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Vocal modulation during courtship increases proceptivity even in naive listeners

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Vocal modulation during courtship increases proceptivity even in naive listeners

Abstract

Speakers modulate their voice when talking to infants, but we know little about subtle variation in acoustic parameters during speech in adult social interactions. Because tests of perception of such variation are hampered by listeners' understanding of semantic content, studies often confine speech to enunciation of standard sentences, restricting ecological validity. Furthermore, apparent paralinguistic modulation in one language may be underpinned by specific parameters of that language. Here we circumvent these problems by recording speech directed to attractive or unattractive potential partners or competitors, and testing responses to these recordings by naive listeners, across both a Germanic (English) and a Slavic (Czech) language. Analysis of acoustic parameters indicates that men's voices varied F_0 most in speech towards potential attractive versus unattractive mates, while modulation of women's F_0 variability was more sensitive to competitors, with higher variability when those competitors were relatively attractive. There was striking similarity in patterns of social context-dependent F_0 variation across the two model languages, with both men's and women's voices varying most when responding to attractive individuals. Men's minimum pitch was lower when responding to attractive than unattractive women. For vocal modulation to be effective, however, it must be sufficiently detectable to promote proceptivity towards the speaker. We showed that speech directed towards attractive individuals was preferred by naive listeners of either language over speech by the same speaker to unattractive individuals, even when voices were stripped of several acoustic properties by low-pass filtering, which renders speech unintelligible. Our results suggest that modulating F_0 may be a critical parameter in human courtship, independently of semantic content.

Keywords: human voice, fundamental frequency, mate choice.

1. Introduction

The human voice is remarkably variable. Aside from communication through verbal content, paralinguistic elements of the voice during speech enable individual recognition and assessment of the speaker's physical characteristics such as sex (Puts, Apicella, & Cárdenas, 2012), body size (Feinberg, Jones, Little, Burt, & Perrett, 2005; Xu, Lee, Wu, Liu, & Birkholz, 2013), physical strength (Sell et al., 2010), femininity (Feinberg, 2008; Feinberg, Jones, DeBruine, et al., 2005), attractiveness (Feinberg, Jones, Little, et al., 2005; Feinberg, Jones, DeBruine, et al., 2005; Xu et al., 2013), conception risk (Pipitone & Gallup, 2008), and sexual maturity (Mulac & Giles, 1996). In humans, perceived attractiveness and mate quality can be manipulated by artificially lowering the pitch of male voices or artificially increasing it in female voices, commensurate with sex-typical vocal properties (Collins, 2000; Feinberg, Jones, Little, et al., 2005). In fact, there is evidence for increased reproductive success in traditional societies for both low-pitched males (Apicella, Feinberg, & Marlowe, 2007), and high-pitched females (Atkinson et al., 2012).

In addition, vocal parameters can be intentionally varied, for example altering the intensity (loudness), rhythm and pitch. The classic example of such intentional modulation is infant directed speech (IDS) (Falk, 2005; Ferguson, 1977), in which adults alter vocal characteristics such as pitch, cadence and intonation contours when speaking to infants. Infants prefer these altered signals over adult-directed speech (Fernald & Kuhl, 1987) and it has been suggested that IDS aids human acquisition of vocal language (Burnham, Kitamura, & Vollmer-Conna, 2002) and might underpin the origins of musicality (Dissanayake, 2000; Trehub, 2003). In human and animal social interactions, modulations of the intensity of speech or vocalisations are often associated with hostility (Collias, 1960; Kudo, 1987) and dominance (Ohala, 1982; Tusing & Dillard, 2000), and changes in intensity contribute to emotional expression (Baker, 2001). Regarding pitch modulations, men lower their voices during competitive interactions when they perceive themselves as physically dominant (Puts, Gaulin, & Verdolini, 2006), and while women have been found to increase voice pitch when directing speech towards attractive faces (Fraccaro et al., 2011), both men and women have also been found to lower their voice pitch when speaking attractive targets of the opposite sex (Hughes, Farley, & Rhodes, 2010). This suggests that, while more evidence for specific types of modulation is needed (e.g. in the case women responding to attractive opposite-sex stimuli), modulations do actually occur. Similar subtle modulation in voices might be expected in courtship contexts. In fact, there is evidence of vocal differences between speech directed towards romantic partners and same-sex friends which can be detected by listeners (Farley, Hughes, & LaFayette, 2013), and intentional voice manipulations make female voices, but not male voices, sound more attractive (Hughes, Mogilski, & Harrison, 2013; see also Fraccaro et al., 2013). Indeed, such modulations occur in other species including frogs (Ryan, 1980), koalas, *Phascolarctos cinereus* (Charlton, Ellis, Brumm, Nilsson, & Fitch, 2012), fallow deer, *Dama dama* (Charlton & Reby, 2011), red deer, *Cervus elaphus* (Reby et al., 2005; Reby, Charlton, Locatelli, & McComb, 2010), and birds. For example, in the zebra finch, *Taeniopygia guttata*, males sing more rapidly to females than when they sing alone, producing syllables with lower spectral variability (Kao & Brainard, 2006).

Studies aiming to measure the effects that acoustic parameters have on human communication are hampered by the confounding influence of verbal content. To address this issue, many studies record voices enunciating vowel sounds or speaking standard sentences, or measure responses to voices with artificially manipulated vocal parameters (e.g. Feinberg, Jones, Little, et al., 2005; Puts, Hodges, Cárdenas, & Gaulin, 2007). These methodologies have provided important insights into the role that vocal parameters play in human communication. Similarly, to study vocal modulation, and unlike research on animals or IDS (where infants understand little or none of the semantic content), it is necessary to control the confounding influence that verbal content may play. Some studies have used scripted speech (e.g. Fraccaro et al., 2011; Hughes et al., 2010), therefore eliminating prosodic variation in vocal acoustic parameters. Although challenging, testing free, unscripted speech is ideal, as standard sentences may not accurately reflect the levels of natural vocal variation; standardised sentences likely limit the kind of spontaneous paralinguistic variation found in normal free speech, as well as the nuance and range of paralinguistic modulation known at least to occur in IDS, which is characterised by an extreme range of pitches, typically starting from a high pitch and containing many glissandos. Finally, while some studies have successfully tested natural vocal variation during speech (e.g. Hodges-Simeon, Gaulin, & Puts, 2010, 2011), apparent paralinguistic modulation in one language may be underpinned by specific parameters of that language (e.g. rhythm, intonation, and use of specific phonemes). Here we circumvented these issues (i.e. the confounding influence of verbal content, using unscripted speech, and the potential effects of one language in paralinguistic modulation) by adopting a cross-language design involving two model languages.

Based on evolutionary theory and the current knowledge of human voices, we hypothesized that males and females would modulate their acoustic parameters (study 1), depending on the sex and attractiveness of the target, to affect the way in which they would be perceived. Because speech intensity is associated with hostility and dominance (Collias, 1960; Kudo, 1987; Ohala, 1982) we expected participants to speak with increased intensity in responses to same-sex targets, in comparison to opposite-sex targets. Furthermore, because emotional expressiveness is attractive (Sprecher, 1989), and changes in intensity improve emotional expression (Baker, 2001), we expected participants to speak with increased variability in intensity when responding to opposite-sex targets, and especially when those targets were attractive. In addition, based on the body of knowledge produced by studies testing perception of manipulated pitch, we predicted that women, and especially men, would emphasise sex-specific vocal characteristics when responding to attractive individuals of the opposite sex (i.e. lowering F_0 in men, and increasing it in females), and that both sexes would increase F_0 variability, in order to sound more attractive to those attractive targets. Additionally, we predicted that these modulations would be detectable by naive listeners (study 2), and that speakers would sound more attractive when speaking to attractive versus unattractive targets.

2. Study 1

First, we tested the possibility that individuals might alter vocal parameters in speech directed at potential romantic partners or competitors depending on the attractiveness of the listener. Recorded voice samples from speakers of two different languages were used to avoid the possibility that apparent paralinguistic modulation in one language might be reinforced by specific parameters of that language (e.g. rhythm, intonation, and use of specific phonemes).

2.1 Method

2.1.1 Participants

We recruited 110 heterosexual participants who were students at the Universities of Liverpool and Stirling (UK) or Charles University (Czech Republic). Of these, 30 were English speaking males (mean age ± SD = 22.6 ± 4.17), 30 English speaking females (21.8 ± 3.96), 25 Czech speaking males (22.8 ± 2.30), and 25 Czech speaking females (21.8 ± 1.84) not suffering from voice hoarseness or nasal congestion. No participant suffered from speech impediments, and all were fluent in English. All participants signed a written consent form.

2.1.2 Target Videos

The stimuli were selected from a group of 40 videos, of about 20 seconds length (mean length ± SD = 19.3 ± 2.60), half of which pictured men (mean age ± SD = 22.5 ± 2.41) and half women (22.1 ± 1.65). Individuals were visible from the waist upwards before a white background and were filmed having been asked to introduce themselves to an attractive person of the opposite sex. Each video was rated for attractiveness on a 1 to 7 scale, by an independent panel of 24 opposite-sex raters. From these, the 3 most attractive and the 3 least attractive male and female videos were selected (12 in total). Individuals seen in the videos did not take part in any of the other experiments.

2.1.3 Experimental Procedure

After the experiment had been explained and written informed consent obtained, participants were shown the twelve target videos, played without sound to avoid possible effects of pitch convergence (Gregory, Green, Carrothers, Dagan, & Webster, 2001), and asked to record a response message to each one. Participants were told that these messages would be presented to opposite-sex participants who would judge them as a potential date: in the case of responses to opposite-sex targets, participants believed their messages were going to be presented to the target they were responding to (i.e. the person in the video), while in the case of responses to same-sex targets, participants were told that their responses were going to be presented to all the opposite-sex targets. Participants were instructed to either explain whether and why they would like to date the person in the video (for opposite-sex targets) or why they should be chosen over the person in the video for a date (for same-sex targets). This scenario was based on a study which produced demonstrable effects on mate preferences (Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004).

After recording their response to each presented target video, participants were debriefed. In total, 1304 recordings were obtained (4 recordings were not collected because the participant recognised the target, and 12 were discarded because of background noise that affected audio quality), with length ranging from 6 to 46 seconds (mean ± SD = 14.70 ± 7.24 s). Additional details are provided in the Supplementary Materials available on-line.

2.1.4 Data Analysis

Each recording was acoustically analysed using Praat© 5.2 to obtain data on intensity (dB) and F_0 (Hz). Values were obtained every 10 ms. F_0 was measured using a noise-resistant autocorrelation method, between 75 and 300 Hz for male voices, and 100 and 500 Hz for female voices. Since recordings were of free speech, we did not analyse formant frequencies as these would be affected by the amount and duration of particular vowels. For intensity, only time points for which the Praat algorithm produced a value of pitch were used; this was done to control for any background noise during silent periods and to ensure that intensity scores were unaffected by differences in pause length or number. Finally, we checked that there were no significant differences in length of recordings after viewing attractive and unattractive targets, or depending on target sex.

Means and standard deviations were then obtained for intensity and F_0, and minimum F_0 for males, for each of the 1304 recordings (descriptive statistics of acoustic measures and length of the recordings are presented in Table S1, in the Supplementary Materials). For these values, mean scores were calculated for each participant according to the attractiveness and sex of the target; because each participant responded to three targets of each sex/attractiveness combination, values used in the analysis were the mean of their three responses to same-sex attractive, same-sex unattractive, opposite-sex attractive, and opposite-sex unattractive targets. These were analysed using repeated-measures generalised linear models (GLM) for each parameter (with Bonferroni-adjusted $\alpha = 0.0125$ because we performed 4 analyses), using sex and language of the participant as between-subjects factors, and sex and target attractiveness as within-subjects factors. We report the within-subjects effects involving attractiveness in Table 1, reflecting the experimental design; the full models are provided in Table S2. Post-hoc pairwise comparisons (*t*-tests) were conducted for significant effects of target attractiveness. All tests are two-tailed. Additional details are provided in the Supplementary Materials available on-line.

2.2 Results and Discussion

Analysis revealed that variability in F_0 (F_0 SD) was particularly sensitive to change in social context compared with the other three parameters (Table 1). There was a significant main effect of target attractiveness, such that F_0 SD increased after viewing attractive compared with unattractive targets. There were also two significant interactions: between target attractiveness, target sex and participant sex (in which men, but not women, raised F_0 SD after viewing attractive individuals in the opposite-sex condition, Fig. 1D), and between target attractiveness and target sex (in which F_0 SD was highest after viewing attractive individuals in the same-sex condition). These interactions indicate that men's F_0 SD was higher in the opposite-sex condition, while women spoke with more variability after viewing attractive romantic competitors (Fig.1D). Previous studies have noted that women are particularly sensitive to attractiveness of perceived competitors, seeking to increase their perceived attractiveness to potential partners relative to other women (Buss & Dedden, 1990; Fisher, 2004), and the differences in F_0 variability that women show after watching same-sex (but not opposite-sex) targets, could be reflecting this. Each of these effects indicate that individuals tended to speak with increased variability in F_0 when motivation was high – in response to perceived attractiveness of potential dates or when competing for a date against an attractive rival. Such variability might serve as a marker of social interest, or help to capture attention of the listener, or could more simply reflect general autonomic arousal in the speaker.

Furthermore, there was striking similarity in these patterns of F_0 SD across the two languages. Post hoc tests showed that differences in F_0 SD during responses to attractive and unattractive individuals of the same or opposite sex (shown in Fig.1D) occurred in almost identical patterns in English and Czech speakers. This is further illustrated by the absence of any significant interaction involving target attractiveness and language (Table 1, lower panel).

In contrast, there were few context-dependent differences in the other vocal parameters and no similar consistency across languages (Table 1). There were no significant differences in mean intensity. For variability in intensity (intensity SD), there was a significant main effect of target attractiveness, such that participants changed their intensity levels more to attractive individuals, but post hoc tests revealed that this effect was driven mainly by English speakers in the opposite-sex condition (Fig.1B). There was also a near significant (after Bonferroni correction) interaction between target attractiveness, target sex and language, in which higher intensity SD occurred after viewing opposite-sex attractive individuals in English but not Czech speakers. Finally, for mean F_0, there was a significant interaction between target attractiveness and language, in which Czech (but not English) speakers spoke with high mean pitch after viewing attractive individuals; the main effect of target attractiveness was not significant (after Bonferroni correction) but tended towards higher pitch after viewing attractive individuals.

On the basis of previous studies testing perception of manipulated pitch, we had expected that men might lower mean F_0 when speaking to attractive opposite-sex targets because modulation might serve to emphasise sex-typical characteristics (Hughes et al., 2010), but there were no significant interaction effects involving participant or target sex, and the only significant effects for F_0 corresponded to higher, not lower, pitch in the attractive condition (in Czech speakers; Fig.1C). However, absence of this expected result can be explained upon recognizing the relative importance of F_0 variability (Table 1; Fig.1): there was a positive correlation between F_0 SD and mean F_0 ($r = 0.46$, $p < 0.001$; Fig. 2A). This suggests that increased variability in F_0 results in higher mean F_0, and that the observed tendency towards higher mean pitch may therefore emerge as a consequence of increasing F_0 variability, rather than being a directly modulated parameter.

Despite this, men's minimum F_0 was significantly lower, in both Czech and English samples, when responding to attractive (M = 82.36 Hz, SD = 6.47) versus unattractive women (M = 86.20 Hz, SD = 9.13) (paired-samples t-test: $t_{54} = 5.41$, $p < 0.001$; Fig. 2B) and, in contrast to the relationship between F_0 SD and mean F_0, F_0 variability and minimum F_0 were not significantly correlated ($r = -0.11$, n = 55, $p = 0.44$). This suggests that F_0 variability and minimum F_0 are independent parameters which might provide different cues of mating intent and mate quality.

3. Study 2

Findings from study 1 indicate that paralinguistic parameters vary depending on the attractiveness of the target, but did not test the perception of this modulation. For it to be functionally relevant and have an effect on mate choice, it must be perceptually detectable and influence proceptivity towards the speaker. Study 2 aimed to investigate whether this is indeed the case.

3.1 Method

In order to test whether paralinguistic modulation is detectable and context-specific, while ruling out influence of verbal content, we presented subsets of 10 pairs of recordings from each language group to naive listeners (English participants who do not speak Czech, and vice versa) in a series of forced-choice tests. Recordings were judged for attractiveness by both opposite- as well as same-sex listeners. To test context-specificity, we conducted a confirmatory test, in which recordings were rated for friendliness instead of attractiveness. Additionally, and to test whether differences in judgement are dependent on F_0 modulation, low-pass filtered versions of the recordings were rated for both attractiveness and friendliness in separate tests.

3.1.1 Participants

For the test using original voice recordings rated for attractiveness, the final sample included 123 participants judging opposite-sex recordings, and 98 judging same-sex recordings. Opposite-sex listeners were 24 men (mean age ± SD = 29.2 ± 9.29) and 35 women (27.3 ± 8.89) in the English sample, and 24 men (26.5 ± 7.11) and 40 women (26.9 ± 5.30) in the Czech sample. For same-sex listeners, the equivalent participant numbers were as follows: 25 (24.4 ± 2.93), 32 (24.4 ± 2.95), 20 (23.2 ± 4.88), and 21 (24.6 ± 6.13), respectively. Informed consent was obtained from all subjects.

For the test using the same original voice recordings rated for friendliness, 131 heterosexual participants were recruited. Here, listeners were presented with both same- and opposite-sex recordings (with order fully randomised). The final sample included 108 participants: 23 men (mean age ± SD = 32.7 ± 11.78) and 44 women (30.4 ± 14.79) in the Czech sample, and 15 men (33.3 ± 9.38) and 26 women (28.2 ± 10.17) in the English sample.

For the tests assessing low-pass filtered voice recordings, 174 heterosexual participants were recruited. Again, listeners were presented with both same- and opposite-sex recordings, and because filtering renders speech unintelligible, we relaxed selection for participants who understood a little of the other language. The final sample included 82 participants judging the recordings in terms of attractiveness, and 92 judging on friendliness. For attractiveness judgements there were 22 men (mean age ± SD = 25.6 ± 3.16) and 21 women (24.8 ± 4.18) in the English sample, and 11 men (25.9 ± 5.89) and 28 women (24.8 ± 6.11) in the Czech sample. Equivalent participant numbers judging friendliness were 25 (26.8 ± 6.70), 30 (25.9 ± 4.12), 20 (24.6 ± 5.33), and 17 (23.0 ± 4.62), respectively.

Additional details regarding the exclusion criteria for these tests are provided in the Supplementary Materials.

3.1.2 Audio samples

We used the recorded responses of the first 10 tested participants from each sex/language combination to the most attractive and the most unattractive females as, in the voice recordings, there was significant variation in F_0 SD for both male and female participants (notice that all participants were told their recordings would be presented to opposite-sex participants to be judged as a potential date). Separate tests were also composed using responses subjected to low-pass filtering (Burnham et al., 2002) using Praat© 5.2 with an upper cut-off of 400 Hz (i.e. removing all frequencies above the cut-off level), and standardised to approximately 9 seconds in length (mean ± SD = 8.98 ± 2.28). Low-pass filtering retains variation in fundamental frequency in the voice samples, including minimum F_0, but removes all spectral information above the cut-off point (including most formants) and renders speech unintelligible. Additional details are provided in the Supplementary Materials.

3.1.3 Experimental Procedure

Rating tests were conducted online and presented to participants in their native language. Participants were presented with each pair of recordings of the opposite linguistic group, in a different randomised order for each listener. Within each pair, the same voice was directed towards an attractive and an unattractive individual. For the original voices, the research was described as a study of vocal preferences in a foreign language. For the low-pass filtered voices, participants were asked to imagine that they were listening to somebody speaking in a nearby room (because filtered recordings sounded somewhat like this). In all tests, participants were asked to select the recording that sounded either more attractive (i.e. "please listen to both recordings and select the one you think sounds more attractive") or friendly (i.e. "please listen to both recordings and select the one you think sounds more friendly") from each pair.

3.2 Results

First, we compared the extent to which listeners preferred recordings directed towards an attractive target with the level expected by chance (0.5) using one-sample t-tests. In response to the original unfiltered voices, the recording directed towards attractive individuals was chosen as more attractive by opposite-sex naive listeners in every case (Fig. 3a): English men speaking to attractive women were preferred by Czech women more often than expected by chance ($t_9 = 15.05$, $P < 0.001$), and the same effect was found for English-speaking women and Czech-speaking men and women ($t_9 = 14.57$, $P < 0.001$; $t_9 = 20.77$, $P < 0.001$; $t_9 = 8.72$, $P < 0.01$, respectively). The same was true of judgments based on the filtered recordings (Fig. 3c): opposite-sex listeners preferred recordings directed towards an attractive target at levels above chance, in each language/sex combination (English men: $t_9 = 3.49$; Czech men: $t_9 = 3.64$; English women: $t_9 = 3.50$; Czech women: $t_9 = 5.21$; $P < 0.01$ in every case). We also asked independent groups of listeners to select the recording that sounded friendlier, rather than more attractive, from both the original (Fig. 3b) and low-pass filtered (Fig. 3d) recordings. In these tasks, judgments of neither opposite-sex nor same-sex listeners differed significantly from chance, except in one case, where original recordings of English speaking males were rated by Czech females ($t_9 = 3.44$; $P < 0.01$; Fig. 3C). However, in this one case, the strength of preference was lower than in the mate choice context.

To compare these effects directly, we used generalised linear models (GLM) (with Bonferroni-adjusted $\alpha = 0.025$ because we performed 2 analyses), with Rater Sex (same, opposite), and Context (attractiveness, friendliness), as within-subjects factors, and Language (Czech, English) and Gender (male, female) as between-subject factors. We tested whether judges preferred responses to attractive individuals depending on the context (attractiveness, friendliness), and sex of the raters (same, opposite), when presented with original, unaltered recordings. We found significant main effects of both context and rater sex (Fig. 3a,b) on the proportion of responses to attractive individuals selected as more attractive or friendly, such that the proportion was significantly higher when recordings were rated for attractiveness than for friendliness ($F_{1,36} = 10.27$, $p < 0.001$) and by opposite-sex compared to same-sex raters ($F_{1,36} = 63.19$, $p < 0.001$). Furthermore, there was a significant interaction between context and rater sex ($F_{1,36} = 50.93$, $p < 0.001$; Fig. 3a,b): in every case, recordings directed towards attractive individuals were chosen as more attractive by a higher proportion of naive opposite-sex listeners (Fig. 3a), but this was not the case when the recordings were rated for friendliness (Fig. 3b). In contrast, neither the language nor the gender of the speakers (nor the interaction between these) had a significant effect on the proportion selected ($F_{1,36} = 3.29$; $F_{1,36} = 0.47$; $F_{1,36} = 1.11$, respectively; $p > 0.05$ in all cases). For full results, see Table S5 in the Supplementary Materials.

Finally, we tested whether these preferences were preserved after stripping the voices of most acoustic information, but retaining F_0. To do this, the recordings were subjected to low-pass filtering with an upper cut-off of 400 Hz (Burnham et al., 2002). Filtered recordings were then presented in two-alternative forced-choice tasks (as with the original, unfiltered recordings) to listeners from the other language group. Again, rater sex had a significant main effect on the proportion of responses to attractive individuals selected as more attractive or friendly (Fig. 3c,d), with opposite-sex raters selecting a higher proportion of responses to attractive targets than same-sex raters ($F_{1,36} = 8.15$, $p < 0.01$). Moreover, and similarly to ratings of original recordings, there was a significant interaction between context and rater sex ($F_{1,36} = 5.81$, $p = 0.021$; Fig. 3a,b), in which recordings directed towards attractive individuals were chosen as more attractive by a higher proportion of naive opposite-sex listeners, and neither the language nor the gender of the speakers, or their interaction, had a significant effect on the proportion selected ($F_{1,36} = 3.06$; $F_{1,36} = 0.27$; $F_{1,36} = 0.15$, respectively; $p > 0.025$ in all cases). Full results are presented in Table S4. The strength of preference for recordings directed towards attractive individuals was reduced in comparison to the original, unfiltered voices, indicating that other acoustic parameters also contribute to vocal judgments, but this test nonetheless suggests that modulation of F_0 is sufficient to influence proceptivity in naive opposite-sex listeners. Together, these tests indicate that listeners respond proceptively to pitch information contained within these recordings, but only within the context of mate choice.

4. General discussion

Although previous results suggest that voice pitch plays a role in human courtship (Fraccaro et al., 2011; Puts et al., 2006), our cross-language experimental design provides new insights into the specific nature and mechanisms of paralinguistic modulation involved in courtship. While the two languages (English and Czech) are both European, they lie on separate branches of the Indo-European family with several millennia of largely independent development (Gray, Atkinson, & Greenhill, 2011) and are sufficiently distinct to ensure that semantic content cannot be understood by monolingual listeners. We thus believe that similarities in paralinguistic modulation, and their influence on proceptivity, provide evidence for robust context-dependent sensitivity across languages, but confirmatory studies in other languages and language families are now called for. At least within the two tested languages, however, modulation of F_0 occurred flexibly within a human courtship context in both men and women, and was sufficient to influence proceptivity towards the speaker independently of listeners' understanding of verbal content. Furthermore, the acoustic analysis revealed that variability in F_0 was especially sensitive to manipulation of social context and varied across social contexts in strikingly similar ways across languages.

Hormonal contraceptive use has been shown to affect evolutionary relevant preferences in potential partners (e.g. Feinberg, DeBruine, Jones, & Little, 2008; Puts et al., 2006; Roberts, Gosling, Carter, & Petrie, 2008), and could potentially explain why modulation in F_0 SD in female participants was apparent in responses to other women, but not to men. Future research specifically controlling for hormonal contraceptive use should be conducted to explore this possibility.

Previous studies of the influence of F_0 variability on attractiveness judgments have produced mixed results. Across individuals, higher F_0 variability has been found to be negatively associated (Hodges-Simeon et al., 2010), or not significantly associated (Riding, Lonsdale, & Brown, 2006), with attractiveness, leading Hodges-Simeon *et al.* (2010) to conclude that further study was needed to determine whether these different findings result from individual differences or contextual variation. Here, our within-subjects design leads us to suggest that, even if individual differences in F_0 variability do not robustly cue attractiveness, speakers do increase variability in F_0 during free speech towards individuals to whom they are attracted.

With the exception of some recent studies (e.g. Hodges-Simeon et al., 2010; Riding et al., 2006) it has generally been assumed that mean F_0 is the key parameter influencing listeners' perception and, specifically, that females prefer low-pitched males. The opposite effect, however, has been reported for red deer, a sexually dimorphic species in which females prefer males with higher F_0 (Reby et al., 2010), questioning the assumption of a general female preference for low-pitched males in mammals. Individual differences in mean F_0 are an important cue for mate quality and attractiveness, but our results suggest that F_0 variability (rather than mean F_0) may be the critical parameter underpinning vocal modulation in human courtship and competition over mates. Men generally tend to speak towards the lower limit of their pitch range (for information regarding human vocal range, see Honorof & Whalen, 2005; Keating & Kuo, 2012), potentially driving mean pitch upwards when they increase variability. Interestingly, men also reached a lower minimum F_0 when responding to attractive women, but minimum F_0 is not correlated with variability, unlike mean F_0. This raises the intriguing possibility that, as low-pitched vocal sounds are physiologically constrained (unlike high pitches; e.g. *falsetto*) (Lieberman & Blumstein, 1988; see also Fitch & Hauser, 1995), producing a low pitch at some point during an interaction might provide sufficient indication of physical masculinity (Puts et al., 2007) while freeing men to 'play' with their pitch, potentially providing independent cues of both mating intent and mate quality. Furthermore, because low-pitched masculine voices might be associated with aggression (Puts et al., 2012) and because masculinity is often associated with negative attributions (Hodges-Simeon et al., 2010), such modulation could potentially enable men to signal both their masculinity and lack of threat simultaneously, thereby moderating the effect of such negative attributions.

These ideas are consistent with previous suggestions that modulation of F_0 is a general mechanism to signal low or high threat in social interactions (see Hodges-Simeon et al., 2010, 2011; Puts et al., 2012). For example, increased F_0 variability has been associated with positive traits such as dynamism, femininity and aesthetic inclinations in male speakers (Addington, 1968) or simply friendliness, because adults tend to exaggerate this trait when speaking to infants (Trainor, Austin, & Desjardins, 2000). Alternatively, decreased F_0 variability occurs in competitive contexts (Hodges-Simeon et al., 2010, 2011) and is associated with higher aggressiveness in both foraging and industrial societies (Puts et al., 2012). Thus it could be argued that our results support this, more general, hypothesis - that modulation in speakers' F_0 variability might influence attractiveness assessment indirectly, by increasing perceived friendliness and low threat. However, our perceptual studies suggest this is unlikely: responses to attractive targets were preferred consistently only by opposite-sex listeners, and only when rated for attractiveness (Fig. 3).

Finally, such variability in paralinguistic prosody in courtship contexts has implications for ideas about the evolution of musicality in humans. One important part of musicality is the ability to process the pitch variations that produce the contours and, ultimately, a melody (Peretz & Coltheart, 2003; Peretz & Hyde, 2003). Others have argued that IDS (in which adults alter vocal characteristics such as pitch, cadence and intonation contours when speaking to infants) could be an important component in the development of musicality (Trehub, 2003), in view of characteristic patterns of vocal modulation by mothers and its detection by infants (Fernald & Kuhl, 1987), as well as the effects of IDS on infants' arousal, focus on the mother and strengthening of mother-infant bonds.

Applying the same logic, we suggest that production of similar kinds of vocal modulation during courtship, and its detection and influence on proceptivity, could also be precursors for the development of musicality. In contrast to IDS, vocal modulation in courtship can also help to explain why music and singing is so prevalent in adulthood (Brown, 2000; Fitch, 2006), and why serenading is so prevalent both historically and crossculturally. Our results thus introduce a new line of support for the hypothesis of an evolutionary origin of music through sexual selection, as first suggested by Darwin (1871).

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Figure Captions

Figure 1. Modulation of acoustic parameters in speech towards same and opposite-sex targets, split by attractiveness category of the targets (attractive: white bars; unattractive: grey bars) and sex of the stimuli (SS: same-sex; OS: opposite-sex). (a) Mean Intensity; (b) Intensity SD; (c) Mean F_0; (d) F_0 SD. Standard deviation (SD) for intensity and F_0 were used as a measure of variability. Bars represent mean ± 1 s.e.m. For interactions, dashed lines represent an effect of target attractiveness (attractive, unattractive); dotted lines represent an effect of target sex (same, opposite). Post-hoc tests, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. For detailed results, see Table S3 in the Supplementary Material.

Figure 2. Relationships between pitch parameters. (a) Correlation between mean F_0 and F_0 variability (F_0 SD) for men's responses to women (English: $r = 0.45$, n = 30, $p = 0.012$; Czech: $r = 0.41$, n = 25, $p = 0.041$; all individuals: $r = 0.46$, n = 55, $p < 0.001$). (b) Men's minimum F_0 in responses to opposite-sex targets (attractive: white bars; unattractive: grey bars). Bars represent mean ± 1 s.e.m. ***$p < 0.001$.

Figure 3. Mean proportion of recordings towards attractive targets that were selected as more attractive (a,c) or friendly (b,d) by naive listeners. (a) Original recordings, selected as more attractive; (b) original recordings, selected as friendlier; (c) low-pass filtered recordings selected as more attractive; (d) low-pass filtered recordings selected as friendlier. The horizontal axis represents the type of recordings used (original, filtered), the context (whether recordings were judged for attractiveness or friendliness), as well as the gender and language

(En.: English; Cz.: Czech) of the speakers in the recordings. In every case, the recordings were rated by judges (opposite-sex: white bars; same-sex: grey bars) from the other linguistic group (i.e. English raters who do not speak Czech, and vice versa). The dotted horizontal line represents a chance level of 0.5. Bars represent mean ± 1 s.e.m. Descriptive statistics are presented in Table S4 in the Supplementary Material.

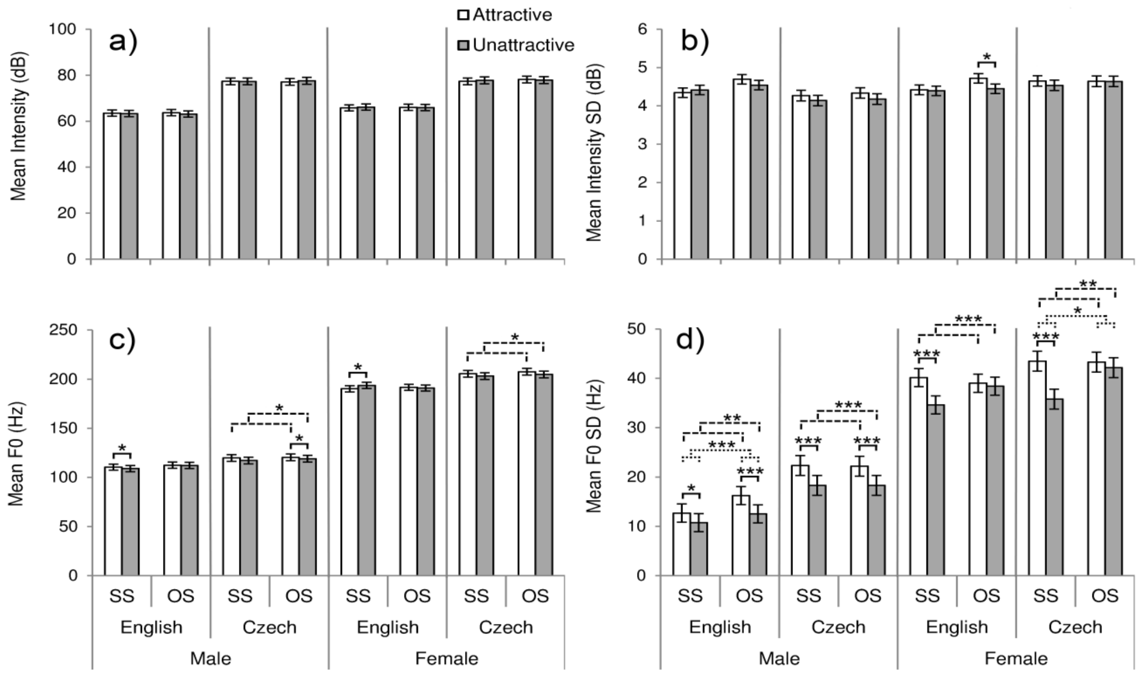
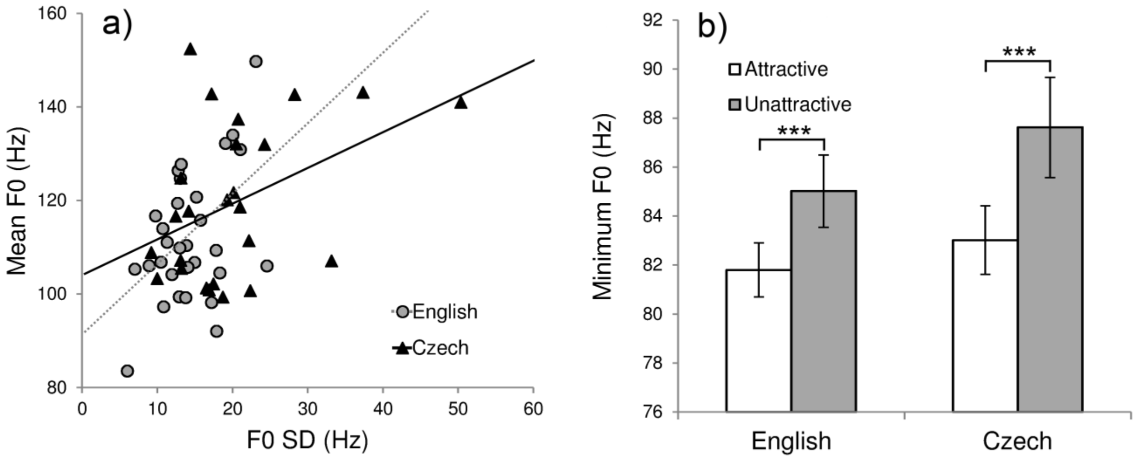

a)
b)
c)
d)
Attractive
Unattractive
Mean Intensity (dB)
Mean Intensity SD (dB)
Mean F0 (Hz)
Mean F0 SD (Hz)
SS OS SS OS SS OS SS OS
English Czech English Czech
Male Female

Figure 1



a)
160
140
120
100
80
Mean F0 (Hz)
0
10
20
30
40
50
60
F0 SD (Hz)
English
Czech
b)
92
90
88
86
84
82
80
78
76
Minimum F0 (Hz)
Attractive
Unattractive
***
***
English
Czech

Figure 2

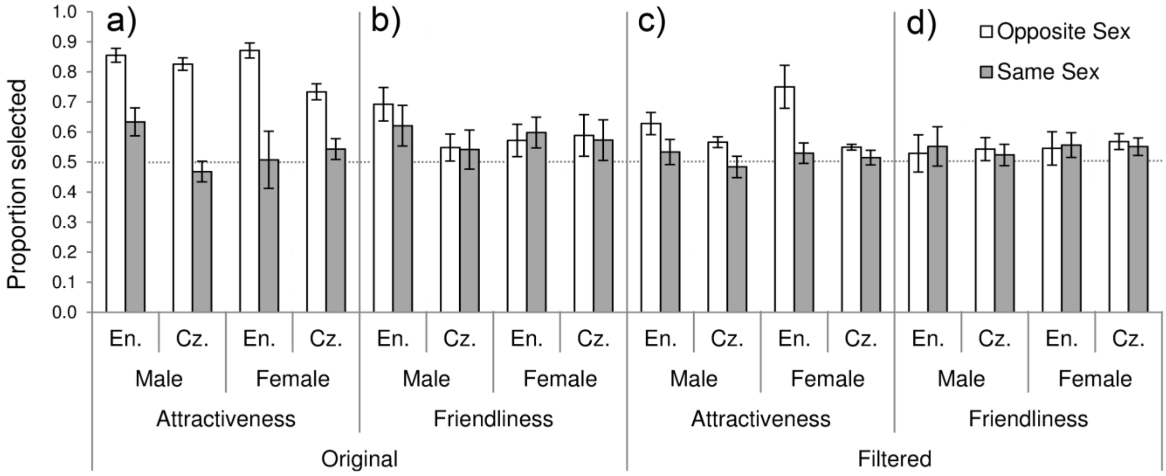

1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Proportion selected
a)
b)
c)
d)
Opposite Sex
Same Sex
En.
Cz.
Male
Female
Attractiveness
Friendliness
Original
Filtered

Figure 3

Table 1. Context-dependent variation in vocal parameters

Effect	Vocal parameter							
	Mean intensity		Intensity SD		Mean F_0		F_0 SD	
Within-subject Effect	*F*	p	*F*	p	*F*	p	*F*	p
TA	0	0.99	**8.18**	**0.005**	4.88	0.029	**68.15**	**<0.001**
TA x PS	0.51	0.476	0.03	0.864	0.83	0.364	0.16	0.687
TA x TS	1.37	0.244	1.98	0.162	0.34	0.563	**9.85**	**0.002**
TA x PS x TS	1.71	0.194	0.19	0.661	3.49	0.065	**17.45**	**<0.001**
TA x L	1.28	0.261	0.01	0.921	**7.27**	**0.008**	2.11	0.15
TA x PS x L	1.41	0.239	1.98	0.163	2.22	0.139	0.02	0.9
TA x TS x L	0.46	0.5	4.08	0.046	0.92	0.339	1.28	0.26
TA x PS x TS x L	1.72	0.193	0.35	0.558	1.01	0.317	0.01	0.921

TA = Target Attractiveness, PS = Participant sex, TS = Target sex, L = Language. Results are from repeated-measures generalized linear models (d.f. = 1, 106 in each case) for each vocal parameter, with Bonferroni adjustment for multiple tests ($\alpha = 0.0125$). Significant effects are in bold. For all results, see table S1 in the Supplementary Materials.