Birds and babies : a comparison of the early development in vocal learners

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1 INTRODUCTION

One of the difficulties of interdisciplinary research is to define complex terms in a way that is comprehensible for researches of all fields involved. In order to combine such definitions and yet keep this thesis readable without too many interruptions for definitions, I included a glossary with definitions for terminology used throughout this thesis (appendix I, p 118). These terms are written in ***bold*** *in the introduction.*

"Hebban olla uogala nestas hagunnan hinase hi(c) (a)nda thu uuat unbidan uue nu" is a well known sentence in Old Dutch[1] dating from approximately the year 1100. Since then the Dutch language has changed substantially. There are different causes for language change, one of them being the cultural transmission of language, where language is transferred from one person to the next or from one generation to the next. Due to 'noise' in the signal transfer in perception or production, changes gradually accumulate. When populations get separated geographically, they go through their own cultural evolution resulting in linguistic variation. The cultural transmission of language exists by virtue of **vocal learning**, a feature that is quite rare in the animal kingdom. Human behavior is usually compared to that of other primates like the chimpanzee, because genetically they are closely related. In terms of language and speech however, the comparison is less appropriate, since non-human primates usually do not seem to learn their vocalizations (Egnor & Hauser, 2004); humans (*Homo sapiens*) are the only primates known to learn their vocalizations. Only a few other animal taxa in the animal kingdom are known to be vocal learners, including songbirds. The vital role of experience with auditory input in the vocal development of humans and songbirds led scientists to instigate comparative research on the two. This does not mean that language or speech and birdsong are the same, but rather that the mechanisms for learning, development and evolution show parallels.

In humans, the cultural transmission of language can lead to the variation that exists between different dialects and languages (Baronchelli et al, 2012). Similarly, in songbirds it can lead to song diversity between populations and individuals Petrinovich and Baptista 1984; Catchpole and Slater 1995 (Gammon et al, 2005). Despite the diversity found in both language and birdsong however, some aspects are remarkably similar between languages (Hyman, 2008; Jakobson, 1941; Jusczyk et al, 2002; Macken & Ferguson, 1981) and songs of the same species of songbirds (Marler & Pickert, 1984; Soha et al, 2009; Soha & Marler, 2000, Fig. 1.1). This may be explained by predispositions or 'innate' biases guiding the change of sounds and structures of languages in a direction that is preferred by the learner's brain. During development, such predispositions may come about in the form of selective attention for certain sounds over others, influencing the learning process (Nelson & Marler, 1993; Soha & Marler, 2001). This would also explain why some sounds are more likely to occur in languages or birdsong populations than other sounds.

Taken together it seems likely that both experience independent processes and experience dependent processes play a role in the acquisition and the evolution of language and birdsong (Lachlan & Feldman, 2003; Yang, 2004). Considerable debate exists, however, on the relative roles of experience dependent and independent processes

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[1] Possibly the sentence is Old English and not Old Dutch (De Grauwe, 2004). The meaning of the sentence in modern English is thought to be: "All birds have a nest except for me and you, what are we waiting for?"

on language learning and evolution. One of the difficulties of trying to disentangle these variables is that it is rather impossible and quite unethical to experimentally manipulate language exposure to human children during development. A solution to this problem is not to control the exposure but to measure it. This can be used to get a grip on the influence of experience dependent and independent processes on vocal learning and how they interact. Questions like the following can be addressed: How often does a certain syllable occur? If syllables occur equally often are they perceived similarly? If they are not, what causes the difference?

Another way to gain insight in the influence of these processes on vocal learning in general is by comparing different species of vocal learners, like songbirds and human beings. By using songbirds as a model for vocal learning it is possible to study the influence of experience dependent and experience independent processes in a more controlled experimental way.

In this thesis I demonstrate how both these processes influence vocal development in human infants and zebra finches (*Taeniopygia guttata)*. Mainly focusing on acquisition of phonemes and elements in human infants and zebra finches respectively, I show that different processes affect vocal acquisition at different developmental stages. In addition, I present an 'element typology' of zebra finch song in order to illustrate how developmental patterns relate to sound patterns found across populations of the same species. Implications for the development and evolution of language and birdsong are discussed.

1.1 SIMILARITIES AND DIFFERENCES BETWEEN LANGUAGE AND BIRDSONG

Many similarities have been described between birdsong and language (Berwick et al, 2011; Bolhuis et al, 2010; Doupe & Kuhl, 1999; Yip, 2006). Similar neural mechanisms have been thought to play a role in vocal learning and memorization, including possible hemispheric lateralization (Moorman et al, 2012; Nottebohm et al, 1976). Both language and birdsong have a hierarchical structure. Language consists of phonemes forming syllables and words, while words form sentences. Zebra finch elements (the smallest units of song) can form syllables and sequences of syllables form a motif (Fig. 1.2). Motifs can be repeated to form a song bout. The most important parallel in relation to this thesis is the vocal learning itself. More detailed aspects of development are similar as well, for instance the presence of a sensitive period and babbling. Babbling is called subsong in birds, which later develops into plastic song and eventually crystallized song (i.e. adult song, fig 1.3b, (Eales, 1985; Immelmann, 1969; Price, 1979; Zann, 1996)). Vocal acquisition seems to be influenced by both experience dependent and independent processes. Similar to dialects in human language, both variation and commonalities are present among vocalizations of birds from different populations of the same species.

In addition to parallels, there are some important differences between birdsong

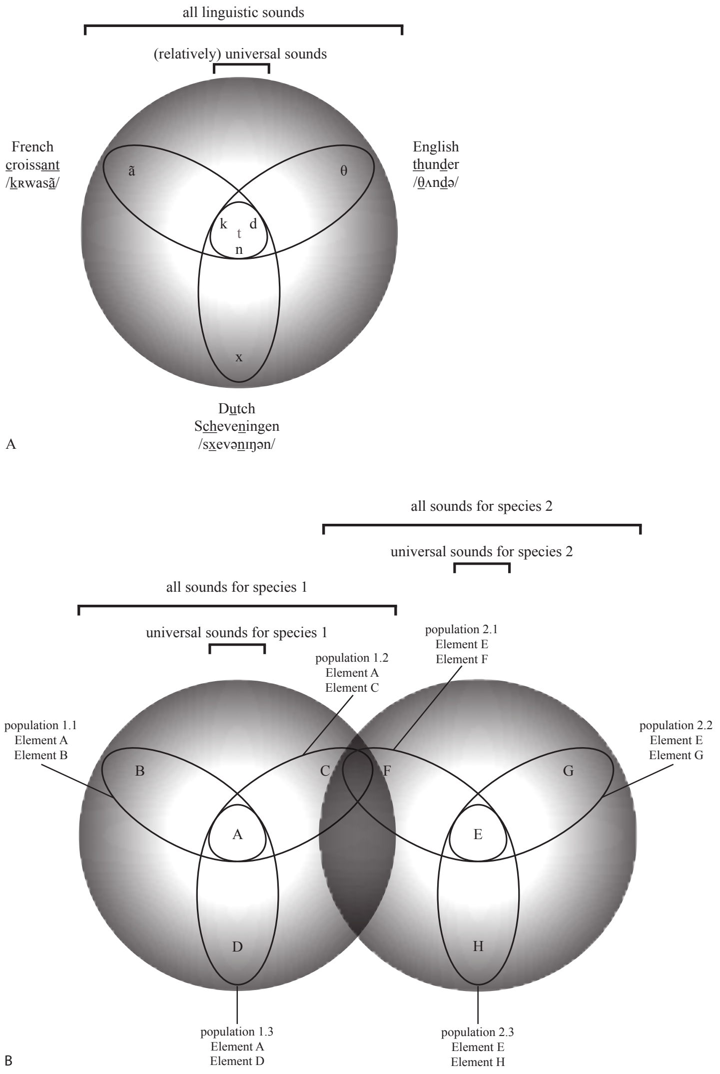

Figure 1.1. Schematic representation illustrating diversity and uniformity in language **(A)** and birdsong **(B).** In language, some sounds are common (relatively universal) across languages whereas others are more specific to certain languages. The sounds /ã/, /θ/ and /x/ are language specific, whereas /k/, /n/ and /d/ are more common. The segment /t/ is thought to be most common across languages **(A).** Similarly, sound diversity and uniformity can be found in birdsong. In contrast to human language, which occurs only in one species, birdsong is present in different species of song birds. Diversity and uniformity can be found across populations within species (as in humans) but also between species **(B)**.

and language. Although some songbirds have quite large repertoires, complex semantics or syntax as in human language has not been found in birdsong to date (Doupe & Kuhl, 1999; ten Cate & Okanoya, 2012). A lively debate is currently going on about whether songbirds can detect recursive patterns. Gentner et al. (2006) claimed that starlings are able to learn a rule of center imbedding and Abe et al (2012) have claimed this too. Both studies, however, have been criticized and alternative explanations for the results have been proposed. In the case of Gentner et al, the birds possibly used a more basic rule to solve the task (van Heijningen et al, 2009). In the study by Abe et al birds may have memorized the test items during training instead of having learnt an abstract syntactical rule (Beckers et al, 2012).

Whereas humans are the only primate species known to learn their vocalizations, the clade of songbirds consists of many different species. Thus, when it concerns birdsong, one has to realize that there is extraordinary diversity both *within and between* the species in what the songs sound like, how they are structured and how they have been shaped by development and evolution. The chipping sparrow (*Spizella passerina*), for instance, sings a relatively simple song consisting of one repeated syllable (Albrecht & Oring, 1995), whereas the nightingale has a repertoire of up to approximately 200 song types (Kipper et al, 2004).

The function of birdsong is also different from the function of human language. Even though language and birdsong are both used for communication, birdsong is used mainly for territory defense or mate attraction. Clear gender differences as found in

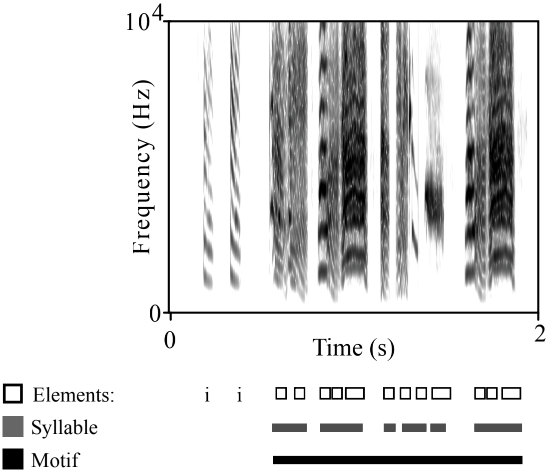

Figure 1.2. A spectrogram of a zebra finch song. A zebra finch song starts with a few introductory notes, followed by one or more motives. A motive consists of a sequence of elements. Elements are grouped into syllables (which are separated by silent intervals).

several songbird species, where most singing behavior is performed by males, are absent in human language.

1.2 Phonological acquisition in human infants

The first issue I address in this thesis is how experience dependent and independent processes influence phonological acquisition in infants. Phonology is the study of sound – phonemes – and how they are organized within and across languages. A **phoneme** is considered the smallest unit in speech. For instance, the consonant /b/ the vowel /ʊ/ and another consonant /k/ are the three phonemes that together form the sounds of the word ‘book’. In language, phonemes are contrastive: substituting phonemes in a word changes the meaning of the word. For example, when in the above mentioned example the phoneme /b/ is substituted by the phoneme /r/, the word turns into ‘rook’ instead of ‘book’. **Phonological typology** is a term used for the study of phonemes and their distribution across languages and dialects. Some phonemes, contrasts and **phonological processes** vary between languages, while others are similar across languages.

Despite linguistic diversity, infants can learn any language they grow up with. There is, on the one hand, considerable variation in language development among children, indicating that the learning process is flexible and experience dependent. On the other hand, certain common patterns can be found both in languages and in language development, indicating that experience independent influences play a role too. The question thus remains how experience dependent and experience independent processes interact during language development.

1.2.1 The relation between language acquisition and typology

Jakobson (1941) already suggested that children acquire “universal” sound contrasts first, regardless of their language environment or culture. He also emphasized the link between language development and patterns found in languages (typology), suggesting first that sounds occurring more often in languages across the world are also likely to be acquired early. Second, he introduced laws of “irreversible solidarity” (or implicational relations) based on cross-linguistic observations of phoneme inventories. These laws specify that one phonemic contrast implies the existence of another, whereby the implied contrasts are those that occur more generally in languages and are acquired first. This relation is not reversible (not every language that has a /t/ also has a /d/)

The observation that some sounds are more likely to appear in languages than others, are more frequent within languages, are acquired earlier, and are more likely to undergo than to trigger phonological processes, has been studied by many other phonologists. The notion of **markedness** is often used to describe these qualitative differences in sound; unmarked sounds are defined as more “universal” (i.e. more common across languages) and are acquired early in development, whereas marked sounds are defined as less common and are acquired later (De Lacy, 2006; Rice, 2007). For this thesis, the most important reason for studying markedness is that both typological as well as developmental data suggest a special status of unmarked sounds. The qualitative difference between marked and unmarked sounds might indicate differences in processing and learning and leads to two potentially contrasting hypotheses.

The first hypothesis is that the special status of unmarked sounds indicates a **predisposition**, a biological sensitivity to specific sounds that have not been heard before. The rationale behind this is that *if* there are predispositions involved in language learning, their effects are likely to show up early in development and therefore they are likely to be common across languages (universal). Alternatively, the second hypothesis is that the higher abundance of unmarked sounds cross-linguistically and in early child language, is a consequence of learning and thus of cultural transmission. This could be due to the fact that within languages the frequency of unmarked sounds is usually high, i.e. markedness correlates with frequency. In other words, the first hypothesis points towards experience independent processes during development and the second to experience dependent processes.

The link between child language data and cross-linguistic data has been further investigated by Zamuner et al (2005). Studying 35 languages, the authors conclude that in coda position (the last position of a word or a syllable) **sonorants** and **coronals** are more abundant across languages than obstruents and labials or dorsals (Zamuner et al, 2005). Child language data, however, show that sonorant and coronals are not the only segments acquired early. Dorsals (for instance /k/) are produced early in coda position as well. In English, sonorants and coronals are frequent but dorsals are as well. In contrast, markedness theories do not predict dorsals to be produced early, leading the authors to conclude that child language data are better explained by input frequency (Zamuner et al, 2005). Nevertheless, they do not claim that acquisition is based on input alone but rather that both theories should be taken into account. For instance, it is unclear whether acquisition of segments in onset position can be explained better by frequency than by markedness. Furthermore, the question remains if this is the case for the very initial set of acquired segments (Levelt & Van Oostendorp, 2007). More importantly, it is not clear why these sounds are so frequent within languages in the first place. Are they frequent due to accumulating cultural transmission or are there other reasons?

In order to further understand language acquisition and its relation to cross-linguistic sound patterns it is necessary to disentangle the effects of markedness, which point to experience-independent effects on acquisition, and the effects of frequency, which point to experience-dependent effects. In this thesis I study these effects separately, in the perceptual behavior of infants. The questions I address are: to which type of information are infants sensitive (experience dependent or –independent)? And how do these sensitivities develop with age? The data known from typology and child language production (markedness) can help to predict when and how development might be affected by experience-independent processes, whereas within language frequency data can give more insight in experience dependent processes.

1.2.2 EXPERIENCE DEPENDENT PROCESSES IN INFANT LANGUAGE ACQUISITION

Throughout this thesis, when I refer to **experience dependent** processes I mean the processes influenced by the learner's exposure to adult language, or adult birdsong in the case of birds. Other experience possibly influences the learning process as well, including practice, self perception, perception of other sounds than speech or birdsong and visual and social experience. The main focus of this thesis is however on auditory input provided by adults.

Several studies have demonstrated the relevance of experience dependent mechanisms to child language acquisition. Jusczyk et al. showed that 9 month old American infants perceptually prefer the most frequently occurring stress pattern of American English (strong- weak, (Jusczyk et al, 1993a). Additionally, unfamiliar words with native language sound patterns are preferred over those with non-native patterns by 9-month-olds (Jusczyk et al, 1993b). This is probably due to the phonotactic probability of the stimuli, since frequently occurring **phonotactic patterns** are also preferred over infrequent ones at 9 months of age (Jusczyk & Luce, 1994). Together these data suggest that around 9 months of age experience dependent processes start to show their effect since infants develop recognition and preference for frequent native language aspects during this period (fig 1.3a). Further evidence for experience dependent processes comes from phoneme discrimination experiments showing that up to the age of 6 months, infants discriminate phonemes from their native language as well as from non-native languages, whereas later in development the capacity to discriminate between non-native phonemes declines. The ability to discriminate native language patterns however increases over the course of development (Kuhl & Meltzoff, 1996; Tsao et al, 2004).

1.2.3 EXPERIENCE INDEPENDENT PROCESSES IN INFANT LANGUAGE ACQUISITION

Frequency of occurrence is often used as a measure of experience dependent processes (Jusczyk et al, 1994; Zamuner et al, 2004). Possible experience independent processes however, could also induce preferences, which in turn could lead to frequent occurrence of the preferred sound too. This means that whenever a frequent sound is preferred by infants, it is not always clear whether the frequency of occurrence in the language is indeed the (only) cause. Experience independent factors like predispositions or an interaction between different factors may cause the preference.

Indications for experience independent factors playing a role in acquisition can

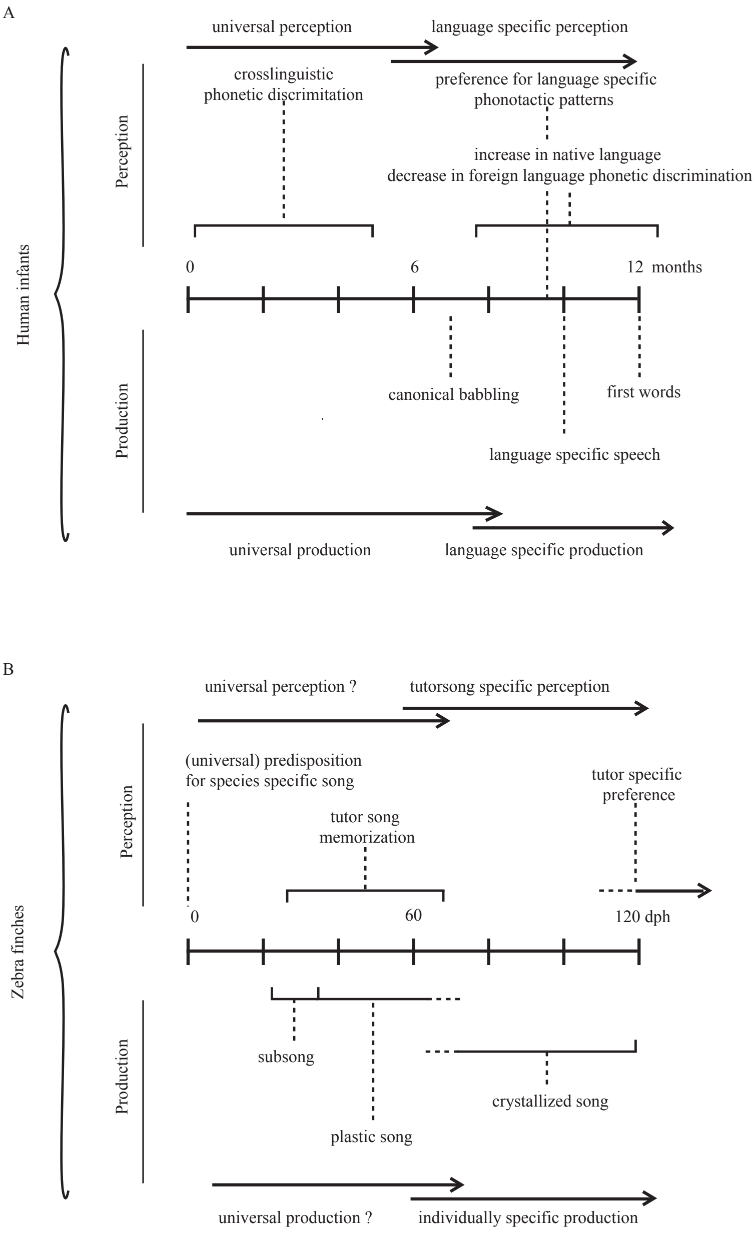

Figure 1.3. Early language and birdsong development. A) shows language development during the first year of life, from universal to language specific. B) shows birdsong development. The exact timeline varies between bird species. The timeline indicated here is representative for zebra finch development.

be found in child language production data. The order in which phonemes are acquired by Dutch children, for instance, cannot be explained by the frequency of these phonemes in the Dutch language (Levelt & Van Oostendorp, 2007). The first consonants that infants produce consistently during babbling can also not be explained by the frequency of occurrence in the speech of these infants' mothers (DePaolis et al, 2011). Furthermore, the way children initially pronounce words often does not match the actual adult pronunciation of the target words. For instance, children tend to omit the coda (the last consonant of a syllable, see example (1.1)) or substitute one phoneme in a word with another (1.2), which is clearly not an effect of exposure to language since these 'mispronunciations' are not available in the input.

(1)Production patterns in early child language production:

CVC →CV (Jacob 1;4/1;5 (Menn, 1976))

Target	*Child Production*
hat	[hæ]
nose	[do]
tape	[dæ]

Dorsal → Coronal (Ruth Hills 2;0 (Ingram, 1974))

Target	*Child Production*
kiss	[tɪ]
key	[ti:]
go	[dou]

Thus, in addition to learning by experience, experience independent processes seem to be involved in language acquisition. How can we explain these experience independent patterns? Constraints on the vocal apparatus (vocal chords, larynx, tongue, teeth and lips) could limit the sounds that can be produced. This is especially true since the infant and child anatomy is different from adult anatomy. Alternatively, phonological explanations for the patterns in 1.1 and 1.2 have been proposed. For instance, example 1.1 can be explained in terms of markedness, because CVC syllables are marked and CV syllables are unmarked, and they therefore replace the marked form. Similarly in example 1.2, dorsals are marked and coronals are unmarked and therefore coronals replace the marked dorsal segments.

These phonological explanations for experience independent patterns imply predispositions for unmarked forms. If predispositions are indeed the cause of these patterns, one might expect a preference for unmarked forms even before production starts. Thus, if infants show a perceptual preference before production and independent of experience, this may indicate the presence of a predisposition. As mentioned before, studies showing a perceptual change in phoneme discrimination and perceptual preferences for native language at 9 months of age point to the existence of experience dependent processes. However, they show that at 6 months of age no evidence is found for a preference for native language stress patterns or frequent phonotactic patterns. Moreover, discriminative abilities in infants younger than 6 months of age are less influenced by experience (however see Kuhl et al, 1992) since infants can still discriminate phonemic contrasts of non-native languages (Kuhl et al, 2006; Rivera-Gaxiola et al, 2005; Tsao et al, 2006). Thus, before 6 months of age perceptual properties seem to be more general across infants growing up in different language backgrounds.

In this thesis I use frequency within language independent of cross-linguistic markedness data to study experience dependent influences. A perceptual preference for frequent sounds within language is expected when experience plays a role. The 'universal' patterns in child and adult language (markedness), independent of within-language-frequency, are used to study possible experience independent predispositions. A perceptual preference for unmarked sounds is thus expected when predispositions play a role. Moreover, by studying the course of development of experience dependent and -independent preferences during the second half of the first year I investigate how experience and predispositions may interact.

1.3 Song acquisition in songbirds

The second aim of this thesis is to study experience dependent and independent processes during vocal acquisition in songbirds. Similar to human speech, birdsong consists of a sequence of different sound units. In zebra finches, the species studied in this thesis, the smallest sound units are called 'elements' (fig. 1.2). Elements are to a certain extent comparable to phonemes, since they are distinguishable separate units and the smallest vocal units described (Zann, 1993). However, because of the lack of meaningful words in birdsong, phonemic contrast is hard to define in birdsong. A similar approach as in the infant study is chosen, using 'typological' information to form predictions about possible experience dependent and independent processes. As with markedness in human language, commonly occurring elements in zebra finch song might indicate predispositions (experience independent) or they may be an effect of cultural transmission and thus experience dependent processes. In zebra finches however, it is possible to control the exposure to elements and thus to disentangle the experience dependent and –independent processes.

The zebra finch is an excellent model species for studying the acquisition of song and the influence of experience dependent and independent processes during this process. Zebra finches are easily maintained in the lab, they breed all year round and have a short developmental period (Doupe & Kuhl, 1999). It has been demonstrated that zebra finches have a sensitive phase for song learning, during which they have to be exposed to song in order to learn to produce normal song later in life (Eales, 1987; Pytte

& Suthers, 2000).

Male zebra finches sing but females do not. Females do produce calls for communicating about, for instance, presence of food or danger (Simpson & Vicario, 1990; Zann, 1996). Even though they do not learn to produce songs, they are able to recognize songs and to develop a preference for their **tutorsong** (Clayton, 1988; Riebel et al, 2002). The fact that females do not sing is convenient because this gives researchers the opportunity to have juvenile birds grow up with their mother only. This way they are raised without song exposure while maintaining relatively natural rearing conditions. Subsequently, these birds can be exposed to songs via a speaker, a method called **tape-tutoring** (nowadays using computer files rather than tapes). This way it is possible to manipulate and control the type of exposure, the amount of exposure and the timing of when the birds are exposed to song, creating a highly controlled setting for examining relative effects of experience dependent and independent processes.

1.3.1 Zebra finch typology

Studying variation in birdsong is not new. Several studies have shown dialects in birdsong (Kroodsma et al, 1999; Marler & Tamura, 1964; Petrinovich & Baptista, 1984). The vocal repertoire may differ between individuals of the same species, and different species differ in the types of elements and complexity. Variation in songs or repertoires of different species should not be confused with variation between different languages, since human language exists in only one species. Therefore it is relevant for drawing parallels between birdsong and language to also study song elements in different populations *within* the same species.

With respect to the zebra finch, relatively little is known about typology. A few studies have described the song elements of a specific population (Holveck et al, 2008; Leadbeater et al, 2005; Sturdy et al, 1999; Zann 1993), and one study describes the song elements in 4 different populations (Sturdy et al, 1999). The purpose for this latter study however, was to form a general and simple classification scheme for describing song of different populations in a similar way. Although the aim was not directly to give a detailed description of differences between populations, the study showed that even with this simple classification, population differences in the distribution of elements were evident. Nothing is known however, about how these within species population differences relate to developmental mechanisms. The same question can be asked for infants: how do experience dependent and independent processes relate to each other and to 'typological' patterns found across populations? In order to answer these questions properly I address developmental issues in this thesis and I present an analysis of the song elements in 13 zebra finch populations in order to come closer to a zebra finch element typology.

1.3.2 EXPERIENCE DEPENDENT PROCESSES IN SONG ACQUISITION

Songbirds learn their songs from adult input. Manipulating input or depriving birds from input severely affects song learning (see Woolley 2012 for review). Zebra finches copy songs to which they have been exposed during a sensitive phase early in life (Immelmann, 1969; Jones et al, 1996). In natural conditions they learn the song of their father or other adult males. In artificial settings it has been shown that zebra finches also learn from auditory input alone (Houx & ten Cate 1999a,b), though live tutoring is more effective (Eales, 1989).

Auditory input is necessary for song recognition and memorization, which induces changes in neural activation. Perceptual preferences for the tutor song have been shown in male and female zebra finches. Also, in response to tutor song, neuronal activation in NCM (caudomedial nidopallium) is positively correlated with the strength of song learning (measured as number of elements copied). This correlation is absent in response to novel song or the bird's own song (Bolhuis et al, 2001; Bolhuis et al, 2000; Terpstra et al, 2004), indicating a relation specifically between auditory experience induced activity and song production.

Even though learning is evident, the role of frequency of occurrence is not so clear. It has even been suggested that the amount of exposure is inversely correlated with song learning (Tchernichovski et al, 1999). Moreover it seems that zebra finches (and probably other songbirds) need only very little experience in order to learn to recognize song (Braaten et al, 2008). After only a day of exposure changes in spine turnover have been shown in the bird's neurons, at least after the first exposure of their life (Roberts et al, 2010). On the other hand, the only factor that seemed relevant for song learning in a study by Houx et al (2000) seemed to be the fact that elements are repeated within a song (and thus appeared more often).

It is thus unclear to what extent the amount of exposure matters, but the type of exposure has been shown to be relevant. Songbirds do not just copy any song but prefer to learn conspecific song. When zebra finches for instance hear both zebra finch song and Bengalese finch song, they will copy the zebra finch song.

1.3.3 Experience independent processes in song acquisition

Previous research on songbirds has indicated how predispositions may play a role in song learning. In most studies, adult song production is used as a measure of learning or selective preference. Isolate birds – raised without song exposure - sing an aberrant of song in which the fine grained acoustic structure of natural song is absent, but some crude features remain (Price, 1979). Cross-fostering experiments for instance have shown that zebra finches copy their own species (**conspecific**) song more accurately than songs of Bengalese finch foster fathers (Clayton, 1989).

Only few studies have examined perceptual predispositions in naïve birds. An experiment in which juvenile zebra fiches could elicit exposure to either conspecific or heterospecific song by hopping on a perch showed more hopping on the perch that generated conspecific song than on the one for heterospecific song (Braaten & Reynolds, 1999). Also, white-crowned sparrow (*Zonotrichia leucophrys*) fledglings produced more begging calls in response to conspecific song than to heterospecific song (Nelson & Marler, 1993; Soha & Marler, 2001) Preference for the own subspecies over other subspecies was not confirmed, but exposure to songs of the own subspecies lead to better discrimination than experience with another subspecies song. This outcome suggests that the perceptual system is more attuned to acoustic features of the own subspecies (Nelson, 2000). Moreover, universal white-crowned sparrow's introductory whistles have been shown to function as a cue for song learning, since songs (even heterospecific ones) are better copied when they contain these universal whistles (Soha & Marler, 2000). This suggests that in addition to a preference for conspecific over heterospecific vocalizations, there are preferences for certain *within-species* element types (independent of song exposure). This has also been shown in a study on grasshopper sparrows, showing that naïve female fledglings respond more to one conspecific song type ('buzz' simple structure and uniform across individuals) than another conspecific one ('warble', complex and possibly individually specific, (Soha et al, 2009).

In summary, similar to what is known for human infants, it seems that both experience dependent and –independent processes are involved in song acquisition. The questions remain however, how and when the different processes are relevant during song learning. In addition, there is not much known about the within-species sensitivities for song features in zebra finches. The questions I address for human infants are asked for zebra finches as well: To which type of information do the young birds show sensitivity and how does this develop over age?

If experience independent processes play a role in early vocal development, preferences are expected for 'universal' within-species properties of song before juveniles are exposed to song. If experience dependent processes are involved, the subsequent exposure to song should have an cumulative effect on these preferences.

1.4 Thesis overview

Significant parallels between birdsong and language have been found. There is evidence for both experience dependent and independent processes involved in vocal development. Several questions remain however, specifically with regard to the relation between predispositions and experience, and to how this could affect uniformity and variety in language and birdsong. In the present thesis I examine the development of perceptual preferences in zebra finches and human infants, aiming to disentangle these effects. Furthermore, I present an analysis of zebra finch songs across populations in order to gain a more detailed view of zebra finch 'typology'.

CHAPTER 2 is aimed at studying the development of perceptual preferences in human infants at 9 and 12 months of age. By carefully balancing the stimuli, we were able to disentangle experience dependent and independent influences on attentional preference. A preference for frequently occurring syllables (in Dutch) is thought to reflect experience dependent mechanisms, whereas preferences for unmarked syllables could indicate experience independent processes. In **homorganic syllables** (which can be viewed as unmarked) the consonant and the vowel share a place of articulation feature. Since these syllables have been shown to appear early in child language and babbling cross-linguistically, a preference for homorganic syllables in perception could also indicate possible experience independent processes.

In CHAPTER 3 I test the preference of male zebra finches for certain types of elements while they are naive to song in order to identify preferences independent of song experience. The stimuli are either common ('universal') or uncommon song elements, similar to unmarked and marked phonemes in human language. Subsequently the birds are tutored with common and uncommon songs and tested for their preference again later in development to examine the effects of experience. Furthermore, an analysis of the produced songs of these same birds is performed to be able to link the perceptual data to the elements that the birds eventually produce.

To take the step towards a zebra finch typology CHAPTER 4 provides an extensive acoustic computational clustering analysis of zebra finch song collected form 13 populations. The distribution of elements across populations and continents is analyzed. In addition an analysis of **phonological syntax** is performed on the same songs to investigate constraints on element sequences. Phonological syntax is a term used in birdsong research to describe the sequence or order of elements or syllables in birdsong. This should not be confused with **syntax** in human language since here it refers to grammar, including grammatical classes. Meaning is usually considered to be dependent on word order here. CHAPTER 4 provides insight in uniformity and variation of elements and sequences across zebra finch populations.

In CHAPTER 5 I discuss in depth the different results in the light of the developmental and evolutionary issues presented above. Findings in human infants and songbirds are compared to determine to what extent new parallels between the two species can be drawn.