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Contextualising courtship: Exploring male body odour effects on vocal modulation

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ABSTRACT

Voice characteristics are important to communicate socially relevant information. Recent research has shown that individuals alter their voices depending on the context of social interactions and perceived characteristics of the audience, and this affects how they are perceived. Numerous studies have also shown that the presence of bodily odours can elicit psychological changes in people. Here, we tested whether the presence of male axillary odour would influence vocal modulations in courtship contexts. We analysed differences in vocal parameters and attractiveness ratings across 950 recordings from 80 participants as they responded to opposite-sex target stimuli. Using these, we tested whether men's and women's vocal parameters and perceived stimuli attractiveness differed in the presence or absence of the odour. We expected women to speak with increased voice F_0, and men to lower their pitch, when exposed to male body odour, especially if it were of high quality. However, neither the presence of male odour, its quality, nor the addition of androstadienone produced any consistent changes in vocal parameters. Nevertheless, rated stimulus attractiveness was predicted by F_0 and especially F_0 variability, suggesting that this is a key parameter in signalling attraction during human courtship, and supporting the idea that vocal modulations are context-sensitive.

1. Introduction

In recent years, numerous studies have shown that the mere presence of odours can bring about psychological changes in people in a range of different contexts. For example, ambient odours can influence people's mood and creativity (Knasko, 1992) and reduce stress (Lehrner et al., 2005). Such effects are not ubiquitous but vary depending on the interaction between specific odours and situations. For example, scents that are perceived to be more associated with one or other gender alter gender-congruent shopping behaviour (Doucé et al., 2016; Spangenberg et al., 2006). Furthermore, subliminal presence of citrus scent, an odour associated with cleanliness, can influence hygienic behaviour (Holland et al., 2005; King et al., 2016), while odours associated with faeces and vomit trigger behaviour associated with disgust and avoidance, including more positive attitude towards safe sex (Tybur et al., 2011) and more conservative attitudes towards sexual behaviour (Adams et al., 2014).

Such effects are not limited to ambient fragrances and those associated with disease risk, but also involve bodily odours and their influence on social interactions. For example, the odours of people in fearful or anxious emotional states can alter brain activation, mood and cognition in others (e.g. Albrecht et al., 2011; Pause et al., 2004). Odours can also influence social judgments in other sensory modalities, as the subliminal presence of male axillary odour alters attractiveness ratings of men's faces by women (Thorne et al., 2002). This effect was supported and extended in a recent study (Mutic et al., 2016) showing that axillary

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odour of both sexes affected the evaluations of masculinity and femininity and the social perception of faces.

At least with attractiveness judgments, we should expect effects to vary depending on the individual odour donor, because perceived odour quality varies between individuals. Just as some individuals have faces that most people would view as relatively attractive (models would be an extreme example), some individuals have relatively attractive body odour. Indeed, some studies report positive correlations between individual facial attractiveness and the perceived pleasantness of their axillary odour (Rikowski and Grammer, 1999; Thornhill et al., 2003; but see Roberts et al., 2011), suggesting that both are underpinned by a common biological mechanism. Although the specific components of axillary odour that are responsible for such effects remain unknown, several studies (Cornwell et al., 2004; Grosser et al., 2000; Jacob et al., 2001; Jacob and McClintock, 2000) focus on a group of naturally occurring steroids, the 16-androstenes, and mainly the compound androstadienone. Although the theoretical relevance of such studies has been questioned (e.g. Wyatt, 2020), researchers have reported numerous effects of androstadienone exposure on individuals. These include effects on positive mood (Jacob and McClintock, 2000), emotional processing (d'Ettorre et al., 2018), assessment of body movement (Ye et al., 2019) and facial information (Hornung et al., 2017; Niu and Zheng, 2020; Parma et al., 2012; Zhou et al., 2014), as well as facial attractiveness judgements, such that presence of androstadienone led to higher attractiveness ratings (Saxton et al., 2008; Verhaeghe et al., 2013).

Voice characteristics are another important means of communicating socially relevant information (e.g., Valentova et al., 2019). Recent research has shown how people alter their voices during social interactions (Leongómez et al., 2021), depending on the social context of such exchange and the perceived characteristics of the audience (for a review, see Pisanski et al., 2016). This has been demonstrated, for example, for interactions in which social status is important (Leongómez et al., 2017; Puts et al., 2006; Sorokowski et al., 2019) and in courtship scenarios (e.g. Leongómez et al., 2014; Pisanski et al., 2018). Voice modulations can increase the prospect of attracting preferred partners, for two reasons. First, the characteristics of an attractive voice can, at least to a certain extent, be imitated or exaggerated (Fraccaro et al., 2011; Leongómez et al., 2014). Second, they exploit the fact that, just like faces and odours, some voices are judged to be relatively more attractive than others.

This latter point illustrates that, in a courtship context, there may be a further correlation between perception of odours and voices, as they may both give information about the underlying quality of an individual as a potential partner, affecting perceived attractiveness (Feinberg et al., 2005). Although the literature on this relationship is scarce, it has been found that odours, according to their hedonic valence, can influence certain acoustic characteristics of voice (Millot and Brand, 2001). In fact, because previous research has showed that (1) women's perception of a man's attractiveness is increased both by the presence of male axillary secretion (Thorne et al., 2002) and exposure to androstadienone (Saxton et al., 2008), and (2) voice modulation is sensitive to attractiveness cues (Leongómez et al., 2014; Pisanski et al., 2018), it is possible that body odours, as signals of the quality of a potential partner, could induce non-conscious vocal modulations in courtship scenarios. However, the potential effects of body odours on voice characteristics have not yet been explored in courtship contexts, for either sex.

In view of this, we set out here to test whether presence of male axillary odour, and androstadienone in particular, would influence vocal modulation in courtship contexts. We used the same experimental paradigm and similar measures of vocal parameters as in Leongómez et al. (2014), to test changes in men's and women's voices as they responded to opposite-sex targets, in the presence and absence of the allocated odour. The vocal parameters we extracted were the mean fundamental frequency (F_0) and its variability (both standard deviation, SD, and coefficient of variation, CV; see Eguchi and Hirsh, 1969), and mean intensity. We also asked participants to rate how attractive they found each target stimulus, and modelled the acoustic parameters as predictors of perceived attractiveness. Despite the study being largely exploratory due to its novelty, we had some specific predictions. First, we predicted that the presence of male body odour and androstadienone would tend to increase the perceived attractiveness of male targets, causing women to speak with increased voice F_0, which tends to be attractive to gynephilic men (Feinberg et al., 2005; Jones et al., 2008). Likewise, given that low F_0 provides a cue of masculinity and dominance (Puts et al., 2007; Wolff and Puts, 2010), we expected men to lower their pitch when exposed to male body odour as a response to perceived intrasexual competition. Finally, we expected both sexes to increase pitch variability when responding to attractive target stimuli (Leongómez et al., 2014).

2. Materials and methods

2.1. Ethics approval

The study was performed in line with the principles of the Declaration of Helsinki. All procedures were approved by the Ethics Committee of the Department of Psychology, Faculty of Natural Sciences, University of Stirling. All participants provided written informed consent and were offered course credit for their participation.

2.2. Participants

We recruited 80 heterosexual participants who were students at the University of Stirling, half of whom were men (mean age ± SD = 20.48 ± 0.41) and half women (20.50 ± 0.49). Participants were not suffering from vocal hoarseness or nasal congestion at the time of testing. To ensure they had a normally functioning sense of smell, all participants were asked to complete a brief screening test, in which they had identify 12 odorants in a multiple choice task with 4 alternatives for each odorant (the Sniffin' Sticks Screening 12 test, www.burghart-mt.de); only data from participants who could correctly identify at least 9 odorants were included in the analysis. One participant (male, 20 years old) correctly identified only 7 and so was excluded from the final sample, but recruitment continued until the final, balanced sample size was achieved.

2.3. Target videos

We used videos that were selected as target stimuli for a previous study (Lengómez et al., 2014). These target stimuli were selected from an initial set of 40 videos: 20 of men (mean age ± SD = 22.5 ± 2.41) and 20 of women (22.1 ± 1.65), each of 20 s length. Their task was presented as: "Please introduce yourself to an attractive person of the opposite sex". Each video was then scored for attractiveness by 24 opposite-sex raters. Based on the mean attractiveness scores, the videos of the 3 most and 3 least attractive men and women were selected for use in the study (12 videos in total).

2.4. Odour stimuli

Body odour samples were collected from 12 men (mean age 21.4 ± 1.9). Each wore a cotton pad in each armpit for one night. They were instructed to wash with unperfumed soap before going to bed, to avoid spicy foods, and to place the pads into the provided sealable bags on waking. These are standard and well-used procedures for axillary odour perception studies (Havlíček et al., 2005; Roberts et al., 2008, 2005). Each odour sample was then frozen immediately until use; freezing does not alter the perception of axillary odours (Lenochova et al., 2009; Roberts et al., 2008). Male odours were subsequently rated for pleasantness by a separate group of people (5 men, 5 women) using a 7-point scale ranging from −3 (very unpleasant) to +3 (very pleasant). Samples from the 4 most pleasant scoring odours were pooled to create a "high quality" (HQ) male odour, while pooling of the 4 lowest scoring odours formed a "low quality" (LQ) male odour. Pooling of such samples to create a composite odour minimises effects of individual differences in odour quality and preference while maintaining the average quality of the constituent samples (Fialová et al., 2018). To create these composites, each cotton pad was shredded into small pieces and mixed in equal parts with the other odours in either the HQ or LQ category, before being frozen in sealable bags. Additional details on odour presentation are provided in the Supplementary material available on-line.

2.5. Experimental procedure

Participants were recruited and participated in this study between November 2011 and May 2012. Each was asked to attend two sessions (experimental and control), spaced between 7 and 14 days apart. Participants were exposed to odour stimuli only during the experimental session; sessions were otherwise identical. Participants were randomly divided into one of 4 experimental odour conditions, according to whether they were exposed to high/low body odour quality (HQ, LQ), and whether androstadienone (ANDR) was added to that odour (the 4 conditions were thus: HQ + ANDR, HQ no ANDR, LQ + ANDR, LQ no ANDR). A group of 10 women and 10 men were allocated to each condition. Sessions were counterbalanced so that for half of the men and women in each group, the control took place in the first session, and for the other half in the second (Fig. 1).

Two hours before each experimental session, the appropriate odour sample was removed from the freezer. At this point, when testing participants from the HQ + ANDR and LQ + ANDR groups, 1 ml of a 250 μM ANDR solution was added by pipette to the odour sample. We used this ANDR concentration to enable comparison with previous studies (e.g. Jacob and McClintock, 2000; Lundström and Olsson, 2005; Saxton et al., 2008) and because it is below the detection threshold for most people (Lundström et al., 2003). Fifteen minutes before the session, the odour sample was placed in the cubicle where the participant would be seated, in a small plastic container wrapped in clean aluminium foil. Odour samples were left in the cubicle for the duration of the experimental session and removed afterwards, leaving the cubicle open and empty for no less than 15 min before they were replaced by new odour samples to test other participants. For control sessions, clean pieces of cotton pads were placed in the same manner, so that participants could not visually differentiate between the control and experimental sessions.

Sessions were conducted in small, quiet testing cubicles with artificial light and no windows. During the session, participants were alone in the cubicle, sitting in front of a laptop, with the plastic container placed directly on the desk between the participant and the laptop, so that the odour sample was about 25 cm below the participant's nose.

The procedure from here on closely followed the methods described in Leongómez et al. (2014), but here we only analyse data from responses to opposite-sex target videos. The study was presented to participants as an experiment on selection of potential mates and relationship formation, examining the relative importance of attractiveness, self-confidence and body language on male and female preferences, as well as to understand the effect that different odours have on these psychological mechanisms. The odours used in the experiment remained undisclosed until participants were fully debriefed after the second session. In both sessions, participants were shown the six opposite-sex target videos, and were asked to record a response message to each one of them using a head mounted microphone. They were told that these messages would be presented to opposite-sex participants who would judge them as a potential date. Based on a study which produced demonstrable effects on mate preferences (Gangestad et al., 2004), participants were instructed to explain whether and why they would like to date the person in the video. Additional details are provided in the Supplementary Material available on-line.

The video targets were presented electronically to participants using E-Prime 2.0 software (Psychology Software Tools, Inc., 2012; www.pstnet.com), and the order of the target videos was fully randomised for each participant/session. Immediately following each video, participants were asked to rate the attractiveness of each target (on a 7-point scale), and monaural audio responses of the participants were digitally recorded using E-Prime (SoundIn object) on a laptop PC, using a ClearChat Stereo Headset (Logitech, 2007), positioning the microphone about 2 cm from the participant's mouth.

As each participant experienced both experimental and control sessions, they recorded a total of 12 responses to opposite-sex targets (6 control, 6 experimental). A grand total of 960 recordings were thus obtained. Eight recordings were discarded because of technical problems or background noise that affected audio quality and subsequent acoustic analysis, so 952 were acoustically analysed. Of these, 2 were excluded from statistical analysis because they did not produce acoustically useable data, so 950 were statistically analysed. Similar to the methods described in Leongómez et al. (2014), each participant responded to 3 targets of each attractiveness category (attractive, unattractive) during both the control and experimental sessions. The values used in the analysis were, therefore, the acoustic values of each participant's 3 responses on each session/attractiveness combination: control/attractive, control/unattractive, experimental/attractive, and experimental/unattractive.

In addition, in the first session and before the experiment, participants were asked to read and sign the consent form, as well as take the short olfactory sensitivity test. In the second session, and after the

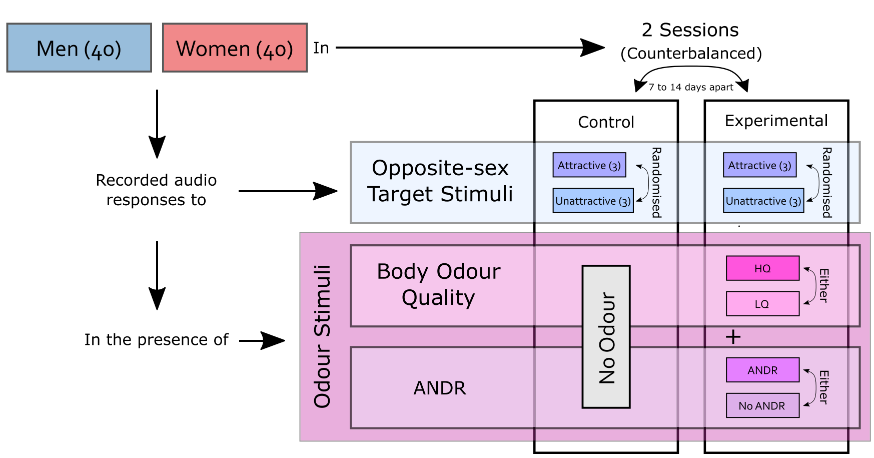

Fig. 1. Experimental design. Diagram of the sessions and stimuli used in each case. The order of session was counterbalanced between participants in each odour stimuli combination (odour quality and ANDR). For body odour quality, HQ = high quality; LQ = low quality. ANDR = androstadienone.

experimental procedure, participants were debriefed. Their data were only retained and analysed if they still gave consent after being fully debriefed.

2.6. Acoustic analysis

Acoustical analyses of the recordings were done following the method described in Leongómez et al. (2014). We used a batch-processing script updated and optimised by Jose Joaquin Atria, based on an original script by Setsuko Shirai (https://www.ucl.ac.uk/~ucjt465/scripts/praat/get_formants_praatlist.praat), in Praat, version 6.0.41 (P. Boersma and D. Weenink, 2018; www.praat.org). Values on intensity (dB), F_0 (Hz), and the first three formants (F_1, F_2, F_3) were obtained every 10 ms. A noise-resistant autocorrelation method (75–300 Hz for male voices, 100–500 Hz for female voices) was used. Additional details are provided in the Supplementary Material available on-line.

2.7. Statistical analysis and mixed modelling

The coding for all statistical analyses, figures, and tables was created in an R Markdown file, using R version 4.0.0 (R Core Team, 2020) and RStudio version 1.3.947. This file is available from the OSF (https://doi.org/10.17605/OSF.IO/GWBHU). The output of that R Markdown file (in PDF format) constitutes the Supplementary Material to this article. All models were fitted using the *lmer* function from the *lmerTest* package (Kuznetsova et al., 2017). All statistical tests are two-tailed. Figures were created using *ggplot2* (Wickham, 2016) and *ggpubr* (Kassambara, 2019), and tables were generated and formatted using *knirt* (Xie, 2015) and *kableExtra* (Zhu, 2019). For a full list of R packages used, see Section 4 in the Supplementary material.

2.7.1. Models of measured variables

To test the effects of the presence or absence of body odour (i.e. control/experimental sessions), the quality of body odour (HQ, LQ), and the presence or absence of added ANDR (+ ANDR, no ANDR) on the acoustic parameters and attractiveness ratings, while taking into account the sex of the participants and the attractiveness category of the target stimuli, we used linear mixed models (LMM). Separate (but with identical factor structure) models were fitted for mean F_0, F_0 SD, F_0 CV, mean intensity, and attractiveness ratings.

Because the main focus was to test the effects of the body odour, and participants were only exposed to these in the experimental session, we only report the main effect of odour Condition, as well as all its interactions with sex, odour quality, ANDR, and Stimuli Attractiveness. We do not report here the main effects of sex, body odour quality, nor the effect of adding ANDR, as these would be confounded with characteristics other than the experimental manipulation, but full factorial models are reported in Section 2.4 of the Supplementary Material (Tables S2, S4, S6, S8 and S10). For all models, Subject (the participant ID), was also included as random factor, with correlated random slopes and intercepts for each participant between Sessions (control, experimental).

In all cases, residuals were closer to a normal or gamma (inverse link) distribution. These models, and their diagnostics (residual distribution, homoscedasticity, and linearity of each fixed factor), are detailed in Section 2.4 of the Supplementary Material.

Contrasts comparing the effect of the condition for each sex, odour quality, ANDR and target stimuli attractiveness category combination (used in model figures), were performed using the functions *emmeans* and *contrast* from the *emmeans* R package (Lenth, 2019).

2.7.2. Models to predict attractiveness ratings

Finally, to explore the association between the perceived attractiveness of each target stimulus to each participant and the acoustic characteristics of their responses, we fitted mixed linear regressions predicting the attractiveness ratings given by participants to each target stimulus, in each session.

In the initial model, fixed predictors were: participant sex, mean F_0, F_0 CV, minimum F_0, (mean) intensity, odour quality and ANDR, as well as the sex × mean F_0, sex × F_0 CV, sex × Minimum F_0, and sex × Intensity interactions. The interaction between participant ID (Subject) and Session was entered as a random intercept factor, to account for the two times that each participant rated and responded to each target stimulus (one in each condition), and to avoid pseudoreplication.

This parameterised initial model was then reduced to include only the most relevant acoustic variables (intermediate model): mean F_0, minimum F_0 and F_0 CV, as well as sex and their interactions with sex were entered as fixed predictors. Finally, this was further reduced, to include as fixed predictors only mean F_0, F_0 CV and sex, with no interactions (final model). The random term remained unaltered in these models.

Initial, intermediate and final models were then compared using the Akaike information criterion (AIC) and Akaike weights and the best-supported model (i.e. the model with the lowest AIC with a ΔAIC higher than two units from the second most adequate model, and higher Akaike weight) is reported (Wagenmakers and Farrell, 2004). To do this, we used the *ICtab* function from the *bbmle* package (Bolker, 2017). Pseudo-R^2 values for these model were obtained using the function *r.squaredGLMM* from the package *MuMIn* (Bartoń, 2020). Once a final model was fitted, model diagnostics were performed.

The residual distribution of the final model was bimodal, and hence differed from a normal distribution. Also, given that the outcome variable (attractiveness ratings) is discrete, Poisson, quasi-Poisson and negative binomial distributions could be tentatively appropriate, but none of these converged, even when separate models were fitted for women and men. Furthermore, the function *check_distribution* from the package *performance* (Lüdecke et al., 2020) showed that the most likely family distribution for this final model was the normal distribution, based on its residuals. Therefore, we used a normal distribution (i.e. a general LMM), but calculated percentile bootstrap confidence intervals for the model estimates, based on 1000 simulations, using the *confint.merMod* function, from the *lme4* package (Bates et al., 2015).

In these models we included F_0 CV and not F_0 SD, for three reasons: first, given that both are measures of F_0 variability, they are highly correlated (see Tables S3 to S5 in the Supplementary Material). Second, unlike F_0 SD, F_0 CV was not significantly correlated with mean F_0 in women, nor in men (Tables S4 and S5 in the Supplementary Material, respectively). Finally, we preferred F_0 CV given that it is a better representation of the perceptual variability, as it takes into account the mean F_0 of each recording (Eguchi and Hirsh, 1969; see also Pisanski et al., 2018). These models, and the diagnostics of the final model (residual distribution, homoscedasticity, and linearity of each fixed factor), are detailed in Section 2.5 of the Supplementary Material.

3. Results

3.1. Descriptives

Descriptive statistics for each measured variable for each group, in each session (control, experimental), and for each target attractiveness category (attractive, unattractive), are presented in Table S1 (female participants) and Table S2 (male participants) in the Supplementary Material.

Fig. 2 shows the distribution of mean F_0 (Hz), F_0 SD (Hz), F_0 CV (Hz), mean intensity (dB), F_1 (Hz), F_2 (Hz), F_3 (Hz), recording length (ms), time recognised as speech (ms), speech proportion (i.e. the proportion of the length of each recording that was recognised as speech), age (years) and attractiveness ratings, for each group of women (Fig. 2A) and men (Fig. 2B).

Bivariate (Pearson) correlations between the continuous variables

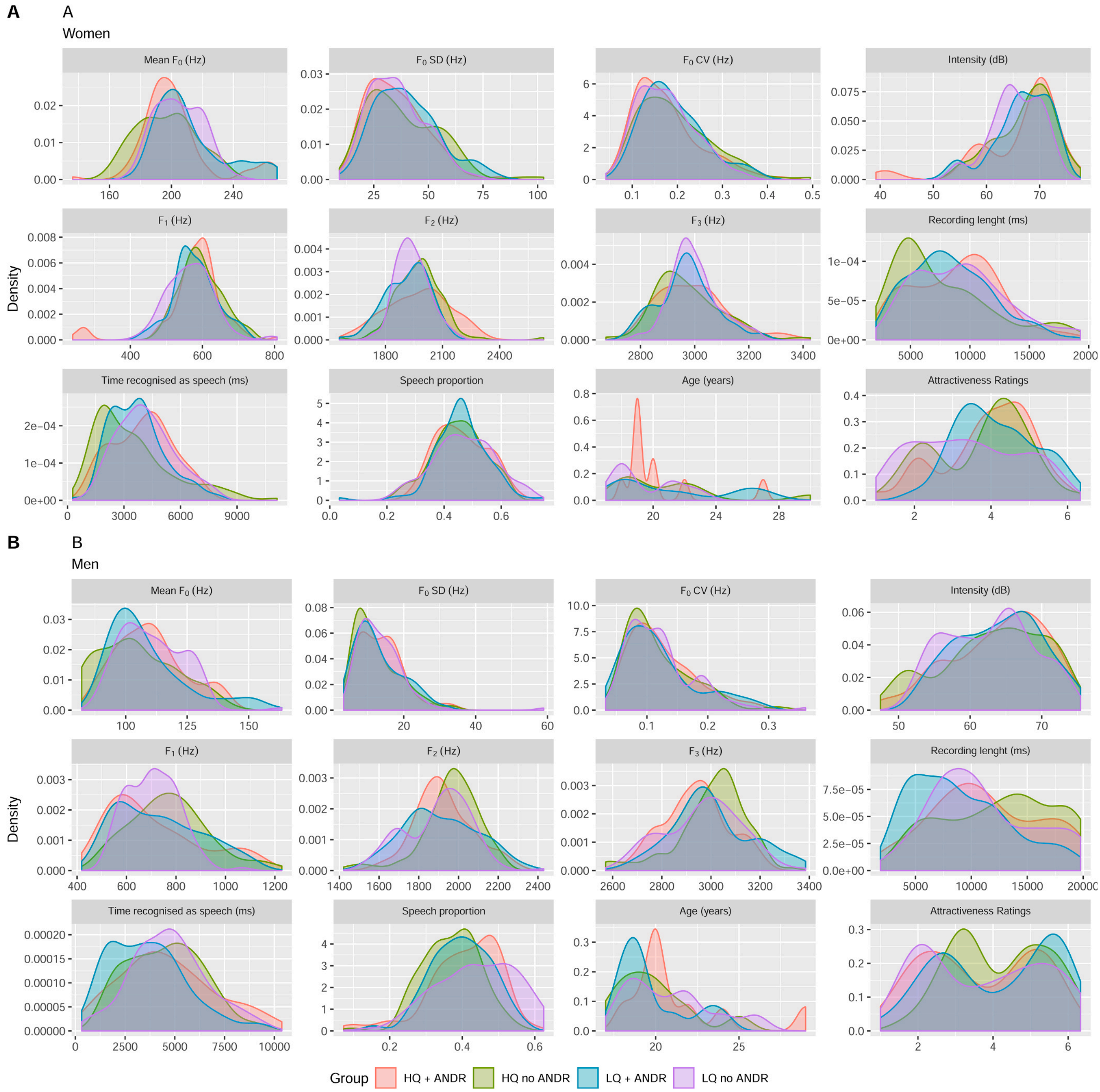

Fig. 2. Distribution of all measured variables by sex and condition. (A) Women. (B) Men. Detailed descriptives are found in Table S1 for women, and Table S2 for men, in the Supplementary material.

included in the statistical models are found in Tables S3 to S5, for all participants combined, men and women, respectively. Mean F_0 was positively and significantly correlated with F_0 SD and Intensity in both men and women, as well as with the length of the recording in men, and marginally positively associated ($r = 0.09$) with the attractiveness ratings given by men. The two measures of F_0 variability, SD and CV, were highly correlated, and were positively associated with mean intensity and (particularly in women) with the attractiveness ratings given to target stimuli.

3.1.1. Time recognised as speech

Time recognized as speech was highly associated with recording length in both women and men (Fig. 3A). The actual speaking time (recognized as speech), although significantly higher for men than for women, was not affected by the presence of body odour (i.e. it did not change between sessions; Fig. 3B).

The proportion of time recognised as speech, however, was significantly higher in women's than in men's responses. That is, although men tended to record longer voice responses, women tended to spend proportionally less time in *silence* (Fig. 3C).

3.2. Models of measured variables

To avoid the possibility that apparent differences between groups might be an artefact of between-subject differences, we tested each participant in two sessions: control (no odour stimuli), and experimental (odour stimuli).

The within-subject effects involving Session are reported in Table 1,

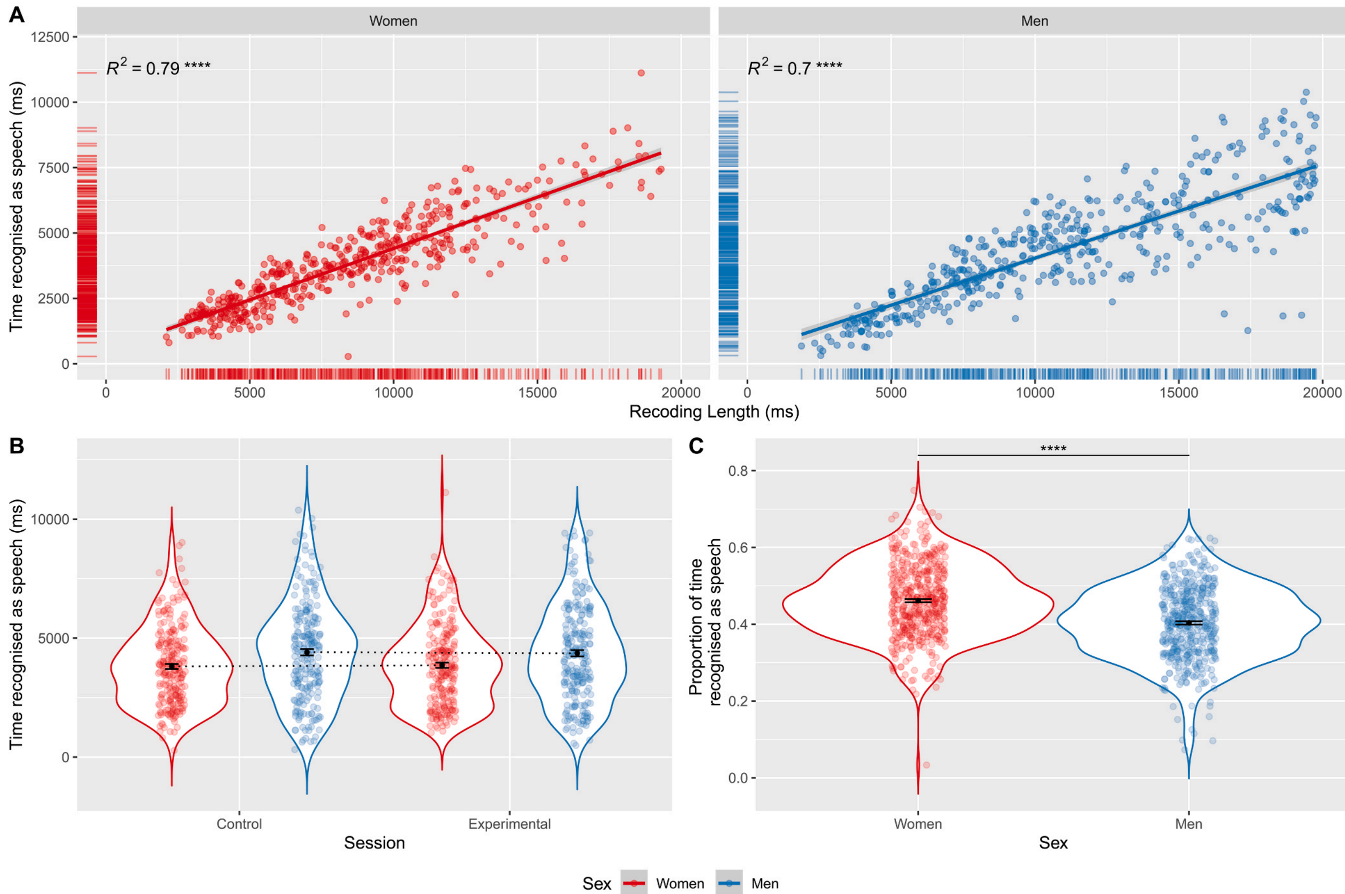

Fig. 3. Differences in time recognised as speech and recoding length. (A) Correlation between time recognised as speech and recoding length. (B) Within-subject differences in time recognised as speech in responses to attractive and unattractive target stimuli. (C) Proportion of time recognised as speech by sex. Comparisons between men and women were performed using *t*-tests: ****$p < 0.0001$.

Table 1
Context-dependent variation in vocal parameters and attractiveness ratings.

Effect	Vocal parameter								Attractiveness ratings	
	Mean F_0		F_0 SD		F_0 CV		Intensity			
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
S	1.44	0.234	3.97	**0.05**	2.66	0.107	0.11	0.736	0.02	0.887
S × SA	1.01	0.316	1.79	0.181	1.14	0.286	1.13	0.288	0	0.956
S × Sex	3.6	0.062	0.54	0.465	0.38	0.539	0.02	0.891	1.83	0.18
S × OQ	0.85	0.36	0.01	0.912	0.05	0.831	0.17	0.677	0.77	0.383
S × ANDR	0.46	0.499	1.19	0.279	0.95	0.334	0.41	0.524	0.06	0.812
S × SA × Sex	2.21	0.137	0.08	0.773	0.06	0.812	0.01	0.929	2.12	0.146
S × SA × OQ	0.13	0.714	0.23	0.633	0.28	0.594	0.25	0.617	0.54	0.465
S × Sex × OQ	0.77	0.382	1.32	0.254	1.32	0.253	0.03	0.856	0.98	0.325
S × SA × ANDR	0.08	0.782	0.97	0.324	1.16	0.282	0.07	0.788	8.77	**0.003**
S × Sex × ANDR	1.39	0.242	1.56	0.215	1.2	0.276	0.35	0.557	1.74	0.191
S × OQ × ANDR	0.52	0.471	1.97	0.165	2.16	0.146	1.44	0.234	0.46	0.501
S × SA × Sex × OQ	0.01	0.932	0.04	0.833	0.47	0.494	1.49	0.223	0.97	0.326
S × SA × Sex × ANDR	0.57	0.449	0.19	0.659	0.13	0.715	0.37	0.546	0.27	0.603
S × SA × OQ × ANDR	0	0.947	1.28	0.259	1.5	0.22	0.47	0.493	0.05	0.819
S × Sex × OQ × ANDR	2.23	0.14	1.36	0.247	1.33	0.252	0.04	0.851	3.08	0.083
S × SA × Sex × OQ × ANDR	1.88	0.171	0	0.947	0.01	0.933	1.72	0.19	2.09	0.149

S = Session (control, experimental); Sex = participants sex (women, men); OQ = odour quality (high quality, low quality); ANDR = androstadienone (ANDR, no ANDR); SA = target stimuli attractiveness (attractive, unattractive). For all results, including all main effects, *df* and Sums of Squares, see Tables S2, S4, S6, S8 and S10 in the Supplementary Material.

reflecting the experimental design (full models, including Satterthwaite's approximation to degrees of freedom and sum of squares, are provided in Tables S2, S4, S6, S8 and S10 in the Supplementary Material).

Analysis revealed that the inclusion of odour stimuli did not have a significant main effect on any of the models for measured acoustic variables (Table 1; Fig. 4A), except for variability in F_0 (measured as F_0 SD), in which the inclusion of body odour in the experimental session caused participants to decrease their pitch variability. However, this effect was only marginally significant, and it was not found when

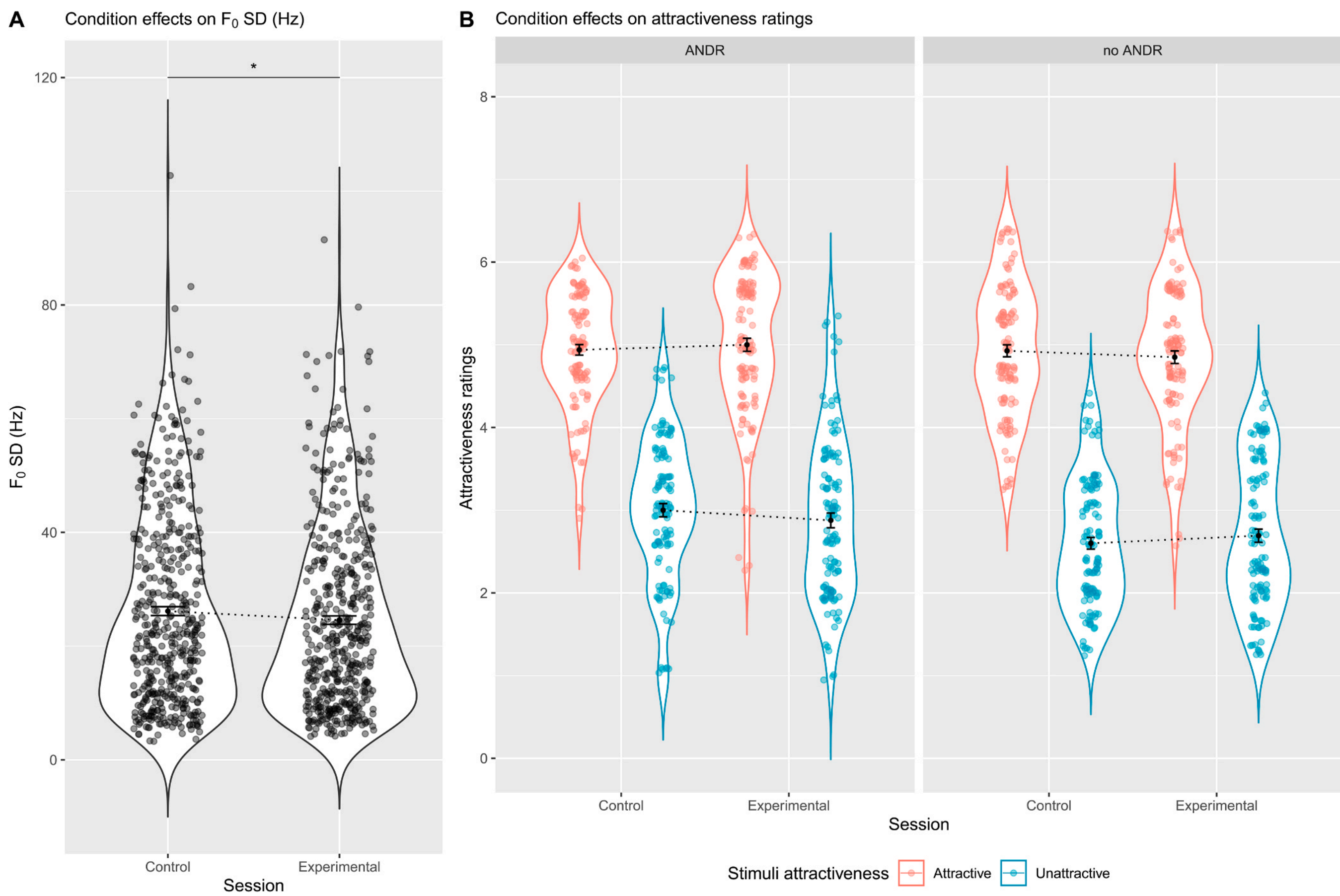

Fig. 4. Significant Session effects and interactions. (A) Main effect of Session for F_0 SD. (B) Interaction between session, target stimuli attractiveness and ANDR for Attractiveness ratings. The black dashed line represents the general within-subject change across sessions (pairwise contrasts using *emmeans*; https://cran.r-project.org/web/packages/emmeans/vignettes/interactions.html). Significant effects of session are represented with solid lines and stars above violin plots: *$p < 0.05$.

variability in F_0 was measured as F_0 CV (i.e. controlling for perceptual variability), suggesting that it was not a robust effect.

In addition, we found a significant, 3-way interaction between session, stimuli attractiveness, and ANDR for the attractiveness ratings given to target stimuli (Table 1; Fig. 4B). The inclusion of body odour (either high or low quality) with added ANDR in the experimental session caused participants to give more extreme ratings to target stimuli (i.e. higher ratings to attractive stimuli and lower ratings to unattractive stimuli). However, for participants who were exposed to male body odour without added ANDR in the experimental session, this effect was in the opposite direction (i.e. a tendency to give lower ratings to attractive, and higher ratings to unattractive, stimuli). Pairwise contrasts, however, showed that these changes (after adjustment for multiple comparisons) between the control and experimental sessions were not significant (Fig. 4B).

3.3. Models to predict attractiveness ratings

The initial mixed linear regressions included Sex, Mean F_0, F_0 CV, (mean) Intensity, odour quality and ANDR, as well as the interactions between sex and mean F_0, sex and F_0 CV, and sex and intensity were included as fixed predictors of the attractiveness rating given to each target stimulus, by each participant in each session. The interaction between subject (participant ID) and session was also kept as a random intercept factor.

In this initial model, only F_0 CV was a significant predictor of the attractiveness ratings (see Table S11, in the Supplementary Material). We then reduced this highly parameterised model to an intermediate model, including only the most relevant acoustic variables: mean F_0, minimum F_0 and F_0 CV, but maintaining sex and the interactions between of sex with mean F_0, minimum F_0 and F_0 CV as fixed predictors, and the interaction between subject and session as a random factor (see Table S12, in the Supplementary Material). Here, again, only F_0 CV was a significant predictor of the attractiveness ratings. This intermediate model was further reduced to only include, as fixed factors, sex, mean F_0 and F_0 CV, in an additive model with no interactions (see Table S13, in the Supplementary Material). The random term was not changed.

This final model, however, was much more likely to be the best of the three models, as revealed by AIC and w_i(AIC) (see Table S14, in the Supplementary Material). The AIC of the final model was about 64 units below that of the initial model, and more than 2 below the intermediate model. In addition, Akaike weights established that the final model, given its increased parsimony and similar predictive power, was most likely to be the best of the three models (in fact, more than three times more likely in comparison to the intermediate model, and several million times more likely to be the best model compared to the initial model).

The final model, however, did not meet the assumptions of residual distribution or homoscedasticity (see Fig. S11 in the Supplementary Material). In particular, the residual distribution was extremely bimodal, even when separate models were fitted for women and men, and no distribution attempted from generalised linear mixed models that converged produced an appropriate model. For this reason, and because a normal distribution was the most probable (see Table S15 in the Supplementary Material), we calculated bootstrap confidence intervals for the model estimates, as this helps in dealing with these issues (Fox, 2016) and can facilitate the assessment of associations even in the absence of p values.

Within this model, sex, mean F_0 and F_0 CV were found to significantly predict attractiveness ratings. Men rated the attractiveness of target stimuli by an estimate of 0.87 units higher than women. For all participants, both mean F_0 and F_0 CV positively predicted attractiveness ratings (Table 2). For each increment of 1 Hz in mean F_0, ratings were estimated to increase by 0.01 units, and by each increment of 1 in F_0 CV, the model estimated an increase of 3.18 points in rated attractiveness (or, to use more realistic F_0 CV units, attractiveness ratings increased by 0.318 units for each 0.1 increment in F_0 CV).

Interestingly, however, while the slope of the association between mean F_0 and the attractiveness ratings predicted by this final model was close to 0 for women, and only slightly positive for men (Fig. 5A), for F_0 CV it was clearly positive not only for both men and women, but for every single participant (Fig. 5B), regardless of the odour condition to which they were exposed.

4. Discussion

4.1. Odour effects on voice modulation and attractiveness ratings

Previous research showed that men's perceived attractiveness to women is increased by the presence of male axillary secretions (Thorne et al., 2002), as well as by exposure to androstadienone (Saxton et al., 2008). Because of this, we expected that men portrayed in the target videos would be regularly perceived as more attractive during the experimental session than the control session, leading women to speak with increased voice F_0, which tends to be attractive to gynephilic men (Feinberg et al., 2005; Jones et al., 2008). Similarly, and because low F_0 signals masculinity and is a robust cue of dominance (Puts et al., 2007; Wolff and Puts, 2010), we expected men to lower their pitch when exposed to male body odour, especially if it was of high quality, as the perception of competition was likely to increase. Contrary to these expectations, the addition of male odour did not produce any consistent changes in vocal parameters. There was only a main effect of pitch variability when measured as F_0 SD, but not when measured as F_0 CV, suggesting that this could thus be an artefact of the measurement of variability without controlling for perceptual differences arising from tone (and sex) of the voice.

However, we did find that the presence of body odour with added ANDR caused participants to tend to give target videos more extreme ratings corresponding to the attractiveness category of the targets, while the presence of body odour without added ANDR caused the opposite tendency in participants of both sexes. While the reasons for these effects are unclear, we speculate that this could be because the presence of male body odour may decrease selectiveness in both women and men, or make targets appear as more similarly attractive (because the odour stimulus, a signal of quality, was always the same for each participant, regardless of the target evaluated). However, the addition of ANDR seem to have had the opposite effect: increasing selectiveness. For example, in women, this could be because the presence of ANDR may increase the preference for attractive targets. In men, instead of increasing the perception of competition for men, ANDR may have boosted their own confidence and/or self-perceived attractiveness, affecting their selectiveness. An explanation for these results would require future studies to specifically control for changes in variables such as self-confidence and self-perceived attractiveness in the presence of ANDR. However, it is important to note that pairwise contrasts revealed that the difference in attractiveness ratings between the control and experimental sessions (for participants exposed to odours either with or without added ANDR, separately), did not reach significance after adjustment for multiple comparisons (see Fig. 4B).

It was unexpected that neither high-quality odour nor added androstadienone had additional effects. It may be that the difference in odour quality between the high and low quality composites was insufficient to elicit quality-related changes in modulation. Using a larger sample of odour donors, and therefore accentuating differences between high- and low-quality odours, could potentially make the effect of odour quality measurable. In addition, measuring participants' subjective evaluations of intensity and pleasantness of the odour stimuli would enable a manipulation check and further exploration of differences in odour condition (e.g., Oren and Shamay-Tsoory, 2019). Alternatively, the lack of effects could be due to methodological choices, including the time that odour samples were left in the cubicle before each session (15 min), and the time that cubicles were left open before testing another participant (>15 min), that may have been insufficient to avoid the residual presence of previously used stimuli, potentially creating some level of smell mixture and confounding any effects of different odour stimuli.

With respect to added androstadienone, there are several possibilities: for example, other constituents of the axillary odour could have a more prominent role in odour evaluation (see d'Ettorre et al., 2018), or these other constituents may be more perceivable in the odour mixture. A more general, evolutionary hypothesis for the lack of effects of ANDR on voice modulation, could be related to an inactivation of the vomeronasal system that would have occurred in catarrhines with the appearance of trichromacy in primates (Gilad et al., 2004; Zhang and Webb, 2003). This tendency can also be observed in primates when comparing nocturnal and diurnal lineages: the former maintain a much greater olfactory brain structure, while the latter have larger cerebral visual structures (Barton et al., 1995). This inactivation could be associated with pseudogenization, in this case leading to decreased functions or changes in the genes related to the vomeronasal organ. In addition, the main olfactory system suffered a progressive inactivation, such that only 70% of the olfactory receptor genes are functional in Old World primates, and only 40% in humans (Gilad et al., 2003), potentially leading to a reduced (or non-existent) role of at least *some* molecules that function as social chemosignals in related species.

Nevertheless, the lack of consistent ANDR effects in our study is consistent with Hare et al. (2017), who found no effects of ANDR on sex perception or evaluation of masculinity-related sex-specific characteristics. Ultimately, the null effect is also in line with recent doubts cast on the existence of specific pheromones in humans and thus should not be expected to have any special effects on any and all cognitive functions and human behaviours (Wyatt, 2015).

Table 2
Final model summary (with bootstrap 95% CI).

	Estimate	Lower 95% CI	Upper 95% CI	Std. Error	df	t	p
(Intercept)	2.02	0.83	3.09	0.59	299.83	3.42	**< 0.001**
Sex (men)	0.87	0.33	1.47	0.29	267	2.98	**0.003**
Mean F_0 (Hz)	0.01	0	0.01	0	274.69	2.1	**0.037**
F_0 CV (Hz)	3.18	1.86	4.61	0.72	714.5	4.39	**< 0.0001**

$R^2_{marginal} = 0.03$, $R^2_{conditional} = 0.13$. Confidence intervals were calculated as the 2.5 and 97.5 percentiles from bootstrap (1000 simulations). Women were used as reference category for Sex. Significant effects are in bold.

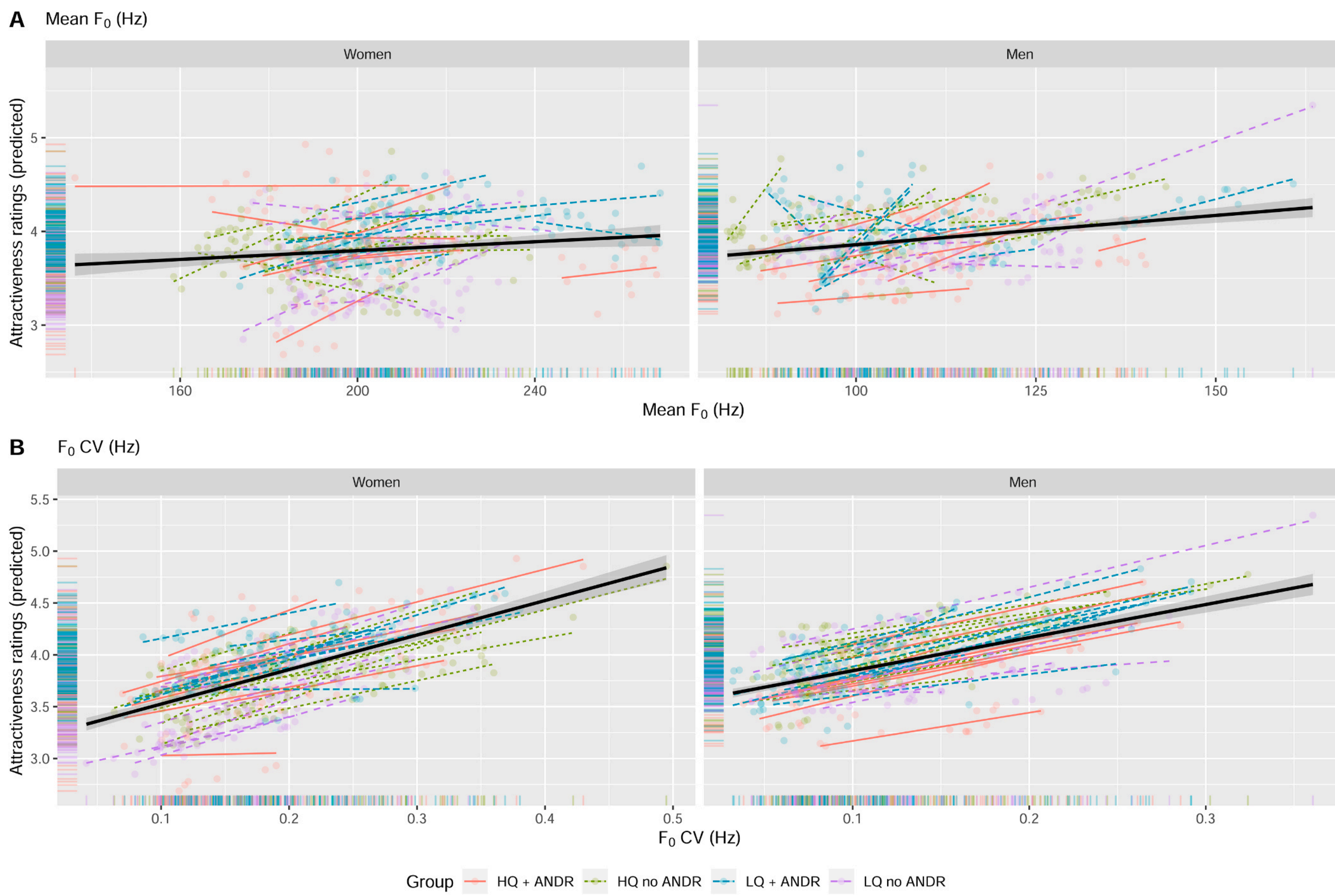

Fig. 5. Single term predictor slopes. Slope of coefficients for each (single term) fixed predictor, against predicted attractiveness ratings for the Final Model (linear relationship between each model term and predicted response), for women (left) and men (right). (A) Mean F_0. (B) F_0 CV. Lines represent the slope for each participant, according to their group. The black line with error represents the general effect.

4.2. Voice characteristics as predictors of perceived attractiveness

Our experimental paradigm was closely based on Study 1 of Leongómez et al. (2014), but there were some important differences. First, of course, the current study incorporated the addition of male body odour and androstadienone in the experimental sessions. Second, it enabled further investigation of vocal modulation in courtship contexts by asking participants to rate each target video, in the two experimental sessions, providing us with the opportunity to test how voice characteristics are related to perceived attractiveness.

Voice modulation, and specifically vocal modulation during courtship, is a complex phenomenon that has gained increasing interest in recent years (e.g. Farley et al., 2013; Fraccaro et al., 2013, 2011; Hughes et al., 2010; Leongómez et al., 2014; Pisanski et al., 2018; for a review see Hughes and Puts, 2021), with important implications for our understanding of vocal communication (Leongómez et al., 2021a,b). Understanding what voice parameters are modulated, in which direction, and what social and perceptual effects these modulations have, are still matters of debate that call for more research. For example, in a tightly controlled experiment, Leongómez et al. (2014) found that both men and women increase pitch variability when responding to attractive target stimuli. The same finding in both sexes suggests pitch variability is a key parameter, but women did so when competing with an attractive woman. In a less controlled but more ecologically valid experiment, Pisanski et al. (2018) recorded participants during real, face-to-face interactions in a speed-dating game, finding that women increased both their average fundamental frequency and its variability (measured as either F_0 SD or F_0 CV) with people they selected as dates. However, although men lowered their F_0 towards individuals selected as dates, their pitch variability (either F_0 SD or F_0 CV) was not correlated with selection of dates.

Such disparities in results could be due to differences in experimental design, such as between responses to muted videos (Leongómez et al., 2014) (to avoid possible effects of pitch convergence; see Gregory et al., 2001), and real-life interactions (Pisanski et al., 2018). Furthermore, participants in the former study were instructed to explain whether and why they would like to go on a date with the person in the video, and this was done in isolation in a cubicle, while in the latter recordings were of free conversations between two participants in a noisy and busy speed-dating game setting. This suggests two things: first, that voice modulations do occur during courtship, and so can play an important part in shaping how we are perceived by others. And second, that vocal modulations are very context sensitive.

Our results, mostly congruent with Leongómez et al. (2014), suggest that pitch variability is modulated according to the attractiveness of the listener in this courtship scenario. Here, our model of perceived attractiveness (measured as attractiveness ratings given to target stimuli), shows that pitch variability (measured as F_0 CV) was a better predictor than mean F_0. Moreover, F_0 CV was predicted to be robust across participants and conditions, and in all fitted models regardless of their complexity. Importantly, F_0 CV is a measure of pitch variability, that controls for perceptual differences that depend on the average pitch of a voice sample.

4.3. Conclusions

Our study is the first to test the effects of male odour quality and ANDR in voice modulation and attractiveness ratings. We did not find support for either odour quality or ANDR effects. Furthermore, we did not detect any consistent effects of the presence of body odour. Although the null effects of ANDR are in line with recent evidence (Hare et al., 2017), the lack of effects of odour quality, and especially of the presence of body odour (vs responses in a no-odour, control session), are somewhat surprising.

However, consistent with evidence of vocal modulations in courtship scenarios, we found that voice characteristics predict attractiveness ratings given to target videos, regardless of the presence or absence of any body odour. Recent evidence, however, is inconsistent regarding the expected direction of such modulations and the relative importance of each acoustic parameter found in different studies (Leongómez et al., 2014; Pisanski et al., 2018). This, we think, suggests that human voice modulation is extremely context-sensitive; for example, it could be that an attractive opposite-sex person could elicit an increase in pitch variability (Leongómez et al., 2014), while the presence of people nearby (as in Pisanski et al., 2018) could create an opposite tendency to decrease these modulations, therefore confounding these effects. If this is true, experimental tests of vocal modulation in courtship (and likely other) scenarios would need to consider these differences and their potential confounding effects.

Declarations

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Compliance with ethical standards

All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional research committee and with the 1964 Helsinki Declaration and its later amendments or comparable ethical standards. Written informed consent was obtained from all individual adult participants included in the study.

CRediT authorship contribution statement

Juan David Leongómez: Conceptualisation, Methodology, Formal analysis, Software, Data curation, Writing- original draft preparation, Visualization, Investigation, Funding acquisition. **Oscar R. Sánchez**: Writing - original draft preparation, Funding acquisition. **Milena Vásquez-Amézquita**: Writing - original draft preparation, Writing - review & Editing. **S. Craig Roberts**: Conceptualisation, Methodology, Writing - original draft preparation, Writing - review & Editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no conflict of interest.

Data and code availability

All data used for this article are openly available at the OSF (https://doi.org/10.17605/OSF.IO/53BZK). Code to perform data wrangling, tables, figures, and all analyses, is available in PDF ('Supplementary-Material.pdf') and *R Markdown* ('Supplementary-Material.Rmd') formats, so that it can be fully reproduced and explored in depth (https://doi.org/10.17605/OSF.IO/GWBHU).

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.beproc.2021.104531.

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