

Anatomical biasing and clicks: Evidence from biomechanical modeling

Scott Reid Moisik^{1,*} and Dan Dediu²

¹Linguistics and Multilingual Studies, Nanyang Technological University, Singapore, SG 639798 and

²Language and Genetics, Max Planck Institute for Psycholinguistics, Wundtlaan 1, 6525 XD Nijmegen, The Netherlands

*Corresponding author: Scott.Moisik@ntu.edu.sg

Abstract

It has been observed by several researchers that the Khoisan palate tends to lack a prominent alveolar ridge. A biomechanical model of click production was created to examine if these sounds might be subject to an anatomical bias associated with alveolar ridge size. Results suggest the bias is plausible, taking the form of decreased articulatory effort and improved volume change characteristics; however, further modeling and experimental research is required to solidify the claim.

Key words: clicks; hard palate; alveolar ridge; anatomical biasing.

1. Introduction

This article examines the production of the speech sounds known as clicks in the context of a three-dimensional biomechanical simulation. Specifically, we ask whether differences in the shape of the palate might influence certain aspects of click production, such as the muscular effort/articulatory ease, following [Kirchner \(1998\)](#) and [Napoli et al. \(2014\)](#), or the dynamics of lingual cavity rarefaction. This work is situated within the larger context of research that seeks to address the question of whether variation in human vocal tract anatomy and physiology constitutes a systematic bias or pressure on speech sound systems. Such biases, while interesting at the level of individual variation, might also show localized patterns corresponding to wider populations of speakers sharing certain vocal tract traits.

It is an undeniable fact that human populations vary in certain systematic ways in their anatomy and physiology. This is true at both micro- and macroscopic levels, and advances in genetics will continue to elucidate the extent of these patterns of variation across populations.

Early in the development of modern phonetic and phonological science, several proposals (e.g. [Vendryès 1902](#); [Brosnahan 1961](#)) were made which held that some of the diversity observed in speech sound systems around the globe might be due to systematic variation observed in the anatomy and physiology of the vocal tract, in addition to the other factors driving language change and diversification. These ideas were dismissed as implausible, on the grounds that any human being can learn any human language. And it is indeed an incontrovertible fact that normal variation of the human vocal tract does not preclude an individual from acquiring any spoken language, including the subtleties of regional accents. But simply being able to speak a language intelligibly and with the right accent does not mean that the speech produced will be identical to that of all other speakers. There will still be subtle differences in speech production strategies from one speaker to the next, and the questions we need to ask are whether these differences are systematically influenced by patterns of variation in vocal tract morphology and whether such variation is structured across

populations and ultimately has consequences that influence how the speech sound systems of these populations change over time. This work is thus aligned with recent research that inquires about the influence of environmental factors on phonological systems (e.g. Everett 2013; Everett et al. 2015) and is fundamentally concerned with the adaptive nature of language to language external factors and the forces that shape linguistic diversity (Dediu et al. 2017, in press; Lupyán and Dale 2016).

As it stands, the hypothesis that systematic, cross-population variation in vocal tract morphology is a factor that shapes phonological diversity across the globe, has never been tested by means of empirically driven methods such as modeling and experimentation. So ruling it out seems to have been a premature move. It also seems to have resulted in the unfortunate side effect that details of vocal tract shape are rarely correlated to production variables in phonetic research. A relatively recent return to the question of whether normal vocal tract variation can indeed exert such biases reflects the unresolved nature of the problem. Many examples exist for such research examining the individual level (e.g. Tiede et al. 2005; Brunner et al. 2009; Stone et al. 2013; Weirich and Fuchs 2013), and these are laden with implications for impacts at broader levels, with some researchers even suggesting it may be a driver of change of certain aspects of entire phonological systems (e.g., Allott 1994; Dediu 2011; Stavness et al. 2013; Dediu et al. 2017, in press).

1.1 Why examine click production?

In the present study, we focus on the case of clicks. Clicks merit investigation because of their rarity as phonemes, their very circumscribed distribution globally, and their apparent articulatory complexity relative to other speech sounds—facts which suggests there are biases against the phonological incorporation of these sounds. Clicks are mainly found in languages of southern and eastern Africa, and they are primarily

associated with the so-called Khoisan languages (actually a group of mostly independent language families, although we use ‘Khoisan’ throughout to refer to these, including Kx’a, San, and Tuu), and the isolates Hadza and Sandawe. Clicks are also found in several Nguni Bantu languages (including Zulu, Xhosa, Ndebele, Swazi, and Sotho) and Dahalo, a Southern Cushitic language, all of which have evidently borrowed clicks through generations of extensive contact with various Khoisan languages (Traunmüller 2003; Güldemann 2007). Independent development of clicks is unattested throughout the rest of the globe—except for the curious case of Damin, a male ritual language of the Lardil tribe of Australia, which employs a limited inventory of five click sounds and was possibly the result of conscious design by its speakers (Güldemann 2007).

Our inspiration for the present study comes from observations by Engstrand (1997), Traunmüller (2003: 4), and Demolin (pers. comm.) that clicks may be subject to a production bias grounded in the morphology of the palate. The ultimate source for this idea comes from Traill (1985: 101–2), who remarks in his dissertation (on the subject of !Xóõ, a language of the Khoisan group) that one cannot use the term *alveolar* to describe post-dental clicks in !Xóõ since four of his five subjects ‘do not have an alveolar ridge’ (101). One of these palates is reproduced in Fig. 1 along with a comparison to the palate of author S.R.M., which exhibits a sizeable alveolar ridge prominence.

While such variation could easily be owing to Traill’s limited sample of !Xóõ palates (although Traill notes that the pattern holds for the San in general, citing van Reenen 1964), it is well established that other members of the Khoisan group show a degree of uniformity of head and palate morphology that distinguishes these groups from other nearby non-Khoisan populations. For example, van Reenen and Allen (1987) compare palatal measures made on plaster dental casts of Central Kalahari Bushmen (a sample comprised of individuals

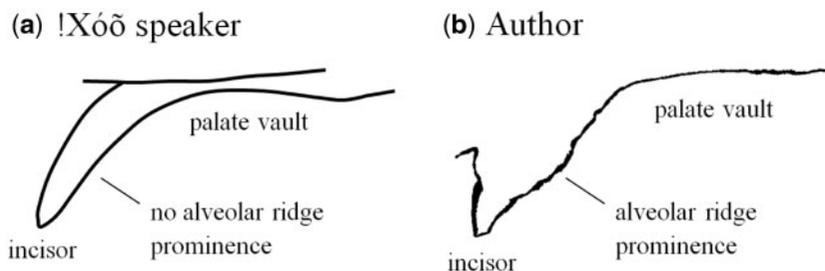


Figure 1. Mid-sagittal palate profiles: (a) an example of a !Xóõ speaker’s palate (retracing of Fig. 24 from Traill, 1985: 107) and (b) the palate of author SRM.

from the !Kung, Auen, Naron, Dukwe, and Heikun tribes); Vassekela Bushmen (originating from Angola); and Herero-speaking individuals, mainly Himbas, for contrast. Note that the former two groups (the Bushmen) consist of speakers of Khoisan click languages, but Herero (a Bantu language) lacks clicks. The most relevant measurements from this study, shown in Table 1, are of palate height at various locations and were obtained with a palatometer, which spans the dental arch at a given pair of reference teeth (canines, second pre-molars, and second molars) and provides the distance from the level of the gums to the palate roof. Limited judgement of palate contour can be made with reference to the height observed at the canines relative to the (second) pre-molar and molar heights. Sample sizes in this study are large (minimum of 76 and maximum of 158). The Bushmen groups generally have narrower and shallower palates, and the anterior flatness (i.e. lack of a prominent alveolar ridge reflected by highest scores for palate height in the canine region) is confirmed. The Vassekela Bushmen are intermediate, but classified with the Himbas as having a ‘shelved’ palate: low at the front but suddenly increasing in height toward the back. The Bushmen palates were not necessarily shorter than those of the Himba.

Similar work by Winkler and Kirchengast (1993) compares 110 male !Kung San (who speak a Khoisan language of Namibia) with a group of 138 males from Kenya and Uganda (containing both Bantu- and Nilotic-speaking individuals). Citing related work (in German) by Winkler (1993; which contains the same samples in addition to 25 non-Khoisan women of similar ethnic background to the corresponding males), Winkler and Kirchengast (1993) state that the !Kung San palate is shorter, narrower, and shallower and characterized by a concave profile. Note, however, that the term *concave* may be in error since, in the original source (i.e. Winkler 1993: 85), the qualitative results identify the ‘konvex’ (convex) profile as most frequent among the !Kung San.

Bearing this in mind, the results of Winkler (1993) indicate 57.3 per cent of !Kung San palates but only 26.1 per cent of the Kenyan palates are classified as convex, the rest being ‘gerade’ (straight) (and only five Kenyan palates being ‘konkav’ (concave)). Note that Winkler and Kirchengast (1993) do not provide a detailed listing of the specific languages spoken by the non-Khoisan group, that is, the Bantu and Nilotic speakers. However, it is stated that most of the Bantu-speaking individuals are from the Taita Hills, and the language of this area, Taita/Dabida, lacks clicks; and clicks are not found in Nilotic languages.

Images of a small selection of palates in profile from the van Reenen and Allen (1987) and Winkler (1993) papers clearly reveal that some Khoisan palate profiles feature a prominent alveolar ridge shape, and, likewise, some non-Khoisan palates appear to feature smooth profiles lacking a prominent alveolar ridge. The results of van Reenen and Allen (1987) showing higher intercanine heights for their Bushmen (Khoisan) sample, might need to be interpreted as reflecting a more complex shape difference than just the alveolar ridge prominence. As can be judged from Winkler’s San Proband 26 (for the figure, refer to Winkler (1993, fig. 4, ‘middle below’)), a prominent alveolar ridge seems to correspond to a low intercanine height, while the palate in Winkler’s San Proband 83 (1993, fig. 4, ‘below’) shows a much higher intercanine height and a more drooping alveolar ridge bulge immediately behind the incisors. But a rather shallow slope of the anterior alveolar margin, as in the non-San (Kenyan) Proband 895 and 1040 (see Winkler (1993, fig. 1, ‘middle’ and ‘below’, respectively)), can also result in relatively low intercanine heights; it could be said that while these palates lack a prominent alveolar ridge, the shape provides less space in the part of the palate anterior to the premolars. (Note that based on the measurements from van Reenen and Allen (1987), the very high intercanine height of San Proband 83, while extreme in its approaching of the

Table 1. Mean \pm SD, range (minimum–maximum), and significance comparisons (at $\alpha = 0.01$; Y = significant, N = not significant) for the palate height measurements in van Reenen and Allen (1987: 488)

Palate height	Bushmen (B)	Vassekela (V)	Himba (H)	B–V	B–H	V–H
C–C	5.35 \pm 1.64 (2.00–10.00)	4.78 \pm 1.66 (2.00–10.00)	4.72 \pm 1.54 (1.50–9.50)	Y	Y	N
P ² –P ²	12.35 \pm 2.24 (7.00–17.50)	13.95 \pm 2.16 (9.00–19.00)	13.85 \pm 2.28 (9.00–19.00)	Y	Y	N
M ² –M ²	13.43 \pm 2.06 (9.50–19.00)	15.33 \pm 2.28 (11.00–21.00)	15.57 \pm 2.37 (8.00–22.00)	Y	Y	N

Measures given in mm. Height abbreviations: C–C = intercanine; P²–P² = inter-second-premolar; M²–M² = inter-second-molar.

inter-second-premolar height, is not out of range.) Thus, the relationship between shape and the interdental measures of van Reenen and Allen (1987) is not so straightforward. In the interest of simplicity, we focus here just on the alveolar ridge prominence, but the variation of anterior palate shape found within various members of the so-called Khoisan group, and also exhibited by non-Khoisan groups, and its complex relationship with simple quantitative measures does need to be kept in mind (and could form the basis of further inquiry into the relation between palate shape and click articulation).

Craniometric data (Howells 1973) show that Bushmen (Khoisan) palates (for males or females) do tend to be smaller in comparison to many other populations (Fig. 2). Note that Zulus, whose language has clicks, fall toward the upper end of these variables. A morphometric study of the human mandible (Cramon-Taubadel 2011) places the San (of the Khoisan group) within the hunter-gatherer jaw class (featuring narrow and elongated mandibular bodies and shorter and more vertically oriented rami), but they do not stand clearly apart from other members of this group.

In short, it seems that the Khoisan palate is distinguishable from palates of other groups, and that the trend of a lack of a prominent alveolar ridge detected in Traill's X-rays may indeed be representative of the Khoisan group, although gene flow with neighbouring groups and the resultant differentiation of palate shape (e.g. as reflected in the Vassekela) is a possibility, and it should be kept in mind that palate shape cannot be categorically distinguished between Khoisan and non-Khoisan populations. Rather it is complex and subject to variation, including within the various Khoisan

populations, and while the anterior palate may be 'lacking an alveolar ridge' for many, in no way is it the case that all such speakers lack an alveolar ridge prominence. Bearing this in mind, we now proceed to discussion of testing the palate shape bias.

1.2 Palate morphology and clicks: hypotheses

Briefly, to produce a lingual (i.e. not bilabial) click, the tongue must first form an enclosed space between the anterior occlusion (which defines the click's place of articulation) and the velar-uvular region of the palate. Clicks do not typically require the tongue be flush against the palate, and, in fact, there is very often a central gap, as observed in X-ray (Ladefoged and Traill 1984; Traill 1985), static palatography (Traill 1985; Thomas-Vilakati 1999), and ultrasound (e.g. Miller et al. 2009) studies. The next step is to generate the lingual (or velaric) ingressive airstream, which depends on rarefaction of the air driven by localized lowering of the tongue body (the exact location and displacement pattern of which is dependent upon click place of articulation). Finally, the lingual seal is suddenly broken by the rapid release of the anterior occlusion, and the pressure differential created through rarefaction generates a flow discontinuity that yields a transient acoustic signal audible as a click.

Our goal was to probe into the possibility that palatal morphology has consequences for click production and that this, in turn, might speak to a production bias which has led to the establishment and maintenance of clicks as speech sounds. The general question we ask is:

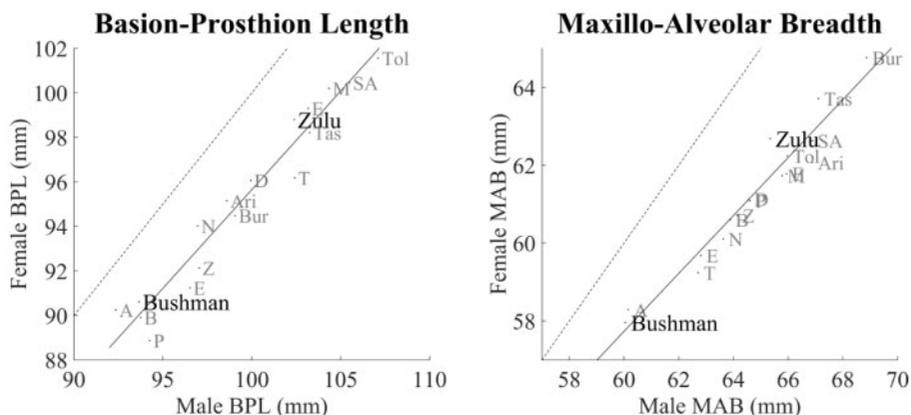


Figure 2. Basion-prosthion length (BPL; proxy for palate length) and maxillo-alveolar breadth (MAB; proxy for palate width). Data from Howells (1973). A = Andaman, Ari = Arikara, B = Berg, Bur = Buriat, D = Dogon (Mali), E = Egyptian, E = Eskimo, M = Mokapu, N = Norse, P = Peru, SA = South Australian, T = Teita (Kenya), Tas = Tasmanian, Tol = Tolai, Z = Zalavar. Dashed line = hypothetical 1:1 sexual dimorphism; Solid line = regression line.

what effect, if any, does palate shape have on the production of clicks?

To address this question, we narrow our focus on the biomechanics of click production, and, on the alveolar ridge, which was identified as an important factor by other researchers and has some support in available anthropometric studies. (Palatal dimensions may also be important, but, in this version of the model, these factors were not explored.) Given this focus on the alveolar ridge, we suggest the following hypotheses regarding alveolar ridge shape and click production: (1) a smooth palatal profile requires less articulatory effort to form click stricture since the anterior tongue does not need to deform as much to form the lingual seal; (2) a smooth palate provides better volume change characteristics (presumably for achieving efficient aero-acoustic effects in click production, although this was not modeled).

To test these hypotheses, we assume that total muscle force is a good proxy for articulatory effort (following Kirchner (1998) and Napoli et al. (2014)). We also constrain our attention to the production of clicks which involve contact between the tongue tip/blade and the anterior palate, as these clicks are most relevant to hypothesis (1). Our simulations are place-abstract, but they most closely resemble dental clicks.

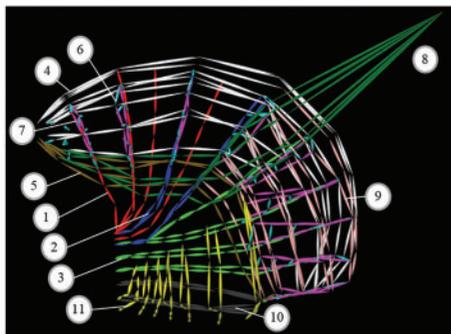
2. Methodology: click simulation in ArtiSynth

The biomechanical simulation of click production was created using the ArtiSynth biomechanical modeling toolkit (www.artisynth.org; last accessed: March 10,

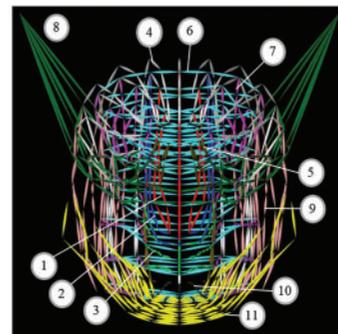
2017 see Lloyd et al. 2012). The model is based on the three-dimensional finite-element (FE) tongue (referred to as the *original tongue* here) integrated with rigid-body skeletal structure for the maxilla and mandible as originally presented in Buchaillard et al. (2009; and used in several subsequent studies; see Nazari et al. 2011; Stavness et al. 2011, 2013). An earlier version of this model was described in Moisik and Dediu (2015), in which several problems with the original tongue FE model were identified in its application to simulating clicks. The new version of the tongue model presented here is based on a finer discretization using a 4-mm hexahedral interior voxelization and symmetric surface construction. Then, based on the surface mesh of the original tongue, several operations were performed, including registration of the muscles of the original tongue, individuation of the midline fascicles of several muscles (including mylohyoid, geniohyoid, genioglossus, superior and inferior longitudinal), refinement of the genioglossus muscle by adding two interposed fascicles each for the anterior and medial portions of this muscle, and the liberation of each midline fascicle of the genioglossus muscle (as a whole). Muscles of the tongue model are shown in Fig. 3. The purpose of these changes was to make a much more realistic click simulation possible than with the original tongue model (for more discussion of the issues faced with the original model, see Moisik and Dediu 2015).

Alveolar ridge shape was systematically manipulated to simulate its effects on click production. To do this, it was first necessary to smooth the original maxillary geometry, which features a prominent alveolar ridge. Smoothing was

(a) Tongue Muscles (Left)



(b) Tongue Muscles (Front)



- genioglossus anterior (1)
- genioglossus medial (2)
- genioglossus posterior (3)
- superior longitudinal (4)
- inferior longitudinal (5)
- transversus (6)
- verticalis (7)
- styloglossus (8)
- hyoglossus (9)
- geniohyoid (10)
- mylohyoid (11)

Figure 3. Muscles of the FE tongue (a) left (b) front: red, 1=genioglossus anterior; blue, 2=genioglossus medial; light green, 3=genioglossus posterior; white, 4=superior longitudinal; brown, 5=inferior longitudinal; cyan, 6=transversus; magenta, 7=verticalis; dark green, 8=styloglossus; pink, 9=hyoglossus; gray, 10=geniohyoid; yellow, 11=mylohyoid. For reasons of visualization, neither medial braches (see text) nor individuated fascicles of the genioglossus portions are shown explicitly here. Colour version available online.

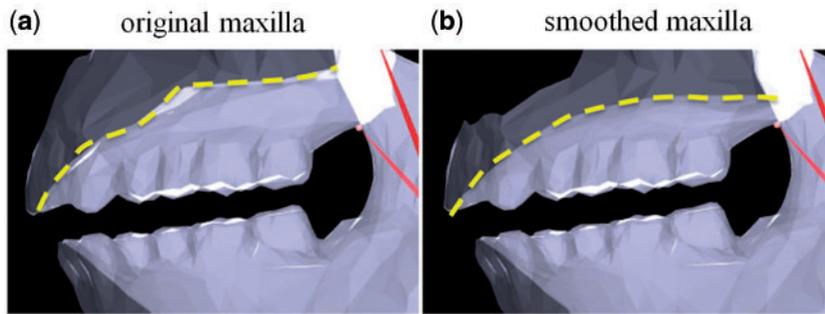


Figure 4. Geometry (a) before (i.e. original maxilla) and (b) after (i.e. smoothed maxilla) maxillary smoothing in the region of the alveolar ridge (midsagittal profile). The dashed line highlights the contour of the mesh for comparison. Colour version available online.

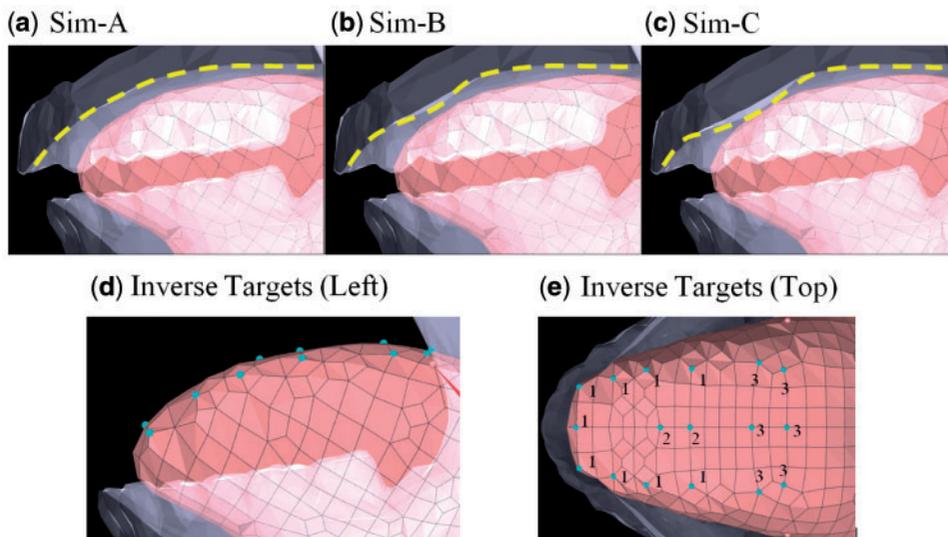


Figure 5. Mesh warping to control alveolar ridge size (a–c) and inverse target design (d and e). The three simulation conditions are depicted: (a) Sim-A, no warping, ‘smooth ridge’; (b) Sim-B, mild warping, ‘small ridge’; (c) heavy warping, ‘big ridge’. The dashed line highlights the change in profile. Arrows show longitudinal locations of inverse-simulation nodes (see text below). Inverse targets are visualized as enlarged/numbered nodes on the FE tongue and are seen in their starting position. See text for discussion of the numbers 1–3 near inverse nodes in (e). Colour version available online.

accomplished manually using tools in Blender (www.blender.org last accessed: March 10, 2017) to deform the anterior palatal geometry such that the alveolar ridge convexity was entirely removed. Results of this process are illustrated in Fig. 4.

Next, to experimentally manipulate the shape of the alveolar ridge, a spherical warping field was used. This field radially displaces only certain mesh vertices within a limited radius of the origin of the warping field (which was placed approximately above the anterior nasal spine). The magnitude of the displacement is given by

$d = (r - p)/r$, where p is the Euclidean distance between a given vertex and the warping origin, and r is the radius of the warping field. The different grades of warping used are shown in Fig. 5 (note that the warping in Sim-B is intermediate between Sim-A and Sim-C).

Finally, ArtiSynth’s inverse controller was used to simulate the dynamics of click production. This controller, familiar from the field of robotics, takes temporal targets of nodal locations of the geometry as input and outputs a parsimonious set of muscle activations which achieve these temporal targets within the limitations set

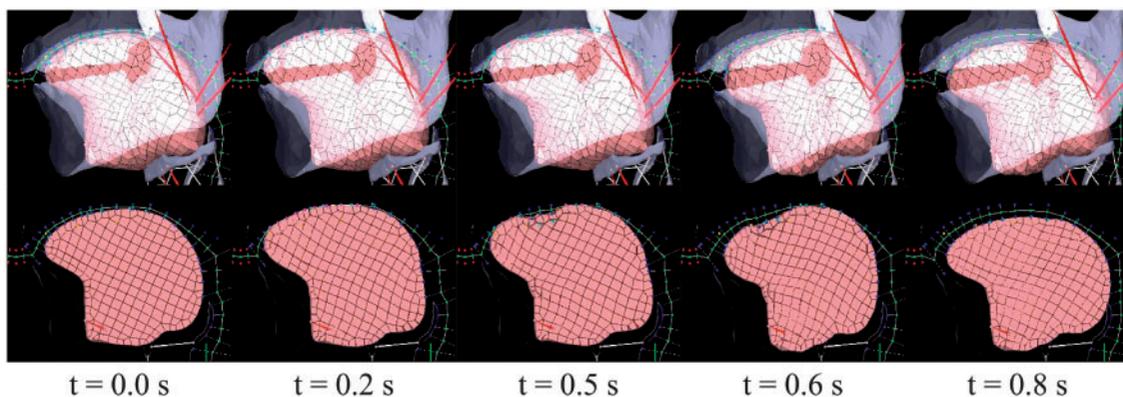


Figure 6. Appearance of Sim-A at several key moments in time, including the start ($t=0.0$ s, first from left), constriction ($t=0.2$ s, second from left), maximum rarefaction ($t=0.5$ s, middle), front release ($t=0.6$ s, second from right), and back release ($t=0.8$ s). The white line shows the airway centerline. Colour version available online.

by tissue contacts, inertia, and material properties. Inverse targets were associated with FE nodes at locations shown in Figs 5d and e (enlarged/numbered nodes). An idealized and place-neutral lingual click was defined as follows: first, all inverse targets were positioned at a short distance beyond the projection of each target's corresponding FE node onto the nearest face of the maxilla mesh along the line of projection (thus, in each simulation, constriction is relative to maxilla shape); then, with reference to Fig. 5e, the midline nodes numbered 2 were displaced to a position about 5 mm below their resting state positions (this simulated rarefaction); shortly thereafter, all targets numbered 1 were displaced to a position about 5 mm below their starting positions (simulating release of the front closure); finally targets at 3 were likewise returned to a position about 5 mm below their starting positions (simulating release of the back closure). Note that no attempt was made to simulate the initial presence of an enclosed airspace during the establishment of palatal contact.

For comparison and control, an idealized velar stop was created using only the inverse targets for the posterior most medial node numbered 3 in Fig. 5e. This causes the tongue to bulge upward toward the palate with the tip and front part of the dorsum retracted, approximating a basic velar stop.

For both the click and velar stop conditions, three 1 s simulations were run, which correspond with the geometries in Fig. 5. One set was run with the mandible set to dynamic (the free jaw condition) and the other held the mandible fixed in place (the fixed jaw condition). Gravity was enabled in all simulations. (The free jaw click simulations are examined in detail in the results below, and the other simulations are discussed

summarily, but more details on these can be found in the Supplementary Appendix.)

To evaluate model performance, three response variables were measured. Muscle force was observed by summing force magnitude readings for all fibers and axial muscles in the model. Following Kirchner (1998; also see Napoli et al. 2014), this force sum was then integrated over time to produce a measure of articulatory effort. (Note that, technically, the integral of force over time is associated with a vector quantity called *impulse*, the unit of which is Ns. Here, since we are dealing with a quantity of force magnitude, we view the integral as an accumulation of force, rather than as impulse, and the use of N for the unit of articulatory effort reflects this.) For all simulations (including the velar stops), volume in the region of lingual rarefaction was observed by summing tubular volumes computed by means of a rudimentary vocal tract airway, which tracks cross-sectional distance of the airway and thus provides diameters for this purpose (the airway can be seen in Fig. 6). Finally, measurements of palate shape was made following the concept of the method in van Reenen and Allen (1987); particular focus is given to intercanine palate height, the measurement of palate height using the midpoint of the chord formed by shortest distance between the canines along their lingual gingival margin.

3. Results

In Fig. 6 are screen shots of the model as it appears in the free jaw condition for Sim-A (smooth palate). For videos of the twelve simulations, see Supplementary Material (three warping conditions X two jaw conditions X and two consonant types). Despite the

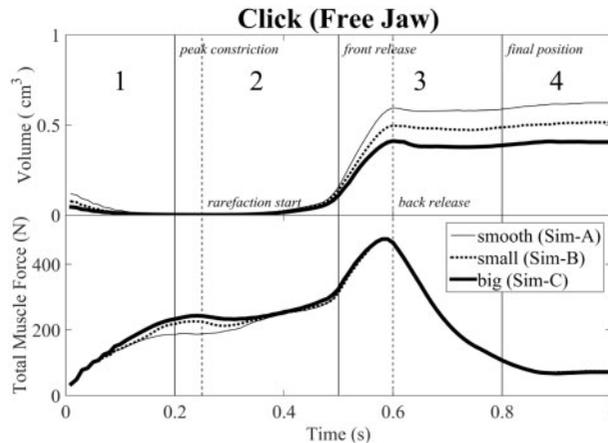


Figure 7. Lingual cavity volume (top) and total muscle force (bottom) for the click simulations (free jaw condition) under the three degrees of warping (see Fig. 5). All signals have been smoothed with a moving average filter. Vertical lines mark key events (individually labeled) and large numbers between these mark articulatory phases: these are (1) onset, (2) rarefaction, (3) release, and (4) rest.

complexity of the gesture, requiring the tongue to deform considerably, and the challenges imposed by collision computation between the tongue and the palatal surface, the model appears to do well to replicate an idealized click.

Results for volume change and total muscle force are presented in Fig. 7. Overall, the effect of having a larger alveolar ridge, given the same relative palatal contact requirements and the same absolute lingual resting and return states, is to reduce the rate and amount of volume gain during release of the front closure (phase 3, Fig. 7) and to increase the articulatory effort, as gauged by total muscle force, in producing and maintaining closure while enlarging the air space. The difference is most evident toward the end of the onset (phase 1, Fig. 7) when the constriction is being formed and during the early part of the rarefaction (phase 3, Fig. 7). Toward and at the point of front release (see solid vertical line marked *front release*, Fig. 7), the difference in muscle force output diminishes and then goes away entirely. This indicates that the key differentiating factor is in the palate contact and difference in lingual deformation required across the different conditions. Fixing the mandible (fixed jaw condition, see Fig. 11 in Supplementary Appendix), does not make a marked change to the results but the difference in muscle force output is enhanced somewhat. A further consideration is that more muscle force is exerted *despite* the fact that the more prominent alveolar ridge shapes reduce the distance that the anterior tongue needs to travel in order to make contact with the palate. The fact that the velar stop simulations (see Supplementary Appendix) are not

differentiated in this way further supports the interpretation that contact and deformation are what drive the observed difference in total muscle force.

Integrated total muscle force by the first three phases for the click and velar stop simulations (both in the free jaw condition) is shown in Fig. 8, and Table 2 provides relative changes (expressed as percentages) between simulation B compared to A and C compared to A for all simulations, confirming the observation that force output increases only for the click simulations. The velar stop simulations are virtually indistinguishable in terms of total muscle force output in the case of the fixed jaw condition; the difference is more appreciable for the free jaw condition between A and B, but not A and C, but, more importantly, the click simulations show a difference that is an order of magnitude larger than this and the majority of the difference arises during the contact phases (1 and 2, onset and rarefaction). In general, the durational characteristics of both simulation types are idealized and, especially in the case of the velar stop, particularly long. This makes comparing the integrated total muscle force values between these two simulation types infeasible. One can observe, however, that the velar stop exhibits less peak muscle force (see Supplementary Figs 12 and 13) than the clicks (see Fig. 7; and Supplementary Fig. 11), and the click is particularly demanding during release.

When examining specific muscle contributions (for the free jaw condition, see Fig. 9; see Supplementary Appendix for the fixed jaw condition and for comparison with the velar stop simulations), it is apparent that the transversus linguae (TR) and genioglossus posterior

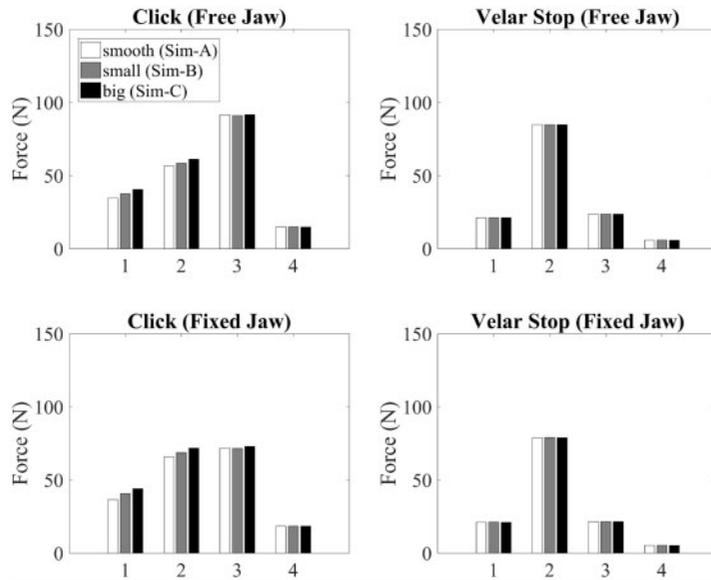


Figure 8. Integrated total muscle force by phase for the click (left) and velar stop (right) simulations. Numbers on abscissa mark phases: 1 = onset; 2 = rarefaction (click)/sustain (velar stop); 3 = release; and 4 = rest. Relative differences between B versus A and C versus A are given in Table 2. See Supplementary Appendix for further details on the other simulations (click in the fixed jaw condition and velar stops).

Table 2. Percentage change of integrated total force over time between Sim-A and the subsequent simulations

	Phase 1	Phase 2	Phase 3	Phase 4	Total
Total force: Sim-B vs. Sim-A					
click, free jaw	5.97	4.13	-0.22	0.02	3.44
click, fixed jaw	2.12	3.40	0.09	0.57	2.43
velar stop, free jaw	0.36	0.20	0.24	1.23	0.27
velar stop, fixed jaw	0.01	0.00	0.02	0.49	0.03
Total Force: Sim-C vs. Sim-A					
click, free jaw	16.63	8.31	0.90	0.02	7.56
click, fixed jaw	11.92	7.15	0.11	-0.98	5.52
velar stop, free jaw	0.00	0.00	0.00	-0.05	0.00
velar stop, fixed jaw	-0.06	0.06	0.03	-0.09	0.03

Definition of phases differs between consonant types (for clicks, refer to Fig. 7; for velar stops, refer to Supplementary Fig. 12).

(GP) are dominant, especially during rarefaction (phase 2, Fig. 9). These muscles, especially in phase 1, account for a large part of the difference in muscle effort as a function of alveolar ridge size (from Sim-A to Sim-C). The TR muscle is associated with intrinsic lingual shaping to form and maintain contact against the palate because it draws the lateral edges of the tongue medially and thereby, through hydrostatic principles, causes the tongue to bulge upward into the palate. GP helps to raise the dorsum of the tongue (as in close vowels like [i] and [u]) but also fronts the tongue. Mylohyoid (MH) and superior longitudinal (SL) likewise increase with alveolar ridge size during phases 1 and 2. However, not

all muscles' force output increase as a function of alveolar ridge size: styloglossus (SG) and genioglossus anterior (GA) actually decrease somewhat. GA is the muscle responsible for generating the cavitation. The difference here though is so small that it does not counteract the general increasing trend. At click release, (phase 3, Fig. 9) geniohyoid (GH) is activated along with verticalis linguae (VE). This latter muscle, in combination with GA, is evidently involved in drawing the anterior tongue down; the presence of GH may support TR in preventing excessive dropping of the tongue and in the maintenance of the back stricture, which is yet to release at this point.

Intriguingly, the muscles responsible for the mandible, grouped as the temporalis (TE), masseter (MA), pterygoids (PT), and digastric (DI), are mostly silent. This is the case even when the mandible lowers during

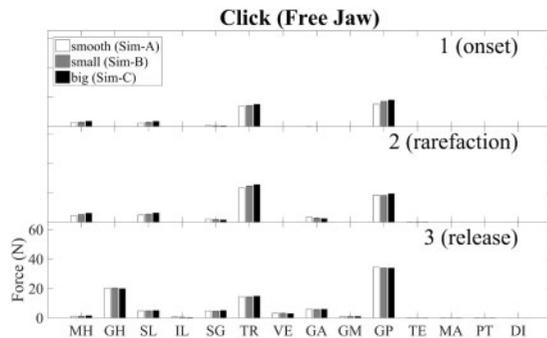


Figure 9. Integrated muscle force for onset (0.0–0.25 s), rarefaction (0.25–0.50 s), and release (0.50–0.80 s) phases of an idealized click (free jaw condition), corresponding to 1, 2, and 3 in Fig. 7a. Muscles: MH = mylohyoid; SL = superior longitudinal; SG = styloglossus; TR = transversus; VE = verticalis; GA = genioglossus anterior; GM = genioglossus medial; GP = genioglossus posterior; TE = temporalis; MA = masseter; PT = pterygoids (internal and external); DI = digastric (anterior and posterior bellies). Scale and units are the same for all ordinate axes shown but only labeled on the bottom axis.

the sequence as is evident in Fig. 6. It is probable that, since no explicit inverse targets were set for this structure, it is mostly passive in the click simulation, lowering in response to the lingual actions during release and with the help of gravity. (Note, as shown in the Supplementary Appendix, the other click simulations in the fixed jaw condition seen in Supplementary Fig. 11 demonstrate similar general behavior, although the exact quantity of force output varies somewhat. The velar stop simulations show heaviest reliance on the GP muscle, as depicted in Supplementary Figs 12 and 13).

As a final examination of the effect of anterior hard palate shape on the production of clicks compared to that of velar stops, consider Fig. 10. The top row of plots shows total muscle force during the onset phase (when contact is formed) as a function of intercanine palate height for all simulations. The bottom row shows the maximum absolute value observed within the release phase for the time derivative of volume. For the clicks, while force is inversely related to intercanine palate height, it is positively correlated with an increasing rate of change in volume over time. For the velar stop, there is no correlation between intercanine palate height and force, and, while the correlation is positive between intercanine palate height and volume, the slope and intercept of this

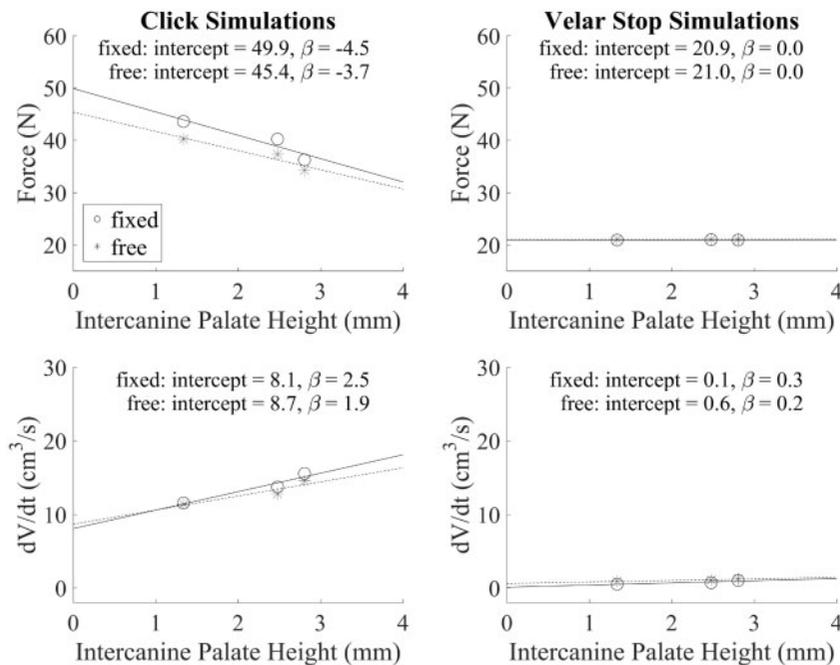


Figure 10. Scatter plots showing correlation between intercanine palate height and integrated total muscle force during the onset phase (top; 1 in Fig. 7) and between intercanine palate height and the maximum absolute value of the time derivative of volume during the release phase (bottom; 3 in Fig. 7) for the click simulations (left) and velar stop simulations (right). Solid line = fixed jaw condition regression line; dashed line = free jaw regression line.

function are much lower than those for the clicks. Since intercanine palate height is used to gauge the prominence of the alveolar ridge (with lower values indicating a more prominent or bulging ridge), it is apparent that having a palate with a higher value of intercanine palate height provides an advantage in terms of force required to produce a click and in terms of the rate of volume change when clicking. The latter is particularly important for click acoustics, since it is the rate of change of cavity volume at release that gives clicks their acoustic energy, with a greater derivative capable of generating more acoustically intense clicks (Stevens 1998: 123): this is due to the proportionality between rate of change of the constriction dimensions and the rate of change of flow. Relative changes during phase 3 (expressed as percentages) between Sim-B versus Sim-A and Sim-C versus Sim-A are given in Table 3. The percentage-wise changes are similar in the fixed jaw condition, but quite a bit higher in the free jaw condition. However, what really matters in this case (unlike that of total muscle force) is the absolute value. When one looks at the absolute values of volume change over time in Fig. 10, it is evident that the clicks have a rate of change about an order of magnitude greater than the velar stops. Because of its importance in click aero-acoustics, the absolute value must be given primacy in interpreting the difference between the two types of consonants, clicks and velar stops.

4. Discussion and conclusion

With this model we have attempted to investigate the claim that alveolar ridge size or prominence has an influence on the articulatory effort required to produce clicks. While the results would suggest that it does, some caveats need to be considered first. The muscle outputs are reasonable and fit with common descriptions of what effect these muscles have on tongue shape (e.g. Zemlin 1998). However, validation of these muscle activation patterns would be difficult to achieve with electromyography (and the authors are unaware of any such

Table 3. Percentage (and absolute) change during phase 3 (release) in the maximum absolute value of the time derivative of volume (cm^3/s) between Sim-A and the other warping conditions

	Sim-B vs. Sim-A	Sim-C vs. Sim-A
click, free jaw	-11.78 (-1.83)	-25.72 (-4.00)
click, fixed jaw	-12.37 (-1.80)	-21.83 (-3.18)
velar stop, free jaw	-29.27 (-0.29)	-48.99 (-0.49)
velar stop, fixed jaw	-13.91 (-0.17)	-27.44 (-0.34)

study for click articulation). One source of support comes from the previous iteration of this model, where the muscle responses are comparable (Moisik and Dediu 2015) despite considerable differences in the design of the tongue. Also, while this model represents an improvement over its predecessor (Moisik and Dediu 2015), certain infelicities still exist, such as the rather small amount of rarefaction attainable. Also note that no fluid–structure interaction was simulated: this is a purely biomechanical simulation. In reality it may be that the negative pressure generated from rarefaction requires heightened muscle forces during the rarefaction phase and this could change the results. The viscosity of saliva on the tongue and palate may also influence click biomechanics and consideration of these forces could be incorporated into future models. Another matter is that a model such as the one described here has a large number of free parameters, and while every effort was made to keep the parameters physiologically realistic (and adhere to the settings documented in the preceding models upon which this model is based), a number of choices still need to be made. Hard palate morphology, particularly as concerns the shape of the alveolar ridge, was parameterized using a rudimentary technique, that of spherical warping. Future work could incorporate more advanced parametric models (Janssen et al. 2015) and statistical models based on three-dimensional intraoral scan data. An important set of choices is in the design of the inverse targets and their timings. There are many ways to do this, and the results could differ substantially from one design to another. This problem is also coupled with the problem of ArtiSynth’s numerical stability, which is generally very good, but there are nonetheless regions of the parameter space that cannot be explored simply because the numerical computations will not allow for it. The inverse targets used in these simulations represent a considerable amount of experimentation to find a solution that is both stable and fair (and ideally also produces aesthetically pleasing click visualizations). Obviously, the way forward would be to drive the simulation using actual data (such as real-time magnetic resonance imaging of click production), but this represents a serious undertaking and poses equally difficult choices to the designer. That and it is not possible (yet) to get good-quality three-dimensional data of click production, which is what is really required. Finally, no attempt has been made to model the active contribution of the soft palate in the formation of the velar closure in click production (which may occur even if the velopharyngeal port needs to be closed as in an oral click). These aspects need to be resolved in future refinements to the model.

With these considerations of the limitations of this ArtiSynth model of click production in mind, the results are consistent with the hypotheses introduced in section 1.2: (1) more muscle force is required to form click stricture with a larger alveolar ridge, and (2) all things being equal, the smoother the palate and the more rapid and larger the volume change. We suspect that greater articulatory effort (estimated through the integral of total muscle force) will have a negative bias on click appearance and maintenance at the diachronic scale. Although the click and velar stop simulations are primarily meant to be compared in terms of the relative effects of manipulating alveolar ridge shape, in absolute terms the click also requires greater articulatory effort overall. As discussed, larger and faster volume change ought to produce acoustically stronger click bursts with better (more perceptually salient) transient properties. It also provides a wider range of volumes achievable depending on other factors, and this should increase the reliability of click production (cf. Brunner et al. 2009). Modeling the acoustics would help to clarify if there are gains of perceptual consequence associated with the Khoisan palate shape. With an acoustic model, it may be possible to evaluate the influence of atmospheric pressure, which has been identified as possibly relevant in accounting for the distribution of ejectives (Everett 2013) and could, if anything, negatively influence click production (since the Khoisan languages are located at high elevation ~1500 m, where atmospheric pressure is low, the requisite pressure differential between the cavity and the ambient air would be less than that at lower altitudes and thus diminish the intensity of the click burst). A perceptual influence of palate shape on click production might be rather less direct than simply influencing the intensity of the burst: anatomical factors (and their sensorimotor effects) have been demonstrated to negatively impact the ability of infants to discriminate non-native speech sounds (Bruderer et al. 2015). Favorable palate shapes for producing clicks might thus benefit perceptual acuity for clicks via motor–auditory interactions (as proposed in the motor theory of speech perception; e.g. Liberman and Mattingly 1985).

This modeling supports the notion that alveolar ridge shape may be a source of biasing on clicks, but one that is weak at best. The borrowing of clicks by non-Khoisan groups with possibly quite different palate sizes (e.g. see Zulu, Fig. 2) and shapes support this interpretation of a weak bias. Likewise, gene flow in the region (exemplified by the Vassekela) has occurred for generations, and this has evidently introduced different distributions of palate shape phenotypes (van Reenen and Allen 1987). Clicks are also used *very* commonly for paralinguistic

purposes (Gil 2013), such as the ‘tsk-tsk’ in English to express disapproval, they serve conversational regulatory purposes (Wright 2011; Ogden 2013), and they are often spontaneously produced by children and by parents interacting with their children (relatedly, see Nathan 2001). What this shows is that in no way can the proposed bias act deterministically. But, despite these contrary details, it should also be considered that the Khoisan have the largest inventories of click sounds among all of the languages with clicks (Güldemann 2007). Likewise, clicks used as paralinguistic devices are not strictly equatable to phonological clicks, since these latter types are subject to articulatory coordination (in the speech stream) of a different and possibly more constrained nature. Finally, while weak biases may not be easily detectable on the individual level, they should not be dismissed. One of the key findings of studies on the cultural evolution of language is *bias amplification*, which results from the nonlinear phenomenon of language transmission (Kirby et al. 2007; Dediu 2011): it could be then that even weak biases might have an impact on the larger timescales of the cultural evolution of language.

Another complication is that vocal tract traits other than hard palate shape differ between ethnic groups (Howells 1973), some of which may be adaptive (e.g., Cramon-Taubadel 2011; Butaric and Maddux 2016). Our study focuses only on the alveolar ridge shape. The other structure with the most immediate relevance to the production of clicks is obviously the tongue, but nothing is known about how this varies in the groups of interest. Given the deformability of the tongue, morphological variation may be less relevant (but not entirely so), at least by comparison to that of the rigid structures. And it is clear that hard palate shape is by no means simple to characterize. Focusing just on the alveolar ridge prominence may be an overly simplistic way of approaching the issue. The model also does not take into account palate dimensions because the goal was to keep the model simple and focus on the alveolar ridge, but one can imagine how a narrow palate might facilitate click seal formation (although tongue size is relevant here, too). Palate size might also influence the amount of pressure exerted by the tongue on the teeth (Proffit et al. 1975). Future iterations of the model could examine these variables (palate width, length, and so forth) in addition to the subtler aspects of hard palate morphology.

A further issue is that the model abstracts away from place of articulation. The abstraction of place of articulation here is justified by the fact that all lingual clicks tend to appear similar to one another at the onset of stricture, and it is only when the rarefaction cavity forms that the

clicks can be distinguished by place of articulation (Ladefoged and Traill 1984). However, place is likely important, and the details of muscle forces and volume change characteristics are very likely to be a function of click place of articulation. In particular, given the relative rarity of palatal clicks and their resistance to borrowing (found only in Yeyi outside of the Khoisan group, see Fulop et al. 2003), these may be most strongly subject to a bias. The direction of lingual motion in such clicks is different and could be a source of differential articulatory efficiency determined by palate shape. There is also diachronic evidence that palatal (and alveolar) clicks are more subject to change than other types of clicks (Traill 1986). This leaves unexplained the bilabial clicks, which do not depend on the anterior lingual contact as the lingual clicks do. The fact that bilabials are commonly attested as conversational turn-taking regulatory elements (Wright 2011; Ogden 2013) but palatal clicks are not is suggestive of the bias. Bilabial clicks, but not palatal clicks, are also reported as ‘epiphenomenal’ (epenthetic/excrescent) productions, such as *as/mŋ*/being realized as *[mɔŋ]*, in languages such as Kinyarwanda (Demolin 2016) and German (Simpson 2007), and may have even influenced sound change in the Indo-European languages (Ohala 1995). We also cannot forget, however, that clicks must be subject to other constraints, such as perceptual ones, the importance of which should not be underestimated. For instance, Best et al. (1988) demonstrated that clicks are different from other speech sounds in terms of phonological attunement (with adults possessing an infant-like ability to perceive non-native contrasts in Zulu clicks). How this constitutes a bias against clicks is not clear (perhaps it is that they are difficult to attune to, making them poor candidates as phonemes, which seem to require this), but it at least suggests that clicks might be subject to different perceptual processing than other speech sounds. So if having the right palate shape lowers the threshold to click adoption and maintenance, a perceptual bias against clicks might keep this threshold altogether high (preventing isolated bilabial clicks from entering an inventory). We intend to explore different places of click articulation in subsequent modeling work.

Taking a step back, this work can be situated within the larger context of ongoing investigation into the adaptiveness of linguistic structure to various factors (for a survey, see Dediu et al. 2017, in press), including demographics (Lupyan and Dale 2010), environmental conditions (Everett 2013; Everett et al. 2015), and even genetics (Dediu and Ladd 2007), in addition to consideration of how language is organized as a system of communication (for discussion of this idea in relation to clicks, see Fleming, this issue). To this we add inter-

population morphological variation of vocal tract anatomy as another possible factor that, taken together, shapes the ‘fitness’ landscape upon which language evolves, in the long (evolutionary) and short (cultural) term. The results from our biomechanical model do support the proposed bias, but further support is needed to verify that such a bias indeed exists. First, although the literature supports clinal but local group differences in hard palate shape between the speakers of the so-called Khoisan languages and neighboring speakers of non-click languages, we have not established here that the distribution of palate shape phenotypes heavily favors a non-prominent alveolar ridge in the Khoisan to the exclusion of all other populations. In any case, our work does not in any way support interpreting the result as a deterministic factor, since clicks can be employed phonologically by speakers who differ considerably from the Khoisan shape, at least in terms of overall palate dimensions (such as the Zulu), and not all speakers of Khoisan languages ‘lack an alveolar ridge’, as Traill (1985) put it (one of his five participants does exhibit an alveolar ridge prominence; also see van Reenen and Allen 1987 and Winkler 1993). Second, while the biomechanical model is a promising means to quantify the elusive parameter of articulatory effort, it needs to be supported with experimental evidence to give it grounding in the real world. To address these shortcomings, we have conducted a large experimental study (called ‘ArtiVarK’) featuring anatomical and speech production imaging data of an ethnically diverse group of participants who were trained to produce clicks. The results of this study may further support the bias, or allow us to rule it out more confidently. If the results are in favor of the bias, then it would certainly motivate further investigation into the matter of clicks (along the lines identified above), but it would also spur investigation into how morphological variation of the vocal tract might similarly bias *other* types of speech sounds. The finding that anatomical (morphological) biases exist would be of considerable relevance to our understanding of the adaptability of language.

Supplementary data

Supplementary data is available at *Journal of Language Evolution* online.

Acknowledgements

This work would not have been possible without the support of the many fine people who develop and maintain ArtiVarK, including Ian Stavness, Sidney Fels, John Lloyd, Peter Anderson, Antonio Sanchez, and Bryan Gick, among many

others. We offer our humble thanks to the ArtiSynth team and all those who have contributed to the project. We also wish to thank the Editor, Hannah Little, for her efforts in coordinating this volume (and the special satellite meeting on language evolution held at the 18th International Congress of Phonetic Sciences in Glasgow, UK) and we thank the reviewers for their helpful commentary of this work.

Funding

This work is part of the G[3]bils project funded by the Netherlands Organisation for Scientific Research (NWO) VIDI grant 276-70-022 to D.D.

Conflict of interest statement. None declared

References

- Allott, R. (1994) 'Motor Theory of Language: The Diversity of Languages', in Wind J. et al. (eds.) *Studies in Language Origins*, Vol. 3, pp. 125–60. Amsterdam & Philadelphia: John Benjamins Publishing Company.
- Best, C. T. et al. (1988) 'Examination of Perceptual Reorganization for Nonnative Speech Contrasts: Zulu Click Discrimination by English-Speaking Adults and Infants', *Journal of Experimental Psychology: Human Perception and Performance*, 14/3: 345–60. <https://doi.org/10.1037/0096-1523.14.3.345>.
- Brosnahan, L. F. (1961) *The Sounds of Language: An Inquiry into the Role of Genetic Factors in the Development of Sound Systems*. Cambridge: W. Heffer and Sons.
- Bruderer, A. G. et al. (2015) 'Sensorimotor Influences on Speech Perception in Infancy', *Proceedings of the National Academy of Sciences*, 201508631. <https://doi.org/10.1073/pnas.1508631112>.
- Brunner, J. et al. (2009) 'On the Relationship Between Palate Shape and Articulatory Behavior', *The Journal of the Acoustical Society of America*, 125/6: 3936–49. <https://doi.org/10.1121/1.3125313>.
- Buchaillard, S. et al. (2009) 'A Biomechanical Model of Cardinal Vowel Production: Muscle Activations and the Impact of Gravity on Tongue Positioning', *The Journal of the Acoustical Society of America*, 126/4: 2033–51
- Butaric, L. N., and Maddux, S. D. (2016) 'Morphological Covariation Between the Maxillary Sinus and Midfacial Skeleton among Sub-Saharan and Circumpolar Modern Humans', *American Journal of Physical Anthropology*, 160/3: 483–97 <https://doi.org/10.1002/ajpa.22986>.
- Cramon-Taubadel, N. V. (2011) 'Global Human Mandibular Variation Reflects Differences in Agricultural and Hunter-Gatherer Subsistence Strategies', *Proceedings of the National Academy of Sciences*, 108/49: 19546–51. <https://doi.org/10.1073/pnas.1113050108>.
- Dediu, D. (2011) 'Are Languages Really Independent from Genes? If Not, What Would a Genetic Bias Affecting Language Diversity Look Like?', *Human Biology*, 83/2: 279–96. <https://doi.org/10.3378/027.083.0208>.
- et al. (2017, in press). 'Language is Not Isolated from Its Wider Environment: Vocal Tract Influences on the Evolution of Speech and Language', *Language and Communication*.
- , and Ladd, D. R. (2007) 'Linguistic Tone is Related to the Population Frequency of the Adaptive Haplogroups of Two Brain Size Genes, ASPM and Microcephalin', *Proceedings of the National Academy of Sciences*, 104/26: 10944–9.
- Demolin, D. (2016) 'Clicks, Stop Bursts, Voids and the Timing of Articulatory Gestures in Kinyarwanda', *Studies in African Linguistics*, 45/1–2: 141–60.
- Engstrand, O. (1997) 'Why are Clicks so Exclusive', in *Papers from Fonetik 97, The Ninth Swedish Phonetics Conference, held in Umeå, May 28–30, 1997*, Vol. 4, pp. 191–4. Department of Phonetics, Umeå University.
- Everett, C. (2013) 'Evidence for Direct Geographic Influences on Linguistic Sounds: The Case of Ejectives', *PLoS ONE*, 8/6: e65275. <https://doi.org/10.1371/journal.pone.0065275>.
- Everett, C. et al. (2015) 'Climate, Vocal Folds, and Tonal Languages: Connecting the Physiological and Geographic Dots', *Proceedings of the National Academy of Sciences*, 201417413. <https://doi.org/10.1073/pnas.1417413112>.
- Fulop, S. A. et al. (2003) 'Yeyi Clicks: Acoustic Description and Analysis', *Phonetica*, 60/4: 231–60 <https://doi.org/10.1159/000076375>.
- Gil, D. (2013) 'Para-Linguistic Usages of Clicks', in Dryer M. S., and Haspelmath M. (eds.) *The World Atlas of Language Structures Online*. Leipzig: Max Planck Institute for Evolutionary Anthropology. Retrieved from <http://wals.info/chapter/142>.
- Güldemann, T. (2007). *Clicks, Genetics, and 'proto-world' from a Linguistic Perspective*. Inst. für Afrikanistik. Retrieved from https://www.researchgate.net/profile/Tom_Gueldemann/publication/40853197_Clicks_genetics_and_proto-world_from_a_linguistic_perspective/links/559645ad08ae99aa62c75bb0.pdf; last accessed March 10, 2017.
- Howells, W. W. (1973) 'Cranial Variation in Man: A Study by Multivariate Analysis of Patterns of Difference among Recent Human Populations', *Papers of the Peabody Museum of Archaeology and Ethnology*, 67: 1–259.
- Janssen, R. et al. (2015). 'Bezier Modelling and High Accuracy Curve Fitting to Capture Hard Palate Variation', in *Proceedings of the 18th International Congress of Phonetic Sciences [online only]*. Glasgow, UK. Retrieved from <http://pubman.mpdl.mpg.de/pubman/faces/viewItemOverviewPage.jsp?itemId=escidoc:2271364>; last accessed March 10, 2017.
- Kirby, S. et al. (2007) 'Innateness and Culture in the Evolution of Language', *Proceedings of the National Academy of Sciences*, 104/12: 5241–5. <https://doi.org/10.1073/pnas.0608222104>.
- Kirchner, R. (1998) 'An Effort-Based Approach to Lenition', Doctoral dissertation, UCLA, Los Angeles, California.
- Ladefoged, P., and Traill, A. (1984) 'Linguistic Phonetic Descriptions of Clicks', *Language*, 60/1: 1–20. <https://doi.org/10.2307/414188>.
- Liberman, A. M., and Mattingly, I. G. (1985) 'The Motor Theory of Speech Perception Revised', *Cognition*, 21/1: 1–36. [https://doi.org/10.1016/0010-0277\(85\)90021-6](https://doi.org/10.1016/0010-0277(85)90021-6).

- Lloyd, J. E. et al. (2012). 'ArtiSynth: A Fast Interactive Biomechanical Modeling Toolkit Combining Multibody and Finite Element Simulation', in Payan Y. (ed.) *Soft Tissue Biomechanical Modeling for Computer Assisted Surgery*, pp. 355–94. Berlin, Germany: Springer.
- Lupyan, G., and Dale, R. (2010) 'Language Structure Is Partly Determined by Social Structure', *PLoS ONE*, 5/1: e8559. <https://doi.org/10.1371/journal.pone.0008559>.
- , and ——— (2016) 'Why Are There Different Languages? The Role of Adaptation in Linguistic Diversity', *Trends in Cognitive Sciences*, 20/9: 649–60 <https://doi.org/10.1016/j.tics.2016.07.005>.
- Miller, A. et al. (2009) 'Rarefaction Gestures and Coarticulation in Mangetti Dune !Xung clicks', in Uther M. et al. (eds.) *Proceedings of the 10th Annual Conference of the International Speech Communication Association*. pp. 2279–82. Brighton, UK: Casual Productions.
- Moisik, S. R., and Dediu, D. (2015) 'Anatomical Biasing and Clicks: Preliminary Biomechanical Modelling', in H. Little (ed.), *Proceedings of the 18th International Congress of Phonetic Sciences [ICPhS 2015] Satellite Event: The Evolution of Phonetic Capabilities: Causes, Constraints, Consequences*, pp. 8–13. Glasgow: ICPhS. Retrieved from <http://pubman.mpdl.mpg.de/pubman/faces/viewItemOverviewPage.jsp?itemId=escidoc:2166182>; last accessed March 10, 2017.
- Napoli, D. J. et al. (2014) 'On the Linguistic Effects of Articulatory Ease, with a Focus on Sign Languages', *Language*, 90/2: 424–56. <https://doi.org/10.1353/lan.2014.0026>.
- Nathan, G. S. (2001) 'Clicks in a Chinese Nursery Rhyme', *Journal of the International Phonetic Association*, 31: 2. <https://doi.org/10.1017/S0025100301002043>.
- Nazari, M. A. et al. (2011) 'Shaping by Stiffening: A Modeling Study for Lips', *Motor Control*, 15/1: 141–68.
- Ogden, R. (2013) 'Clicks and Percussives in English Conversation', *Journal of the International Phonetic Association*, 43/03: 299–320. <https://doi.org/10.1017/S0025100313000224>.
- Ohala, J. J. (1995) 'A Probable Case of Clicks Influencing the Sound Patterns of Some European Languages', *Phonetica*, 52/3: 160–70. <https://doi.org/10.1159/000262167>.
- Proffit, W. R. et al. (1975) 'Lip and Tongue Pressures Related to Dental Arch and Oral Cavity Size in Australian Aborigines', *Journal of Dental Research*, 54/6: 1161–72 <https://doi.org/10.1177/00220345750540061101>.
- Simpson, A. P. (2007) 'Acoustic and Auditory Correlates of Non-Pulmonic Sound Production in German', *Journal of the International Phonetic Association*, 37/2: 173. <https://doi.org/10.1017/S0025100307002927>.
- Stavness, I. et al. (2011) 'Coupled Hard-Soft Tissue Simulation with Contact and Constraints Applied to Jaw-Tongue-Hyoid Dynamics', *International Journal for Numerical Methods in Biomedical Engineering*, 27/3: 367–90
- et al. (2013) 'A Biomechanical Modeling Study of the Effects of the Orbicularis Oris Muscle and Jaw Posture on Lip Shape', *Journal of Speech, Language, and Hearing Research*, 56/3: 878–90. [https://doi.org/10.1044/1092-4388\(2012\)12-0200](https://doi.org/10.1044/1092-4388(2012)12-0200).
- Stevens, K. N. (1998). *Acoustic Phonetics*. Cambridge, Massachusetts: The MIT Press.
- Stone, M. et al. (2013) 'Frequency of Apical and Laminal/s/in Normal and Post-glossectomy Patients', *Journal of Medical Speech Language Pathology*, 20/4: 106–11.
- Thomas-Vilakati, K. D. (1999). *Coproduction and Coarticulation in IsiZulu Clicks*. Los Angeles, California: UCLA.
- Tiede, M. K. et al. (2005) 'Perturbed Palatal Shape and North American English/r/Production', *Journal of the Acoustical Society of America*, 117: 2568–9.
- Truill, A. (1985) 'Phonetic and Phonological Studies of !Xóõ Bushman', in *Quellen zur Khoisan-Forschung*, Vol. 1. Hamburg: Helmut Buske Verlag.
- (1986) 'Click Replacement in Khoe', in Vossen R. and Keuthmann K. (eds.), *Contemporary Studies on Khoisan*, Vol. 2, pp. 301–20. Hamburg: Helmut Buske.
- Traumüller, H. (2003) 'Clicks and the Idea of a Human Protolanguage', *Reports from the Department of Phonetics, Umeå University (PHONUM)*, 9: 1–4.
- van Reenen, J. F. (1964) 'Dentition, Jaws and Palate of the Kalahari Bushman', *Journal of the Dental Association of South Africa*, 19: 1–37.
- , and Allen, D. W. (1987) 'The Palatal Vault of the Bushman (San), Vassekela and Himba', *The Journal of the Dental Association of South Africa = Die Tydskrif Van Die Tandheelkundige Vereniging Van Suid-Afrika*, 42/8: 489–92.
- Vendryès, J. (1902) 'Some Thoughts on Sound Laws', in Keiler A. R. (ed.), *A Reader in Historical and Comparative Linguistics*, pp. 109–120. New York: Holt, Rinehart and Winston.
- Weirich, M., and Fuchs, S. (2013) 'Palatal Morphology Can Influence Speaker-Specific Realizations of Phonemic Contrasts', *Journal of Speech, Language, and Hearing Research*, 56/6: S1894–908. [https://doi.org/10.1044/1092-4388\(2013\)12-0217](https://doi.org/10.1044/1092-4388(2013)12-0217)
- Winkler, E. M., and Kirchengast, S. (1993) 'Metric Characters of the Hard Palate and their Cephalometric Correlations in Namibian !Kung San and Kenyan Tribes', *Human Biology*, 65/1: 139–50.
- Winkler, E.-M. (1993) 'Qualitative und quantitative Merkmale des harten Gaumens bei südwestafrikanischen Saniden und ostafrikanischen Negriden [Qualitative and quantitative characteristics of the hard palates of South-West African San and East African Negroes]', *Homo*, 44/1: 74–91.
- Wright, M. (2011) 'On Clicks in English Talk-In-Interaction', *Journal of the International Phonetic Association*, 41/2: 207–29. <https://doi.org/10.1017/S0025100311000144>.
- Zemlin, W. R. (1998). *Speech and Hearing Science: Anatomy and Physiology*, 4th edn. Boston, London, Toronto, Sydney, Tokyo, and Singapore: Allyn and Bacon.