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**TEMPORAL CHANGE IN THE CALLING BEHAVIOUR OF AN
ISOLATED KILLER WHALE (*Orcinus orca*)**

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Master's dissertation in Marine Sciences - Marine Resources

- Specialization in Marine Biology and Ecology-

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ABSTRACT

Killer whales are highly social animals and rely on acoustic communication for social interactions. Groups of whales have a shared repertoire of vocalizations that can include between 3 and 17 different call types. Killer whales are thought to learn these repertoires from their mothers and their groups, though the mechanisms involved in this process are still relatively unknown. This is partly due to the challenges in assigning sounds to a specific whale in the wild, and the difficulty in following that whale's vocal development through a significant period of time. In this study we catalogue the acoustic repertoire of an individual killer whale in isolation – Morgan – during two different sampling periods nearly one year apart, December 2010 and November 2011. We describe Morgan's vocal repertoire based upon analysis of 17,240 discrete call vocalizations, with emphasis on how the repertoire is organized and how the vocalizations are shaped. We also compare the two periods and try to assess changes in Morgan's vocal behaviour.

Morgan's repertoire appears to be composed by 21 units. These units are small sections of vocalizations that, isolated or combined, create 124 new discrete "call types". The results indicated significant differences between sampling periods, with a higher randomness of unit association for the two-unit combinations in November 2011. There were also significant differences in the distributions between sampling periods, both for the total usage of units and for the usage of two-unit combinations. Some reasons behind those differences could be the fact that Morgan developed a hearing impairment, either before she was found or during her time in the Dolfinarium Harderwijk, or that Morgan was in acoustic isolation during a critical development phase for vocal production learning. Further analysis of the interval between the two examined sampling periods is necessary to understand how the changes occurred, helping us comprehend the reasons behind them. New recordings made in Loro Parque, after Morgan was moved there, are being analysed. Future work will use those recordings to explore how changes in vocal behaviour and repertoire occur in killer whales.

RESUMO

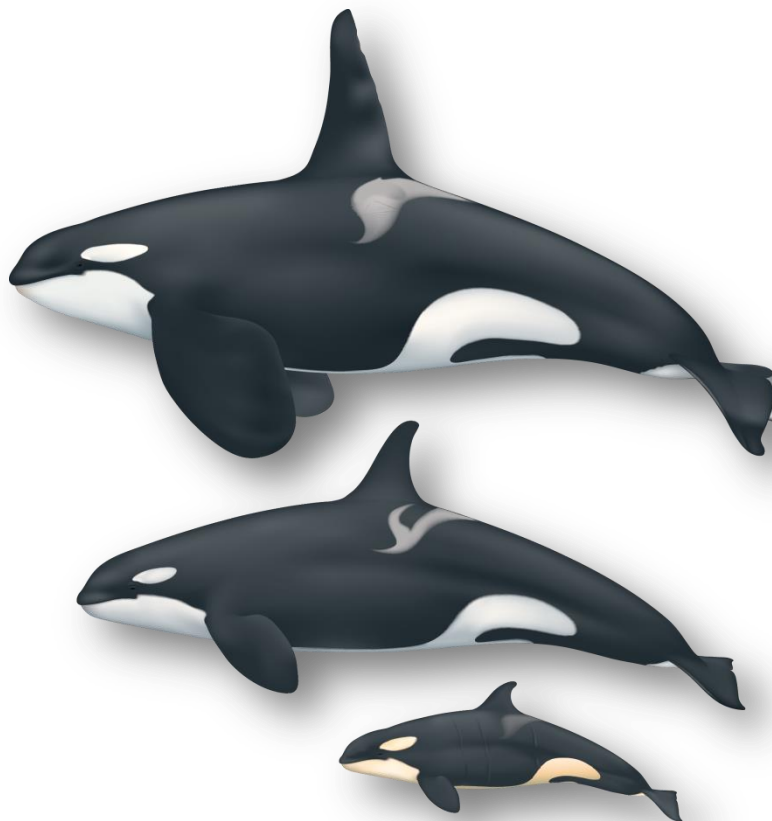
As orcas são consideradas animais altamente sociais, e dependem de comunicação acústica para interagir socialmente. Grupos de orcas partilham repertórios de vocalizações que podem conter entre 3 e 17 vocalizações diferentes. Pensa-se que aprendam estes dialectos através das suas progenitoras e grupo social, embora os mecanismos envolvidos neste processo sejam ainda relativamente desconhecidos. A dificuldade em estudar este assunto deve-se à complexidade de, no estado selvagem, discriminar as vocalizações de orcas específicas e seguir o seu desenvolvimento vocal durante um período de significativo. Neste estudo catalogamos o repertório acústico de uma orca em isolamento – Morgan – durante dois períodos de amostragem distintos, com quase um ano de intervalo entre os mesmos, Dezembro de 2010 e Novembro de 2011. Descrevemos o repertório vocal da Morgan baseado na análise de 17,240 vocalizações, com especial ênfase na sua estrutura e organização e como as vocalizações são compostas. Comparamos também os dois períodos de amostragem e tentamos avaliar alterações no comportamento vocal da Morgan.

O repertório da Morgan aparenta ser estruturado e baseado em 21 unidades. Estas unidades são secções menores de vocalizações que, quando isoladas ou em combinações com outras unidades, criam 124 novas vocalizações. Os resultados indicam que houve diferenças estatisticamente significativas entre os períodos de amostragem, com uma maior aleatoriedade na associação de unidades, para combinações de duas unidades, em Novembro de 2011. Adicionalmente, houve diferenças significativas entre os dois períodos no total de ocorrências de unidades e na ocorrência de combinações compostas por duas unidades. Estas diferenças podem-se dever ao facto de a Morgan ter sofrido uma diminuição na capacidade auditiva, durante o tempo que esteve no Dolfinarium Harderwijk ou antes de ter sido encontrada, ou devido ao facto de ter estado em isolamento durante uma fase de desenvolvimento crítica para a aprendizagem de produção de vocalizações. Estudos adicionais devem ser conduzidos de modo a que se possa compreender como ocorreram estas alterações e as razões que possam estar na origem das mesmas. Gravações acústicas, feitas recentemente no Loro Parque, para onde a Morgan foi transferida entretanto, serão analisadas. Estudos subsequentes com estas gravações, irão explorar a ocorrência de alterações de comportamento vocal e repertório acústico em orcas.

INTRODUCTION

The killer whale (*Orcinus orca*, Linnaeus, 1758 – Figure 1) is the only living species in the genus *Orcinus*. They are the largest members of the *Delphinidae* family, Order *Cetartiodactyla*, Suborder *Odontoceti* (Baird, 2002; Ford, 2008). They can be found in every ocean (Ford, 1991), but are more common in coastal and higher latitude areas, with a distribution that appears to be tied to regions of higher ocean productivity (Forney and Wade, 2006).

Figure 1 – Killer whale illustration featuring, from top to bottom, a male, a female and a calf (illustration by Uko Gorter).



Despite their wide distribution, killer whales appear to specialise on specific types of prey and some sympatric ecotypes have been recognised and described as having different genetics, morphology, social structure and behaviour (American Cetacean Society *et al.*,

2011; Barrett-Lennard, 2000; Filatova *et al.*, 2012; Foote *et al.*, 2011, 2014; Ford *et al.*, 2000; Pitman and Ensor, 2003; Yurk, 2005). The term ecotype was first proposed by Turesson (1922) as an “ecological unit to cover the product arising as a result of the genotypical response of an ecospecies to a particular habitat”. In the North Pacific, three ecotypes have been defined – Resident, Transient and Offshore. **(1)** Residents prey mainly on chinook salmon (*Oncorhynchus tshawytscha*, Walbaum, 1792) and live in large groups with a fairly stable social structure (Ford, 2008; Ford and Ellis, 2006; Ford *et al.*, 2000; Ivkovich *et al.*, 2010), **(2)** Transients live in smaller groups, with a less stable social structure, and feed mainly on other marine mammals and occasionally on sharks (Baird and Dill, 1995; Ford *et al.*, 1998), **(3)** Offshores are the less studied ecotype, their social structure is not well known but are thought to feed mainly on fish (Ford *et al.*, 2011). Foote *et al.* (2011) suggested the existence of three “differentiated populations” in the North Atlantic. **(1)** A population associated with the North Sea, Norwegian and Icelandic herring stocks (*Clupea harengus*, Linnaeus, 1758), **(2)** a population associated with the Northeast mackerel stock (*Scomber scombrus*, Linnaeus, 1758) and **(3)** a population partially associated with a stock of North Atlantic bluefin tuna (*Thunnus thynnus thynnus*, Linnaeus, 1758). Pitman & Ensor (2003) provided descriptions for three different forms of killer whale occurring in Antarctic waters. **(1)** Type A killer whales that prey mainly on Antarctic minke whales (*Balaenoptera bonaerensis*, Burmeister, 1867), **(2)** Type B, which prey mainly on seals, and **(3)** Type C, that has only been recorded feeding on Antarctic toothfish (*Dissostichus mawsoni*, Norman, 1937).

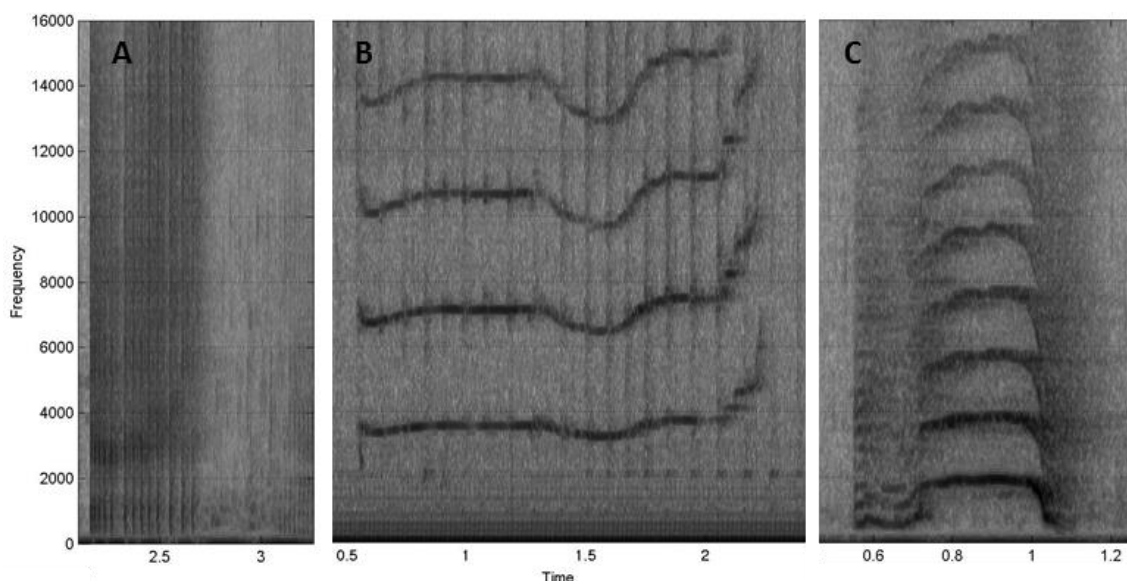
The most well-studied populations are in the Northeast Pacific, off the coast of British Columbia. Here, studies started in the 1970s and contributed to most of what we currently know about killer whales’ social structure, behaviour and communication (Bigg *et al.*, 1990; Ford, 1991; Ford *et al.*, 2000). Northeast Pacific resident populations are organized into matrilineal groups, where the matrilineal group is the smallest social unit and consists of a fairly stable group in which the male offspring stays with its mother even throughout adult life, and may comprise individuals of up to four generations (Bigg *et al.*, 1990; Ford, 1991). Different matrilineal groups combine to form pods, which was defined as “the largest cohesive group of individuals within a community that travelled together for the majority of time” (Bigg *et al.*, 1990).

Killer whales are highly social animals (Bigg *et al.*, 1990; Ford, 1984; Ford *et al.*, 2000; Hoyt, 1990; Janik, 2009). The group living structure may bring advantages to individuals, for instance by increasing foraging efficiency (Bertram, 1978). Like other social animals, killer whales rely highly upon communication for social interactions, and acoustic communication appears to be particularly important for this species. Other types of

communication are often difficult or less efficient in the marine environment these animals live in (Miller *et al.*, 2004; Myrberg, 1980), so vocal communication plays a key role in delphinids' social structure and behaviour (Ford, 1991; Janik, 2009; Janik and Slater, 2000; Kremers *et al.*, 2012; Miller *et al.*, 2004). Studies on cetacean social behaviour suggest a positive association between sociality and acoustic repertoire, specifically a correlation in the complexity of whistles and tonal sounds with group size and social structure (May-Collado *et al.*, 2007). They likely use sounds to communicate (Ford, 1989; Richardson and Greene, 1995), and keep contact between members of the same group (Ford, 1989, 1991), and echolocation sounds to localize objects, obstacles, prey and other individuals (Au, 1993).

Killer whale vocalizations can be classified into three basic categories: **(1) Clicks** (click trains when produced in series) consist of a very short sound pulse with energy spread over a wide range of bandwidths (Figure 2 – A), and are used primarily for echolocation (Barrett-Lennard *et al.*, 1996; Ford, 2008; Schevill and Watkins, 1966); **(2) Whistles** can be continuous or segmented, non-pulsed tonal signals, consisting of a narrowband component with few or no harmonic sidebands (Figure 2 – B), with fundamental frequencies generally ranging between 6 and 12 kHz, although they can range as low as 1.5 kHz and as high as 18 kHz, and are thought to have an important role in close range communication in killer whales (Ford and Fisher, 1982; Thomsen *et al.*, 2001, 2002). Some populations have been reported to produce whistles at much higher frequencies, ranging up to 75 kHz (Samarra *et al.*, 2010a); **(3) Pulsed calls** consist of burst-pulsed sounds (Janik, 2009), with high pulse repetition rates up to 5000 pulse/second, as opposed to clicks, that have repetition rates between 6 and 17 click/second, (Ford and Fisher, 1982; Schevill and Watkins, 1966). They were described by Schevill & Watkins (1966) as “screams” and are fairly complex, with numerous frequency modulations and harmonics, and may have energy distribution between 500 Hz and 25 kHz (Figure 2 – C).

Figure 2 – Killer whale sounds. **A** – Clicks; **B** – Whistle; **C** – Pulsed call. The frequency axis is measured in Hertz (Hz) and the time axis is measured in seconds (s).



Pulsed calls are the most common sound produced by killer whales. They are traditionally classified into discrete categories based upon their stereotyped characteristics, which appear to be stable over time. Pods have a limited repertoire of pulsed call types, ranging from 7 to 17 call types per pod, averaging 10.7 calls per pod in the Northeast Pacific (Ford, 1987), and from 3 to 16 call types, averaging 9.0 call types per pod in Norway (Strager, 1995).

An alternative view on killer whale vocalizations, as proposed by Shapiro *et al.* (2011) for the Norwegian killer whale population and Yurk *et al.* (2002) for the southern Alaska resident population hypothesizes that some vocalizations may be produced by recombining subsets of other calls. For this study they will be referred to as **units**. This conceives the notion that individuals would generate complete vocalizations using a method of sequencing specific units, in a similar fashion to songbirds (Fee *et al.*, 2004; Glaze and Troyer, 2006; Williams and Staples, 1992).

The stable structure of the Northeast Pacific killer whale groups allowed researchers to understand that pods share the same repertoire or part of their repertoire of discrete calls. These similarities within the same group and consistent structural variations between different pods' repertoires form a system of dialects (Ford, 1987). Dialects are sets of vocalizations shared by individuals of a given species, but that differ discretely from the vocal features of other groups of individuals (Baker and Cunningham, 1985). These dialects are stable over several years within each individual group, but differ between

Pods (Ford, 1984, 1989, 1991). Pods that share some or all of the call types in their repertoire are called vocal clans (Ford, 1984, 1991). Differences in call repertoires are related to genetic distance, in such way that increasing differences in vocal repertoire translate in increased genetic differences between killer whales (Deecke *et al.*, 2010; Filatova *et al.*, 2012; Hoelzel *et al.*, 2007; Yurk *et al.*, 2002).

Vocal dialects are common in birds (Baker and Cunningham, 1985), but unusual in mammals, being mostly present in humans (Labov, 2001), bats (Boughman, 1997; Esser and Schubert, 1998) and marine mammals (Ford, 1991; Rendell and Whitehead, 2003).

Killer whales are thought to learn these call repertoires and pass it on to the offspring and members of the group, as it happens in humans, birds and other marine mammals (Bowles *et al.*, 1988; Crance *et al.*, 2014; Deecke *et al.*, 2000; Foote *et al.*, 2006; Ford, 1991; Janik, 2009). The vocal dialect is passed on, thus maintaining a vocal tradition through time (Foote *et al.*, 2006; Janik and Slater, 2000, 2003; Yurk, 2005).

As mentioned above, vocal learning is rather common in birds, but comparatively less well-known in mammals (Janik and Slater, 1997, 2000). This makes it harder to understand the mechanisms underlying vocal learning. The process of vocal learning can be divided in two phases, as suggested by Foote *et al.* (2006): (1) sensory learning phase, in which a learning individual listens to the vocalizations from one or more “tutors” (Doupe and Kuhl, 1999; Wilbrecht and Nottebohm, 2003), (2) sensorimotor learning phase, in which the individual experiments and acquires the motor skills required to match the vocalization to the shape he had previously learned (Doupe and Kuhl, 1999; Marler, 1991; Marler and Peters, 1982; West and King, 1988). Early vocalizations tend to be inconsistent (Bowles *et al.*, 1988), but as they practice and further develop their vocal production, the individuals start producing stereotyped discrete calls (Janik and Slater, 1997).

Studying the vocal development of killer whale calls in the wild is particularly challenging because killer whales live and travel in groups making it difficult to ascribe specific sounds to a particular individual. It is, therefore, practically unmanageable to study and follow an individual’s vocal development through a given period of time. Thus, little is known about the development of vocal behaviour in this species (Bowles *et al.*, 1988).

In this study we catalogue and examine Morgan’s vocal repertoire, and its development. Morgan (Figure 3) is a female killer whale, brought into captivity in June 2010. She was found emaciated and by herself on June 23rd, near the island of Schiermonnikoog, in the Waddenzee, the Netherlands, in a region characterized by shallow muddy areas. Morgan

was taken to the Harderwijk Dolfinarium facilities for rehabilitation. She weighed 430 kg and had a body length of 343 cm upon admission (van Elk, 2010). Based on her body size, Morgan was estimated to be 18-24 months old. The reason behind Morgan's stranding was unclear, with no gross pathology being found except for skin abrasions and severe malnourishment. Following a period of rehabilitation, an assessment was made of the releasability of Morgan (van Elk, 2010) and a final decision was made to transfer Morgan to another park with suitable conditions to hold a killer whale. During the process of arranging for a transfer, Morgan was kept in Harderwijk, which led to an isolation period of over 1 year.

Samarra *et al.* (2010) matched some of Morgan's calls to the herring-feeding killer whale population in Norway, showing that Morgan originated from Norway and included calls from this population in her repertoire. Morgan was alone in captivity through a period of one year, making it possible to assess the development of her repertoire during a time that is considered critical for vocal learning and development, given her young age. In this study we have the rare opportunity to describe the vocal repertoire of a single individual, where the calls can be unmistakably assigned to one killer whale, over a period of one year. We then compare two sampling periods, one in the beginning and one at the end of the one year period alone in captivity. In this study we test a call division hypothesis, dividing the vocalizations into units (Shapiro *et al.*, 2011; Yurk *et al.*, 2002).

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Figure 3 – Morgan.

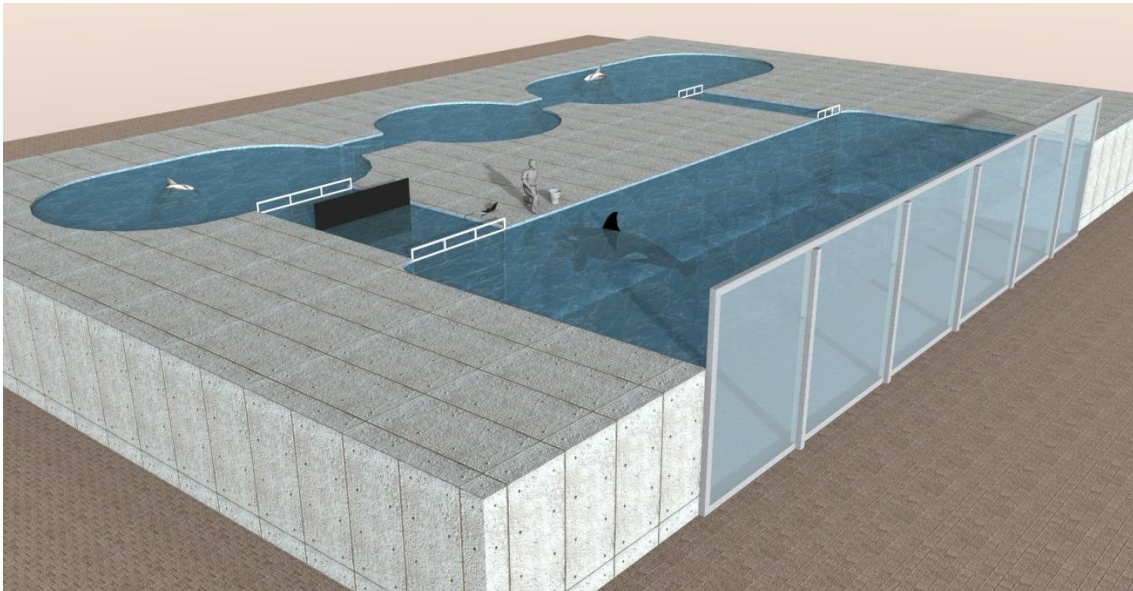


METHODS

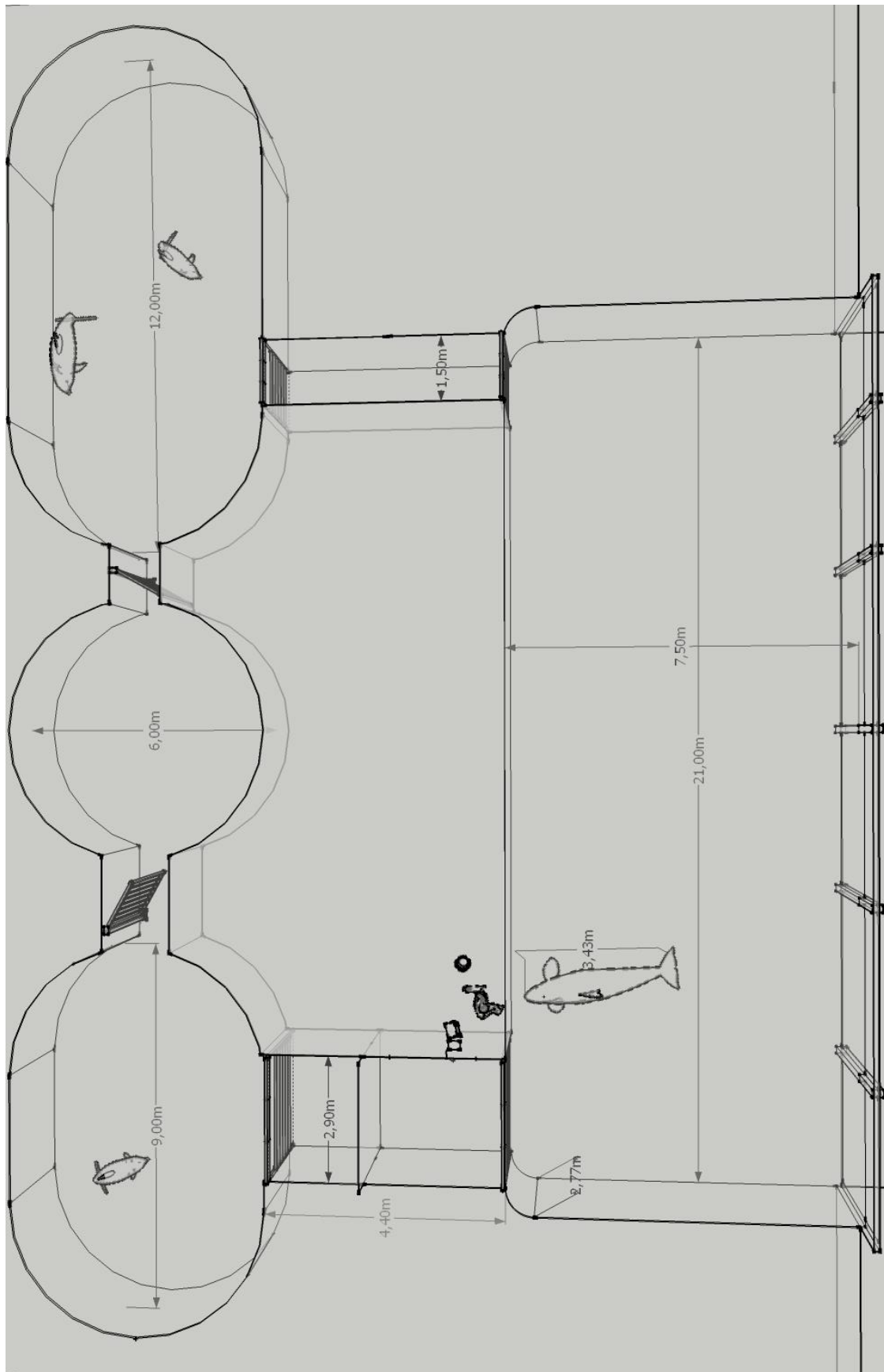
Subject

The subject of this study was an individual killer whale – Morgan. During the time spent in Harderwijk, Morgan was held in a pool of dimensions 21.00 x 7.50 x 2.80 meters, in isolation (Scheme 1 and 2). Bottlenose dolphins (*Tursiops truncatus*, Gervais, 1855) occupied an adjacent pool and although their vocalizations could be heard, the animals were never in physical contact. Two tunnels connected the pool where Morgan was held to the bottlenose dolphin pool. The two tunnels were gated on both ends the entire time Morgan was in the pool. These metal gates stopped physical contact between Morgan and the bottlenose dolphins but visual and acoustic contact was possible. In addition to the metal gates, a gate blocking visual and considerably reducing acoustic contact was in place for the majority of the time on one of the tunnels. This was the tunnel where the hydrophone was placed (Scheme 3). A 3D model of the facility was made using SketchUp 8 (Schell and Esch, 2000) and rendered using IRender nXt (Render Plus Systems Inc., 2014).

Scheme 1 – 3D representation of the facility where Morgan was being held in Harderwijk.



Scheme 2 – 2D graphic representation of the pool system where Morgan was being held in Harderwijk.

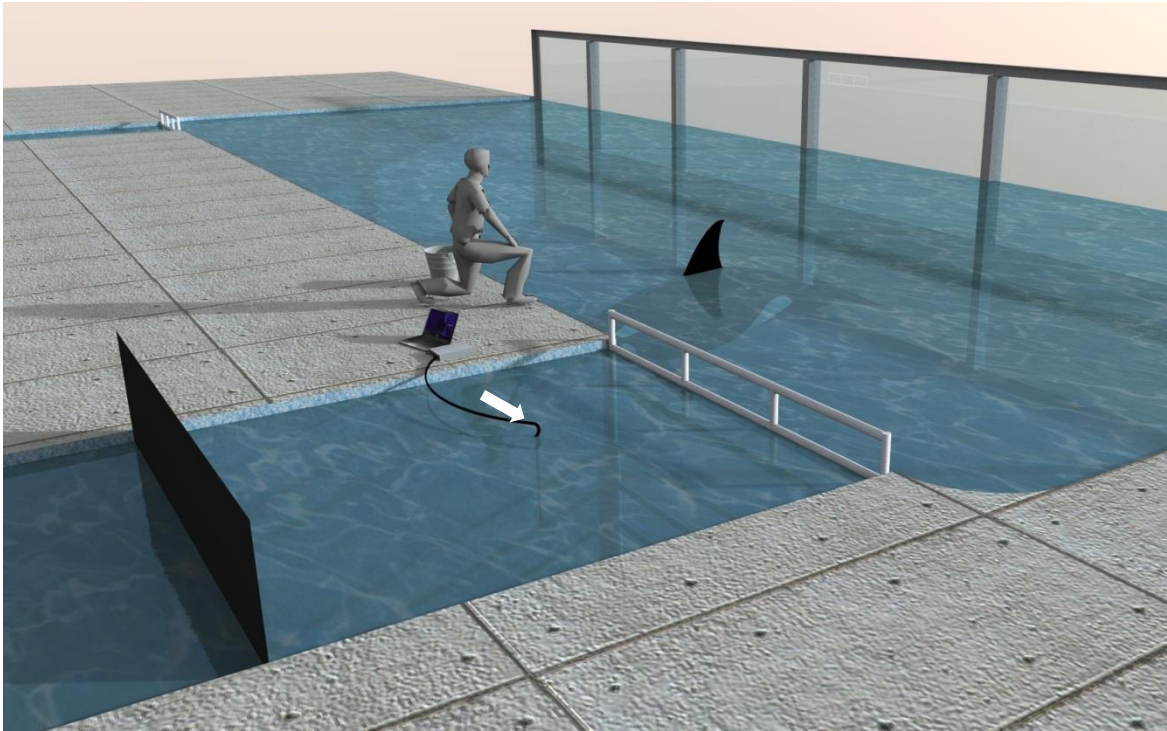


In November 2011 Morgan was transferred to Loro Parque, in Santa Cruz de Tenerife, Spain. Behavioural observations by the trainers indicated that the animal was not showing any response to sound cues or stimuli, suggesting that she might have a hearing impairment. In November 2012 Lucke *et al.* (2013) subjected the whales in Loro Parque to audiometry tests, playing tone pips, pure tones and broad band clicks to the animals and measuring the auditory evoked potential (AEP) - “small neuronal signals produced by the brain in response to hearing a sound” (Lucke *et al.*, 2013) - of each one. The results presented showed no AEP for Morgan, indicating that she suffered from hearing deficit. However, it was not possible to determine whether the hearing deficit was total or partial, limited to specific frequencies. The study concluded that Morgan’s hearing ability was at least 20 to 30 dB lower than the hearing sensitivity of the rest of the whales tested in Loro Parque.

Data collection

Data were collected by recording the vocalizations of one individual killer whale, Morgan, in a pool facility (Harderwijk Dolfinarium). Acoustic recordings were made using a High Tech Instruments HTI-96-MIN hydrophone with pre-amplifier, with a flat frequency response between 0.002 and 30 kHz. The hydrophone was connected to an Edirol UA-25 soundcard, and recording on to a laptop using PAMGUARD (Gillespie and Mellinger, 2008) at a sampling rate of 96 kHz. The hydrophone was placed behind a gate, in a channel connecting the pool where Morgan was being held and the pool where bottlenose dolphins were held (Scheme 3).

Scheme 3 – 3D representation of the recording setup. The location of the hydrophone is indicated by the white arrow.



Two periods of acoustic recordings were analysed. The first period of acoustic recordings was conducted in December 2010, shortly after Morgan was brought into the Dolfinarium; the second period of acoustic recordings was conducted in November 2011, shortly before Morgan was moved to Loro Parque. These two different sampling sessions were enough apart in time that we could assess whether there were any changes in the repertoire over time, for the period when she was alone in captivity. Recordings were conducted continuously for 92 hours in December 2010 and 170 hours in November 2011, resulting in a total of 262 hours of recordings, in which the sounds could be unquestionably ascribed to Morgan.

Data analysis and repertoire classification

The acoustic recordings were analysed manually and the vocalizations were marked on a scale of 1 to 3, depending on their quality and distinctness, using Adobe Audition CS6 (Adobe Systems Inc., 2012; Blackmann-Harris window; FFT=2048).

Even though some whistles were also ascribed to Morgan, only pulsed calls were analysed. Although it was possible to hear bottlenose dolphin vocalizations occasionally,

in most cases these were clearly distinguishable from Morgan's sounds as they were much lower in intensity. Fainter sounds that could not be undoubtedly ascribed to Morgan were not marked. A total of 26,343 calls with sufficient quality (3, on a scale of 1 to 3) were classified and analysed.

Classification was conducted by visual and aural assessment of the calls by one observer, based on the time-frequency contour of recorded calls. MATLAB R2010a (MathWorks Inc., 2010) was used to create spectrograms of each call. The spectrograms were created with the frequency range limited to 16 kHz, 2048-point Fast Fourier Transformation, Hann window function and 87.5% overlap between frames.

The calls were, in a first approach, classified traditionally as call types (Ford, 1987). The call types were later divided into units, and classified as combinations of units, when appropriate (Shapiro *et al.*, 2011; Yurk, 2005). The criteria used to consider a segment of a call as a unit were the following: it is the smallest divisible section in a call; appears isolated (as a discrete vocalization) at least once and/or; appears in different positions (order) in different vocalizations (Figure 6).

Units were classified into discrete categories by analysing their time-frequency contours. The resulting categories included some variation (unit sub-types), such as presence or absence of specific components, e.g. the high-frequency component (HFC). The proposed units were labelled alphanumerically, starting with the unit type (e.g. A, G), followed by the sub-type (e.g. i or ii – Figure 5) and an apostrophe ['] indicating the presence or absence of HFC, when applicable (Figure 4). The calls were labelled by adding together the units that composed those calls by the order they were produced (Figure 6).

Figure 4 – Different subtypes of the same unit. Note the HFC (indicated by the white arrow) is present in panel **A** (unit subtype Gi), but absent in panel **B** (unit subtype Gi').

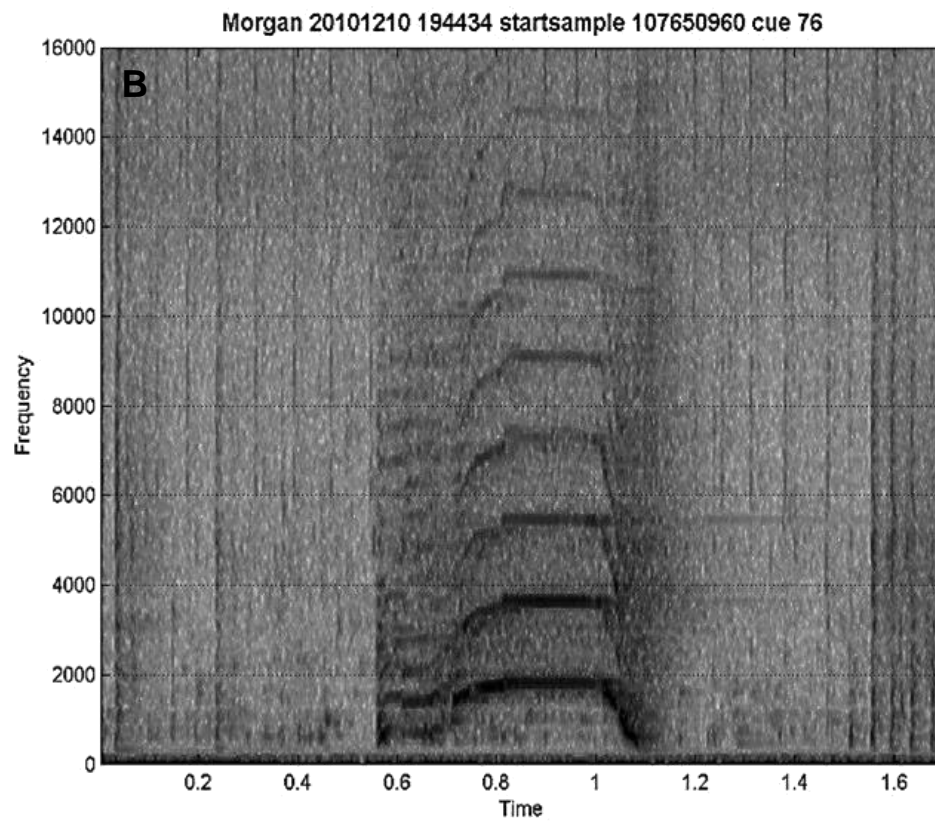
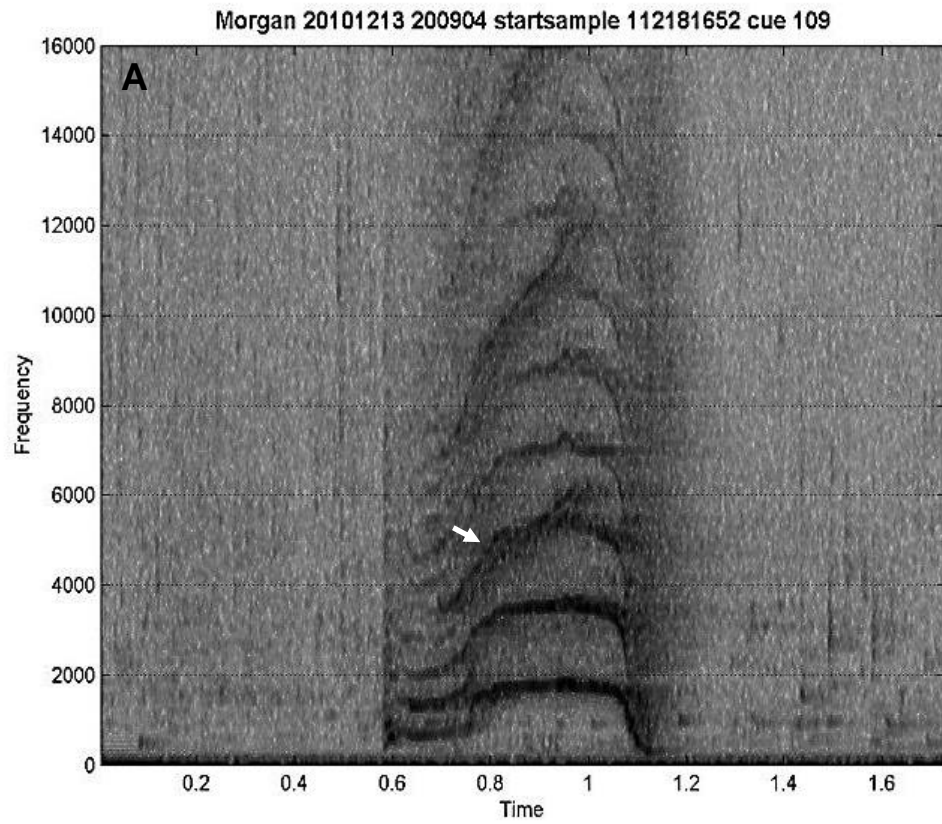


Figure 5 – Labelling the calls: combination of units Ai' and Gi compose call Ai'+Gi.

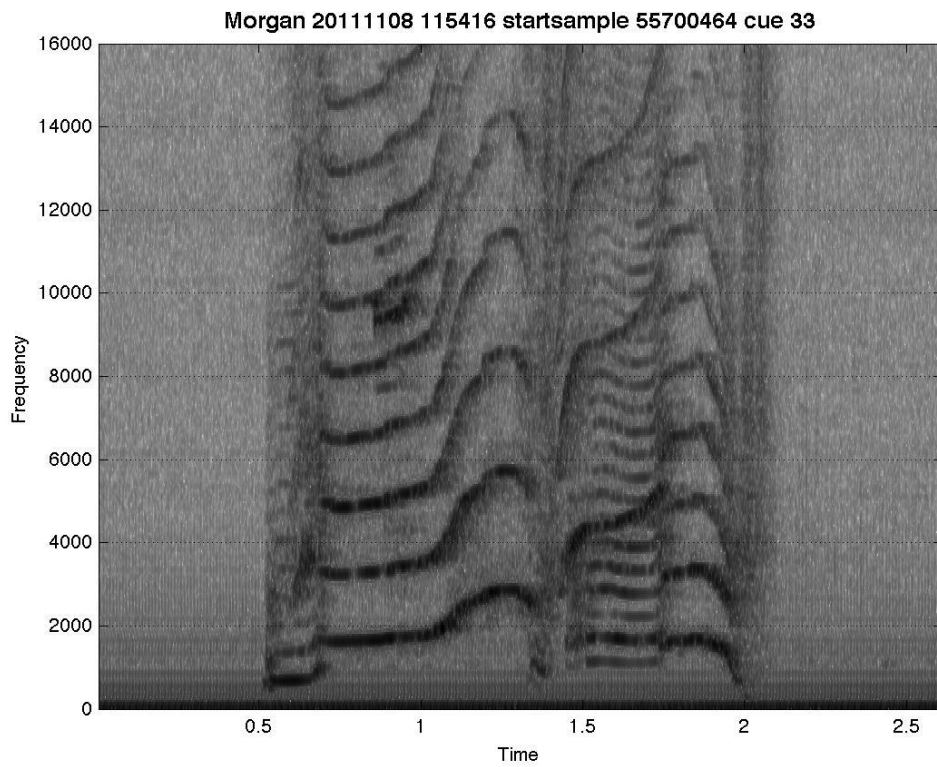
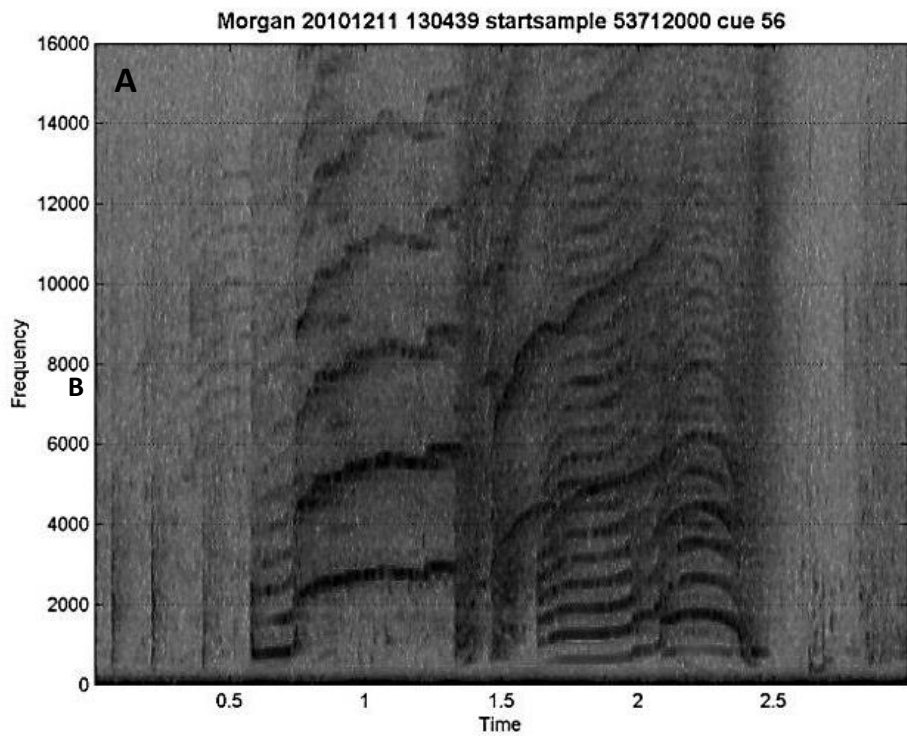
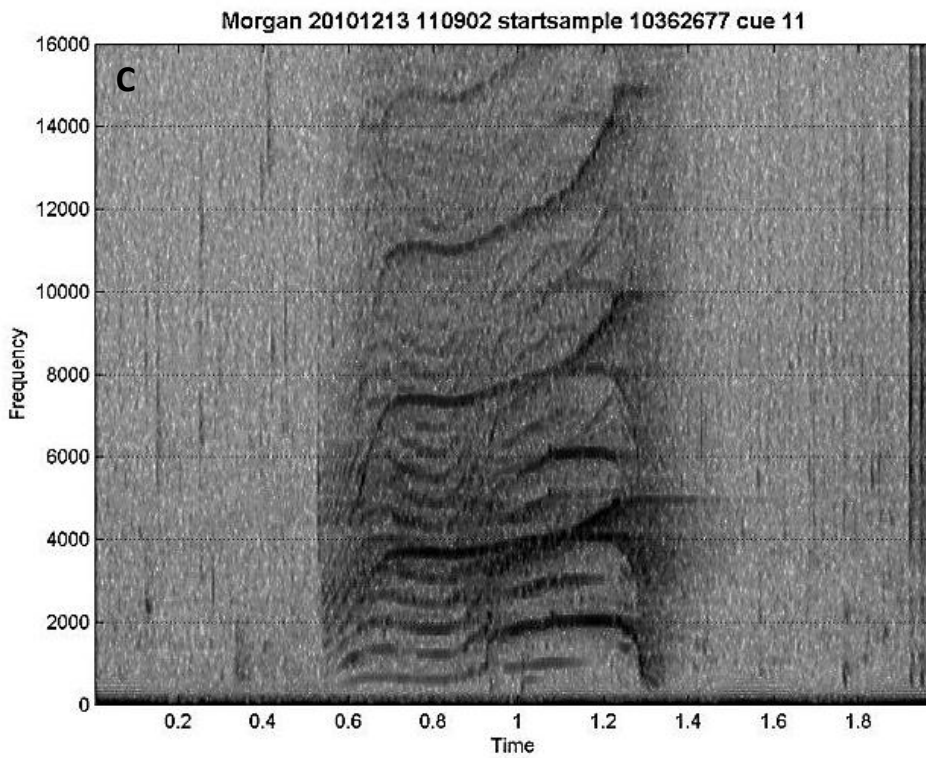
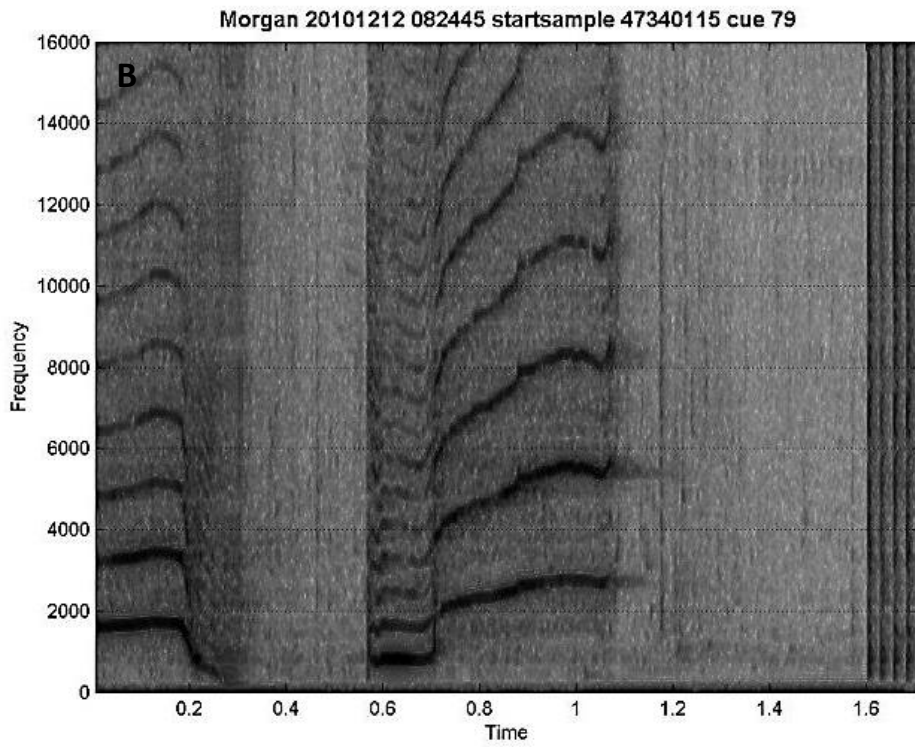


Figure 6 – Division of calls into units: the call in panel A (B+Gi) is composed of the units present in panel B (B) and in panel C (Gi).



F

Figure 6, continued



Statistical analysis

A descriptive statistical analysis was carried out using Microsoft Excel 2010 (Microsoft Corporation, 2010). A nonparametric Friedman's Rank Sum Test was performed using R (R Core Team, 2014) to assess whether there were any significant differences in the number of total occurrences of units between December 2010 and November 2011. The same test was used for the number of two-unit based combinations, which represented the majority in Morgan's repertoire (Table 4). The combinations that had a structure of Unit+HFC were not accounted for in the statistical tests, because the high-frequency component alone was not considered a unit.

To analyze differences in call rate between sampling periods the recordings were divided into ten minutes intervals using MATLAB (MathWorks Inc., 2010). The means and medians of the distribution of discrete calls was then compared with R (R Core Team, 2014) using a two-sample Wilcoxon test (Mann-Whitney test) and a two-sample Mood test, respectively.

Information theory

Information theory is a branch of applied mathematics developed by Claude E. Shannon (1948). It is used to study, among other things, fundamental limits for reliably communicating data. The quantitative measure of information is entropy, which is usually expressed in the number of bits needed to store or communicate a message. Entropy quantifies the uncertainty involved in predicting a specific outcome for a specific source (Attneave, 1959). In this study it is used as a natural language processing mechanism.

Kullback-Leibler divergence (also called information divergence, information gain, or relative entropy, is given by the equation $D_{KL}(P||Q) = \sum_{i=1}^N \ln\left(\frac{P_i}{Q_i}\right) P_i$) was used to compare the relative entropy between the sampling periods of 2010 and 2011, and we calculate the maximum possible entropy for two-unit combinations using 21 units. We measure the entropy as a way of quantifying the structural constraints for each period. R (R Core Team, 2014) was used to compute the empirical Kullback-Leibler divergence between the first and the second unit in two-unit based combinations, the most frequently produced combinations (with more than one unit) for both sampling periods. Denoted as $D_{KL}(P||Q)$, is the divergence of Q from P, Q and P being the distribution of the second and first unit respectively. It measures the expected numbers of additional bits that would be used to code samples from the first units (P)

using a code based exclusively on the second units (Q), rather than a code based on the first units. It translates into the predictability of having a given unit after another. The higher the relative entropy between two distributions, the lower the predictability of having a given unit following another. As stated by Suzuki *et al.* (2006) “a source with larger entropy produces a greater variety of alternative messages than a source with a smaller entropy”.

RESULTS

Data analysed

262 hours of acoustic recordings were analysed. A total of 26,343 calls were marked and classified. 17,240 were classified as discrete calls, making 65% of the total of calls produced. Only these calls were further analysed. Of those 206 hours, 92 were recorded in December 2010 and 170 in November 2011.

Division in units

The division of discrete calls resulted in 7 types of units (A-G), 5 of which further classified into unit subtypes (Table 1). This classification was made when there were subtle differences between units with some common features and not sufficiently different to be considered a different unit type (e.g. Ai and Aii, Figure 7), similarly to the classic classification into call types/subtypes (Ford and Fisher, 1982). In some cases, units were identical in every aspect except that one contained a HFC while the other did not. To illustrate this variation, an apostrophe was used after each unit type to identify the absence of HFC in that unit (e.g. Ai'). A total of 21 different units was found to be produced by Morgan. These units were combined into 124 different calls, 84 observed in December 2010 and 88 in November 2011.

Figure 7 – Differences between unit subtypes: A – Unit Ai; B – Unit Aii.

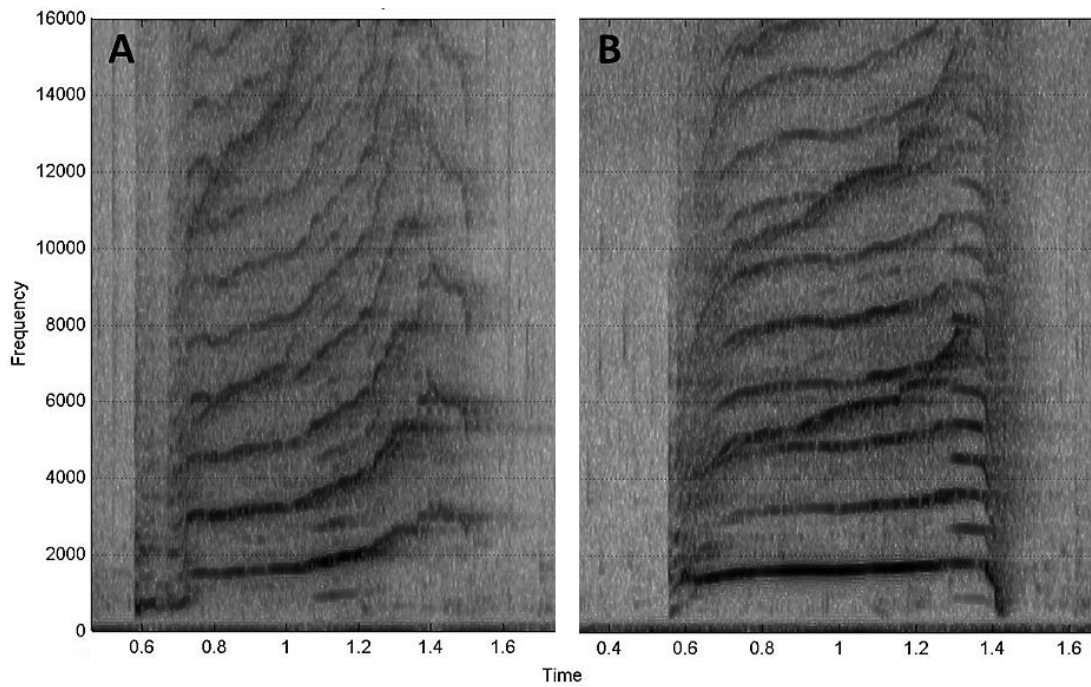


Table 1 – List of identified unit types and unit subtypes. The ‘ indicates absence of a high-frequency component.

Unit Types	Unit Subtypes
A	Ai Ai' Aii Aii'
B	B
C	Ci Ci' Cii Cii'
E	Ei Ei' Eii Eii'
F	Fi Fi' Fii Fii'
G	Gi Gi' Gii
Z	Z

The spectrograms below (Figures 8 to 28) present the different unit types and subtypes that composed Morgan’s vocal repertoire. Whenever possible, multiple spectrograms are provided to show some of the variability within unit subtypes:

Figure 8 – Unit subtype Ai

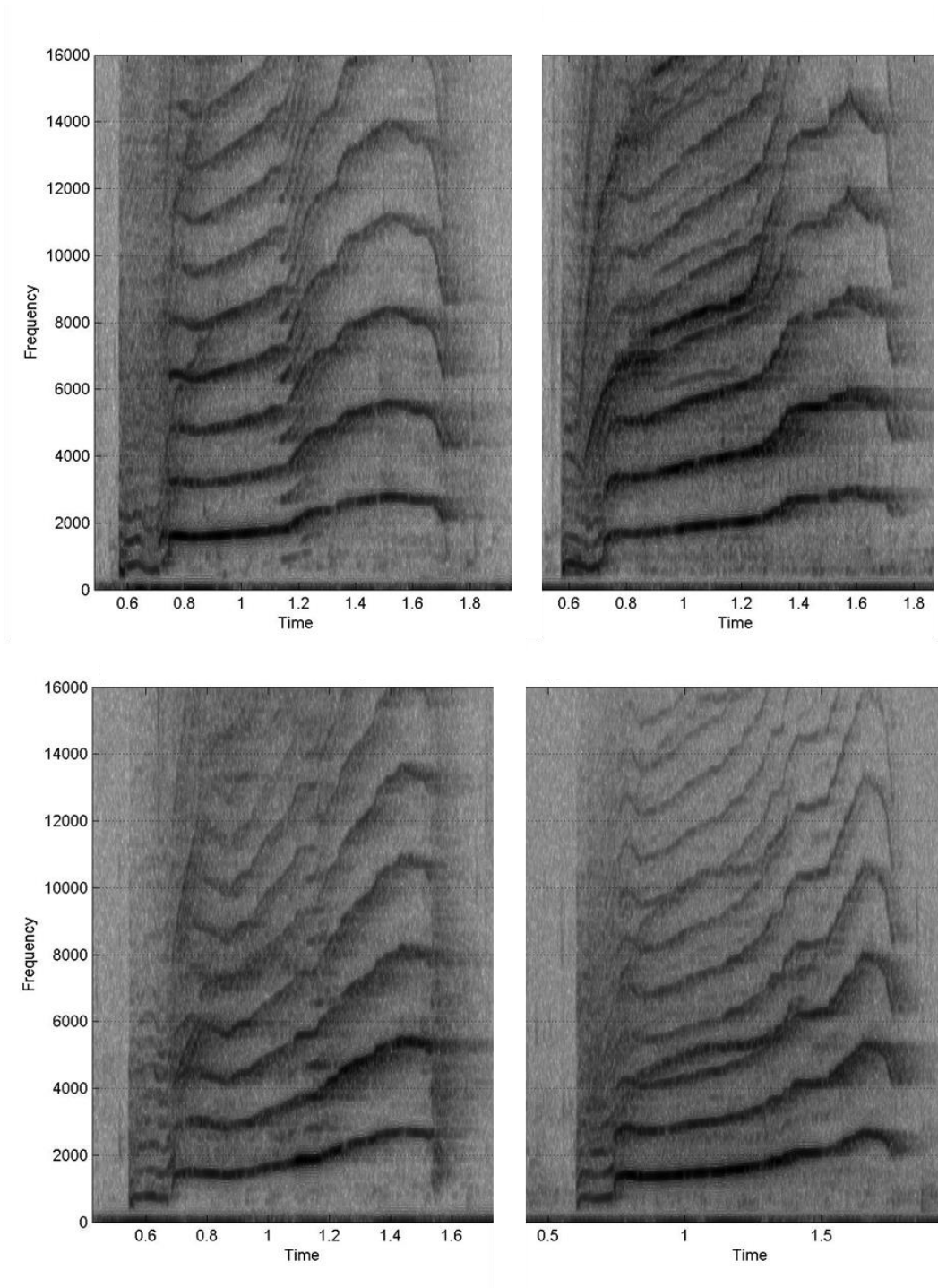


Figure 9 – Unit subtype Ai'

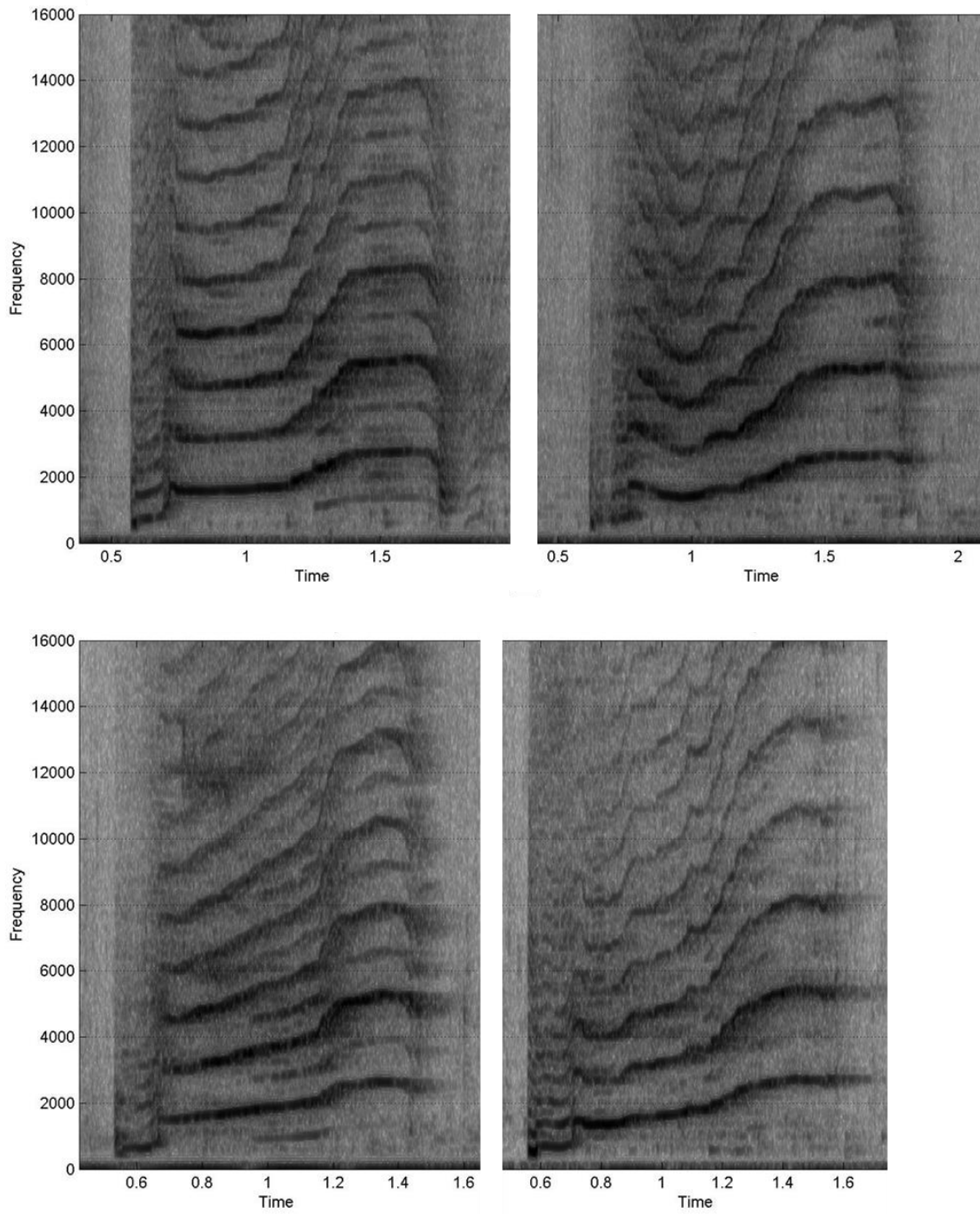


Figure 10 – Unit subtype Aii

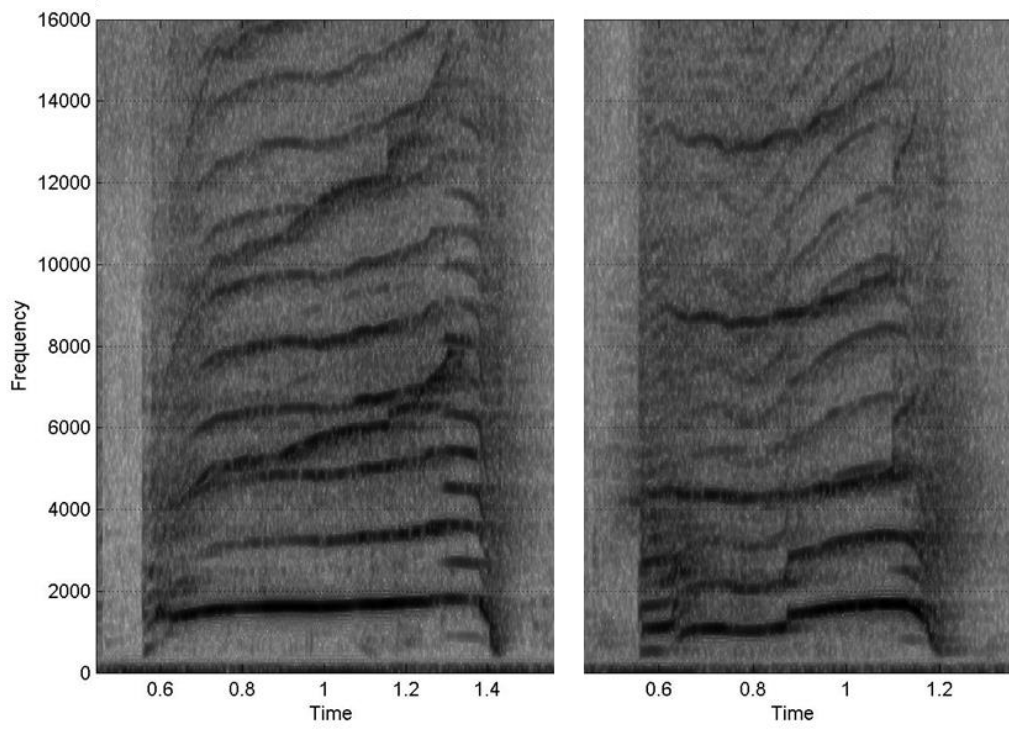


Figure 11 – Unit subtype Aii'

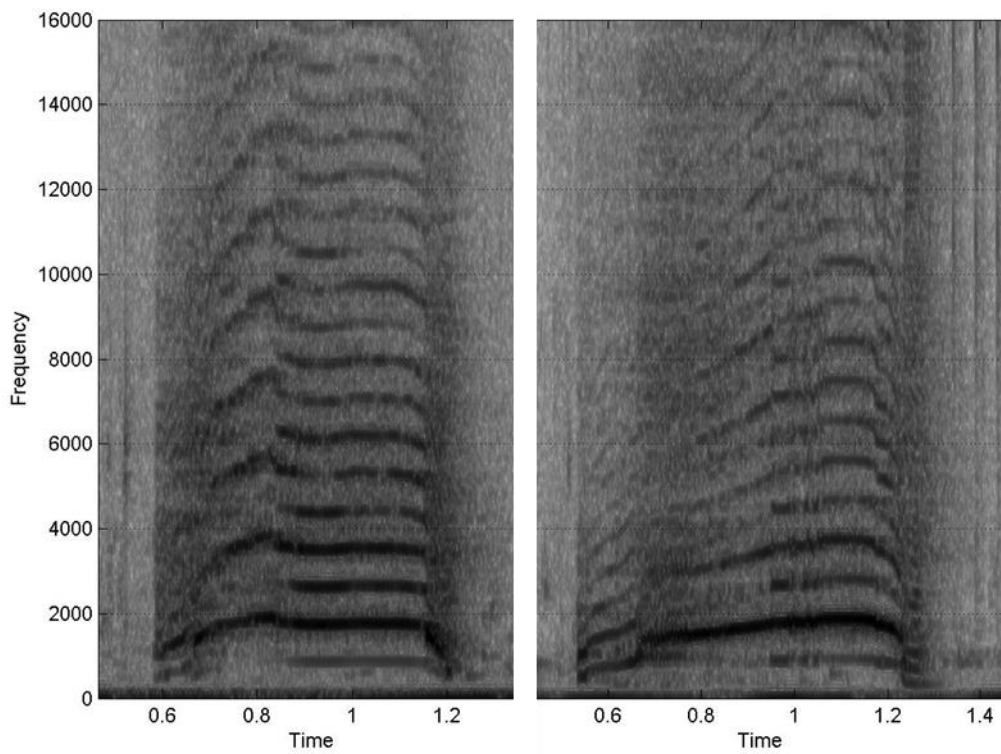


Figure 12 – Unit type B

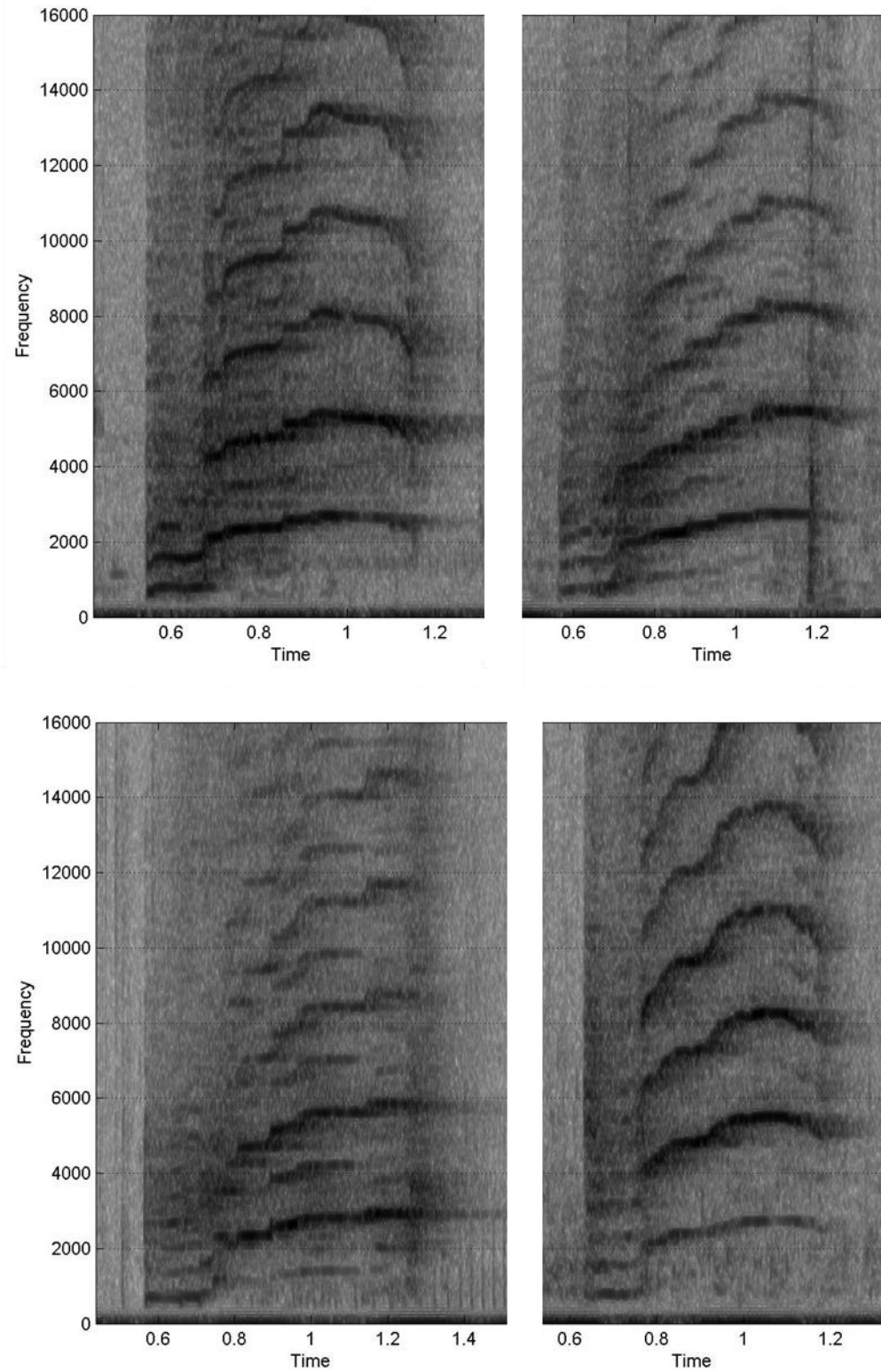


Figure 13 – Unit subtype Ci

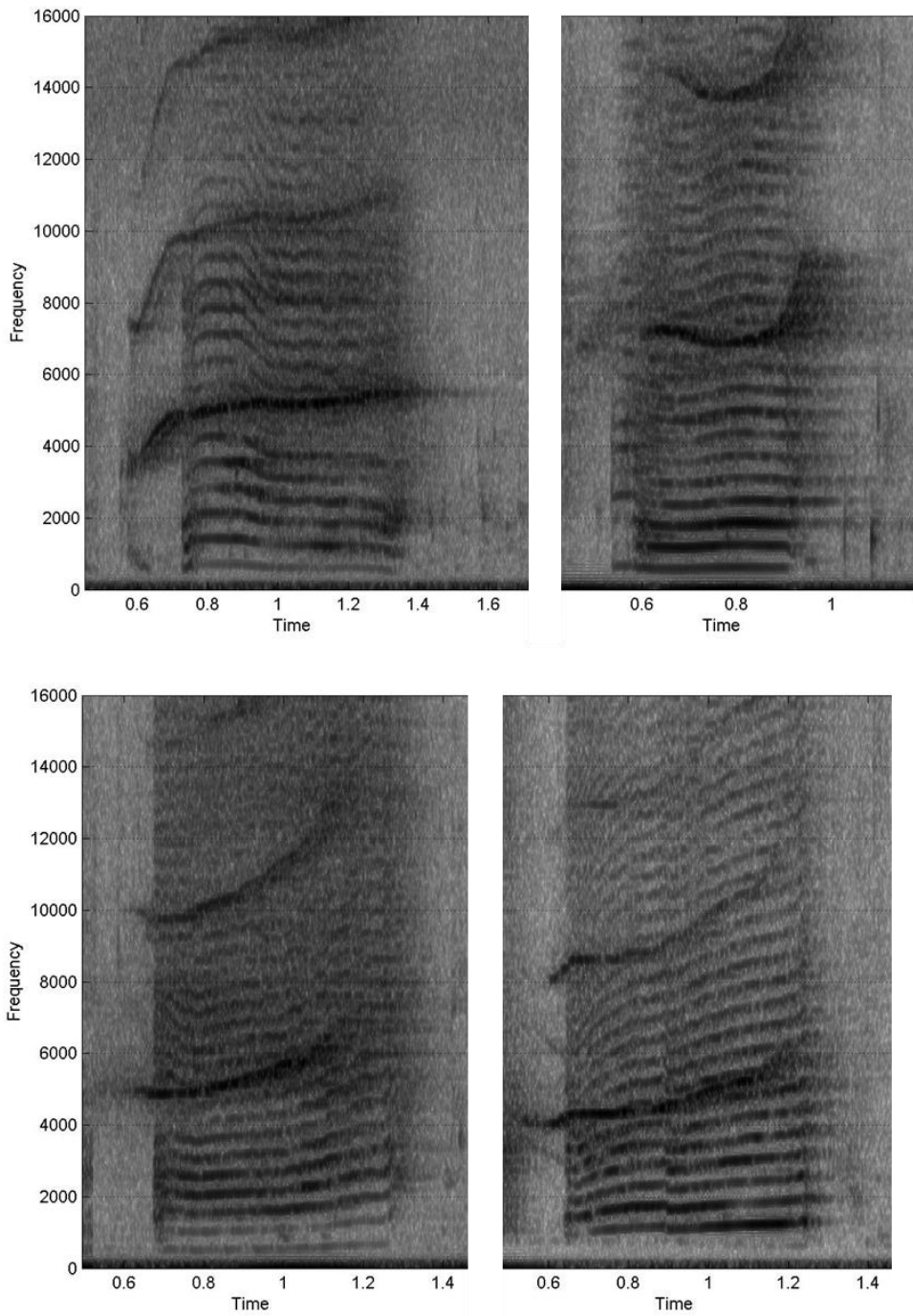


Figure 14 – Unit subtype Ci'

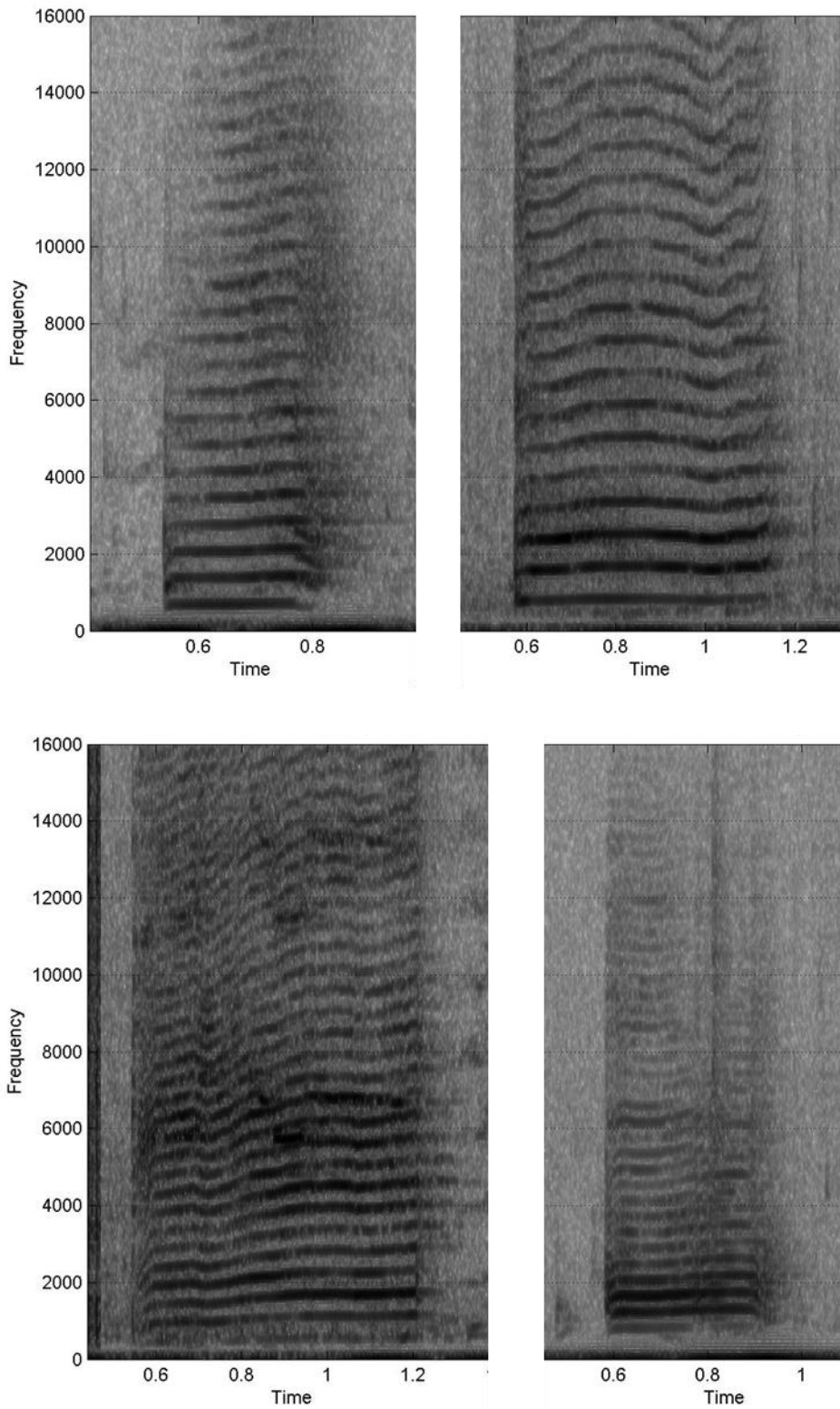


Figure 15 – Unit subtype Cii

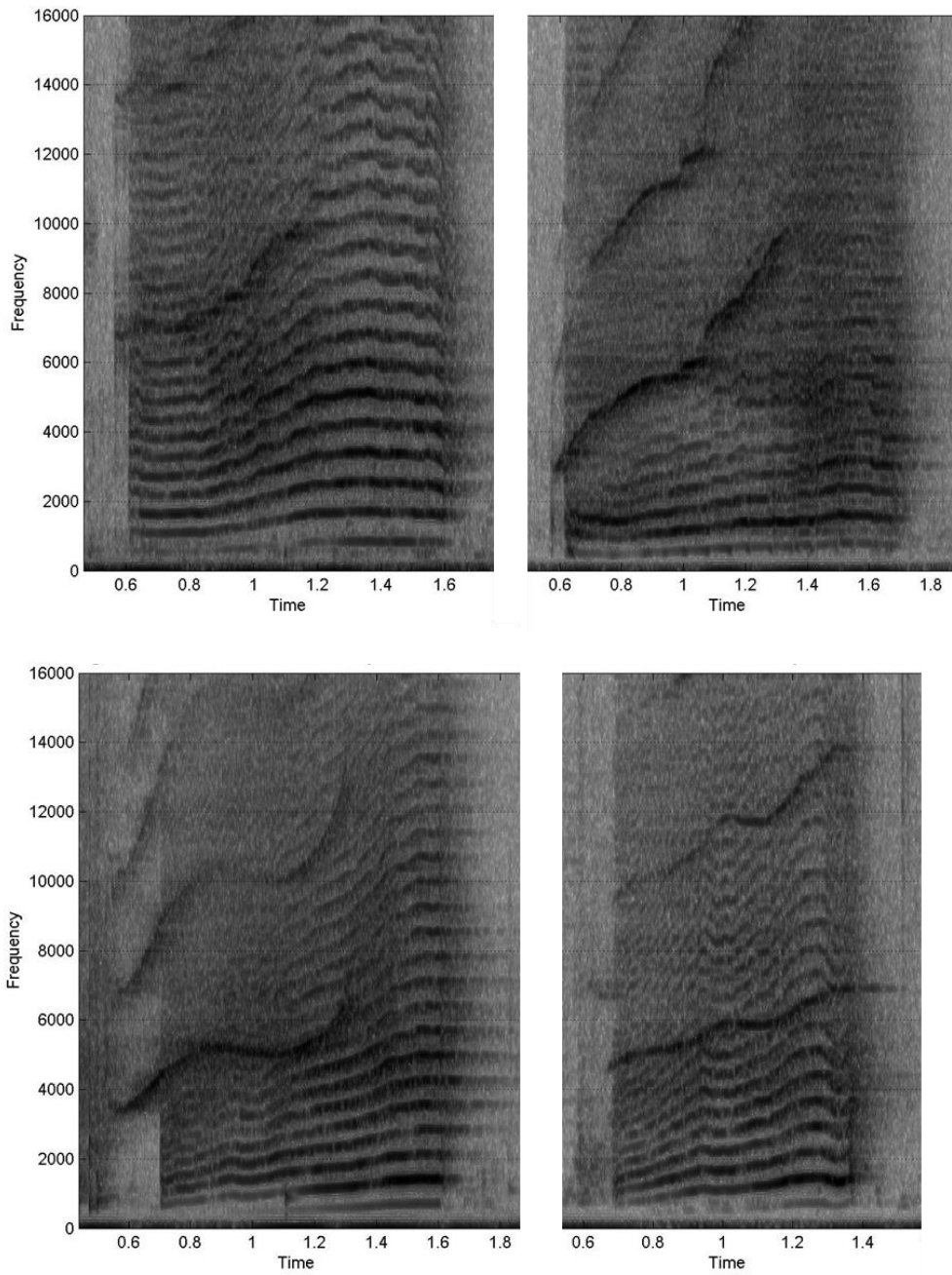


Figure 16 – Unit subtype Cii'

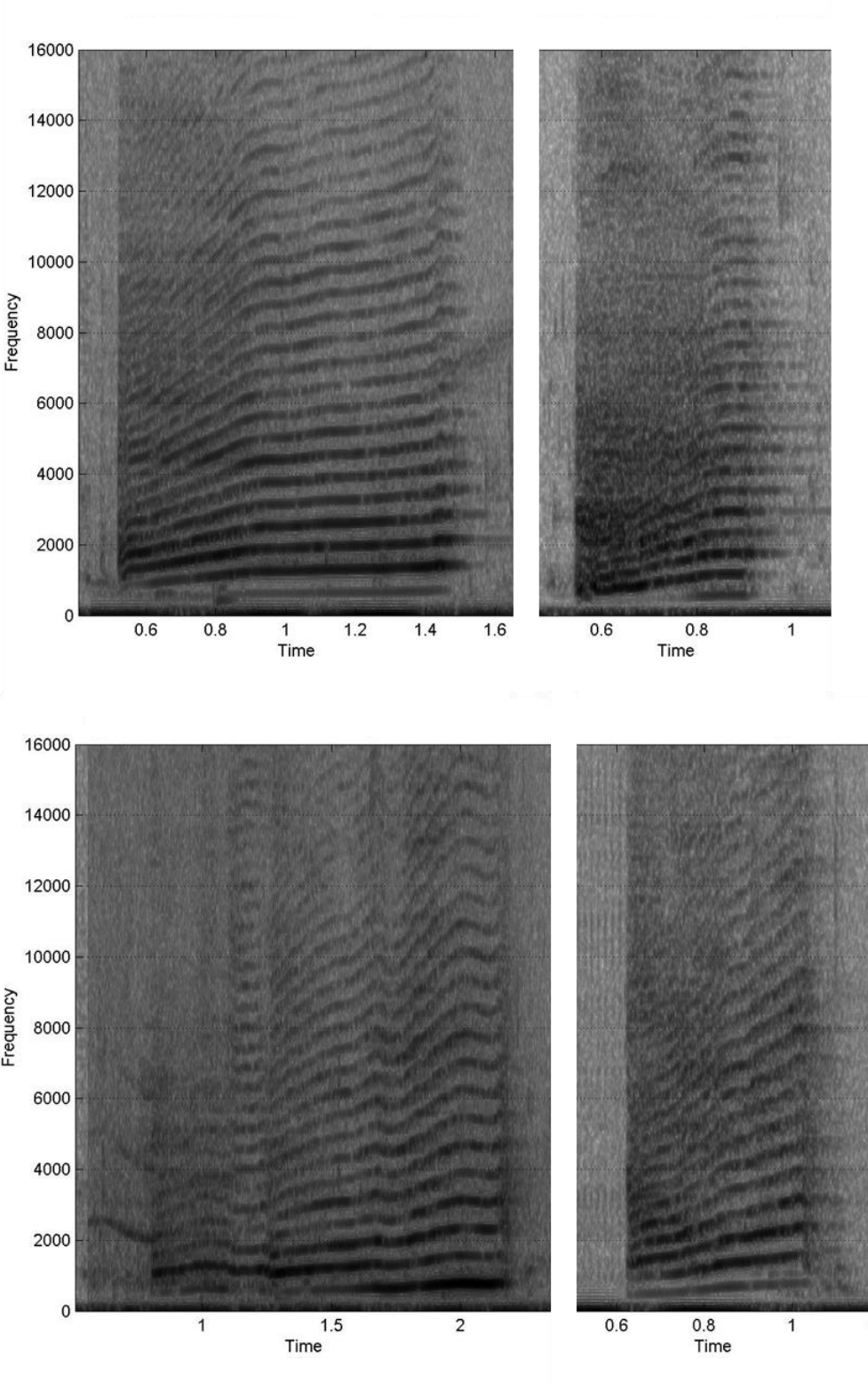


Figure 17 – Unit subtype Ei

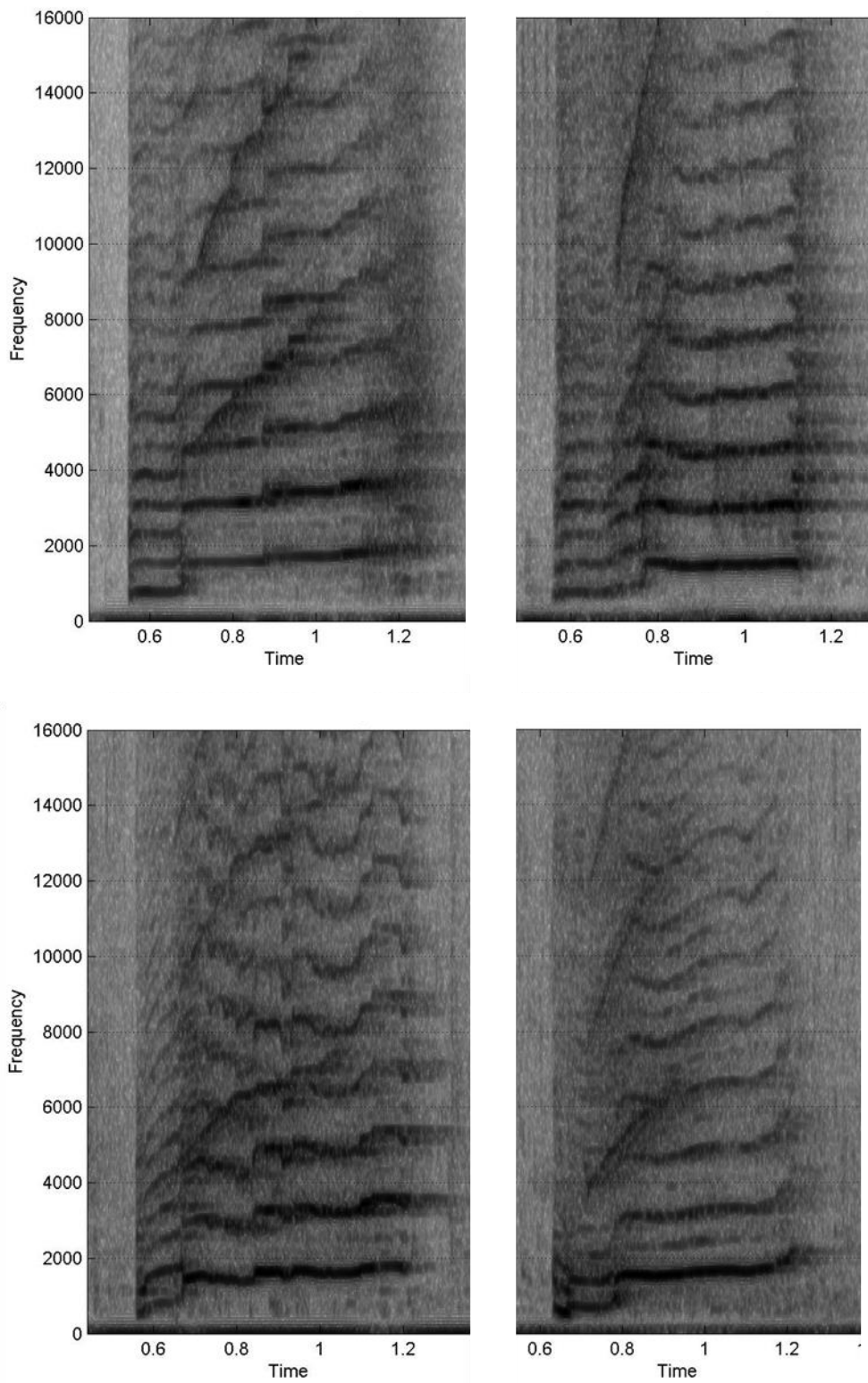


Figure 18 – Unit subtype Ei'

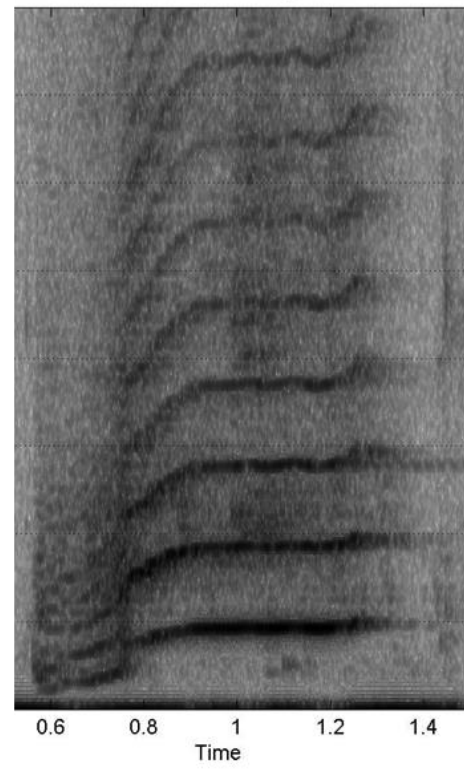
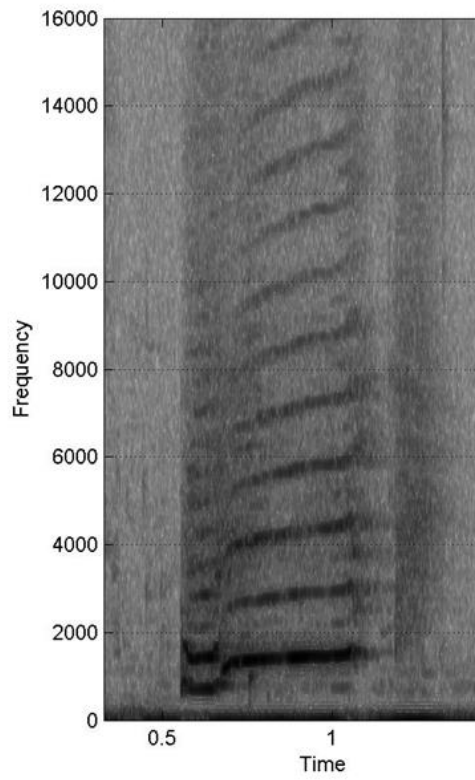
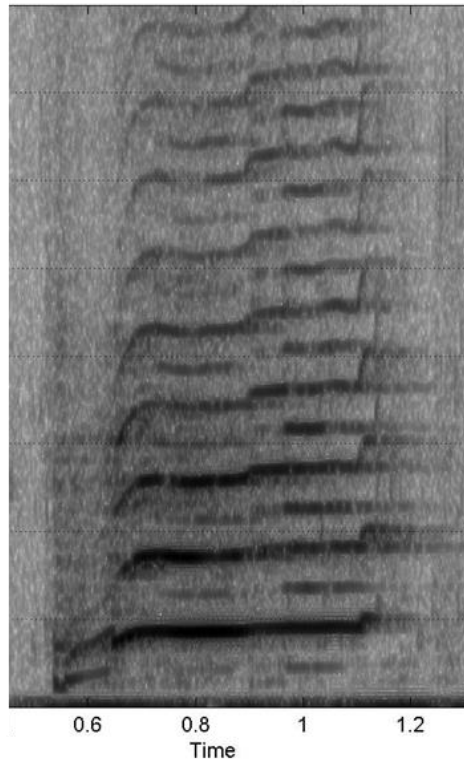
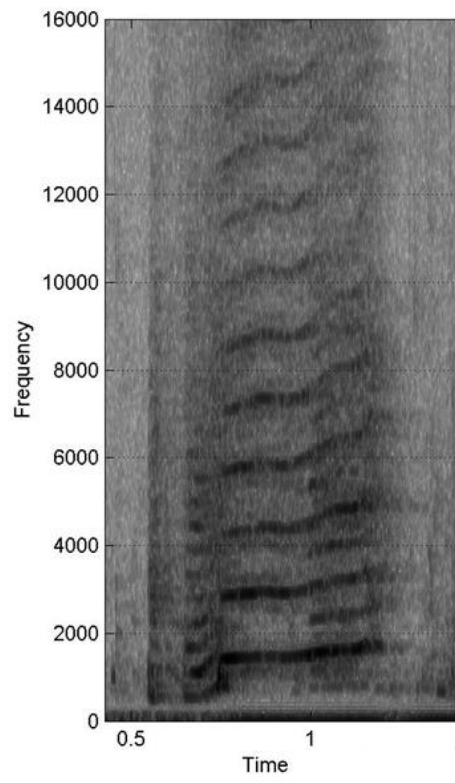


Figure 19 – Unit subtype Eii

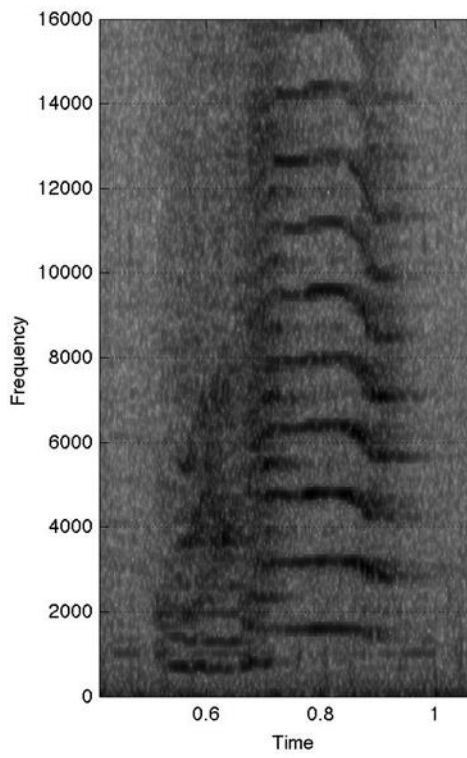
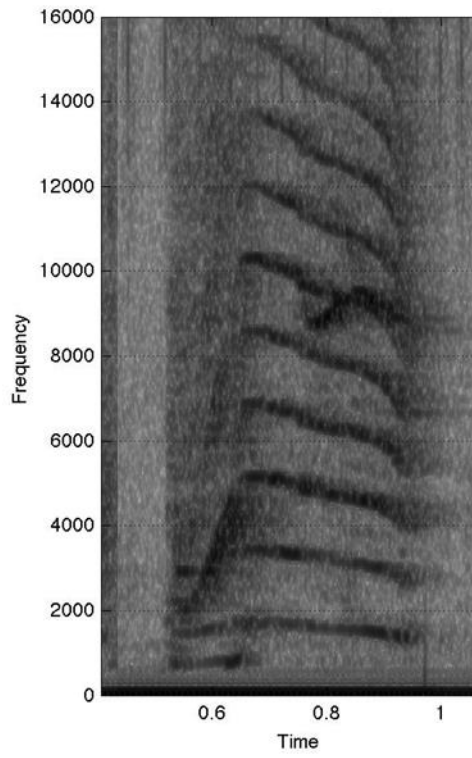


Figure 20 – Unit subtype Eii'

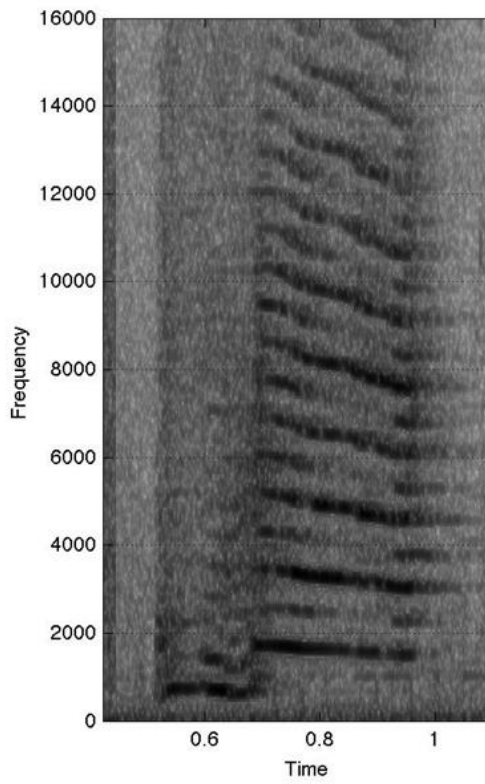
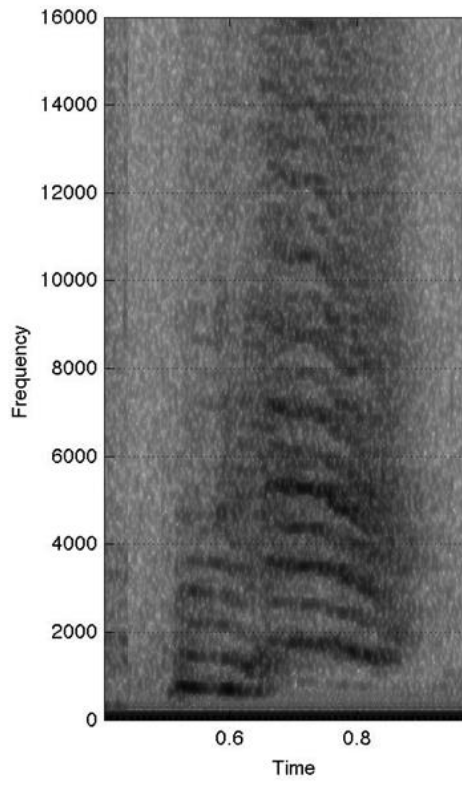


Figure 21 – Unit subtype Fi

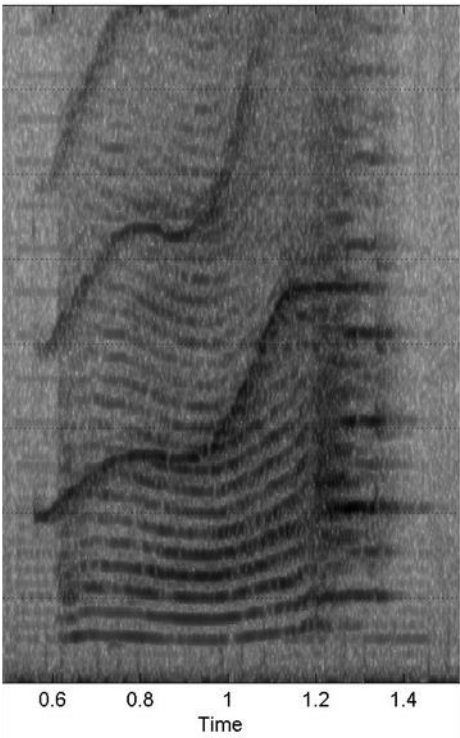
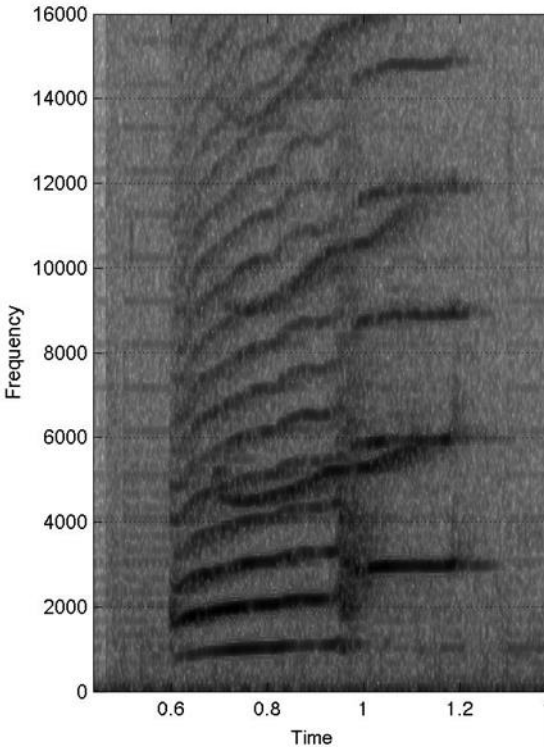
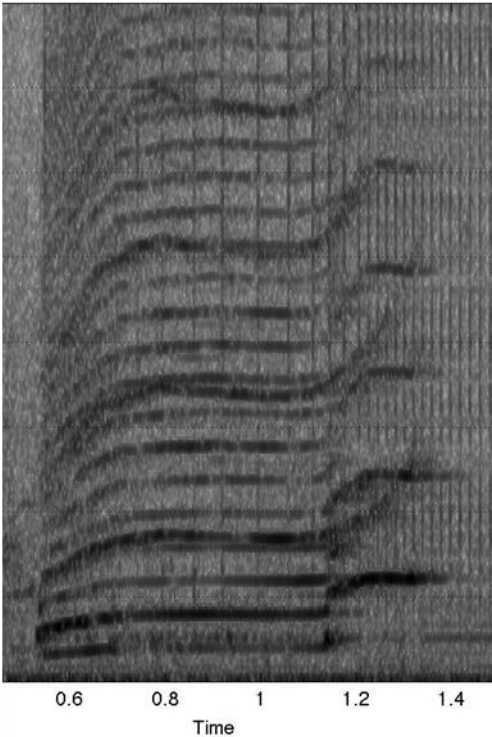
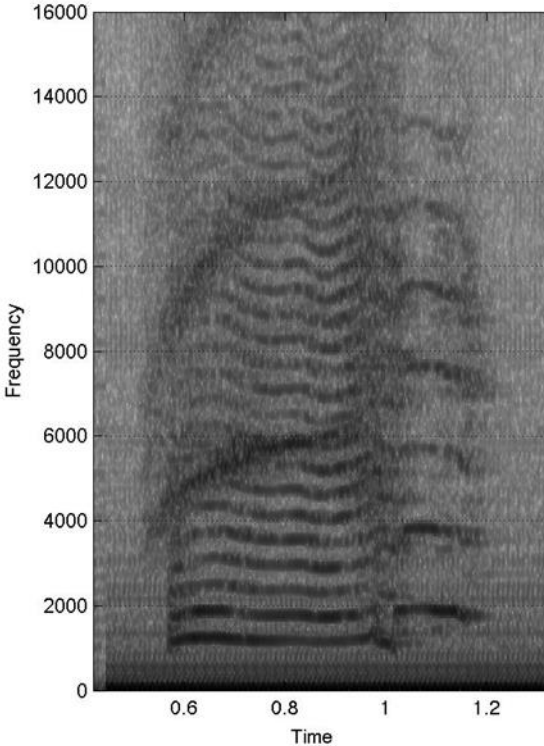


Figure 22 – Unit subtype Fi'

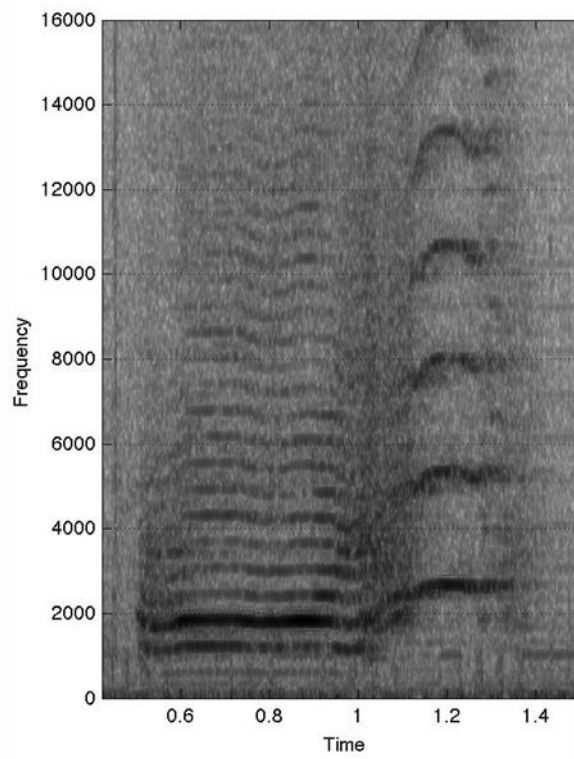
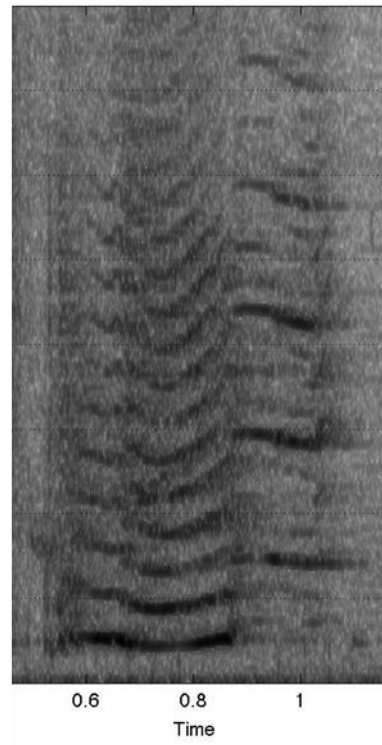
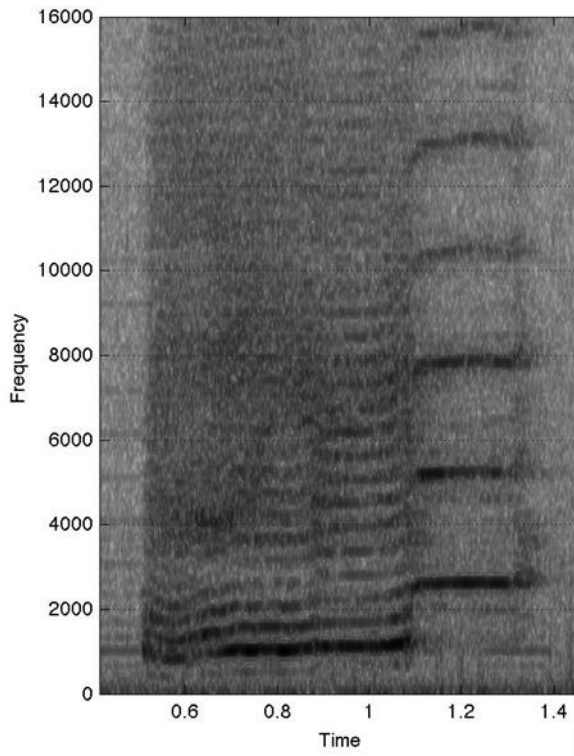


Figure 23 – Unit subtype Fii

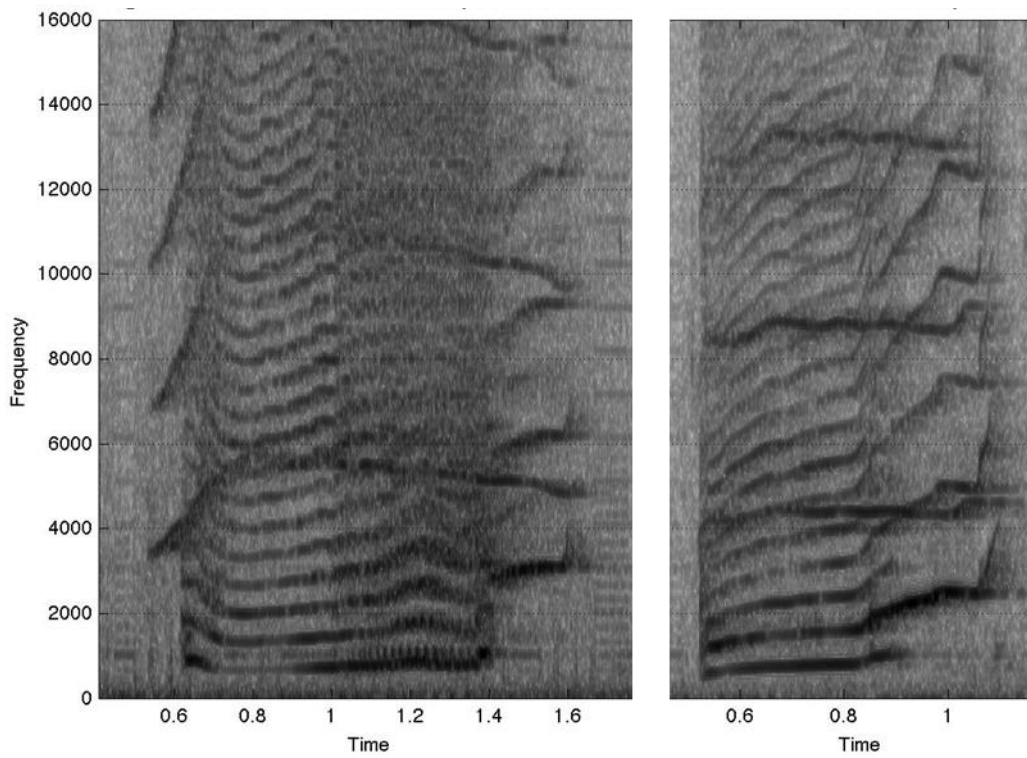
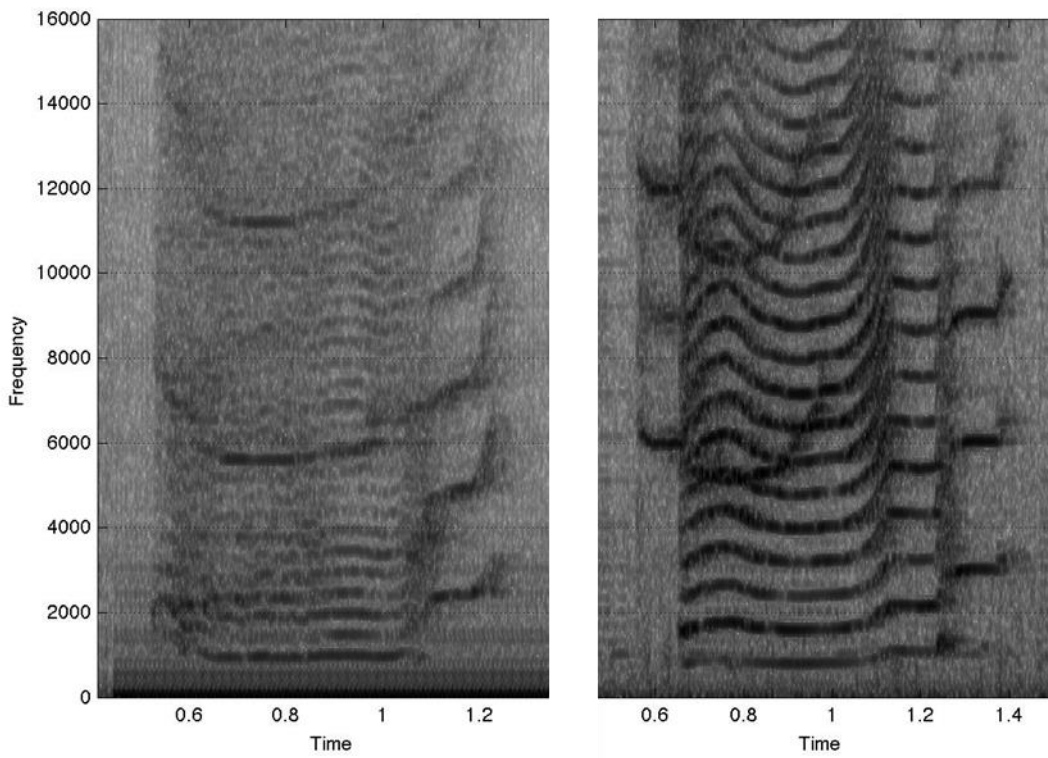


Figure 24 – Unit subtype Fii'

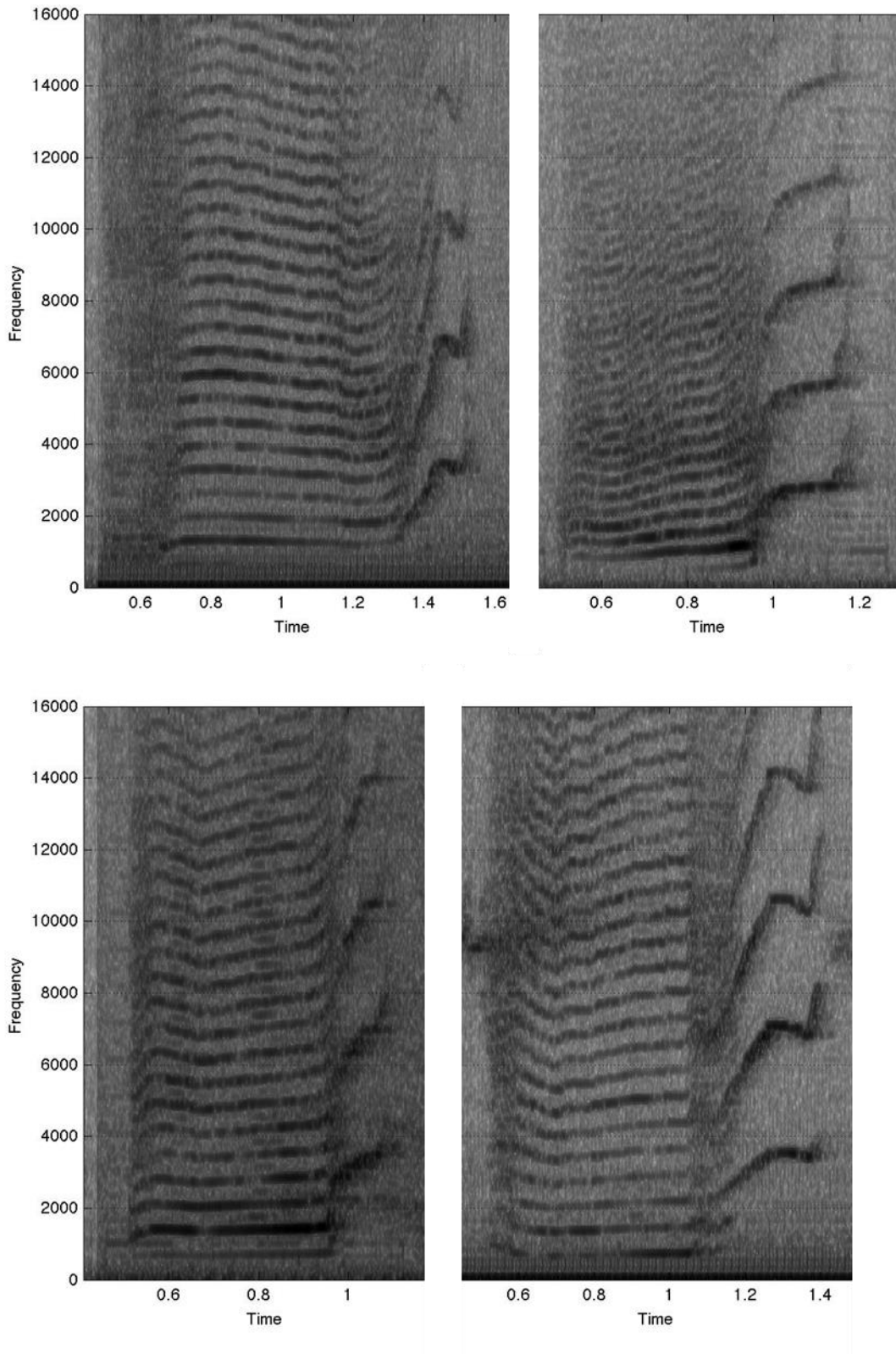


Figure 25 – Unit subtype Gi

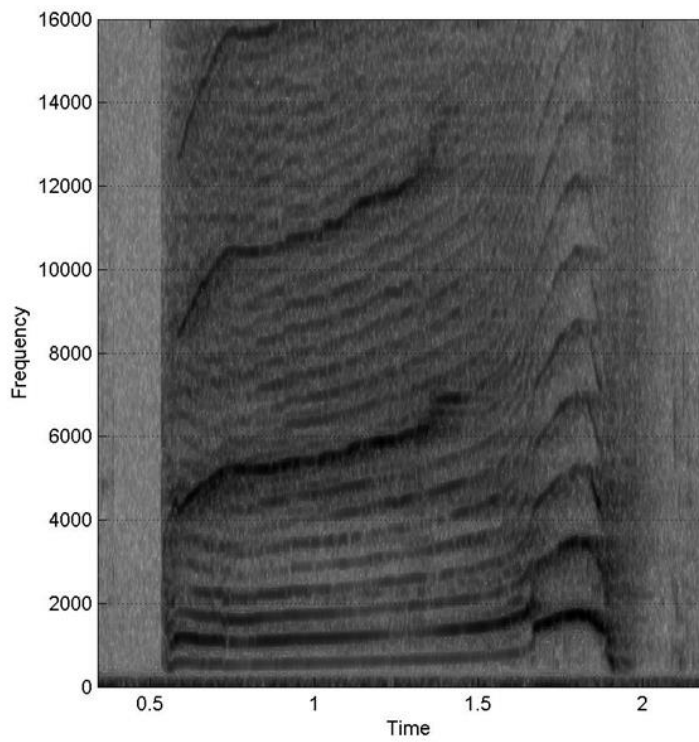
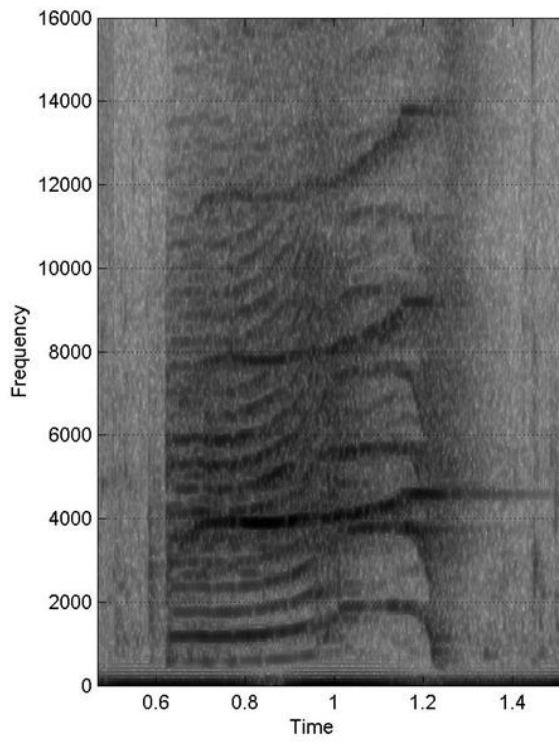


Figure 26 – Unit subtype Gi'

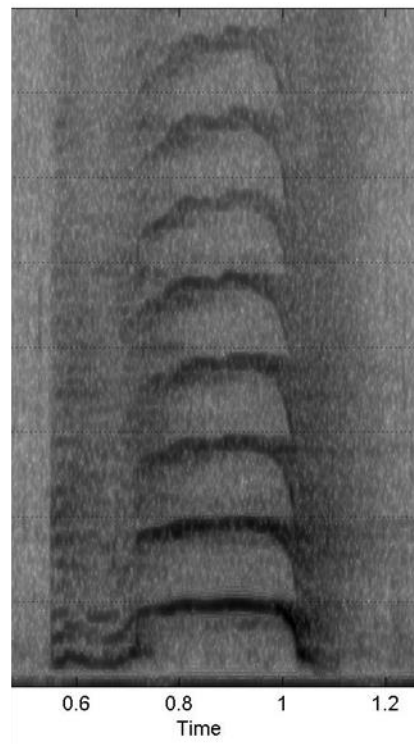
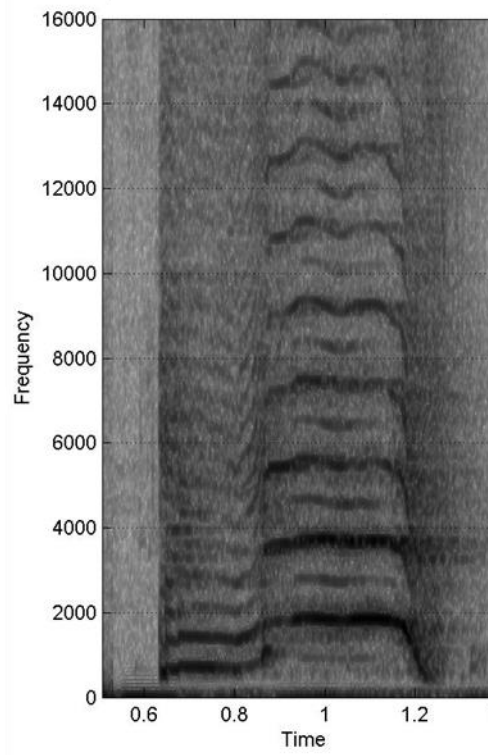
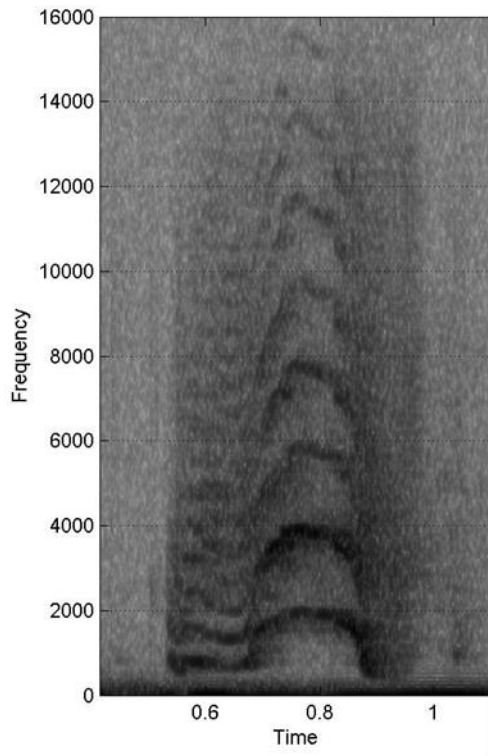


Figure 27 – Unit subtype Gii

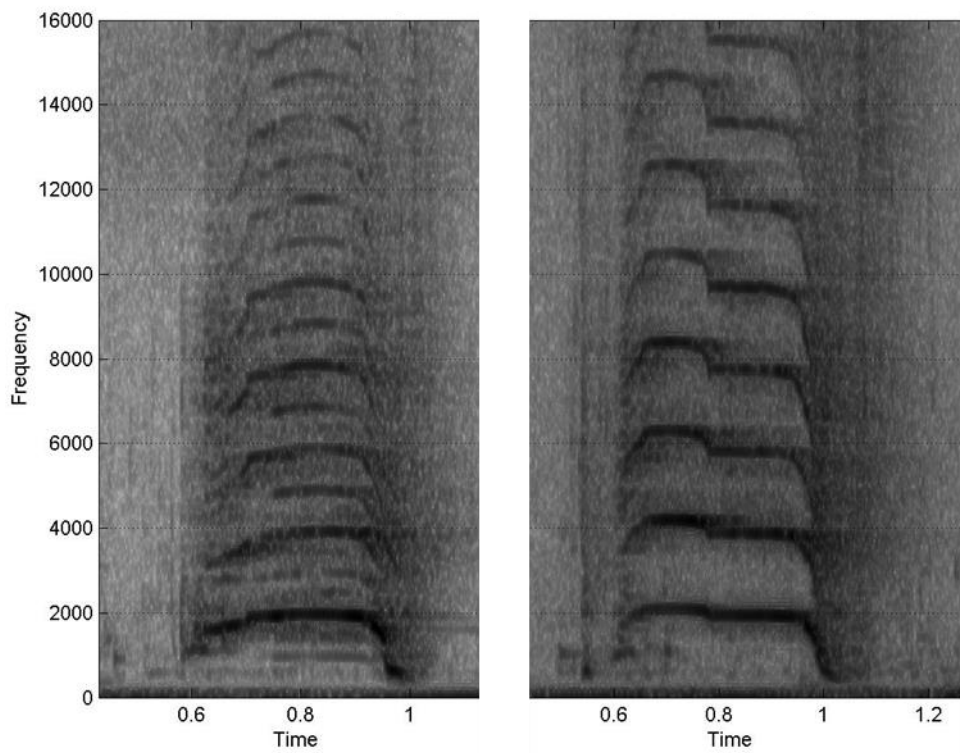
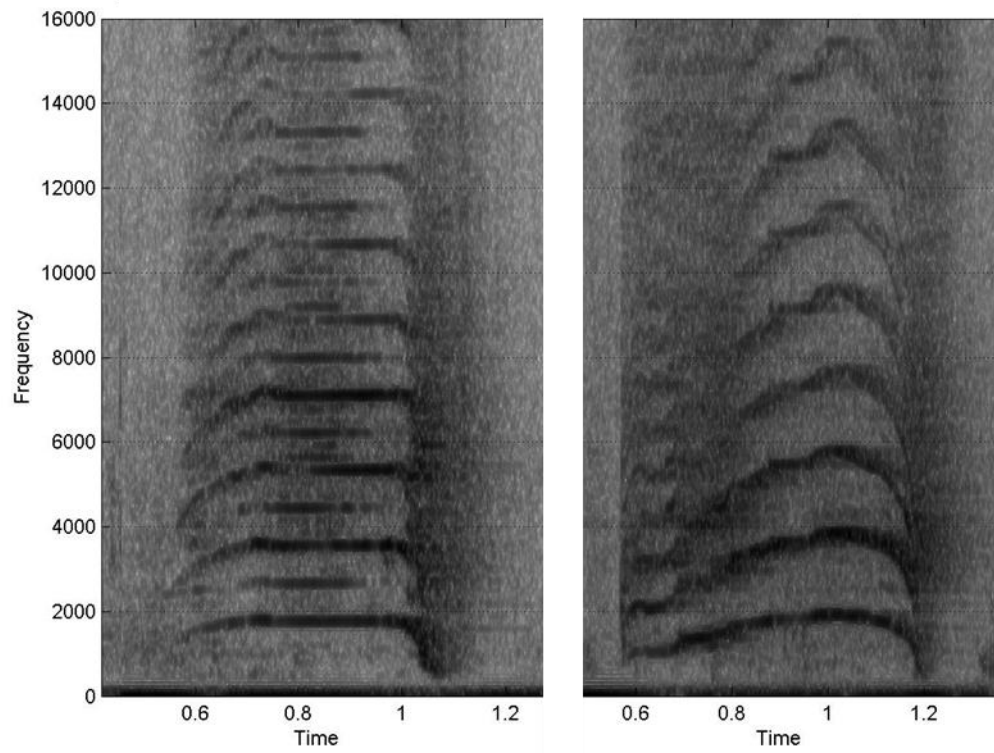
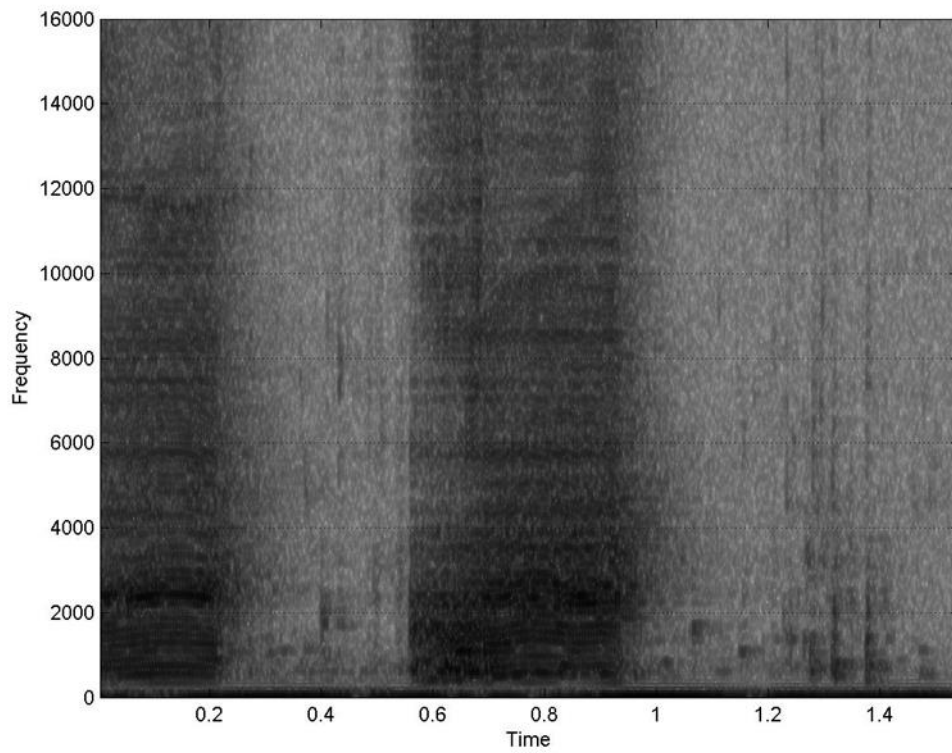
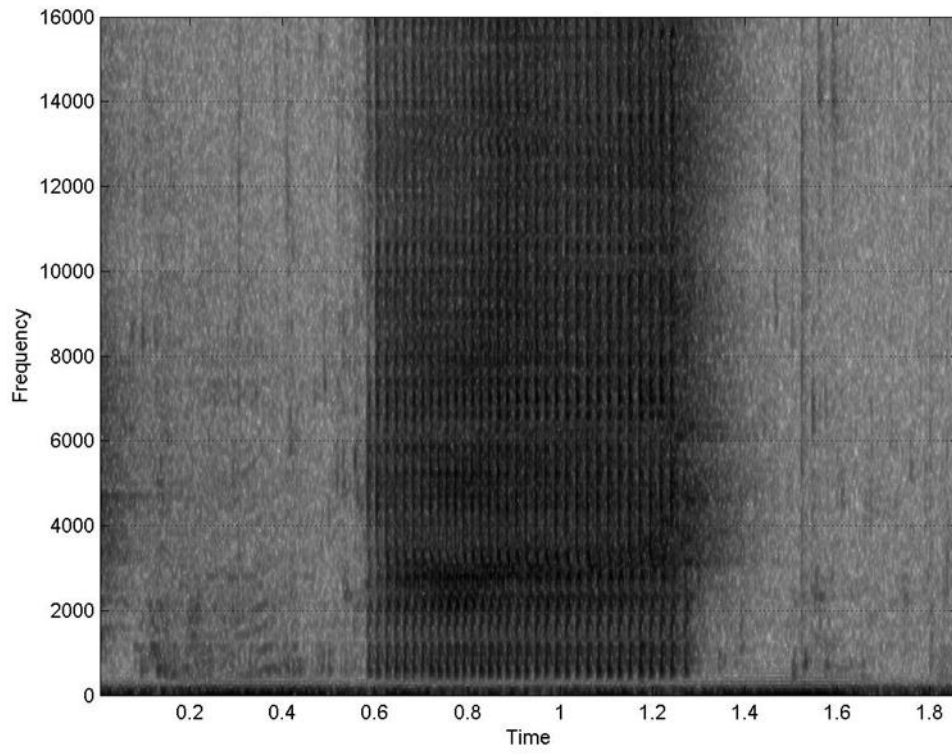


Figure 28 – Unit type Z



Describing Morgan's repertoire changes over time

To investigate whether there were changes in Morgan's vocal repertoire throughout the ~1 year period of sampling, the first and second period were analysed separately. In the tables below are highlighted, for both sampling periods, the units that represented more than 5% of the repertoire (Table 2), and the ten most used combinations (Table 3). There was a radical reduction in the percentage of variable calls between the two sampling periods, with the observations of variable calls decreasing from 23.8% in December to 2.3% in November 2011.

Table 2 – List of units and respective number of occurrences and relative percentage for the sampling periods of December 2010 and November 2011.

Unit	2010 December		2011 November	
	Nº units	Percentage (%)	Nº units	Percentage (%)
Ai	911	5.5	253	2.2
Ai'	807	4.9	850	7.3
Aii	18	0.1	0	0
Aii'	24	0.1	0	0
B	2448	15	838	7.2
Ci	940	5.7	1514	12.9
Ci'	46	0.3	118	1.0
Cii	28	0.2	16	0.1
Cii'	12	0.1	18	0.2
Ei	48	0.3	0	0
Ei'	109	0.7	3	0.03
Eii	23	0.1	342	2.9
Eii'	68	0.4	504	4.3
Fi	160	1	131	1.1
Fi'	7	0	149	1.3
Fii	11	0.1	53	0.5
Fii'	0	0	91	0.8
Gi	2878	17	798	6.8
Gi'	4177	25	1895	16.2
Gii	485	2.9	190	1.6
Z	3400	20	3936	33.6
HFC	5058	30	3059	26.2
Total units	16600	100	11699	100

Table 3 – List of combinations and respective number of occurrences and relative percentage produced in December 2010 and November 2011.

	2010		2011	
	DECEMBER		NOVEMBER	
	N	%	N	%
Ai	57	0.5	26	0.4
Ai'	71	0.7	37	0.6
Ai'+Ci	122	1.2	339	5.1
Ai'+Ci'	8	0.1	14	0.2
Ai'+Ci'+Z	0	0.0	4	0.1
Ai'+Ci+Z	0	0.0	70	1.1
Ai'+Cii	0	0.0	1	0.0
Ai'+Fi	3	0.0	23	0.3
Ai'+Fi'	0	0.0	8	0.1
Ai'+Fi'+Z	0	0.0	4	0.1
Ai'+Fi+Ci	4	0.0	13	0.2
Ai'+Fi+Z	0	0.0	9	0.1
Ai'+Gi	467	4.4	89	1.3
Ai'+Gi'	2	0.0	0	0.0
Ai'+Gii	80	0.8	0	0.0
Ai'+HFC	15	0.1	9	0.1
Ai'+HFC+Gii	1	0.0	0	0.0
Ai'+HFC+Z	1	0.0	0	0.0
Ai'+Z	33	0.3	230	3.5
Ai+B+Gi	1	0.0	0	0.0
Ai+Ci	160	1.5	175	2.6
Ai+Ci+Z	0	0.0	66	1.0
Ai+Cii	1	0.0	0	0.0
Ai+Ei	1	0.0	0	0.0
Ai+Fi	47	0.4	1	0.0
Ai+Fi'	6	0.1	0	0.0
Ai+Fi+Ci	4	0.0	0	0.0
Ai+Fi+Gi	1	0.0	0	0.0
Ai+Fi+Z	0	0.0	3	0.0
Ai+Fi+Z+Cii	1	0.0	0	0.0
Ai+Gi	575	5.4	2	0.0
Ai+Gii	33	0.3	0	0.0
Ai+HFC	14	0.1	0	0.0
Ai+Z	10	0.1	6	0.1
Aii	18	0.2	0	0.0
Aii'	24	0.2	0	0.0

Table 3, continued

	N	%	N	%
B	66	0.6	18	0.3
B+Ci	605	5.7	472	7.1
B+Ci'	14	0.1	4	0.1
B+Ci'+Z	0	0.0	9	0.1
B+Ci+Gii	1	0.0	0	0.0
B+Ci+Z	0	0.0	170	2.6
B+Eii+Ci'	1	0.0	0	0.0
B+Fi	66	0.6	13	0.2
B+Fi'	0	0.0	2	0.0
B+Fi'+Z	0	0.0	1	0.0
B+Fi+Ci	6	0.1	2	0.0
B+Fi+Gi	1	0.0	0	0.0
B+Fi+Z	0	0.0	6	0.1
B+Fi+Z+Ci	1	0.0	0	0.0
B+Fii	6	0.1	2	0.0
B+Gi	1425	13.5	54	0.8
B+Gi'	11	0.1	3	0.0
B+Gi+Z	2	0.0	0	0.0
B+Gii	73	0.7	0	0.0
B+HFC	16	0.2	0	0.0
B+Z	143	1.4	82	1.2
B+Z+Ci	1	0.0	0	0.0
B+Z+Fi	5	0.0	0	0.0
B+Z+Gi	3	0.0	0	0.0
Ci	32	0.3	77	1.2
Ci'	23	0.2	45	0.7
Ci'+Z	0	0.0	17	0.3
Ci+Z	0	0.0	24	0.4
Cii	26	0.2	4	0.1
Cii'	12	0.1	8	0.1
Cii'+Z	0	0.0	9	0.1
Cii+Z	0	0.0	2	0.0
Ei	36	0.3	0	0.0
Ei'	72	0.7	2	0.0
Ei'+Ci	0	0.0	1	0.0
Ei'+Z	36	0.3	0	0.0
Ei'+Z+Gi'	1	0.0	0	0.0
Ei+Gi	2	0.0	0	0.0
Ei+Z	9	0.1	0	0.0
Eii	4	0.0	136	2.0
Eii'	9	0.1	81	1.2
Eii'+B+Ci	1	0.0	0	0.0
Eii'+Z	58	0.5	420	6.3
Eii'+Z+Ci	0	0.0	3	0.0
Eii+Z	17	0.2	206	3.1

Table 3, continued

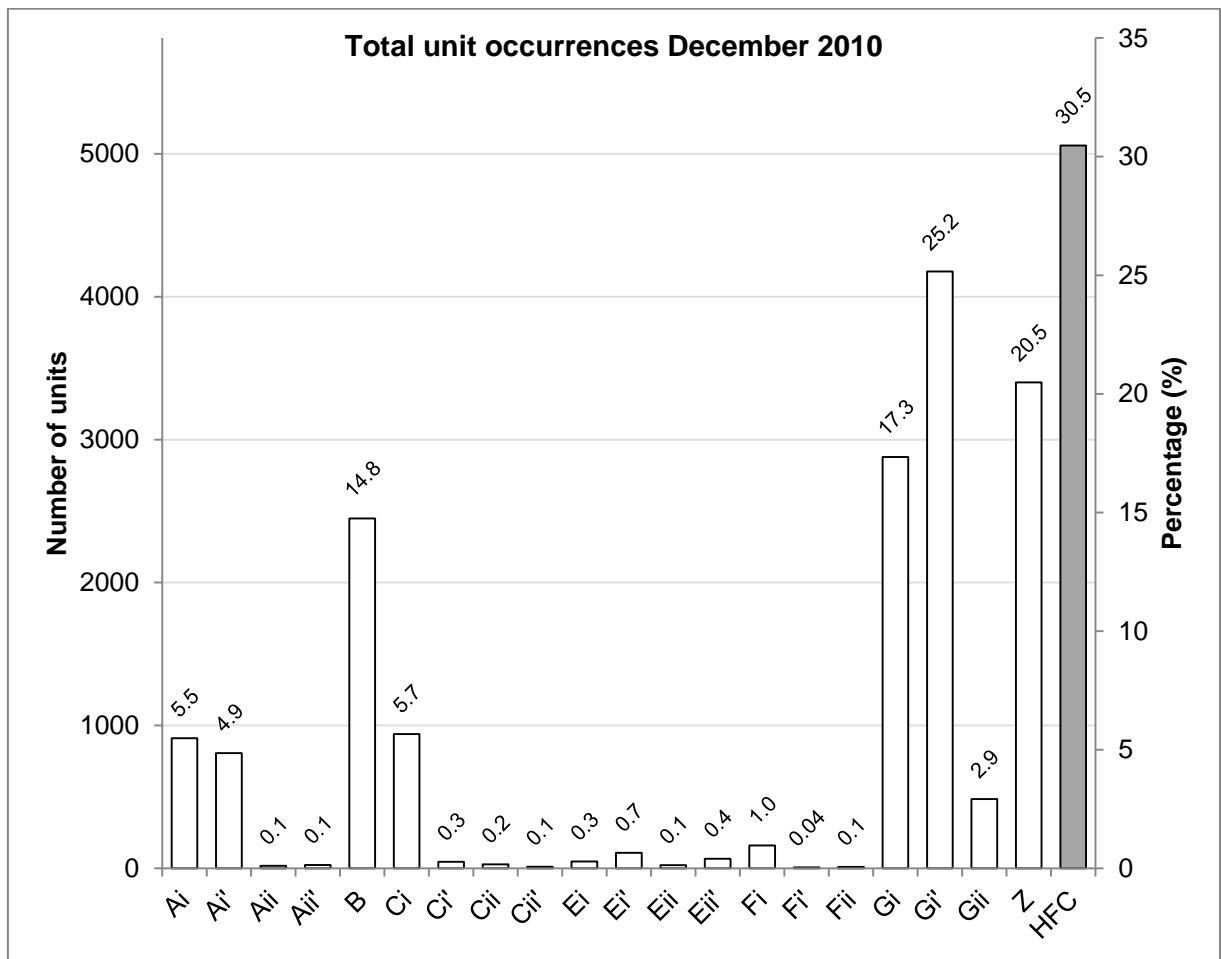
	N	%	N	%
Eii+Z+Z+Z+Z	1	0.0	0	0.0
Fi	15	0.1	34	0.5
Fi'	1	0.0	80	1.2
Fi'+Ci'	0	0.0	11	0.2
Fi'+Fi'	0	0.0	5	0.1
Fi'+Z	0	0.0	41	0.6
Fi+Ci	0	0.0	1	0.0
Fi+Z	0	0.0	16	0.2
Fii	11	0.1	42	0.6
Fii'	0	0.0	74	1.1
Fii'+Z	0	0.0	17	0.3
Fii+Z	0	0.0	8	0.1
Gi	395	3.7	259	3.9
Gi'	4016	37.9	982	14.8
Gi'+Z	8	0.1	841	12.6
Gi'+Z+Ci	3	0.0	36	0.5
Gi+Z	2	0.0	326	4.9
Gi+Z+Ci	0	0.0	7	0.1
Gi+Z+Gi	0	0.0	3	0.0
Gii	189	1.8	172	2.6
Gii+Z	1	0.0	18	0.3
Z	3	0.0	3	0.0
Z+Ci	0	0.0	42	0.6
Z+Ci'	0	0.0	6	0.1
Z+Ci'+Z	0	0.0	6	0.1
Z+Ci+Z	0	0.0	25	0.4
Z+Cii	0	0.0	2	0.0
Z+Cii'	0	0.0	1	0.0
Z+Cii+Z	0	0.0	7	0.1
Z+Fi	0	0.0	2	0.0
Z+Fii	0	0.0	1	0.0
Z+Gi	3	0.0	49	0.7
Z+Gi'	7	0.1	12	0.2
Z+Gi'+Z	1	0.0	0	0.0
Z+Gii	1	0.0	0	0.0
Z+Z	901	8.5	449	6.8
Z+Z+Gi	0	0.0	5	0.1
Z+Z+Gi'	136	1.3	21	0.3
Z+Z+Gii	102	1.0	0	0.0
Z+Z+Z	205	1.9	37	0.6
Z+Z+Z+Gi	0	0.0	1	0.0
Z+Z+Z+Gii	4	0.0	0	0.0
Z+Z+Z+Z	41	0.4	6	0.1
TOTAL	10590	100	6650	100

Table 4 – Number of occurrences and number of different combinations composed by one, two and three or more units, in December 2010 and November 2011.

Combinations	DECEMBER 2010		NOVEMBER 2011	
	N	different comb	N	different comb
single unit	5080	20	2080	18
two-unit	4981	38	4056	45
three-unit and more	529	26	514	25
TOTAL	10590	84	6650	88

In December 2010 a total of 18,300 calls were identified. Of these, 10,590 (57.9%) were considered discrete stereotyped calls and were included in the analysis. The rest were composed of 18.3% aberrant and 23.8% variable calls. The 10,590 discrete calls were subdivided into 16,600 units, with different production rates (Figure 29).

Figure 29 – Histogram of unit occurrences. Numbers above bars indicate the percentage of total unit usage that each unit represented. HFC indicates the number of times the high-frequency component was observed.



There was a high degree of variation in the occurrence of units (Table 3). In most cases, units were combined to produce calls. Combinations could be of different units and/or of repetitions of the same unit (e.g., call Z+Z+Z). Table 4 shows the total numbers of calls in which units were used, either as a single unit or combinations of units.

The ten most frequently used calls (single units or combinations of units) made up 84.2% of all the discrete calls produced by Morgan during this sampling period. All the remaining calls represented 15.8% of the discrete calls produced. The call composed of the single unit Gi' was the most commonly produced, representing 37.9% of all discrete calls produced (Figure 30).

Figure 30 – The ten most frequently produced calls and respective numbers of occurrences. Numbers above bars indicate the percentage of discrete calls that each call type represented.

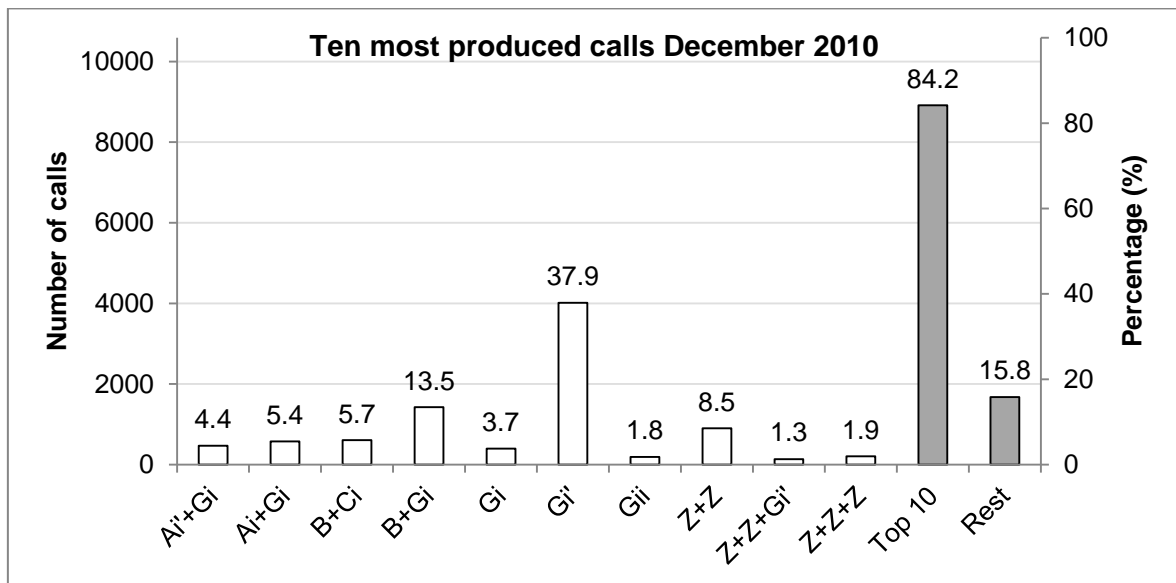


Table 5 – Units used by Morgan and number of discrete calls in which they were used.

Unit	N° of calls used in	Percentage (%)
Ai	911	8.6
Ai'	807	7.6
Aii	18	0.2
Aii'	24	0.2
B	2448	23.1
Ci	940	8.9
Ci'	46	0.4
Cii	28	0.3
Cii'	12	0.1
Ei	48	0.5
Ei'	109	1.0

Table 5, continued

Unit	Nº of calls used in	Percentage (%)
Eii	23	0.2
Eii'	68	0.6
Fi	160	1.5
Fi'	7	0.1
Fii	11	0.1
Gi	2878	27.2
Gi'	4177	39.4
Gii	485	4.6
Z	1716	16.2
HFC	5058	47.8
Total calls	10590	100

As it is possible to observe in Table 5, the unit Z was used in 16.2% of all discrete calls analysed, and the high-frequency component was used in less than half of the calls produced. There were 13 units that were used in less than 5% of the calls.

November 2011

Although the recording duration for the second sampling period was longer than the first (170 hours compared to 92 hours in December 2010), in November 2011 a total of only 8,043 calls were recorded. This represents a call rate of 47.3 calls/hour, in comparison to a call rate of 198.9 calls/hour in December 2010. In contrast to December 2010 when the total amount of discrete calls was ~58%, 82.7% of the 8,043 calls recorded in November 2011 (corresponding to 6,650 calls) were classified as discrete calls. The discrete calls were subdivided into 11,699 units (Figure 31). The rest was composed of 15% aberrant and 2.3% variable calls.

The ten most frequently used calls (single units or combinations of units) and respective values are presented in Table 5. The ten most used calls made up 68% of all discrete calls produced during this sampling period (Figure 32). All other calls constitute 32% of the discrete calls produced.

Figure 31 – Total unit occurrences. Numbers above bars indicate the percentage of total unit usage that each unit represented. HFC indicates the number of times the high-frequency component was observed.

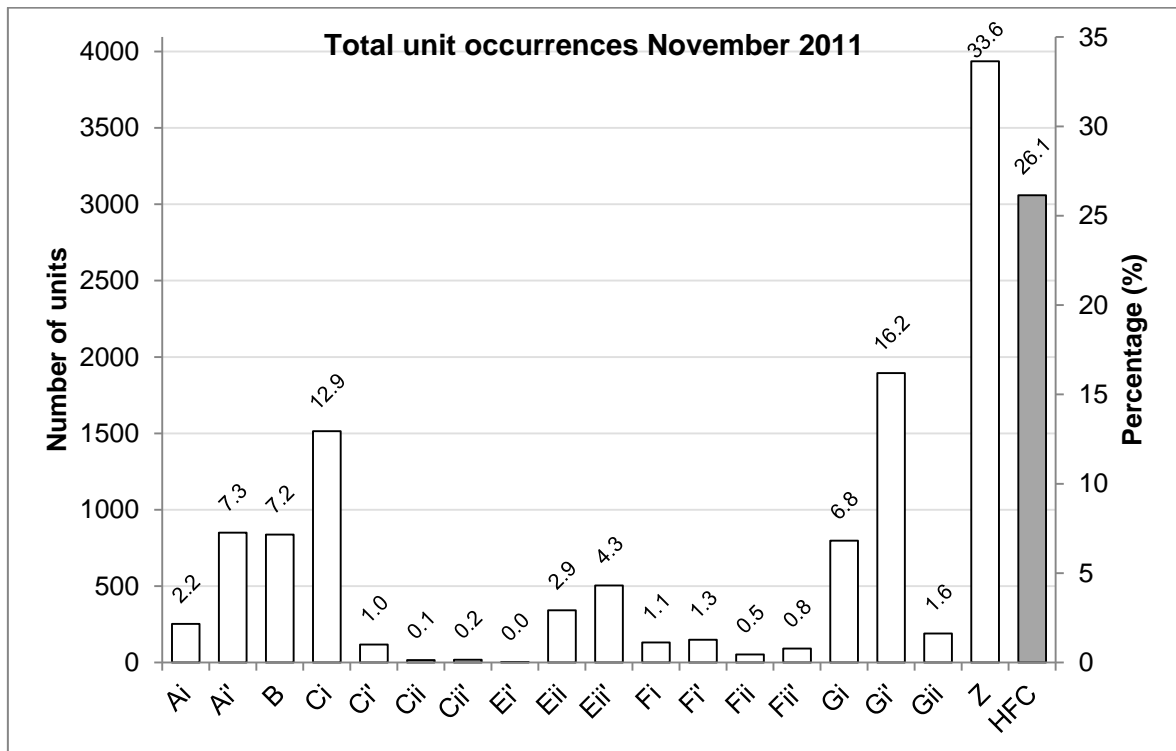


Figure 32 – The ten most frequently produced calls and respective numbers of occurrences.

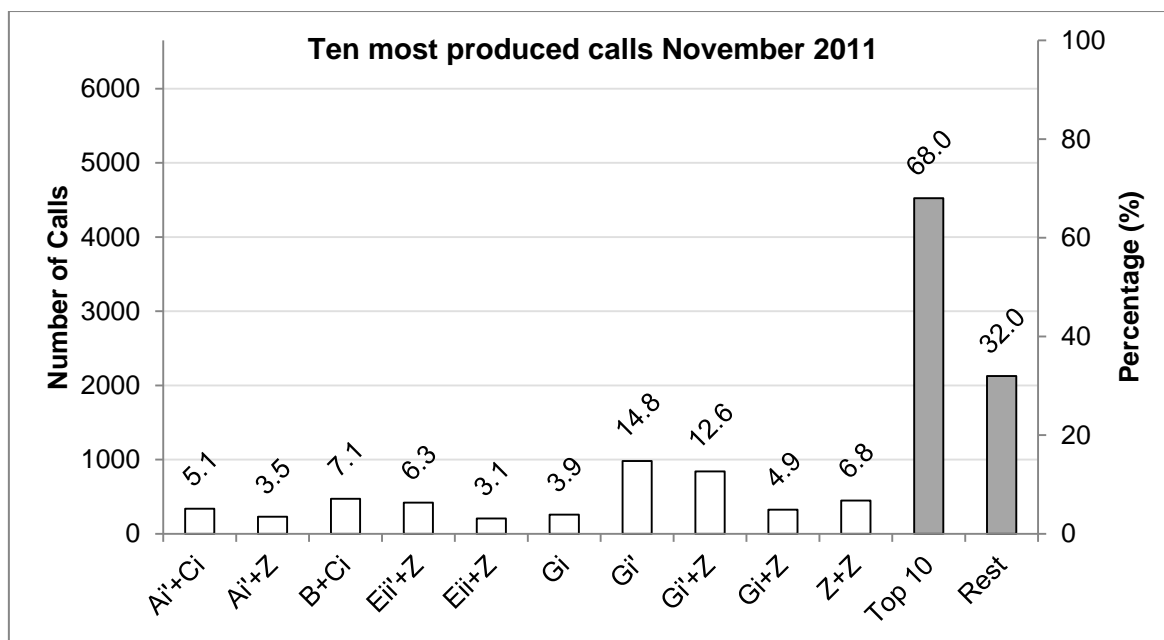


Table 6 – Units used by Morgan and number of discrete calls they were used in.

Unit	Nº of calls used in	Percentage (%)
Ai	253	3.8
Ai'	850	12.8
B	838	12.6
Ci	1514	22.8
Ci'	118	1.8
Cii	16	0.2
Cii'	18	0.3
Ei'	3	0.1
Eii	342	5.1
Eii'	504	7.6
Fi	131	2.0
Fi'	144	2.2
Fii	53	0.8
Fii'	91	1.3
Gi	795	12.0
Gi'	1895	28.5

Table 6, continued

Unit	N° of calls used in	Percentage (%)
Gii	190	2.9
Z	3329	50.1
HFC	3059	46.0
Total calls	6650	100

As it is possible to observe in Table 6, the unit Z was used in ~50% of all calls produced, and the high-frequency component was used in less than half of the calls produced. Ten of the units were used in less than 5% of the calls.

Statistical comparison

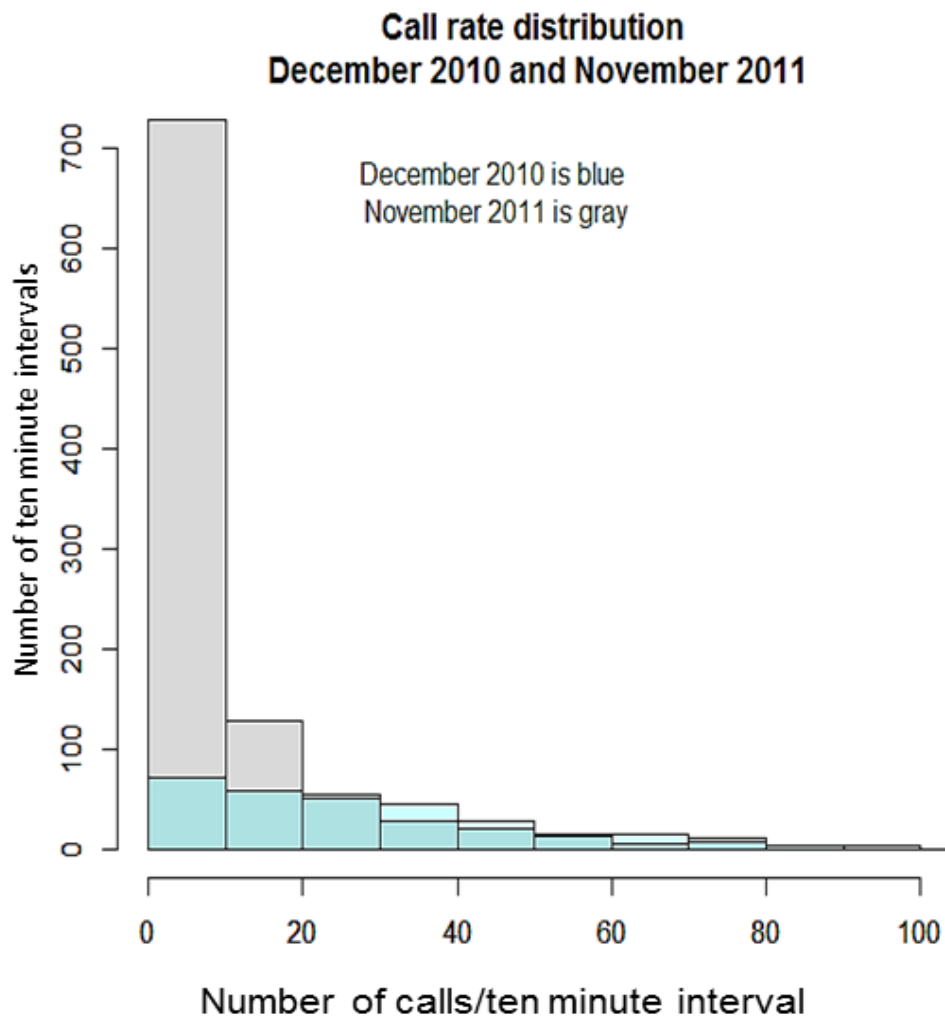
The Friedman Rank Sum Test weighed the occurrences of each unit for the sampling periods of December 2010 and November 2011, testing whether or not the distribution of occurrences per unit was the same across the two sampling periods.

The results showed that there was a significant difference in the distribution of occurrences per unit between the two sampling periods (Friedman chi-squared = 34.2; d.f. = 20; $p = 0.025$).

The same test was computed for one- and two-unit calls, testing whether the distribution of occurrences of the 77 different combinations was the same for December 2010 and November 2011. The results indicated a statistically significant difference in the distribution between the two sampling periods (Friedman chi-squared = 99,96 d f = 76, p-value = 0.0397).

The results for the two-sample Wilcoxon and Mood test indicated statistically significant differences for both the means (Wilcoxon $W = 241819$, $p < 2.2^{-16}$) and the medians (Mood $Z = 5.7815$, $p = 7.402^{-09}$) in the distribution of calls per unit of time, respectively. Figure 33 shows the distributions of the numbers of calls for every ten minutes interval for both sampling periods.

Figure 33 – Overlapping histograms of the distributions of calls per ten minutes intervals for December 2010 (in blue) and November 2011 (in grey).



Kullback-Leibler divergence

The maximum possible number of totally random two-unit combinations was calculated to be $21^2 = 2^2 \log_2 21 = 441$ with equal probability. The real number of different two-unit combinations produced by Morgan was 56. The maximum entropy for the two-unit combinations was also computed as 4.39 bits. This is the maximum entropy value, translated as minimum predictability for unit association. The relative entropy for December 2010 was 0.71 bits and for November 2011 was 1.08 bits. This difference in the relative entropy indicates that there was a higher predictability for the two-unit combinations in December 2010.

DISCUSSION

Morgan produced a wide number of vocalizations during the study period which resulted from the combination of units, as presented in the results section. The division and classification of vocalizations into units was used for the analysis because her vocalizations seemed to be produced by putting together, and in specific order, smaller calls or sections of other vocalizations, resulting in a large number of different vocalizations with familiar contours. A similar method of classification had already been suggested in two previous studies (Shapiro *et al.*, 2011; Yurk, 2005), and given the high variability of Morgan's repertoire and the number of possibilities given by the recombination of units, this method was more descriptive than the traditional classification of vocalizations into call types and subtypes (Ford, 1989).

The number of different discrete combinations that Morgan produced (124) contrasts greatly with the number of call types observed in other killer whale pods, which varies from 7 to 17 subtypes in the Northeast Pacific (Ford, 1987) and from 3 to 16 in Norway (Strager, 1995). However, Morgan produced only 21 different units that were combined to produce the 124 discrete call combinations. Previous studies that used section-based-structure to describe killer whale repertoires (Shapiro *et al.*, 2011; Yurk, 2005) considered between 11 and 26 sections. Although the criteria for dividing the vocalizations were different between all three studies, the number of sections the repertoire was divided into was remarkably similar.

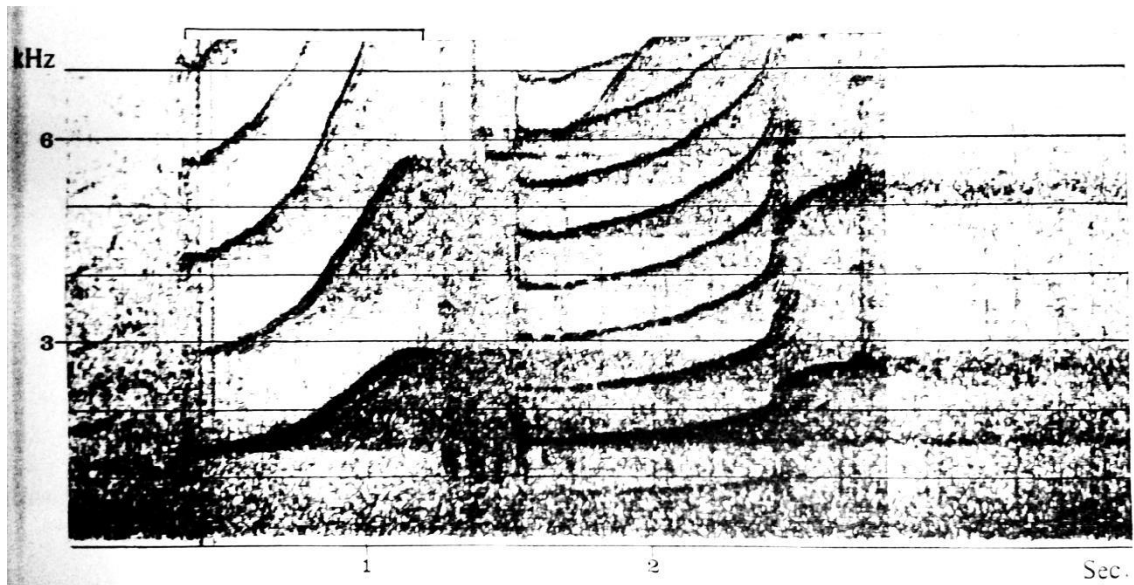
Some of these units' combinations were only observed once, but were accounted for, because they were composed by a combination of discrete units. The discrete vocalizations varied in the number of units that composed them, ranging from one (a single unit, e.g. Ai) to five (e.g. Eii+Z+Z+Z+Z), although the most frequently used calls were composed of one and two (93.64% of all the combinations produced). Morgan produced 21 different units and combined them into 124 different vocalizations. Of these, 58 were composed of two units (two-unit combinations) and 45 were composed of three or more units. This is not a vast number of combinations, given that the possibilities for free combinations using up to two units would total 462, and when using up to three 3 units the total would be 9723 different possible combinations. This leads to the conclusion that the use of units and the order they are put together was not random, but that there is a process of learning a specific repertoire (Bowles *et al.*, 1988) associated with this. The order in which the units appeared when put together to create longer vocalizations appears not to have been arbitrary. It suggests the existence of a set of rules, a strong

structural arrangement, a syntax, as suggested by Suzuki *et al.* (2006) for humpback whales (*Megaptera novaeangliae*, Borowski, 1781). The idea of an existing set of rules for the construction of combinations is supported by the Kullback-Leibler divergence, which shows that the relative entropy for the two-unit combinations for both sampling periods was substantially less than the maximum possible entropy of 4.39 bits, indicating that the association of units was not random. The existence of a set of rules would be a determinant factor to the total size of Morgan's vocal repertoire. As shown in the results, the maximum number of two-unit combinations with a completely random association index was 441, and the actual number of two-unit combinations produced by Morgan was 56, which is 7 times smaller.

Although the total number of combinations produced was fairly higher in December 2010, the number of occurrences for two-unit and for three-unit and more combinations was similar between the two sampling periods, and the most significant difference can be observed in the production rate of single units alone, with substantially more single-unit calls in December 2010 than November 2011 (Table 4).

The vocalizations composed by what were considered discrete units totalled ~65% of all call utterances produced, the rest being classified as aberrant and variable. Shapiro *et al.* (2011) suggested that Norwegian killer whales may assemble some of their calls putting together sections from a repertoire of "subunits". This structure would mean less memory requirements to the individuals, when compared to the whole call type structure, specifically given the variability and possibility of call subtypes that could exist. This is reinforced by the observation that Morgan's vocalizations, like other Norwegian whales' compound calls (Figure 34), sometimes consisted of combinations of Norwegian killer whales' stereotyped calls (Shapiro, 2008; Strager, 1993, 1995).

Figure 34 – Norwegian compound call N14i, composed by sections highly similar to Morgan’s units Ai’ and Fi’ (adapted from Strager, 1993).



New vocalizations could be created by forming new combinations, adding units or changing their order in already existing vocalizations, suggested also by the number of combinations that Morgan produced only once, as if she was experimenting.

Some variable and aberrant vocalizations consisted of combinations of a discrete unit and a variable section, suggesting that variable and aberrant calls may not be as distant from discrete calls as they are usually considered, being possible to observe a gradual variation, rather than a gap between the two categories. This could also shed some light on how the units and their order and combinations are chosen in the first place. However, to fully understand the processes by which variable and aberrant calls are produced, more recordings of other individuals would be required, given that Morgan’s situation was highly specific due to her hearing impairment.

Although most vocalizations were constructed from a set of shared units, the high-frequency component kept the same general contour in most of the vocalizations in which it was used (Figure 35). The units are shared across the repertoire of vocalizations, and only two (Aii and Aii’ – Figure 36) were used alone, and were the only two units never observed paired with any other unit to create a new vocalization.

Figure 35 – **A** – Unit type Ai; **B** – Unit type Ci; **C** – Unit type Ei; **D** – Unit type Gi. Note the high-frequency component (indicated by the white arrow) keeps the same rough contour across the four unit types.

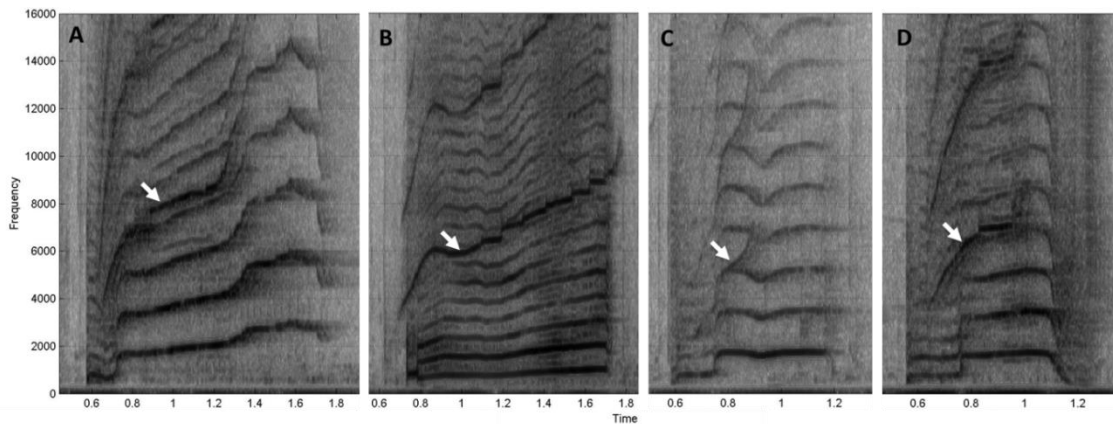
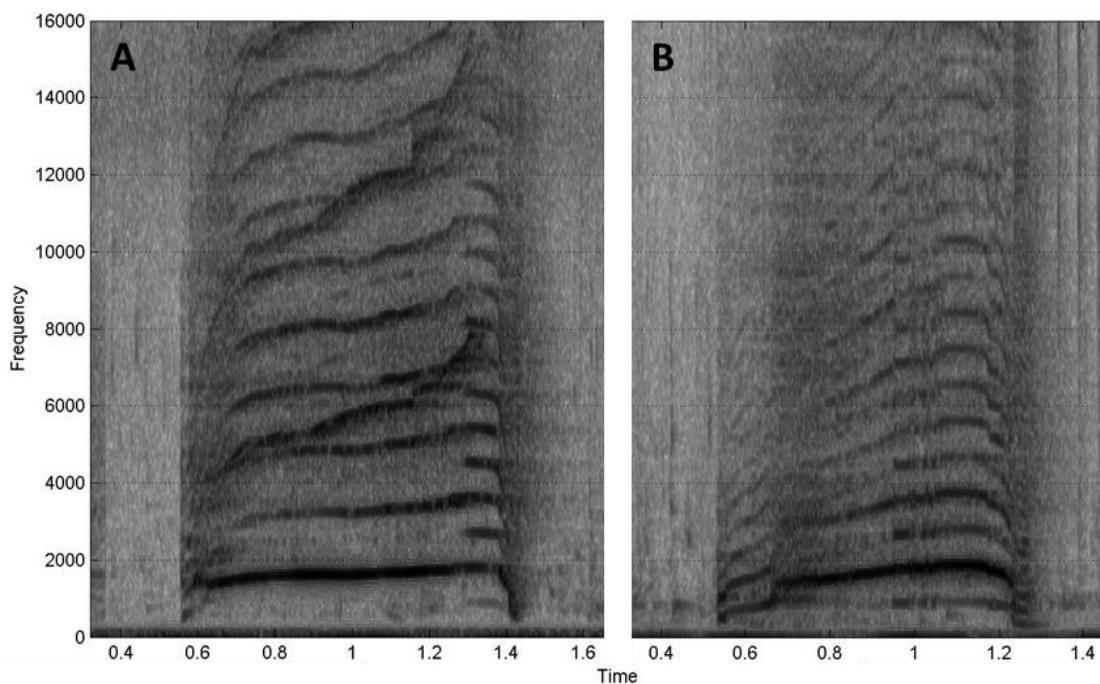


Figure 36 – Unit Aii (panel **A**) and Aii' (panel **B**) were only observed alone, never paired with other units.



Differences between sampling periods

The differences in Morgan's acoustic behaviour between the sampling periods of December 2010 and November 2011 are striking, when it comes to call rate and the ratio between discrete and variable/aberrant vocalizations. In this interval of 11 months there

was a reduction in the call rate from 198.9 to 47.3 calls/hour. Differences in the call rates were considered to have statistical significance based upon the results of the Wilcoxon and Mood two-sample tests.

The percentage of discrete vocalizations had a remarkable increase, from ~58% in December 2010 to ~83% in November 2011. The percentage of variable calls decreased from 24% to 2%. When it comes to unit usage, the major difference was an increase from ~16% to ~50% in the usage frequency of calls with the unit Z, and the dropping of unit type Aii, that was not present in November 2011. The results of the Friedman Rank Sum tests indicate that there was a significant difference between the two sampling periods in the distribution of total occurrences of units and occurrences of two-unit combinations. The results of the Kullback-Leibler entropy test showed that the level of relative entropy for the period of December 2010 (0.71 bits) was lower than that of November 2011 (~1.08 bits). This difference in the relative entropy indicates that there was a higher predictability for the two-unit combinations in December 2010. The degree of uncertainty of the second unit relative to the first one is higher in November 2011. This is in part due to the number of different two-unit combinations produced in November 2011 (44) being higher than in December 2010 (35), and also to the fact that the occurrences are more evenly distributed throughout those combinations in November 2011. When trying to explain these changes, there are different factors specific to this study that should be taken into account:

1) Hearing loss – As stated previously, hearing exams concluded that Morgan has a hearing impairment (Lucke *et al.*, 2013). However, it is not possible to determine when the hearing loss happened, and exactly how severe it is. Not much is known about how hearing loss might affect vocalizations of cetaceans. Not only the hearing loss itself, but the degree of hearing loss is thought to impact their behaviour, assuming that different forms of hearing deficiency can lead to different consequences. For example, false killer whales (*Pseudorca crassidens*, Owen, 1846) with partial hearing loss in specific frequencies may shift the peak frequency of the clicks they produce to match frequencies they can still hear (Kloepper *et al.*, 2010). If Morgan already had a hearing impairment before arriving in Harderwijk it could be a plausible explanation for the high variability in the vocalizations, given that an individual that has limited or no feedback from the vocalizations it produces might increase the variation in the contour of the vocalizations, leading to a decrease in the relative frequency of occurrence of discrete calls. Adult songbirds that were deafened only produced accurately 36% of the song syllables produced prior to the deafening procedure, indicating that continued auditory feedback is essential to maintaining a discrete repertoire (Nordeen and Nordeen, 1992; Sober and Brainard, 2009). Brainard and Doupe (2000) suggest that the increasing variation of both

speech and birdsong after deafening may result from an accumulation of “drifts” in vocal control structures. It could also explain the increase in the Kullback-Leibler divergence in this study, which translates in an increase of the randomness of association of units, possibly due to the lack of aural feedback. However, this limited feedback could also result in a different outcome, where an individual reduces the range of vocalizations it produces, opting for producing fewer units or combinations. In this case, it may choose to produce vocalizations that were developed further during the learning phase, discarding others and experimenting less. This might explain the reduction in the percentage of variable calls throughout the period that Morgan was in Harderwijk.

2) Critical speech/vocal learning phase – According to the first reports, Morgan was around 18 to 24 months old when she was found (van Elk, 2010). If those estimates were correct, it could mean that the separation from her mother and the rest of the group occurred during a critical phase for learning the group repertoire (Bowles *et al.*, 1988; Foote *et al.*, 2006), leading to her experimenting more during her first year in Harderwijk.

Some of Morgan’s vocalizations had a high degree of similarity to stereotyped calls from Norwegian killer whale pods (Samarra *et al.*, 2010b), suggesting that the units in her repertoire were learned while she was still with her group. Assuming that vocal learning was required for acquiring these calls into her repertoire, this would mean that at least some of the combinations Morgan produced were based on her pod’s repertoire and that she would have acquired these sounds before suffering the hearing loss. Thus, this would suggest that Morgan’s hearing impairment was not fully developed at birth. Like children’s babbling (Doupe and Kuhl, 1999) and songbirds’ subsong (Catchpole and Slater, 2003; Marler and Peters, 1982; Thorpe, 1958) during speech and birdsong development phase, respectively, killer whales were reported to emit highly irregular vocalizations at an early stage (Bowles *et al.*, 1988; Foote *et al.*, 2006). This “babbling” is thought to have an important role in the development of correct speech and singing ability for humans and songbirds (Doupe and Kuhl, 1999). This plasticity in the human speech and birdsong decreases with time, resulting in a more consistent set of vocalizations. This could also explain the drop in variability of Morgan’s vocalizations during the interval between the sampling periods, independent of when she suffered hearing loss.

3) Isolation – Morgan was isolated during her period in Harderwijk, with no contact with any other individuals, although there was acoustic and distant visual contact with bottlenose dolphins held in a neighbouring pool. This may have had an impact on how Morgan’s repertoire evolved. Studies in some passerine song-birds that also learn their repertoires from tutors show that an early learning phase is crucial for the development of

a stereotyped song (Catchpole and Slater, 2003; Doupe and Kuhl, 1999; Marler and Peters, 1982), and that the absence of exposure to others' songs may result in production of abnormal songs (Marler, 1970; Thorpe, 1958). There are also reports that indicate the importance of this exposure in humans, where children with little or no social contact do not develop normal speech (Doupe and Kuhl, 1999).

Being isolated means that Morgan would not have had feedback from peers when a vocalization was produced, thus giving no social meaning or context to vocalizations, possibly explaining the reduction in call rate and the increase in relative entropy, or uncertainty for the two-unit combinations from 2010 to 2011. The fact that Morgan was alone might have increased the randomness of association of units to construct calls.

Although killer whale vocalizations are not considered to be context-specific, there can be some relative usage differences when accounting for 'social' and 'non-social' behaviours or contexts (Ford, 1989; Hoelzel and Osborne, 1986). Weiß *et al.* (2006) showed that mothers of new-born calves and their matriline change their calling behaviour, producing more often family-specific calls, as if teaching the calf first the acoustic "family badge". This might also explain changes in the frequency of usage of a specific unit or combination.

All these particular factors combined give a high degree of uncertainty as to which factors determined Morgan's acoustic production patterns. Various indefinite and uncontrollable aspects, such as not being able to quantify Morgan's hearing loss or knowing exactly when it occurred, might have influenced the results, for example the high number of total combinations produced, making it challenging to precisely explain the results obtained. This makes Morgan a unique subject to study the development of the vocal repertoire and behaviour an individual killer whale with a hearing deficit. A similar study with more controlled conditions would be of high significance to understand to what extent deafness could have influenced the results of this study.

Further analysis would be necessary to assess how the changes in vocal behaviour reported here occurred, examining the recordings made during the interval between the two sampling periods. Understanding whether the changes were gradual or sudden could help comprehend the reasons behind them. A different analysis for the distribution of call usage frequency which groups equal and sequential combinations within a given period of time, to account for likely bouts of calling in Morgan's call production behaviour would be recommended.

Further analysis of recordings from the pool facility in Loro Parque may also shed some light into vocal learning. When Morgan was transferred from Harderwijk to Loro Parque she brought a different set of vocalizations into a group that had already a described shared dialect (Kremers *et al.*, 2012). Observing whether or not there were any changes in the vocal behaviour of whales with different backgrounds and how those changes occur, will help us to further understand the processes of vocal production learning in killer whales.

CONCLUSIONS

This study allowed the cataloguing and analysis of the vocal repertoire of a wild-born young killer whale during a period of time when it was held in isolation. This provided a rare opportunity where sounds could be undoubtedly ascribed to an individual and followed through a significant interval of time. Therefore, we could evaluate changes in vocal behaviour during a development period considered crucial for vocal production learning.

There were significant changes in Morgan's vocal behaviour between the two sampling periods. A number of different reasons including the possibility that Morgan have been deaf when she was found or might have become deaf during the time in Harderwijk, or alternatively due to the isolation conditions in Harderwijk.

This study provides a description and analysis of evolution of an individual killer whale vocal repertoire. This key information will be the basis for subsequent studies where we compare the repertoires of Morgan and the whales of Loro Parque, to where she was moved, to better understand the processes of vocal learning in killer whales.

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