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Whistling shares a common tongue with speech: bioacoustics from real-time MRI of the human vocal tract

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Most human communication is carried by modulations of the voice. However, a wide range of cultures has developed alternative forms of communication that make use of a whistled sound source. For example, whistling is used as a highly salient signal for capturing attention, and can have iconic cultural meanings such as the catcall, enact a formal code as in boatswain's calls or stand as a proxy for speech in whistled languages. We used real-time magnetic resonance imaging to examine the muscular control of whistling to describe a strong association between the shape of the tongue and the whistled frequency. This bioacoustic profile parallels the use of the tongue in vowel production. This is consistent with the role of whistled languages as proxies for spoken languages, in which one of the acoustical features of speech sounds is substituted with a frequency-modulated whistle. Furthermore, previous evidence that non-human apes may be capable of learning to whistle from humans suggests that these animals may have similar sensorimotor abilities to those that are used to support speech in humans.

1. Introduction

Whistling produces a loud and pitched sound that approximates a sine wave. These sounds travel well over large distances [1] and are easy to discern from other biological sounds by the rare occurrence of pure-tone sine waves in nature. These features have made whistling a viable alternative sound source for human communication when signal fidelity may be more important than signal complexity [2,3].

Whistling may be a more robust channel in contexts where the voice is unreliable, such as communication over long distances or in poor weather. For example, naval vessels maintain a traditional code of boatswain's calls, in which arbitrary combinations of whistles correspond to simple commands [4,5]. Furthermore, a number of cultures have developed whistled proxies of spoken language [6]. In these languages, the whistled frequency stands in for one of the acoustical features that would normally be carried by the voice [6–8]. Whistled languages encode less information from which to identify the intended speech sounds than voiced speech, but are more robust to long-distance communication. The narrow frequency band of the whistle gives it more power per unit of spectral bandwidth, increasing its signal-to-noise ratio and the effective range of communication [1–3].

Whistles are physical phenomena that occur when airflow interacts with objects to produce a positive feedback loop. For example, the hole-tone whistle is produced when a jet of air passes through two constrictions [9,10]. The space between the constrictions forms a resonator that selectively amplifies particular

frequencies. Pressure fluctuations at the surface of the jet propagate backwards and are amplified according to the characteristics of the resonator [11,12]. Ring-shaped vortexes are formed in the downstream jet at the frequency of the resonant cavity. The perceptual property of this periodic waveform is the pitch of the whistle.

Many whistled codes used by humans are produced with the aid of the hands or an instrument, but the most basic form of whistling is the bilabial whistle. Though common knowledge suggests that whistling is primarily determined by the action of the lips, the tongue has an active role. Shadle [11] hypothesized that the lips form a constriction through which a jet of air is forced and that a resonant cavity behind the lips and bounded by the tongue determines the frequency that is whistled.

The tongue is a muscular organ that is divided into extrinsic and intrinsic muscle groups [13,14]. The extrinsic lingual muscles originate in osseous structures, such as the mandible and hyoid bone, and insert in the body of the tongue with the primary function of changing the tongue's position. The intrinsic lingual muscles make up the body of the tongue itself and serve to reconfigure the shape of the tongue to produce the dextrous movements required by both swallowing and speech. The human tongue, in particular, receives dense and complex innervation, which may support fine motor control [15–17]. The changing shape of the tongue is used during speech to create narrow constrictions in the oral cavity that divide the vocal tract into a series of resonant cavities [18–20]. Together, these cavities selectively amplify a combination of frequency bands that encode the vowel sounds of speech [20–22].

Two previous studies provide support for the role of the tongue in whistling. Kaburagi *et al.* [23] used magnetic resonance imaging to gather still images of one individual. Qualitatively, it appeared from these images that the configuration of the tongue varied by the frequency being whistled with gross similarity to vowel production. Azola *et al.* [24] gathered X-ray cineradiographic images from two individuals providing evidence that the space between the tip of the tongue to the incisors forms a resonant cavity as with speech.

We used real-time anatomical MRI to collect videographic data with high contrast between the tongue and the surrounding vocal tract. We modelled the cross-sectional shape of the tongue to quantify tongue movements in their entirety and applied functional principal components analysis to explore variation in the tongue shapes that whistlers employed. This approach provided a quantitative, generalizable and holistic description of the tongue's role in whistling.

2. Material and methods

(a) Participants
Six participants (three male, including authors M.B. and B.G.S.) with no speech-motor or auditory deficits were recruited from Maastricht University. Participants had varied cultural backgrounds, including German, Dutch, Canadian, Australian and American, and ages ranging from 20 to 33.

(b) Procedure
Each participant performed three sound production tasks while undergoing real-time magnetic resonance imaging (rtMRI). In separate runs, each participant was instructed to (1) whistle a continuous siren spanning the range of frequencies that they could reliably produce, (2) whistle a chromatic scale of discrete
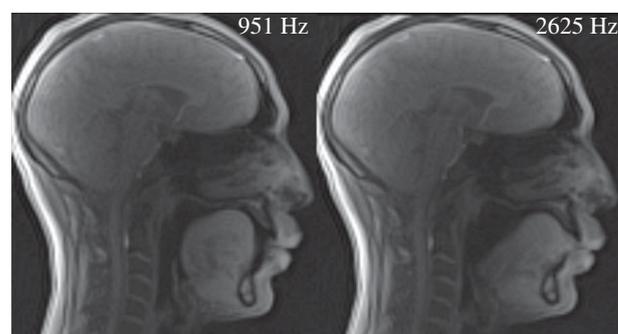
Figure 1. Still images of the highest and lowest frequency whistled by one participant whistling a continuous siren.

notes over the same range, and (3) produce a whistle with conventionalized meaning (a 'catcall' was familiar to all participants despite diverse cultural backgrounds). Participants were instructed to produce sound as part of a breath phrase of approximately 8 s and to breathe normally. Participants' heads were constrained by foam pillows in the MRI.

(c) Real-time magnetic resonance imaging
Real-time MRI collects a series of anatomical images from a mid-sagittal slice of the head and neck (figure 1). Images were collected on a Siemens 3 T Magnetom Prisma Fit at the Maastricht Brain Imaging Centre with the LiveView pulse sequence [25]. T1-weighted images were collected with an acquisition time of 60 ms (sampling rate 16.67 Hz) over a single mid-sagittal slice with thickness = 8 mm, in-plane resolution = 2 mm × 2 mm, field-of-view = 256 × 256 mm, repetition time = 2.58 ms, echo time = 1.64 ms and flip angle = 8°. K-space was sampled over 125 radial spokes. Scan durations were controlled manually and ranged from 88 to 98 s per run. Two runs (call, discrete scale) from one participant were discarded due to scanner malfunction or poor signal-to-noise ratio in imaging data. A third run (discrete scale) from a separate participant was discarded due to poor audio recording quality.

(d) Acoustical measurement
Audio recordings were collected continuously throughout the scanning session using an MRI-compatible microphone attached to the side of the head coil (sampling frequency 44 100 Hz, quantization 32-bit). Recordings were anti-alias filtered by applying a low-pass filter at the sampling frequency prior to digitization. Audio and rtMRI data were synchronized by aligning the onset of acoustical artefacts associated with MRI acquisition with the first image volume.

Acoustical MRI artefacts were then removed using the noise reduction algorithm in AUDACITY [26]. The spectral profile of the acoustical MRI artefact was estimated from a period after the onset of the MRI-related noise in each scanning run and before the onset of whistling and this noise component was down-weighted across the recording (noise reduction = 48 dB, sensitivity = 1.5, frequency smoothing = 3 bands). Two iterations of this procedure sufficiently filtered the acoustical waveform. Recorded waveforms were visually inspected in PRAAT (v. 6.0.36) [27] by an experienced acoustical analyst (M.B.) to identify remaining artefacts and omit corresponding time points from further analysis.

Whistling frequency measurements were extracted semi-automatically with an in-house PRAAT script. The script extracted the fundamental frequency by autocorrelation and calculated the mean frequency within a window equal to half the rtMRI sampling rate centred at each image acquisition.

(e) Tongue shape measurement
The edge of the tongue was detected in each frame automatically using a custom MATLAB script [28,29]. A trace was then computed
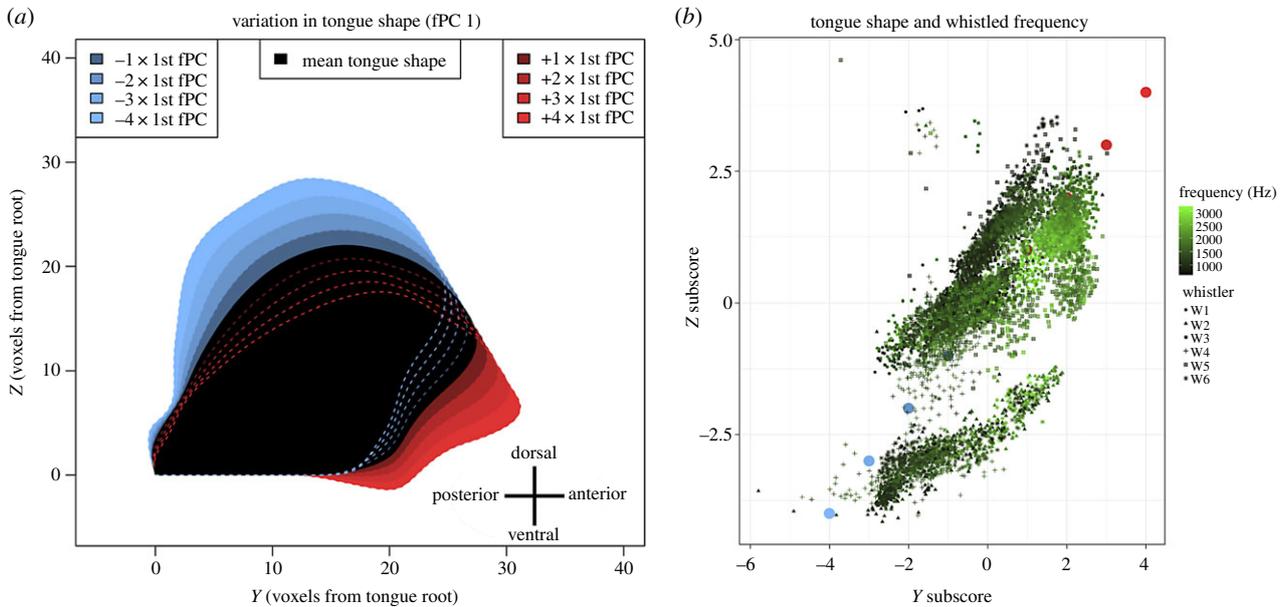
Figure 2. (a) Mean shape of the tongue (black) framed by shapes marking the first functional principal component (red to blue). Successive shades of red mark tongue shapes with fPC1 scores of +1 to +4. Successive shades of blue mark tongue shapes with fPC1 scores of −1 to −4. Dashed lines continue each shaded area where they would otherwise be obscured. (b) Scatterplot showing Y and Z subcomponent scores of fPC1 for each frame. Colour hue indicates the frequency being whistled at each frame. Symbols indicate the whistler that contributed to each point. Large background circles are fictive data points plotted for the purpose of facilitating the interpretation of fPC scores only. Each fictive point indicates the fPC1 score associated with the tongue shape of the same colour in (a). The origin corresponds to the mean tongue shape. (Online version in colour; for greyscale edition, the first fPC spans from left to right through successive shades of grey and is plotted with increasing luminance.)

from tongue-edge maps using the tongue root as a reliably identifiable point of origin. This produced a continuous function of Y (anterior–posterior) and Z (ventral–dorsal) coordinates that capture the shape of the tongue. The coordinate values were centred to create an image space with the origin at the centre of mass of the tongue in each frame for analytical purposes. Figures are plotted with origins at the tongue root to facilitate visualization.

(f) Functional data analysis

Spatially smooth representations of the tongue contour were created by modelling each tongue trace with a B-spline with a basis set of cubic polynomials placed at every second sample along the trace using the *fda* package implemented in R [30,31]. Smoothing parameters were chosen by generalized cross-validation. The length of each trace was normalized to the mean to remove the confounding influence of the cross-sectional size of the tongue and to ensure that tongue splines were modelled with a consistent number of knots.

Variation in tongue shape was explored using functional principal components analysis (fPCA) [32]. Functional PCA explores patterns of variation in the shapes of functions around a mean shape [33]. Much like discrete PCA, fPCA seeks principal components that maximize variation between observations [34–36]. The principal components of discrete PCA are eigenvectors that map each component back onto a set of discrete variables. The principal components of functional PCA are eigenfunctions that map each component back onto variations in shape (electronic supplementary material, file S1). fPCA was conducted simultaneously on functions of Y and Z coordinates to produce a two-dimensional description of tongue shape variation. This approach has the benefit of partitioning anterior–posterior (Y) and dorsal–ventral (Z) functions, and yields separate Y and Z principal component subscores. These subscores can be interpreted as the degree to which the shape of the tongue is deformed along the Y or Z plane in each MRI frame.

A separate examination of the fPCs for each participant and each whistling task confirmed that the components were highly consistent across participants and tasks. The data were therefore combined and fitted to a linear mixed-effects model with the dependent variable of whistled frequency, with Y and Z subscores as regressors. The model accounted for random factors of Participant and Condition with random slopes for the effects Y and Z subscores at each level of the random factors [37]. This approaches the maximal random effects structure [38], though random effects of Condition were not nested within Participant due to a failure of more complex models to converge [Hz $\sim 1 + Y + Z + Y:Z + (1 + Y + Z + Y:Z \mid$ Whistler$) + (1 + Y + Z + Y:Z \mid$ Condition$)$]. Significance was assessed by F-tests with degrees of freedom determined by Satterthwaite's approximation for degrees of freedom, at an alpha level of 0.05.

3. Results

The first two fPCs accounted for 62% and 17% of the total variance in tongue contour. These functional components describe a dimension from (1) low-forward to high-back tongue position and (2) high-forward to low-back tongue position (figures 2 and 3). As each fPC describes a distinct dimension of tongue shapes, we report separate models for each principal component. Across both fPCs, Y subscores were clearly associated with whistled frequency. Electronic supplementary material, files S2–S4 contain representative MR videography clips synced with audio. This relationship is summarized by the β parameters reported below. These indicate the increase in whistled frequency per increase of 1 unit of fPC score (equivalent to adjacent tongue shapes in figures 2 and 3).

Y subscores on the first functional principal component predicted the frequency that was being whistled ($F_{1,8.5} = 6.5$, $p = 0.03$, $\beta = 399.1$, CI = [92.9, 705.3]). Z subscores were poor predictors of whistled frequency ($F_{1,5.5} = 2.1$, $p = 0.21$, $\beta = -200.1$, CI = [−473.5, 75.3]) and no interaction was apparent between subscores ($F_{1,8.4} = 0.01$, $p = 0.94$, $\beta = 4.5$, CI = [−112.1, 121.0]). An anterior–ventral tongue position was associated with high-frequency whistling ($R^2 = 0.61$; figure 2).
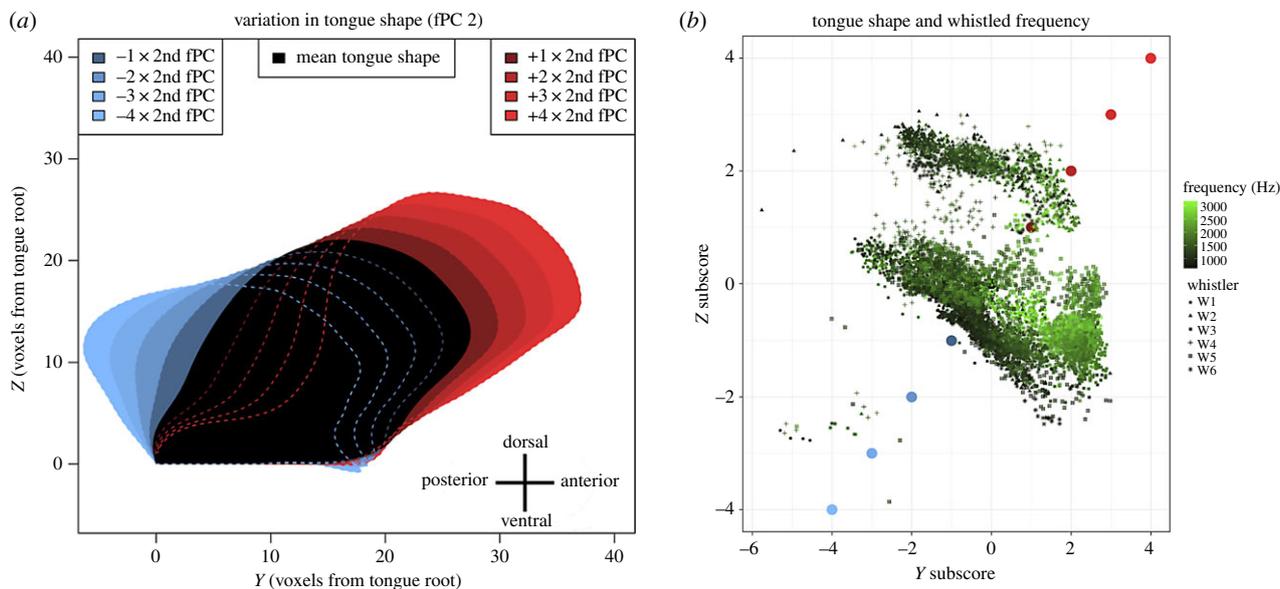
Figure 3. (a) Mean shape of the tongue framed by shapes describing the second functional principal component. (b) Scatterplot showing Y and Z subcomponent scores of fPC2 for each frame. (Online version in colour; for greyscale edition, the first fPC spans from left to right through successive shades of grey and is plotted with increasing luminance.)

Y subscores on the second functional principal component also predicted the frequency that was being whistled ($F_{1,8.8} = 5.8$, $p = 0.04$, $\beta = 297.0$, CI = [56.2, 537.8]). Z subscores were poor predictors of whistled frequency ($F_{1,5.6} = 1.9$, $p = 0.22$, $\beta = 222.7$, CI = [−96.5, 541.8]) and no interaction was apparent between subscores ($F_{1,8.6} = 0.04$, $p = 0.84$, $\beta = 13.8$, CI = [−115.2, 142.8]). An anterior–dorsal tongue position was associated with high-frequency whistling ($R^2 = 0.60$; figure 3).

4. Discussion

We used rtMRI to demonstrate that the shape of the tongue is strongly associated with the frequency of bilabial whistling in humans, such that forward configuration of the tongue produced the highest frequencies regardless of tongue height. This mechanism was consistent across contexts, including simple but highly artificial siren sounds, music-like discrete chromatic scales and complex calls with culturally imposed meaning. This is consistent with Shadle's hypothesis that the tongue shapes a resonant cavity behind the lips to determine the whistled frequency [11]. Tongue configurations that reduce the size of the resonant cavity between the incisors and the tongue amplify pressure fluctuations with shorter wavelengths (i.e. higher frequencies). Our approach modelled the entire cross-sectional surface of the tongue. Though the posterior tongue may be ancillary to whistled sound production, its movement is nonetheless a part of whistled sound production.

(a) A shared bioacoustical mechanism with speech

The same mechanism determines the frequency of whistling and the identities of spoken vowels. Vowel sounds are produced by shaping resonant cavities within the vocal tract [19,20,32]. These resonant cavities selectively amplify certain frequency bands of the voice, called formants, which together encode the identity of spoken vowels [18,39]. For example, a low-back tongue position produces a high first formant (F1) and low second formant (F2), as in the sound /ɑ/ (odd). A high-forward tongue position produces a low F1 and high

F2, as in the sound /i/ (even). The most anterior of these resonant cavities, which determines the second formant in the context of the speech, is a strong driver of whistled frequency. We observed whistled frequencies ranging from 600 to 3100 Hz, which spans the values of the second formant that encode vowel sounds [40–42].

We observed two fPCs of tongue shape: one capturing variation from low-back to high-forward tongue configurations and a second capturing variation from high-back to low-forward tongue configurations. Forward configurations of the tongue were associated with high frequencies across components, suggesting that multiple tongue configurations may produce similar bioacoustical effects. These alternative modes of production may provide an avenue to study motoric degrees of freedom in this muscular system [43].

The shared bioacoustics of whistling and vowel production may inform the study of whistled languages. Twelve whistled languages have been documented, though anecdotal reports suggest that they may be more abundant [2,6]. The most well studied of these is Silbo Gomero of the Canary Islands, in which whistling is used as a sound source in place of the voice [44]. Silbadors produce loud hand-assisted whistles to communicate over long distances over mountainous terrain. They describe producing Silbo as whistling while moving one's tongue as though to pronounce words in spoken Spanish [44]. The effect is to approximate spoken Spanish, with the whistled frequency standing in for the second formant (F2) of Spanish vowels [6,7]. Similar whistled proxies have been described for French [45], Turkish [46] and Greek [47], among other languages [2,6]. Though the simpler acoustical structure of whistling encodes less information than the voice, even amateur whistlers are highly precise [48]. The common bioacoustical mechanisms of speaking and whistling may explain the emergence of whistled proxies across diverse languages and cultural groups.

(b) A bioacoustical clue to the evolution of speech

Whistling may provide a novel avenue to understand the evolution of speech-motor abilities through the comparative study of human and non-human apes. Though whistling

has not been observed in non-human apes in the wild, at least one species (*Pongo* spp.) can learn to whistle in captivity [49,50]. In most instances, it has not been possible to determine whether these animals spontaneously imitated their caretakers or were explicitly trained. In one case, this behaviour was observed to transfer between cohabitating animals, demonstrating the potential for cultural transmission [49]. This behaviour has provided evidence that orangutans have voluntary control over the upper lip, lower lip and respiratory muscles, which are readily accessible to external observation. Our study, along with that of Azola *et al.* [24], demonstrates the strong involvement of the tongue in human bilabial whistling. Whistling in non-human apes may provide a useful animal model for the study of sensori-motor capacities that support speech. Dynamic imaging in non-human apes is needed to confirm that the tongue is similarly involved when these species whistle, in line with broad similarities in vocal tract anatomy [51].

corresponds with the bioacoustical mechanism that produces the second formant in vowel production. This finding is consistent with the link between whistled languages and the spoken languages for which they act as a proxy. Comparative research with non-human apes that have learned to whistle may provide further insights into the evolution of the lingual-motor skills that support speech.

5. Conclusion

The tongue is a strong determinant of the frequency of oral whistling, with forward tongue configurations associated with higher frequencies. This lingual component of whistling

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