Speech across species : on the mechanistic fundamentals of vocal production and perception

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3

Vocal tract articulation revisited: the case of the monk parakeet

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Birdsong and human speech share many parallels with respect to vocal learning and development. However, vocal production mechanisms have long been considered to be different. The vocal organ of songbirds is more complex than the human larynx, leading to the hypothesis that vocal variation in birdsong originates mainly at the sound source while in humans is primarily due to vocal tract filtering. However, several recent studies have indicated the importance of vocal tract articulators such as beak and oropharyngeal-esophageal cavity. In contrast to most other bird groups, parrots have a prominent tongue raising the possibility that tongue movements may be of significant importance in vocal production in parrots, but evidence is rare and observations often anecdotal. In the current study we used X-ray cinematographic imaging of naturally vocalizing monk parakeets (*Myiopsitta monachus*) to assess which articulators are possibly involved in vocal tract filtering in this species. We observed prominent tongue height changes, beak opening movements and tracheal length changes suggesting an important role of tongue and beak in producing a resonance cavity and identifying the trachea as another vocal articulator. We also found strong positive correlations between beak opening and amplitude as well as changes in tongue height and amplitude in several types of vocalizations. Our results suggest considerable differences between parrot and songbird vocal production while at the same time parrots vocal articulation might more closely resemble human speech production.

Manuscript

Introduction

In recent years birdsong has become the focus of many scientists interested in the cognitive, neural, genetic and physiological mechanisms underlying human speech and language. The fact that songbirds and humans exhibit many parallels in vocal learning and perception (e.g. Doupe & Kuhl 1999; Ohms *et al.* 2010a) has established songbirds as an excellent model system in which to study the underlying mechanisms in both birds and humans (Bolhuis *et al.* 2010). Also, cognitive mechanisms related to syntax detection might be comparable in humans and songbirds although results are controversial (Gentner *et al.* 2006; van Heijningen *et al.* 2009).

However, while there are numerous analogies there are differences too, especially regarding vocal production. In humans the primary sound source is located in the larynx and voiced speech sounds are produced by a pair of vibrating vocal folds (Titze 2000). The generated acoustic signal is subsequently filtered by shaping the vocal tract using different articulators such as tongue and lips (Ladefoged 2006). This leads to amplification of different frequency regions within the broad-band spectrum of human speech sounds.

The vocal organ of birds on the other hand, the syrinx, is located at the basis of the trachea in the interclavicular air sac (Suthers & Zollinger 2004) and in the case of Oscine songbirds consists of two sets of vibrating labia located at the cranial end of each of the primary bronchi (Goller & Larsen 1997) which are capable of independent motor control (Suthers 1990). This enables songbirds to sing with two voices simultaneously or switch between both sets of labia while singing, depending on the frequencies produced (Suthers 1990; Suthers *et al.* 1994; Suthers *et al.* 2004; Zollinger & Suthers 2004). The more complex vocal organ of songbirds initially led to the hypothesis that acoustic variation predominantly arises at the sound source and that in contrast to human speech acoustic filtering by the vocal tract only plays a minor role in birdsong production (Greenewalt 1968).

Most bird species studied produce relatively narrow-band, tonal songs which lack the complex resonance patterns prominent in human speech. It has been shown, however, that the sound generated at the source can exhibit harmonic overtones (Beckers *et al.* 2003) and that cyclical movements of the hyoid skeleton or expansion of the cervical esophagus filter these out of the signal by tuning the oropharyngeal-esophageal cavity (OEC) to the fundamental frequency of the song (Riede *et al.* 2004; Riede *et al.* 2006; Riede & Suthers 2009). Additionally, in zebra finches (*Taeniopygia guttata*) which produce a wide range of broad-band note types, expansion of the OEC has also been found to affect frequency patterns by shifting energy to relatively lower frequencies while amplitude generally increases (Ohms *et al.* 2010b). Other articulators involved in avian vocal tract filtering include beak movements and gape widths (Hoese *et al.* 2000; Podos *et al.* 2004; Nelson *et al.* 2005) making clear that there is increasing evidence for the importance of vocal tract filtering in the production of avian vocalizations.

Interestingly, observations of naturally vocalizing and speech-imitating parrots, which have a simpler syrinx with only one pair of vibrating labia (Larsen & Goller 2002) suggest that tongue movements play an important role in vocal production too (Nottebohm 1976; Patterson & Pepperberg 1994; Beckers *et al.* 2004). Compared to songbirds the parrot tongue is morphologically very different in that it contains many intrinsic muscles and its surface is more like the human tongue: a fleshy, rather flexible structure (Homberger 1986) that might be moved in a horizontal and vertical plane within the oral cavity. So far, however, evidence on this subject is rare and observations are often anecdotal. Studies on a speech-imitating African grey parrot *(Psittacus erithacus)* have suggested that this bird can, similarly to humans, adjust the front-back position of its tongue in order to imitate human articulatory patterns while it lacks, contrary to humans, extensive control over the high-low dimension (Patterson & Pepperberg 1994; Warren *et al.* 1996). Another experimental approach evaluating the significance of tongue movements in monk parakeet (*Myiopsitta monachus*) vocalizations has demonstrated that moving the tongue horizontally in the mouth cavity can lead to frequency and amplitude changes in acoustic resonance patterns (Beckers *et al.* 2004). However, no direct observations of tongue movements in naturally vocalizing parrots exist to date nor is it known whether parrots, like songbirds, exhibit a cyclical movement of the hyoid skeleton causing an expansion of the OEC.

In the current study we address these questions by using X-ray cinematographic imaging of the vocal tract during natural vocalizations of monk parakeets. We report on tongue height changes and beak movements during sound production and how these strongly correlate with amplitude. Furthermore we found evidence for tracheal shortening during vocalizing.

Material and Methods

Subjects

The monk parakeets used in this study had been obtained from a U.S. Department of Agriculture pest control program in Florida and were housed in pairs or individually in metal cages (43 cm deep x 44.5 cm wide x 50 cm tall) in the same room under a 14L:10D schedule prior to the experiment. During the experiment all birds were moved in their home cages into the room that contained the X-ray apparatus to stimulate the respective focal bird to vocalize. Food and water were provided *ad libitum* at all times and wooden toys in the cages served as enrichment. X-ray recordings were obtained from four monk parakeets of which three fulfilled our criteria for good lateral views and were included in further analysis.

X-ray cinematography and song recordings

A Series 9800 mobile C-arm and 1 k x 1 k neurovascular work station (OEC Medical Systems, Inc.) was used to obtain X-ray videos of spontaneously vocalizing monk parakeets. This apparatus generated a digital signal of 30 pulses/s and a 1000 x 1000 image resolution. The duration of each X-ray pulse was 10 ms. The focal bird was transferred into a metal cage of the same dimensions given above in which two opposite sides of the cage were replaced by plexiglass panels and enabled recording the bird in a lateral view with the head of the bird being about 5 cm in front of the intensifier screen. The digital signal of the X-ray apparatus was recorded on a Sony GVD-1000 NTSC digital video cassette recorder, mini DV format. Sound was simultaneously recorded using a directional microphone (Audio Technica model AT835b) which was positioned about 0.5 m from the bird. Afterwards relevant sequences of the X-ray movies were digitized and rendered at 30 frames/s (video) and concurrent vocalizations were digitized at 48 kHz sampling rate using the software Vegas Video, Sonic Foundry, Madison, WI, USA, version 5.0. All data files were corrected for a recording delay of approximately 114 milliseconds in the video relative to the audio.

Marker implantation

In all four birds a stainless steel ball (SIS Type 316, 1.59 mm diameter, Small Parts Inc.) with a diameter of 1.59 mm was inserted dorsally under the skin of the neck. This sphere provided a size reference when measuring anatomical distances from the X-ray videos. Additionally, two of the monk parakeets were anesthetized and the trachea was exposed through a small mid-ventral incision in the skin of the neck and two pieces of silver wire (ca. 2 mm long x 0.16 mm diameter) (Engelhard Fine Wire) were attached with tissue adhesive (3 M Vetbond) to two tracheal rings. These markers were about 13 mm apart in bird 2 and about 10 mm in bird 3. In order to better follow tongue movements during X-ray recordings, we implanted a short piece (ca. 1.5 mm) of the same silver wire into the tongue bottom about 1.5 mm from the tip of the tongue of bird 1. The wire was inserted into the hole made by a 26 ga hypodermic needle and the incision was sealed with a micro-drop of tissue adhesive. All of the described procedures were performed under isoflurane anesthesia administered with a calibrated anesthetic gas vaporizer (Fluotec) through a mask at a concentration of ~1.5 to 2.0% in air.

Anatomical measurements

Only those video sequences in which the birds' heads were clearly laterally oriented towards the X-ray beam were used for measuring anatomical distances during sound production. The distances measured were: (1) 'beak movement' represented by the distance between the dorsal point of the beak- skull transition and the ventral point of the lower mandible where the bones form a strong symphysis, (2) 'tongue height' which was defined as the distance between the tongue's ventral surface measured about 1.5 mm from the tip of the tongue and the same point of the lower mandible as measured in 'beak movement' and (3) 'tracheal shortening' which was determined by changes in the distance between the tracheal markers (Fig. 3.1). These measurements were performed using MaxTRAQ Lite+, version 2.2.0.1 (Innovision Systems Inc.) by manually selecting points of interests in each successive frame. From the coordinates of each selected point distances were automatically calculated between the points. Ten repeated measures of beak movement in the same frame had a standard deviation of 0.12 mm whereas the distance measured between two metal bars had a standard deviation of 0.14 mm.

Acoustic measurements were done with sound analysis software (Praat, version 4.6.09, freely available at www.praat.org; Boersma 2001).

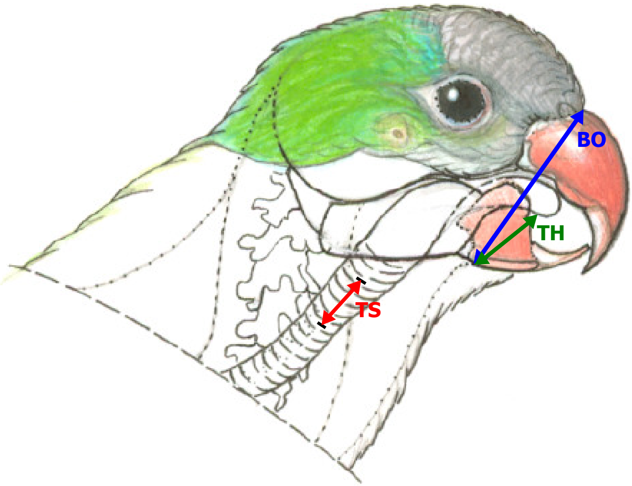

Figure 3.1. Anatomical measurements.

Lateral view of a monk parakeet indicating the distances measured. Beak opening (BO) describes the distance from the dorsal edge of the beak-skull transition to the ventral edge of the lower mandible where the bones form a strong symphysis. Tongue height (TH) is defined by the distance between the ventral surface of the tongue about 1.5 mm from the tip and the lower mandible and tracheal shortening (TS) measures the distance between two tracheal markers.

Results

Vocalizations

Adult monk parakeets produce nine different call types in various contexts, e.g. territorial defense, pair bonding and flock integration, which differ in temporal as well as spectral parameters (Martella & Bucher 1990). In the current study, however, only a subset of these vocalizations was uttered during recording sessions, consisting of contact and greeting calls as well as chatter sounds.

The most common call type produced by the monk parakeets in our study was the contact call (Fig. 3.2a), a short (180.66 ms ± 9.17 s.d. between animals), strongly frequency-modulated (FM) call with discrete, harmonically related frequency bands, which is uttered in many contexts by both sexes (Martella & Bucher 1990). We recorded several instances of contact calls of three birds that met the criteria specified in the methods section to be included in the analysis.

The second-most common call produced by the monk parakeets in this study was the greeting call (Fig. 3.3a) which is considerably longer and more variable in duration (455.70 ms ± 234.39 s.d. between individuals) and does not exhibit the fast FM typical for contact calls. It consists of a spectrally complex pattern with amplified frequency bands that are indicative of formants (Beckers *et al.* 2004) and that exhibit some FM, especially at the beginning of a call.

Furthermore, each of the parakeets produced several sounds which are referred to as chatter (Martella & Bucher 1990). These sounds are mostly characterized by short harmonic stacks which at times exhibit some FM. In the case of bird 1 these short harmonic sounds alternate with notes that exhibit fast FM (Fig. 3.4a).

Articulatory movements

All monk parakeets in this study generally showed the same articulatory movements of beak and tongue when producing contact and greeting calls. Although these call types differed from each other in acoustic structure, no obvious difference in the movement patterns of tongue and beak was detected that could explain the acoustic variation and FM between call types.

Beak opening increased substantially before the onset of a contact call and the tongue which usually rests high in the oral cavity, so that it touches the upper mandible, moves downwards and retracts a bit thereby creating a large oral resonance cavity (Fig. 3.5). Just after call onset both beak gape and tongue height reached their maximum mean displacement with beak movement ranging from 5.57 to 6.68 mm and tongue height ranging from 2.92 to 4.31 mm (Table 3.1). This position was maintained for the duration of the call, after which both articulators returned to their original position.

The movement patterns for beak and tongue during greeting calls were rather similar to those described in contact calls. However, in longer greeting calls the initial beak opening movement proceeded more gradually compared to contact calls, reaching its maximal displacement towards the end of the call, while tongue height decreased faster at the beginning of the greeting call and remained low throughout its duration (Fig. 3.3b). Additionally, beak gape did not increase as much as it did during contact calls with a mean maximum displacement ranging from 4.78 to 6.28 mm whereas tongue depression seemed to be slightly higher in two of the birds (Table 3.2). Furthermore it was noticeable that greeting calls were produced over a wide range of intensities and there was a strong relationship between acoustic power and magnitude of articulatory movements (Fig. 3.6 b,e; see below). Therefore we divided greeting calls into two groups depending on mean acoustic power measured over the whole call. All greeting calls below 66 dB were referred to as ‘soft greeting calls’ whereas everything above this threshold was simply referred to as ‘greeting calls’. Mean maximum beak movement was on average 3.3 times as high in greeting calls compared to soft greeting calls whereas tongue displacement differed on average only by a factor of 1.9 (Tables 3.2 and 3.3). This suggests that tongue height might be relatively more important than beak gape in generating spectral features which are similar in loud and soft greeting calls while beak gape might mainly affect amplitude.

Figure 3.4 shows the cyclical movements of beak and tongue during the production of two alternating chatter sounds. It is apparent that the magnitude of change of both beak opening and tongue height was less in the second and fourth note compared to the first and third. Examining the corresponding video revealed a strikingly opposite pattern of cyclical tongue movement between these two note types. During the production of the first and third note the tip of the tongue and antero-dorsal part of the tongue body first moved caudally following the movement of the lower mandible while the postero-dorsal part of the tongue body remained higher on a vertical axis. However, during the second part of the sound, which consisted of upward FM sweeps, the postero-dorsal part of the tongue body pushed downwards now forming a horizontal plane with the rest of the structure before the anterior part of the tongue moved rostrally to its resting position high up in the mouth cavity touching the upper mandible. In the second and fourth note this pattern was reversed with the postero-dorsal part of the tongue body moving caudally just before the onset of the note. During the first part of the note the rest of the tongue then completed its caudal movement and again formed a horizontal plane with the postero-dorsal part of the tongue body which was lifted a bit during the second part of the note before the tongue as a whole moved rostrally to its resting position.

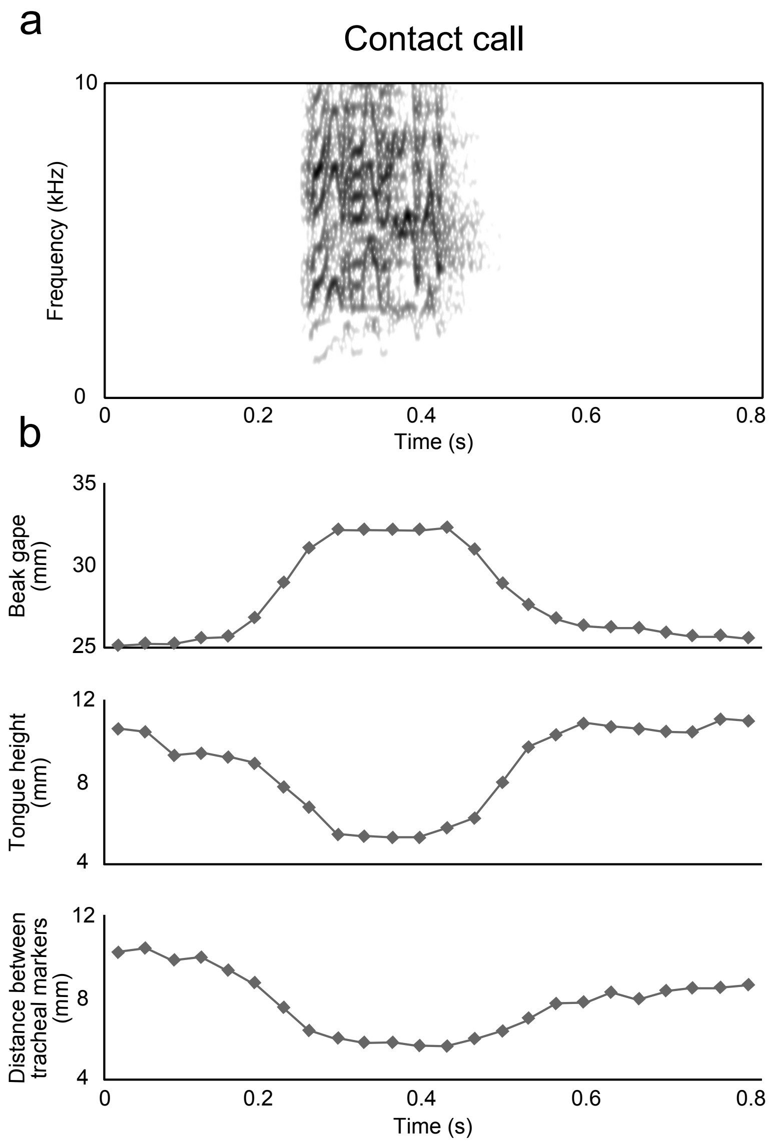

Figure 3.2. Articulatory patterns during contact call production.

Contact calls are accompanied by movements of different articulators. **(a)** Spectrogram of a contact call produced by bird 3. **(b)** Beak opening, tongue depression and tracheal shortening over the course of the contact call displayed in panel (a). kHz, kilohertz; mm, millimeters; s, seconds.

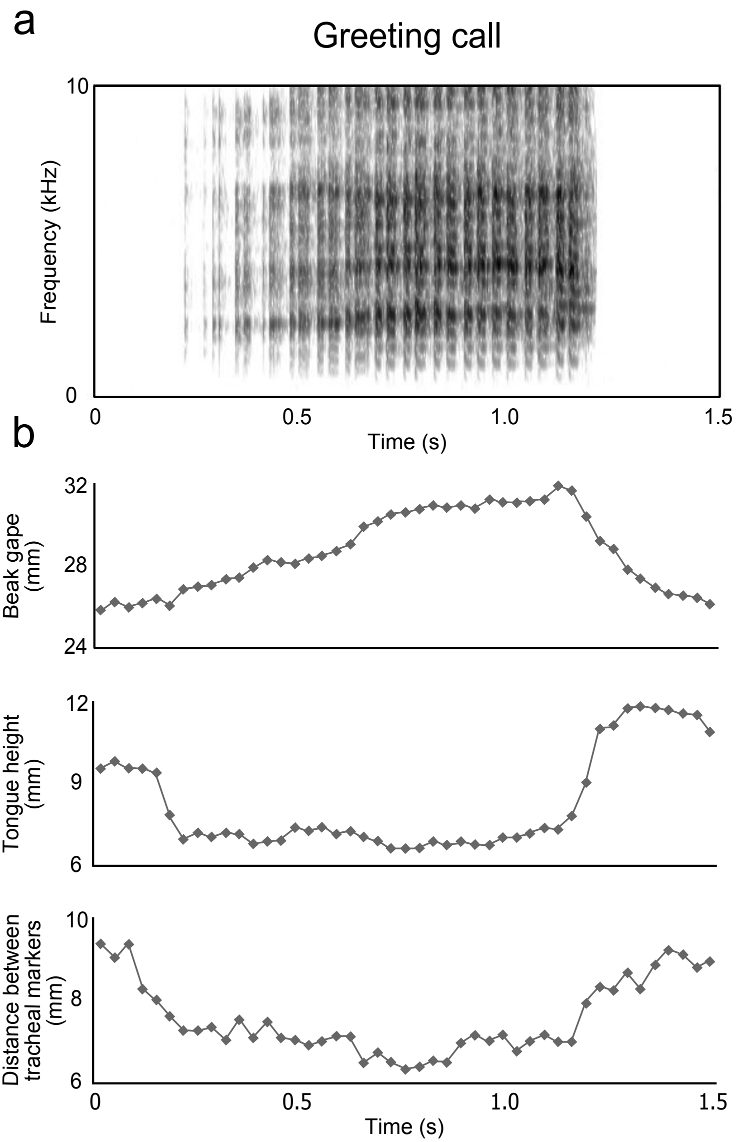

Figure 3.3. Articulatory patterns during greeting call production.

Similar to contact calls, greeting calls are accompanied by changes in the same articulators as described for contact calls. **(a)** Spectrogram of a greeting call produced by bird 3. **(b)** Beak opening, tongue depression and tracheal shortening over the course of the greeting call displayed in panel (a). kHz, kilohertz; mm, millimeters; s, seconds.

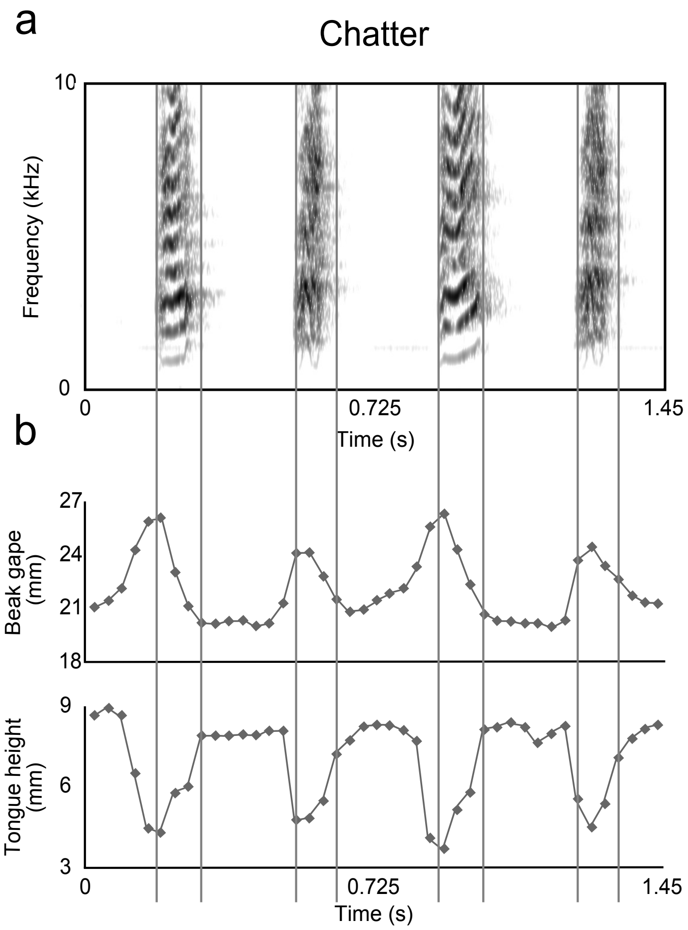

Figure 3.4. Articulatory patterns during chatter sounds.

This figure represents articulatory movements during the production of two alternating chatter sounds of bird 1. **(a)** Spectrogram of chatter sounds. **(b)** Beak opening and tongue depression during the production of the chatter sounds illustrated in panel (a). Note that both beak and tongue reach their maximum displacement just after the onset of the sound while most of the sound is produced when the articulators already move back to their original position. kHz, kilohertz; mm, millimeters; s, seconds.

Changes in tracheal length

In birds 2 and 3 we implanted silver wire markers onto the trachea which could be traced during sound production. In bird 2 these markers were attached to the trachea 18 and 31 mm from the glottis. In bird 3 the markers were implanted 24 and 34 mm from the larynx. The total length of the trachea from glottis to syrinx was 55 mm in bird 2 and 65 mm in bird 3. In both contact and greeting calls the distance between these markers changed substantially over the course of call production with a mean maximum shortening ranging from 5.70 mm in bird 2 to 3.40 mm in bird 3 during contact calls, from 4.78 mm in bird 2 to 3.03 mm in bird 3 during greeting calls and from 1.15 mm in bird 2 to 2.22 mm in bird 3 during soft greeting calls (Tables 3.1-3.3). Postmortem investigation of the trachea revealed that it had very little resistance to substantial changes in length in both birds. Calculating predicted resonances of the tracheas modeled as stopped tubes yields resonances at 1570 Hertz and 1330 Hertz respectively for bird 2 and 3. Both of these values fall within the range of spectral peaks measured over the course of greeting calls.

Table 3.1. Articulator displacement during contact calls.

Bird ID	**Beak opening (mm)**	**Tongue depression (mm)**	**Tracheal shortening (mm)**
1	5.57 ± 0.98; *n* = 6	2.92 ± 0.82; *n* = 6	
2	6.50 ± 1.04; *n* = 10	4.00 ± 0.47; *n* = 10	5.70 ± 0.08; *n* = 2
3	6.68 ± 0.89; *n* = 28	4.31 ± 0.60; *n* = 28	3.40 ± 1.20; *n* = 7

This table lists the mean maximum beak opening movement, tongue depression and tracheal shortening in millimeters per bird inlcuding standard deviation and total number of calls measured. ID, identity; mm, millimeters.

Table 3.2. Articulator displacement during greeting calls.

Bird ID	**Beak opening (mm)**	**Tongue depression (mm)**	**Tracheal shortening (mm)**
1	4.78 ± 1.11; *n* = 4	3.85 ± 1.32; *n* = 4	
2	6.28 ± 0.50; *n* = 4	4.79 ± 1.12; *n* = 4	4.78; *n* = 1
3	5.19 ± 1.15; *n* = 1	4.11 ± 0.92; *n* = 13	3.03 ± 1.24; *n* = 13

This table is equivalent to table 3.1 but lists measurements for greeting calls instead. ID, identity; mm, millimeters.

Table 3.3. Articulator displacement during soft greeting calls.

Bird ID	Beak opening (mm)	Tongue depression (mm)	Tracheal shortening (mm)
2	0.77 ± 0.63; *n* = 6	1.66 ± 0.99; *n* = 6	1.15 ± 0.86; *n* = 2
3	2.70 ± 1.87; *n* = 10	3.03 ± 1.39; *n* = 10	2.22 ± 1.05; *n* = 10

This table is equivalent to tables 3.1 and 3.2 and gives articulator measurements for soft greeting calls. ID, identity; mm, millimeters.

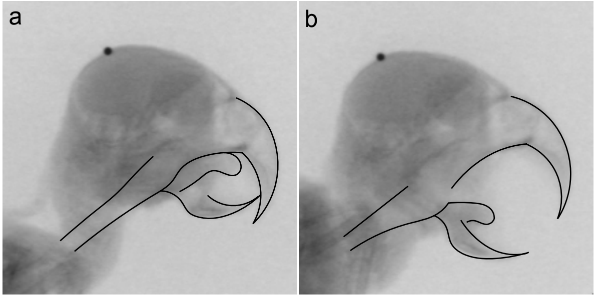

Figure 3.5. X-ray images.

This figure shows two X-ray frames of the same monk parakeet **(a)** prior to vocalizing and **(b)** during contact call production. Beak, tongue and trachea are highlighted by black lines.

Relationship between articulators and intensity

The fast FM patterns characteristic for contact calls are likely to be caused by the sound source and only marginally influenced by articulatory movements of the upper vocal tract since 1) in both contact and greeting calls tongue and beak movements as well as tracheal contraction are comparable and 2) changes in articulatory configurations are slow compared to FM. Changes in resonance patterns of greeting calls, however, are likely to be influenced by articulator movements. Unfortunately it was not possible to establish clear relationships between articulator configuration and formant changes because it is not clear how the sound source behaves in this species which therefore precludes extracting the filter characteristics. However, we detected positive correlations between articulator movements (beak opening, tongue height change and tracheal contraction) and intensity for greeting calls and chatter sounds in several birds (Fig. 3.6, Table 3.4). We did not find a correlation between beak movements and intensity and tongue height changes and intensity for contact calls, although this might be due to the fact that contact calls are generally rather loud calls and there is little variation in intensity.

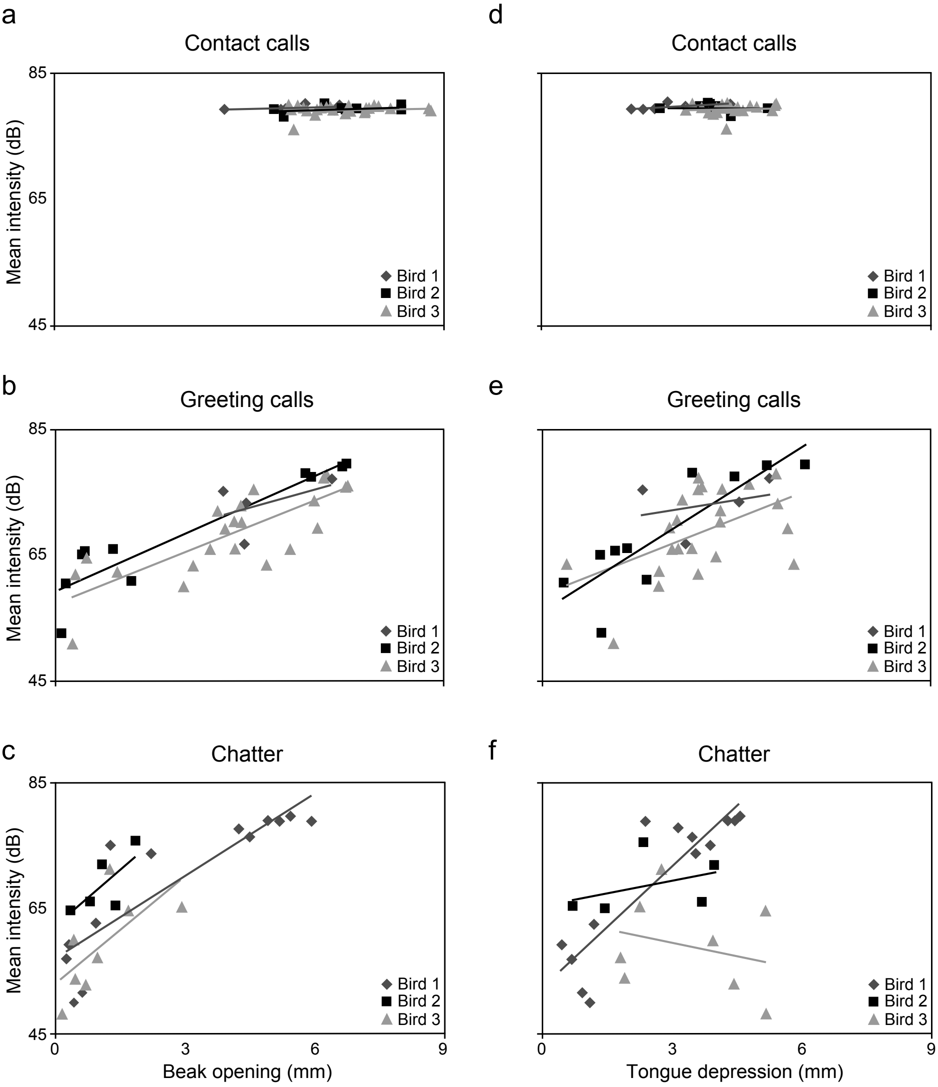

Figure 3.6. Correlations between articulator displacements and vocalization intensity.

This figure shows six scatter plots in which **(a)** beak opening and intensity for contact calls, **(d)** tongue depression and intensity for contact calls, **(b)** beak opening and intensity for greeting calls, **(e)** tongue depression and intensity for greeting calls, **(c)** beak opening and intensity for chatter sounds and **(f)** tongue depression and intensity for chatter sounds are plotted against each other for all three birds. Table 3.4 lists which of these correlations are significant. dB, decibel; mm, millimeters.

Table 3.4. Correlations between distances and intensity.

Distance measured	Vocalization		Bird 1	Bird 2	Bird 3
Beak opening	contact call	Spearman's rho	0.257	0.231	-0.035
		p	0.623	0.521	0.858
		n	6	10	28
	greeting call	Spearman's rho	0.400	0.915	0.816
		p	0.600	**< 0.01**	**< 0.01**
		n	4	10	23
	chatter	Spearman's rho	0.918	0.700	0.762
		p	**< 0.01**	0.188	**0.028**
		n	13	5	8
Tongue depression	contact call	Spearman's rho	0.657	-0.103	0.151
		p	0.156	0.777	0.442
		n	6	10	28
	greeting call	Spearman's rho	0.400	0.867	0.532
		p	0.600	**< 0.01**	**< 0.01**
		n	4	10	23
	chatter	Spearman's rho	0.813	0.600	0.286
		p	**< 0.01**	0.285	0.493
		n	13	5	8
Tracheal shortening	contact call	Spearman's rho			-0.179
		p			0.702
		n			7
	greeting call	Spearman's rho			0.397
		p			0.061
		n			23
	chatter	Spearman's rho			0.587
		p			**0.045**
		n			12

This table shows the correlations between three distances measured (beak opening, tongue depression and tracheal contraction) and mean intensity for all vocalizations measured. Intensity was measured over the whole vocalization. Significant p-values are printed bold. *n*, number of vocalizations measured.

Discussion

Our study is the first to investigate vocal tract articulation in a naturally vocalizing parrot species using X-ray cinematographic imaging. Our results demonstrate that monk parakeet vocalizations are accompanied by prominent changes in beak gape, tongue position and tracheal length. These findings are partly consistent with what has been previously reported for an African grey parrot imitating speech (Warren *et al.* 1996). While previous studies have indicated that retraction and extension of the tongue between back and front positions, respectively, seem to be particularly important to mimic human speech (Warren *et al.* 1996) and modulate formant patterns (Beckers *et al.* 2004), our results show that monk parakeets especially manipulate the high-low dimension when vocalizing while they might be able to move their tongue in a horizontal plane more than they actually do when communicating naturally. Given that monk parakeets can mimic human speech, which seems to require extensive control over the front-back position of the tongue, one wonders why they do not use this dimension as much in their own vocalizations. Nevertheless it is obvious from the videos that tongue position also changes with respect to frontedness, although it is difficult to reliably quantify these patterns.

Beak gape which has been found to correlate with frequency changes in many bird species (Hausberger *et al.* 1991; Westneat *et al.* 1993; Hoese *et al.* 2000; Podos *et al.* 2004; Goller *et al.* 2004) also changes up to 6.68 mm, in the index of beak gape used in the current study, in vocalizing monk parakeets although we could not establish a quantitative relationship with frequency patterns. However, it seems that beak gape and tongue position can change independently from each other at least to a certain degree since we observed prominent tongue movements in soft greeting calls while beak gape changed only slightly. Therefore we can conclude that tongue position is not merely incidental to beak opening, a question that arose in a previous study (Warren *et al.* 1996).

Furthermore the strong tracheal shortening which we observed on the videos provides convincing evidence for a new type of vocal articulator in birds. The shortening is accompanied by a caudal movement of the lower mandible and the hyoid skeleton and although it might be a passive process resulting from the movements of other articulators it is very likely to have an effect on the sound produced. A former study (Daley & Goller 2004) investigating tracheal length changes in singing zebra finches found that at the beginning of a song bout and between motifs tracheal length decreased. While the initial contraction was actively mediated by syringeal muscles the shortening within the motif seemed to be the result of pressure changes in the interclavicular air sac and could not be related to frequency patterns of the song. However, length changes were small (<0.2 mm) within a song and represented only about 3 % of the length of the trachea and therefore are unlikely to have a strong effect on resonance patterns. Even within the family *Psittacidae* the degree to which the trachea can contract seems to vary noticeably between species since in African grey parrots the trachea can only stretch about 10 % (Pepperberg *et al.* 1998) while in our monk parakeets the trachea showed very little resistance to tracheal shortening. Future research will have to reveal how exactly acoustic features of vocalizations are influenced by tracheal length changes.

We also found a significant positive correlation between beak opening and amplitude in greeting calls in two of the three birds. The same significant correlation was found for tongue height change and amplitude in the greeting calls of the same birds. The reason why we did not find a correlation in one of the birds between beak movement and amplitude as well as tongue height change and amplitude for greeting calls is most probably due to the small sample size of only 4 greeting calls that were of sufficient quality for analysis (Table 3.4). The analysis revealed more positive correlations for chatter sounds in some individuals but not for contact calls, likely because contact calls were generally rather loud and showed little variation in amplitude (Fig. 3.6 a, d). These findings largely agree with earlier reports on zebra finches producing loud notes with large beak gapes (Ohms *et al.* 2010b).

Judging from the X-ray videos it seems that monk parakeets do not expand the cervical end of the esophagus to form a large OEC as do songbirds. In accordance with this observation is the fact that when obtaining silicone casts of the oral cavity from dead monk parakeets no silicone entered the esophagus while the cranial part of the trachea and the glottis were filled with silicone. Further research is needed to clarify if the esophagus contributes to vocal production in parrots at all.

Overall we have shown that monk parakeets use several articulators when producing species-specific sounds with tongue height changes, beak gape opening and tracheal length changes being the most obvious movements. However, tongue movements in the horizontal direction, although less prominent, are also likely to affect sound production while other possible articulators such as glottal opening still have to be identified. Experimentally manipulating such structures and obtaining cineradiographic data on mimicking parrots would provide further insight into the mechanisms underlying vocal production and would be of great interest for comparing the role of the tongue in human speech production and in parrot speech imitation.

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