testosterone seems to influence both such that traits that are perceived as masculine are often also perceived as dominant (see definitions section).

Women prefer video displays of dominant male behaviour (Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004), images of men with more masculine (Johnston et al., 2001) and less feminine (Penton-Voak & Perrett, 2000; Penton-Voak et al., 1999) face shapes most when conception risk is high, and when looking for short-term partners (Little et al., 2002). By contrast, women's preferences for increased femininity in male face shape are heightened when conception risk is low (Johnston et al., 2001; Penton-Voak & Perrett, 2000; Penton-Voak et al., 1999) and when seeking long-term partners (Little et al., 2002).

None of the above studies assessed the relationship between women's attractiveness and masculinity preference, yet women's mate value may affect commitment from male partners (see Little et al., 2001; Magrath & Komdeur, 2003; Penton-Voak et al., 2003; Trivers, 1972). Attractive women (as rated by self and others) and women with low (feminine) waist-to-hip ratios have stronger preferences for masculinity and facial symmetry than less attractive and masculine women (Little et al., 2001; Penton-Voak et al., 2003). Women's psychological condition (low scores on anxiety and depression scales) also positively predicts preferences for apparent health in faces (Jones, Little, Boothroyd, Feinberg et al., In Press).

Taking a comparative approach, in certain fish species with high paternal investment, female attractiveness and condition influence preferences for sexually dimorphic traits in males (Bakker, Kunzler, & Mazzi, 1999; Lopez, 1999). Perhaps similar variation in preferences is found in humans.

If facial masculinity and vocal masculinity both reflect circulating testosterone levels (and/or pubertal and intrauterine testosterone levels, see chapter 4 for review) then women who perceive themselves to be relatively more attractive may also have stronger vocal masculinity preferences than women who perceive themselves to be relatively less attractive. I tested the above hypothesis in two independent samples. In the first study, I tested if women's self-rated attractiveness predicted their preferences for masculine sounding men's voices. Studies have shown that voice pitch (fundamental frequency) is inversely related to pubertal and adult testosterone levels (Dabbs & Mallinger, 1999; Harries et al., 1998; Harries et al., 1997) and possibly intra-uterine testosterone levels (see chapter 4 for review), and to ratings of attractiveness, masculinity, age, perceived health (Collins, 2000, chapters 5 & 6) and dominance (see chapters 8 & 9; Ohala, 1983, 1984). Therefore, in study 2, I evaluated whether women's self-rated attractiveness related to preferences for voices manipulated in pitch (see chapter 6). Self-rated attractiveness of face and body has been shown to correlate positively with facial attractiveness as rated by other individuals (Penton-Voak et al., 2003). Thus, self-rated attractiveness is a likely indicator of actual attractiveness. In both studies, I hypothesised that women who considered themselves relatively more attractive would have stronger preferences for masculine voices than women who consider themselves to be relatively less attractive.

Study 1 – Natural voices

2 Methods

2.1 Participants

Participants included 11 males (aged 20-23) who provided the vocal samples and 66 heterosexual females (aged 18-24) who rated the voices. Participants were paid $10 for participating and were students at Rutgers University.

2.2 Voice recordings

Male participants were recorded speaking the American English [common English spelling in "", IPA spelling in ()] "A" (ε□) "E" (ι]) "I" (α□)"O" (oY)and "U" (φυ]) with a Rode NT-2 cardioid condenser microphone (www.rode.com). Voices were encoded using 16-bit quantisation and 44.1 kHz sampling rate. Explanation about why 44.1 kHz sampling rate was used can be found in chapter 5. To ensure amplitude and temporal variation did not affect ratings, all voices were normalised to 87dB RMS and the duration of each vowel was normalised to 0.5 seconds (without altering pitch) with Sonic Foundry's SoundForge v5.0.

2.3 Procedure

Women listened to the male voices and rated their attractiveness and masculinity on a scale from one to 15. The order of voices and ratings were randomised. Participants also reported their age. Women rated their self-rated attractiveness on a 15-point scale (1=very unattractive, 15=very attractive). The question was: "How attractive do you consider yourself to be?"

2.4 Statistical Analysis

Mean attractiveness and masculinity ratings were calculated for each vocaliser to test the overall relationship between attractiveness, masculinity, and fundamental frequency.

To create masculinity preference scores for each listener, first I calculated average masculinity ratings across listeners for all 10 vocalisers. The vocalisers were then ranked on perceived masculinity. Next, I averaged the attractiveness ratings of the 5 voices that were rated most masculine and separately averaged the attractiveness ratings the 5 voices rated least masculine sounding. Finally, for each listener, the average attractiveness rating for the 5 least masculine sounding voices was subtracted from the average attractiveness rating for the 5 most masculine sounding voices. A high number represents a strong masculinity preference, whereas a low (negative) number represents a strong femininity preference. All correlations were calculated with Spearman's rank order correlation to reduce effects of potential outliers. Two-tailed p-values are reported.

3 Results

Mean masculinity ratings correlated with mean attractiveness ratings for each voice (R_s=0.745, n=10, p=0.003). I observed a positive relationship between female participants' self-rated attractiveness and their preferences for masculine sounding voices (R_s=0.265, n=66, p=0.032). A partial correlation showed that the positive relationship between self-rated attractiveness and preference for masculine sounding voices was independent of the age of the listener (R_{63}=0.265, p=0.028).

4 Discussion

Women's self-rated attractiveness predicted preferences for masculine sounding voices. There were some caveats, however, to the methods of this study. I used unmanipulated voices. Thus, there could be an interaction between accent and perceived masculinity that could potentially explain the findings. Furthermore, voices were manipulated in duration, which may have more adverse effects in the current study than in chapter 5 because here, diphthong vowels were used. Therefore, formant transitions could potentially sound unnatural (although upon debriefing of participants, none of the 66 women reported that any voice sounded unnatural). Furthermore, these results could be influenced by women's self-confidence.

Study 2

In study 1, I found that women's self-rated attractiveness predicted preferences for masculine sounding voices. Due to potential methodological caveats, I chose to replicate this study with better methods. In study 2, I investigated if findings from study 1 extend to preferences for men's voices that had been manipulated in masculinity (pitch). Stimuli were generated from men speaking sentences to improve the ecological validity of vocal attractiveness studies. Penton-Voak et al. (2003) explored the relationship between self and other-rated facial attractiveness, waist-to-hip ratio and masculinity preferences. If body, facial and vocal attractiveness are interrelated (Collins & Missing, 2003; Hughes et al., 2004; Thornhill & Grammer, 1999, chapter 10) then they may have similar effects on masculinity preferences. To test this idea, I also explored how self-rated attractiveness for different aspects of appearance, face, body and voice, influenced masculinity preferences.

2 Methods

2.1 Participants

Participants included 5 men who provide vocal samples and 21 heterosexual women who rated the voices (aged 18-24). Participants were paid £4 per hour pro rata for participation and were undergraduate students from the University of St Andrews.

2.2 Voice recordings

Five men's voices were recorded speaking the 1^{st} sentence of the rainbow passage (Fairbanks, 1960): "When sunlight strikes raindrops in the air, they act as a prism and form a rainbow". I used an Audio-Technica AT4041 cardioid condenser microphone and recorded directly onto computer hard disk at 44.1 kHz sampling rate and 16-bit quantisation. Explanation about why 44.1 kHz sampling rate was used can be found in chapter 5. Here accent will not be an issue because I used a within-subjects design (within-vocaliser) to analyse voice preferences, comparing voices with lowered fundamental frequencies to voices with raised fundamental frequencies.

2.3 Acoustic measurements

Pitch of voice was measured using Praat's autocorrelation algorithm (Boersma & Weenink, 2001). Pitch was searched for between 65 and 300 Hz with a Hanning window length of 0.05s (see chapters 5 & 6).

2.4 Voice manipulations

To masculinise and feminise men's voices, I raised and lowered pitch by 20Hz (sensu chapter 6) using the pitch-synchronous overlap add (PSOLA) algorithm in Praat audio software (Boersma & Weenink, 2001). This manipulation leaves time, amplitude and formant frequencies relatively undisturbed, whilst manipulating the fundamental frequency (and corresponding harmonics) of periodic sounds. Finally, amplitude of each voice was normalised to 87dB RMS. The mean male voice pitch (for vowels) is 124Hz (Childers & Wu, 1991). The mean voice pitch before manipulations was slightly lower than mean ($\underline{M}$=118, s.d.=19.58). The mean pitch of masculinised voices was 99Hz (s.d.=19.06). The mean pitch of feminised voices was 137Hz (s.d.=20.11). Figure 7-1 displays spectrograms of manipulated voices.

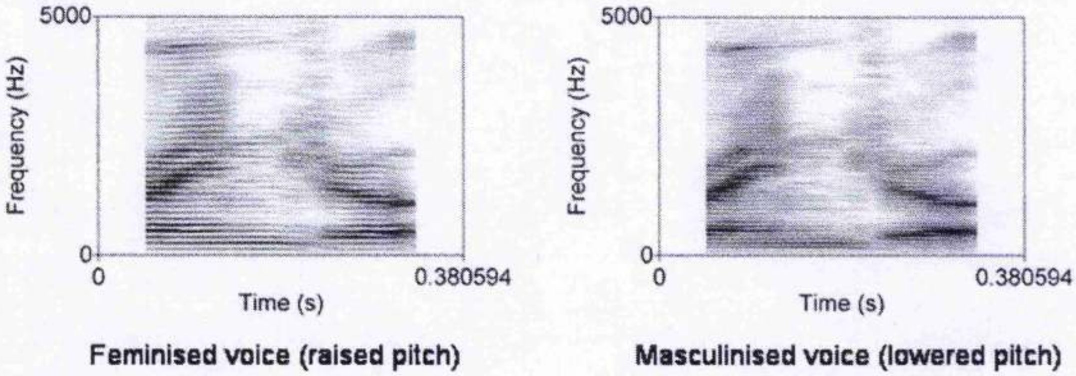


Figure 7-1. Spectrograms of the pitch-manipulated word "rainbow". Harmonic spacing is equal to the fundamental frequency (pitch) (Ladefoged, 1996). Harmonics are the horizontal lines that ascend the plots. Therefore, the difference in pitch between the two manipulations can be seen by noting the difference in the spacing of the harmonics.

2.5 Procedure

Manipulated voices were presented in random order amongst 35 filler voices (unmanipulated male voices used to disguise the manipulation). Participants listened to each voice and rated it on a 7 point scale (1=very unattractive/feminine, 7=very attractive/masculine). Masculinity and attractiveness ratings were conducted in separate blocks by the same participants. Self-rated attractiveness (unqualified, face, body, and voice) were scored on four different 7-point scales with the same anchors (1=very unattractive, 7=very attractive). Although unconventional, to test for potential effects of self-confidence, women rated their self-confidence when talking to members of the opposite sex on a 7-point scale (1=not at all confident, 7=very confident).

2.6 Statistical analysis

For each listener a mean attractiveness and masculinity rating was created for the mean of the 5 voices with raised pitch and a separate mean for the 5 voices with lowered pitch. To create masculinity preference scores, for each female listener, the mean of her attractiveness ratings for the 5 feminised voices (pitch raised) was subtracted from the mean of her attractiveness ratings of the 5 masculinised voices (pitch lowered). Pitch does affect other attributions (see chapter 6), but here I focus on masculinity because that is what has been done in many other studies (see definitions section for further explanation and references). Because of time constraints, one cannot have every voice rated for every attribution imaginable in every study.

3 Results

3.1 General preferences

Voices lowered in pitch were more masculine (t_{20}=9.522, $p<0.0001$) and attractive (t_{20}=4.915, $p<0.0001$) sounding than those with raised pitch.

3.2 Self-rated attractiveness

General (unqualified) self-rated attractiveness was correlated significantly with self-rated facial attractiveness and self-rated body attractiveness. Table 7-1 shows intercorrelations between different measures of self-rated attractiveness.

Table 7-1. Intercorrelations (Spearman's Rho correlation) among different measures of self-rated attractiveness (SRA).

N=21	**General SRA**	**SRA Face**	**SRA Body**
SRA Face	0.66**		
SRA Body	0.78**	0.41	
SRA Voice	0.22	0.08	0.16

**denotes two-tailed significance at $p<0.01$; *denotes significance at $p<0.05$

Table 7-2. Descriptive statistics of the different self rated attractiveness (SRA) measures. A repeated-measures ANOVA revealed that measures of self-rated attractiveness were significantly different ($F_{3,57}=4.453$, $p=0.007$). Self-rated facial attractiveness scores were higher than general self-rated attractiveness scores, which were higher than self-rated body attractiveness scores, which were higher than self-rated voice attractiveness scores.

1-7 scale	General SRA	SRA Face	SRA Body	SRA Voice
Min	3	2	2	2
Max	5	5	5	5
Mean (S.D.)	4.33	4.41	3.80	3.57
S.D.	0.66	1.01	1.11	0.93

3.3 Self-rated attractiveness and vocal masculinity preferences

Self-rated attractiveness of the body correlated significantly with vocal masculinity preferences. Table 7-3 shows r values of correlations between measures of self-rated attractiveness and vocal masculinity preferences.

Table 7-3. Correlations between self-rated attractiveness and vocal masculinity preferences.

	General SRA	SRA Face	SRA Body	SRA Voice
R value of correlation between SRA measures and vocal masculinity preferences	0.366	0.203	0.585**	0.172

**=p=0.007

The correlation between self-rated attractiveness of the body and masculinity preferences remained significant after controlling for age of the listener ($R_{17}=0.582$, $p=0.009$).

No measure of self-rated attractiveness or masculinity preference correlated significantly with self-confidence when talking to members of the opposite sex (all $R<0.367$, all $p>0.12$). When controlling for self-confidence when talking to members of the opposite sex, the correlation between self rated attractiveness of the body and masculinity preferences remained significant ($R_{17}=0.574$, $p=0.01$).

4 Discussion

In study 1 (using natural voices manipulated only in duration), I found that masculine sounding voices were attractive, supporting Collins (2000). In study 2 (using a manipulation), I found that lowering men's voice pitch enhanced attractiveness ratings. This finding supports those from chapter 6, but the current study used sentences rather than vowels, thus increasing the ecological validity of such studies.

Vocal masculinity relates to indices of testosterone (Dabbs & Mallinger, 1999), dominance (chapters 8 & 9; Ohala, 1983, 1984), sexual maturity (Harries et al., 1998; Harries et al., 1997; Huber et al., 1999) and perceived health (chapter 6). I found individual differences in vocal masculinity preferences. Therefore selecting men with cues associated with high testosterone might not be the optimal choice for all women as men with relatively high testosterone are less likely to be in committed relationships and invest less in offspring than men with relatively low testosterone (Burnham et al., 2003; Gray, 2003; Gray, Chapman et al., 2004; Gray et al., 2002).

I found evidence in voice preferences that converges with evidence from studies of face preferences (Jones, Little, Boothroyd, Feinberg et al., In Press; Little et al., 2001; Penton-Voak et al., 2003). Women have preferences that may reflect a world in which masculine men are willing to commit to relatively more attractive women than relatively less attractive women may be. This last point appears to hold regardless of whether female attractiveness is measured by self-rated attractiveness (Little et al., 2001), other-rated attractiveness (Penton-Voak et al., 2003), or by waist-to-hip ratio (Penton-Voak et al., 2003).

The difference in observed preferences between women who judge themselves as more and less attractive is beneficial to more women who assess themselves as more attractive if they can obtain paternal investment and the benefits associated with masculine traits, e.g. dominance (Mazur et al., 1997; Mueller & Mazur, 1996; Salvador et al., 2003; Salvador et al., 1999; Swaddle & Reierson, 2002, chapter 9) and good long-term medical health (Rhodes et al., 2003) from the same (masculine) man.

The difference in observed preferences between women who perceive themselves as more and less attractive is beneficial to women who find themselves less attractive since preferences for increased levels of femininity in men may bring them benefits of increased paternal investment, which in turn may enhance reproductive success (see Little et al., 2001; Penton-Voak et al., 2003; Trivers, 1972). The later strategy may be particularly advantageous when less attractive women seek extra-pair copulations with masculine men, and these offspring are raised by the more committed, feminine man (Gangestad & Thornhill, 1997; Penton-Voak et al., 1999; Trivers, 1972).

Self-rated attractiveness of the body appeared to be the more important than other measures of self-rated attractiveness in relation to vocal masculinity preferences. Self-rated attractiveness of the body also was most strongly correlated with self-rated attractiveness in general (unqualified self-rated attractiveness). Perhaps this reflects the importance of body shape portrayed in the media. Alternatively the positive correlation between only self-rated attractiveness of the body and voice masculinity preferences could simply reflect the fact that there was more variance in self-rated attractiveness of the body than other measures of self-rated attractiveness.

The relationship between self-rated attractiveness and vocal masculinity preferences remained significant when controlling for age in both samples. Therefore, although age may predict masculinity preferences, it does not appear to mediate the findings reported here. Furthermore, in study 2, self-reported self-confidence when speaking to the opposite sex. Although this is an unconventional measure, self-confidence did not appear to drive the reported results. This may not, however, extend to established inventories of self esteem.

In summary, I found that women's self-perceived attractiveness predicts strength of preference for masculine aspects of men's voices in 2 independent samples using both natural variation and manipulations of vocal masculinity. In general, masculine men are less likely to invest in relationships and offspring than feminine men (Burnham et al., 2003; Gray, 2003; Gray, Chapman et al., 2004; Gray et al., 2002). The findings reported here, coupled with those by Little et al. (2001) and Penton-Voak et al. (2003) suggest that women who perceive themselves as attractive may be able to secure greater commitment from masculine men than their counterparts with relatively low self-images.

Chapter 8[1]

Trait oestrogen level and menstrual cycle shifts in preferences for vocal masculinity

1 Rationale

Masculine traits in men indicate long-term health (Rhodes et al., 2003), higher reproductive success (Mueller & Mazur, 1997, 1998; Pawlowski et al., 2000), but reduced commitment to relationships and investment in offspring (Burnham et al., 2003; Gray, 2003; Gray, Chapman et al., 2004; Gray et al., 2002). By contrast, feminine traits in men indicate a higher probability of relationship commitment and paternal investment (Burnham et al., 2003; Gray, 2003; Gray, Chapman et al., 2004; Gray et al., 2002). Women exhibit stronger facial masculinity preferences during the most fertile phase of the menstrual cycle (late-follicular phase) than at other times (Johnston et al., 2001; Penton-Voak & Perrett, 2000; Penton-Voak et al., 1999). Menstrual cycle shifts in facial masculinity preferences have been observed when women evaluated men's faces for short-term relationships (Penton-Voak et al., 1999) and when relationship context was not specified (Johnston et al., 2001; Penton-Voak & Perrett, 2000; Penton-Voak et al., 1999).

Masculinity in men's face shape is preferred by women more for short-term than long-term relationships (Johnston et al., 2001; Little et al., 2002; Penton-Voak et al., 2003;

[1] Please refer to the definitions section for notes on how I use the terms masculinity/femininity and dominance. They are not used interchangeably in this chapter, even though it may appear so.

Penton-Voak et al., 1999). Preferences for male facial masculinity are influenced by the attractiveness and femininity of the female judges (Little et al., 2001; Penton-Voak et al., 2003). While relatively unattractive and masculine women demonstrated stronger preferences for masculine males as short-term partners than as long-term partners, the effect of relationship context on masculinity preferences was weaker for attractive, feminine women (Little et al., 2001; Penton-Voak et al., 2003). This effect of own attractiveness and femininity on women's masculinity preferences is thought to occur because more attractive, feminine women may be better able to obtain commitment from masculine men during long-term relationships (Clark, 2004; Gangestad & Simpson, 2000; Little et al., 2001; Penton-Voak et al., 2003). Given that attractive and feminine women have more stable masculinity preferences across relationship contexts than unattractive and masculine women do, attractive and feminine women should show less variation in their preferences for masculine males during the menstrual cycle than unattractive and masculine women.

Fundamental frequency (an acoustic measure of voice pitch) in men is related negatively to testosterone throughout pubertal development (Harries, Hawkins, Hacking, & Hughes, 1998; Harries et al., 1997) and during adulthood (Dabbs & Mallinger, 1999) and possibly pre-natal testosterone (see chapter 4, for review). Collins (2000) and chapter 6 found that low fundamental frequency and large apparent vocal-tract length (indicated by narrow spacing of formant frequencies) independently predicted perceived masculinity (and potential correlates thereof). Fundamental frequency is associated negatively with attractiveness (Collins, 2000; chapters 5, 6 & 7) and perceived dominance (Ohala, 1983, 1984; chapter 9) of men's voices. Enhancing masculine characteristics in voices (lowering fundamental frequency and increasing apparent vocal-tract length) using audio software (www.praat.org) also increased women's attributions of masculinity and attractiveness to male voices (chapters 5, 6 & 7). Moreover, human male vocal attractiveness is highly related to masculinity (Collins, 2000, chapter 6) and human men with attractive voices self-reported more mating success than men with unattractive voices (Hughes et al., 2004, but see chapter 4 for alternate explanation of their results).

Testosterone enhances somatic tissue development (Notelovitz, 2002). Thus vocal-tract length and testosterone should be positively related as the differences between men and women's vocal-tract lengths are larger than what can be accounted for by sexual dimorphism in height (Fitch & Giedd, 1999). As vocal-tract length increases, formant dispersion decreases (Fitch, 1997). Closely spaced formants are associated with large body size in rhesus macaques (*Macaca mulatta*, Fitch, 1997), dogs (*Canis familiaris*, Riede & Fitch, 1999) red deer (*Cervus elaphus*, Reby & McComb, 2003), and humans (*Homo sapiens*, Collins & Missing, 2003; Gonzalez, 2004; Rendall et al., 2005). Chapter 6, Smith et al. (2005), and Fitch (1994) found that increasing apparent vocal-tract length in human voices increased perceived body size (body size was the attribution used in these studies, not height or weight). It is relevant here that researchers have found that taller men had higher reproductive success (Mueller & Mazur, 2001; Pawlowski et al., 2000).

Using voices manipulated in formant dispersion (apparent vocal-tract length) and fundamental frequency, I tested if women's preferences for male and female voices, manipulated along the dimension of masculinity (i.e. fundamental frequency and formant dispersion), were affected by menstrual cycle. In light of chapter 6 and Collins (2000), I predicted that masculinised men's voices (voices with lowered pitch and increased apparent vocal-tract length) would be preferred to feminised men's voices (voices with raised pitch and decreased apparent vocal-tract length). Next I predicted that masculinity preferences for men's voices would be stronger when conception risk is high (late-follicular phase) than when conception risk is low (early-follicular and luteal phases). This would parallel findings for facial masculinity.

Gangestad et al. (2004) found that women's preferences for dominant behavioural displays in video clips (including voices perceived as dominant) are strongest during the late-follicular phase of the menstrual cycle. Gangestad et al. (2004) did not test for variation in women's preferences for dominant voices. Also, Gangestad et al. (2004) did not determine whether their observed cyclic shift in attraction to dominance in men was due to a change in sensitivity to dominance across the menstrual cycle, or a change in attraction to dominance across the menstrual cycle. I sought to address the above by asking women to assess attractiveness and dominance of voices across the menstrual cycle and determining if ratings of dominance (sensitivity to dominance) and/or attraction to dominant sounding voices changes cyclically. This is also useful in determining if any possible results are due to a general response bias to the vocal manipulation.

Ohala (1983, 1984) found and suggested that low voice pitch and/or increased vocal-tract lengths are used as dominance displays across species. Therefore, women may rate voices with lower pitch and increased apparent vocal-tract length as more dominant that voices with raised pitch and decreased apparent vocal-tract length.

As feminine and attractive women showed the least variation when evaluating attractiveness of masculinised faces in long-term and short-term contexts (Little et al., 2001; Penton-Voak et al., 2003), I predicted that women with high average (trait) oestrogen (an index of femininity and reproductive health in women, Jasienska et al., 2004; Law Smith et al., In press; Moran et al., 1999; Zaadastra et al., 1993) would have relatively stable preferences for masculinity across the menstrual cycle. By contrast, I predicted that women with low average oestrogen would show the most marked masculinity preference change across the cycle.

I tested for menstrual cycle shifts in preferences for manipulated masculinity in both men's and women's voices. If cyclic shifts in preferences are linked to mate-choice then such shifts would be present for men's but not women's voices. If may be however that menstrual cycle shifts have no costs, in which case they could occur for both sexes of voices.

2 Materials and Methods

2.1 Voice recordings

Four men's and 4 women's voices were recorded, speaking monopthong vowels "eh" (ɛ) "ee" (ɩ˥) "ah" (A˥) "oh" (oʊ) "oo" (ʊ˥) (symbols in parentheses are International Phonetic Alphabet symbols) with an Audio-Technica AT4041 cardioid condenser microphone in a quiet room from a distance of approximately 20 cm. The voices were encoded directly onto computer hard disk in mono at 44.1 kHz sampling rate and 16-bit quantisation using Sonic Foundry's Sound Forge 6.0 (see chapter 5 for explanation of why 44.1 kHz sampling rate was used). The voices, when manipulated, spanned the normal range of fundamental frequencies of adult men and women (average pitch across all 5 vowels of manipulated voices in men: 105-142Hz, M=121.91Hz, s.d.=3.45; women: range 194-250Hz, M=208.53, s.d=15.00).

2.2 Acoustic measurements

All acoustic measurements and manipulations were conducted using Praat v4.0 (www.praat.org). Each vowel was measured separately. Fundamental frequency was measured using Praat's autocorrelation algorithm. Male fundamental frequencies were searched for between 65 and 300Hz and female fundamental frequencies were searched for between 100 and 600Hz. Fundamental frequencies were averaged across vowel sounds for each vocaliser.

The first (lowest) four formant frequencies of each vowel sound were measured in order to obtain estimates of vocal-tract length. Formant frequencies were measured using the Linear Predictive Coding Burg algorithm. The first set of predictions (using Praat's default input parameters) was plotted as dots overlaid on frequency-time spectrograms. Subsequently Praat's input parameters (maximum formant and number of formants to search for) were adjusted to obtain the best visual fit of the predicted formants onto the observed formants (chapter 6). The algorithm produced a mean formant frequency, averaged across voiced windows of each vowel sound. Formant dispersion (the average distance between successive formants, Fitch, 1997) was used to estimate vocal-tract length. Formant dispersion (from Fitch, 1997) was calculated as [(F4-F3)+(F3-F2)+(F2-F1)] /3 where F1-F4 represents formant frequencies 1-4. As per fundamental frequency, formant dispersion was averaged across vowels for each vocaliser.

2.3 Acoustic manipulations

All manipulations were carried out using Praat's Pitch-Synchronous Overlap Add (PSOLA) algorithm (www.praat.org). The manipulations (sensu chapter 6), were achieved by raising or lowering the entire sound spectrum (while preserving duration of utterance) such that the formant frequencies would produce the target vocal-tract lengths. Next, the fundamental frequency was manipulated (using the PSOLA algorithm, www.praat.org) to the appropriate values. To create feminised voices, the fundamental frequency of each voice was raised by 20Hz and formant dispersion was increased by 50Hz (5%). To create masculinised voices, the fundamental frequency of each voice was lowered by 20Hz and formant dispersion was decreased by 50Hz (5%). Here each vowel's duration was normalized to 500ms (using the PSOLA algorithm, www.praat.org) to control for variation in spoken vowel duration between individuals. Amplitude was normalized to 87 dB RMS. Table 8-1 displays descriptive statistics on acoustic properties of manipulated voices. Figure 8-1 shows spectrograms of manipulated voices.

Table 8-1. Mean and standard deviation (in parentheses) of fundamental frequency (F0) and formant dispersion (Fdisp) of voices after acoustic manipulations (in Hz). Values before manipulation are the midpoint between manipulated values.

	Men's voices		**Women's voices**	
	Masculinised	*Feminised*	*Masculinised*	*Feminised*
F0 [Hz]	102 (3.36)	142 (3.54)	189 (13.91)	228 (16.09)
Fdisp [Hz]	1025 (72)	1124 (85)	1192 (50)	1299 (73)

Figure 8-1

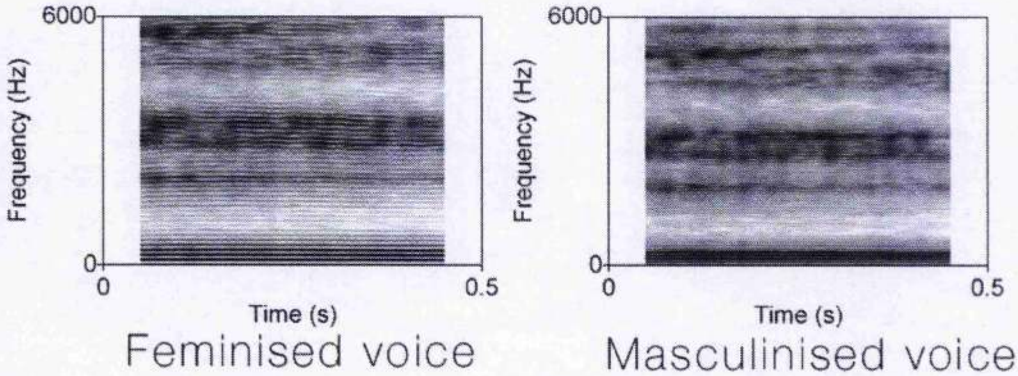


Figure 8-1. Spectrograms of the vowel "ee" from one male vocaliser. Harmonics (thin horizontal lines) are integer multiples of the fundamental frequency (Ladefoged, 1996), thus change in pitch can be noted by the harmonic spacing. Formant frequencies are the thick, dark, horizontal bands. Therefore, formant dispersion can be seen by noting the spacing between formants.

2.4 Participants

Twenty-six female participants aged 18 to 23 (M=19.5, SD=1.29) were screened for and satisfied the following criteria: reported they were heterosexual, were not using hormonal contraception (and had not been using hormonal contraceptives for 3 months), cycled regularly (self-report), had urine samples (without blood contamination), and reported no hearing problems.

2.5 Procedure

Female participants completed a block of testing once a week, for a period of 4-6 weeks. On each test day participants provided a urine sample, completed voice preference tests and completed a short questionnaire.

2.6 Hormone assays

Oestrone-3-glucuronide (E3G), the primary urinary metabolite of oestrodial and pregnanediol-3-glucuronide (P3G), the primary urinary metabolite of pregnanediol were measured. Both E3G and P3G are most concentrated in early morning urine samples. Urinary creatinine concentration is a measure of urinary excretion rate (which can alter the concentration of metabolite in urine). Thus to control for urinary excretion rate, E3G levels were divided by creatinine concentration levels (Hillier, Morrell, & Urquhart, 2002/2003). E3G and P3G are expressed as ratios: E3G:createnine and P3G:createnine. As both E3G and P3G were corrected for with creatinine, for brevity, henceforth I discuss E3G:createnine and P3G:createnine as E3G and P3G concentration ratios.

Upon scheduling time of experimentation, prior to testing, participants were each given empty, sterilised urine collection vials. Women deposited approximately 25ml of urine from mid-stream of their first urination on each day of testing. Urine was frozen at -20°C until time of analysis.

The assays used a direct competitive ELISA 96-well plate system. Urine samples, diluted in assay buffer, were incubated with labelled antigen [E3G or P3G conjugated to horseradish peroxidase] in the presence of rabbit anti-steroid antibody [respectively, anti-P3G antibody (RAB F 27/7/87) or anti-E3G antibody (RAB 1) (MRC/AFRC Comparative Physiology Research Group, Institute of Zoology, London)]. Bound and free antigens were separated using solid-phase goat anti-rabbit immunoglobulin (IgG). The plates were washed and bound antigen was detected by incubation with the substrate *o*-phenylenediamine and the developed reaction was detected using a plate reader at 492 nm.

Intra and inter-assay variations (CVs) were assessed by multiple analyses of a number of samples. The samples (low, medium, and high concentrations) were aliquoted and stored at -20° C, a new aliquot being used for each assay. For intra-assay variation, three samples were assayed ten times within the same assay. This was repeated on four occasions over a period of two weeks. For inter-assay variation, three samples were assayed in 42 assays over a period of eight weeks. The intra-assay CV was less than 10% on each occasion. The intra-assay CV was greater than 10% on only two occasions (11.2 and 12.9%). At the three levels: low, medium, and high, the intra-assay CVs for E3G were 11.0, 6.4 and 4.8%, respectively. At the three levels, low, medium, and high, the intra-assay CVs for P3G were 10.6, 69.6, and 45.5% respectively.

2.7 Voice ratings

Each stimulus was composed of five vowels from each vocaliser (in the order "ah", "ee", "eh", "oh", "oo", presented at 500ms intervals). The order of stimuli was randomised. Participants were allowed *ad-libitum* repetitions of each voice, played at an adjustable volume via headphones, to ensure ratings were private. To ensure further privacy, computer stations were separated by screens. Participants were instructed to select their rating of each voice for attractiveness and dominance on 7 point scales on the computer monitor (1=very unattractive, 7= very attractive; 1=very subordinate, 7=very dominant). Men's and women's voices were rated in two separate blocks, the order of which was randomised.

2.8 Questionnaires

In addition to hormonal analysis, menstrual cycle information was collected via self-report (diary data). To determine day of menstruation and length of menstrual cycle, participants reported the number of days since the onset of their last period of menstrual bleeding and their average menstrual cycle length. Date of onset of period following study completion was also collected via email. I calculated cycle day by the backwards counting method (see Gangestad et al., 2004). Additionally, participants reported hormonal contraceptive use (current or in the last 3 months). Sexual orientation was reported on a 7 point scale (1= completely homosexual, 4= bisexual, 7= completely heterosexual). Age was also self-reported.

2.9 Menstrual cycle classification

From diary data, test days between 14 and 21 days until next onset of menses (i.e. the late-follicular phase) were first assigned to the high conception risk group and all other days assigned to the low conception risk group (Penton-Voak et al., 1999). Subsequently, diary data was verified using P3G ratios (sensu Jones et al., 2005). If participants whose diary data indicated that they were in the late-follicular phase did not have P3G concentration ratios <0.5, I classified data from these times as non-fertile.

Eleven women completed testing in the fertile phase only once, 12 completed testing in the fertile phase twice, and 2 women completed testing in the fertile phase 3 times. Two women completed testing in the non-fertile phases twice, 10 completed testing in the non-fertile phases 3 times, and 13 women completed testing in the non-fertile phases 4 times. Where women completed testing in more than one fertile and/or non-fertile phase, average scores (within each phase) were used (sensu Jones et al., 2005). Differences between phases in number of times participants were tested reflect the fact that only 1 week was used to categorise the fertile phase, whereas 3 weeks were used to categorise non-fertile phases.

2.10 Statistical analysis

Mean ratings for each listener were calculated by averaging attractiveness ratings of the 4 same-sex voices of each manipulation type (masculinised or feminised) every time they rated voices for each cycle phase (fertile or non-fertile). When participants did not rate all voices, they were excluded from that specific analysis. My hypotheses contained directional predictions thus allowing 1-tailed probability estimates. To increase the robustness of the reported effects, and to reduce probability of type 1 errors, 2-tailed probability estimates were used.

Average (trait) E3G concentration was computed by calculating the mean of the previously computed average fertile level and average non-fertile E3G concentration from all urine samples collected from each participant. Analyses using either average late-follicular E3G, or average (late-follicular and luteal) E3G produced comparable results. 1-sample Kolmogorov-Smirnov tests revealed that all variables were normally distributed (all $p>0.05$).

3 Results

Late-follicular and non-fertile E3G concentration ratios were positively correlated with non-fertile E3G concentration ratios ($r_{25}=0.598$, $p=0.002$). Late-follicular and non-fertile P3G concentration ratios were not significantly correlated ($r_{25}=0.307$, $p=0.136$). A paired sample t-test showed that the fertile and non-fertile groups did not differ significantly in order of testing (t_{23}=1.172, p=0.253).

3.1 Men's voices

3.1.1 Dominance

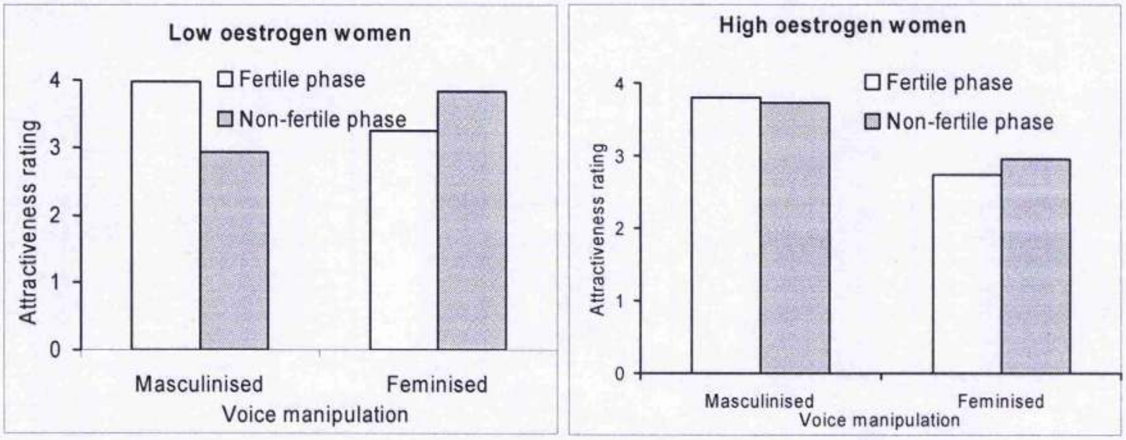
A mixed-design ANOVA [within-subject factors: cycle phase (fertile/non-fertile) and voice manipulation (masculinised/feminised), covariate: average E3G concentration] showed that masculinised voices were perceived more dominant than feminised voices ($F_{1,20}$=4.382, p=0.049). There were no other significant effects on vocal dominance (all $F_{1,20}$<3.152, p>0.09). Using E3G split on the group mean as a between subjects factor revealed no additional qualifications to this result. In each group (high and low E3G), at all menstrual cycle phases masculinised voices were perceived as more dominant than feminised men's voices.

3.1.2 Attractiveness

A mixed-design ANOVA [within-subject factors: cycle phase (fertile/non-fertile) and voice manipulation (masculinised/feminised), covariate: average E3G concentration] revealed a trend for women to prefer masculinised men's voices over feminised men's voices ($F_{1,23}$=3.591, p=0.071). An interaction between oestrogen and cycle phase also tended towards significance ($F_{1,23}$=3.538, p=0.072). Women with high E3G concentration tended to prefer men's voices more when more fertile than when less fertile. An interaction was observed between cycle phase and voice manipulation on attraction to men's voices ($F_{1,23}$=7.47, p=0.012). Femininity in men's voices was preferred more in times of low conception risk, whereas masculinity in men's voices was preferred more in times of high conception risk. This interaction was qualified by average E3G concentrations ($F_{1,23}$=5.948, p=0.023). Women with low E3G concentrations showed stronger cyclic shifts in preferences for masculinity in men's voices than women with high E3G concentrations (see Fig.1). No other effects were significant (all $F_{1,23}$<2.755, p>0.111).

To provide understanding of the results, female subjects were split according to average E3G concentration and comparing the two groups in an ANOVA with average E3G concentrations as a between-subjects factor instead of a covariate. Figure 8-2 shows that, while both groups of women preferred masculinity more when fertile than non-fertile, this shift was most pronounced in women with lower E3G concentration.

Figure 8-2. E3G-dependent menstrual-cycle shifts in preferences for manipulated men's voices.



Preferences were analysed in a mixed-design ANOVA [within-subject factors: cycle phase (fertile/non-fertile) and voice manipulation (masculinised/feminised), between-subjects factor: E3G concentration (low/high)]. Masculinised men's voices were preferred to feminised men's voices ($F_{1,25}$=31.139, p<0.0001). There was a significant interaction between E3G concentrationl, cycle phase and voice manipulation ($F_{1,25}$=4.34, p=0.048). Women with low E3G preferred men's voices more when fertile than when non-fertile, whereas women with high E3G did not exhibit this shift in preferences. All other relationships were non-significant (all $F_{1,25}$<0.358, p>0.070). From the graph it can be inferred that for women with low E3G, feminised voices were preferred to masculinised voices in the non-fertile phase. At all other times, masculinised voices were preferred to feminised voices.

Mixed-design ANOVAs [within-subject factor: menstrual cycle phase (fertile/non-fertile), covariate: average P3G concentration] diminished the strength of the previously observed menstrual cycle shift in vocal masculinity preferences ($F_{1,23}$=3.823, p=0.063). There was no significant interaction between average P3G and menstrual cycle shifts for vocal masculinity preferences $F_{1,23}$=32.732, p=0.112). Using P3G split on the group mean as a covariate revealed no qualifications to this result.

3.2 Women's voices

3.2.1 Dominance

A mixed-design ANOVA, [within-subject factors: cycle phase (fertile/non-fertile) and voice manipulation (masculinised/feminised), covariate: E3G concentration] revealed that masculinised women's voices were perceived as more dominant than feminised female voices ($F_{1,19}$=14.75, p=0.001). No other relationships were significant (all $F_{1,19}$<2.045, p>0.169). Adding E3G concentration as a between-subjects factor instead of as a covariate did not reveal any qualifications to this result.

3.2.2 Attractiveness

A mixed-design ANOVA [within-subject factors: cycle phase (fertile/non-fertile) and voice manipulation (masculinised/feminised), covariate: E3G concentration] showed an overall effect of cycle phase on attraction to women's voices. Women preferred women's voices more when fertile than when not fertile ($F_{1,19}$=5.645, p=0.028). This effect was qualified by average E3G concentrations. Women with high average oestrogen preferred women's voices more when fertile, whereas women with low E3G concentration preferred women's voices more when not fertile ($F_{1,19}$=8.231, p=0.010). No other observed relationships were significant (all $F_{1,25}$<0.416, p>0.526). Adding E3G concentration as a between-subjects factor instead of as a covariate did not reveal any qualifications to this result.

4 Discussion

I found that masculinising (lowering fundamental frequency and increasing apparent vocal-tract length) male voices increased their attractiveness, replicating findings from chapter 6 (see figure 8-2, caption). There was only one case in which femininity was preferred to masculinity, which was in the non-fertile phase, for women with low E3G concentrations. The implications of this finding are discussed below. I also found that masculinised (voices with lowered fundamental frequency and increased apparent vocal-tract length) male and female voices were perceived as more dominant than feminised voices at all menstrual cycle phases, regardless of whether the listeners had high or low E3G concentrations. This supports findings that pitch of voice was negatively associated with attributions of dominance in voices (Ohala, 1983, 1984). These findings support research showing that testosterone itself and testosterone related traits correlates with various measures of dominance (see Salvador, 2005, for review; Swaddle & Reierson, 2002).

I found that women prefer vocal masculinity in men (but not women) more when fertile than non-fertile. This extends to the vocal domain, findings by Penton-Voak et al (1999), Penton-Voak & Perrett (2000) and Johnston et al (2001), who found women increased their facial masculinity preferences at peak fertility.

As masculinised men's voices were rated more dominant than feminised voices, menstrual cycle shifts in preferences for dominant sounding voices were observed, supporting findings by Gangestad et al. (2004). Attributions of dominance to voices varying in pitch and apparent vocal-tract length did not change across the menstrual cycle. Dominant sounding voices (or voices with acoustic features associated with masculinity) become more attractive to women when fertile. Women did not change the way they attributed dominance to voices when fertile as compared to when less fertile.

I found women with higher E3G concentration exhibited the smallest menstrual cycle shifts in vocal masculinity preferences. If the cost associated with choosing masculine men as long-term partners is lower for feminine and attractive (high oestrogen) women, i.e. they are more able to secure masculine men for long-term partners (Gangestad & Simpson, 2000; Little et al., 2001; Penton-Voak et al., 2003), menstrual cycle shifts in masculinity preferences may not surface. If the cost associated with choosing masculine men as long-term partners is higher for masculine and unattractive (low oestrogen) women, menstrual cycle shifts in masculinity preferences may be more pronounced.

Within-individual change in progesterone appears to be more important for within subject changes in mate preferences during the menstrual cycle than change in E3G concentration is (Jones, Little, Boothroyd, DeBruine et al., In Press). Between-individual variation in oestrogen (or concentration of oestrogen metabolites), however, appears to be a better predictor of between subject variation in the magnitude of cyclic shifts in masculinity preferences than between subjects variation in progesterone level.

It should be noted that there are perceptual scales of pitch (e.g. ERB, Bark, Mel, and Semitone scales, Stevens, 1998; Traunmüller, 1990), different than the Hz scale. Absolute frequency changes may be easier to detect in masculinised voices than in feminised voices and in male than female voices. Therefore, my manipulations may not have been perceptually equivalent. I found, however, that the manipulations were strong enough to drive attributions of dominance in both sexes. Nonetheless, it is entirely possible that no menstrual-cycle shifts in preferences were observed in women's voices because of the lower perceptual value of the manipulation in women's voices. More research is necessary to clarify this point.

As menstrual cycle affected attributions of attractiveness but not attributions of dominance in men's voices, this particular effect cannot be explained by a decrease in cortical sensitivity to sounds varying in pitch at the luteal phase (Walpurger et al., 2004). In other words, if general acoustic sensitivity underlies my results then I would expect equal cyclic change in attractiveness ratings and dominance ratings. This did not occur.

An overall effect was found of women preferring both men's and women's voices more (i.e. using higher numbers on the rating scale) when fertile than non-fertile. This may be linked to elevated serotonin (elevating mood) mid-cycle (Wihlback et al., 2004) or reduction in cortical sensitivity to sounds varying in pitch in the luteal phase (Walpurger et al., 2004).

Although not investigated here, the present results may be qualified by relationship context. Penton-Voak et al. (1999) found menstrual cycle shifts in masculinity preferences were more pronounced when women were evaluating faces in a short-term context than a long-term context. Clark (2004) found that masculine women (as indicated by digit-ratio and mental-rotation ability) had less restricted socio-sexual inventory scores (e.g. preferred and had more short-term relationships) (see Gangestad & Simpson, 2000) than feminine women. Hughes & Gallup (2003) found feminine women (as indicated by waist-to-hip ratio) reported that they were more likely to be in long-term relationships than masculine women were. Therefore, women preferring short-term relationships should show larger cyclic shifts in masculinity preferences than women preferring long-term relationships. Puts (2005) found that women preferred voices with lower frequencies more when evaluating them as potential short-term partners than when evaluating them as potential long-term partners.

In summary, menstrual cycle shifts in and preferences for perceived dominance in voices manipulated along the dimension of masculinity (pitch and apparent vocal-tract length) were found in men's but not women's voices. The size of cyclic shifts was smaller in women with high average levels of oestrogen metabolites. Feminine and attractive women may secure masculine men as long-term partners (Little et al., 2001; Penton-Voak et al., 2003). Thus when trade-offs between male genetic quality (e.g. dominance and long-term health, see Rhodes et al., 2003) and paternal investment are less of an issue (e.g. for attractive, feminine and/or high oestrogen women), menstrual cycle shifts in preferences for masculinity and/or perceived dominance may be less pronounced. Future studies on menstrual cycle shifts in preferences should consider underlying condition as a qualifying factor to help unravel the mystery of female mate preferences.

Chapter 9[2]

Shifts in testosterone relate to shifts in dominance attributions to men's voices

1 Rationale

In men, masculine, testosterone-dependent traits are used as cues to apparent dominance. Swaddle & Reierson (2002) found men's faces, altered in shape characteristics reflecting changes in face shape that occur during puberty, were rated more dominant than those with face shapes characterized by pre-pubertal (i.e. lower) testosterone levels. Penton-Voak and Chen (2004) found women rated faces of men with higher testosterone more masculine than faces of men with lower testosterone. Rated facial dominance of men entering a military academy predicted their rank later in their military careers (Mueller & Mazur, 1996, 1997). Testosterone related traits are often rated as both masculine and dominant, even though masculinity and dominance are not the same attributions. Nevertheless, attributions of dominance have predicted outcomes of social interactions.

Pitch of voice has been found to correlate negatively with testosterone at puberty and in adulthood (Dabbs & Mallinger, 1999; Harries et al., 1998; Harries et al., 1997). Formant dispersion, a correlate of vocal-tract length, predicts body size (height and/or weight) in rhesus macaques, *Macaca mulatta* (Fitch, 1997), dogs, *Canis familiaris* (Riede & Fitch, 1999), red deer *Cervus elaphus* (Reby & McComb, 2003) and humans *Homo sapiens*

[2] Please refer to the definitions section for notes on how I use the terms masculinity/femininity and dominance. They are not used interchangeably in this chapter, even though it may appear so.

(Collins & Missing, 2003; Gonzalez, 2004; Rendall et al., 2005). In humans, vocal-tract length might be related to testosterone because testosterone enhances bone growth through development (Fitch & Giedd, 1999; Notelovitz, 2002). In chapter 6, I found that male voices manipulated to have lowered voice pitch and increased apparent vocal-tract length were rated more attractive, masculine, larger and older than those with raised voice pitch and decreased apparent vocal-tract lengths. Furthermore, Ohala (1983, 1984) both suggested and found that voice pitch and vocal-tract length both are cues to dominance.

Testosterone is related positively to status-seeking behaviour, physical dominance, self-efficacy and social dominance (see Salvador, 2005, for review). Also, testosterone and cortisol change in response to competition (see Salvador, 2005, for review). Pitch and vocal-tract length may be related to perceptions of dominance (Ohala, 1983, 1984). Subordinate men tend to shift their speaking fundamental frequency to that of more dominant men (Gregory, 1994; Gregory, Dagan, & Webster, 1997; Gregory & Webster, 1996), thus it is known that perceptions of dominance affect vocal behaviour. If testosterone increases one's own sense of dominance status, then men may attribute less dominance to voices when their own testosterone is higher than when their own testosterone is lower. This effect may be particularly true when men rate the voices of low status (subordinate) men who may have feminine vocal features (i.e. high pitch and small apparent vocal-tract length).

I sought to take advantage of the natural variation in men's testosterone and cortisol to investigate how attributions of dominance to voices relate to testosterone and/or cortisol changes. Testosterone level in men varies such that it is highest in the morning, falls during the day, and increases during sleep (Dabbs, Jr., 1990). As men age, the nocturnal increase in testosterone is smaller such that diurnal variation in testosterone is less prominent (Diver, Imtiaz, Ahmad, Vora, & Fraser, 2003). Like testosterone, men's cortisol levels vary such that cortisol is highest in the morning, lowers throughout the day, and then rises again overnight (Ice, Katz-Stein, Himes, & Kane, 2004). By measuring the magnitude of change in testosterone and cortisol levels, I sought to establish whether dominance attributions are linked to current levels of either hormone.

To test if changes in testosterone and cortisol predict dominance ratings of voices varying in masculinity, I the manipulated men and women's voices along the dimension of masculinity (i.e. vocal differences between men and women: pitch and vocal-tract length) and asked men to rate the voices for dominance in the morning and afternoon. Following Ohala (1983, 1984), I hypothesised that masculinised voices would be perceived as more dominant than feminised voices. If testosterone increases one's self-perceived dominance then when men's testosterone is raised, men might lower their perceptions of dominance of other men's voices. I tested these hypotheses.

By measuring men's responses to male and female voices, I sought to establish if any changes in attributions were a general response to stimuli varying in masculinity (by masculinity I mean manipulations fundamental and formant frequencies, not a replacement for the word dominance), or specific to one sex. If men change attributions of dominance to men's voices but not women's voices, it is likely that any observed changes in dominance attribution would be more relevant to intrasexual competition than otherwise.

2 Methods

2.1 Participants

Participants provided informed consent and protocols were approved by the University of St Andrews ethics committee. Participants included 58 students at the University of St Andrews. Five men aged 21-31 (M=24, SD=4.25), and four women aged 18-25 (M=19.5, SD=1.29) provided voices for stimuli and the remaining 49 men aged 18-25 (M=20.68, SD=2.15) rated voices for dominance.

2.2 Stimuli generation

Stimuli were the voices from chapter 8, but I added one additional man's voice. Participants were recorded, speaking the vowel sounds "eh" (ε) "ee" (ι˥) "ah" (A˥) "oh" (oʊ) "oo" (ʊ˥) (symbols in parentheses are International Phonetic Alphabet symbols) with an Audio-Technica AT4041 condenser microphone in a quiet room. Voices were encoded at 44.1 kHz sampling rate and 16-bit quantisation as uncompressed ".wav" files directly onto computer hard disk. Manipulations and measurements were performed with

Praat software v4.2 (www.praat.org). Each vowel sound was manipulated and measured separately. Masculinised voices were produced by lowering the pitch (fundamental frequency) by 20Hz and decreasing formant dispersion by 50Hz (5%) using the pitch-synchronous overlap add (PSOLA) algorithm (www.praat.org). The converse was done to create feminised voices. Subsequently, to control for between vocaliser variation in loudness and vowel duration, time was normalised to 500ms using the PSOLA algorithm (Boersma & Weenink, 2001) and amplitude was normalised to 87.5 dB RMS.

Fundamental and formant frequencies were measured using an identical technique to chapter 8. Formant dispersion was used as a correlate of vocal-tract length. I calculated formant dispersion as $[(F_4-F_3)+(F_3-F_2)+(F_2-F_1)]/3$, where F_n represents formant frequencies 1-4 (Fitch, 1997). All measurements were averaged across vowels per vocaliser, and then across vocalisers per manipulation. Table 9-1 displays descriptive statistics for acoustic properties of the voices. Figure 9-1 shows spectrograms of the vowel "ee", from a typical manipulated male voice.

Table 9-1. Mean and standard deviation (in parentheses) of fundamental frequency (F0) and formant dispersion (Fdisp) of voices after acoustic manipulations. "Masculinised" refers to voices with lowered fundamental frequency and increased apparent vocal-tract length (not to be confused with dominance attributions). "Feminised" refers to voices with raised fundamental frequency and decreased apparent vocal-tract length (not to be confused with dominance attributions).

	Men's voices		**Women's voices**	
	Masculinised	*Feminised*	*Masculinised*	*Feminised*
F0 [Hz]	97(18)	136(18)	189 (14)	228 (16)
Fdisp [Hz]	1005(77)	1106(85)	1192(50)	1299(73)

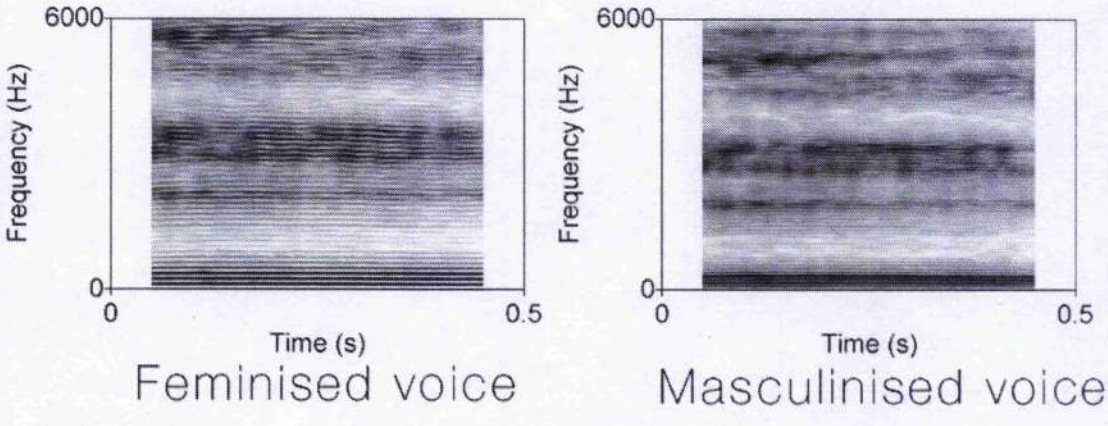


Figure 9-1. Spectrograms of masculinised (lowered pitch and increased apparent vocal-tract length) and feminised (raised pitch and decreased apparent vocal-tract length) versions of the vowel "ee" from a typical vocaliser. The fundamental frequency is higher in the feminised voice and is visible as larger harmonic spacing (thin horizontal lines). Lower fundamental frequencies have closer harmonic spacing (Ladefoged, 1996). Formant frequencies are the thick dark horizontal bands on each plot. The formant dispersion (represented by the distance between the dark bands on the plot) is smaller in the masculinised than in the feminised voice. Larger formant dispersion corresponds to a shorter vocal-tract (Fitch, 1997).

2.3 Testosterone and cortisol assays

Male participants deposited between 3 and 5 mL of saliva upon arrival to the laboratory each morning and afternoon of testing. Saliva was then frozen at -20°C until analysis. Six highly discoloured saliva samples were excluded from analysis as they were most likely contaminated with blood. Hormonal data were assayed by Martin Sharpe and Emad Al-Al-Dujaili at the biological sciences lab at Queen Margaret University College, Edinburgh, using an 'in-house' enzyme linked immunosorbant assay (ELISA). The assay procedure was based on the indirect, competitive binding technique with samples first extracted using di-ethyl ether. Four mL of ether was added to 500μl of sample, vortex mixed for 10 minutes and then frozen at -80°C until the aqueous phase was frozen. The unfrozen ether was de-canted and evaporated with forced nitrogen. Samples were finally reconstituted with 500μl of assay buffer and vortex mixed prior to assay. Assay sensitivity was 0.5pg/mL; inter and intra-assay coefficients, obtained over 50 assay runs, were 6.8% and 2.7% respectively; cross reactivity with related compounds was minimal and the standard curve was highly reproducible (r=0.998). Salivary cortisol levels were also determined by an in-house cortisol ELISA using the same indirect assay procedure. Cross-reactivity with cortisone was 1.2%, corticosterone 1.4%, Deoxy-cortisol 1%, testosterone 0.4% and other steroids <0.5%. Intra and inter assay precision values were 3.2% and 5.7% respectively. The assay also involved an extraction step and recovery studies for a range of cortisol levels from 2.6-40.8 ng/mL were 91.8% to 106.7%. Assay sensitivity was 0.05ng/mL.

2.4 Procedure

Men followed the same procedure in the morning and afternoon. Male and female voices were presented via computer in separate randomised blocks in random orders. Each computer was separated by blinds and participants listened to the voices via headphones to increase privacy. Volume was adjusted to a comfortable level at the beginning of each session and participants listened to voices with unmonitored *ad-libitum* repetitions. Perceived dominance of each voice was assessed using a 7-point scale (1=very subordinate, 7=very dominant).

2.5 Exclusion criterion

As noted above, participants with contaminated saliva samples (n=6) and those reporting hearing problems (n=4) were excluded from the analysis. As age increases, diurnal variation in testosterone decreases (Diver et al., 2003). I therefore excluded participants over the age of 25 years (n=1, see Dabbs & Mallinger, 1999). Some of the participants were excluded on more than one criterion. Thus, the final number of participants was 38.

3 Results

3.1 Shifts in hormone levels

Paired sample t-tests confirmed that testosterone and cortisol levels were higher in the morning than the afternoon (testosterone: t_{37}=2.25, p=0.037; cortisol: t_{37}=2.99, p=0.005).

A few males had higher testosterone in the afternoon than in the morning. Therefore, subsequent analyses grouped dominance ratings of voices by testing time when testosterone was higher and testing time when testosterone was lower (regardless of whether this occurred in the morning or in the afternoon).

3.2 Men's voices

For each participant, unsigned magnitude of testosterone change was calculated by subtracting the lower testosterone level from the higher testosterone level. Magnitude of cortisol change was calculated by subtracting the cortisol from level from the time of testing when testosterone was lowest from the cortisol level from the time of testing when testosterone was highest. Dominance ratings were the dependent variable.

A mixed-design ANOVA [within subject factors: testing time based on testosterone level (high testosterone/low testosterone) and voice manipulation (masculinised/feminised), between subjects factor: order of testing (high testosterone tested 1^{st}/low testosterone tested 1^{st}), covariates: magnitude of testosterone change and magnitude of cortisol change] tested for the above effects on dominance ratings of men's voices (i.e. the dependent variable was dominance rating). There was a main effect of testing time classified by testosterone level (high vs low) on dominance ratings ($F_{1,36}$=4.626, p<0.038). All voices were rated less dominant at times when men's testosterone was high than at times when men's testosterone was low. Masculinised men's voices (i.e. those with lowered pitch and increased apparent vocal-tract length) were rated more dominant than feminised men's voices (i.e. those with raised pitch and decreased apparent vocal-tract length, $F_{1,36}$=21.895, p<0.001). There was a 3-way interaction among testing time classified by testosterone level (high vs low), voice manipulation (masculine/feminine: i.e. lowered pitch and increased apparent vocal-tract length/raised pitch and decreased apparent vocal-tract length) and magnitude of testosterone change ($F_{1,36}$=5.172, p=0.029), but not magnitude of cortisol change ($F_{1,36}$=0.897, p=0.350). The amount that men's testosterone changed was positively related to the amount that their dominance attributions changed. No other effects were significant (all F>2.16 p>0.15).

Post-hoc t-tests were run to investigate if the interaction between testing time classified by testosterone level (high vs. low) and dominance ratings was driven by changes to both masculinised and feminised voices or to one direction of voice manipulation. Attributions of dominance to masculinised voices did not change from testing time characterised by high testosterone to testing time characterised by low testosterone (t_{38}=0.333, p=0.741), but feminised voices were rated more dominant at the testing time when men's testosterone was lower than at the testing time when men's testosterone was higher (t_{38}=-2.58, p=0.014). This is illustrated in figure 9-2.

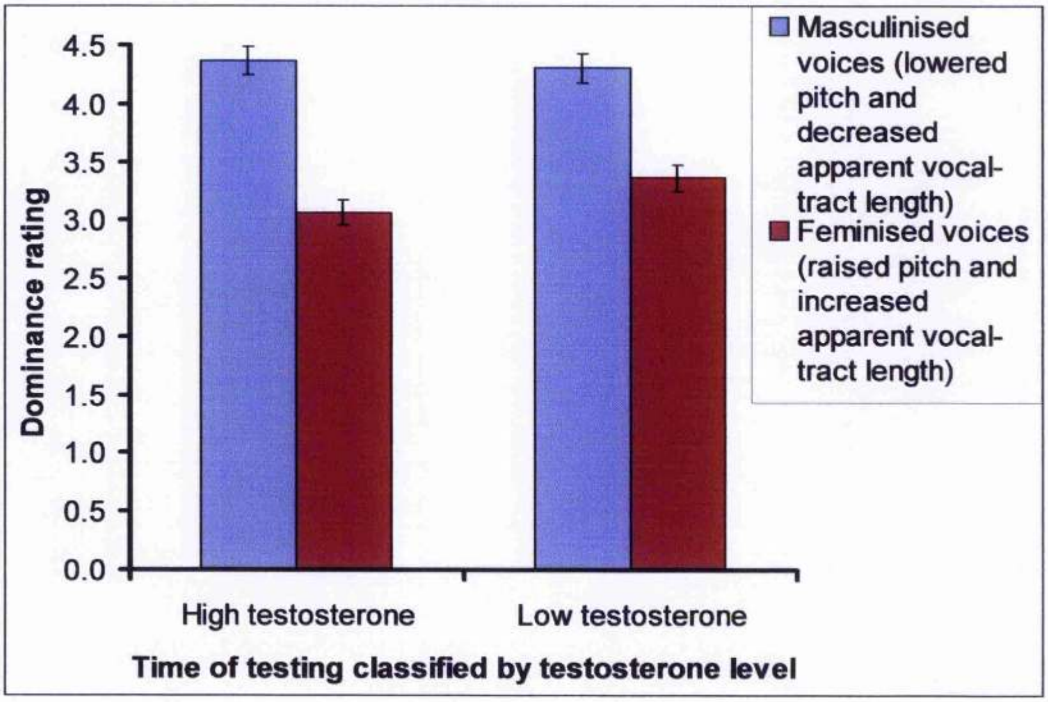


Figure 9-2. Changes in dominance attributions and testing time classified by testosterone level. Feminised voices were always rated less dominant than masculinised voices. Attributions to masculinised voices did not change. Feminised voices were rated more dominant at testing times when men's testosterone was low than at testing times when men's testosterone was high. The change in attributions to feminised voices appears to be strong enough to drive a main effect of testosterone on ratings of all voices.

The above analysis was repeated, but instead of using magnitude of hormone changes, average cortisol and testosterone levels were used. Here, only the effect of voice manipulation on dominance ratings was significant ($F_{1,36}$=11.61, p=0.002). All other effects were not significant (All F<3.39, all p>0.73).

3.3 Women's voices

A mixed-design ANOVA [within subject factors: testing time characterised by testosterone level (high/low) and voice manipulation (masculinised/feminised; i.e.

lowered pitch and increased apparent vocal-tract length/raised pitch and decreased apparent vocal-tract length), between subjects factor: order of testing (high testosterone 1^{st}/low testosterone 1^{st}), covariates magnitude of testosterone change and magnitude of cortisol change] tested for the above effects on dominance ratings of women's voices. I also performed a subsequent analysis with average testosterone and average cortisol rather than the changes in testosterone in cortisol. In both models, no effects were significant (all $F<2.473$, all $p>0.125$).

Paired-sample t-tests did reveal, however, that masculinised (lowered pitch and increased apparent vocal-tract length) women's voices were rated as more dominant that feminised (raised pitch and decreased apparent vocal-tract length) women's voices at both testing times (time characterised by high testosterone: $t_{38}=2.745$, $p=0.009$; time characterised by low testosterone: $t_{38}=2.654$, $p=0.012$).

4 Discussion

I observed a diurnal shift in testosterone, supporting the existing literature (Dabbs, Jr., 1990), but this shift was reversed in some men. Therefore, I classified data by testing time by high and low testosterone, rather than time of day. Furthermore, as others have suggested and found (Ohala, 1983, 1984), men with masculinised vocal features were perceived as more dominant than those with feminised vocal features. The finding that masculinised women's voices were more dominant than feminised women's voices is novel, although this was only found in the t-tests, not the ANOVAs. My finding supports the proposal that vocal traits associated with testosterone and body size (Dabbs &

Mallinger, 1999; Fitch & Giedd, 1999; Gonzalez, 2004; Notelovitz, 2002; Ohala, 1983, 1984) act as dominance cues to men in both men and women's voices. Gregory and colleagues (1990; 1994; 1997; 1996) have shown that subordinate men change their pitch to that of dominant men. Thus, my findings that pitch and vocal-tract length combined are used as cues to dominance extend previous behavioural findings to attributions.

Men and women can raise their voices in pitch by large amounts, lowering voice pitch, however, is limited by the physical constraints of vocal-fold length, stress and density (Titze, 1994, pp 191-217). Exaggerating vocal-tract length can be achieved by lowering the larynx and lip protrusion (see Fitch & Giedd, 1999, for review). Thus vocal-tract length and pitch are not necessarily honest signals of body size and testosterone; nonetheless I did find that perceivers do associate the two combined acoustic cues with dominance. Furthermore, the perception that these acoustic features signal dominance is consistent with the perception that the same acoustic features also relate to perceptions of body size, weight, masculinity (and correlates thereof) and attraction (Collins, 2000; Fitch, 1994; Smith et al., 2005, chapters 5-8).

Dominance ratings of men's voices were lowest at testing times when testosterone was highest. Post-hoc tests revealed that men perceived feminised (raised pitch and decreased apparent vocal-tract length) men's voices as less dominant in when own testosterone was higher than when own testosterone was lower. Men's attitudes towards masculinised (lowered pitch and increased apparent vocal-tract length) men's voices did not change. These findings support my original hypothesis that if testosterone increases one's own sense of dominance, then when men's own testosterone is elevated, men may rate voices (particularly feminised voices, i.e. those with raised pitch and decreased apparent vocal-tract length) as less dominant than when own testosterone is lower. There might have been no change in dominance attributions to masculinised (lowered pitch and decreased apparent vocal-tract length) men's voices because they were perceived equally dominant at all times of testing.

Men with the largest magnitude of testosterone change showed the largest change in attributions of dominance to men's voices. The magnitude of men's testosterone change, positively predicted the difference in attributions of dominance to masculinised (lowered pitch and increased apparent vocal-tract length) and feminised (raised pitch and decreased apparent vocal-tract length) men's voices. The magnitude of cortisol change, average of testosterone and cortisol were not related to the amount that attributions changed. This suggests that the changes in dominance attributions that I observed were related to how current testosterone level affects current perceptions, and not necessarily related to how trait (or baseline) hormone levels affect men's overall perceptions.

The results reported here cannot be due to repeated exposure to the stimuli as (1) there was no effect of order of testing and (2) there was an interaction among magnitude of voice manipulation, testing time characterised by testosterone level and magnitude of testosterone change on dominance ratings of men's voices. Furthermore, these effects were not due to general arousal, or an artefact of testing time as cortisol change did not covary with strength of dominance attributions to men's voices. Nevertheless, cortisol is likely to play role in other areas of social perception as anxiety, stress and depression predict women's attitudes towards healthy looking faces (Jones, Little et al., In Press).

The testosterone-related shifts in dominance attributions were specific to men's voices. There are two interpretations here. First, the results may suggest that the observed effects were specific to male-male competition and thus were not a result of a general response to stimuli varying in masculinity. Second, the ability to discriminate a change in pitch depends on absolute pitch. Absolute frequency changes in may be easier to detect in masculinised voices than in feminised voices. Absolute frequency changes could also be easier to detect in male than female voices. Although men rated feminised women's voices as less dominant than masculinised women's voices, this result was not consistent between the t-tests and the ANOVAs. Thus, as the vocal manipulations may have been more difficult to discern in women's voices, this may have led to the lack of consistent results in women's voices.

I found that variation in men's testosterone levels was positively linked to variation in attributions of dominance to manipulated masculine traits in men's voices. This suggests that men's perception of dominance in men's voices is dependant on the expression of dominant traits in the signaller and in the perceiver's hormonal state.

Chapter 10

The voice and face of woman: one ornament that signals quality?

General rationale

It is well documented that in women, indices of mate quality are correlated across multiple modalities. Women with attractive faces have been shown to have attractive bodies (Thornhill & Grammer, 1999) and attractive voices (Collins & Missing, 2003). Body shape and vocal attractiveness are also inter-correlated (Collins & Missing, 2003; Hughes et al., 2004). Correlations between cross-modal indices of mate quality extend to facial attractiveness and attractiveness of body odour (Rikowski & Grammer, 1999). Furthermore, male preference strength for femininity in female faces was found to correlate with male preference strength for female-typical putative pheromones (Cornwell et al., 2004). It has been suggested that interrelationships between feminine characteristics reflect underlying reproductive health and hormonal profile, (Thornhill & Gangestad, 1999) and age (Collins & Missing, 2003).

Pitch of voice (Abitbol et al., 1999; Van Borsel et al., 2000) and facial femininity (Thornhill & Gangestad, 1999) may both be related positively to oestrogen and negatively to testosterone levels. Within the normal range, oestrogen is positively linked to reproductive development, health and the expression of femininity (Alonso &

Rosenfield, 2002). If pitch of voice and facial femininity both reflect oestrogen levels, pitch of voice and facial femininity may both be ornaments signalling the same underlying quality (see Thornhill & Grammer, 1999, for discussion). Study 1 tested whether correlations between facial and vocal attractiveness that exist at the subjective level (Collins & Missing, 2003) can be extended to objective measures of facial and vocal femininity. Here I investigated the relationship between facial-metric femininity (sensu Penton-Voak et al., 2001) and pitch of voice. I predicted that if facial femininity and pitch of voice reflect sex hormone levels, females with feminine face shapes should also have higher pitched voices.

Femininity is attractive in women's faces (O'Toole et al., 1998; Perrett, Lee et al., 1998b; Rhodes et al., 2000) and voices (Collins & Missing, 2003). Thus it is not surprising that facial and vocal attractiveness correlate (Collins & Missing, 2003). Therefore measures of vocal femininity should predict facial attractiveness. In study 2, average facial prototypes (Benson & Perrett, 1993; Tiddeman, Burt, & Perrett, 2001) were constructed from women with relatively low-pitched voices and facial prototypes of women with relatively high-pitched voices. Two populations of women were studied. In study 2, the attractiveness of these 'average' prototype images was evaluated by men in a forced-choice design where preference strength was also measured. Formulation of average faces is a useful tool to reduce noise prevalent in correlational studies as averaging highlights qualities common to the groups and suppresses those that are distinctive to individuals in the groups (see Benson & Perrett, 1993; Tiddeman et al., 2001). It was predicted that men would prefer the prototype faces of women with high-pitched voices to prototype faces of women with low-pitched voices. In study 3, I tested if the relationship between voice pitch and facial attractiveness extended to the natural faces that made up the prototypes in study 2.

Study 1

1 Rationale

The aim of study 1 was to determine the relationship between objective measures of femininity in face shape (facial-metric femininity, sensu Penton-Voak et al., 2001, who demonstrated that these measurements are sexually dimorphic) and femininity of voice (fundamental frequency). It was predicted that women with relatively feminine faces would also have relatively high-pitched voices. Collins & Missing (2003) proposed that the link between feminine facial and vocal qualities reflects chronological age. I examined this proposal by testing if age correlated with facial and vocal femininity, and by controlling for chronological age when analysing the relationship between facial and vocal femininity.

2 Methods

2.1 Participants

This study comprised two independent samples. Participants included 52 white female undergraduate students (mean age=19.6, SD=2.1) from the University of St Andrews, Scotland, and 56 white female undergraduate students (mean age=18.4, SD=0.72) from the University of McMaster, Canada. One UK participant was removed from the analysis because her facial-metric femininity score was more than 3 standard errors away from the group's mean, leaving 51 UK participants as the final number of participants in the sample. One UK participant did not report her age and was excluded from analyses involving age.

2.2 Photographs

Images of women's faces were captured under diffuse lighting with neutral facial expression, in front of a standardised background. In the UK, a digital camera captured the images uncompressed, at a resolution of 1200 X 1000 pixels, with 24-bit RGB (red, green, blue) colour encoding. In Canada, images were captured under diffuse lighting at 1800 X 2400 pixel resolution with 32-bit RGB colour encoding and 1:11 jpeg compression.

2.3 Facial-metric femininity measures

Facial-metric femininity was measured using an identical technique to Penton-Voak et al. (2001) but here the scale was reversed such that high numbers indicate feminine face shapes and low numbers indicate masculine face shapes. Penton-Voak et al. (2001) found women had larger eyes, smaller lower face to face height ratio, more prominent cheekbones, larger distance from eyes to eyebrows, and a larger face width to lower face height ratio than men did. Thus, five measurements were taken (see Fig. 10-1) from full colour images. These measures were all z-scored so that each trait would have the same scale. Consistent with Penton-Voak et al. (2001), an index of facial-metric femininity was calculated as –[*Z*(lower face height/face height)-*Z*(face width/lower face height)-*Z*(eye size)-*Z*(mean height of eyebrow above top of eye)-*Z*(cheekbone prominence)].

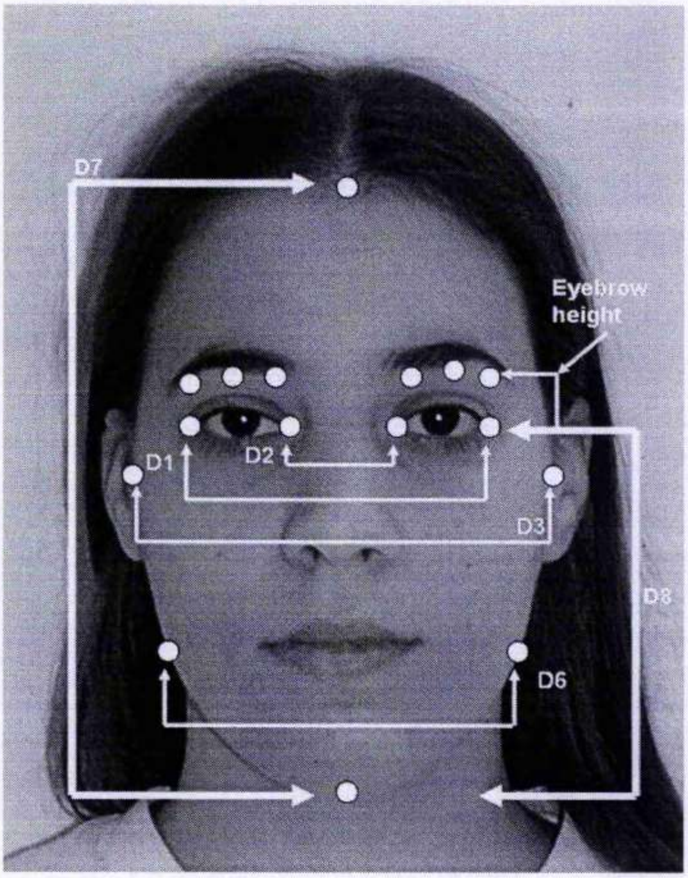


Figure 10-1. Landmarks used in facial-metric femininity measurement technique. Facial masculinity measurements: eye size [(D1-D2)/2], lower face/face height (D8/D7), cheekbone prominence (D3/D6), face width/lower face height (D3/D8), and mean eyebrow height (mean distance from eyebrow to top of the eye).

2.4 Voice recordings

In the UK, female participants were recorded speaking the English monopthong vowel sounds "eh" (ε) "ee" (ι˥) "ah" (A˥) "oh" (oυ) "oo" (υ˥) (symbols in parentheses are International Phonetic Alphabet symbols) with an Audio-Technica AT4041 condenser microphone (*see* http://www.audio-technica.com). The voices were recorded onto computer hard disk using Sonic Foundry's SoundForge (*see* http://www.soundforge.com) at 44.1 kHz sampling rate and 16-bit quantisation and saved as uncompressed "wav" files.

In Canada, methods of voice recording differed. A Labtec, Verse 504 microphone was used. Participants spoke two additional vowel sounds: "uh" (℘) and "ih" (I). All sounds were included in averages.

2.5 Fundamental frequency measurement

Each vowel sound was analysed separately using Praat software (www.praat.org). Fundamental frequency was measured using Praat's autocorrelation algorithm. Fundamental frequency measurement technique was identical to that used for women in chapter 5. Mean fundamental frequencies were measured by averaging the fundamental frequency of each voiced window across the entirety of each vowel sound. Subsequently fundamental frequencies were averaged across vowels for each vocaliser.

2.6 Statistical analysis

Normal distribution for femininity, voice pitch and age was examined in both samples (after removing the one UK participant whose facial-metric femininity score was a statistical outlier). 1-sample Kolmogorov-Smirnov tests indicated that only the distribution of participants' age from the Canadian sample differed from normal ($z=1.981$, $p=0.001$; all other $z<1.23$, $p>0.09$). Zero-order correlations were tested using Pearson's correlations in SPSS v11.0. Partial correlations were run to explore potential effects of chronological age.

3 Results

UK women with more feminine faces had higher pitched voices ($r_{52}=0.340$, $p=.015$). Canadian women with more feminine faces also had higher voice pitches ($r_{56}=0.363$, $p=.006$). Neither in Canada nor the UK did facial-metric femininity or pitch of voice correlate with age (all $|r|<0.267$, all $p>0.114$). Furthermore, correlations between facial-metric femininity and pitch of voice remained significant after controlling for age (UK: $r_{47}=0.317$, $p=0.026$; Canada: $r_{53}=0.358$, $p=0.007$).

4 Discussion

In this study, it was found that women with more feminine faces had higher pitched voices. This suggests that femininity of face and voice reflect a common underlying quality. This relationship was independent of age. Although age may be related to femininity in a population with a broader age spectrum (Deffenbacher, Johanson, & O'Toole, 1998; O'Toole, Price, Vetter, Bartlett, & Blanz, 1999), age cannot account for the findings reported here for populations of young adult females. Future studies could include wider age ranges to examine, with greater detail, the effects of age on the relationship between voice pitch and facial masculinity.

Study 2

1 Rationale

The aim of study 2 was to test if faces (Benson & Perrett, 1993; Tiddeman et al., 2001) of women with high-pitched voices differed in attractiveness than faces of women with low-pitched voices. Facial prototypes, constructed from many individual faces were used as they highlight qualities common to groups, and suppress distinctive qualities (Perrett et al., 1994). It was hypothesised that men would prefer the average facial prototypes of women with high-pitched voices, to those with low-pitched voices.

2 Methods

2.1 Participants

Female participants included 123 female students at the University of St Andrews and the Canadian participants from study 2. UK female participants' ages were self-reported and ranged from 17 to 27 (M=20.6, SD=1.86). 338 male participants were recruited via the worldwide web. Male participants' age was also self-reported and ranged from 16 to 65

(M=26.59, SD=9.46). Many published studies have used internet-based tests to assess face preferences and other behaviours (Fessler & Navarrete, 2003; Jones, Perrett et al., In Press; Little et al., 2001; Little & Jones, 2003; Little, Jones, Penton-Voak, Burt, & Perrett, 2002a; Little, Penton-Voak, Burt, & Perrett, 2003; Oates & Wilson, 2002), and the use of web based methods has become common practice in psychology (Kraut et al., 2004). Studies have shown that laboratory and internet based tests of face preferences produce similar results (Buchanan, 2000; Jones et al., 2005; Jones et al., 2005; Wilson & Daly, 2004).

2.2 Image capture and voice recordings

Voices were recorded and images were captured in identical fashion to study 1.

2.3 Stimuli generation

Using computer graphics software (www.perceptionlab.com), digital images were delineated using 186 landmark points. Facial prototypes averaging shape, colour and texture information were constructed (Benson & Perrett, 1993; Tiddeman et al., 2001) out of the images of women from the UK with the 24 highest-and 25 lowest-pitched voices and Canadian women (from the sample in study 2) with the 15 highest-and 14 lowest-pitched voices. Figure 10-2 displays the facial stimuli. Images were made symmetrical by first mirror flipping the image and second, averaging colour, shape and texture information with that of the original image (see Jones et al., 2004). Subsequently these images were masked around the perimeter of the face to reduce cues from clothing and hairstyle.

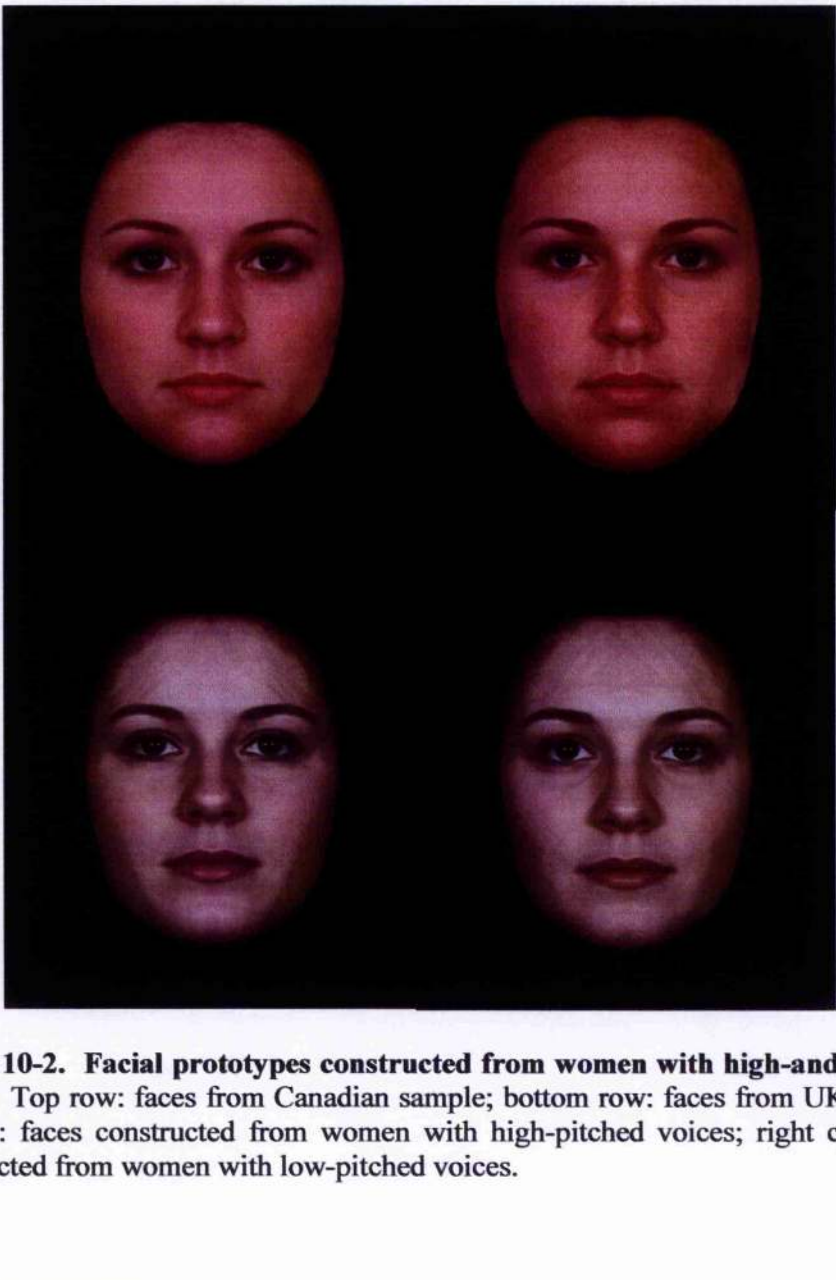


Figure 10-2. Facial prototypes constructed from women with high-and low-pitched voices. Top row: faces from Canadian sample; bottom row: faces from UK sample; left column: faces constructed from women with high-pitched voices; right column, faces constructed from women with low-pitched voices.

2.4 Procedure

Image pairs were presented side by side via the internet at size 397x499 pixels amongst filler items. Participants reported sex and age. Faces were rated in a forced-choice paradigm, in which raters could select strength of preference for either face. The 8 point scale was labelled "guess", "slightly prefer", "prefer" and "strongly prefer" for each image. These scores were later converted to a numerical scale from 0 to 7 (0=highly prefer prototype faces of women with low-pitched voices, 7=highly prefer prototype faces of women with high-pitched voices). Side of presentation of face pairs was fully counterbalanced and order was randomised. Before analysis, potential repeat participants were removed by excluding repeat IP addresses (Kraut et al., 2004).

3 Results

In the Canadian sample, women making up the facial prototype of low-pitched voices had a mean voice pitch of 186.35 Hz (s.d.=8.39) and a mean age of 18.64 years (s.d.=0.84). Women making up the facial prototype of high-pitched voices had a mean voice pitch of 236.05 (s.d.=9.72) and a mean age of 18.13 (s.d.=0.64). An independent sample t-test revealed that the two groups differed significantly in pitch of voice (t_{27}=-14.7, p<0.0001) but not in age (t_{27}=1.843, p=0.076).

In the UK sample, women making up the facial prototype of low-pitched voices had a mean pitch of 182.68Hz (s.d.=5.9) and a mean age of 21.25 (s.d.=2.23). UK women making up the facial prototype of high-pitched voices had a mean pitch of 236.01 Hz (s.d.=16.3) and a mean age of 20.32 (s.d.=1.44). An independent sample t-test revealed that the two groups differed significantly in pitch of voice (equal variance not assumed: Levene's test for equality of variances, $F_{1,47}$=15.412, p<0.001; Brown-Forsythe t-test, $t_{30.415}$=-15.096, p<0.0001) but not age (t_{47}=1.692, p=0.097).

One-sample t-tests showed that, for both Canadian and UK image pairs, men preferred the faces of women with high-pitched voices significantly above the chance value of 3.5 (Canada: $t_{337}=12.1$, M=4.71, S.E.=0.1, $p<0.0001$; UK: $t_{337}=3.294$, M=3.84, S.E.=0.103, $p=0.0001$).

Study 3

1 Rationale

Study 3 tested whether men and women prefer faces of women with high pitched voices to those with low-pitched voices. The stimuli used here were natural faces as to test if findings from study 2 extended to more ecologically valid stimuli.

2 Methods

2.1 Participants

Participants included 41 students at the University of St Andrews (17 men and 24 women), and the faces that were used to construct averages in study 2. Ten men and 10 women rated Canadian faces. Seven men rated all UK faces, whilst two sets of 7 women rated each ½ of the UK faces. Age of raters was not recorded.

2.2 Stimuli

Facial stimuli were masked (as in study 2) to reduce cues from hair and clothing.

2.3 Procedure

Faces were displayed on screen in random orders. Attractiveness of each face was rated on a 7 point scale (1=very unattractive, 7=very attractive).

3 Results

Cronbach's alpha test showed that inter-rater agreement was high ($\alpha > 0.7$). Thus all ratings were Z-scored within group and then ratings from men and women were averaged (as there was agreement between men and women as per which faces were attractive). A univariate ANOVA [dependent variable: facial attractiveness, between-groups factors: pitch of voice (high or low), sample (UK or Canada), and covariate: age of face] tested the relationship between pitch of voice and facial attractiveness. The faces of women with high pitched voices were found more attractive than the faces of women with low pitched voices $F_{(1,71)}=88.6$, $p<0.001$. There were no other significant interactions (all $F_{(1,72)}<0.339$, $p>0.562$).

Table 10- 2. Mean and S.D. of ages. S.D. is in ()

Study #	Participants	Age Mean(s.d.)
Study 1	UK	18.4 (0.72)
	Canada	19.6 (2.1)
Studies 2 & 3	UK stimuli	18.64 (0.84)
	Canada stimuli	19.6 (2.1)
	Raters (study 2)	26.59 (9.46)

4 Discussion

In study 1, femininity of women's face shapes correlated with pitch of voice in both the UK and Canadian samples. This effect was robust to different recording methods, including microphone type and phonation, different photographic conditions, as well as phenotypic variation across continents. In populations with a wide age range, younger women may have more feminine facial and vocal features than older women. The relationship between facial femininity and pitch of voice reported here however, was not due to age. This suggests that although age contributes to female femininity (Deffenbacher et al., 1998; O'Toole et al., 1999), female femininity also independently reflects qualities such as hormonal status and reproductive health (Alonso & Rosenfield, 2002; Jasienska et al., 2004; Law Smith et al., In Press; Moran et al., 1999; Zaadastra et al., 1993). The correlation between facial femininity and voice pitch supports the idea that cues to underlying quality are concordant in face and voice. Thus findings by Collins and Missing (2003), that female facial and vocal attractiveness correlate, may reflect that faces and voices signal common information about the degree to which femininity is expressed in an individual.

In two independent samples in studies 2 and 3, it was found that facial prototypes and natural faces (respectively) of women with high-pitched voices were more attractive than those with low-pitched voices. These findings extend those of Collins & Missing (2003); vocal femininity was a predictor of facial attractiveness. Male preferences for femininity as indicated by face and voice are potentially adaptive as expression of pitch of voice and facial femininity may be positively linked to oestrogen (Abitbol et al., 1999; Alonso & Rosenfield, 2002; Thornhill & Gangestad, 1999), which is, in turn, positively linked to reproductive health and development (see Alonso & Rosenfield, 2002 for review). Although perceived age may contribute to attractiveness ratings in studies 2 and 3, and perceived age is positively related to facial and vocal masculinity (see Deffenbacher et al., 1998; O'Toole et al., 1999, chapters 5 & 6), attributions of age will not have influenced the objective assessment of facial and vocal masculinity in study 1. It is possible that when considering larger age ranges, age may have a greater effect on the relationship between vocal and facial masculinity.

In summary, I showed that objective measures of vocal and facial femininity are correlated and that vocal femininity can predict facial attractiveness.

Chapter 11

The relative role of femininity and averageness is aesthetic judgements of women's voices

1 Rationale

It is hypothesised that averageness is a major component of attractiveness. People prefer average configurations in faces and non-face objects (Halberstadt & Rhodes, 2000, 2003; Langlois & Roggman, 1990; Little & Hancock, 2002; Penton-Voak & Perrett, 2000). There are indications that men prefer women's faces that deviate systematically from average configuration (Perrett et al., 1994). Shifting female face shape away from average, towards feminine configuration increased attractiveness (Penton-Voak et al., 1999; Perrett et al., 1998; Rhodes et al., 2000). This finding does not appear to reflect potential sample biases as it occurred in two Caucasian and two Asian populations. It appears that both averageness and femininity make positive contributions to the attractiveness of women's faces (Langlois & Roggman, 1990; Little & Hancock, 2002; Penton-Voak & Perrett, 2000).

Due to individual differences in preferences for men's faces, evidence that shifting men's face shape away from average, and the direction away from average that might enhance attractiveness is equivocal (Fink & Penton-Voak, 2002; Penton-Voak & Perrett, 2000). Perrett et al. (1998) and Rhodes et al. (2000) found overall preferences for feminised men's faces, whereas Johnston et al. (2001) found overall preferences for masculinised men's faces. Cornwell et al. (2004) observed preference for male facial shape that was close to average levels of masculinity. Thus for male faces, the relative importance of averageness and sexual dimorphism is unclear.

People also prefer averageness of non-vocal auditory stimuli (i.e. music, Repp, 1997). In the domain of vocal attractiveness, however, shifting male voice pitch (fundamental frequency) towards masculine values enhanced vocal attractiveness (chapter 6), but this study did not explore the possible effect of starting pitch of voices. If averageness is more important than masculinity, then masculinising an already masculine male voice should make it less attractive. Several factors have been reported to contribute to individual differences in women's preferences for masculinity (see Penton-Voak & Perrett, 2000, for review). The psychological literature, however, has not yet revealed differences in men's preferences for femininity. I therefore sought to study the importance of averageness and femininity for men's judgments of women's voices.

The average young adult woman's voice pitch (220Hz), is nearly double the average adult man's voice pitch (124Hz) (Bachorowski & Owren, 1999; Childers & Wu, 1991). Collins & Missing (2003) found a positive correlation between measured voice pitch and rated attractiveness in women, but did not report mean pitch or range of their sample. Thus it is unclear if their (Collins & Missing, 2003) findings were due to preferences for voices with average pitch or preferences for high-pitched voices. Due to the correlational nature of the study, these findings could also have reflected unmeasured vocal characteristics (see chapters 5 & 6).

In the present study I tested if lowering and raising pitch (sensu chapters 6 & 7) independent of other vocal characteristics has the same effect on attraction to voices when the starting pitch of the voices was average, lower than average (i.e. masculine) and higher than average (i.e. feminine). If increasing pitch in female voices that are already more feminine than average increases their attractiveness, this would demonstrate that preferences for feminine female voices outweigh preferences for averageness in vocal stimuli. Furthermore, there could be ceiling level to pitch preferences such that when raised too high, men do not prefer this because of a number of reasons (e.g. sounds too young). I also tested if the manipulations of voices with different starting pitches produced pairs that were perceptually equivalent.

2 Methods

2.1 Participants

Protocols were approved by the University of St Andrews ethics committee. Female participants were 15 undergraduates from the University of St Andrews aged 18-23 (M=20, s.d.=1.69). Male participants were 20 men aged 17-28 (M=20.29, s.d.=2.86).

2.2 Voice recordings

Female participants were recorded speaking the English vowel sounds "eh" (ɛ) "ee" (ι˥) "ah" (A˥) "oh" (oʊ) "oo" (ʊ˥) (symbols in parentheses are International Phonetic Alphabet symbols) with an Audio-Technica AT4041 condenser microphone (*see* http://www.audio-technica.com). Voices were recorded onto computer hard disk using Sonic Foundry's SoundForge (*see* http://www.soundforge.com) at 44.1 kHz sampling rate and 16-bit quantisation and saved as uncompressed "wav" files.

2.3 Stimuli generation

Each vowel sound was manipulated separately. Fundamental frequency was manipulated using the Pitch-Synchronous Overlap Add (PSOLA) method (www.praat.org). The PSOLA method allows selective manipulation of pitch (fundamental frequency and corresponding harmonics) independently of formant frequencies (see chapters 6 & 7). To feminise voices, the fundamental frequency of each voice was raised by 20Hz (see chapters 6 & 7). The converse was done to masculinise voices. Amplitude of each vowel was normalized to 87.3dB RMS. Voices were then converted to MPEG layer 3 audio format (mp3), uncompressed at 11.025 kHz sampling rate at 128 kbps bit-rate using the LAME 3.93 encoder. The conversion from "wav" to "mp3" did not affect frequencies at all (correlations between fundamental and formant frequencies between "wav" and "mp3" had r-values of 1). Figure 11-1 shows spectrograms of manipulated voices.

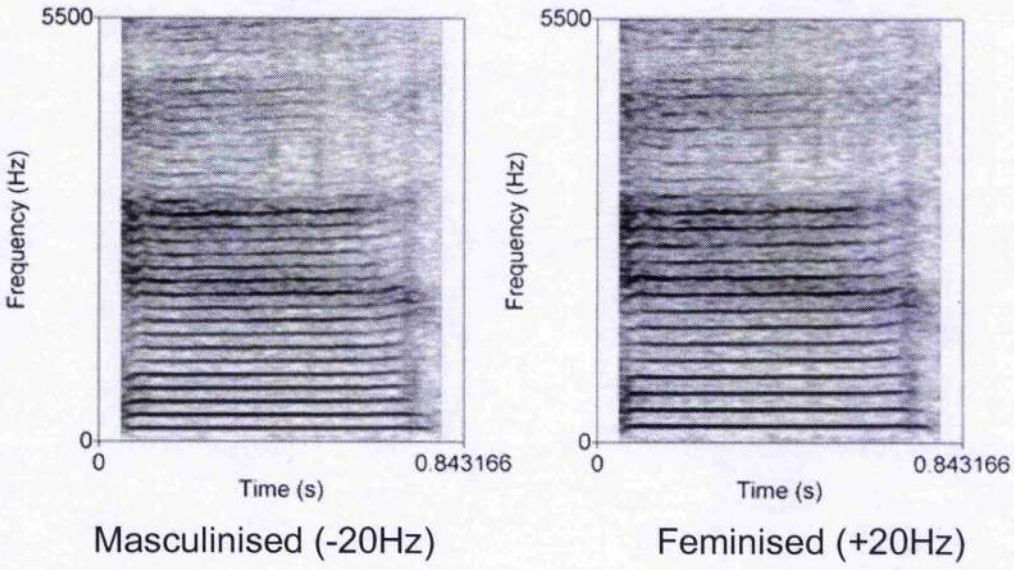


Figure 11-1. Spectrograms of manipulated vowel "ee" from a vocaliser with a starting fundamental frequency of 220Hz. Harmonics are the horizontal lines ascending the two plots. Harmonic spacing is equal to the fundamental frequency (Ladefoged, 1996). Thus the voice raised by 20 Hz has broader harmonic spacing than the voice lowered by 20 Hz.

2.4 Acoustical analysis

After stimuli were generated, each vowel sound was analysed separately using Praat software (www.praat.org). Absolute pitch (fundamental frequency in Hz) was measured using Praat's autocorrelation algorithm. Pitch measurement technique was identical to that used in chapters 6 & 7, except pitch was searched for between 100 and 600Hz (as recommended for women's voices by www.praat.org). Formant frequency measurement technique was identical to that in chapter 5. Mean pitch was measured by averaging the pitch of each voiced window across the entirety of each vowel sound. Subsequently mean pitch was averaged across vowels for each vocaliser. Table 11-1 shows descriptive statistics for pitch in Hz of manipulated voices. I also measured pitch using the following perceptual pitch scales: equivalent rectangular bandwidth (ERB) and Bark, using the same technique as mentioned above for pitch measurement in Hz.

Table 11-1. Descriptive statistics of manipulated voices. Mean (in Hz) and standard deviation (in parentheses) of fundamental frequencies (pitch) of manipulated voices at each level of starting pitch.

Starting pitch	Masculinised	Feminised
Low pitch (200Hz)	180(1.40)	220(1.40)
Average pitch (220Hz)	200(0.26)	240(0.26)
High pitch (241Hz)	221(0.95)	261(0.95)

Table 11-2. Descriptive statistics of formants frequencies of unmanipulated voices. Mean and standard deviation of formant frequencies 1-4 (F1-F4) and their dispersion [Fdisp=(F4-F3)+(F3-F2)+(F2-F1)] /3 (Fitch, 1997).

Acoustic measurement	Low starting pitch	Average starting pitch	High starting pitch
F1	584 (99.7)	530 (66.2)	534 (65.5)
F2	1725 (219.8)	1773 (86.1)	1840 (109.4)
F3	2848 (81.6)	2937 (207.4)	3004 (100.8)
F4	4008 (246.8)	4067 (162.2)	4122 (20.9)
Fdisp	1141 (64.1)	1179 (48.9)	1196 (26.2)

2.4 Procedure

Voices were presented using a forced choice paradigm. Participants listened to 15 pairs of manipulated voices (each pair consisting of masculinised and feminised versions of a single identity). Side of presentation and order of stimuli presentation were fully randomised. Participants were instructed to listen to both voices (separately) through headphones and then select which voice was more attractive. Participants were allowed unmonitored *ad-libitum* stimulus repetitions.

3 Results

1-sample Kolmogorov-Smirnov tests showed that men's responses were normally distributed (all $z<1.055$, $p>0.215$). 1-way ANOVAs showed that the pitch groups (high, average, and low) that women were divided into did not differ significantly in age ($F_{2,12}=0.061$, $p=0.941$) or formant qualities (i.e. formant frequencies 1-4 and formant dispersion: all $F_{2,12}<1.659$, all $p>0.230$).

For each group of voices, low, average and high, the percentage of feminine voices chosen was calculated. One sample t-tests (chance value=50%) revealed that men preferred femininity in voices with low starting pitch ($t_{19}=5.659$, $p<0.001$), voices with average starting pitch ($t_{19}=4.198$, $p<0.001$) and in voices with high starting pitch ($t_{19}=2.156$, $p=0.044$).

A repeated-measures ANOVA [between-subjects factor: starting pitch (high/ average/low] revealed a linear effect of starting pitch on number of feminised voices preferred ($F_{1,19}$=5.153, p=0.035). Increasing pitch in voices with low starting pitch had the greatest effect on attractiveness enhancement. See figure 11-2 for a graphic representation of statistics.

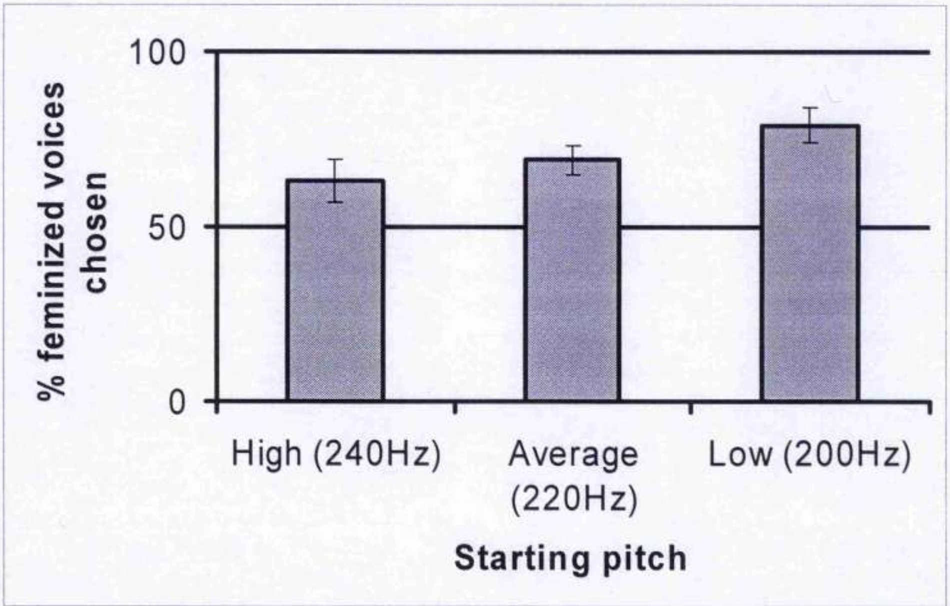


Figure 11-2. Preferences for femininity outweigh preferences for averageness. At each starting pitch, men preferred voices with raised pitch to voices with lowered pitch above the chance value of 50%. The manipulation had a greater effect on the voices with the lowest starting pitch than those with the highest starting pitch.

The pitch manipulation had its strongest effect when the starting pitch was lowest. As perceptual scales of pitch are not linear in relation to absolute pitch, pitch discrimination requires smaller change in absolute pitch at lower starting frequencies than at higher starting frequencies (Ladefoged, 1996; Stevens, 1998; Traunmüller, 1990). I sought to determine if the linear effect of starting pitch on the amount femininity was preferred was due to differences in ability to discriminate between manipulations at different starting pitches.

Table 11-3 shows manipulation strength in absolute and perceptual pitch scales (Hz, Bark & ERB). To determine if manipulations at each pitch level were perceptually equivalent, I calculated pitch differences between manipulations at each pitch level. In each transformation from the Hz scale, I found that the strength of manipulations did vary slightly on Bark and ERB scales.

Table 11-3. Mean differences in pitch (feminised voice-masculinised voice) for each starting level of pitch, using different pitch scales. Manipulations of voices starting at higher pitches may have sounded slightly less manipulated than manipulations of voices starting at lower pitches.

Starting pitch	**Difference in Hz**	**Difference in Bark**	**Difference in ERB**
Low (200Hz)	40	0.45	0.84
Average (220Hz)	40	0.44	0.81
High (240Hz)	40	0.43	0.78

4 Discussion

For voices at each starting pitch, increasing pitch increased the attractiveness of women's voices. This finding is consistent with evidence from the facial literature that increasing female feminine characteristics enhances attractiveness (Perrett, al., 1998; Rhodes et al., 2000). The finding that increasing pitch enhances women's vocal attractiveness is also consistent with Collins & Missing (2003) who found a positive association with pitch and attractiveness in unmanipulated voices. The fact that increasing pitch enhanced the attractiveness of voices that were already higher pitched than average prior to the vocal manipulation indicates that men preferred voices with feminine characteristics to average characteristics. This finding holds regardless of potential differences in perceived manipulation strength at different starting pitch levels. Although averageness is attractive in faces (Langlois & Roggman, 1990; Little & Hancock, 2002), non-face objects (Halberstadt & Rhodes, 2000, 2003) and in music (Repp, 1997), men's preferences for exaggerated feminine female traits in both faces and voices appear to outweigh general preferences for averageness.

There may be 3 potential explanations for the linear effect of starting pitch on percentage of feminised voices preferred suggests that there is a positive.

1) **Non-linear relationship between pitch and attractiveness**. Collins & Missing (2003) found a linear relationship between women's voice pitch and attractiveness but did not test for non-linearities. I found that increasing pitch had a bigger effect on the attractiveness of voices that had a low starting pitch than on voices with a higher starting pitch. To determine if this is explanation holds, all other possibilities must be ruled out.

2) **Perceptual differences in pitch perception.** Additional acoustical analysis revealed that the manipulations may not have been perceptually equivalent at each starting pitch. Therefore, the linear effect of starting pitch on femininity preferences may explain by differences between perceptual and absolute pitch. To determine if this is the case, future studies could be run with voices manipulated on the dimension of perceived pitch.

3) **Ceiling/floor on pitch preferences.** There could be a limit as to how much raising pitch increases the attractiveness of women's voices. If manipulated too high, the voices might sound too child-like to be attractive as a sexual partner. There could also be a lower limit to what pitch level is attractive in women's voices. If a voice pitch is too low, it may not be attractive because at menopause, women's voices pitch lowers (Abitbol et al. 1999). Thus low voice pitch in women can signal that the vocalisers are not very fertile. To determine if this is the case, additional studies with more levels of pitch could be conducted.

In summary, I demonstrated that men prefer femininity over averageness in women's voices. Men may prefer women with high-pitched voices because high voice pitch is associated with pro-social stereotypes (Berry et al., 1994; Zuckerman & Driver, 1989), youth (Collins & Missing, 2003; Huber et al., 1999; Linders et al., 1995; Zuckerman & Driver, 1989; Zuckerman et al., 1995) and hormonal markers of fertility (Abitbol et al., 1999; Chae et al., 2001; Van Borsel et al., 2000). Men may prefer femininity to averageness in women's voices for any or all of these reasons (possibly subject to limits).

Chapter 12

General discussion

1 Dominance of voice and intrasexual competition

In within each sex (chapters 8 & 9), voices with relatively masculine acoustic characteristics (low fundamental frequency and large apparent vocal-lengths) were perceived as more dominant than voices with relatively feminine acoustic characteristics (high fundamental frequency and small apparent vocal-tract length) were rated. Women also rated masculinised (lowered fundamental frequency and increased apparent vocal-tract length) men's voices as dominant and attractive. This is similar to what Ohala (1983, 1984) found and hypothesised (i.e. voice pitch and apparent vocal-tract length are used as dominance cues). Although men in this thesis were not explicitly competing when rating voices, they are recognising traits that may signal dominance. Women preferred men with dominant sounding voices. These voices contained enhanced sexually dimorphic characteristics. Thus, in the voice, I have observed that intrasexual competition interacted with intersexual selection. Furthermore, men preferred women with higher pitched voices to lower pitched voices (chapter 10). Sexual selection may have a role in maintaining current levels of sexual dimorphism in voices. This leads in to the next topic: whether sexual dimorphism of the voice is undergoing (or underwent) disruptive, directional and/or stabilising selection.

2 Disruptive, directional and stabilising selection

To re-iterate, disruptive selection selects against the mean of the traits, causing a bimodal distribution in trait size. Directional selection selects against one extreme of a trait and drives the mean trait in the opposite direction of the extreme selected against. Stabilising selection selects against both extremes of a trait, thus maintaining the current mean of a trait (see Trivers, 1985).

If we consider selection of fundamental frequency at the species level, then there is evidence for disruptive selection occurring now or possibly having occurred in the past. In other words, for both men and women, androgynous voice pitch, or voice pitch close to the mean of men and women (averaged together) is unattractive. Men with high pitched voices and women with low pitched voices seem to be the least attractive in most conditions. Thus, it is likely that at some time in our evolutionary past, there was a selection pressure to drive sexual dimorphism in voice pitch to its current level. To determine if within each sex there is stabilising selection for voice pitch is more difficult to evaluate given the data reported in this thesis. In support of directional selection are the results of the correlational studies (chapter 5) and in studies with voice manipulations (chapters 6-11, excluding chapter 9), women preferred men's voices with pitch below the population mean, whereas men preferred women's voices with pitch above the population mean. Thus, there is selection against androgyny as mentioned before.

Within each sex I observed directional selection for voice pitch. Women preferred men's voice pitch that was below the population mean. Men preferred women's voice pitch above the population mean. Whether there are limits as to how high a women's voice pitch can be and still be attractive and how low a man's voice pitch can be and still be attractive, however, cannot be determined by the data reported in this thesis. It is possible that voice pitch may be maintained at current levels if there is a non-linear interaction between voice pitch and attractiveness (i.e. too high of a pitch and too low of a pitch are both unattractive in both sexes). In Chapter 11, there is some evidence of a non-linear interaction between women's voice pitch and attractiveness, but this could be confounded by the perceptual difference between manipulations. Future research should address this issue.

To further complicate matters, there is not yet adequate data on how voice pitch relates to actual reproductive success. Voice pitch of monozygotic twins is more similar than voice pitch of same-sex dizygotic twins (Debruyne et al., 2002). Therefore, voice pitch has a heritable component. What is unknown is if men with low pitched voices and women with high pitched voices actually have higher reproductive success than their counterparts. Without this data, it cannot be determined if preferences for low pitch in men's voices and high pitch in women's voices translates to an actual reproductive advantage.

3 What happened to vocal-tract length?

There are accounts of taller men (Mueller & Mazur, 2001; Pawlowski et al., 2000) and shorter women (Nettle, 2002a, 2002b) having higher reproductive success than shorter men and taller women. Vocal-tract length is a positive correlate of height (Fitch &

Geidd, 1999) and formant dispersion is a negative correlate of vocal-tract length (Fitch, 1997). Therefore, it is reasonable to assume that in general, women would prefer men with lower formant dispersion and men would prefer women with higher formant dispersion.

In chapter 5, I did observe that men had significant preferences for higher formant dispersion in women's voices, but this was confounded by the duration manipulation. I do have unpublished data showing that when manipulating formant dispersion independently of pitch in women's voices (as was done in chapter 6 for men's voices), men did prefer women with increased formant dispersion. In support of this, Collins & Missing (2003) found that formant dispersion did correlate positively with attractiveness of women's voices. The voices used by Collins & Missing (2003) were of different durations, thus it is necessary for future correlational studies to control for duration of utterance by means of extracting a portion of each vowel that is of equal length, and then ramping the amplitude of the onset and offset, or for manipulations to be performed that do not affect time or pitch (see chapter 6).

In chapters 5 & 6, I observed no evidence for women to have general preferences for men with lower formant dispersion. Collins (2000) also did not find any evidence of women's preferences for formant qualities, but this data could have been confounded by duration of utterance (here, duration of utterance was not controlled for) and measures of raw formants were entered into a principal components analysis along with formant dispersion rather than using formant dispersion on its own as a variable in analysis.

Formant dispersion is a more robust correlate of vocal-tract length than average formants or raw formants because formant dispersion is robust to the effects of the glottis being open or closed during phonation has on formant frequencies (e.g. differences between open-closed and open-open tube models of the vocal-tract, see Fitch & Hauser, 2002). Therefore, there may have been an undetected relationship between formants and attractiveness in the study of Collins (2000). Nevertheless, formant dispersion did not correlate with attractiveness of men's voices in chapter 5, nor did manipulations of apparent vocal-tract length (which changed formant dispersion) affect attractiveness ratings of men's voices (in general). Thus, the manipulation was either too subtle to detect, other acoustic cues overshadow possible effects of formant dispersion on attractiveness or there is no general preference for large vocal-tracts in men's voices. Because the manipulation of apparent vocal-tract length in chapter 6 was strong enough to affect other attributions (size, masculinity and age), it is likely that there is no general preference for vocal-tract size. Just because there was not general preference for low formant dispersion in men's voices, however, does not mean that formant dispersion is not used in mate choice decisions. This leads us to the next topic: assortative mating.

4 Assortative preferences

4.1 Assorting for attractiveness?

I found that women who rated themselves more attractive had stronger preferences for masculine aspects of men's voices than women who rated themselves less attractive. This finding is not necessarily a demonstration of assortative preferences for attractiveness in the classical sense because although pitch and perceived masculinity are highly associated with vocal attractiveness, there is variance in attractiveness unexplained by masculinity. Furthermore, it is still unknown if these individual differences in preferences are carried over into reproductive behaviour. Nevertheless, it may be adaptive for less attractive women to include less attractive men in their mate-search behaviour in order to expand their potential pool of mates. More attractive women may be able to afford to be more selective than less attractive women may be able to be.

4.2 Assorting for body size

I observed assortative preferences for size in chapter 6. Taller and heavier women preferred men's voices with apparent vocal-tract lengths that were manipulated to be longer, whereas shorter and thinner women preferred men's voices with apparent vocal-tract lengths that were manipulated to be shorter. As vocal-tract length is a correlate of height and weight (Fitch & Geidd, 1999), these data support the idea that women have assortative preferences for male body size (height and weight). These data are different than those reported by Pawlowski (2003) who found that women's height negatively predicted their preference for height differences between men and women in line drawings. The study in chapter 6 did not compare preferences for relative heights, nor did Pawloski (2003) test for assortative preferences for absolute height so it is unknown if one set of results contradicts or qualifies the other. Furthermore, it can be imagined that there assortative preferences for relative and absolute height might actually be able to occur simultaneously and independently of each other.

Assortative preferences for height may have an adaptive function. Muller & Mazur (2001) reviewed data showing that partners dissimilar in height were more likely to have abnormal outcomes of the pregnancies.

Indeed, assortative preferences for height have been found in speed dating scenarios (Kurzban & Weeden, 2005). Studies have shown that cross-culturally, married and/or cohabited men and women are often of similar heights and weights (for recent evidence, see Salces et al., 2004; Silventoinen et al., 2003; Ginsberg et al., 1998, although many other studies exist showing similar results). Thus it is likely that assortative preferences for size (height and weight) carry over into assortative mating.

5 Misuse of pitch as a cue to size

While auditory cues to size (i.e. vocal-tract length) appear to affect mate-choice relevant decisions, pitch alters perceptions of body size (e.g. height and weight), but does not relate to actual body height or weight (Lass & Brown, 1978). This misuse of pitch as a cue to body size has perplexed researchers (Fitch & Hauser, 1995) as humans appear to have the cognitive capacity to learn that fundamental frequency is not associated with body size among adults of the same sex (Lass & Brown, 1978). Indeed, red deer (*Cervus elaphus*), who may have a lower cognitive capacity than humans, appear to react to formant dispersion, rather than fundamental frequency (McComb, 1991; Reby & McComb, 2003; Reby et al., 2005), when females attend to males and when males attend to males. So why does this misperception persist in humans?

Fitch & Hauser (1995) reviewed the topic of why pitch affects attributions of size but does not relate to actual height or weight among adults, within a sex. First, voice pitch is proportional to vocal fold length and thickness (Titze, 1994). Pubertal and adult male vocal folds are 63% longer than pre-pubertal male vocal folds, whereas pubertal and adult female vocal folds are 34% longer than pre-pubertal vocal folds (Kahane, 1982). Kahane (1978) found that men's larynges grow 50% larger than female larynges do at puberty. As Kahane (1982) notes, length of the vocal folds does not necessarily account for all of the variance in voice pitch between men and women. Vocal fold thickness must also play a role. For example, all 6 strings on a guitar are the same length, but vibrate at different frequencies. The thicker strings vibrate at lower frequencies than the heavier strings. On electric guitars, for example, strings can be made of the same material, and thus have the same density. Thus, it is the mass of the string (or vocal-fold), its length and its stiffness that influence the frequency at which it vibrates (Titze, 1994).

Second, because the larynx is made not made of bones (although anchored by the hyoid), and is suspended in the vocal tract by muscles and tendons, allowing vertical movement. The vocal folds (and the larynx) can grow independently of the rest of the body. Neck circumference, rather than height or vocal-tract length correlates with fundamental frequency in adult men and women (see Titze, 1994, for review; Feinberg, unpublished data).

Third, among children, and between men and women, pitch is negatively related to age and height (Huber et al., 1999; Rendal et al., 1995; Titze, 1994). Titze (1994) also notes that in general, larger objects produce lower frequencies than smaller objects. Hauser (1993) showed that among species, the larger species tended to have lower fundamental frequencies than the smaller species, although there were numerous exceptions to the rule. Thus, Fitch & Hauser (1995) hypothesised that because of the relationships between fundamental frequency and size among children and between sexes, people may over-generalise this perception to adults (within a sex).

Ohala (1984) proposed that fundamental frequency and vocal-tract length are used as dominance cues across species and across cultures in humans. In support of this I found that both men and women perceived men's voices with low fundamental frequency and large vocal-tract lengths more dominant than men's voices with high fundamental frequency and short vocal-tract lengths. Gregory and colleagues (1990; 1997; 1996) showed that indeed, subordinate vocalisers converge on the fundamental frequency of dominant vocalisers, thus showing behaviourally that pitch is used as a dominance cue, further supporting findings by Ohala (1984) and myself (chapters 8 & 9). Thus, even though fundamental frequency may not reliably relate to height, it may signal affect or intention to dominate.

Even though fundamental frequency may signal dominance, it does not fully explain why people do not learn that fundamental frequency is not a cue to body size in adults of a given sex. One further insight into the dilemma is that there might be little cost associated with the misuse of fundamental frequency as a cue to body size. After all, visual information on height and weight would certainly override auditory information if the two were in conflict. Shorter men can still be socially dominant and signal dominant intentions (e.g. Henry Winkler aka "The Fonz" is 5'7"). Thus, if there is disparity between two signals (e.g. visual and auditory information about height), individuals may choose the more reliable of the two. This leads us to the next topic of discussion: multiple cues to mate quality, why they exist and what they mean.

6 Multiple ornaments signalling mate quality

6.1 Multiple messages in the voice

As we have seen in the case of voice pitch misrepresenting body size (height and weight) among same-sex adults and formant frequencies accurately representing body size (height and weight), there can be multiple cues to mate quality. There are different theories about how multiple cues interact to signal mate quality. The case of fundamental frequency and formant frequencies signalling body size (height and weight) and/or dominance might fit different theories about multiple ornaments, depending on interpretation of what these acoustic features are signalling. Formant dispersion is an informative cue to body size (height and weight, Fitch & Geidd, 1999; Fitch, 1997; Collins & Missing, 2003). In other words, formant dispersion provides accurate information about the body size (height and weight) of the individual. Fundamental frequency on the other hand does not provide accurate information about adult body size (height and weight), but does indicate age (Huber et al., 1999) and sex (Childers & Wu, 1991; Rendall et al., 2005), which also relate to body size (height and weight).

Fundamental frequency also may relate to perceived dominance (Ohala, 1983, 1984; Chapters 8 & 9) and inheritable immunity to infection (see chapter 3 for discussion). Therefore, if fundamental frequency is considered only as a body size (height and weight) indicator in same-sex adults then it is an uninformative cue. Alternatively, if fundamental frequency is considered as an indicator of body size (height and weight) via stage of development and sex, dominance and/or inheritable immunity to infection, then fundamental and formant frequencies might be informative cues that signal multiple messages (Møller & Pomiankowski, 1993; Johnstone, 1997; see Candolin, 2002, for review). According to Candolin (2002), when assessed together, multiple messages can be used to assess overall quality. Furthermore, the sex that is choosing can pick one trait over the other, in terms of which trait is more relevant to increasing fitness, given current ecological conditions.

In the case of women's mate selection of fundamental frequency and formant dispersion, fundamental frequency seems to be more important than formant dispersion, although it is not known if this is due to female choice, or perceptual differences in manipulation strength of fundamental and formant frequencies in this thesis. Further research is needed to clarify this last point.

6.2 Multiple ornaments that signal the same quality

In women, voice pitch (Abitbol et al., 1999) and facial femininity (Law Smith et al., In Press) may both be related to oestrogen levels and are correlated positively (Chapter 10). Thus, voice pitch and facial femininity may both be signalling fertility. Thus, these data are more likely to fit the back-up cues model (multiple traits signal the same information about mate quality and thus are back-up copies of the same signal) rather than the multiple messages model (multiple traits convey different information about mate quality but are nevertheless correlated, see Candolin, 2002, for review). Each trait signals the same quality, but there is always a degree of error involved. Therefore, having multiple cues (or back-up cues) signalling the same quality can reduce the assessor's error in evaluating the individual's overall quality.

7 If men's faces and voices signal the same qualities, why do women's preferences for sexual dimorphism appear to be inconsistent across modalities?

7.1 General preferences

Men's preferences for femininity appear to be consistent across facial and vocal domains (chapter 5, 10, 11; Collins & Missing, 2003; Perrett et al., 1998; Rhodes et al., 2000). This was discussed above when discussing multiple ornaments signalling the same quality. Evidence for women preferring masculine vocal features (in particular, low voice pitch) is unequivocal (see chapters 5, 6, 7, 8, Collins, 2000; Puts, 2005). Evidence for women preferring masculine facial features, however, is equivocal (see Perrett et al., 1998; Rhodes, 2000; Johnston, 2001). In some studies women prefer masculinised men's faces and in some studies women prefer feminised men's faces. This seems strange because women's preferences for male-typical putative pheromones and preferences for facial masculinity appear to be positively correlated (Cornwell et al., 2003). One possibility is that in men, voice pitch appears to be used as a cue to health (whether correctly or incorrectly, see chapter 6) as well as perceived masculinity. Shape-only transformations of men's faces may not provide cues to apparent health, whereas manipulations of perceived health in the face alter attributions of masculinity and health (Boothroyd et al., 2005). I have unpublished data showing that women's preferences for voices with lowered pitch correlate positively with preferences for faces with increased apparent health (which also look more masculine) as opposed to faces with decreased apparent health (which look more feminine). The same vocal preferences for decreased pitch do not correlate with preferences for shape-only facial masculinity transforms (which do not alter health perceptions). Thus, arguably, the difference in preferences for male facial and vocal masculinity may have its origins in the type of manipulation used in the study. Manipulations of only face shape may fail to capture cues to perceived health. Therefore, studies manipulating only face shape may be producing an erroneous picture of preferences amongst women. When perceived health information in the face is discarded, women's preferences for vocal masculinity and facial masculinity do not correlate. When perceived health information in the face is included, women's preferences for facial masculinity and vocal masculinity do correlate. Other explanations will follow.

7.2 Menstrual-cycle variation in preferences

An alternative explanation, to the disparity between women's preferences for masculinity in the voice and face than the one mentioned above, may be menstrual cycle variation in masculinity preferences. Although women's overall preferences for voices and faces appear to be disparate, they way preferences change over the menstrual cycle is synchronous. For both faces and voices, women prefer higher levels of masculinity when fertile than at other parts of the menstrual cycle (Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000; Johnston et al., 2001; Jones et al., 2005; Putz, 2005; Chapter 8). Thus, as there is an interaction between women's hormonal status and preferences for masculinity, to me, general preferences seem less important because they are qualified. What is interesting is that even though there may be disparity between general preferences for masculinity in voices and faces, the reduction in preferences for femininity in the late-follicular menstrual cycle is consistent across modalities.

These preferences for masculinity may reflect that men with higher testosterone invest less in their offspring than men with lower testosterone (Burnham et al., 2003; Gray, 2003; Gray et al., 2004; Gray et al., 2002). Consistency in menstrual cycle shifts in masculinity preferences across modalities suggests that and that at some level women are aware that faces and voices convey common information about the masculinity of the individual (Penton-Voak & Chen, 2004; Dabbs & Mallinger, 1999).

8 Conclusions

In summary, I have consistently found that men prefer feminine aspects of women's voices and women prefer masculine aspects of men's voices. Furthermore, strength of preferences and attributions appear to be dependent on hormonal status and self-perceptions. As there are preferences for sexual dimorphism in the voice, it is apparent that some time in our evolutionary past, there was disruptive selection in voice pitch at the species level and directional selection for voice pitch within each sex. Future research should try to determine the limits of how high or low fundamental frequencies can be and still remain attractive (i.e. whether or not selection pressure on voice pitch is stabilising). Furthermore, long-term studies should be conducted to determine how these preferences relate to whom people end up mating with and how vocal traits relate to actual reproductive success.

References

Abitbol, J., Abitbol, P., & Abitbol, B. (1999). Sex hormones and the female voice. *Journal of Voice, 13*(3), 424-446.

Ahnesjö, I., Kvarnemo, C., & Merilaita, S. (2001). Using potential reproductive rates to predict mating competition among individuals qualified to mate. *Behavioral Ecology, 12*(4), 397-401.

Alonso, L. C., & Rosenfield, R. L. (2002). Oestrogens and puberty. *Best Practice & Research Clinical Endocrinology & Metabolism, 16*(1), 13-30.

Amir, O., & Kishon-Rabin, L. (2004). Association between birth control pills and voice quality. *Laryngoscope, 114*(6), 1021-1026.

Amir, O., Kishon-Rabin, L., & Muchnik, C. (2002). The effect of oral contraceptives on voice: Preliminary observations. *Journal of Voice, 16*(2), 267-273.

Andersson. (1994). *Sexual Selection*. Princeton: Princeton University Press.

Archer, J., Birring, S. S., & Wu, F. C. W. (1998). The association between testosterone and aggression among young men: Empirical findings and a meta-analysis. *Aggressive Behavior, 24*(6), 411-420.

Bachorowski, J. A., & Owren, M. J. (1995). Vocal Expression of Emotion - Acoustic Properties of Speech Are Associated with Emotional Intensity and Context. *Psychological Science, 6*(4), 219-224.

Bachorowski, J. A., & Owren, M. J. (1996). Vocal expression of emotion is associated with vocal fold vibration and vocal tract resonance. *Psychophysiology, 33*, S20-S20.

Bachorowski, J. A., & Owren, M. J. (1999). Acoustic correlates of talker sex and individual talker identity are present in a short vowel segment produced in running speech. *Journal of the Acoustical Society of America, 106*(2), 1054-1063.

Baird, D. D., Weinberg, C. R., Zhou, H. B., Kamel, F., McConnaughey, D. R., Kesner, J. S., et al. (1999). Preimplantation urinary hormone profiles and the probability of conception in healthy women. *Fertility and Sterility, 71*(1), 40-49.

Bakker, T. C. M., Kunzler, R., & Mazzi, D. (1999). Sexual selection - Condition-related mate choice in sticklebacks. *Nature, 401*(6750), 234-234.

Barker, B. A., & Newman, R. S. (2004). Listen to your mother! The role of talker familiarity in infant streaming. *Cognition, 94*(2), B45-B53.

Bateman, A. J. (1948). Intrasexual selection in *Drosophila*. *Heredity, 2*, 349-368.

Bedard, C., & Belin, P. (2004). A "voice inversion effect?" *Brain and Cognition, 55*(2), 247-249.

Belin, P., Zatorre, R. J., Lafaille, P., Ahad, P., & Pike, B. (2000). Voice-selective areas in human auditory cortex. *Nature, 403*(6767), 309-312.

Benson, P. J., & Perrett, D. I. (1993). Extracting Prototypical Facial Images from Exemplars. *Perception, 22*(3), 257-262.

Berry, D. S., & Hansen, J. S. (2000). Personality, nonverbal behavior, and interaction quality in female dyads. *Personality and Social Psychology Bulletin, 26*(3), 278-292.

Berry, D. S., Hansen, J. S., Landrypester, J. C., & Meier, J. A. (1994). Vocal Determinants of 1st Impressions of Young-Children. *Journal of Nonverbal Behavior, 18*(3), 187-197.

Boersma, P., & Weenink, D. (2001). Praat. http://www.praat.org: Summer Institute of Linguistics.

Booth, A., Johnson, D. R., & Granger, D. A. (1999). Testosterone and men's health. *Journal of Behavioral Medicine, 22*(1), 1-19.

Boothroyd, L. G., Jones, B. C., Burt, D. M., Cornwell, R. E., Little, A. C., Tiddeman, B. P., et al. (2005). Facial masculinity is related to perceived age but not perceived health. *Evolution and Human Behavior, 26*(5), 417-431.

Buchanan, T. (2000). Internet research: self-monitering and judgements of attractiveness. *Behavior Research Methods Instruments and Computers, 32*, 521-527.

Burg, V. D. (1958). Myoelastic-aerodynamic theory of voice production. *Journal of Speech and Hearing Research, 1*, 227-244.

Burnham, T. C., Chapman, J. F., Gray, P. B., McIntyre, M. H., Lipson, S. F., & Ellison, P. T. (2003). Men in committed, romantic relationships have lower testosterone. *Hormones and Behavior, 44*(2), 119-122.

Burton, A. M., & Bonner, L. (2004). Familiarity influences judgments of sex: The case of voice recognition. *Perception, 33*(6), 747-752.

Burton, L. A., Henninger, D., & Hafetz, J. (2005). Gender differences in relations of mental rotation, verbal fluency, and SAT scores to finger length ratios as hormonal indexes. *Developmental Neuropsychology, 28*(1), 493-+.

Buss, D. M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioural and Brain Sciences, 12*, 1-49.

Campos, L. D., Otta, E., & Siqueira, J. D. (2002). Sex differences in mate selection strategies: Content analyses and responses to personal advertisements in Brazil. *Evolution and Human Behavior, 23*(5), 395-406.

Candolin, U. (2003). The use of multiple cues in mate choice. *Biological Reviews, 78*(4), 575-595.

Cartwright, J. (2000). *Evolution and human behavior: Darwinian perspectives on human nature*. Cambridge: MIT Press.

Chae, S. W., Choi, G., Kang, H. J., Choi, J. O., & Jin, S. M. (2001). Clinical analysis of voice change as a parameter of premenstrual syndrome. *Journal of Voice, 15*(2), 278-283.

Chaffkin, L. M., Luciano, A. A., & Peluso, J. J. (1993). The Role of Progesterone in Regulating Human Granulosa-Cell Proliferation and Differentiation Invitro. *Journal of Clinical Endocrinology and Metabolism, 76*(3), 696-700.

Chatterjee, S., & Das, N. (1995). Physical and Motor Fitness in Twins. *Japanese Journal of Physiology, 45*(3), 519-534.

Chen, C. C. G., & Parker, C. R. (2004). Adrenal androgens and the immune system. *Seminars in Reproductive Medicine, 22*(4), 369-377.

Childers, D., & Wu, K. (1991). Gender recognition from speech. Part II: Fine analysis. *Journal of the Acoustic Society of America, 90*, 1841-1857.

Collins, S., & Missing, C. (2003). Vocal and visual attractiveness are related in women. *Animal Behaviour, 6*, 997-1004.

Collins, S. A. (2000). Men's voices and women's choices. *Animal Behaviour, 60*, 773-780.
Collins, S. A., & Missing, C. (2003). Vocal and visual attractiveness are related in women. *Animal Behaviour, 65*, 997-1004.
Cornwell, R. E., Boothroyd, L., Burt, D. M., Feinberg, D. R., Jones, B. C., Little, A. C., et al. (2004). Concordant preferences for opposite-sex signals? Human pheromones and facial characteristics. *Proceedings of the Royal Society of London Series B-Biological Sciences, 271*(1539), 635-640.
Creel, S. (2001). Social dominance and stress hormones. *Trends in Ecology & Evolution, 16*(9), 491-497.
Csizmadi, I., Collet, J. P., Benedetti, A., Boivin, J. F., & Hanley, J. A. (2004). The effects of transdermal and oral oestrogen replacement therapy on colorectal cancer risk in postmenopausal women. *British Journal of Cancer, 90*(1), 76-81.
Dabbs, J. M., Jr. (1990). Salivary testosterone measurements: Reliability across hours, days, and weeks. *Physiology and Behavior, 48*(1), 83-86.
Dabbs, J. M., & Mallinger, A. (1999). High testosterone levels predict low voice pitch among men. *Personality and Individual Differences, 27*(4), 801-804.
Daly, M., & Wilson, M. (2001). Risk-taking, intrasexual competition, and homicide. *Nebraska Symposioum on Motivation, 47*, 1-36.
Darwin, C. (1871). *The descent of man, and selection in relation to sex*. Princeton: Princeton University Press.
de La Rochebrochard, E., & Thonneau, P. (2002). Paternal age and maternal age are risk factors for miscarriage; results of a multicentre European study. *Human Reproduction, 17*(6), 1649-1656.
Debruyne, F., Decoster, W., Van Gijsel, A., & Vercammen, J. (2002). Speaking fundamental frequency in monozygotic and dizygotic twins. *Journal of Voice, 16*(4), 466-471.
Deffenbacher, K. A., Johanson, J., & O'Toole, A. J. (1998). Facial aging, attractiveness, and distinctiveness. *Perception, 27*(10), 1233-1243.
Dickey, R. P., Olar, T. T., Taylor, S. N., Curole, D. N., & Matulich, E. M. (1993). Relationship of Endometrial Thickness and Pattern to Fecundity in Ovulation Induction Cycles - Effect of Clomiphene Citrate Alone and with Human Menopausal Gonadotropin. *Fertility and Sterility, 59*(4), 756-760.
Diver, M. J., Imtiaz, K. E., Ahmad, A. M., Vora, J. P., & Fraser, W. D. (2003). Diurnal rhythms of serum total, free and bioavailable testosterone and of SHBG in middle-aged men compared with those in young men. *Clinical Endocrinology, 58*(6), 710-717.
Drew, S. V. (2001). Oestrogen replacement therapy and ovarian cancer. *Lancet, 358*(9296), 1910-1910.
Eissa, M. K., Obhrai, M. S., Docker, M. F., Lynch, S. S., Sawers, R. S., & Newton, J. R. (1986). Follicular-Growth and Endocrine Profiles in Spontaneous and Induced Conception Cycles. *Fertility and Sterility, 45*(2), 191-195.
Enlow, D. H., & Moyers, R. E. (1971). Growth and architecture of face. *Journal of the American Dental Association, 82*(4), 763.
Fecteau, S., Armony, J. L., Joanette, Y., & Belin, P. (2005). Sensitivity to voice in human prefrontal cortex. *Journal of Neurophysiology, 94*(3), 2251-2254.

Feinberg, D. R., & Jacobson, A. S. (June 2001). *Human mate choice and female preferences for male voices: correlation with symmetry and sexual behavior.* Paper presented at the 13th Human Behaviour and Evolution Society (HBES) Conference, London , England , UK.

Fessler, D. M. T. (2003). No time to eat: An adaptationist account of periovulatory behavioral changes. *The Quarterly Review of Biology, 78*(1), 3-21.

Fessler, D. M. T., & Navarrete, C. D. (2003). Domain-specific variation in disgust sensitivity across the menstrual cycle. *Evolution and Human Behavior, 24*, 406-417.

Fink, B., Grammer, K., & Thornhill, R. (2001). Human (*Homo sapiens*) Facial Attractiveness in Relation to Skin Texture and Color. *Journal of Comparative Psychology, 115*(1), 92-99.

Fink, B., & Penton-Voak, I. (2002). Evolutionary psychology of facial attractiveness. *Current Directions in Psychological Science, 11*(5), 154-158.

Firman, R. C., Simmons, L. W., Cummins, J. M., & Matson, P. L. (2003). Are body fluctuating asymmetry and the ratio of 2nd to 4th digit length reliable predictors of semen quality? *Human Reproduction, 18*(4), 808-812.

Fisher, M. L. (2004). Female intrasexual competition decreases female facial attractiveness. *Proceedings of the Royal Society of London Series B-Biological Sciences, 271*, S283-S285.

Fisher, R. A. (1930). *The Genetical Theory of Sexual Selection*. New York: Oxford University Press Inc.

Fitch, W. T. (1994). *Vocal tract length and the evolution of language.* Brown University.

Fitch, W. T. (1997). Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *Journal of the Acoustical Society of America, 102*(2), 1213-1222.

Fitch, W. T. (2000a). The evolution of speech: a comparative review. *Trends in Cognitive Sciences, 4*(7), 258-267.

Fitch, W. T. (2000b). The phonetic potential of nonhuman vocal tracts: Comparative cineradiographic observations of vocalizing animals. *Phonetica, 57*(2-4), 205-218.

Fitch, W. T., & Giedd, J. (1999). Morphology and development of the human vocal tract: A study using magnetic resonance imaging. *Journal of the Acoustical Society of America, 106*(3), 1511-1522.

Fitch, W. T., & Hauser, M. D. (1995). Vocal production in nonhuman primates: acoustics, physiology and functional constraints on "Honest" advertising. *American Journal of Primatology, 37*, 191-219.

Fitch, W. T., & Hauser, M. D. (2002). Unpacking "Honesty": Vertebrate Vocal Production and the Evolution of Acoustic Signals. In A. M. Simmons, R. F. Fay & A. N. Popper (Eds.), *Acoustic Communication* (pp. 65-137). New York: Springer.

Fitch, W. T., Neubauer, J., & Herzel, H. (2002). Calls out of chaos: the adaptive significance of nonlinear phenomena in mammalian vocal production. *Animal Behaviour, 63*, 407-418.

Fitch, W. T., & Reby, D. (2001). The descended larynx is not uniquely human. *Proceedings of the Royal Society of London Series B-Biological Sciences, 268*(1477), 1669-1675.
Folstad, I., & Karter, A. (1992). Parasites, bright males, and the immunocompetence handicap. *American Naturalist, 139*, 603-623.
Frost, P. (1988). Human skin color: A possible relationship between its sexual dimorphism and its social perception. *Perspectives in Biology and Medicine, 32*(38-58).
Furlow, F. B., Armijo-Prewitt, T., Gangestad, S. W., & Thornhill, R. (1997). Fluctuating asymmetry and psychometric intelligence. *Proceedings of the Royal Society, 264*, 823-829.
Gangestad, S. W., Simpson, J. A., Cousins, A. J., Garver-Apgar, C. E., & Christensen, P. N. (2004). Women's preferences for male behavioral displays change across the menstrual cycle. *Psychological Science, 15*(3), 203-207.
Gangestad, S. W., & Thornhill, R. (1997). The evolutionary psychology of extrapair sex: The role of fluctuating asymmetry. *Evolution and Human Behavior, 18*, 69-88.
Gangestad, S. W., & Thornhill, R. (2003). Facial masculinity and fluctuating asymmetry. *Evolution and Human Behavior, 24*(4), 231-241.
Gangestad, S. W., Thornhill, R., & Yeo, R. A. (1994). Facial attractiveness, developmental stability, and fluctuating asymmetry. *Ethology and Sociobiology, 15*, 73-85.
Getty, T. (2002). Signaling health versus parasites. *American Naturalist, 159*(4), 363-371.
Gonzalez, J. (2004). Formant frequencies and body size of speaker: a weak relationship in adult humans. *Journal of Phonetics, 32*(2), 277-287.
Gray, H. (1918). *Anatomy of the human body* (20 ed.). Philadelphia: Lea & Febiger.
Gray, P. B. (2003). Marriage, parenting, and testosterone variation among Kenyan Swahili men. *American Journal of Physical Anthropology, 122*(3), 279-286.
Gray, P. B., Chapman, J. F., Burnham, T. C., McIntyre, M. H., Lipson, S. F., & Ellison, P. T. (2004). Human male pair bonding and testosterone. *Human Nature-an Interdisciplinary Biosocial Perspective, 15*(2), 119-131.
Gray, P. B., Kahlenberg, S. M., Barrett, E. S., Lipson, S. F., & Ellison, P. T. (2002). Marriage and fatherhood are associated with lower testosterone in males. *Evolution and Human Behavior, 23*(3), 193-201.
Greenlees, I. A., & McGrew, W. C. (1994). Sex and Age-Differences in Preferences and Tactics of Mate Attraction - Analysis of Published Advertisements. *Ethology and Sociobiology, 15*(2), 59-72.
Greenwood, D. D. (1997). The mel scale's disqualifying bias and a consistency of pitch-difference equisections in 1956 with equal cholear distances and equal freqeuncy ratios. *Hearing Research, 103*, 199-224.
Gregory, S. W. (1990). Analysis of Fundamental-Frequency Reveals Covariation in Interview Partners Speech. *Journal of Nonverbal Behavior, 14*(4), 237-251.
Gregory, S. W. (1994). Sounds of Power and Deference - Acoustic Analysis of Macro Social Constraints on Micro-Interaction. *Sociological Perspectives, 37*(4), 497-526.

Gregory, S. W., Dagan, K., & Webster, S. (1997). Evaluating the relation of vocal accommodation in conversation partners' fundamental frequencies to perceptions of communication quality. *Journal of Nonverbal Behavior, 21*(1), 23-43.

Gregory, S. W., & Webster, S. (1996). A nonverbal signal in voices of interview partners effectively predicts communication accommodation and social status perceptions. *Journal of Personality and Social Psychology, 70*(6), 1231-1240.

Grimes, D. A., Gallo, M. F., Grigorieva, V., Nanda, K., & Schulz, K. F. (2005). Steroid hormones for contraception in men: systematic review of randomized controlled trials. *Contraception, 71*(2), 89-94.

Halberstadt, J., & Rhodes, G. (2000). The attractiveness of nonface averages: Implications for an evolutionary explanation of the attractiveness of average faces. *Psychological Science, 11*(4), 285-289.

Halberstadt, J., & Rhodes, G. (2003). It's not just average faces that are attractive: Computer- manipulated averageness makes birds, fish, and automobiles attractive. *Psychonomic Bulletin & Review, 10*(1), 149-156.

Hamilton, W. D., & Zuk, M. (1982). Heritable true fitness and bright birds: a role for parasites? *Science, 218*, 384-387.

Hanson, H. M., & Chuang, E. S. (1999). Glottal characteristics of male speakers: Acoustic correlates and comparison with female data. *Journal of the Acoustical Society of America, 106*(2), 1064-1077.

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. *Journal of Laryngology and Otology, 112*(5), 451-454.

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.

Harris, J. A., Vernon, P. A., & Boomsma, D. I. (1998). The heritability of testosterone: A study of Dutch adolescent twins and their parents. *Behavior Genetics, 28*(3), 165-171.

Hauser, M. D. (1993). The Evolution of Nonhuman Primate Vocalizations - Effects of Phylogeny, Body-Weight, and Social-Context. *American Naturalist, 142*(3), 528-542.

Hauser, M. D. (1996). *The Evolution of Communication*. Cambridge, Massachusites: Massichusites Institute of Technology Press.

Hertrich, I., & Ackermann, H. (1995). Gender-Specific Vocal Dysfunctions in Parkinsons-Disease - Electroglottographic and Acoustic Analyses. *Annals of Otology Rhinology and Laryngology, 104*(3), 197-202.

Hertrich, I., Lutzenberger, W., Spieker, S., & Ackermann, H. (1997). Fractal dimension of sustained vowel productions in neurological dysphonias: An acoustic and electroglottographic analysis. *Journal of the Acoustical Society of America, 102*(1), 652-654.

Hiort, O. (2002). Androgens and puberty. *Best Practice & Research Clinical Endocrinology & Metabolism, 16*(1), 31-41.

Hooven, C. K., Chabris, C. F., Ellison, P. T., & Kosslyn, S. M. (2004). The relationship of male testosterone to components of mental rotation. *Neuropsychologia, 42*(6), 782-790.

Hosoda, M., Stone-Romero, E. F., & Coats, G. (2003). The effects of physical attractiveness on job-related outcomes: A meta-analysis of experimental studies. *Personnel Psychology, 56*(2), 431-462.

Huber, J. E., Stathopoulos, E. T., Curione, G. M., Ash, T. A., & Johnson, K. (1999). Formants of children, women, and men: The effects of vocal intensity variation. *Journal of the Acoustic Society of America, 106*(3), 1532-1542.

Hughes, S. M., Dispenza, F., & Gallup, G. G. (2004). Ratings of voice attractiveness predict sexual behavior and body configuration. *Evolution and Human Behavior, 25*(5), 295-304.

Hughes, S. M., & Gallup, G. G. (2003). Sex differences in morphological predictors of sexual behavior - Shoulder to hip and waist to hip ratios. *Evolution and Human Behavior, 24*(3), 173-178.

Hughes, S. M., Harrison, M. A., & Gallup, G. G. (2002). The sound of symmetry. Voice as a marker of developmental instability. *Evolution and Human Behavior, 23*, 173-180.

Ice, G. H., Katz-Stein, A., Himes, J., & Kane, R. L. (2004). Diurnal cycles of salivary cortisol in older adults. *Psychoneuroendocrinology, 29*(3), 355-370.

Jasienska, G., Ziomkiewicz, A., Ellison, P. T., Lipson, S. F., & Thune, I. (2004). Large breast and narrow waist indicate high reproductive potential in women. *Proceedings of the Royal Society of London Series B-Biological Sciences, 271*, 1213-1217.

Johnston, V. S., Hagel, R., Franklin, M., Fink., B., & Grammer, K. (2001). Male facial attractiveness: Evidence for a hormone-mediated adaptive design. *Evolution and Human Behavior, 22*, 251-267.

Jones, B. C., Little, A. C., Boothroyd, L., DeBruine, L. M., Feinberg, D. R., Smith, M. J. L., et al. (2005). Commitment to relationships and preferences for femininity and apparent health in faces are strongest on days of the menstrual cycle when progesterone level is high. *Hormones and Behavior, 48*(3), 283-290.

Jones, B. C., Little, A. C., Boothroyd, L., Feinberg, D. R., Cornwell, R. E., DeBruine, L. M., et al. (In Press). Women's physical and psychological condition independently predict their preference for apparent health in faces. *Evolution and Human Behavior.*

Jones, B. C., Little, A. C., Burt, D. M., & Perrett, D. I. (2004). When facial attractiveness is only skin deep. *Perception, 33*(5), 569-576.

Jones, B. C., Little, A. C., Feinberg, D. R., Tiddeman, B. P., Penton-Voak, I. S., & Perrett, D. I. (2004). The relationship between shape symmetry and visible skin condition in male facial attractiveness. *Evolution and Human Behavior, 25*, 24-30.

Jones, B. C., Little, A. C., Penton-Voak, I. S., Tiddeman, B. P., Burt, D. M., & Perrett, D. I. (2001). Facial symmetry and judgements of apparent health. Support for a "good genes" explanation of the attractiveness - symmetry relationship. *Evolution and Human Behavior, 22*, 417-429.

Jones, B. C., Perrett, D. I., Little, A. C., Boothroyd, L., Cornwell, R. E., Feinberg, D. R., et al. (2005). Menstrual cycle, pregnancy and oral contraceptive use alter attraction to apparent health in faces. *Proceedings Of The Royal Society Of London Series B-Biological Sciences, 272*(1561), 347-354.

Jones, D. (1995). Sexual Selection, Physical Attractiveness, and Facial Neoteny - Cross-Cultural Evidence and Implications. *Current Anthropology, 36*(5), 723-748.

Judge, T. A., & Cable, D. M. (2004). The effect of physical height on workplace success and income: Preliminary test of a theoretical model. *Journal of Applied Psychology, 89*(3), 428-441.

Kahane, J. C. (1978). Morphological-Study of Human Prepubertal and Pubertal Larynx. *American Journal of Anatomy, 151*(1), 11-19.

Kahane, J. C. (1982). Growth of the Human Prepubertal and Pubertal Larynx. *Journal of Speech and Hearing Research, 25*(3), 446-455.

Kenrick, D. T., & Keefe, R. C. (1992). Age Preferences in Mates Reflect Sex-Differences in Reproductive Strategies. *Behavioral and Brain Sciences, 15*(1), 75-&.

Kersing, W., Dejonckere, P. H., van der Aa, H. E., & Buschman, H. P. J. (2002). Laryngeal and vocal changes during vagus nerve stimulation in epileptic patients. *Journal of Voice, 16*(2), 251-257.

Kokko, H., & Jennions, M. (2003). It takes two to tango. *Trends in Ecology & Evolution, 18*(3), 103-104.

Kotby, M., Titze, I., & Saleh, M. (1991). Perturbation measures in different types of dysphonia. *Folia Phoniatrica, 44*(1-2), 40-41.

Koziel, S., & Pawlowski, B. (2003). Comparison between primary and secondary mate markets: an analysis of data from lonely hearts columns. *Personality and Individual Differences, 35*(8), 1849-1857.

Kraut, R., Olson, J., Banaji, M., Bruckman, A., Cohen, J., & Couper, M. (2004). Psychological research online - Report of board of scientific affairs advisory group on the conduct of research on the Internet. *American Psychologist, 59*, 105-117.

Ku, J. H., Kim, M. E., Jeon, Y. S., Lee, N. K., & Park, Y. H. (2002). Factors influencing testicular volume in young men: results of a community-based survey. *Bju International, 90*(4), 446-450.

Kvarnemo, C., & Ahnesjö, I. (1996). The dynamics of operational sex ratios and competition for mates. *Trends in Ecology & Evolution, 11*(10), 404-408.

Ladefoged, P. (1996). *Elements of Acoustic Phonetics* (2nd ed.). Chicago: University of Chicago Press.

Langlois, J. H., & Roggman, L. A. (1990). Attractive Faces Are Only Average. *Psychological Science, 1*(2), 115-121.

Lass, N., & Brown, W. (1978). Correlational study of speakers' heights, weights, body surface areas, and speaking fundamental frequencies. *Journal of the Acoustic Society of America, 63*, 1218-1220.

Law Smith, M. J., Perrett, D. I., Jones, B. C., Cornwell, R. E., Moore, F. R., Feinberg, D. R., et al. (In Press). Facial appearance signals reproductive hormonal levels in adult females. *Proceedings of the Royal Society of London, Series B*.

Law Smith, M. J., Stirrat, M. R., Coetzee, V., Jones, B. C., Cornwell, R. E., Feinberg, D. R., et al. (In Prep). Reproductive and stress hormones, apparent health and human face colour.

Linders, B., Massa, G., Boersma, B., & Dejonckere, P. (1995). Fundamental voice frequency and jitter in girls and boys measured with electroglottography:

influence of age and height. *International Journal or Pediatric Otorhinolaryngology, 33*, 61-65.

Linville, S. E. (1985). Acoustic characteristics of perceived versus actual vocal age in controlled phonation by adult females.

Lipson, S., & Ellison, P. (1996). Comparison of salivary steroid profiles in naturally occurring conception and non-conception cycles. *Hum. Reprod., 11*(10), 2090-2096.

Little, A. C., Burt, D. M., Penton-Voak, I. S., & Perrett, D. I. (2001). Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. *Proceedings of the Royal Society of London Series B-Biological Sciences, 268*(1462), 39-44.

Little, A. C., & Hancock, P. J. B. (2002). The role of masculinity and distinctiveness in judgments of human male facial attractiveness. *British Journal of Psychology, 93*, 451-464.

Little, A. C., & Jones, B. C. (2003). Evidence against perceptual bias views for symmetry preferences in human faces. *Proceedings of the Royal Society of London Series B-Biological Sciences, 270*(1526), 1759-1763.

Little, A. C., Jones, B. C., Penton-Voak, I. S., Burt, D. M., & Perrett, D. I. (2002a). Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape. *Proceedings of the Royal Society of London Series B-Biological Sciences, 269*(1496), 1095-1100.

Little, A. C., Penton-Voak, I. S., Burt, D. M., & Perrett, D. I. (2003). Investigating an imprinting-like phenomenon in humans Partners and opposite-sex parents have similar hair and eye colour. *Evolution and Human Behavior, 24*(1), 43-51.

Lopez, S. (1999). Parasitized female guppies do not prefer showy males. *Animal Behaviour, 57*, 1129-1134.

Low, B. (2000). *Why Sex Matters: A Darwinian Look at Human Behavior*. Princeton: Princeton University Press.

Lutchmaya, S., Baron-Cohen, S., Raggatt, P., Knickmeyer, R., & Manning, J. T. (2004). 2nd to 4th digit ratios, fetal testosterone and estradiol. *Early Human Development, 77*(1-2), 23-28.

Ly, L. P., Liu, P. Y., & Handelsman, D. J. (2005). Rates of suppression and recovery of human sperm output in testosterone-based hormonal contraceptive regimens. *Human Reproduction, 20*(6), 1733-1740.

Magrath, M. J. L., & Komdeur, J. (2003). Is male care compromised by additional mating opportunity? *Trends in Ecology & Evolution, 18*(8), 424-430.

Maisey, D., Vale, E., Cornelissen, P., & Tovée, M. (1999). Characteristics of male attractiveness for women. *The Lancet, 353*(9163), 1500.

Manning, J. T., Brundred, P. E., & Flanagan, B. F. (2002). The ratio of 2nd to 4th digit length: A proxy for transactivation activity of the androgen receptor gene? *Medical Hypotheses, 59*, 334-336.

Manning, J. T., Bundred, P. E., Newton, D. J., & Flanagan, B. F. (2003). The second to fourth digit ratio and variation in the androgen receptor gene. *Evolution and Human Behavior, 24*, 399-405.

Manning, J. T., Trivers, R. L., Singh, D., & Thornhill, R. (1999). The mystery of female beauty. *Nature, 399*(6733), 214-215.

Manning, J. T., Wood, S., Vang, E., Walton, J., Bundred, P. E., van Heyningen, C., et al. (2004). Second to fourth digit ratio (2D : 4D) and testosterone in men. *Asian Journal of Andrology, 6*(3), 211-215.

Mazur, A., & Booth, A. (1998). Testosterone and dominance in men. *Behavioral and Brain Sciences, 21*, 353-397.

Mazur, A., & Mueller, U. (1996). Channel modeling: From West Point cadet to general. *Public Administration Review, 56*(2), 191-198.

McComb, K. E. (1991). Female choice for high roaring rates in red deer, Cervus-Elaphus. *Animal Behaviour, 41*, 79-88.

Moran, C., Hernandez, E., Ruiz, J. E., Fonseca, M. E., Bermudez, J. A., & Zarate, A. (1999). Upper body obesity and hyperinsulinemia are associated with anovulation. *Gynecologic and Obstetric Investigation, 47*(1), 1-5.

Mueller, U., & Mazur, A. (1996). Facial dominance of West Point cadets as a predictor of later military rank. *Social Forces, 74*(3), 823-850.

Mueller, U., & Mazur, A. (1997). Facial dominance in Homo sapiens as honest signaling of male quality. *Behavioral Ecology, 8*(5), 569-579.

Mueller, U., & Mazur, A. (2001). Evidence of unconstrained directional selection for male tallness. *Behavioral Ecology and Sociobiology, 50*(4), 302-311.

Nettle, D. (2002a). Height and reproductive success in a cohort of British men. *Human Nature-an Interdisciplinary Biosocial Perspective, 13*(4), 473-491.

Nettle, D. (2002b). Women's height, reproductive success and the evolution of sexual dimorphism in modern humans. *Proceedings of the Royal Society of London, Series B, 269*, 1919-1923.

Newman, M. L., Sellers, J. G., & Josephs, R. A. (2005). Testosterone, cognition, and social status. *Hormones and Behavior, 47*(2), 205-211.

Newman, S. R., Butler, J., Hammond, E. H., & Gray, S. D. (2000). Preliminary report on hormone receptors in the human vocal fold. *Journal of Voice, 14*(1), 72-81.

Notelovitz, M. (2002). Androgen effects on bone and muscle. *Fertility and Sterility, 77*(4), S34-S41.

Oates, K., & Wilson, M. (2002). Nominal kinship cues facilitate altruism. *Proceedings of the Royal Society of London Series B-Biological Sciences, 269*(1487), 105-109.

O'Carroll, R. E. (1998). Placebo-controlled manipulations of testosterone levels and dominance. *Behavioral and Brain Sciences, 21*(3), 382-+.

O'Connor, D. B., Archer, J., Hair, W. M., & Wu, F. C. W. (2001). Effects of exogenous testosterone (T) on self-reported and partner-reported aggression in men. *Aggressive Behavior, 27*(3), 220-221.

O'Connor, D. B., Archer, J., & Wu, F. C. W. (2004). Effects of testosterone on mood, aggression, and sexual behavior in young men: A double-blind, placebo-controlled, cross-over study. *Journal of Clinical Endocrinology and Metabolism, 89*(6), 2837-2845.

O'Connor, D. B., Archer, J., & Wu, F. W. C. (2001). Measuring aggression: Self-reports, partner reports, and responses to provoking scenarios. *Aggressive Behavior, 27*(2), 79-101.

O'Doherty, J., Winston, J., Critchley, H., Perrett, D., Burt, D. M., & Dolan, R. J. (2003). Beauty in a smile: the role of medial orbitofrontal cortex in facial attractiveness. *Neuropsychologia, 41*(2), 147-155.

Ohala, J. J. (1983). Cross-Language Use of Pitch - an Ethological View. *Phonetica, 40*(1), 1-18.

Ohala, J. J. (1984). An Ethological Perspective on Common Cross-Language Utilization of F0 of Voice. *Phonetica, 41*(1), 1-16.

O'Toole, A. J., Deffenbacher, K. A., Valentin, D., McKee, K., Huff, D., & Abdi, H. (1998). The perception of face gender: The role of stimulus structure in recognition and classification. *Memory & Cognition, 26*(1), 146-160.

O'Toole, A. J., Price, T., Vetter, T., Bartlett, J. C., & Blanz, V. (1999). 3D shape and 2D surface textures of human faces: the role of "averages" in attractiveness and age. *Image and Vision Computing, 18*(1), 9-19.

Otta, E., Abrosio, F. F. E., & Hoshino, R. L. (1996). Reading a smiling face: Messages conveyed by various forms of smiling. *Perceptual and Motor Skills, 82*(3), 1111-1121.

Parsa, V., & Jamieson, D. (2000). Identification of pathological voices using glottal noise measures. *Journal of Speech, Language, and Hearing Research, 43*, 469-485.

Pawlowski, B. (2003). Variable preferences for sexual dimorphism in height as a strategy for increasing the pool of potential partners in humans. *Proceedings of the Royal Society of London Series B-Biological Sciences, 270*(1516), 709-712.

Pawlowski, B., & Dunbar, R. I. M. (1999). Impact of market value on human mate choice decisions. *Proceedings of the Royal Society of London Series B-Biological Sciences, 266*(1416), 281-285.

Pawlowski, B., Dunbar, R. I. M., & Lipowicz, A. (2000). Evolutionary fitness - Tall men have more reproductive success. *Nature, 403*(6766), 156-156.

Pawlowski, B., & Jasienska, G. (2005). Women's preferences for sexual dimorphism in height depend on menstrual cycle phase and expected duration of relationship. *Biological Psychology, 70*(1), 38-43.

Pawlowski, B., & Koziel, S. (2002). The impact of traits offered in personal advertisements on response rates. *Evolution and Human Behavior, 23*(2), 139-149.

Penton-Voak, I., & Perrett, D. I. (2000). Consistency and individual differences in facial attractiveness judgements: An evolutionary perspective. *Social Research, 67*(1), 219-244.

Penton-Voak, I. S., & Chen, J. Y. (2004). High salivary testosterone is linked to masculine male facial appearance in humans. *Evolution and Human Behavior, 25*, 229-241.

Penton-Voak, I. S., Jacobson, A., & Trivers, R. (2004). Populational differences in attractiveness judgements of male and female faces: Comparing British and Jamaican samples. *Evolution and Human Behavior, 25*(6), 355-370.

Penton-Voak, I. S., Jones, B. C., Little, A. C., Baker, S., Tiddeman, B., Burt, D. M., et al. (2001). Symmetry, sexual dimorphism in facial proportions and male facial attractiveness. *Proceedings of the Royal Society of London Series B-Biological Sciences, 268*, 1617-1623.

Penton-Voak, I. S., Little, A. C., Jones, B. C., Burt, D. M., Tiddeman, B. P., & Perrett, D. I. (2003). Female condition influences preferences for sexual dimorphism in faces of male humans (Homo sapiens). *Journal of Comparative Psychology, 117*(3), 264-271.

Penton-Voak, I. S., & Perrett, D. I. (2000a). Consistency and individual differences in facial attractiveness judgements: an evolutionary perspective. *Social Research, 67*, 219-245.

Penton-Voak, I. S., & Perrett, D. I. (2000b). Female preference for male faces changes cyclically: Further evidence. *Evolution and Human Behavior, 21*(1), 39-48.

Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K., et al. (1999). Menstrual cycle alters face preference. *Nature, 399*(6738), 741-742.

Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K., Rowland, D., & Edwards, R. (1999). Symmetry and human facial attractiveness. *Evolution and Human Behavior, 20*, 295-307.

Perrett, D. I., Hietanen, J. K., Oram, M. W., & Benson, P. J. (1992). Organization and Functions of Cells Responsive to Faces in the Temporal Cortex. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences, 335*(1273), 23-30.

Perrett, D. I., Lee, K. J., Penton-Voak, I., Rowland, D., Yoshikawa, S., Burt, D. M., et al. (1998). Effects of sexual dimorphism on facial attractiveness. *Nature, 394*, 884-887.

Perrett, D. I., May, K. A., & Yoshikawa, S. (1994). Facial shape and judgements of female attractiveness. *Nature, 368*, 239-242.

Petrie, M. (1994). Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature, 371*(6498), 598-599.

Pinto, N. B., & Titze, I. R. (1990). Unification of Perturbation Measures in Speech Signals. *Journal of the Acoustical Society of America, 87*(3), 1278-1289.

Price, T., Schluter, D., & Heckman, N. E. (1993). Sexual Selection When the Female Directly Benefits. *Biological Journal of the Linnean Society, 48*(3), 187-211.

Puts, D. A. (2005). Mating context and menstrual phase affect women's preferences for male voice pitch. *Evolution and Human Behavior, 26*(5), 388-397.

Putz, D. A., Gaulin, S. J. C., Sporter, R. J., & McBurney, D. H. (2004). Sex hormones and finger length - What does 2D : 4D indicate? *Evolution and Human Behavior, 25*(3), 182-199.

Ramig, L., Scherer, R., & Titze, I. (1984). Acoustic correlates of aging. *Journal of the Acoustical Society of America, 76*(S1), S59.

Reby, D., & McComb, K. (2003). Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Animal Behaviour, 65*, 519-530.

Reby, D., McComb, K., Cargnelutti, B., Darwin, C., Fitch, W. T., & Clutton-Brock, T. (2005). Red deer stags use formants as assessment cues during intrasexual agonistic interactions. *Proceedings of the Royal Society B-Biological Sciences, 272*(1566), 941-947.

Rendall, D., Kollias, S., Ney, C., & Lloyd, P. (2005). Pitch (F-0) and formant profiles of human vowels and vowel-like baboon grunts: The role of vocalizer body size and voice-acoustic allometry. *Journal of the Acoustical Society of America, 117*(2), 944-955.

Repp, B. H. (1997). The aesthetic quality of a quantitatively average music performance: Two preliminary experiments. *Music Perception, 14*(4), 419-444.

Rhodes, G., Chan, J., Zebrowitz, L. A., & Simmons, L. W. (2003). Does sexual dimorphism in human faces signal health? *Proceedings of the Royal Society of London Series B-Biological Sciences, 270*, S93-S95.

Rhodes, G., Hickford, C., & Jeffery, L. (2000). Sex-typicality and attractiveness: Are supermale and superfemale faces super-attractive? *British Journal of Psychology, 91*(1), 125-140.

Riede, T., & Fitch, T. (1999). Vocal tract length and acoustics of vocalization in the domestic dog (Canis familiaris). *Journal of Experimental Biology, 202*(20), 2859-2867.

Rikowski, A., & Grammer, K. (1999). Human body odour, symmetry and attractiveness. *Proceedings of the Royal Society of London Series B-Biological Sciences, 266*, 869-874.

Roberts, M. L., Buchanan, K. L., & Evans, M. R. (2004). Testing the immunocompetence handicap hypothesis: a review of the evidence. *Animal Behaviour, 68*, 227-239.

Roberts, S. C., Havlicek, J., Flegr, J., Hruskova, M., Little, A. C., Jones, B. C., et al. (2004). Female facial attractiveness increases during the fertile phase of the menstrual cycle. *Proceedings of the Royal Society of London Series B-Biological Sciences, 271*, S270-S272.

Roberts, S. C., Little, A. C., Gosling, L. M., Perrett, D. I., Carter, V., Jones, B. C., et al. (2003). *Human facial attractiveness and MHC.* Paper presented at the Human Behavior and Evolution Society Annual Meeting, University of Nebraska-Lincoln, Lincoln, Nebraska, USA.

Robles, L., & Ruggero, M. A. (2001). Mechanics of the Mammalian Cochlea. *Physiol. Rev., 81*(3), 1305-1352.

Roumen, F., Doesburg, W. H., & Rolland, R. (1982). Hormonal Patterns in Infertile Women with a Deficient Post- Coital Test. *Fertility and Sterility, 38*(1), 42-47.

Ruscio, M. G., & Adkins-Regan, E. (2003). Effect of female brooding behaviour on male mate choice in Japanese quail, Coturnix japonica. *Animal Behaviour, 65*, 397-403.

Salvador, A. (2005). Coping with competitive situations in humans. *Neuroscience and Biobehavioral Reviews, 29*(1), 195-205.

Santoro, N., Goldsmith, L. T., Heller, D., Illsley, N., McGovern, P., Molina, C., et al. (2000). Luteal progesterone relates to histological endometrial maturation in fertile women. *Journal of Clinical Endocrinology and Metabolism, 85*(11), 4207-4211.

Schaal, B., Tremblay, R. E., Soussignan, R., & Susman, E. J. (1996). Male testosterone linked to high social dominance but low physical aggression in early adolescence. *Journal of the Academy of Child and Adolescent Psychiatry, 35*(10), 1322-1331.

Shackelford, T. K., Weekes-Shackelford, V. A., LeBlanc, G. J., Bleske, A. L., Euler, H. A., & Hoier, S. (2000). Female coital orgasm and male attractiveness. *Human Nature-an Interdisciplinary Biosocial Perspective, 11*(3), 299-306.

Singh, D. (1993). Body shape and women's attractiveness: The critical role of waist-to-hip ratio. *Human Nature, 4*(3), 297-321.

Singh, D. (1995a). Female health, attractiveness, and desirability for relationships: Role of breast asymmetry and waist-to-hip ratio. *Ethology and Sociobiology, 16*(6), 465-481.

Singh, D. (1995b). Female Judgment of Male Attractiveness and Desirability for Relationships - Role of Waist-to-Hip Ratio and Financial Status. *Journal of Personality and Social Psychology, 69*(6), 1089-1101.

Smith, C. A., & Stillman, S. (2002). What do women want? The effects of gender and sexual orientation on the desirability of physical attributes in the personal ads of women. *Sex Roles, 46*(9-10), 337-342.

Smith, D. R. R., Patterson, R. D., Turner, R., Kawahara, H., & Irino, T. (2005). The processing and perception of size information in speech sounds. *Journal of the Acoustic Society of America, 117*(1), 305-318.

Steinberger, E., Rodriguez-Rigau, L. J., Smith, K. D., & Held, B. (1981). The menstrual cycle and plasma testosterone level in women with acne. *Journal of the American Academy of Dermatology, 4*, 54-58.

Stevens, K. (1998). *Acoustic Phonetics*. Cambridge: MIT Press.

Stewart, D. R., Overstreet, J. W., Nakajima, S. T., & Lasley, B. L. (1993). Enhanced Ovarian-Steroid Secretion before Implantation in Early Human-Pregnancy. *Journal of Clinical Endocrinology and Metabolism, 76*(6), 1470-1476.

Strassberg, D. S., & Holty, S. (2003). An experimental study of women's Internet personal ads. *Archives of Sexual Behavior, 32*(3), 253-260.

Studer, L., Aylwin, A., & Reddon, J. (2005). Testosterone, sexual offense recidivism, and treatment effect among adult male sex offenders. *Sexual Abuse-a Journal of Research and Treatment, 17*(2), 171-181.

Swaddle, J. P., & Reierson, G. W. (2002). Testosterone increases perceived dominance but not attractiveness in human males. *Proceedings of the Royal Society of London Series B-Biological Sciences, 269*(1507), 2285-2289.

Tan, U., Okuyan, M., Albayrak, T., & Akgun, A. (2003). Sex differences in verbal and spatial ability reconsidered in relation to body size, lung volume, and sex hormones. *Perceptual and Motor Skills, 96*(3), 1347-1360.

Thornhill, R., & Gangestad, S. W. (1999). Facial attractiveness. *Trends in Cognitive Sciences, 3*(12), 452-460.

Thornhill, R., Gangestad, S. W., & Comer, R. (1995). Human female orgasm and mate fluctuating asymmetry. *Animal Behaviour, 50*, 1601-1615.

Thornhill, R., & Grammer, K. (1999). The body and face of woman: One ornament that signals quality? *Evolution and Human Behavior, 20*(2), 105-120.

Thornhill, R., & Palmer, C. (2001). *A Natural History of Rape: Biological Bases of Sexual Coersion*. Cambridge: MIT Press.

Tiddeman, B. P., Burt, D. M., & Perrett, D. I. (2001). Prototyping and transforming facial texture for perception research. *IEEE Computer Graphics Applications, 21*, 42-50.

Titze, I., & Winholtz, W. (1993). Effect of microphone type and placement on voice perturbation measurements. *Journal of Speech and Hearing Research, 36*(6), 1177-1119.

Titze, I. R. (1994). *Principles of Voice Production*. Englewood Cliffs, New Jersey: Prentice Hall.

Tovée, M. J., Brown, J. E., & Jacobs, D. (2001). Maternal waist-to-hip ratio does not predict child gender. *Proceedings of the Royal Society of London Series B-Biological Sciences, 268*(1471), 1007-1010.

Tovée, M. J., & Cornelissen, P. L. (1999). The mystery of female beauty. *Nature, 399*(6733), 215-216.

Tovée, M. J., & Cornelissen, P. L. (2001). Female and male perceptions of female physical attractiveness in front-view and profile. *British Journal of Psychology, 92*, 391-402.

Traunmüller, H. (1990). Analytical Expressions for the Tonotopic Sensory Scale. *Journal of the Acoustical Society of America, 88*(1), 97-100.

Tremblay, R. E., Schaal, B., Boulerice, B., Arseneault, L., Soussignan, R. G., Paquette, D., et al. (1998). Testosterone, physical aggression, dominance, and physical development in early adolescence. *International Journal of Behavioral Development, 22*(4), 753-777.

Trivers, R. (1985). *Social Evolution*. Menlo Park: The Benjamin/Cummings Publishing Company, Inc.

Trivers, R. L. (1972). Parental investment and reproductive success. In B. Campbell (Ed.), *Sexual Selection and the Descent of Man* (pp. 1871-1971). Chicago: Aldine Publishing Company.

Trivers, R. L., Manning, J. T., Thornhill, R., Singh, D., & McGuire, H. (1999). Jamaican Symmetry Project: Long-term study of fluctuating asymmetry in rural Jamaican children. *Human Biology, 71*(3), 417-430.

Tusing, K. J., & Dillard, J. P. (2000). The sounds of dominance - Vocal precursors of perceived dominance during interpersonal influence. *Human Communication Research, 26*(1), 148-171.

Van Borsel, J., De Cuypere, G., Rubens, R., & Destaerke, B. (2000). Voice problems in female-to-male transsexuals. *International Journal of Language and Communication Disorders, 35*(3), 427-442.

Van den Berghe, P. L., & Frost, P. (1986). Skin color preference, sexual dimorphism and sexual selection: A case of gene-culture co-evolution? *Ethnic and Racial Studies, 9*, 87-88.

Van Roo, B. L. (2004). Exogenous testosterone inhibits several forms of male parental behavior and stimulates song in a monogamous songbird: The blue-headed vireo (Vireo solitarius). *Hormones and Behavior, 46*(5), 678-683.

Van Valen, L. (1962). A study of fluctuating asymmetrty. *Evolution and Human Behavior, 16*, 125-142.

Walpurger, V., Pietrowsky, R., Kirschbaum, C., & Wolf, O. T. (2004). Effects of the menstrual cycle on auditory event-related potentials. *Hormones and Behavior, 46*(5), 600-606.

Wang, X. Q., Lu, T., Snider, R. K., & Liang, L. (2005). Sustained firing in auditory cortex evoked by preferred stimuli. *Nature, 435*(7040), 341-346.

Waynforth, D., & Dunbar, R. I. M. (1995). Conditional Mate Choice Strategies in Humans - Evidence from Lonely Hearts Advertisements. *Behaviour, 132*, 755-779.

Weatherhead, P. J., & Robertson, R. J. (1979). Offspring Quality and the Polygyny Threshold - Sexy Son Hypothesis. *American Naturalist, 113*(2), 201-208.

Wedekind, C., Seebeck, T., Bettens, F., & Paepke, A. J. (1995). MHC - Dependent mate preferences in humans. *Proceedings Of The Royal Society Of London Series B-Biological Sciences, 260*(1359), 245-249.

Wihlback, A. C., Poromaa, I. S., Bixo, M., Allard, P., Mjorndal, T., & Spigset, O. (2004). Influence of menstrual cycle on platelet serotonin uptake site and serotonin(2A) receptor binding. *Psychoneuroendocrinology, 29*(6), 757-766.

Wilson, E. O. (1975). *Sociobiology: The new synthesis*. Cambridge: Harvard University Press.

Wilson, M., & Daly, M. (2004). Do pretty women inspire men to discount the future? *Proceedings of the Royal Society of London Series B-Biological Sciences, 271*, S177-S179.

Wolfe, V., & Martin, D. (1997). Acoustic correlates of dysphonia: types and severity. *Journal of Communication Disorders, 30*, 403-416.

Yu, D. W., & Shepard, G. H. (1999). The mystery of female beauty - Reply. *Nature, 399*(6733), 216-216.

Zaadastra, B. M., Seidell, J. C., Vannoord, P. A. H., Tevelde, E. R., Habbema, J. D. F., Vrieswijk, B., et al. (1993). Fat and female fecundity - Prospective-study of effect of body-fat distribution on conception rates. *British Medical Journal, 306*(6876), 484-487.

Zahavi, A. (1975). Mate selection: A selection for a handicap. *Journal of Theoretical Biology, 53*, 205-214.

Zuckerman, M., & Driver, R. (1989). What sounds beautiful is good: The vocal attractiveness stereotype. *Journal of Nonverbal Behavior, 13*, 67-82.

Zuckerman, M., Miyake, K., & Elkin, C. S. (1995). Effects of Attractiveness and Maturity of Face and Voice on Interpersonal Impressions. *Journal of Research in Personality, 29*(2), 253-272.

Appendix:
Definitions

To avoid misinterpretation of some things I wrote in this thesis, I will define some key terms that might be misinterpreted. The terms I use may not be standard definitions across disciplines, but will give the reader a full understanding as to how these terms are used in this thesis.

Condition – whilst in much animal research, condition means health, Penton-Voak et al. (2003) used the term "condition" to mean mate value, encompassing attractiveness, femininity and health. Therefore, I use condition in the sense that Penton-Voak et al. did. In this thesis, "condition" encompasses health (physical and/or mental), attractiveness and femininity, but I try to be specific about which type of condition I am speaking of.

Dominance –I use *dominance* in terms of behaviour and perception.

> **Dominant behaviour** – "[actions with the] apparent intent to achieve or maintain high status, or to obtain power, influence or valued prerogatives – over a conspecific (Mazur & Booth, 1998, pg. 21).
>
> **Dominance perception** – people often are asked to rate a face or voice in terms of how dominant it looks or sounds. Thus, this perception may or may not relate to dominant behaviour. I try to clarify by stating "Dominant looking.", or "Dominant sounding…"

Femininity & Masculinity – when voices are not explicitly rated for masculinity and femininity, the terms masculinity and femininity are used in this thesis to mean the physical differences between men and women, which are often also differences between pre-pubertal and post-pubertal men. In terms of faces, this could be face shape, colour and/or texture. In terms of voice, I use masculinity and femininity to mean pitch and/or vocal-tract length. This is a standard way of discussing masculinity in the human attractiveness literature (see Perrett et al., 1998; Rhodes et al., 2000; Johnston et al., 2001; Jones et al., 2005; Little et al., 2001;2002;2003; Penton-Voak et al., 1999; Penton-Voak & Perret, 2002; Fink & Penton-Voak, 2002; Gangestad et al., 2003; O'toole, 1998; and many more).

As a convention, I use masculinity/femininity to denote the type of manipulation used, whereas dominance is the attribution given to the voices (or faces). Masculinity can also be attributed to voices (as in chapters 5, 6 & 7). In particular studies where masculinity is not rated, when I use the term masculinity, I am referring to fundamental frequency and/or formant dispersion or the differences between men's and women's faces. Pitch and apparent vocal-tract length manipulations affect perceptions of masculinity, size, age, health, attractiveness and dominance. I do not use the term masculinity as a replacement for these other attributions.

Thus, in chapters 8 & 9, I often have voices that were manipulated in masculinity rated for dominance. I also say in these chapters that hormones predicted attraction to or attributions of dominance to voices varying in masculinity. This does *not* mean that I think masculinity and dominance are the same things. I mean here that the manipulation was a manipulation along the dimension of the differences between men and women (masculinity/femininity), and the attributions of attractiveness and dominance were what were given to the voices by the raters in the studies.

Pitch – I use pitch and fundamental frequency interchangeably in this thesis. Pitch is often defined as the perception of fundamental frequency. I use the two terms interchangeably because if a sound is filtered such that the fundamental frequency is removed, fundamental frequency can still be perceived and calculated via harmonic spacing, which is equal to the fundamental frequency.

Sampling rates – throughout this thesis, unless otherwise noted, voices were recorded and played back at 44.1 kHz sampling rate, which encompasses the range of human hearing. All acoustic analyses and manipulations were conducted at 11.025 kHz sampling rate to increase frequency resolution. This is done automatically by the software used in this thesis.

Size – when I use the word "size", I mean height and weight or any combination thereof. Height and weight are normally correlated, so I use the attribution of size in this thesis to reduce the number of variables used. The word "size" (meaning height and/or weight) has been used in many studies relating voices to physical characteristics or perceptions thereof (including, but not limited to: Fitch, 1994; Smith et al., 2005; Puts, 2005; Reby & McComb, 2003; Rendall et al., 2005; Fitch & Geidd, 1999; Fitch, 1997; Fitch & Hauser

1995). Furthermore, the words "body size" appear in 16,057 journal articles indexed on web of science and 216,307 journal articles indexed on Pub Med. Therefore, I am fully justified in my use of the word "size" throughout this thesis. When researchers use the terms height or weight, I used the terms height or weight (unless otherwise noted). When researchers used the word "size" then I also used the term "size".

I know of one case (Collins & Missing, 2003) where body size did not refer to height and/or weight (although there may be others). In this study, the authors use body size to mean a composite measure of body circumference. This study, however, is the exception, not the rule.