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### ► To cite this version:

Arnaud Tognetti, Valérie Durand, Melissa Barkat-Defradas, Astrid Hopfensitz. Does he sound cooperative? Acoustic correlates of cooperativeness. *British Journal of Psychology*, 2020, 111 (4), pp.823-839. 10.1111/bjop.12437 . hal-03169806

**HAL Id: hal-03169806**

**<https://hal.science/hal-03169806>**

Submitted on 13 Nov 2023

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# Does he sound cooperative? Acoustic correlates of cooperativeness

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The sound of the voice has several acoustic features that influence the perception of how cooperative the speaker is. It remains unknown, however, whether these acoustic features are associated with actual cooperative behaviour. This issue is crucial to disentangle whether inferences of traits from voices are based on stereotypes, or facilitate the detection of cooperative partners. The latter is likely due to the pleiotropic effect that testosterone has on both cooperative behaviours and acoustic features. In the present study, we quantified the cooperativeness of native French-speaking men in a one-shot public good game. We also measured mean fundamental frequency, pitch variations, roughness, and breathiness from spontaneous speech recordings of the same men and collected saliva samples to measure their testosterone levels. Our results showed that men with lower-pitched voices and greater pitch variations were more cooperative. However, testosterone did not influence cooperative behaviours or acoustic features. Our finding provides the first evidence of the acoustic correlates of cooperative behaviour. When considered in combination with the literature on the detection of cooperativeness from faces, the results imply that assessment of cooperative behaviour would be improved by simultaneous consideration of visual and auditory cues.

The manifestation of cooperation and trust across contexts has been the focus of much research in economics, biology, and psychology. Decisions about interpersonal interactions that require cooperation are influenced by relatedness (kin selection), spatial constraints (e.g., spatial selection, multi-level selection), and reputation (Hamilton, 1964; Nowak, 2006; Rand & Nowak, 2013; West, Griffin, & Gardner, 2007). It remains unknown, however, how cooperative partners can be identified in the absence of these contextual factors. One possibility is that people use phenotypic cues to assess the cooperative intent of potential partners.

Studies that examined the existence of such cues focus primarily on facial traits. Discriminating between high and low altruistic individuals, and estimating their trustworthiness and cooperation, is fast, spontaneous, and intuitive processes (Bonnenfon,

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Hopfensitz, & De Neys, 2013, 2017; Dzhelyova, Perrett, & Jentsch, 2012), which are based on both static and dynamic facial cues. For example, only a few seconds are needed to predict the trustworthiness or cooperation of a target individual from a picture of his/her face (Bonnefon *et al.*, 2013; De Neys, Hopfensitz, & Bonnefon, 2015) or a silent video clip (Fetchenhauer, Groothuis, & Pradel, 2010; Oda, Yamagata, Yabiku, & Matsumoto-Oda, 2009). Individuals' assessments and decisions regarding a cooperative other rely on facial cues, including width-to-height ratio (Little, Jones, DeBruine, & Dunbar, 2013; Stirrat & Perrett, 2010, 2012) and the presence of a genuine (i.e., Duchenne) smile (Brown, Palameta, & Moore, 2003; Centorrino, Djemai, Hopfensitz, Milinski, & Seabright, 2015; Johnston, Miles, & Macrae, 2010; Oda, Naganawa, Yamauchi, Yamagata, & Matsumoto-Oda, 2009; Reed, Zeglen, & Schmidt, 2012). In addition, facial cues of cooperativeness are reliable and valid across cultures (Tognetti, Berticat, Raymond, & Faurie, 2013; Tognetti, Yamagata-Nakashima, Faurie, & Oda, 2018).

Nevertheless, evolutionary ecology highlights the adaptive advantage of *multimodal* signalling in animal communication (Hebets & Papaj, 2005). For example, the *redundant signal hypothesis* suggests that multiple cues considered in combination provide a better estimate than any single cue (Groyecka *et al.*, 2017; Moller & Pomiankowski, 1993). Accordingly, cooperativeness might also be best identified by considering multiple cues.

One likely contributing factor is the voice. As with faces, vocal cues influence the perception of a speaker's social traits. For example, digital manipulation of speech recordings (raising or lowering vocal pitch) alters ratings related to trustworthiness, although this association seems to be context-dependent. Lower-pitched male voices are perceived as *less* trustworthy in economic trust games (Montano, Tigue, Isenstein, Barclay, & Feinberg, 2017; O'Connor & Barclay, 2017; Torre, White, & Goslin, 2016) and mating contexts (i.e., more likely to cheat; O'Connor & Barclay, 2017; O'Connor, Re, & Feinberg, 2011), but *more* trustworthy in general (Oleszkiewicz, Pisanski, Lachowicz-Tabaczek, & Sorokowska, 2017; Schirmer, Feng, Sen, & Penney, 2019; Tsantani, Belin, Paterson, & McAleer, 2016), or when trust is linked to the political context (Klofstad, Anderson, & Nowicki, 2015; Klofstad, Anderson, & Peters, 2012; Tigue, Borak, O'Connor, Schandl, & Feinberg, 2012). Vocal cues also influence ratings of cooperativeness. For example, male voices are perceived as *less* likely to 'contribute to a mutually beneficial goal' when they have a low pitch, but *more* likely to cooperate when they exhibit wide pitch variations in combination with a low pitch (Knowles & Little, 2016).

The voice's influence on the perception of a speaker's social traits could stem from the pleiotropic effect of testosterone on both vocal pitch and cooperative or trust-related behaviours (O'Connor & Barclay, 2017). Indeed, the surge of testosterone during puberty causes the vocal folds to grow longer and thicker through androgen receptors in the epithelial cells of the vocal folds, thus lowering vocal pitch (larger vocal folds mechanically vibrate more slowly than smaller ones; Harries, Hawkins, Hacking, & Hughes, 1998). Testosterone continues to influence vocal pitch through adolescence (Hodges-Simeon, Gurven, & Gaulin, 2015; Pedersen, Møller, Krabbe, & Bennett, 1986) and adulthood (Dabbs & Mallinger, 1999; Evans, Neave, Wakelin, & Hamilton, 2008; Puts, Apicella, & Cárdenas, 2012). Testosterone is also associated with cooperative or trust-related behaviours, but its influence is context-dependent. For example, men with higher levels of testosterone report lower cooperativeness on the self-report altruism scale (Harris, Rushton, Hampson, & Jackson, 1996), a greater likelihood of exploiting their partner's trust in a trust game (Takagishi, Takahashi, & Yamagishi, 2011), and more punitive acts towards other players in ultimatum games (Burnham, 2007). Men with artificially raised testosterone levels are also less generous in ultimatum games (Zak *et al.*,

2009, but see Cueva *et al.*, 2017). Nevertheless, during intergroup competition, men who have high testosterone levels are more cooperative and generous with in-group members (Diekhof, Wittmer, & Reimers, 2014; Reimers & Diekhof, 2015).

Findings that link testosterone with vocal pitch and cooperative behaviour motivated previous research to examine how fundamental frequency (the acoustic correlate of vocal pitch) influences the perception of a speaker's social traits. Such perceptions, could, however, be influenced by other acoustic features such as pitch variations, jitter, and harmonics-to-noise ratio (HNR), which are proxies for intonation, vocal roughness, and breathiness, respectively (Hillenbrand & Houde, 1996; Rabinov, Kreiman, Gerratt, & Bielamowicz, 1995). Indeed, all of these acoustic criteria are sexually dimorphic and thus potentially influenced by sexual hormones such as testosterone. Relevant evidence indicates that, compared with women, men have less variance in fundamental frequency (more monotonous; Puts *et al.*, 2012), but higher and lower values of jitter and HNR, respectively (Graddol, 1989; Van Borsel, Janssens, & De Bodt, 2009). One study showed a weak association between testosterone and pitch variations (Puts *et al.*, 2012), whereas some authors suggest that jitter and HNR are sensitive to hormonal influx because both relate to oscillations of the vocal folds, which are influenced by circulating androgens (Pisanski *et al.*, 2016). Moreover, pitch variations, jitter, and HNR influence listeners' perceptions of cooperativeness or trustworthiness (Belin, Boehme, & McAleer, 2017; Knowles & Little, 2016; McAleer, Todorov, & Belin, 2014; Ponsot, Burred, Belin, & Aucouturier, 2018; Schirmer *et al.*, 2019; Weirich, 2008). State-of-the-art vocal manipulations of pitch highlight the major influence that pitch variations have on perceptions of a speaker's social traits (Belin *et al.*, 2017; Ponsot *et al.*, 2018), such that voices with greater variations in pitch (i.e., more dynamic, less monotonic) are rated as more cooperative than voices with less variations (Knowles & Little, 2016). One interesting finding indicated that women perceive low-pitched male voices as the *least* cooperative when they have small pitch variations, but as the *most* cooperative when they have greater variations (Knowles & Little, 2016). It remains unknown, however, whether acoustic features co-vary in the way they influence the perception of a speaker's social traits. Most importantly, it is unknown whether acoustic features of the voice are associated with *actual* cooperative behaviours, and not only with *perceived* cooperativeness. Thus, it is crucial to disentangle whether inferences of traits from voices are based on dubious stereotypes, or facilitate the detection of cooperative partners.

In the present study, we investigated the existence of acoustic correlates of cooperativeness, by (1) relating cooperative behaviour in an economic social-dilemma game to acoustic parameters measured from recordings of spontaneous speech and (2) examining the potential role of testosterone in this association. Specifically, we quantified the cooperativeness of native French-speaking men in a standard public good game. This game represents a stylized model of a community in which each individuals' well-being depends on their own and others' contributions (Ledyard, 1995). Individually, each individual is best off if s/he contributes nothing and relies on others' efforts to create social benefits by behaving cooperatively. The external validity of the public good game was demonstrated previously by linking individuals' contributions to the public good with cooperative behaviours in naturally occurring situations (Fehr & Leibbrandt, 2011; Rustagi, Engel, & Kosfeld, 2010). We also measured mean fundamental frequency, pitch variations, roughness, and breathiness from spontaneous speech recordings of the same men, and we collected saliva samples to measure their testosterone levels. In line with the previous literature, we hypothesized that men's contributions to the public good would

be associated with vocal-acoustic characteristics due to the influence of testosterone on both cooperative behaviours and acoustic features.

## Methods

The protocol concerning recruitment procedures and data collection was approved by the ethical committee of Toulouse School of Economics - Institute for Advanced Study in Toulouse (#2016-10-001). We obtained written informed consent from all participants.

### Participants

Origin (Ordin & Mennen, 2017; Zimmerer, Jügler, Andreeva, Möbius, & Trouvain, 2014), language (Andreeva *et al.*, 2014; Pépiot, 2014), sexual orientation (Baeck, Corthals, & Borsel, 2011; Gaudio, 1994; Munson, McDonald, DeBoe, & White, 2006), and smoking (Sorensen & Horii, 1982) influence acoustic characteristics. Hence, in the present study we only used the voice recordings of participants that were native French speakers, born in metropolitan France, had French parents and European grandparents, and who neither smoked, nor reported to be homosexual. We expected that approximately 15% of show-ups would not fulfil these prerequisites. As a result, a total of 81 men were recruited as participants in our study, leading to an estimated number of approximately 70 useable observations for speech analysis. Numbers were based on estimated sample size requirements ( $N = 62$ ) for a linear model with 4 explanatory variables with 80% power,  $\alpha = 0.05$ , and  $R^2 = 0.15$  (*pwr.f2.test* function of the *pwr* package in R). Male participants were randomly selected from a pool of more than 4,000 volunteers from the University of Montpellier. None of them had previously participated in a public good game experiment.

From November 2016 to February 2017, 12 experimental sessions took place at the Laboratory of Experimental Economics in Montpellier (University of Montpellier, France). All sessions started at 2 p.m. Each session started in a computer laboratory where participants first played a public good game. Upon completion, they were invited to a separate room for speech recordings.

### Measure of cooperativeness

To quantify cooperation, we used the public good game (Ledyard, 1995). This game, which is considered the benchmark for experimental research on social dilemmas, represents a stylized model of a community in which each individuals' well-being depends on own and others' contributions. Individually, each member is best off if s/he contributes nothing and relies on others' efforts to create social benefits by behaving cooperatively.

The public good game was run on a computer network (interface programmed with LE2M – Software for the Economic Experiments of Montpellier developed by D. Dubois and JM. Rousselle). To prevent visual contact, each participant was seated in an individual cubicle containing a computer terminal. Communication between participants was not allowed. At the beginning of each session, participants received a written copy of the instructions (for details see the Supporting Information). To implement common knowledge of the game and the task, the principal investigator (AT) also read the instructions aloud. Questions were allowed and were answered privately. We checked participants' understanding of the instructions by a computerized questionnaire. To

guarantee experimenter–subject and subject–subject anonymity, a subject number was assigned to each participant.

In each session, participants played, in groups of two, a one-shot linear public good game followed by a conditional contribution in the same game (we followed procedures of Fischbacher *et al.* (2001); for details see the SM). The one-shot public good game is classically used to measure cooperativeness and has the advantage to provide a continuous measure of cooperativeness but does not control for the participants' beliefs. Conditional contributions do control for individuals' beliefs and allow categorization of individuals according to type (as defined by Fischbacher *et al.* (2001); see also the SM). However, only two categories are generally highly represented: *conditional cooperators* (individuals who are willing to contribute more to a public good the more others contribute) and *free-riders* (individuals who do not contribute to a public good regardless of others' contributions).

At the beginning of the one-shot public good game, participants were randomly assigned into pairs. Each participant received an initial endowment of 20 tokens. Then, each player independently decided how to allocate his endowment between a private and a common account. Allocation decisions yielded payoffs in euros. Each token allocated by a subject to his private account paid off 1.50€ for himself while the common account paid off 0.90€ to each member of the pair (marginal per capita return, MPCR = 0.6). It was made clear that each token allocated to the common account would provide exactly the same payoff to each member of the pair regardless of the contributor. From these parameters, it follows that the utilitarian optimum and the efficient symmetric outcome is for all group members to contribute their entire endowments to the public account. However, even under these specifications, it still remains in each individual's self-interest to contribute zero.

After the one-shot public good game, participants were asked, in an incentive compatible way, how much they would contribute if they could condition their contributions on their partner's one (conditional choice).

All participants were informed about their final payoff at the end of the entire experimental session to avoid any potential influence on speech recordings. Average earnings were  $32 \pm 5.60$  € (Mean  $\pm$  SD), and each subject was paid in private.

## **Speech recordings and analyses**

### *Recordings*

At the end of the public good game, each participant was invited to enter individually another room for the speech recordings. A single investigator conducted all the recordings (MBD) which took place in a quiet room of the laboratory of Experimental Economics in Montpellier. We recorded spontaneous speech due to its stronger ecological validity compared with scripted speech (Puts, Hodges, Cárdenas, & Gaulin, 2007; Suire, Raymond, & Barkat-Defradas, 2018). Thus, participants were asked to describe a picture regarding global warming (Figure S1). Once they finished describing the picture, spontaneous speech was elicited by asking: 'Do you think that ecological actions by individual citizens are sufficient to reduce the impact of global change or even to halt it?' (our translation from the original French question).

We used the complete answer produced by participants as material for acoustic analysis. Answers to semi-directive open questions limit content variation while inducing

participants to use a more natural voice, as their attention is concentrated on the expression of their own personal opinions.

We recorded speech samples using a linear PCM recorder with a sampling rate of 22 kHz, 16bits, mono, which were saved into .wav files. To control for intensity, participants were instructed to speak within a constant distance of 15 cm from the recorder.

### *Speech analyses*

Participants who were native French speakers, born in metropolitan France, who had native French parents and European grandparents, and who neither smoked, nor reported to be homosexual were eligible for speech analysis. Our final sample consisted of 64 men (Mean age  $\pm$  SD = 21.6  $\pm$  3.3 years), a majority of which were students (55 out of 64 participants).

The 64 speech samples were analysed using the speech analysis software Praat© version 5.1.45. (Paul Boersma and David Weenink, Phonetic Sciences, University of Amsterdam, [www.praat.org](http://www.praat.org)). Pitch floors were set to 70 Hz with a ceiling of 250 Hz. Other settings were kept as default. For each participant, we extracted values for four acoustic parameters via the voice report menu: mean fundamental frequency (mean F0, the acoustic correlate of vocal height, in Hz), variations of fundamental frequency (proxy of intonation, F0-SD in Hz), jitter (proxy of vocal roughness, in %), and the HNR (proxy of vocal breathiness, in dB).

### **Saliva collection and testosterone assays**

Testosterone concentrations (pg/mL) were measured in saliva samples. This non-invasive technique yields testosterone levels that are highly correlated with free testosterone levels (Ellison, 1988; Vittek, L'Hommedieu, Gordon, Rappaport, & Louis Southren, 1985). At the start of the experiment, each participant was given one labelled tube and straw (Salicaps kits; IBL-Hamburg, Hamburg, G) to collect saliva. Contamination of saliva samples was minimized by instructing participants not to eat, drink (except plain water), smoke, chew gum, or brush their teeth for one hour before the session. Because the change of testosterone rate in the diurnal cycle is the lowest in early afternoon (Dabbs, 1990b), saliva samples were collected at 2.00 p.m. Samples were kept refrigerated during the experiment and then stored at  $-80^{\circ}\text{C}$ . Testosterone levels were analysed by luminescence immunoassay (LIA) technique, using LIA Testosterone kits (IBL, Hamburg). The assay of each sample was replicated twice, and only measures whose intra-assay CV was lower than 10% were used.

### **Additional data**

Sociodemographic questionnaires were also administered (see SM) at the end of the session (after public good game and speech recording sessions). We obtained self-reports on nationality, mother tongue, country of birth of parents and grandparents, sexual orientation, and smoking habits, to use this information as exclusion criteria during data analysis (see above). Moreover, since age, level of education and body mass index (BMI) affect cooperative behaviours, acoustic characteristics, or testosterone levels (e.g., Dabbs, 1990a, 1990b, 1992; Ellison *et al.*, 2002; Gachter & Herrmann, 2009; Jasienska, Jasienski, & Ellison, 2012; Lukas, Campbell, & Ellison, 2004; Schötz & Müller, 2007; Sutter & Kocher,

2007; Torre & Barlow, 2009), we also collected self-reports on age and education and measured and weighted each participant, to allow statistical control for these potentially confounding variables.

### Statistical analyses

To examine whether acoustic characteristics were associated with unconditional contributions to the public good, we used a censored regression model (Tobit model, *censReg* function of the *censReg* package in R). This type of model enables us to control for the fact that contributions had an upper and a lower bound, since players could not contribute less than 0 or more than 20 tokens to the public good. Our explanatory variables were the four acoustic parameters discussed above (mean F0, F0-SD, jitter, HNR). We also added testosterone level to examine its potential influence on contributions to the public good.

We, then, examined whether conditional cooperators ( $N = 44$ ) and free-riders ( $N = 11$ ), the two main categories measured by the conditional contributions (Figure S2), differed in terms of acoustic parameters, by using a logistic regression (*glm* function with a binomial error structure of the *stats* package in R). We used the four acoustic parameters and testosterone level as explanatory variables.

Because co-occurring acoustic parameters are likely to be intercorrelated (e.g., Leongómez *et al.*, 2014; Werth, Voigt, Döllinger, Eysholdt, & Lohscheller, 2010), we checked for multicollinearity by calculating the variance inflation factor (VIF) for all explanatory variables (*vif* function of the *car* package in R). We ruled out potential bias from multicollinearity as all variables demonstrated a low value of VIF for both models ( $VIF < 2.46$ ).

Finally, in order to examine the influence of testosterone level on men's speech, we performed four linear models, one for each acoustic parameter studied (i.e., mean F0, F0-SD, jitter, and HNR). Each acoustic parameter was used as a response variable, and we included testosterone level as an explanatory variable.

We also controlled for the robustness of our results by doing the same models but controlling for several confounding factors known to affect acoustic characteristics, testosterone levels, and cooperative behaviours such as age, BMI, level of education, and duration of the speech.

Statistical analyses were performed using R, version 3.4.2 (R Core Team, 2017). Following the recommendations found in Schielzeth (2010), we centred every continuous variable (including the explanatory variables) in all the models in order to make the effects more easily biologically interpretable.

## Results

Average contributions to the public good, testosterone levels, and acoustic characteristics were similar to results from previous studies using similar subject pools (Suire *et al.*, 2018; Tognetti, Dubois, Faurie, & Willinger, 2016). Participants allocated slightly less than half of their endowment to the public good (Mean  $\pm$  SD =  $8.45 \pm 6.96$  tokens). The mean testosterone level was  $122.91 \pm 44.08$  pg/mL. Mean fundamental frequency ranged between 82.45 and 144.78 Hz (Mean  $\pm$  SD =  $113.59 \pm 13.86$  Hz), pitch variations ranged between 7.14 and 31.30 Hz ( $14.37 \pm 4.88$  Hz), jitter ranged from 1.52% to 5.41% ( $2.68 \pm 0.73$  %), and HNR ranged from 9.10 to 15.52 dB ( $12.06 \pm 1.68$  dB). Also in line

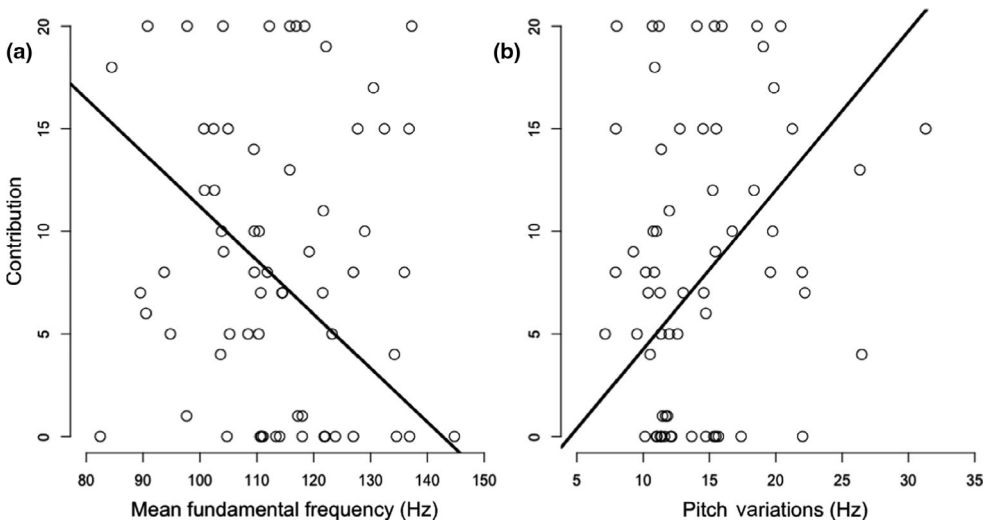


with the existing literature (e.g., Leongómez *et al.*, 2014; Werth *et al.*, 2010), we observed a significant positive correlation between fundamental frequency and pitch variations ( $r = .54, N = 64, p < .0001$ ) and a significant negative correlation between jitter and HNR ( $r = -.68, N = 64, p < .0001$ ). No other significant correlation was observed between the acoustic characteristics ( $-.17 > r > .16, N = 64, .18 > p > .55$  for all correlations).

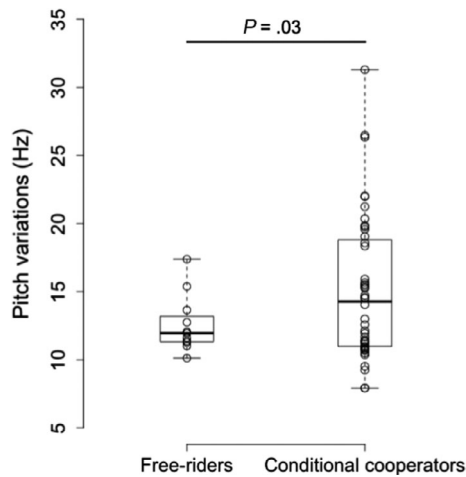
The censored regression model examining the potential association between acoustic characteristics and cooperative behaviours showed that both mean F0 and F0-SD were significantly associated with men's contributions to the public good (see Table S1.A). Lower-pitched voice men ( $\beta = -0.26, SE = 0.12, 95\% CI = [-0.49, -0.03], \chi^2(1, N = 64) = 5.19, p = .02$ , Figure 1a) and men displaying more pitch variations ( $\beta = 0.77, SE = 0.32, 95\% CI = [0.14, 1.40], \chi^2(1, N = 64) = 5.74, p = .02$ , Figure 1b) were more cooperative in a social-dilemma situation. Jitter ( $\beta = -3.42, SE = 2.41, 95\% CI = [-8.15, 1.31], \chi^2(1, N = 64) = 2.00, p = .16$ ), HNR ( $\beta = 0.02, SE = 1.09, 95\% CI = [-2.11, 2.15], \chi^2(1, N = 64) < 0.01, p = .98$ ), or testosterone level ( $\beta = -0.01, SE = 0.03, 95\% CI = [-0.06, 0.05], \chi^2(1, N = 64) = 0.02, p = .88$ ) were not significantly associated with men's contributions to the public good (see Table S1.A).

Consistently, the logistic regression showed that conditional cooperators displayed significantly more pitch variations ( $\beta = 0.24, SE = 0.13, 95\% CI = [0.02, 0.54], \chi^2(1, N = 55) = 4.70, p = .03$ ) than free-riders (Figure 2) but no difference concerning vocal pitch ( $\beta = -0.03, SE = 0.03, 95\% CI = [-0.10, 0.03], \chi^2(1, N = 55) = 0.94, p = .33$ ), jitter ( $\beta = 0.44, SE = 0.64, 95\% CI = [-0.79, 1.79], \chi^2(1, N = 55) = 0.48, p = .49$ ), HNR ( $\beta = 0.55, SE = 0.33, 95\% CI = [-0.05, 1.29], \chi^2(1, N = 55) = 3.23, p = .07$ ), or testosterone level ( $\beta = 0.01, SE = 0.01, 95\% CI = [-0.007, 0.03], \chi^2(1, N = 55) = 1.36, p = .24$ ) was found (see Table S2.A).

Finally, testosterone level did not significantly influence men's mean F0 ( $\beta < -0.01, SE = 0.04, F(1,62) = 0.04, p = .84$ ), F0-SD ( $\beta < 0.01, SE = 0.01, F(1,62) = 0.23,$



**Figure 1.** Contribution to the public good as a function of (a) the mean fundamental frequency (the acoustic correlate of vocal pitch) and (b) the pitch variations (acoustic correlate of intonation). Both the raw data ( $N = 64$ ) and the predicted values from the censored regression model are shown. A censored regression model indicated that men's contributions to the public good are significantly associated with both mean F0 ( $\beta = -0.26, SE = 0.12, p = .02$ ) and F0-SD ( $\beta = 0.77, SE = 0.32, p = .02$ ).



**Figure 2.** Box plot representation of the pitch variations exhibited by the two main categories measured by the conditional contributions: free-riders ( $N = 11$ ) and conditional cooperators ( $N = 44$ ). Medians (thick lines), first and third quartiles, and whiskers representing the entire data range, and individual data points are indicated. A logistic regression indicated that pitch variations significantly differ between free-riders and conditional cooperators ( $p = .03$ ).

$p = .63$ ), jitter ( $\beta < -0.01$ ,  $SE = 0.01$ ,  $F(1,62) = 1.05$ ,  $p = .31$ ), or HNR ( $\beta < -0.01$ ,  $SE = 0.01$ ,  $F(1,62) = 0.24$ ,  $p = .63$ ) (Table S3.A).

The results found were robust to the inclusion of various confounding variables such as age, BMI, level of education, and duration of speech. Specifically, qualitatively similar effects of both F0 and F0-SD were obtained (Tables S1.B S2.B), and none of the confounding variables significantly influenced the outcome variables (see panels B of Tables S1–S3).

## Discussion

Several acoustic features influence the perception of how trustworthy and cooperative the speaker is (Belin *et al.*, 2017; Knowles & Little, 2016; Montano *et al.*, 2017; O'Connor & Barclay, 2017; Oleszkiewicz *et al.*, 2017; Ponsot *et al.*, 2018; Tigue *et al.*, 2012; Tsantani *et al.*, 2016). Their influence could stem from the pleiotropic effect of testosterone on both acoustic features and cooperative behaviours (O'Connor & Barclay, 2017). It is unknown, however, whether acoustic features are associated with actual cooperative behaviour and whether testosterone mediates this association. In this study, we present evidence that both vocal pitch and its variations are related to cooperative behaviour in an incentivized social-dilemma game: the public good game. However, no effect of testosterone level on cooperation, or on any of the other acoustic features studied, was found. Overall, our study provides the first evidence of the existence of acoustic correlates of cooperativeness.

Specifically, our results indicate that men's contributions to the public good are significantly and negatively associated with fundamental frequency and significantly and positively with its variations. When we compared the acoustic traits between conditional cooperators and free-riders (the two main categories as defined in Fischbacher *et al.* (2001)), we found that conditional cooperators exhibit significantly higher pitch

variations than free-riders. Taken together, our results suggest that highly cooperative men have deeper voices and exhibit greater variations in their intonation compared to less cooperative men.

The present results are consistent with the only previous study examining jointly the influence of vocal pitch and its variations on the perception of a speaker's cooperativeness (Knowles & Little, 2016). Indeed, Knowles and Little (2016) found that male voices were perceived as the most likely to cooperate when they exhibited high pitch variations in combination with a low pitch (although it was found for women's but not for men's ratings). Vocal pitch and its variation are, thus, associated in the same way with both cooperative behaviours and perceived cooperativeness. It, therefore, indicates that inferences of cooperativeness from voices might actually facilitate the detection of cooperative partners. This sets the ground for future research, namely whether particular combinations of acoustic traits influence ratings of cooperativeness and to which degree these acoustic cues of cooperativeness are reliable or could be manipulated through conscious control of the speaker (e.g., by lowering voice pitch or by increasing speech's intonation).

Behavioural decisions in the public good games (contributions to the public good) and in the trust game (amounts sent to the other player) are highly correlated (Galizzi & Navarro-Martínez, 2018; Peysakhovich, Nowak, & Rand, 2014), which suggests a strong association between cooperativeness and trustworthiness. Hence, similarly to cooperativeness, vocal pitch and its variations are also likely to be used as cues of trustworthiness. In fact, both acoustic features influence perception of how trustworthy a speaker is. For example, lower-pitched male voices and voices with high pitch variations are perceived as more trustworthy in general (Belin *et al.*, 2017; Oleszkiewicz *et al.*, 2017; Schirmer *et al.*, 2019; Tsantani *et al.*, 2016) or when trust is linked to the political context (Klofstad *et al.*, 2015, 2012; Tigue *et al.*, 2012). It remains unknown, however, whether these acoustic features correlate with *actual* trustworthiness, and not only with *perceived* trustworthiness.

The existence of vocal cues of cooperativeness could stem from the pleiotropic effect of testosterone on both cooperative behaviours (Burnham, 2007; Diekhof *et al.*, 2014; Reimers & Diekhof, 2015; Takagishi *et al.*, 2011) and vocal pitch (Dabbs & Mallinger, 1999; Evans *et al.*, 2008; Puts *et al.*, 2012). As testosterone has immunosuppressive effects (*immunocompetence handicap hypothesis*: Folstad & Karter, 1992; Rantala *et al.*, 2012; but see: J. Nowak, Pawłowski, Borkowska, Augustyniak, & Drulis-Kawa, 2018), men with (costly) lower pitch might benefit from a higher biological quality (Arnocky, Hodges-Simeon, Ouellette, & Albert, 2018; Hodges-Simeon *et al.*, 2015). In addition, they may also be more socially dominant (Puts *et al.*, 2012; Puts, Gaulin, & Verdolini, 2006; Puts *et al.*, 2007). Accordingly, because of their underlying qualities, including access to resources, men with lower pitch would be more cooperative than men with higher pitch because they could better afford the costs associated with cooperative behaviours while receiving reputational benefits (Raihani & Smith, 2015; Sylwester & Roberts, 2010; Tognetti, Berticat, Raymond, & Faurie, 2012; Tognetti *et al.*, 2016). This condition-dependent mechanism could ensure the reliability of the vocal cues of cooperativeness. However, in the present study testosterone levels did not seem to affect cooperation or any of the acoustic features studied. Testosterone is a multiple-effect hormone which is influenced by numerous biological and environmental factors and pathways. As such, it is generally difficult to correlate testosterone levels to other biological or behavioural traits. In addition, we could only collect one sample of saliva for hormonal assays, which might not accurately reflect a participant's basal testosterone level.

Although the present study retains many strengths, it is also subject to several limitations. In particular, it is the first to investigate the existence of acoustic correlates of cooperativeness in speech production. However, the investigation is restricted to French men. To provide broader conclusions, it should not only be extended to women, but to other populations as well. In addition, we did not conduct a perceptual study using our recordings to examine whether listeners use acoustic features as a social cue in a behavioural economic task. Indeed, we recorded individuals' free speech due to its stronger ecological validity (Puts *et al.*, 2007; Suire *et al.*, 2018), but this type of recordings is not suitable for perceptual studies, as recordings roughly differ in duration and semantic content. Finally, we used state-of-the-art methodology in economics to quantify and categorize individuals according to type (Fischbacher *et al.*, 2001). However, we compared two categories with unbalanced sample sizes ( $N_{\text{Free-rider}} = 11$  vs.  $N_{\text{conditional cooperators}} = 44$ ) and the sample size of the free-riders was limited (although its proportion (18%) mimics the proportion found in the general French population; Frey, 2017). Hence, we cannot exclude the possibility that the acoustic differences found between free-riders and conditional cooperators arose from this specific and particular sample of 11 free-riders. It seems, nevertheless, unlikely as the results found using this categorization are qualitatively similar to the ones we found using a continuous measure of cooperativeness (i.e., contributions to the public good).

To conclude, the present study provides evidence that at least two acoustic features (vocal pitch and its local variations) could be used as cues of cooperativeness. Facial cues enable individuals to discriminate between high and low cooperative individuals with an above chance accuracy (Bonnefon *et al.*, 2013, 2017; Fetchenhauer *et al.*, 2010; Little *et al.*, 2013; Oda, Naganawa, *et al.*, 2009; Reed *et al.*, 2012; Stirrat & Perrett, 2010, 2012; Tognetti *et al.*, 2013) but the accuracy of face-based cooperation detection is rather low (Bonnefon *et al.*, 2017). Hence, by highlighting the fact that cooperativeness is advertised by several cues across multiple sensory modalities, our findings pave the way for further investigations examining whether the assessment of cooperative behaviour is improved by simultaneous consideration of both visual and auditory cues.

## Acknowledgements

We are very grateful to D. Dubois for his help during experimental sessions and the Laboratory of Experimental Economics of Montpellier (LEEM, University of Montpellier) for hosting the experiment. We also thank A. Suire, A. Vergès, and J. Gourragné for their help in acoustic analyses and all of the participants in our study. Financial support by PEPS CNRS HomoVox, SINT-ANR-15-CE33-0005-01 and ANR Labex IAST is gratefully acknowledged. This is contribution ISEM 2019-254.

## Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Received 4 April 2019; revised version received 28 October 2019

### Supporting Information

The following supporting information may be found in the online edition of the article:

**Figure S1.** Picture shown to the participants when we recorded their spontaneous speech.

**Figure S2.** Conditional contributions per subject. Subjects were classified following the procedure of Fischbacher, Gächter and Fehr (2001)

**Table S1.** Censored regression models investigating the effect of men's speech on contributions to the public good ( $n = 64$  men).

**Table S2.** Logistic regressions investigating whether free riders ( $n = 11$ ) relatively to conditional cooperators ( $n = 44$ ) differ in term of acoustic parameters.

**Table S3.** Linear regressions examining the effect of testosterone on each of the four acoustic parameters studied ( $n = 63$ ).